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Ontogenetic and sex-specific differences in density-dependent habitat selection of a marine fish population

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Abstract. The spatial dynamics of species are the result of complex interactions between density-independent and density-dependent sources of variability. Disentangling these two sources of variability has challenged ecologists working in both terrestrial and aquatic ecosystems. Using a novel spatially explicit statistical model, we tested for the presence of density-independent and density-dependent habitat selection in yellowfin sole (*Limanda aspera*) in the eastern Bering Sea. We found specificities in the density-dependent processes operating across ontogeny and particularly with gender. Density-dependent habitat expansion occurred primarily in females, and to a lesser degree in males. These patterns were especially evident in adult stages, while juvenile stages of both sexes exhibited a mix of different dynamics. Association of yellowfin sole with substrate type also varied by sex and to a lesser degree with size, with large females distributed over a wider range of substrates than males. Moreover, yellowfin sole expanded northward as cold subsurface waters retracted in summer, suggesting high sensitivity to arctic warming. Our findings illustrate how marginal habitats can play an important role in buffering density-dependent habitat expansion, with direct implications for resource management. Our spatially explicit modeling approach is effective in evaluating density-dependent spatial dynamics, and can easily be used to test similar hypotheses from a variety of aquatic and terrestrial ecosystems.

Key words: Bering Sea; climate change; density dependence; habitat selection; marginal habitats; spatial distribution; yellowfin sole.

Introduction

The spatial distribution of organisms is generally not homogeneous in space and time as a result of habitat heterogeneity and complex mechanisms of habitat selection (Chesson 1998). A multitude of factors are known to play a role in determining the spatial dynamics of species, and they can be broadly classified as density-independent, changing with environmental variability, and density-dependent, changing with demography (Sutherland 1983). Environmentally-driven habitat selection is directly related to individual-level responses to different biotic and abiotic features that are unequally distributed in space and across habitats. This results in how different proportions of a population use different habitats (Křivan and Sirot 2002). With unlimited resources, a species' fundamental niche could potentially explain most of its habitat selection (Hutchinson 1957). However, in the presence of limited resources, the quality of a habitat is also a function of the density of individuals. As the density increases in a habitat, its quality decreases, promoting the movement of individuals toward unoccupied habitats with less environmentally suitable conditions (Rosenzweig 1991). If all individuals are capable of choosing the most suitable habitat available, their fitness should be homogeneous throughout the species' range (i.e., "ideal free distribution"; Fretwell and Lucas 1969).

Three models have been proposed to describe a species' density and distribution according to variations in global population abundance (Fig. 1). In the constant-density model (CM), increases in global abundance are characterized by maintaining a constant density in the core area of the distribution and adjusting the area covered (Hilborn and Walters 1992). This pattern of distribution has been observed for species where there are major limits to increasing densities in high-quality sites (e.g., nesting sites). Consequently, habitat expansion prevents intraspecific competition from increasing in the core of the distribution (Iles and Sinclair 1982, Gill et al. 2001, Gunnarsson et al. 2005). The second model, the proportional-density model (PM), describes a condition in which local densities vary proportionally to the global abundance and the area occupied remains invariant (Hilborn and Walters 1992, Petitgas 1997, Balbontin and Ferrer 2008). In this case, geographic expansion can be limited by lack of suitable habitats (Stephens at al. 2002), by very specific

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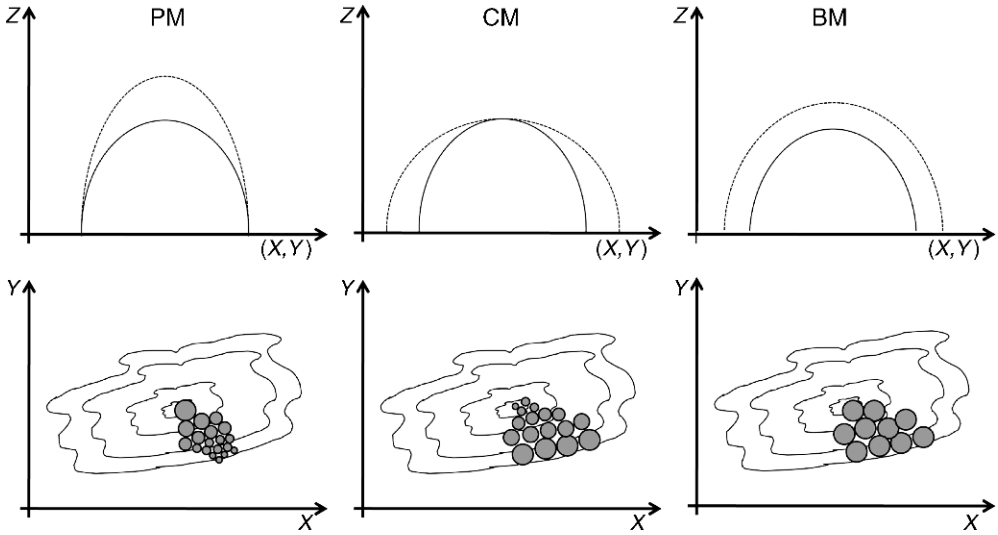

FIG. 1. Schematic of three theoretical models of density-dependent spatial dynamics, from left to right: the proportional density model (PM), the constant density model (CM), the basin model (BM). The top row shows local density (Z) variations across space (X, Y) between two levels of population abundance. The bottom row shows density isoclines, and the size of the bubbles represents the expected increase in local density.

biotic and abiotic requirements that markedly reduce the fitness in suboptimal habitats (Stephens et al. 2002), or by conditions of low densities where space and resources are not limiting (Rodenhouse et al. 1997, Balbontin and Ferrer 2008). The third model, also known as the basin model (BM), represents an intermediate situation between the CM and PM models. Here, geographic distribution and density covary in relation to variations in population abundance (Sutherland 1983, MacCall 1990). A graphical representation of how local population abundance changes in relation to global population abundance should reveal which of the three dynamics is occurring. In particular, as population abundance increases, the PM dynamic is expected to show major increases of local densities in the core areas of the distribution, and progressively lower increases at the boundaries (Fig. 1). In contrast, the CM dynamic would show a higher increase at the boundaries of the distribution and low or no variation in the highest density areas (Fig. 1). As a combination of the two previous scenarios, the BM dynamic would show rather homogeneous density variations throughout the areas and habitats occupied by the population regardless of its local densities (Fig. 1).

The three proposed scenarios do not necessarily occur in isolation, and are dependent upon other variables. For instance, physiological and behavioral differences between the sexes and across ontogeny may differentially affect the spatial distribution of individuals in a population. A vast body of literature demonstrates how responses to environmental factors can change throughout the life cycle of organisms across different taxa (e.g., Werner and Gilliam 1984, Ebenman and Persson 1988), but rarely has ontogenetic variability been investigated in relation to spatially density-dependent processes (but see Swain and Sinclair 1994, Swain 1999, Stephens et al. 2002, Simpson and Walsh 2004). Fishery related data (e.g., spatial distribution of catches or survey abundance estimates) offer a unique opportunity for investigating complex spatiotemporal dynamics of wild populations, due to the intensity and richness of information collected. Furthermore, fisheries data are mostly collected in highly productive environments, such as upwelling or subarctic regions, which are also likely to experience high interannual variation of environmental conditions (e.g., temperature, ice cover, wind stress). Therefore, the analysis of fishery data is well suited for testing alternative ecological hypotheses on habitat selection along contrasting environmental and demographic conditions.

Our objectives were twofold. First, we developed a new class of models that are capable of detecting spatially variable density-dependent and density-independent relationships. The second objective was to test whether there are gender and body-size differences in the way in which density-dependent habitat selection operates in a large marine population. We employed two approaches of spatial ecology that are rarely used in combination, namely geostatistics and regression analysis (Ciannelli et al. 2008). The results are thus presented in two main sections: the first focused on density-dependent dynamics using geostatistical aggregation curves (Matheron 1981), and the second focused on a novel spatially explicit regression model to assess the joint effects of density-dependent and density-independent forcing. In both approaches, we separated

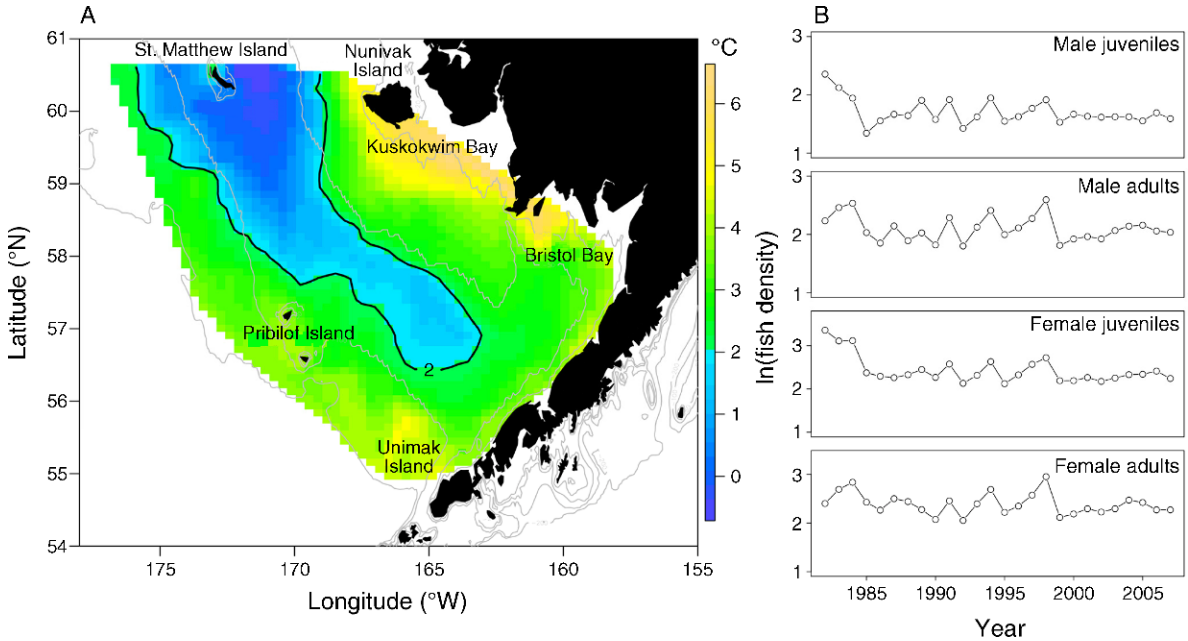

FIG. 2. (A) Map of the eastern Bering Sea shelf showing the 20-, 50-, 100-, and 200-m isobaths, and average summer bottom temperature (1982–2007) with the 2°C isotherm (black line). (B) Annual mean fish density (ln[density], where density is measured as fish/km^2) of yellowfin sole as estimated from survey data for juvenile males, adult males, juvenile females, and adult females.

effects across ontogeny and sex, and tested whether such separation is consistent with the observed data. In pursuing our analysis, we developed a new class of spatially explicit regression models that can be readily applied to other systems and species where spatial variations of species–habitat associations are expected.

MATERIAL AND METHODS

We used the yellowfin sole (*Limanda aspera*) in the eastern Bering Sea (EBS) to test our hypotheses of spatial population dynamics. Yellowfin sole is a relatively slow-growing and long-lived fish species (>20 years; Wilderbuer et al. 1992), with females reaching maturity at approximately 30.7 cm in total length and 10.5 years of age (Nichol 1995). Males mature at smaller size than females, at approximately 20.3 cm in total length and 6.5 years of age (Wilderbuer et al. 1992). As with most flatfish, the spatial distribution of yellowfin sole is strongly influenced by sediment type (McConnaughey and Smith 2000), depth, and temperature (Swartzman et al. 1992, Nichol 1997, Spencer 2008). Differences in the bathymetric and spatial distribution between sexes and different age groups have been reported previously (Bakkala 1981, Wilderbuer et al. 1992, Nichol 1997, 1998). Juveniles distribute along an ontogenetic gradient of depth, moving toward deeper waters with increasing body size, while mature fish are known to migrate to shallower waters mainly during spawning (Nichol 1997). Males also appear to be distributed nearer to shore than females (Nichol 1998). Few explanations driving these differences between sex and ontogeny have been elucidated. Dispersion indices and central tendency approaches have not provided a definitive understanding of the influence of density dependence in yellowfin sole spatial distribution patterns (McConnaughey 1995, Spencer 2008).

Study area

We studied yellowfin sole on the continental shelf of the EBS, which is one of the most productive marine ecosystems in the world. The wide shelf (Fig. 2) is often divided into three domains that are distinguished by their bathymetry (coastal, <50 m; middle, 50–100 m; outer, 100–200 m) and hydrographic properties (Kinder and Schumacher 1981). The presence of an isolated mass of cold subsurface waters in summer over the middle shelf of the Bering Sea, identified by the 2°C isotherm (Fig. 2; Maeda 1977, Khen 1988), has been reported as one of the dominant hydrographic features affecting fish distribution (Wyllie-Echeverria and Wooster 1998, Ciannelli and Bailey 2005, Mueter and Litzow 2008).

The data

Yellowfin sole data were collected during the annual groundfish survey conducted by the U.S. National Marine Fisheries Service during 1982–2007 (Appendix A). The sampling design was based on a fixed regular grid of 37 × 37 km, and sampling occurred over a period of six to eight weeks during late spring and summer (Stauffer 2004, Lauth and Acuna 2007). The survey gear selectivity approximates an increasing asymptotic curve for fish larger than 22 cm in total length, with a 50% retention probability at 17 cm in

total length (Wilderbuer et al. 2008). The data set used for our analyses was restricted to stations that have been sampled throughout most of the time series, thus excluding a limited number of hauls in the northernmost part of the study area that were inconsistently sampled. Analyses were conducted under two different levels of gender and ontogenetic aggregation, and results were compared in order to evaluate the importance of aggregation level. In the first level, we calculated local fish densities as the total number of fish caught per swept area (number of fish/km^{-2}) for each haul, and in the second, local densities for each haul were calculated separately for the two sexes and two length groups, as identified by a preliminary depth-preference analysis (Appendix B).

To characterize the spatial heterogeneity of yellowfin sole abundance a number of physical and oceanographic parameters were used as co-located variables in the statistical models. These were bottom temperature (T) and sediment size (K, expressed in units of Φ [$-\log_2$(diameter), measured in mm]; see Smith and McConnaughey 1999). Previous studies have indicated that these parameters are important determinants of yellowfin sole distribution (McConnaughey and Smith 2000, Mueter and Litzow 2008, Spencer 2008).

Under the assumption that different sex-stage groups contribute equally to competition within each group, overall population size estimates were used as predictors of density-dependent sources in spatial distribution patterns. These global abundance estimates were obtained from the stock assessment model of the North Pacific Fishery Management Council (Wilderbuer et al. 2008).

Geostatistical model

We used geostatistical aggregation curves to detect density-dependent spatial dynamics of yellowfin sole in the EBS. The shape of these curves was used as one criterion to distinguish among the three theoretical models of density-dependent spatial dynamics (i.e., CM, PM, and BM; Fig. 1). Aggregation curves have been applied to determine spatial changes as a function of variation in population abundance (Matheron 1981, Petitgas 1997, 1998).

The geostatistical aggregation curve, $P(T)$, describes the maximum proportion of fish that can be found in a certain proportion of area. It was described by the curve on the T–P space joining the points (T_j, P_j), $j = 1, 2, \ldots, n$, where T_j is the proportion of the total area occupied by population densities (z) larger than z, and P_j is the proportion of fish that are encountered at densities larger than z. The T_j and P_j curves were respectively formulated as follows:

$$T_j = \frac{\sum_{i=1}^{j} a_i}{A}$$

and

$$P_j = \frac{\sum_{i=1}^{j} a_i z_i}{Q}$$

where a_i is the swept area with fish density z_i and $z_1 > z_2 > \cdots > z_n$, A is the total surveyed area, and Q is total sample size. The shape of the $P(T)$ curve is described by the space selectivity index (Ssp), which represents a measure of departure from a homogeneous distribution as described by a diagonal in the aggregation curve plot (Petitgas 1998). The Ssp was calculated as the area lying between the $P(T)$ curve and this diagonal.

Variations in population abundance will have different effects on the shape of the $P(T)$ curve and the value of the Ssp index, under different spatially density-dependent dynamics (Petitgas 1998). In the CM model, the distribution becomes smoother as population size increases, decreasing the space selectivity index. A PM model is characterized by proportionality between the increment of population size and local density, resulting in a $P(T)$ curve and the Ssp index that are invariant to population abundance. In the BM model, both local abundance and habitat increase as a function of increasing global population size. Variations in the shape of the $P(T)$ curve under this dynamic are expected to be the same as in CM, but local densities in the core of the distribution are expected to increase in this case (Fig. 1).

Because the Ssp index is informative of the level of aggregation of a population, we investigated its relationships with the size of the population to infer the type of density-dependent habitat selection that the population is experiencing. Data were analyzed on an annual time step, and Ssp was calculated for each year. Interannual differences in the shape of the $P(T)$ curve were tested statistically using a bootstrap approach on the pairwise comparisons among all Ssp values (Manly 1996, Petitgas 1998). It should be noted however, that the use of geostatistical aggregation curves and Ssp index cannot uniquely distinguish among the three hypothesized density-dependent habitat selection dynamics, and additional information on local densities is also required.

Regression model

We modeled the abundance of yellowfin sole in the EBS using generalized additive models (GAM; Wood 2006). These are regression techniques where the relationships between dependent and independent covariates is modeled with a smoothing term and therefore are desirable in our application for their ability to model nonlinearities that often characterize biological systems. The regression analysis was restricted to non-zero hauls. A total of 5780 hauls were used to model yellowfin sole density over 26 years, with an average of 222 local fish density estimates per year.

The regression models tested for both environmentally driven processes and spatial density-dependent dynamics. Three different formulations were used: one spatially invariant and two spatially variant coefficient models. The use of these three formulations allowed us to distinguish among the alternative theoretical models of spatial density dependence described in Fig. 1, and also to test whether there were spatially variable relationships between species abundance and water temperature. In all formulations, the dependent variable $x_{t,y,(\varphi,\lambda)}$ was the natural logarithm of yellowfin sole index of abundance at a particular location φ,λ (identified by longitude and latitude degrees), at time t (day of year), in year y. The spatially invariant model was expressed as follows:

$$x_{t,y,(\varphi,\lambda)} = a + \alpha B_y + g_1[t] + g_2[T_{(\varphi,\lambda)}] + g_3[K_{(\varphi,\lambda)}] + s_1(\varphi,\lambda) + e_{t,y,(\varphi,\lambda)} \quad (1)$$

where g and s are one-dimensional (Wood 2004) and two-dimensional (Wood 2003) smoothing functions, respectively, a is the intercept, B and T are the standardized and shifted population size from assessment and bottom temperature respectively, α is the slope for population size effect that is assumed to be uniform throughout the region, K is sediment size, t is Julian day, and $e_{t,y,(\varphi,\lambda)}$ is a normally distributed error term. Although we used co-located environmental variables, the formulation assumes that the effects of temperature and sediment size are invariant over the entire range of yellowfin sole distribution. For testing a variable spatial effect of bottom temperature and population size, we introduced locally variable coefficient terms (Hastie and Tibshirani 1993; see Bacheler et al. 2009 for an ecological application). The first variable coefficient model introduces the spatial effect of bottom temperature only and was formulated as follows:

$$x_{t,y,(\varphi,\lambda)} = a + \alpha_1 B_y + \alpha_2 T_{(\varphi,\lambda)} + g_1[t] + g_2[K_{(\varphi,\lambda)}] + s_1(\varphi,\lambda) + s_2(\varphi,\lambda)T_{(\varphi,\lambda)} + e_{t,y,(\varphi,\lambda)}. \quad (2)$$

The second formulation includes the spatial effects of both temperature and population size

$$x_{t,y,(\varphi,\lambda)} = a + \alpha_1 B_y + \alpha_2 T_{(\varphi,\lambda)} + g_1[t] + g_2[K_{(\varphi,\lambda)}] + s_1(\varphi,\lambda) + s_2(\varphi,\lambda)T_{(\varphi,\lambda)} + s_3(\varphi,\lambda)B_y + e_{t,y,(\varphi,\lambda)} \quad (3)$$

where α_1 and α_2 are the population size and bottom temperature associated slopes, respectively, assumed to be uniform throughout the region, and s_2 and s_3 are bi-dimensional smoothing functions that describe the local variation in fish density per unit increase in bottom temperature and population size, respectively. Due to model identifiability (i.e., to guarantee a unique solution for all model parameters; Huang 2005), smoothed terms were centered around 0, and a constant (a) was added to the predictions to scale back to original values. However, the zero constraint does not necessarily hold for the spatially variable terms s_2 and s_3 since an increase of, for instance, population size may cause an increase of local abundance throughout the study region. To overcome this problem, we included globally linear terms for B and T. Hence, the effects of s_2 and s_3 should be interpreted as variations around the overall linear effects α_1 and α_2.

The spatially explicit variant coefficient formulations identify yellowfin sole habitat where density was more affected by an increase or decrease of bottom temperature and population size. Our models assume there is a local, linear relationship between bottom temperature and population size with local abundance, but that the linear coefficients vary smoothly throughout the whole study area. The parametric form of the density-dependent term B in model 1 and 2 assumes a uniform and linear density variation throughout the areas where yellowfin sole is present, regardless of its local density, as described by the BM model. Alternatively, the variable coefficient term in Eq. 3 assumes a spatially heterogeneous density-dependent effect as theorized by the dynamics of PM and CM. However, the spatial arrangement of the variable coefficient (s_3 terms) allows for the PM and CM dynamics to be distinguished (Fig. 1).

Regression models were compared based on the genuine cross validation score (gCV). Each model was fitted to a reduced dataset with 200 random observations removed, and average squared prediction error of the 200 removed cases was calculated. The procedure was repeated 500 times and the gCV was obtained as the mean of this error statistic (Ciannelli et al. 2007). A similar procedure was used to choose among aggregated and sex- and size-disaggregated models. In the case of the disaggregated models, estimates for each sex and size were summed for each of the reduced data sets, and then the mean squared prediction error was calculated and compared to the aggregated abundance observations. The average of 1000 realizations was taken as the final statistic for comparing the prediction performances of the aggregated and disaggregated models.

Results

Bimodal distributions were observed in the depth preference of both yellowfin sole sexes, with marked preferences for very shallow waters in the first length classes and for fish of intermediate lengths (Appendix B). Rapid change in depth preference was detected at 24 cm total length for male and 30 cm total length for female yellowfin sole (Appendix B). These natural breaks were consistent with previous knowledge on the size of maturity for females (Nichol 1995), and were slightly larger for males (Wilderbuer et al. 1992). The two identified size thresholds were used to classify juvenile and adult yellowfin sole for subsequent analyses.

Geostatistical model

The space selectivity index (Ssp), inversely proportional to the spatial spread of the population, was

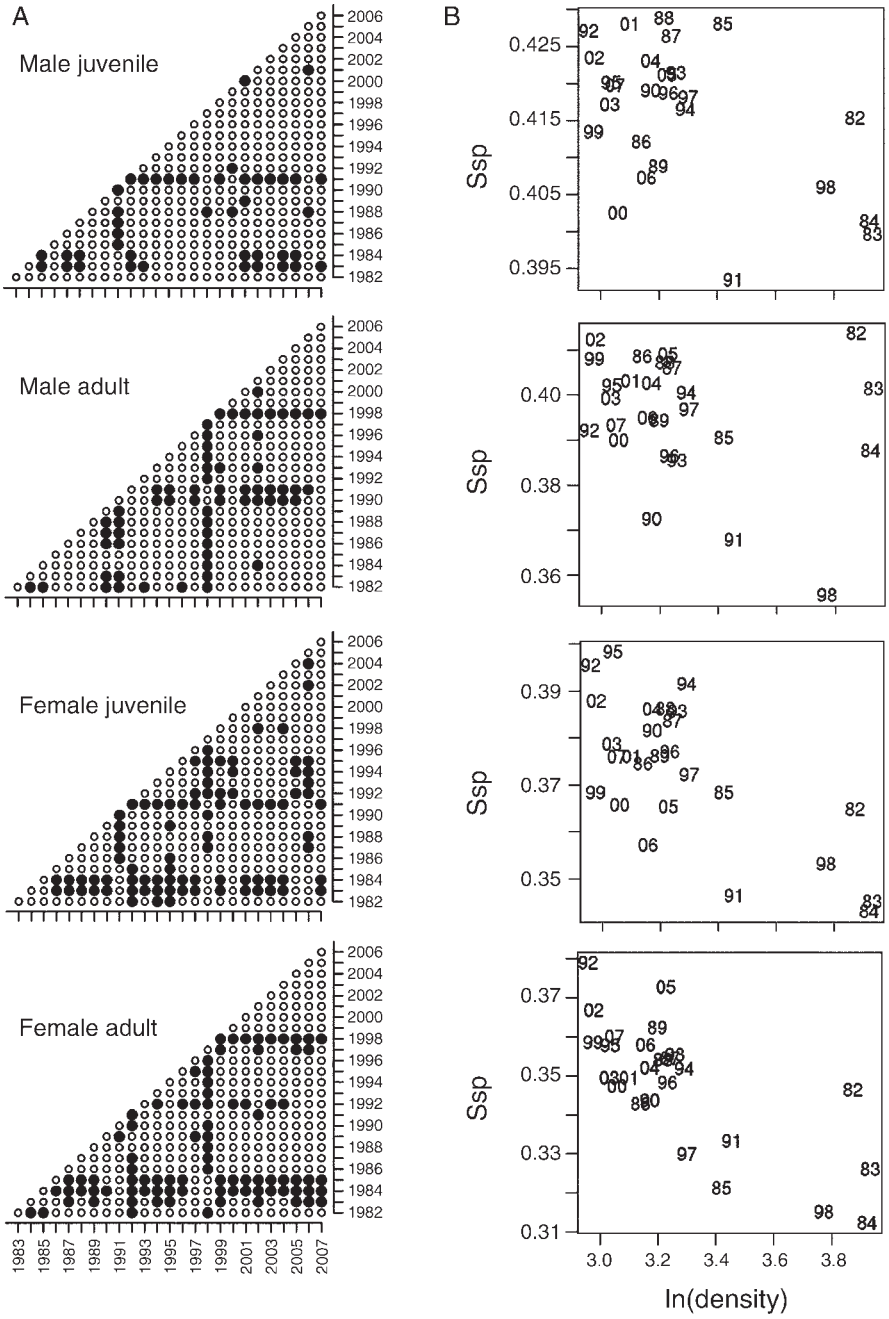

FIG. 3. (A) Pairwise comparisons of yellowfin sole space selectivity indices for 1982–2007 (solid points are 95% statistically significant different, from 1000 bootstrap replicates). (B) Bivariate plot of the estimated annual space selectivity index (Ssp) and the annual mean ln(density) of yellowfin sole from the survey (numbers refer to years).

calculated for each year, sex, and maturity stage combination. We found that a limited number of Ssp comparisons were significantly different (Fig. 3). Females had the highest proportion of significant yearly pairwise comparisons, 26% for juveniles and 27% for adults, while in males significant comparisons were less frequent (19% for adults and 13% for juveniles). This suggests stronger expansion and contraction of the distribution of females, typical of BM and CM dynamics, than for males. The space selectivity index values were plotted against the average of the logarithm local fish density to test for the presence of density-dependent patterns relating the level of aggregation in the spatial distribution and the annual population size (Fig. 3). A significant negative relationship was found between these two variables for juvenile females ($R =$

TABLE 1. Aggregated spatially invariant and spatially variant coefficient models of yellowfin sole density in the eastern Bering Sea.

Model	Predictor variables							Dev. expl. (%)	gCV
	B_y	$g_1[t]$	$g_2[T_{(\varphi,\lambda)}]$	$g_3[K_{(\varphi,\lambda)}]$	$s_1(\varphi, \lambda)$	$s_2(\varphi, \lambda)T_{(\varphi,\lambda)}$	$s_3(\varphi, \lambda)B_y$		
1	0.17**	8.78**	6.27**	8.39**	28.00**			74.4	0.968
2	0.18**	8.73**	0.17**	7.44**	28.12**	27.97**		75.6	0.949
3	0.18**	8.90**	0.17**	7.35**	28.75**	27.40**	25.19**	76.5	0.934

Notes: Estimated degrees of freedom (or linear coefficient in the case of parametric terms) and statistical significance are shown for each term, as well as deviance explained (%) and genuine cross validation (gCV) scores. Variables are defined in *Material and methods: Regression model.*

* $P \leq 0.05$; ** $P \leq 0.01$.

0.68, $P = 0.01$), adult females ($R = 0.79$, $P < 0.01$), and juvenile males ($R = 0.46$, $P < 0.01$), but not for adult males ($R = 0.18$, $P = 0.19$). Because the space selectivity index is inversely related to the level of spatial aggregation in the distribution, a negative relationship is representative of both dynamics BM and CM, while a lack of significant relationship is expected by a dynamic lacking expansion such as PM.

Regression model

Model formulations that included a variable coefficient term for both bottom depth and population size (model 3) were statistically superior to all others for both aggregated and disaggregated (i.e. sex- and size-specific) models (Table 1, Table 2). Hereafter, we exclusively focus on the results of the disaggregated model because it significantly outperformed the aggregated model (average squared prediction error of 0.691 compared to 0.746). Throughout the remainder of the *Results* section we describe the average spatial patterns for each sex and stage. This initial description is needed as a background for the following section where we describe the effect of population abundance on local densities. We then describe the effect of other density-independent variables included in the model on the local abundance of yellowfin sole.

Predictions of the mean distribution patterns confirmed the general preference of yellowfin sole for the coastal and middle shelves of the EBS, but with differences between the four groups examined, particularly for adult fish (Fig. 4). Juveniles of both sexes concentrated on the shelf between Nunivak Island and Bristol Bay, with a core area of aggregation at the edge of the coastal shelf, at approximately 50 m depth. The shallow waters of Bristol Bay were more important for juvenile males than juvenile females (Fig. 4). Adults of both sexes were found in high concentrations in Bristol Bay and on the shelf between Nunivak Island and Bristol Bay, but preferred shallower waters compared to juveniles. A third area of concentration of adult males occurred at the limit between the narrow coastal and wide middle shelves north of the Alaska Peninsula, while the distribution of adult females extended northwestward along the middle shelf at the depth of 50–80 m until 58°–59° N latitude (Fig. 4).

TABLE 2. Sex- and size-specific spatially invariant and spatially variant coefficient models of yellowfin sole density in the eastern Bering Sea.

Model and group	Predictor variables							Dev. expl. (%)	gCV
	B_y	$g_1[t]$	$g_2[T_{(\varphi,\lambda)}]$	$g_3[K_{(\varphi,\lambda)}]$	$s_1(\varphi, \lambda)$	$s_2(\varphi, \lambda)T_{(\varphi,\lambda)}$	$s_3(\varphi, \lambda)B_y$		
1									
juv male	0.17**	6.27**	5.59**	3.84**	28.18**			66.1	0.994
adu male	0.04**	2.68**	6.04**	8.17**	27.45**			72.7	0.891
juv female	0.25**	5.48**	6.47**	7.92**	28.13**			62.1	1.009
adu female	0.04**	8.72**	6.61**	8.70**	28.04**			57.5	0.898
2									
juv male	0.17**	6.49**	0.09**	1.00**	27.07**	26.36**		67.7	0.975
adu male	0.04**	3.04**	0.17**	7.49**	27.29**	27.61**		73.6	0.879
juv female	0.26**	5.53**	0.14**	6.98**	27.71**	26.51**		63.3	0.997
adu female	0.05**	8.71**	0.17**	8.28**	29.00**	26.91**		58.6	0.890
3									
juv male	0.17**	6.00**	0.10**	1.00*	28.17**	25.61**	21.46**	68.5	0.968
adu male	0.04**	5.05**	0.18**	7.57**	28.70**	26.69**	22.45**	74.5	0.873
juv female	0.26**	6.14**	0.14**	6.99**	28.89**	25.70**	21.75**	64.4	0.986
adu female	0.04**	8.95**	0.15**	8.17**	29.00**	27.02**	25.40**	60.4	0.879

Notes: Estimated degrees of freedom (or linear coefficient in the case of parametric terms) and statistical significance are shown for each term, as well as deviance explained (Dev. expl., %) and genuine cross validation (gCV) scores. Abbreviations are: adu, adult; juv, juvenile.

* $P \leq 0.05$; ** $P \leq 0.01$.

Sex- and size-specific differences were observed in the spatial response to population size (Fig. 4A). An increase in population size was estimated to have a positive effect on juvenile male densities over most of their range, and especially in the coastal and middle shelf waters in the southern EBS where medium local densities occurred. A bimodal distribution in the response of adult males to variations in the population size was observed between Bristol Bay, corresponding to the peak of their distribution, and shallow depths along the Alaska Peninsula toward Unimak Island. In contrast to juvenile males, a positive density effect in juvenile females was manifested at the outer margin of their distribution, along the deeper portion of the middle shelf, and the shelf break between Unimak and Pribilof Islands, east of the Pribilofs, and on the middle shelf toward St. Matthew Island (Fig. 4). Adult females lacked a positive response to population size in the core of their distribution on the middle and coastal shelves, as was observed for juvenile females.

Yellowfin sole showed a general positive response to sediment size (corresponding to low values of Φ) with some differences between the two sexes and to a lesser degree between juveniles and adults (Fig. 5). Adult males had the highest positive response for larger sediment size (i.e., coarse sand), while adult females had a clear positive response for intermediate values of sediment size (i.e., fine sand) at approximately 2.5Φ (Fig. 5).

The overall effect of bottom temperature in the spatially invariant models was characterized by a steep negative effect for temperatures below 0°C for all the sex and size groups examined (Appendix C). The variable coefficient formulations showed a common and positive response to bottom temperature throughout the study region, albeit with some spatial variation in the degree of such response. Increases in temperature had a major positive effect in the northern part of the study area on the continental shelf southeast of St. Matthew Island, and in the south, off the Alaska Peninsula and over the narrow shelf off Unimak Island (Fig. 4). Only for adult females did the positive effect extend throughout the whole shelf in the 30–60 m depth range.

Discussion

We found that marked differences in the spatial dynamics characterized the specific patterns of different ontogenetic and sex groups of the yellowfin sole population in the EBS. The specificity of the density-dependent processes that we found in the two sexes and life stages examined represents a poorly explored level of complexity in the spatial dynamics of animal populations. For all sex- and size-groups, the variant coefficient model was selected over the invariant model, demonstrating that density dependence plays a role in driving the spatial dynamics of yellowfin sole, and that it is a spatially heterogeneous process. As demonstrated by geostatistical aggregation curves, females were more responsive to increments in population size than males.

The regression analysis was instrumental in further distinguishing among different density-dependent habitat selection models and in defining particular regions where local increases in abundance were more likely to be found. For juvenile females, we estimated increased local densities throughout the EBS, suggesting an intermediate dynamic between BM and CM. In contrast, adult female distribution expanded toward suboptimal habitats on the middle shelf and upper slope, and even showed a decrease in the core area of their distribution, suggesting high intraspecific competition and indicating that a CM model best describes adult female spatial dynamics.

Juvenile males expanded southward from their core distribution when population size increased, but also increased in local abundance within their core range, suggesting a mixture of BM and CM dynamics. In agreement with the PM model, the increase of adult male densities mostly occurred on the coastal shelf of Alaska where their abundance was highest, as also suggested by the geostatistical approach. Moreover, an expansion of adult male distribution was also predicted at the edge of the Alaska Peninsula. Therefore, the spatial dynamics of this group are difficult to describe with a single theoretical model.

In many flatfish species (e.g., plaice, *Pleuronectes platessa*; flounder, *Plathichthys flesus*; dab, *Limanda limanda*; sole, *Solea solea*) females grow to a larger size and body volume than males (Van der Veer et al. 2001) and provide greater reproductive investment (Rijnsdorp and Ibelings 1989, Van der Veer et al. 2001). Results of dynamic energy budget models (Kooijman 2000), as well as field and laboratory experiments (Lozan 1992, Van der Veer et al. 2001), have related the greater reproductive investment of female flatfish to unequal food intake between the two sexes. We contend that the higher energetic requirement of females likely drives their density-dependent habitat expansion. Interestingly, larger yellowfin sole have greater prey diversity in their diet (Lang 1991), a feature that can facilitate habitat expansions. Compared to males, we also found that female density is higher over a larger range of sediment size. Thus, it appears that the spatiotemporal dynamics of yellowfin sole result from a complex balance of intraspecific competition, energetic budget, and sediment associations, all of which combine to constrain yellowfin sole habitat expansion to the continental shelf and upper slope areas of the EBS. There may still be additional sources of population distribution variability, such as predation or currents and drift pathways during the pre-settling early life stages. However, an examination of these other sources of variability was beyond the scope of this study.

Our analyses indicate that temperature and sediment size are important density-independent variables affecting yellowfin sole spatial distribution. In agreement with previous studies (e.g., McConnaughey and Smith 2000),

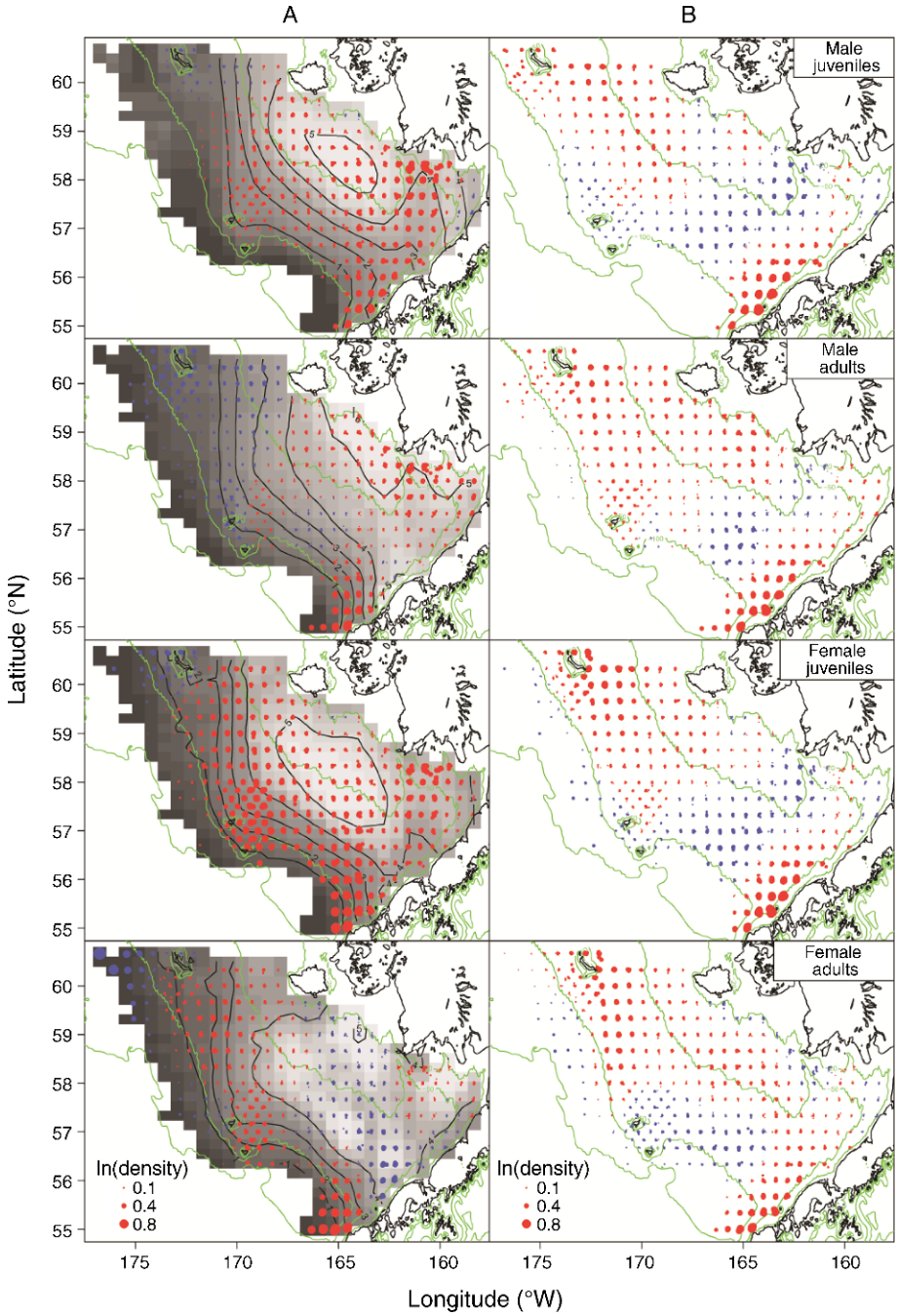

FIG. 4. (A) Spatial effects of population size overlaid with the average distribution of yellowfin sole for each sex and length group during the 26-year time period, as predicted from the variable coefficient model. (B) Spatial effects of bottom temperature. Circle size is proportional to the estimated variation in yellowfin sole log(density) for one-unit increments in the value of both standardized population size and bottom temperature. Red and blue bubbles indicate an increase and decrease, respectively; Green lines show the 20-, 50-, 100-, and 200-m depth isobaths.

our results have shown that yellowfin sole have a greater affinity for sandy bottoms, but variable sex- and life-stage-specific associations also occur. For example, males appear to associate more with larger sediments compared to females, as a result of their nearer shore distribution. Moreover, considering the larger body size attained by females, ontogenetic variations in the diet of yellowfin sole (Bakkala 1981) may contribute to explain differences in the response to sediments.

The variable coefficient formulation demonstrates how part of the nonlinear response of yellowfin sole to temperature has a spatial structure. This approach also

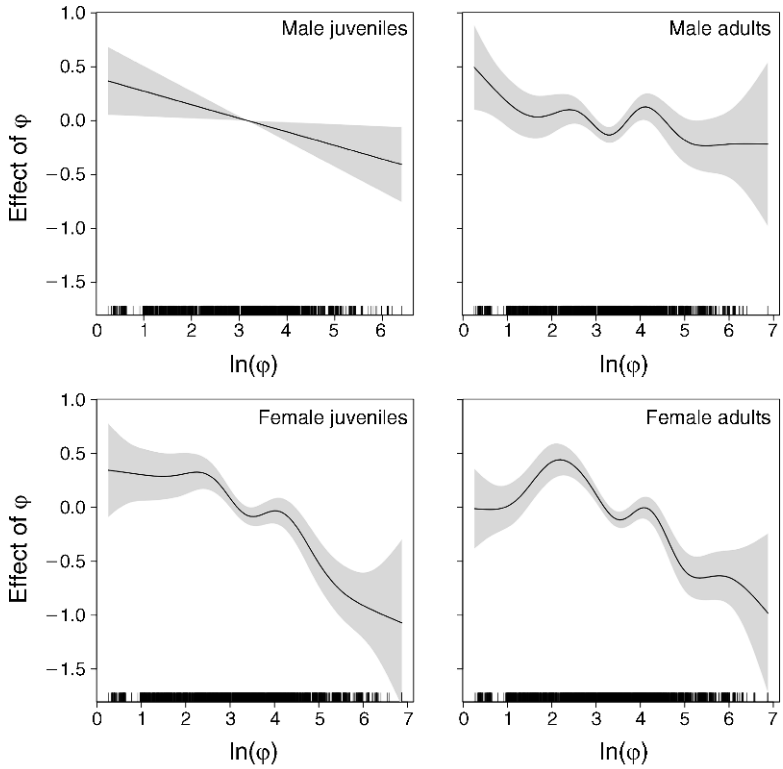

FIG. 5. Effect of sediment size (φ) on yellowfin sole abundance as estimated from variable coefficient models for juvenile and adult males and females, with the shaded regions indicating the 95% confidence interval.

reveals the spatial pattern of the bottom temperature effect and its strong association with the spatial distribution of the cold pool. A northward expansion of yellowfin sole is predicted as temperature increases and the cold pool contracts. This result needs to be interpreted in relation to the current warming trend of arctic regions and its ecological and management implications for marine populations (Grebmeier et al. 2006). However, it is important to note that the variability in bottom temperature is not homogeneously distributed throughout the EBS. Typically, the southern EBS experiences larger seasonal and inter-annual variations than the northern part (Kinder and Schumacher 1981). Yellowfin sole appear to be more tolerant of low temperatures than other subarctic species. The overall negative response for temperatures below 0°C can explain the lack of correlation with the 2°C isotherm of the cold pool found by previous studies (Mueter and Litzow 2008, Spencer 2008).

Changes in spatial distribution with population size have been found for several marine and terrestrial organisms (i.e., Swain 1999, Gill et al. 2001, Balbontin and Ferrer 2008), including some flatfish (i.e., Brodie et al. 1998, Simpson and Walsh 2004, Spencer 2008). However, Shepherd and Litvak (2004) argued that, in many cases, spatial dynamics are assumed to be influenced solely by density-dependent factors, and rarely are environmental processes properly and simultaneously taken into account. The difficulty of detecting local variations of population density in relation to its global abundance and environmental forcing variables have led most authors to assume rather than test the existence of density-dependent habitat selection in animal populations (Shepherd and Litvak 2004). The space selectivity index from geostatistical aggregation curves is able to detect variations in the allocation of biomass across space, but like other central tendency indices (Swain and Wade 1993, Bethke and Taylor 1996, Swain 1999), cannot identify the locations where these variations occur (Petitgas 1998). The analytical framework we have developed integrates central tendency indices with advanced regression models. Most importantly, this approach simultaneously takes into account multiple sources of variability such as density-dependent and density-independent processes. We showed here how variable coefficient models represent an efficient way to investigate spatial density dependence. They allow a proper testing of different theoretical density-dependent dynamics through a spatially explicit approach.

Our study demonstrates that spatiotemporal dynamics are the result of complex interactions between density-independent and density-dependent sources of variability that act differently throughout ontogeny and sex. In the case of an exploited resource such as yellowfin sole, the specificity in the response to internal

and external driving forces has an immediate implication for the spatially-explicit management of this resource. Understanding the spatial dynamics of species is a central issue in conservation ecology and fisheries management. The current emphasis on protecting individuals and their essential habitats (Beck et al. 2001) cannot be considered in isolation without an understanding of the variability in both the responses across life stages and the features that contribute to habitat quality. This becomes a management priority for populations like yellowfin sole that experience an important additional source of mortality from harvest. We found that compensatory spatial density-dependent dynamics can promote an expansion of adult female distribution to marginal habitats. This result highlights the importance of peripheral habitats as buffer zones for a viable population expansion, reducing competition in the main areas of the species distribution.

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APPENDIX A

Standardized annual indices of abundance of yellowfin sole in the eastern Bering Sea (*Ecological Archives* E092-015-A1).

APPENDIX B

Calculation of depth preference (*Ecological Archives* E092-015-A2).

APPENDIX C

Effect of bottom temperature from the invariant coefficient model (*Ecological Archives* E092-015-A3).