Distribution and transport patterns of northern rock sole, *Lepidopsetta polyxystra*, larvae in the southeastern Bering Sea

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Abstract

We report the size, abundance, and distribution (horizontal, vertical) of northern rock sole, *Lepidopsetta polyxystra*, larvae collected from ichthyoplankton surveys on the southeastern Bering Sea shelf near Unimak Island, in Unimak Pass, and in the Gulf of Alaska south of Unimak Island. The greatest abundances of larvae occurred within Unimak Pass and in the Bering Sea northeast of Unimak Island. Larvae were smaller and more abundant in 2002 than in 2003. Larval abundance and size varied with depth. Highest abundances were at depths of 10–30 m during the day, and larger fish appeared to migrate from below 20 m to 0–10 m at night. There was evidence of multiple spawning locales and larval dispersal pathways that were depth- and area-specific. Northern rock sole larvae spawned west of Unimak Pass along the Aleutian Islands may be transported northward by the Bering Slope Current. Larvae spawned in the Gulf of Alaska and advected through Unimak Pass are differentially dispersed, primarily to the middle and outer shelves along the 100 m and 200 m isobaths, or along the Alaska Peninsula. Larvae spawned along the Alaska Peninsula east of Unimak Island appear to have the greatest chance of being transported to nursery areas in the coastal domain. Dispersal of near-surface northern rock sole larvae in any of these locations is likely influenced by wind-driven advection, but below-surface (>10 m) northern rock sole larval transport is probably more affected by factors that modulate geostrophic flow rather than wind-driven surface currents.
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Keywords: Distribution; Transport; Larvae; Pleuronectidae; Northern rock sole; *Lepidopsetta polyxystra*; Bering sea

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1. Introduction

Northern rock sole, *Lepidopsetta polyxystra*, is a commercially important pleuronectid flatfish that ranges from St. Lawrence Island to the Aleutian Islands in the Bering Sea and south to Puget Sound, Washington (Mecklenburg et al., 2002). Although distributed primarily on the continental shelf of the eastern Bering Sea and the Gulf of Alaska, northern rock sole are known to occur as far west as the Gulf of Anadyr, Sea of Okhotsk and the northern coast of Hokkaido, Japan (Orr and Matarese, 2000). Previously classified taxonomically as rock sole, *Lepidopsetta bilineata*, the northern rock sole was recently determined to be a distinct species (*L. polyxystra*) with a more northerly range than *L. bilineata*, which is now commonly called southern rock sole (Orr and Matarese, 2000). Though it shares an overlapping distribution with southern rock sole in the Gulf of Alaska, northern rock sole (NRS) comprise the majority of the Bering Sea and Aleutian Islands rock sole populations, where they are managed as a single stock (Orr and Matarese, 2000; Wilderbuer and Walters, 2004). Female rock sole are highly desirable when in spawning condition and are the target of a high value roe fishery in February and March (Wilderbuer and Walters, 2004). In 2003, commercial landings of NRS totaled 35,395 tons, of which 19,492 tons (55%) were retained (i.e. processed as a fishery product; Wilderbuer and Walters, 2004). The value of the northern and southern rock sole fishery for all of Alaska is 3.8 million dollars.

Considered one of the smaller flatfish species, NRS can live up to 18 years and reach weights of 1.5 kg and lengths of 53 cm (females) to 60 cm (males) (Matarese et al., 2003; Wilderbuer and Walters, 2004). Adults in the eastern Bering Sea are demersal, occur at depths <100 m and are associated with muddy substrata lacking vertical relief (Busby et al., 2005). Northern rock sole adults occupy separate summertime feeding and winter spawning distributions on the continental shelf, and spawning occurs during the winter–early spring period of December–March (Wilderbuer and Walters, 2004).

Northern rock sole eggs are demersal and hatching occurs at approximately 3 mm standard length (SL; Matarese et al., 2003). Larvae of NRS are easily identified and distinguishable from larvae of southern rock sole and other Bering Sea flatfishes (Orr and Matarese, 2000). Larvae first appear in the plankton in March, with abundance peaking in April and remaining relatively high through May and June (Matarese et al., 2003). Small larvae (<10 mm SL) are common during winter–spring in the Bering Sea and Gulf of Alaska, but larger larvae are rarely collected in the summer-fall (Matarese et al., 2003; data collected by the Recruitment Processes Program of the Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA). Larvae begin to undergo eye migration at about 15 mm SL, and most NRS stay in the plankton to at least 30 mm SL (Orr and Matarese, 2000; Matarese et al., 2003). During this time young larvae consume small plankton and algae, while early juvenile stages consume larger zooplankton. Juveniles and adults prey on bivalves, polychaetes, amphipods, mollusks and crustaceans (Wilderbuer and Walters, 2004). Early NRS juveniles, presumably residing in coastal areas (see below), are likely preyed upon by nearshore shrimp species, while late-stage juveniles (5–15 cm SL) have been found in the stomachs of walleye pollock, Pacific cod, yellowfin sole, skates and Pacific halibut (Wilderbuer and Walters, 2004).

While juvenile rock sole nursery areas and habitat use in the Gulf of Alaska (GOA) are described, settlement areas and nursery grounds for juveniles in the eastern Bering Sea (EBS) are not as well-documented. Norcross et al. (1995) and Abookire and Norcross (1998) determined that juvenile rock sole in the GOA are found in shallow water (<50 m) on sand or mixed sand substrata. However, at that time, *L. polyxystra* was not recognized as a distinct species (Orr and Matarese, 2000), and it is likely that at least some of the individuals identified as "rock sole" were southern rock sole (*L. bilineata*). However, several years later Hurst and Abookire (2005) collected settled age-0 NRS in shallow waters (7–20 m) in nearshore bays surrounding Kodiak Island, Alaska. Based on the information available for the GOA, it is likely that settlement in nearshore bays and estuaries in the Bering Sea is also an important component of NRS recruitment success.

While the distribution of NRS larvae has been well documented in the Gulf of Alaska (Matarese et al., 2003), this is not the case in the Bering Sea where many fewer ichthyoplankton surveys have been conducted (Matarese et al., 2003). Little is known about northern rock sole larval distribution and size structure in the Bering Sea, and transport pathways from spawning grounds to nearshore nursery areas are unknown. One of the few studies of larval transport in the Bering Sea is that of Wilderbuer et al. (2002) who used an ocean surface current simulation model (OSCURS; Ingraham and Miyahara, 1988) to show that above-average flatfish

recruitment coincided with wind-driven advection of flatfish larvae to presumed juvenile nursery areas. A central tenet of their hypothesis is that flatfish larvae, including larvae of NRS, are mainly present in surface waters in the EBS and thus are significantly affected by decadal-scale variations in ocean surface currents. Our objectives in this study were (1) to examine the vertical and horizontal distribution of northern rock sole larvae in the EBS, (2) to evaluate potential mechanisms of delivery of northern rock sole larvae to presumed settlement and nursery areas in the EBS, (3) to evaluate exchange of northern rock sole larvae from the GOA into the EBS through Unimak Pass, and (4) to relate observed patterns to oceanographic conditions using empirical data and a circulation model.

2. Material and methods

2.1. Study area and sampling procedure

The geographic region of focus was the eastern Bering Sea shelf, near the Alaska Peninsula and Unimak Island. Ichthyoplankton samples were collected on a fixed grid of stations (Fig. 1) during research cruises in 2002 (12–21 May, 81 stations) and 2003 (17–24 May, 60 stations). We also analyzed ichthyoplankton samples collected southeast of Unimak Pass, on separate cruises, to determine whether northern rock sole larvae recruit to the EBS shelf from the GOA. Unimak Pass is a shallow (70 m), narrow (16 km) connection between the GOA and the EBS that has been characterized as a "significant conduit" (Stabeno et al., 1999a) of exchange (Royer, 1981; Stabeno et al., 1995; Stabeno et al., 2002). Ichthyoplankton samples from the Gulf of Alaska were collected on 24–25 May 2002 (11 stations) and on 26 May 2003 (7 stations). Ichthyoplankton samples were collected with 60 cm bongo nets (505 μm mesh) fitted with flowmeters, towed from 10 m off-bottom to the surface; tows in the EBS were to 300 m maximum depth, and in the GOA to 200 m maximum depth. Net depth, conductivity and water temperature were measured at each station using a Sea-Bird SBE 19 conductivity, temperature and depth (CTD) profiler attached in-line between the wire terminus and the bongo net frame.

To obtain quantitative estimates of larval abundance in the surface layer, we used neuston nets (505 μm mesh) fitted with flowmeters deployed at stations (Fig. 1) in Unimak Pass and on the EBS shelf in both years. Neuston collections were not made in the GOA. In 2003, we also used a 1 m² multiple opening and closing net
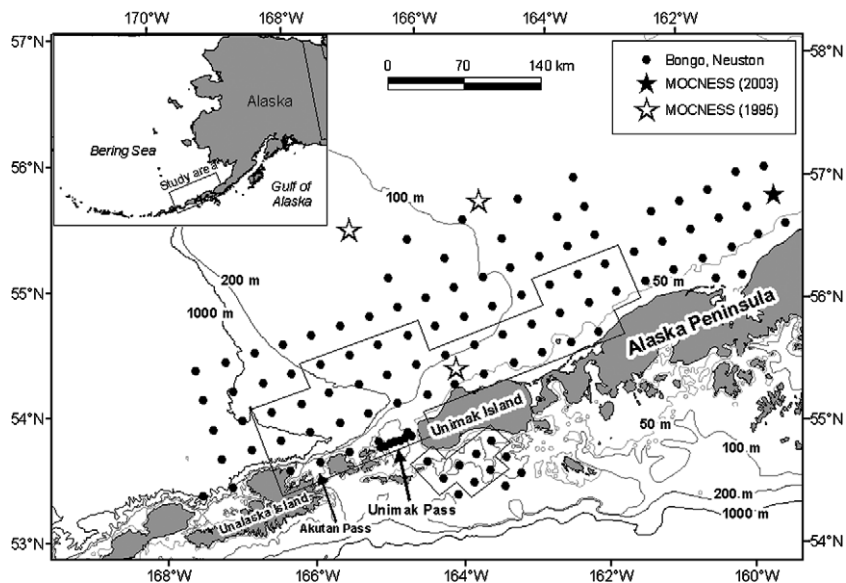

Fig. 1. Bongo and neuston grid station locations in the eastern Bering Sea and Gulf of Alaska for 2002 and 2003, and MOCNESS station locations in the eastern Bering Sea for 1995 and 2003. The subset of bongo and neuston stations occupied in both years is outlined by boxed areas.

environmental sampling system (MOCNESS; Wiebe et al., 1976) to collect depth-discrete samples every 3 h over a 24-h period at one station (depth = 60 m) on the EBS shelf (Fig. 1). Depth strata were: 0–10 m, 10–20 m, 20–30 m, 30–40 m and 40–50 m. Prior to each MOCNESS tow, salinity and temperature data were collected at the same depth strata using a Seabird 911 CTD profiler. In addition, we augmented our investigation by examining historical MOCNESS ichthyoplankton data collected by the Bering Sea Fisheries-Oceanography Coordinated Investigations program (1995). Historical rock sole samples have been conclusively re-identified as either northern or southern rock sole (Orr and Matarese, 2000).

Ichthyoplankton samples were fixed in 5% formalin and sorted by species; individuals were identified to the lowest possible taxon, enumerated, and measured (mm SL) at the Plankton Sorting and Identification Center in Szczecin, Poland. Larval identifications were verified at the Alaska Fisheries Science Center in Seattle, Washington, USA. Larval abundance was expressed as catch 10 m^{-2} for bongo and MOCNESS tows, and as catch 1000 m^{-3} for neuston tows.

2.2. Geographic distribution

We utilized parametric (analysis of variance: ANOVA) and nonparametric (generalized additive model: GAM) statistical techniques to explore relationships between larval abundance and size with respect to year, location, gear type, water depth, temperature, and salinity. Analysis of variance (ANOVA) was utilized to test for differences in larval abundance (fourth root transformed) among stations and between gear types (bongo versus neuston). We standardized abundance to catch per 1000 m^3 when comparing gear types within years. We also examined geographic differences in larval size within each year (using data from bongo tows only). We controlled for possible confounding effects of larval growth over the sampling period by normalizing length data to a projected size on 21 May using an estimated larval growth rate of 0.2 mm d^{-1}. Hurst and Abookire (2005) estimated early juvenile growth rates for northern rock sole in the GOA to be between 0.2 and 0.3 mm d^{-1}, and we conservatively assumed larval growth rates to be similar. Geographic differences in fish length were visualized by grouping stations according to geographic region and larval size structure. Groupings were subjective but were made to examine regional differences in size distribution (using the ANOVA technique) and to elucidate potential dispersal routes.

We considered the average water temperature and salinity at each station as a signature for the different currents in the region. The presence of fronts and/or mixing at the interface of two water masses could be construed as warranting separate consideration. A preliminary examination of the data indicated that temperature and salinity variations only appeared to occur at the natural breaks between landscape features (i.e., isobaths), so we determined that a separate category for possible fronts was not warranted. We related fish length and distribution to each proxy variable by assigning stations to one of three temperature and salinity categories (Table 1). In addition, we examined the effect of bathymetry on abundance and length by assigning each station to one of four water depth categories (Table 1). Abundance and length data for each category were compared using an ANOVA. Multiple comparison tests were used to explore differences among means (Fisher's least significant differences, LSD).

Table 1
Environmental categories and ranges used in analyses of larval abundance and length

Year	Category	Water depth (m)	Temperature (°C)	Salinity
2002	1	0–50	1.9–3.2[a]	26.2–31.5
	2	50–100	3.2–4.0	31.5–32.3
	3	100–200	4.0–5.3	32.3–33.1
	4	>200	–	–
2003	1	0–50	3.8–4.3	30.7–31.5
	2	50–100	4.3–4.9	31.5–32.4
	3	100–200	4.9–6.0	32.4–32.6
	4	>200	–	–

Temperature and salinity values are averages of station profiles. Note differences in temperature and salinity ranges between years.
[a] No larvae were captured in this temperature range in 2002.

We also used ANOVA to compare larval abundance and length between years. However, because geographic coverage of the sample grids between 2 years varied slightly, interannual variations in species abundance and length were examined from a subset of stations (51) occupied in both years of the study (Fig. 1, boxed areas). Interannual variation in larval abundance was evaluated by testing for differences in bongo and neuston catches between years. Interannual variation in larval length was evaluated by testing for differences among larvae collected in bongo tows between years.

Larval abundance and length data were also analyzed using a nonparametric regression technique called the generalized additive model (GAM). The GAM offers advantages over ANOVA because it is less restrictive in its assumptions about the underlying statistical data distribution, and analyzes the independent variables simultaneously, which allows their partial effects to be resolved. In a GAM the covariates are assumed to affect the dependent variable through additive and unrestrictive smooth functions.

We carried out separate GAM analyses for the 2002 and 2003 bongo catch data. Due to the large number of zero observations, a two-stage model was implemented for the abundance analyses; first larval presence/absence was modeled, and second, the number (log-transformed abundance) of larvae was modeled, given that some larvae were observed. A GAM with logit link, binomial error structure was applied in the first stage for modeling, while in the second stage a GAM with an identity link function and Gaussian error distribution was implemented. Given that length data were only available when larvae were present, analysis of larval size (normalized length) required only a one-stage GAM, which also utilized an identity link function and Gaussian error distribution. In each analysis the best fit model was determined by running GAMs with all possible combinations of the covariates (including all possible one-variable models, two-variable models, etc.) and choosing the model with the lowest generalized cross-validation (Gu, 2002; Green and Silverman, 1994).

The independent variables examined in the GAM analyses included water depth, temperature, salinity, and station location. Water temperature and salinity values at each station were averaged over depth. Station location was split into two covariates: *Along Shore* and *Away from Shore*. The *Along Shore* and *Away from Shore* variables (described below) were used in lieu of station latitude and longitude because they were less likely to interact and were more interpretable as meaningful gradients (Venables and Dichmont, 2004). The *Along Shore* variable measured the location of each station along the long-axis of the sampling grid, roughly following the coastline of the Alaska Peninsula from southwest to northeast. *Along Shore* station locations were expressed as the distance (km) to the east of a reference line placed perpendicular to, and bisecting, Unalaska Island. Because geographic coverage of the sample grids between the 2 years varied slightly, this perpendicular reference line bisected the southwestern end of Unalaska Island in 2002, while in 2003 it ran through the northeastern end of Unalaska Island. The *Away from Shore* variable measured the location of each station along the short-axis of the sampling grid, moving away from the Alaska Peninsula from southeast to northwest. *Away from Shore* station locations were expressed as the distance (km) of each station to the north of a reference line placed in roughly the center of the Alaska Peninsula and running parallel to its long-axis.

2.3. Vertical distribution

We examined differences in catch of northern rock sole larvae between the surface layer and the water column within each year by comparing abundance in the neuston tows with abundance in the bongo tows. We also tested for day-night differences in larval abundance in the neuston layer using a nonparametric permutation test (using the program STAT-EXACT). The nonparametric approach was used because there was high incidence of zero catches. We used ANOVA and Fisher's LSD tests to examine differences in abundance and length (mean weighted by CPUE) of larvae collected from MOCNESS sampling. Temperature and salinity profiles taken from corresponding CTD casts were also examined and compared with larval abundance and length from MOCNESS sampling.

2.4. Physical oceanography

We related larval distribution patterns to current patterns in the vicinity using two different approaches. We evaluated potential dispersal of larvae from the GOA into the EBS through Unimak Pass by examining trajectories of "holey-sock", satellite-tracked drifters. All drifters were drogued at ∼40 m to examine low fre-

quency current patterns and to reduce the effects of tidal forcing. Nine trajectories were available for 2002 and eight for 2003. All drifters considered in this study were either released in the GOA and entered the Bering Sea through Unimak Pass, or were released in Unimak Pass or nearby Akutan Pass (Fig. 1).

We evaluated potential dispersal of larvae along the Alaska Peninsula using modeled depth-specific currents from an implementation for the Northeast Pacific of the Regional Ocean Model System (NEP-ROMS; Righi, 2005; Curchitser et al., 2005). Based on previous Regional Ocean Model Systems that use stretched, terrain-following coordinates in the vertical and orthogonal curvilinear coordinates in the horizontal to produce three-dimensional simulated data fields (Hermann and Stabeno, 1996; Hermann et al., 2002), the NEP-ROMS model allows visualization of the vertical profiles of oceanic currents in the eastern Bering Sea. Fifteen simulated floats were initialized in the vicinity of Unimak Island on 1 April of 2002 and 2003. Floats were launched at varying depths from the surface to ~40 m. Daily wind and buoyancy flux estimates, derived from a global model, allowed hindcasting of circulation, salinity, temperature fields and tidal circulation. Simulated floats were tracked for 90 days, and discrete-depth drifter trajectories and endpoints were mapped to examine vertical flow variations in each year.

We examined the endpoints of the simulated drifters to determine the proportion of floats that were retained along the peninsula versus the proportion that were advected towards the north. If drifter endpoints were north of an imaginary line drawn between 54.80° N, 167.55° W and 57.72° N, 161.69° W at the end of the 90-day simulation, then they were considered to be advected to the middle/outer shelf region (usually following the 100 or 200 m isobaths). Endpoints that were south of the line at the end of the simulation were considered to be retained along the peninsula (inside the 50 m isobath). Line position was arbitrarily determined, but roughly bisected divergence between floats moving towards the middle/outer shelf region and those moving towards the peninsula. We compared simulated water movement to observed distribution patterns of northern rock sole larvae to discern if any patterns were identifiable.

3. Results

3.1. Geographic distribution

Absolute abundances of northern rock sole larvae were different between the 2 years of study. Larval abundance was an order of magnitude higher in 2002 than in 2003 (ANOVA, $p < 0.0001$). However, relative differences in distribution were similar. Within each year, larval abundance (catch per 1000 m^3) was significantly lower in the neuston tows than the bongo tows ($p < 0.0001$), indicating that fewer larvae were present in the surface layer than in the water column (Figs. 2 and 3). Since catch in the neuston tows was low, all subsequent analyses of abundance and length were restricted to larvae collected in the bongo tows.

Northern rock sole larvae occurred in large patches in both 2002 and 2003, with highest abundances occurring at stations within and to the northeast of Unimak Pass (Fig. 3). Abundance was reduced west of Unimak Pass, and aggregations west of Unimak Pass appeared spatially separated from those farther east by large gaps. Larval abundance increased eastward along the Alaska Peninsula, though it should be noted that the sampling grid in 2003 extended farther east than in 2002 (Fig. 3). The GAM analyses supported the observation that NRS larvae were separated by mesoscale gaps. Abundance of larvae was significantly affected by the station position, defined in terms of distance along the Alaska Peninsula and away from shore, in both 2002 (Table 2, first and second stage models) and 2003 (Table 3, second stage model). To better understand the effects of these covariates, we examined the fitted contribution of each variable to total larval abundance plotted against the value of the variable (Figs. 4 and 5). In 2002 the *Along Shore* term had a positive effect on larval abundance beginning at about 300 km (Fig. 4b). This is a reflection of the high catch abundances seen at the northeast end of the study area (Fig. 3a), that is, >300 km to the northeast of the sampling grid's southwestern boundary. Likewise in 2003 the positive effect of the *Along Shore* term (Fig. 5b) was reflected in the rather patchy catch abundances seen across the sampling grid (Fig. 3c). The distribution of NRS larvae also appeared to vary with distance from the shoreline. The *Away from Shore* term appeared in the GAM models of abundance for both 2002 (Table 2, ns) and 2003 (Table 3, $p = 0.000$). In both years larvae occurred in the nearshore half of the sampling grid (Figs. 4b and 5b). We noted a lack of station position covariates in the best fit presence/absence models (first stage), with the exception of the significant *Along Shore* term in 2002 (Table
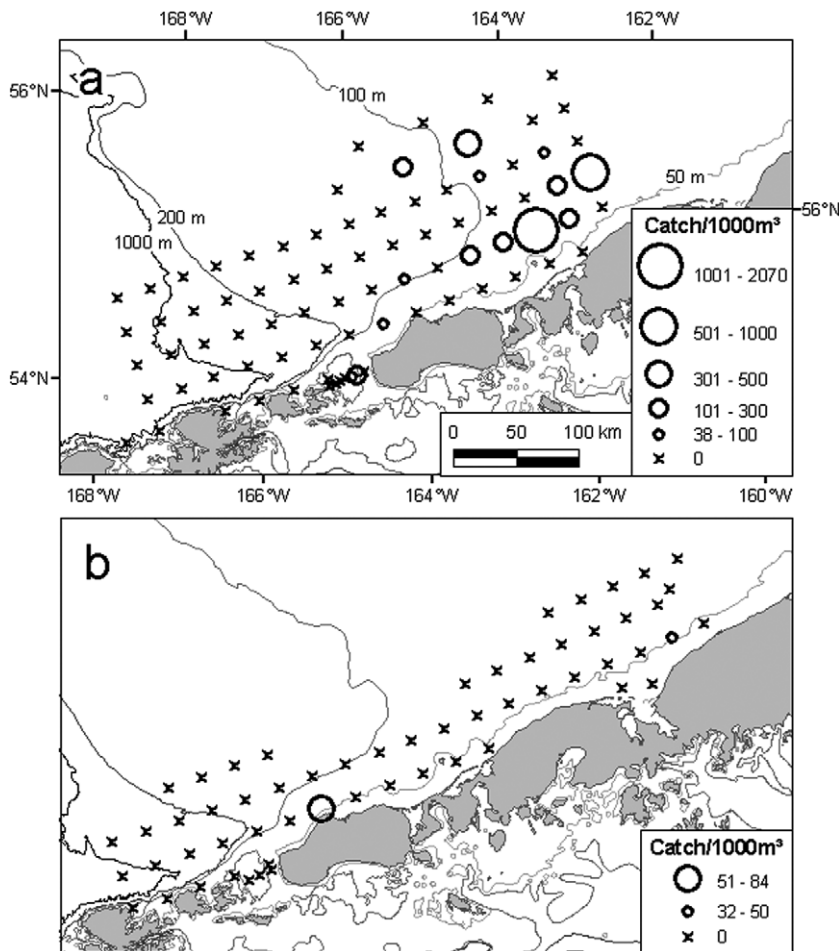
Fig. 2. Distribution of northern rock sole larvae in neuston tows. Catch concentrations (catch 1000 m^{-3}) for (a) 2002 and (b) 2003. Note the difference in concentration scales for the 2 years.

2). However, we caution that the numerous zero observations considered in the first-stage GAM analyses may have masked some of the larvae-covariate relationships.

In addition to geographic location, larval abundance also appeared to be related to water depth, temperature and salinity. Water depth had a significant effect on abundance in both years of this study (ANOVA results; 2002, $p < 0.0001$; 2003, $p = 0.001$). Abundance tended to be highest over depths between 50 and 100 m in 2002, between 100 and 200 m in 2003, and in both years was significantly reduced near the slope (>200 m). Water depth was also a significant explanatory variable in the presence/absence GAM for 2002, although it was not in the best-fit GAM for abundance in that year (Table 2). However, water depth was a covariate in the GAM for abundance for 2003 (Table 3, $p = 0.103$).

In 2002, abundance was also significantly related to salinity (ANOVA, $p < 0.0001$). Abundance was highest in waters with salinities of 31.5–32.4, which were centered over the middle/outer shelf regions (Fig. 3). Abundance was lowest in the high salinity waters (>32.4) that extended over the slope and the western half of the sampling grid. Higher salinities in this area are likely related to intrusions of slope water onto the shelf via the Bering Canyon. The relationship between salinity and abundance was similar in 2003 (ANOVA, $p = 0.065$). Salinity also appeared as a covariate in the best-fit GAM for abundance for 2002 (Table 2), and in the temperature–salinity interaction term in the GAM for presence/absence for 2003 (Table 3). We note here that there was a positive correlation between salinity and water depth in both years ($R^2 = 0.41$, 2002; $R^2 = 0.53$, 2003). In addition, the second best-fit GAM for larval abundance for 2003, which substituted salinity
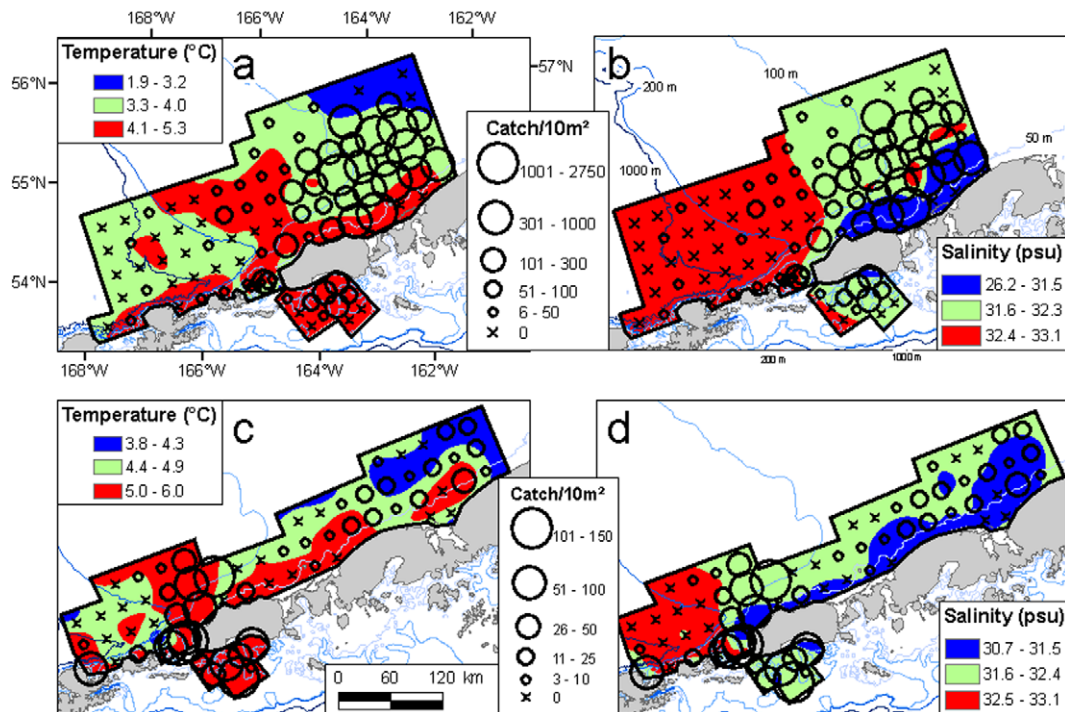
Fig. 3. Distribution of northern rock sole larvae in bongo tows. Catch abundances (catch 10 m^{-2}), and temperature and salinity contours for (a and b) 2002 and (c and d) 2003. Note differences in abundance scales and contour levels between years. Temperature and salinity contour levels correspond to categories 1–3 presented in Table 1.

Table 2
Results of best fit GAMs for northern rock sole distribution in 2002

Statistics	Two-stage modelling		Single model
Model stage	First	Second	na
Data type	Presence/absence	Larval density given presence	Mean length per station
Family	Binomial	Gaussian	Gaussian
Link	Logit	Identity	Identity
n	81	52	51
R-squared (adjusted)	0.752	0.732	0.548
% Deviance explained	80.8	75.0	68.5
GCV score	1.056	0.522	0.482
Covariates (p-values)	Along shore (0.011)[*]	Along shore (0.000)[*]	Away from shore (0.000)[*]
	Temperature (0.001)[*]	Away from shore (0.120)	Water depth (0.003)[*]
	Water depth (0.000)[*]	Temperature (0.099)	Salinity (0.003)[*]
		Salinity (0.242)	Temperature (0.075)

GCV, generalized cross-validation; na, not applicable.
  [*] Significant result ($\alpha = 0.05$).

($p = 0.184$) for depth, explained a similar amount of the deviance (77.1%) in abundance, and had an only slightly higher GCV score (0.692).

Temperature significantly affected abundance in 2003 (ANOVA, $p = 0.002$). Stations at intermediate temperature ranges (~4–5 °C), which occurred throughout the sampling grid, were associated with significantly lower abundances than higher and lower temperature ranges. In addition, temperature appeared as a covariate in the first and second stage best-fit GAMs for both years of this study, although it was only a significant explanatory variable in the GAM for presence/absence for 2002.

Table 3
Results of best fit GAMs for northern rock sole distribution in 2003

Statistics	Two-stage modelling		Single model
Model stage	First	Second	na
Data type	Presence/absence	Larval density given presence	Mean length per station
Family	Binomial	Gaussian	Gaussian
Link	Logit	Identity	Identity
n	60	36	36
R-squared (adjusted)	0.657	0.672	0.496
% Deviance explained	75.8	77.9	55.2
GCV score	0.672	0.668	1.572
Covariates (p-values)	Temperature-salinity interaction (0.026)[*]	Along shore (0.003)[*]	Along shore (0.003)[*]
		Away from shore (0.000)[*]	Away from shore (0.004)[*]
		Temperature (0.090)	Temperature (0.025)[*]
		Water depth (0.103)	

GCV, generalized cross-validation; na, not applicable.
[*] Significant result ($\alpha = 0.05$).

The absolute sizes of northern rock sole larvae were significantly different between 2002 (mean = 7.0 mm SL ± 0.07) and 2003 (mean = 8.6 mm SL ± 0.14) (ANOVA, $p < 0.0001$), though geographic differences in relative size structure within each year were similar (Fig. 6). In both years, the mean length of larvae collected west of Unimak Pass was generally shorter than regions farther east. In 2002, larvae collected from the eastern-most sampling region (Fig. 6, Region E) were longer than those collected from north (Region D, $p = 0.001$) or south (Region A, $p = 0.001$) of Unimak Pass. In 2003, larvae from the eastern-most sampling region (Region F) were shorter than those north (Region D, $p < 0.0001$), in (Region B, $p = 0.001$) and south (Region A, $p < 0.0001$) of Unimak Pass.

The GAM for larval fish length also revealed geographic differences in size structure of NRS larvae; station position was a significant explanatory variable in both years of this study. As with the abundance analyses, we examined the fitted contribution of each variable to total mean larval fish length plotted against the value of the variable (Fig. 7). In 2003 larval fish length appeared to be negatively affected (i.e. fish became smaller) at >350 km to the northeast of the sampling grid's southwestern boundary. This location roughly corresponds to the boundary between Regions E and F in Fig. 6. Although the *Along Shore* term was not a covariate in the 2002 model, we again note that the survey area was truncated in 2002.

In addition to variation in larval fish length with *Along Shore*, the station position *Away from Shore* was a significant explanatory variable in both 2002 (Table 2) and 2003 (Table 3). Considering the nearshore, shallow-water spawning habits of this species, it was not surprising to find that increased distance from shore positively affects larval fish length (Fig. 7). Water depth was also a significant explanatory variable in the 2002 GAM for larval fish length (Table 2). Although Fig. 7 shows we found that fish length was negatively correlated with water depth in 2002, we point out that this relationship was due to a single, outlier data point. We do not have convincing rationale for removing this data point from the formal GAM analyses, though we note that when this outlier was removed from informal GAMs, the fish length-water depth relationship became positive without substantially changing the other relationships expressed within the GAM. ANOVA testing also showed that larval fish length varied significantly with water depth in both years (2002, $p = 0.045$: 2003, $p = 0.048$). In general, smaller fish tended to occur in nearshore, shallow water. In 2002, fish that occurred at depths between 0 and 50 m were significantly smaller than those collected at 50 and 100 m. In 2003, fish collected at depths between 0 and 50 m were significantly smaller than those collected at both 50 and 100 m or 100 and 200 m. There were insufficient length data in the >200 m depth range for analyses.

Salinity appeared as a significant explanatory variable in the GAM analysis for larval fish length for 2002 (Table 2, Fig. 7). Although salinity was not a variable in the best-fit GAM for larval fish length for 2003, the second best-fit model for 2003, which substituted salinity (significant in that model) for temperature, explained a similar amount of the deviance (57.2%) in larval fish length and had a marginally higher GCV score (1.579). These results suggest temperature and salinity were correlated in 2003. Analysis of variance testing on the 2003

(a) First-stage modelling   **(b) Second-stage modelling**
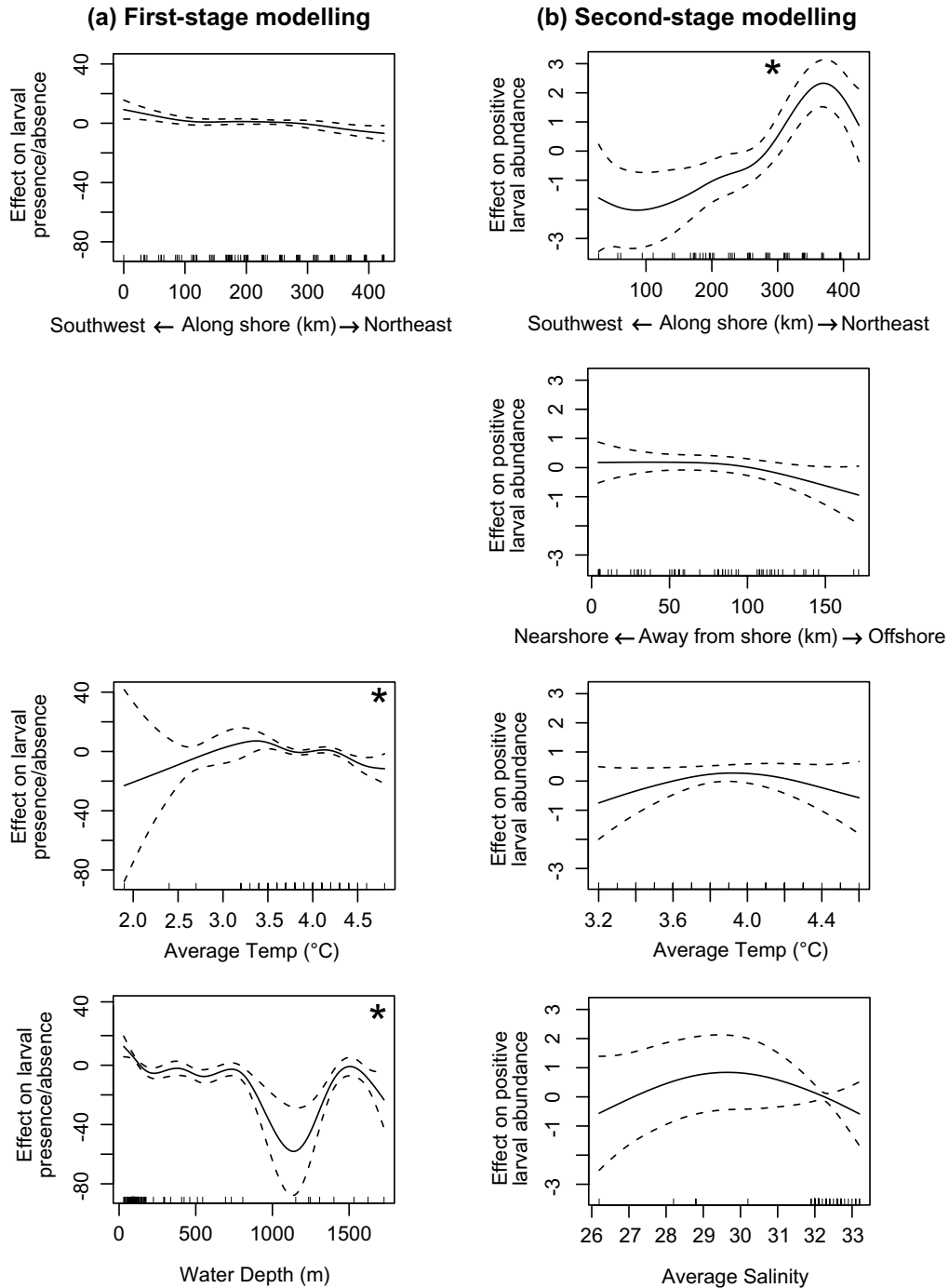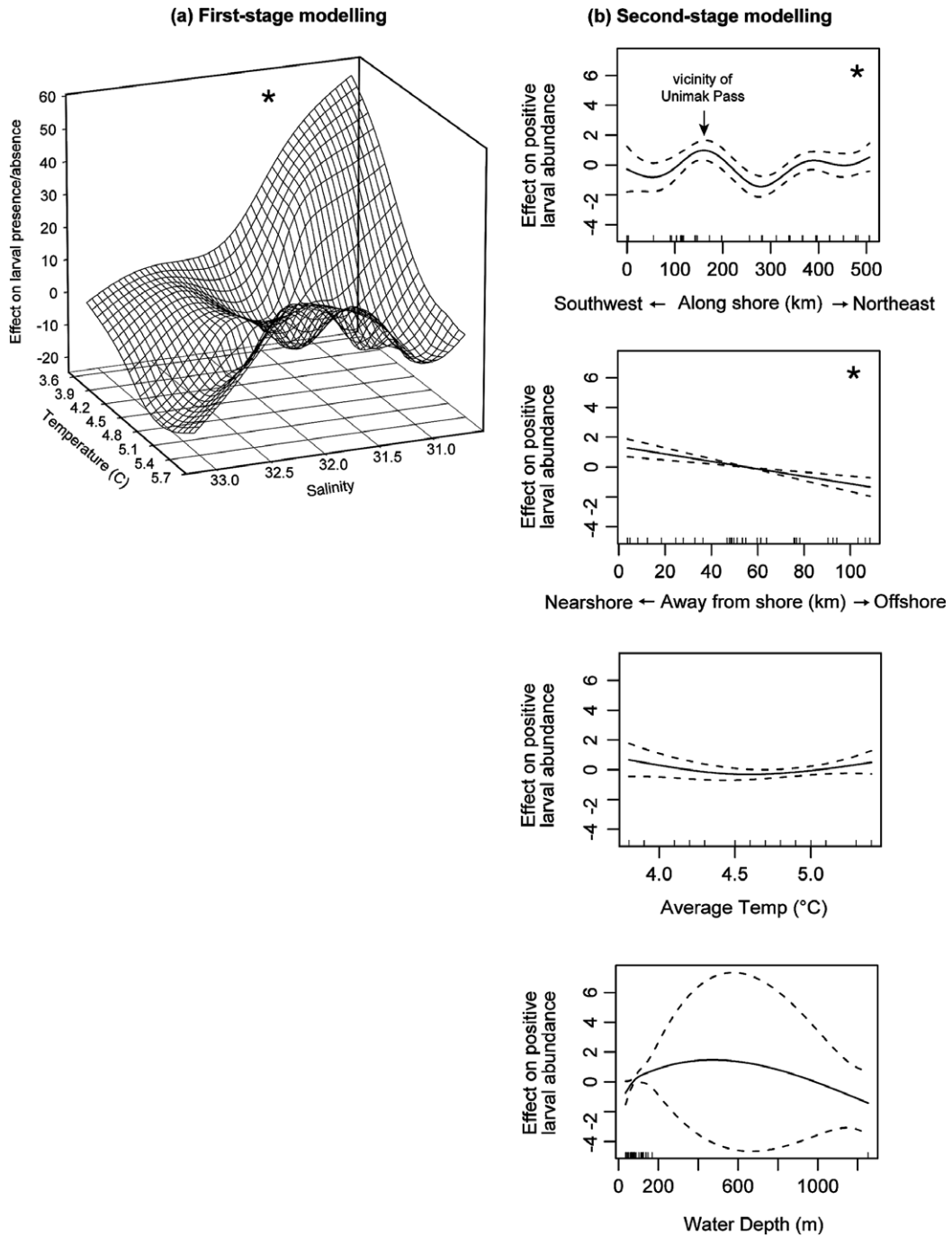

Fig. 4. Results of GAM regression for 2002 (a) NRS larval presence/absence and (b) NRS larval abundance (log) given presence as a function of station position along shore, station position away from shore, water depth, average water temperature, and average salinity. Broken lines represent 2-SE ranges around the covariate main effects. *Variable *p*-value < 0.05.

data also suggested a relationship between fish length and salinity ($p = 0.034$). Northern rock sole larvae caught in high salinity waters (>32.5) were longer than those caught in low salinity waters (<31.5), though this result should be interpreted with caution because of the small sample size. In general, larvae caught north of

Fig. 5. Results of GAM regression for 2003 (a) NRS larval presence/absence and (b) NRS larval abundance (log) given presence as a function of station position along shore, station position away from shore, water depth, average water temperature, average salinity, and the interaction of temperature with salinity. Broken lines represent 2-SE ranges around the covariate main effects. *Variable *p*-value < 0.05.

Unimak Pass, an area characterized by high salinity slope water, were longer than those caught in the eastern-most regions (Fig. 6), which are characterized by low salinity coastal/shelf water (Fig. 3).

Water temperature, averaged over depth at each station, was generally cooler in 2002 (range 2.0–4.5 °C) than in 2003 (4.0–6.0 °C). Although temperature appeared as a significantly factor in all statistical tests
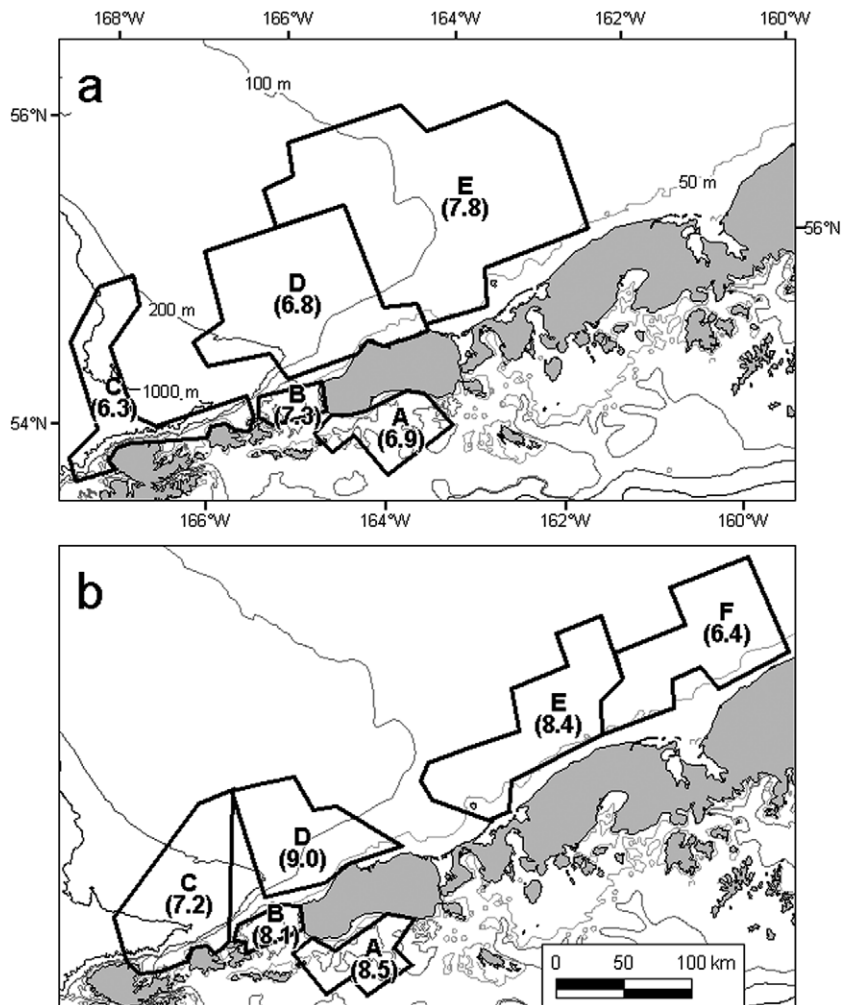
Fig. 6. Regional length groups used to examine geographic differences in size distribution of larvae in (a) 2002 and (b) 2003. Weighted mean length of larvae (mm SL) for each length group indicated in parenthesis.

(GAM and ANOVA) of fish length data, the results were ambiguous. Temperature appeared as a variable in both the 2002 ($p = 0.075$) and 2003 ($p = 0.025$) GAMs of larval fish length (Tables 2 and 3). However, plots of the temperature effects on larval fish length suggest a positive effect (i.e. larger fish) at the low end of the temperature scale (<3.9 °C) in 2002, while in 2003 the larger fish appeared at the high end (>4.8 °C, Fig. 7a and b). Analysis of variance also showed significant temperature effects in both years (2002, $p = 0.037$: 2003, $p = 0.001$). In addition, post hoc testing suggested similar temperature–fish length relationships to those found in the GAM analyses; in 2002 fish caught in moderate temperatures (3.0–4.0 °C) were longer than those caught at warm water temperatures (4.0–5.0 °C), while in 2003 fish caught in warmer water (5.0–6.0 °C) were longer than those caught at temperatures low and moderate for that year (4.0–5.0 °C).

3.2. Vertical distribution

As noted above, larval abundance was significantly higher in oblique (bongo) tows than in surface (neuston) tows in both years. MOCNESS sampling (2003) confirmed that northern rock sole larvae were distributed throughout the water column (Fig. 8). The ANOVA indicated an interaction between diel and depth-related effects on larval fish abundance. Accordingly, day and night samples were separated and vertical differences
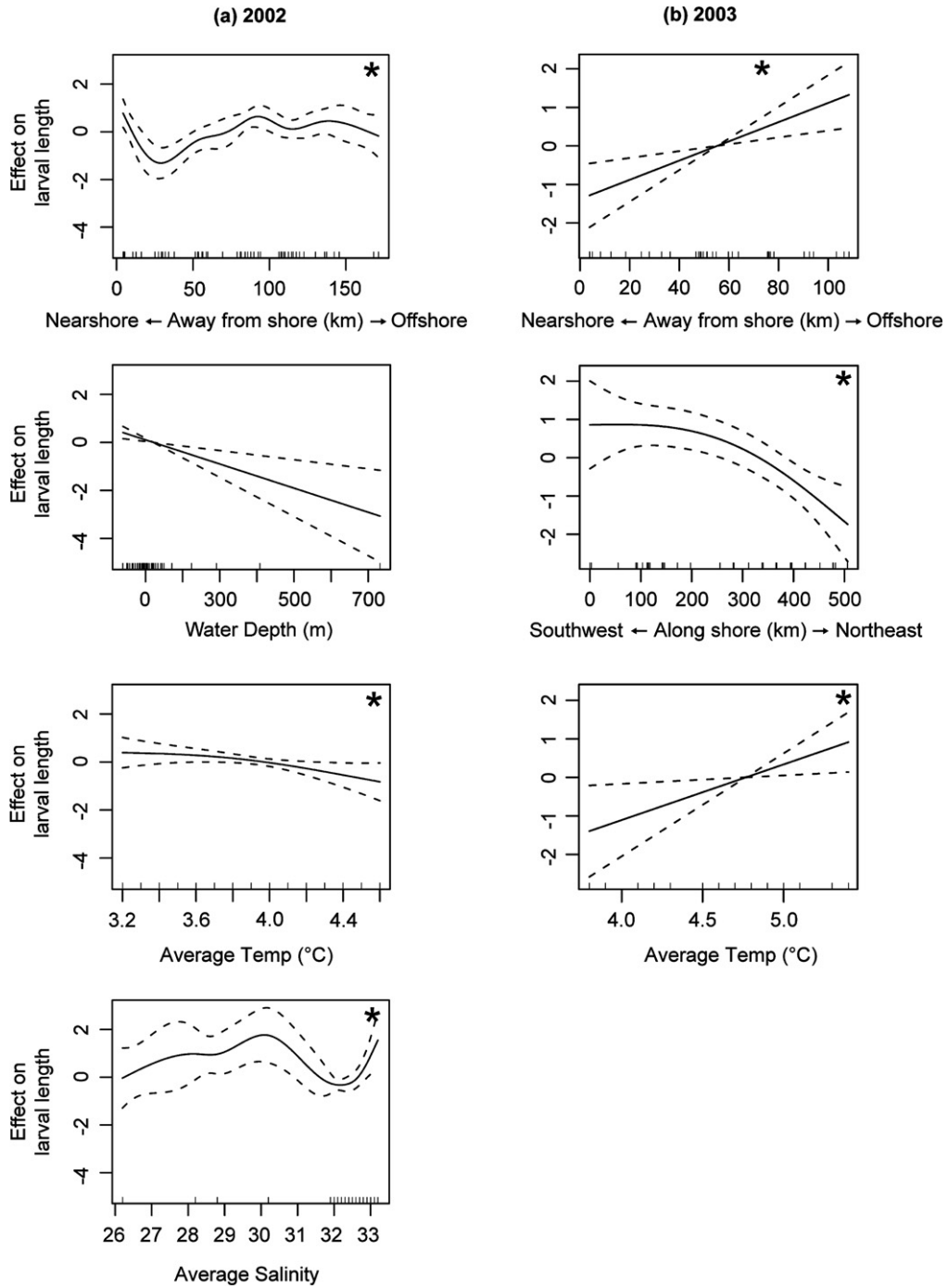
Fig. 7. Results of GAM regression for (a) 2002 and (b) 2003 NRS larval mean length per station as a function of station position along shore, station position away from shore, water depth, average water temperature, and average salinity. Broken lines represent 2-SE ranges around the covariate main effects. *Variable p-value < 0.05.

were re-evaluated. It was determined that significant depth-related differences in abundance occurred only during the day ($p = 0.0002$). Fig. 8 shows that 75% of the daytime catch occurred between 10 and 30 m, and only 2% of the daytime catch occurred in near-surface waters (0–10 m).
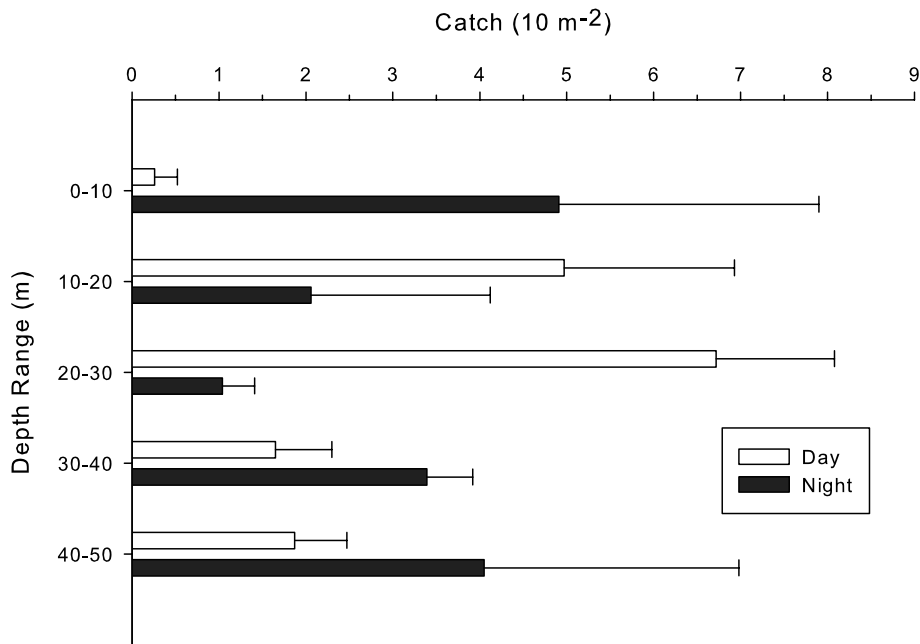
Fig. 8. Mean ($\pm$SE) abundance (catch 10 m^{-2}) of northern rock sole larvae collected from 0 to 50 m depth at a station on the eastern Bering Sea shelf occupied over 24 h in May 2003 (7 day tows, 2 night tows).

There were no significant differences in catch in the neuston gear between day and night (2002, $p = 0.06$; 2003, $p = 0.13$), though we noted a trend toward higher abundances at night. In 2002, the mean daytime abundance in the neuston was 10.2 ± 4.69 individuals 1000 m^{-3} while at night it was 163.1 ± 85.29 individuals 1000 m^{-3}. In 2003, there were no larvae in daytime catches, while at night the mean catch was 5.8 ± 4.38 individuals 1000 m^{-3}.

Further analyses of MOCNESS data (2003) indicated that there were also diel and depth variations of larval fish length (Fig. 9). Length varied significantly with depth during both day ($p = 0.042$) and at night ($p = 0.002$). During daylight, larger fish (6.61–6.75 mm mean SL) occurred at depths below 20 m. However at night, larger fish (8.23–8.48 mm mean SL) migrated to the top 20 m of the water column.

Analyses of historical MOCNESS data collected on the EBS shelf confirmed the observed relationship between depth and abundance. Data were limited; there were only two cruises (April and May 1995) where northern rock sole larvae were collected in MOCNESS sampling (153 mesh) on the EBS shelf. However, analyses of diel patterns from these collections concurred with our observations (Table 4). Larvae were collected below 20 m depth during daylight hours, and above 20 m depth at night. Comparisons of larval size with depth for these tows were deemed inappropriate, since catches were low and since the mesh size (153 μm) used was not ideal for sampling larger larvae.

3.3. Physical oceanography

Generally, drifter trajectories (2002–2003) indicated that the main direction of subsurface flow exiting Unimak Pass was northward, along the 100 and 200 m isobaths. A much smaller portion of flow followed the 50 m isobath northeast along the Alaska Peninsula (Fig. 10). Historical data (nearly 400 trajectories since 1986) confirm this pattern of divergence between the shelf and the peninsula (see Reed and Stabeno, 1996; Stabeno et al., 2002). Specifically in 2002, all nine drifters that were released in, or went through Unimak or Akutan passes, followed trajectories northward onto the EBS shelf (Fig. 10a). Four went through Unimak Pass in spring and early summer of 2002 (three in April; one in May/June), three crossed in late autumn (November/December) and two crossed in mid-winter (December 2002/January 2003). In 2003, eight drifters were deployed in, or went through, Unimak Pass. Seven of these followed a trajectory onto the EBS shelf, and
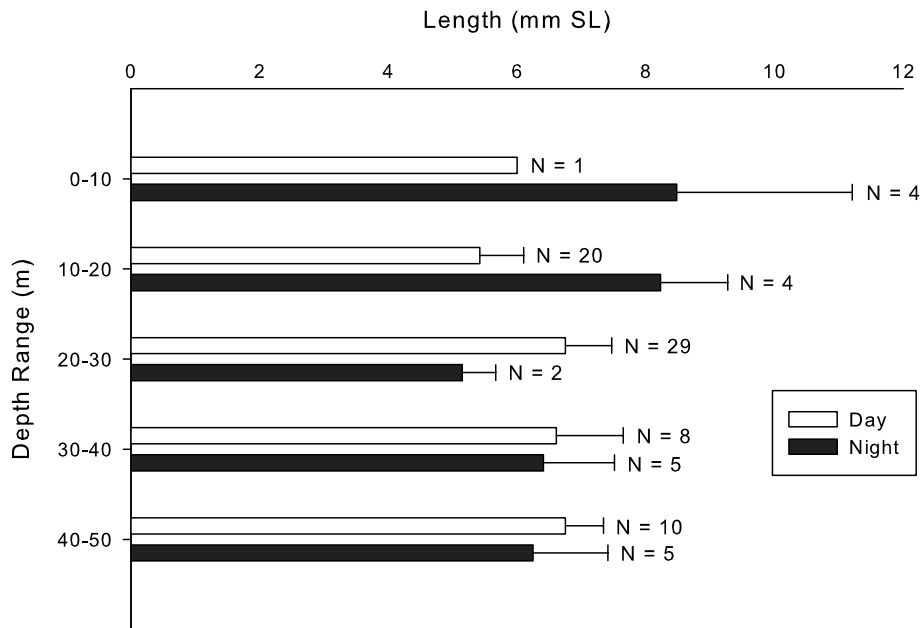
Fig. 9. Mean (±SE) standard length (mm) of northern rock sole larvae collected from 0 to 50 m depth at a station on the eastern Bering Sea shelf occupied over 24 h in May 2003 (7 day tows, 2 night tows).

Table 4
Depth-discrete northern rock sole larval distribution on the EBS shelf (1995)

Cruise	Location	Date	Local time	Depth (m)	Catch $(10 \, m^{-2})$
6MF95	55.07° N, 164.53° W	23 April	10:50 AM (Day)	1–10	1.9
				10–20	0
				20–30	0
				30–40	0
				40–55	9.0
6MF95	56.46° N, 164.60° W	30 April	8:50 PM (Day)	1–10	0
				10–20	0
				20–30	7.2
				30–40	0
				40–55	0
7MF95	55.07° N, 164.53° W	5 May	2:50 PM (Day)	1–10	0
				10–20	2.0
				20–30	12.7
				30–40	3.0
				40–50	6.9
7MF95	56.04° N, 166.41° W	9 May	12:40 AM (Night)	1–20	52.4
				20–30	8.6
				40–50	3.0
				100–115	2.7

Historical samples were collected from two research cruises conducted by the Bering Sea FOCI Program using a 1 m² MOCNESS system with 153 μm mesh nets. Note different depth intervals on 9 May.

only one traveled along the Alaska Peninsula (Fig. 10b). Two of the shelf-bound drifters went through Unimak Pass in early spring (February/March), one crossed in late spring (May) and four crossed in mid-winter (December 2003/January 2004). The drifter that traveled along the Alaska Peninsula went through Unimak Pass in the autumn (October) of 2003.
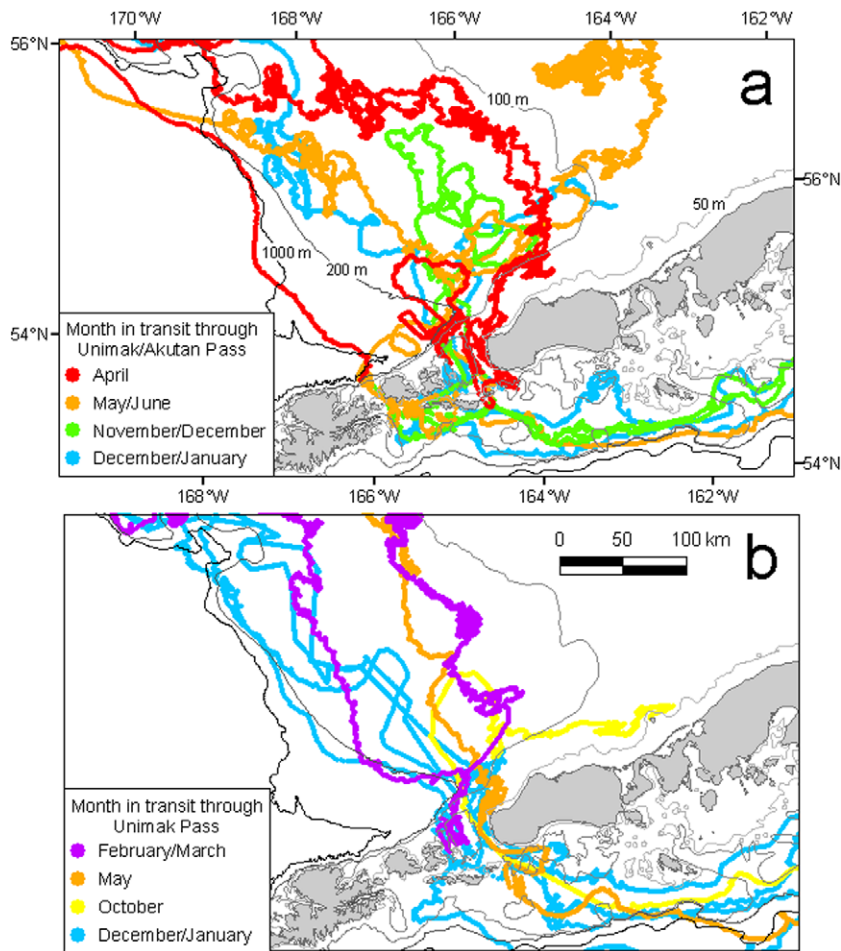
Fig. 10. Satellite-tracked drifter trajectories for (a) 2002 and (b) 2003. Line color indicates the approximate time of year each drifter passed through Unimak or Akutan Pass.

3.4. Model simulations

We evaluated flow along the Alaska Peninsula using modeled currents from NEP-ROMS circulation simulations for 2002–2003. They showed a divergence in flow with the majority of simulated floats moving along the 50 m isobath and a smaller fraction moving along the 100 m and, to a lesser extent, 200 m isobaths (Figs. 11 and 12). Most importantly, the direction of flow appeared to vary with depth. In both years, at the end of the model simulation a greater proportion of floats at depth (>10 m) were entrained along the 50 m isobath (80% in 2002, 84% in 2003) than along either the 100 m or the 200 m isobath (Table 5). However, movement of surface waters (0–10 m) varied between years. After 30 days in the 2002 simulation, there was a relatively even split between 50 m isobath trajectories (59%), and 100 m or 200 m isobath trajectories (41%). However, a wind event recorded on approximately Day 45 (mid-May) drove surface floats off the 50 m isobath and northward along the 100 m isobath (D. Righi, National Oceanic and Atmospheric Administration, Pacific Marine Environmental Laboratory, personal communication). As a result, by day 90 only 31% of the floats were retained along the 50 m isobath, while 69% were entrained along the 100 m and 200 m isobaths. It was apparent from this simulation that wind-forcing substantially influenced the top 10 m of the water column (Table 5). The change in surface float trajectories in 2002 is in marked contrast to surface trajectories in 2003, which showed more uniform movement along the 50 m isobath at all depths. In addition, progression of modeled floats
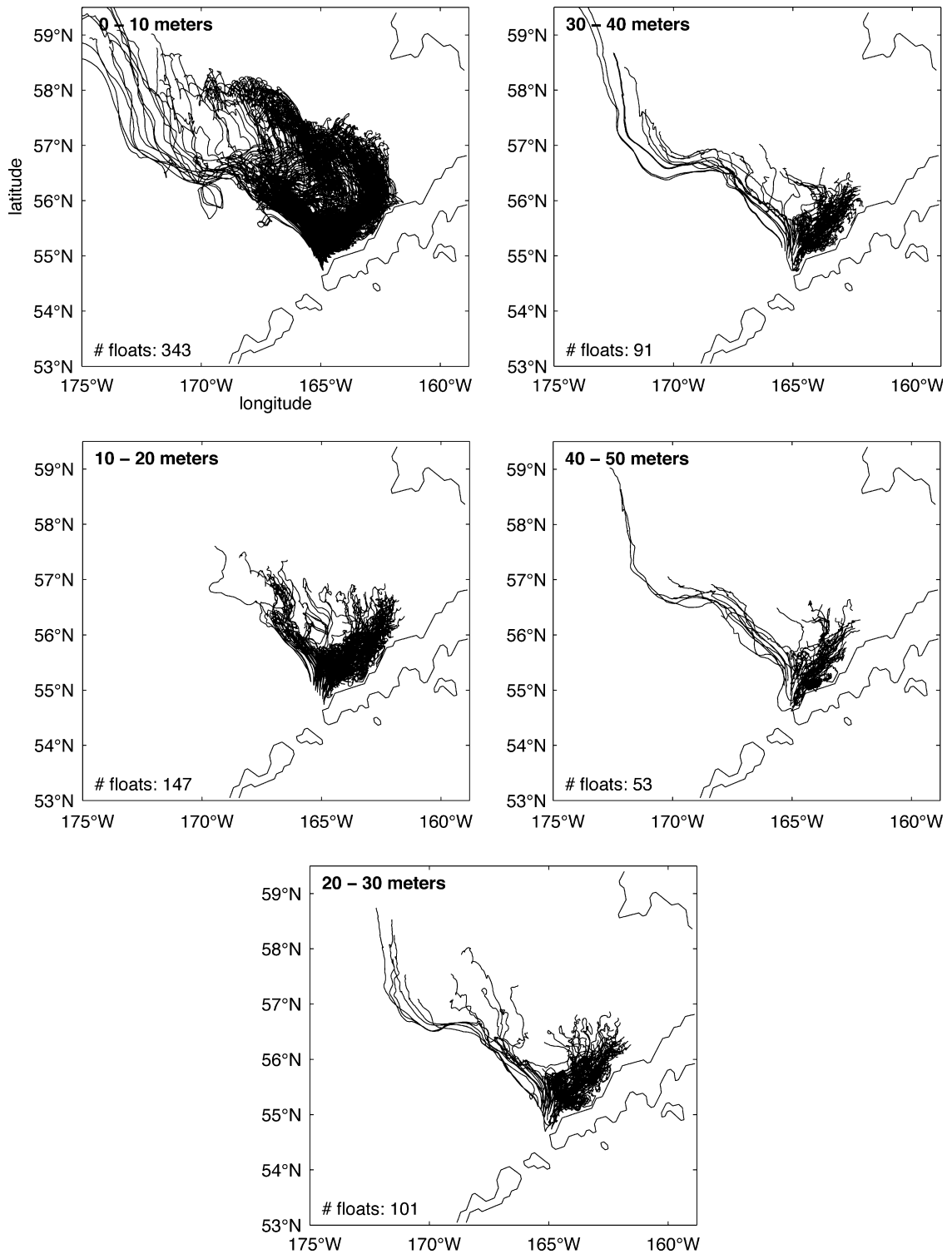
Fig. 11. Depth-discrete trajectories of Northeastern Pacific Regional Ocean Model System (NEP-ROMS) simulated drifters released in 2002. Number of floats initialized between depths ranges indicated in lower left-hand corner of each panel. Position of floats after 30 and 90 days, relative to line that passes through 54.80°N by 167.55°W and 57.72°N by 161.69°W, are shown in Table 5.
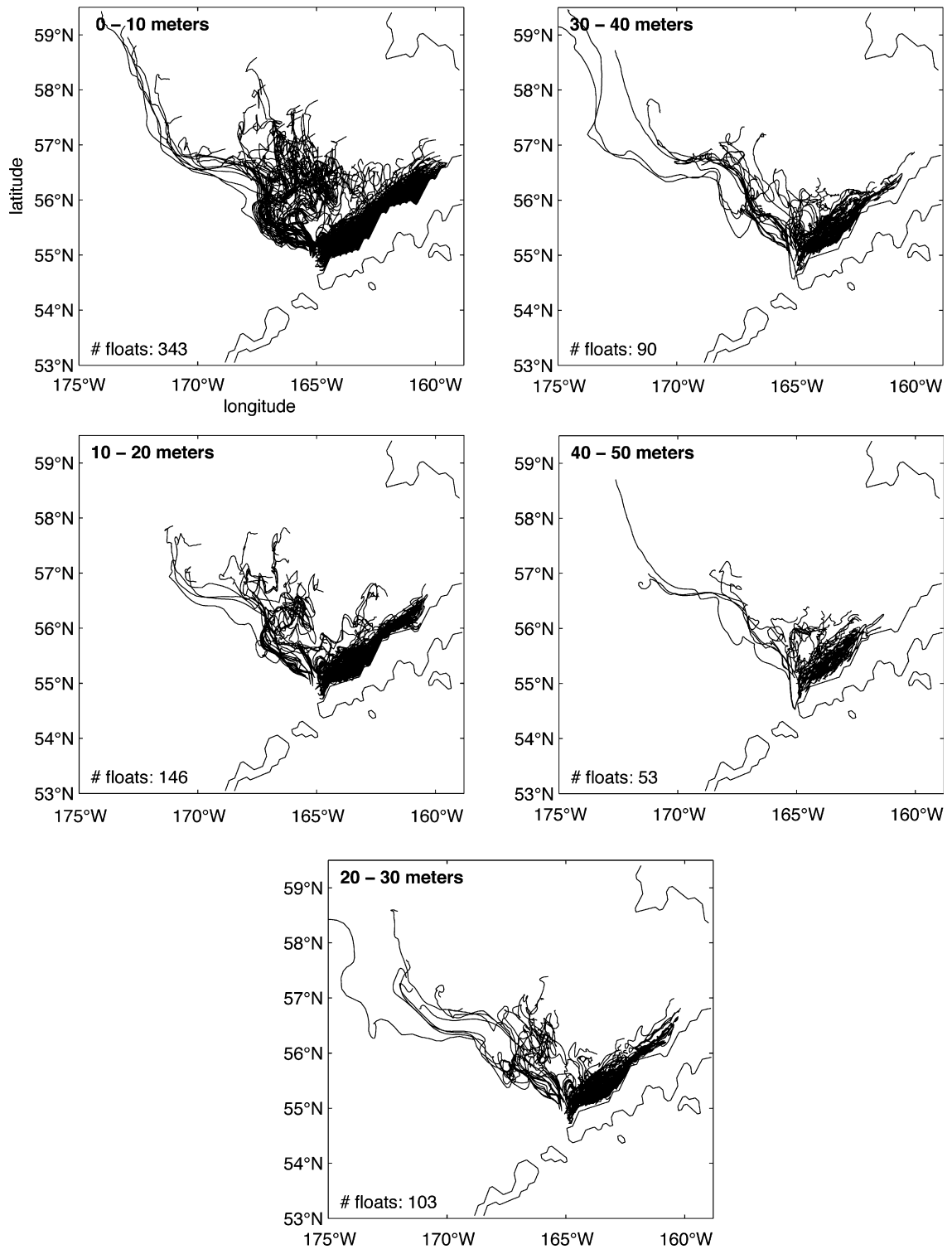
Fig. 12. Depth-discrete trajectories of Northeastern Pacific Regional Ocean Model System (NEP-ROMS) simulated drifters released in 2003. Number of floats initialized between depths ranges indicated in lower left-hand corner of each panel. Position of floats after 30 and 90 days, relative to line that passes through 54.80°N by 167.55°W and 57.72°N by 161.69°W, are shown in Table 5.

Table 5
Number of NEP-ROMS modelled floats moving eastward along the Alaska Peninsula (*East/Peninsula*) or northward towards the middle/ outer EBS shelf (*North/Shelf*) after 30 and 90 days

Year	Depth (m)	30 days		90 days		Total
		East/Peninsula	North/Shelf	East/Peninsula	North/Shelf	
2002	0–10	201	142	105	238	343
	10–20	122	25	116	31	147
	20–30	88	13	84	17	101
	30–40	77	14	70	21	91
	40–50	48	5	42	11	53
2003	0–10	295	48	300	43	343
	10–20	124	22	124	22	146
	20–30	85	18	85	18	103
	30–40	76	14	74	16	90
	40–50	48	5	46	7	53

Position of floats was determined relative to a line that passes through 54.80° N, 167.55° W and 57.72° N, 161.69° W, shown in first panel of Figs. 8 and 9. Floats southeast of line = *East/Peninsula*, floats northwest of line = *North/Shelf*.

penetrated farther eastward along the Alaska Peninsula in 2003, indicating swifter current velocities along the 50 m isobath in that year relative to 2002.

4. Discussion

In 2002 and 2003 northern rock sole larvae were collected: (1) in the vicinity of Unalaska Island, west of Unimak Pass, (2) in the Gulf of Alaska south of Unimak Pass and in Unimak Pass itself, (3) immediately north of Unimak Island, and (4) along the Alaska Peninsula. Mesoscale gaps in larval abundance occurred between these areas (Figs. 3, 4b and 5b). In addition, there were distinct breaks in larval size distribution (Figs. 6 and 7). These observations suggest multiple spawning locations for northern rock sole along the Alaska Peninsula. Further, we found that there were distinct horizontal and vertical differences in currents in this vicinity (Figs. 11 and 12). Movement of water through Unimak Pass tended to be northwards, along isobaths, while flow east of Unimak Island was easterly, across isobaths and parallel to the coast (Fig. 10). We propose that northern rock sole larvae in the EBS are differentially advected from the Unimak Island vicinity, with the direction and speed of transport dependent upon their vertical distribution.

4.1. Interannual variations in abundance

Northern rock sole larvae were smaller and more abundant in 2002 than in 2003. It is unlikely that observed differences were related to variations in larval supply, as examination of adult rock sole (*Lepidopsetta* spp.) distribution in the same region (in summer) suggests that adult rock sole abundance was higher in 2003 relative to 2002 (Acuna and Kotwicki, 2004; Acuna et al., 2003). Rather, it seems more likely that factors associated with timing of spawning played a role in the observed differences. Water temperature data from 2002 and 2003 suggest that ocean temperatures were a degree colder in 2002 than in 2003 (Overland and Stabeno, 2004). Spawning in northern rock sole is probably temperature-dependent, so it is likely that spawning in 2002 occurred somewhat later than in 2003. Accordingly, larvae would be expected to be smaller and more abundant at the time of sampling in 2002, since growth and agents of mortality had less cumulative time to act on the population.

4.2. Larval vertical distribution

Northern rock sole larvae were not uniformly distributed in the water column in the EBS; rather, highest daytime abundances occurred between 10 and 30 m. Larvae were occasionally present in neuston catches, though surface water collections alone do not appear to be sufficient to adequately sample northern rock sole

larvae. We also found that larger, presumably older, larvae move vertically in the water column. Our observations of diel differences in vertical distribution and abundance are corroborated by historical data, and they were consistent with general observations of zooplankton vertical migration patterns in the Bering Sea (Schabetsberger et al., 2000). However, our results are in contrast to previously published reports of vertical distribution of rock sole larvae in the Gulf of Alaska (Haldorson et al., 1993). Those earlier studies showed GOA rock sole concentrated at depths of 5–15 m during the day and migrated deeper (20–30 m depth) at night. It should be emphasized that at the time these earlier studies were undertaken, it was not possible to distinguish between northern and southern rock sole larvae. It is likely that "rock sole" in these studies were a combination of *L. polyxystra* and *L. bilineatus*. We also emphasize that patterns of larval vertical position and movement are flexible, dependent not only on time of day, but potentially also on food availability, tidal stage, temperature, light, presence of internal waves, and more (e.g. Porter et al., 2005). The patterns we present here were based on a series of tows at one location, taken over one 24-h period; additional depth-discrete sampling needs to be conducted in both the GOA and in the EBS to confirm observed differences between the two systems. However, if differences are confirmed, it provides further evidence that there are disparities in fish early life histories between the GOA and the EBS. Other studies that have documented differences between the two systems include that by Kendall (2001), who noted that vertical distribution of walleye pollock (*Theragra chalcogramma*) eggs is strikingly different between the EBS shelf (<30 m) and the GOA (>180 m), and Duffy-Anderson et al. (2003) who demonstrated a higher degree of cannibalism among immature walleye pollock in the EBS relative to the GOA.

4.3. Implications for transport

Our observations of northern rock sole vertical distribution on the EBS shelf further our understanding of oceanographic processes that affect larval flatfish dispersal, and potentially recruitment in the Bering Sea. For example, previous work by Wilderbuer et al. (2002) compared trajectories from a wind-driven surface current model (OSCURS; Ingraham and Miyahara, 1988) with observations of interannual flatfish recruitment patterns. Wilderbuer et al. (2002) demonstrated that above-average flatfish recruitment success was correlated with wind-driven advection of flatfish larvae to inshore nursery grounds. We concur with Wilderbuer et al. (2002) that wind-forced transport of northern rock sole larvae is likely a component of their recruitment success, although surface transport models alone may not be sufficient to predict distribution and transport. In particular, net flow below the wind-mixed layer (15–25 m) is primarily baroclinic, and the majority of northern rock sole larvae were collected from depths below 10 m. Therefore, it is likely that the dispersal of a significant proportion of larvae is influenced by factors that modulate geostrophic flow rather than wind-driven surface currents (<10 m). It should also be noted that deepening of the wind-mixed layer could affect wind-induced transport of northern rock sole larvae even at depth. Likewise, larvae may be able to mitigate the effects of flow variation by altering their position in the water column. Biophysical models that couple larval vertical movement with 3D circulation and hydrography may provide more information on how larval behaviors affect dispersal trajectories.

4.4. Dispersal along the Alaska Peninsula

The regional ocean model used in the present analysis allowed us to account for potential differences between surface and subsurface flow in the EBS. General output from the model (1996–2004) has consistently indicated that flow on the EBS side of Unimak Island diverges in two broad directions (Stabeno et al., 2002; Duffy-Anderson et al., 2005). The eastward component (the Bering Coastal Current (BCC); P. Stabeno, unpublished data) follows the 50 m isobath along the Alaska Peninsula at 2–4 cm s^{-1}. The northwest component follows the 100 m (or 200 m) isobath at 5–8 cm s^{-1} toward the middle and outer domains of the EBS shelf. Sub-tidal (net) flow along the shallow 50 m isobath is both wind-induced and baroclinic, while flow along the 100 m or 200 m isobaths is primarily baroclinic. Data from 2002 to 2003 show that the majority of flow below 10 m moves eastward along the 50 m isobath, while a smaller portion flows along the 100 and 200 m isobaths. Surface flow follows a similar pattern, but may be punctuated by stochastic wind-induced divergence northward (Figs. 11 and 12, Table 5).

Since most northern rock sole larvae occur below the surface layer (>10 m, Figs. 5 and 6), we postulate that they are primarily dispersed from the Unimak Island vicinity by baroclinic flow. The majority of larvae located at depth are likely entrained in the BCC, along the 50 m isobath and dispersed to bays and estuaries in the coastal domain. A smaller portion is entrained in the baroclinic flow along the 100 m or 200 m isobaths and moves northward, with some flux, over the middle or outer shelves (Fig. 10). Interestingly, baroclinic entrainment of larvae in the more robust 100 m and 200 m isobath currents offers a significant probability of delivery to the Pribilof Islands vicinity, an area characterized as supporting increasing abundances of flatfishes since the 1980s (Conners et al., 2002), and a potentially suitable nursery habitat for juvenile northern rock sole (Busby et al., 2005).

Larvae that are spawned east of Unimak Island along the Alaska Peninsula are probably less influenced by flow along the 100 m or 200 m isobaths. Rather, they are primarily influenced by the baroclinic portion of the BCC, and are likely dispersed to bays and estuaries along the Alaska Peninsula and toward Bristol Bay (Fig. 13). Considering this relationship, it is possible that interannual variations in the baroclinc flow of the BCC may be reflected in years of positive or negative NRS recruitment, though we stress that additional studies are needed to test this hypothesis.

Proportionally fewer northern rock sole larvae occur in near-surface waters (0–10 m), but those that do are less likely to be influenced by variations in baroclinicity and are more vulnerable to intermittent wind events. For example, for the 2002 simulation, we noted that NEP-ROMS-modeled floats that had been initialized near the surface (0–10 m) were transported from the Alaska Peninsula northward at approximately 56° N, 161° W. Northward forcing of surface waters on the EBS shelf has been observed in other years as well (Duffy-Anderson et al., 2005). Unlike baroclinic transport northward, wind-forced northward dispersion (Fig 11, and Table 5) is transitory, as well as spatially and temporally unpredictable, so sustained transport to potential nursery areas in the north via this mechanism seems improbable.

4.5. Dispersal through Unimak Pass

We suggest that the majority of northern rock sole larvae collected in Unimak Pass were spawned in the GOA. Previous work has shown that flow into Unimak Pass (a portion of the Alaska Coastal Current) is
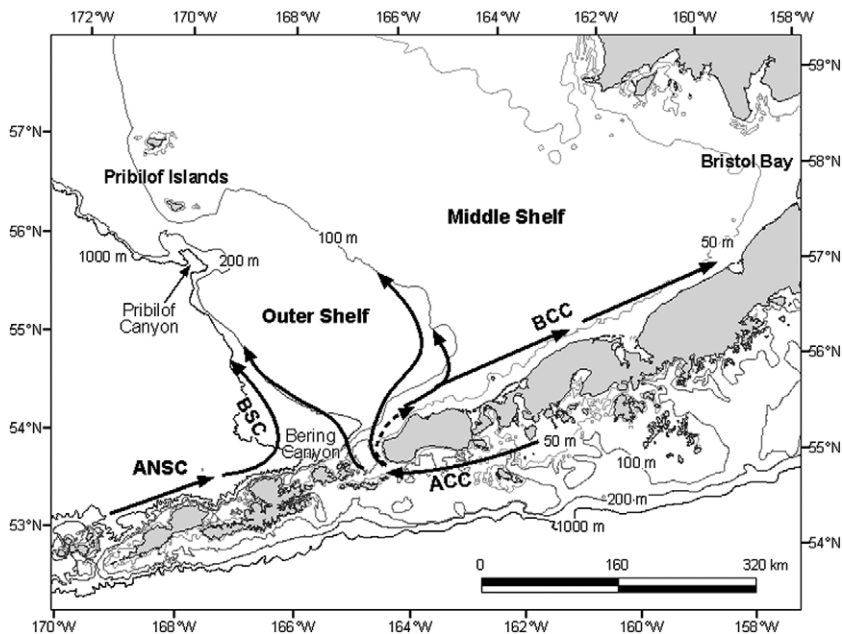

Fig. 13. Major current patterns associated with isobaths in the eastern Bering Sea (shelf and slope). Aleutian north slope current (ANSC), Bering slope current (BSC), Alaska coastal current (ACC) and Bering coastal current (BCC).

typically northward from the Gulf of Alaska into the Bering Sea (Schumacher et al., 1982; Reed, 1987; Stabeno et al., 2002), and we noted that mean size of larvae was similar between the GOA, Unimak Pass, and the EBS shelf north of Unimak Pass. As GOA-spawned larvae are transported through the pass, they are most likely entrained in current flowing northward along the 100 m isobath or along the 200 m isobath. Dispersal may be to nursery areas to the north such as the Pribilof Islands (Fig. 13). It is unknown, however, what the proportional contribution of northern rock sole spawned in the GOA is to recruitment or stock size in the EBS.

To begin to determine the contribution of GOA-spawned northern rock sole to rock sole recruitment in the EBS, it is important to note that there are seasonal differences in the direction of current flow through Unimak Pass. Spring (March–April) flow typically follows the 100 m or 200 m isobaths northwest. Later, however, flow through Unimak Pass has turned sharply to the northeast, presumably merging with and influencing the BCC. This shift in exit trajectory typically occurs by early summer (July) and lasts through late summer (September) (Stabeno et al., 2002). Abundance of northern rock sole larvae peaks in April (Matarese et al., 2003). Since drifter movements through Unimak Pass are predominantly along the 100 m and 200 m isobaths, even as late as mid-May, we postulate that the contribution of GOA-spawned northern rock sole larvae is minimal in juvenile settlement areas along the EBS side of the Alaska Peninsula.

4.6. Dispersal west of unimak pass

Larvae spawned west of Unimak Pass are potentially influenced by the Aleutian North Slope Current and Bering Slope Current (Stabeno et al., 2002). These currents act to modulate dispersal of larvae northward and potentially isolate these individuals from others spawned along the Alaska Peninsula (Fig. 13). Northern rock sole larvae influenced by slope currents may be transported to the continental shelf by flows that connect the basin and the shelf (Stabeno et al., 1999a). In particular, topographic features such as the Bering and Pribilof Canyons may steer and accelerate flow up onto the shelf, advecting and dispersing larvae to the EBS outer shelf (Stabeno et al., 1999b).

5. Conclusions

In summary, evidence of mesoscale gaps in distribution, as well as regional differences in larval size structure, suggest multiple spawning locations for northern rock sole along the Alaska Peninsula in 2002 and 2003. In addition, we show that NRS larvae on the EBS shelf are heterogeneously distributed in the water column, with highest daytime abundances at depths between 10 and 30 m. Relatively few larvae occur near the surface (<10 m), and these are likely affected by variations in wind-induced current patterns. Transport of deeper larvae is probably modulated by factors affecting geostrophic (primarily baroclinic) flow. Northern rock sole larvae appear to migrate vertically and may mitigate depth-discrete flow variations by actively altering their distribution in the water column. Observations of depth-specific flow in and around Unimak Pass, coupled with evidence of multiple northern rock sole spawning sites in this area, indicate that northern rock sole larvae spawned along the EBS side of the Alaska Peninsula may contribute a greater number of recruits to presumably favorable juvenile nursery grounds eastward along the Alaska Peninsula than do those spawned west or south of Unimak Pass.

Acknowledgments

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