Using ecologically based relationships to predict distribution of flathead sole *Hippoglossoides elassodon* in the eastern Bering Sea

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ABSTRACT: This study describes a method for modeling and predicting, from biological and physical variables, habitat use by a commercially harvested groundfish species. Models for eastern Bering Sea flathead sole *Hippoglossoides elassodon* were developed from 3 relationships describing the response of organism abundance along a resource continua. The model was parameterized for 1998 to 2000 trawl survey data and tested on 2001 and 2002 data. Catch per unit effort (CPUE) of flathead sole had a curvilinear relationship with depth, peaking at 140 m, a proportional relationship with bottom water temperature, a positive curvilinear relationship with potential cover (invertebrate sheltering organisms such as anemones, corals, sponges, etc.), a negative relationship with increasing mud:sand ratio in the sediment, and an asymptotic relationship with potential prey abundance. The predicted CPUE was highly correlated (r^2 = 0.63) to the observations (1998 to 2000) and the model accurately predicted CPUE (r^2 = 0.58) in the test data set (2001 and 2002). Because this method of developing habitat-based abundance models is founded on ecological relationships, it should be more robust for predicting fish distributions than statistically based models. Thus, the model can be used to examine the consequences of fishing activity (e.g. reduction in sheltering organisms), changes in temperature (e.g. climate effects) and interaction between variables, and can be modified to incorporate new variables as more information is collected about a species.

KEY WORDS: Fish habitat · Habitat model · Bering Sea · Soft sediment · Flatfish

INTRODUCTION

The multidimensional habitat niche for a given population is defined by its distribution along a combination of multiple resource continua (Hutchinson 1957). For any individual continuum, the relationship between the resource and population abundance can be described by any of a series of increasingly complex equations based on ecological relationships that should determine the population distribution. These include: (1) linear relationships of abundance and resources (Friedlander & Parrish 1998), (2) a density-dependent response, whereby abundance increases along a resource gradient until intraspecific competition leads to decreasing or stabilized abundance (i.e.

Iles & Beverton 2000), and (3) an approximate normal or dome-shaped distribution along a resource gradient (May 1973, Murawski & Finn 1988). In theory, parameterization of the mathematical constructs of these relationships will provide a robust method for predicting population distribution.

In contrast to the ecological relationships mentioned above, the analysis of habitat use of fish populations has largely used statistical models to characterize observed distributions without *a priori* consideration of ecological theory or mechanisms. These models include simple comparisons of habitat use between areas of high and low density (McConnaughy & Smith 2000), categorical analysis regression trees (Norcross et al. 1999) and generalized additive models (Swartzman et

al. 1992, O'Brian & Rago 1996, Stoner et al. 2001, Simpson & Walsh 2004, Walsh et al. 2004). General additive models (GAMs) have the advantage of exhibiting non-linear response curves describing the relationship between fish distributions and habitat, but the shape of the response curves may be difficult to explain in terms of organism ecology. It is notable that existing statistical habitat models are rarely used for prediction (but see Stoner et al. 2001 for exception), because the statistical relationships describing existing distributions may not be applicable to future distributions (Beutel et al. 1999). Utilization of ecological relationships provides the advantages of nonlinearity in modeling distributions across habitats, a distribution response for each habitat variable that is justifiable based on organism ecology, and therefore a more robust prediction of future organism distribution across habitats than traditional statistical models.

The characterization of habitat use is also dependent on the habitat variables used in the analysis. For example, Swartzman et al. (1992) modeled 5 eastern Bering Sea flatfish species (rock sole *Lepidopsetta* sp., Alaska plaice *Pleuronectes quadrituberculatus*, flathead sole *Hippoglossoides elassodon*, yellowfin sole *Pleuronectes asper* and Greenland turbot *Reinhardtius hippoglossoides*) using a GAM with temperature and depth as predictor variables, and concluded that depth is the primary factor influencing flatfish distributions. However, McConnaughy & Smith (2000) noted that sediment characteristics differed between areas of high and low flatfish abundance and proposed that differences in the availability and quality of prey may explain sediment preferences among the same 5 species of flatfish and arrowtooth flounder *Atheresthes stomais*. Incorporating a full suite of habitat variables into the analyses is important for determining the factors that determine fish distribution.

The primary objective of this study was to develop and demonstrate a method of predicting fish distribution and abundance across multiple resource continua based on the ecological relationships described above. We used log-likelihood methods to fit ecologically-based models to catch data, utilizing multiple habitat variables including potential prey, potential cover, temperature, sediment type and depth. Flathead sole in the eastern Bering Sea was chosen as the species to illustrate this method because (1) an annual fishery-independent trawl survey documents flathead sole distribution, abundance and related habitat data, (2) the survey samples the depth and temperature range of flathead sole, and (3) flathead sole abundances vary across the geographic range of the survey. Flathead sole are distributed throughout the North Pacific Ocean from Monterey, California, to the Chukchi Sea (Kramer et al. 1995), and are a component of Bering Sea commercial bottom-trawl fisheries, with annual catches averaging 18 000 t since 1990 (North Pacific Fishery Management Council 2003). Flathead sole spawning occurs in the spring, as eggs are present in April to early July over the outer domain (>100 m depth) of the eastern Bering Sea shelf (Grigorev & Fadeev 1995). As with many flatfish species, the buoyant eggs and larvae are transported to nursery grounds in shallow inshore areas (Alderdice & Forrester 1974, Haldorson et al. 1993, Abookire & Norcross 1998). Juvenile flathead sole exhibit strong preferences for specific depth and sediment ranges in coastal embayments in the Gulf of Alaska (Abookire & Norcross 1998), but the distribution of adult and subadult flathead sole relative to habitat features are for the most part unknown, particularly in the Bering Sea. Our hypothesis was that flathead sole catches across the Bering Sea shelf would be related to food availability, temperature, depth, sediment type and shelter available. Modeling was conducted on 4 groups of the catch data (all flathead sole combined, subadults, mature females and mature males) over 3 yr of Bering Sea trawl surveys. The best-fitting model was then tested on data collected during the subsequent 2 surveys.

MATERIALS AND METHODS

Collection. Data for this study were collected during annual trawl surveys conducted by the National Marine Fisheries Service (NMFS) from 1998 to 2002 during the summer months (Acuna et al. 2003). Stations for the trawl survey are evenly distributed over a 20 nautical mile grid system on the eastern Bering Sea shelf, except in 2 areas where additional stations have been placed within the grid system (Fig. 1). An 83-112 eastern otter trawl equipped with net mensuration gear, bottom contact sensor and temperature–depth recorder (SeaBird SBE 39) was towed for 30 min on the seafloor through the middle of each grid cell (see Acuna et al. 2003 for detailed description of the Bering Sea trawl survey methods, gear and data). Depths of the survey ranged from 16 m near Nunivak Island to >180 m along the Bering Sea shelf edge. Only tows with good performance and suitable bottom contact (Gary Walters, NOAA NMFS RACE, pers. comm.) were used in the analysis. The number of good-performance tows ranged from 349 in 1999 to 355 in 2001. Tows with a recorded catch of flathead sole, but with no size information were discarded, resulting in a total of 1758 useable tows over 5 yr (Table 1).

Adult flathead sole were divided into 2 groups based on their total body length taken from each haul:
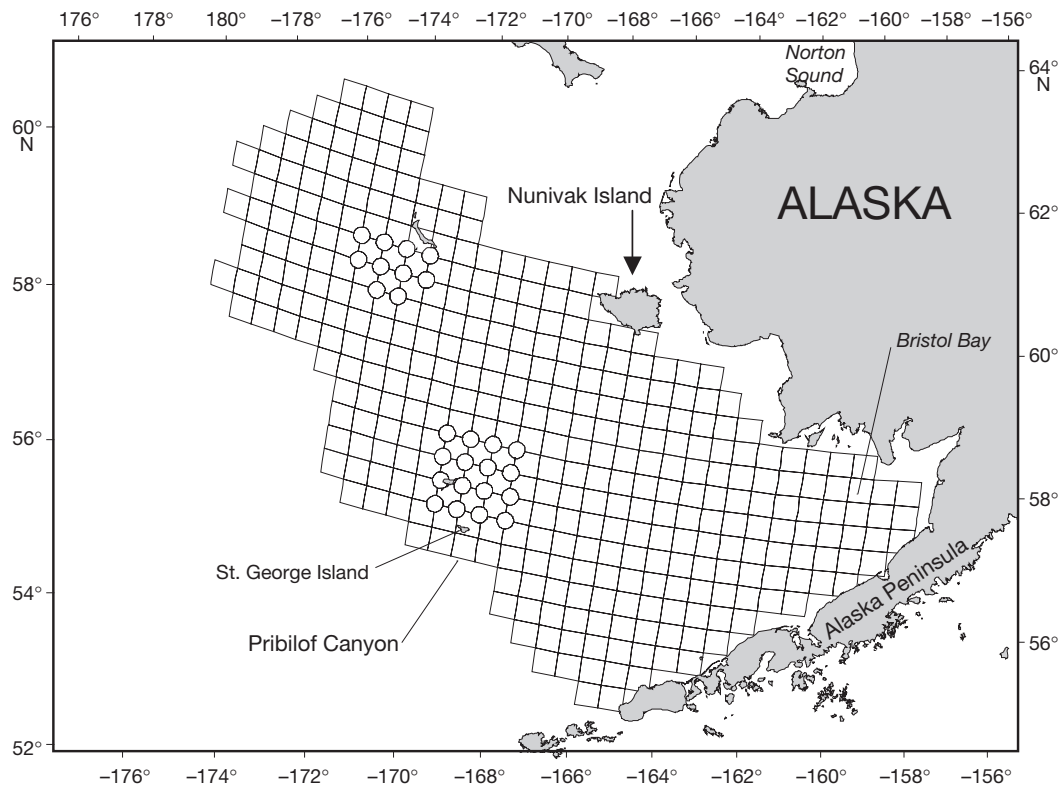
Fig. 1. Map of the Bering Sea showing 20 nautical mile grid of survey stations. In each summer from 1998 to 2002, 1 survey trawl was conducted near the center of each box of the grid; 1 survey trawl was also conducted using same method near the center of each circle in each summer

subadults and mature adults. The mature adults were further divided into males and females. Juvenile fish <150 mm in total length (TL) (Holladay & Norcross 1995, Abookire et al. 2001) were not included in the analysis because they were rarely caught by the research trawl and were assumed to have different distributions based on previous research (Norcross et al. 1997, Abookire & Norcross 1998). Subadult fish were defined as those <300 mm in TL (younger than 9.7 yr), the estimated age and size of 50% maturity (Stark 2004), and >150 mm TL (older than age 1+ yr). Subadults included males and females combined in a single group, but adult fish (>300 mm TL) were divided into male and female segments. Catch per unit effort (CPUE) was estimated for each group as no. captured ha^{-1} swept by the net during each tow in the NMFS trawl survey.

Habitat variables. Habitat variables were chosen based on their hypothesized importance for growth, survival and regulation of metabolism. The suite of variables included depth, temperature, potential cover, sediment type (defined as mud:sand ratio) and potential prey. Bottom temperature and depth were averaged during the period of bottom contact of each trawl

haul. For tows with no associated temperature data, a temperature value was linearly interpolated from the closest adjacent stations in the survey grid sampled on the same day.

In this analysis, potential cover was defined as epibenthic organisms and associated organic material that extend above the sea bottom. Taxa included soft and hard corals, surface bivalves and empty bivalve shells, ascidians, gastropods, sponges, anemones, bryozoans and sea pens. Potential cover was estimated as the combined catch per unit effort of sheltering organ-

Table 1. *Hippoglossoides elassodon.* Mean CPUE and standard error (SE), for adult flathead sole, and number of trawl survey stations occupied each year for modeled data (1998 to 2000) and test data (2001 and 2002)

| Year | CPUE (no. ha^{-1}) | | n |
	Mean	SE	
1998	38.05	5.69	350
1999	22.72	2.23	349
2000	23.36	2.31	351
2001	32.08	3.45	355
2002	30.02	4.01	353

isms recovered from each trawl (kg ha^{-1}), and used as an index of available epibenthic shelter.

Sediment type data were derived from Smith & McConnaughey (1999), and were assumed to be constant over the years. Sediment characteristics in the Bering Sea from a number of studies have been compiled into a database containing 2587 observations (Smith & McConnaughey 1999). Because the point locations of the sediment size data do not correspond to the survey stations, the predicted mud.sand ratio at the survey stations was obtained from ordinary kriging (Isaaks & Srivastava 1989). The sand classification encompassed sediment ranging from very fine to very coarse sand ($-1 < \phi < 4$), while the mud classification encompassed sediment from clay to coarse silt ($\phi > 4$) (Wentworth 1922). Larger-grained sediments (gravel) occurred in significant quantities (>10% by weight) at only 20 of the 358 trawl stations, and thus gravel was not included in the definition of sediment type. To satisfy the stationarity assumption, an overall trend from low mud:sand ratios in the central shelf to high ratios in the northwest shelf was removed with a local regression scatterplot smoother, and kriging was conducted on the residuals from this trend. This trend can be explained by stronger wave energy in nearshore, shallow locations being sufficient to suspend smaller particles, with sediment size generally decreasing with increasing distance from shore. Areas of medium and fine silt occur in the southwestern and northwestern shelf, respectively. A spherical variogram model was fit to data with a maximum distance of 250 km and checked for isotropy. The predictions from the krigged surface were then added to the underlying trend to obtain predicted values of the mud:sand ratio at each trawl survey station.

Flathead sole prey on mysids, euphausids, decapods (including shrimp and pagurid crabs), juvenile walleye pollock (<200 mm TL) and, especially, ophiurids (Pacunski et al. 1998). All these groups are epibenthic species, and all except mysids and euphausids are commonly captured in trawl surveys. Mysids and euphausids comprise <6% of the flathead sole diet measured by weight (Pacunski et al. 1998), and were considered a minor diet component. The total catch per unit effort (kg ha^{-1}) of those prey items captured in the trawl survey was summed for each station as an index of potential prey. In some trawls (n = 8), walleye pollock were not measured for total length. In these cases the average individual weight (total catch weight/total catch numbers) was calculated. If the average individual weight was less than 0.5 kg, the catch was assumed to be composed of entirely juvenile fish; if the average weight was greater than 0.5 kg, the entire catch was assumed to be adults.

Model structure. Prior to fitting the parameters for each model, CPUE data were log + 1 transformed, so in the following equations CPUE refers to the log-transformed data. A model of flathead sole CPUE was estimated, whereby CPUE is a function (f) of the 5 habitat variables depth (D), temperature (T), potential cover (C), mud:sand ratio (M), potential prey (P) and an error term (ε):

$$\text{CPUE} = f(D) + f(T) + f(C) + f(M) + f(P) + \varepsilon \quad (1)$$

The relationships between flathead sole CPUE and habitat variables were estimated using one of 3 equations. The most complex equation had 3 parameters, and represented the response of CPUE as a dome-shaped function of the habitat variables, so that:

$$\text{CPUE}_h = \alpha_h + \beta_h X_h + \delta_h X_h^2 \quad (2)$$

Here, X_h is habitat variable h, while β_h, δ_h, and α_h are parameters fitted to the data. The second equation describes CPUE as a density-dependent function of the habitat variables, so that:

$$\text{CPUE}_h = a_h X_h e^{-b_h X_h} \quad (3)$$

In this case, a_h and b_h, are the parameters fit. The simplest equation utilized predicted flathead sole density as proportional to the habitat variables X_h, so that:

$$\text{CPUE}_h = a_h X_h \quad (4)$$

where a_h is the only parameter fit in the equation.

All components of CPUE were combined prior to fitting the parameters. For example, the initial (full) model for the analyses estimated 15 parameters and included depth (Eq. 2), temperature (Eq. 2), mud:sand ratio (Eq. 2), potential cover (Eq. 2) and potential prey (Eq. 2), so that:

$$\begin{aligned}
\text{CPUE} = &\; \alpha_D + \beta_D X_D + \delta_D X_D^2 + \alpha_T + \beta_T X_T + \delta_T X_D^2 + \\
&\; \alpha_C + \beta_C X_C + \delta_C X_C^2 + \alpha_M + \beta_M X_M + \delta_M X_M^2 + \\
&\; \alpha_P + \beta_P X_P + \delta_P X_P^2 + \varepsilon
\end{aligned} \quad (5)$$

All 15 parameters for the suite of habitat variables were fit simultaneously.

The errors, ε, were then assumed to be distributed log-normally, and modeling parameters were estimated by minimizing the negative log-likelihood (Hilborn & Mangel 1997):

$$-\ln(L) = \sum \left[\log(\sigma) + \frac{1}{2}\log(2\pi) + \frac{(Y - \hat{Y})^2}{2\sigma^2} \right] \quad (6)$$

where σ is estimated analytically by:

$$\sigma = \sqrt{\frac{\sum (Y - \hat{Y})^2}{n - 1}} \quad (7)$$

L is the likelihood, Y are the observed CPUE data and $\hat{Y}$ are the predicted values.

Models were reduced by sequentially removing 1 parameter for each variable (i.e. the depth relationship was changed from Eqs. 2 to 3), and parameters were refit. The models were compared using the Akaike information criterion (AIC) for non-nested models to determine the best-fitting model:

$$AIC = L + 2P \qquad (8)$$

where P is the number of parameters in Model M (Akaike 1992). The best 14-parameter model was then evaluated against the full 15-parameter model. Next, the process was repeated, eliminating another parameter and testing the resulting 13-parameter models to the best 14-parameter model. This process was repeated until reduction in the number of parameters resulted in no reduction in AIC score, and this final model was deemed best for the data set analyzed. The correlation between the observed and predicted values was used to determine the percentage of variance in the CPUE data set explained by the model. Deviations (observed values minus predicted values) for the model were explored through examination of residuals via a geographic information system (GIS) to examine spatial patterns.

Model cross-validation. Once a final model was determined for the 1998 to 2000 trawl survey data, the model was tested on flathead sole catch data from the Bering Sea trawl surveys of 2001 and 2002. The 2001 and 2002 catch data, depth, temperature, potential cover, mud:sand ratio and potential prey for each station were compiled into a matrix. The parameters from the best-fitting model for 1998 to 2000 were used to predict the 2001 and 2002 flathead sole distribution. The error of the model for 2001 and 2002 data was calculated as the observed CPUE minus the CPUE predicted using the 1998 to 2000 model and parameters, and the percentage of explained variance in the 2001 and 2002 CPUE data was estimated.

RESULTS

Catch of flathead sole ranged from 0 to 4694 individuals in 1998 to 2000 , with 20% of the trawl hauls capturing zero flathead sole. The catch was evenly divided between mature adults (53%) and subadults (47%), and the mature adults were composed of 46% females and 54% males. Trawl survey data were collected at depths ranging from 16 to 188 m, with stations fairly evenly distributed at depths between 35 and 135 m (Fig. 2). Bottom water temperatures during the 1998 to 2000 trawl surveys ranged from −1.7 to 6.6°C and most temperatures were between 0 and 4°C (Fig. 2). The catch of potential cover ranged from 0 to 1366 kg ha^{-1}, and at most sites the CPUE of invertebrates was less
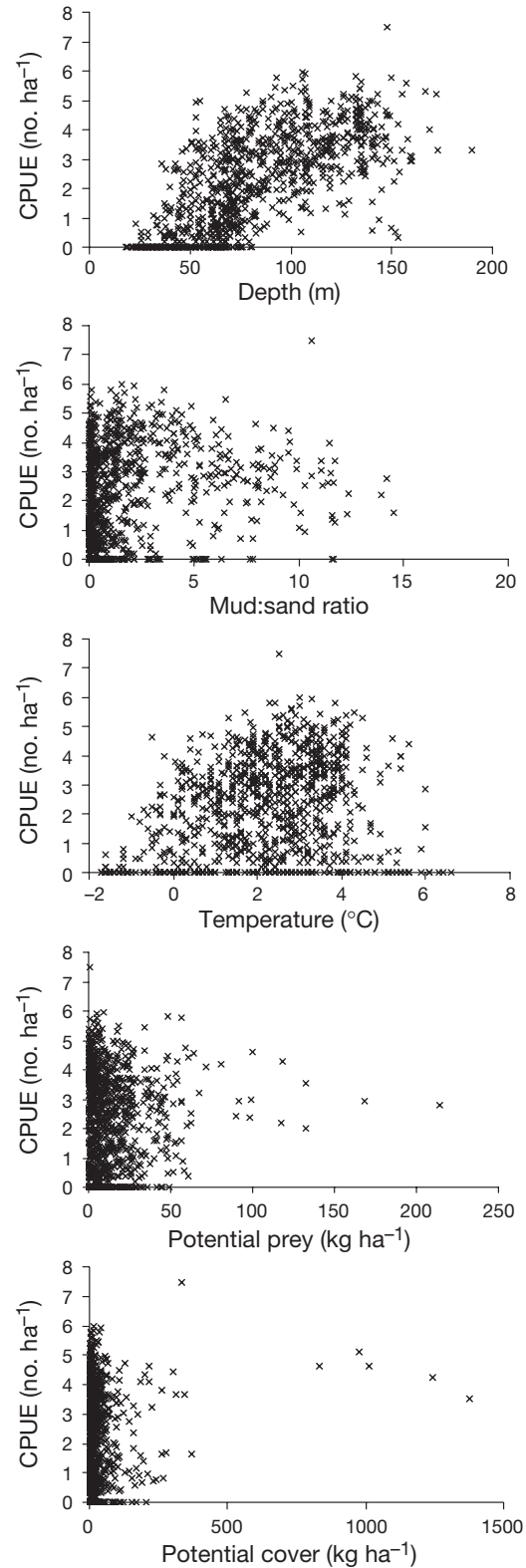

Fig. 2. *Hippoglossoides elassodon.* Distributions of flathead sole catch per unit effort (CPUE) across habitat variables for 1998 to 2000 trawl survey data. Mud:sand ratio predicted from krieged data (Smith & McConnaughey 1999); other habitat data collected on 1050 trawl survey tows
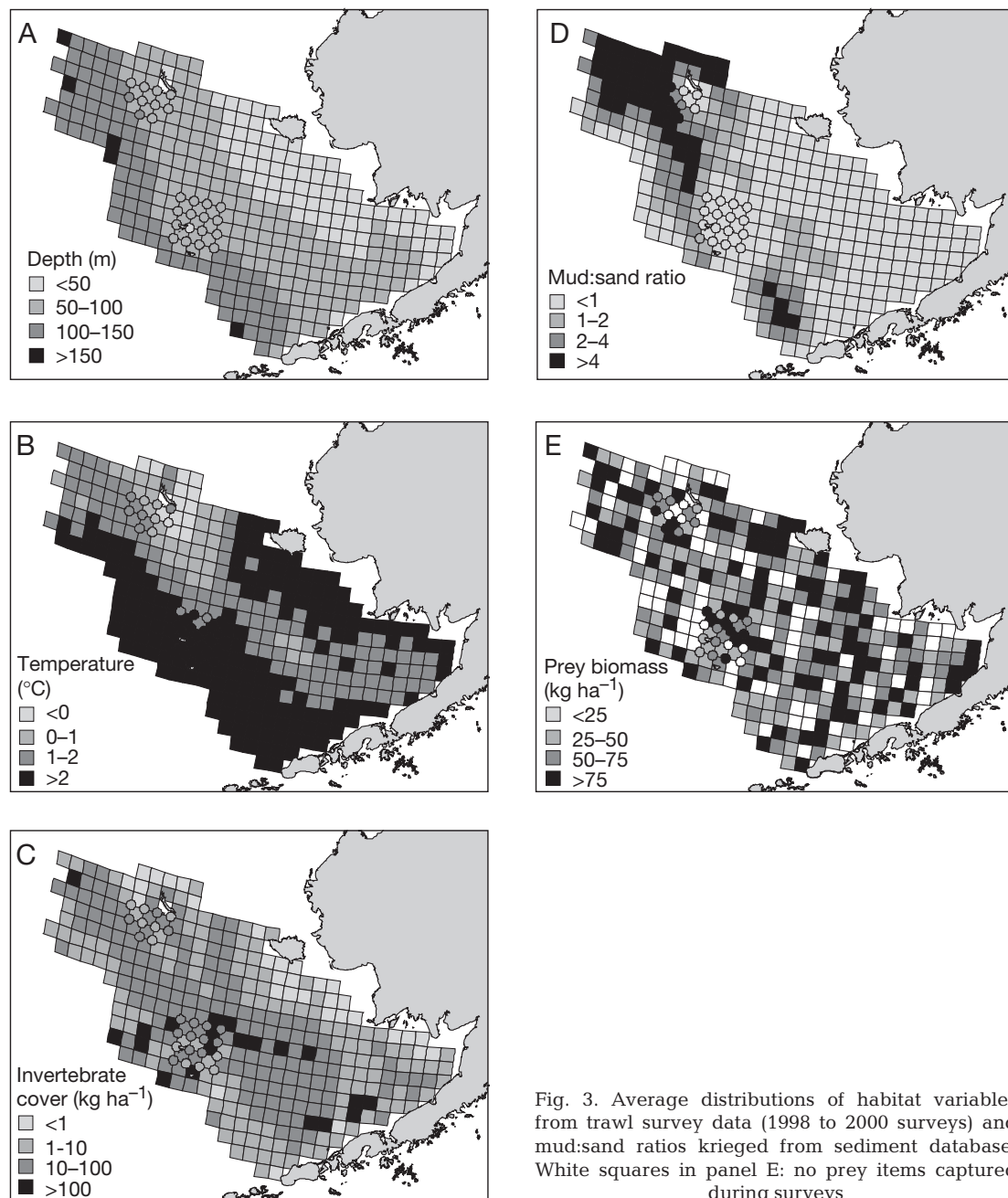
Fig. 3. Average distributions of habitat variables from trawl survey data (1998 to 2000 surveys) and mud:sand ratios krieged from sediment database. White squares in panel E: no prey items captured during surveys

than 45 kg ha^{-1} (Fig. 2). The mud:sand ratio ranged from 0 to 14 (Fig. 2). Over 50% of the sites had sediment samples composed of mostly sand-sized particles, and thus mud:sand ratios of <1. Total potential prey ranged from 0 to 214 kg ha^{-1}, with the majority of sites having less than 20 kg ha^{-1} of flathead sole diet components. The mid-shelf region (depths between 50 and 100 m) was dominated by temperatures from –1 to 2°C, had variable mud:sand ratios and was interspersed with large volumes of potential cover (Fig. 3). High catches of flathead sole prey items were distributed

across the entire shelf, with no apparent pattern. Mud-dominated stations were mostly in the northern outer-shelf region (Fig. 3).

The best model of flathead sole (combined subadults and adults from 1998 to 2000) habitat-use included all 5 habitat variables; depth, temperature, potential cover, mud:sand ratio and potential prey (Table 2). This model was reduced from the original 15-parameter model to a 10-parameter model. The 10-parameter model predictions were highly correlated ($r^2 = 0.63$) to the observations, and the majority of

Table 2. *Hippoglossoides elassodon.* Best-fitting models for flathead sole habitat use. For each group of flathead sole (by maturity and by sex) the full model was the 15-parameter model of Eq. (5); for each habitat variable, the number of parameters and equation are shown in body of table (see 'Materials and methods' for definitions). Number of parameters (P) for each model, Akaike information criterion (AIC) for full and reduced models, and r^2 value for observed versus predicted values are given. –: variable not included in model

Data set	Depth	T	Potential cover	Mud:sand ratio	Potential prey	P	AIC model		r^2
							Full	Reduced	
Combined	2 (Eq. 3)	1 (Eq. 4)	3 (Eq. 2)	2 (Eq. 3)	2 (Eq. 3)	10	1552	1524	0.63
Mature females	2 (Eq. 3)	2 (Eq. 3)	–	2 (Eq. 3)	–	6	1422	1404	0.41
Mature males	3 (Eq. 2)	2 (Eq. 3)	3 (Eq. 2)	1 (Eq. 4)	–	9	1411	1399	0.41
Subadults	3 (Eq. 2)	1 (Eq. 4)	3 (Eq. 2)	3 (Eq. 2)	2 (Eq. 3)	12	1465	1457	0.60

predictions (67%) fell within 1.0 of the observed CPUE, which is approximately 50% of the overall mean CPUE = 2.12 (Fig. 4). The model included depth as a 2-parameter model (Eq. 3), whereby flathead sole CPUE decreased at depths of <140 m (Fig. 5). The model predicted a linear relationship between CPUE and temperature with a slope of 0.29 (Eq. 4, Fig. 5). The relationship between potential cover followed Eq. (2), with an exponential increase in flathead sole CPUE with increasing potential cover (Fig. 5). Flathead sole CPUE decreased sharply at mud:sand ratios >0.1 (Eq. 3, Fig. 6). Flathead sole CPUE increased to an asymptote at potential prey >30 kg ha^{-1} (Fig. 5).

Modeling was also carried out on subadult fish and the 2 sexes of mature adults separately, for a total of 3
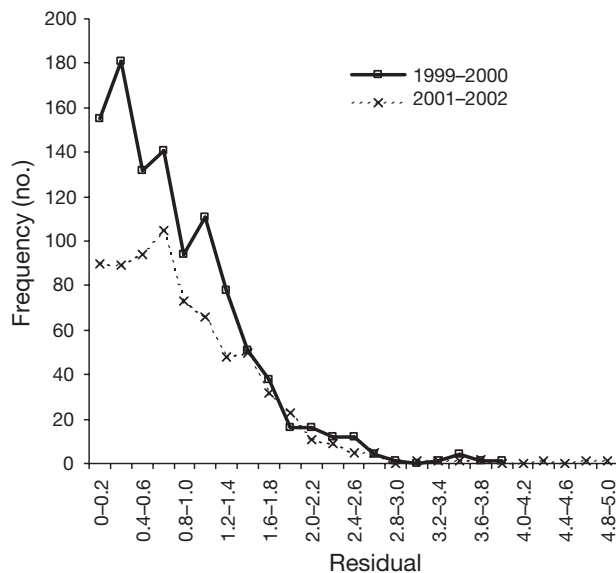

Fig. 4. *Hippoglossoides elassodon.* Frequency (no.) histogram of absolute values of residuals from observed and predicted CPUE. For 1998 to 2000 , predicted data generated from best-fitting model of flathead sole habitat use (n = 1050); for 2001 and 2002, predicted data generated from best-fitting model of flathead sole habitat-use developed from analysis of 1998 to 2000 data (n = 708)

more modeling analyses. The best-fitting model for mature females explained only 41% of the variance in the CPUE data, and contained the depth, temperature and mud:sand ratio variables (Table 2). The major differences between the female and combined flathead sole model was that the female–temperature relationship followed Eq. (3), while the potential cover and potential prey variables were dropped from the analysis. The best-fitting model of male habitat association also explained 41% of the variance in the data set (Table 2), and was the similar to the model for combined adult flathead sole. The major difference between the combined and male flathead models was the elimination of the potential prey variable from the latter analysis. When subadults were modeled, the best-fitting model was similar to the model of all flathead sole, but did not explain as much of the variance in the data set (Table 2). The only differences between the subadult model and the combined flathead sole model were in the depth and mud:sand ratio variables. The model of all flathead sole combined fitted the data much better than any of the individual models divided by maturity and sex, and was thus chosen as the best model for examination of the test data.

The best-fitting model equations and parameters developed for the 1998 to 2000 data (Fig. 5) were utilized to test the model on the 2001 and 2002 trawl survey data. The majority of individual predictions (64%) fell within 1.0 of the observed CPUE, which was again <50% of the overall mean CPUE = 2.16 (Fig. 4). The fit of the model to the test data was almost as good as the original fit on the 1998 to 2000 data (Fig. 6), as the predicted values were also highly correlated (r^2 = 0.58) to the observations. The model fit was adequate for the majority of the CPUE observations from 1 to 5, but the model had difficulty predicting the largest observations of flathead sole CPUE, as well as trawl hauls where zero flathead sole were captured.

Spatial plots of model residuals indicate that the model tended to under-predict (positive residuals) observed CPUE in the southern region of the Bering
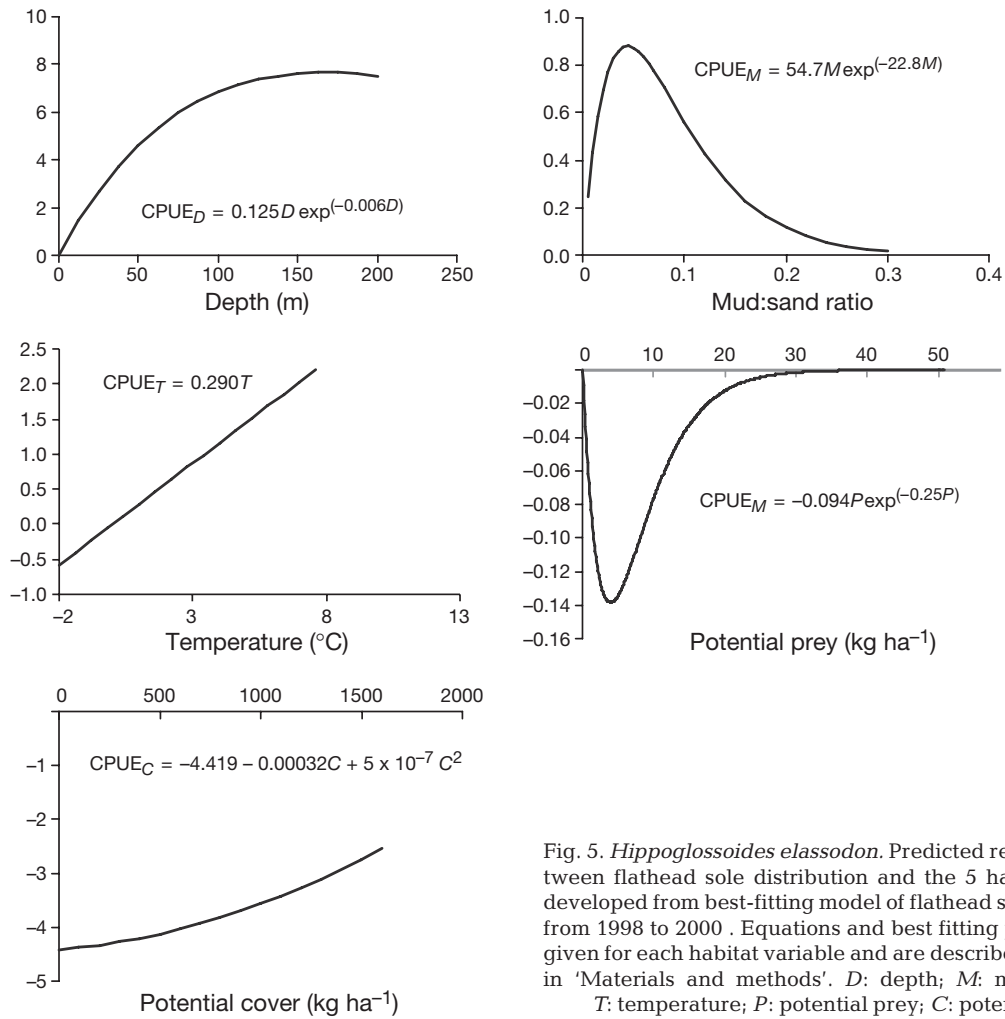
Fig. 5. *Hippoglossoides elassodon.* Predicted relationships between flathead sole distribution and the 5 habitat variables developed from best-fitting model of flathead sole distribution from 1998 to 2000 . Equations and best fitting parameters are given for each habitat variable and are described in Eqs. 2 to 4 in 'Materials and methods'. *D*: depth; *M*: mud:sand ratio; *T*: temperature; *P*: potential prey; *C*: potential cover
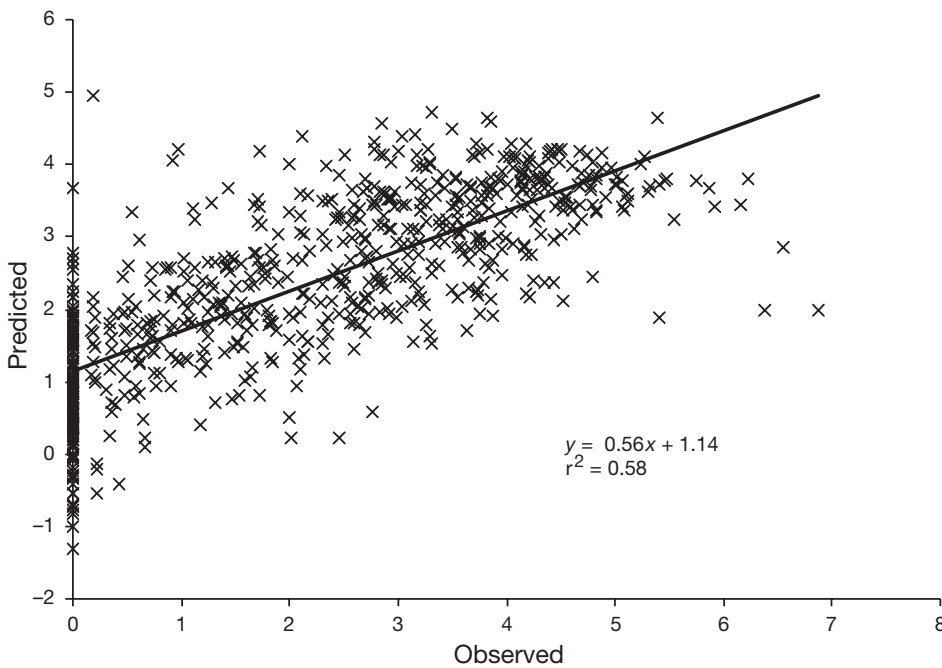
$$CPUE_D = 0.125 D \exp^{(-0.006D)}$$

$$CPUE_M = 54.7 M \exp^{(-22.8M)}$$

$$CPUE_T = 0.290 T$$

$$CPUE_M = -0.094 P \exp^{(-0.25P)}$$

$$CPUE_C = -4.419 - 0.00032 C + 5 \times 10^{-7} C^2$$

$$y = 0.56x + 1.14$$
$$r^2 = 0.58$$

Fig. 6. *Hippoglossoides elassodon.* Predicted and observed CPUE values for test data set of the Bering Sea flathead sole for 2001 and 2002. Predicted data generated from best-fitting model of flathead sole habitat-use developed from analysis of 1998 to 2000 data
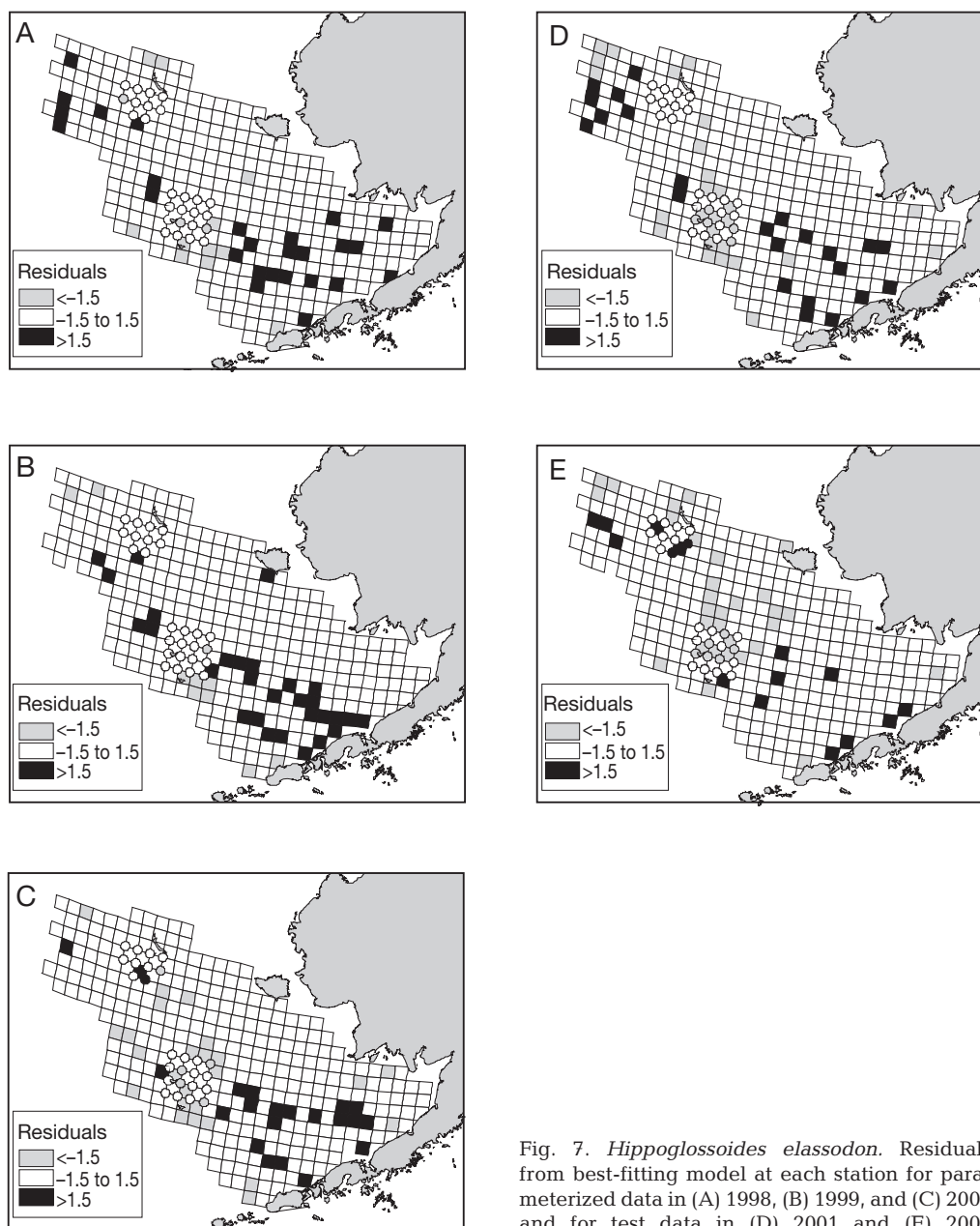
Fig. 7. *Hippoglossoides elassodon.* Residuals from best-fitting model at each station for parameterized data in (A) 1998, (B) 1999, and (C) 2000 and for test data in (D) 2001 and (E) 2002

Sea shelf in 1998 to 2000, while over-predicting the observed CPUE in the central shelf (Fig. 7). In 2001 and 2002, positive and negative residuals were more evenly distributed across the shelf. The largest positive deviations from the observed data occurred near the northern Aleutian chain and Bristol Bay in all years. The largest negative deviations occurred most consistently around the edge of Pribilof canyon, south of St. George Island, although large negative deviations also occurred through the middle of the Bering Sea shelf (Fig. 7).

DISCUSSION

The summer distribution and catch of flathead sole in the eastern Bering Sea can be predicted using depth, temperature, potential cover, mud–sand ratio and the potential prey at each trawl survey site. As with other flatfish species in the Bering Sea, depth is a primary factor in determining the distribution of flathead sole (Swartzman et al. 1992, Zimmermann & Goddard 1996, Nichol 1998). The peak depth distribution (~140 m) of flathead sole places them within the outer domain of

the Bering Sea shelf (Schumacher & Kinder 1983). This area of the shelf is typically dominated by the degree of ice cover over the winter and spring (Wyllie-Echeverria & Ohtani 1999). Production is controlled by spring water-column stability determined by the timing and location of ice retreat (Niebauer et al. 1981). In years of strong ice cover, a pool of water colder than 2°C forms in summer on the middle and outer shelf (Wyllie-Echeverria & Ohtani 1999) and can persist throughout the summer. Previous investigations of flathead sole distribution on the Bering Sea shelf indicated that water temperatures below 2°C and higher than 4.3°C were avoided by flathead sole (Mineva 1964). Additionally, studies of energy requirements have found high Q_{10} values for flathead sole, indicating a relatively narrow thermal range (Paul et al. 1995). Our analysis is consistent with the lower temperature boundary, as modeling indicated a steep decline in flathead CPUE below 2°C, and suggests that flathead sole avoid the pool of colder water on the mid-shelf. In this analysis, however, the model did not predict any decline in CPUE at higher temperatures. The lack of a declining CPUE trend at higher temperatures may be an artifact of the small number of trawl survey collections at temperatures greater than 4°C.

Sediment characteristics have often been found to influence the distribution of flatfishes. In this study, sediment type (as represented by the mud:sand ratio) exhibited a strong relationship with the summer distribution of flathead sole. Flathead sole CPUE increased sharply as the mud:sand ratio increased, and then the effect of sediment on CPUE declined to near zero at mud:sand ratios >0.3. A previous analysis of flathead sole distribution in the Bering Sea using the same sediment data (but an earlier period of trawl survey data) indicated that this species preferred areas of mixed sand and mud, where its primary prey item (ophiuriods) was present in high densities (McConnaughey & Smith 2000). The diet data presented by McConnaughey & Smith (2000) suggest that flathead sole are generalist feeders, consuming walleye pollock when occupying sandy areas and ophiuriods when occupying mixed mud and sand areas. In this study, increases in potential prey resulted in increased flathead sole CPUE, while the effect of sediment type was only important to the flathead sole catch over a small range of values, consistent with the dietary explanation for sediment preference proposed by McConnaughey & Smith (2000).

Other studies of flatfish distribution have found that the presence of structure can increase the density of individuals. Sheltering structure such as benthic invertebrates, overlying litter, etc. are associated with increased abundance of juvenile flatfish in nursery areas (Howell et al. 1999, Stoner & Titgen 2003), and presumably enhance survival through mitigation of predation (Orth et al. 1984, Fernandez et al. 1993, Laurel et al. 2003, Stoner & Titgen 2003) or collection of prey in areas of complex benthic structure (Stevens & Anderson 2000). In the current study, the presence of invertebrate sheltering organisms in the trawl survey was predicted to increase the abundance of flathead sole in the catch. There was no available information from the Bering Sea trawl surveys to identify other types of structure, such as sand waves, that could alternatively provide shelter for flathead sole. Western Bristol Bay, where unusual bed forms (sand waves, faults and seafloor depressions) have been mapped using sidescan sonar (Schwab & Molnia 1987, Marlow et al. 1999), was a location where the model predicted lower values than were observed. Sand waves have also been observed at other locations in the Bering Sea outside the region included in the trawl survey (Field et al. 1981, Hunter et al. 1982). Therefore, the trawl survey catch of potential cover does not account for all types of shelter available to demersal fishes.

Correlations among the initial group of habitat variables made it difficult to partition the amount of flathead sole CPUE accounted for by individual variables (Table 3). Most of these relationships were weakly significant (r < 0.10) with the exception of the sediment–depth (0.44) and sediment–temperature (0.25) correlations. Independence among the 5 variables was not a necessary assumption of this modeling effort; however, it does complicate the interpretation of the results. For example, some variability in the catch that was attributed to depth in the model may have actually been a function of changes in sediment type, as sampling moved deeper. However, removal of either depth or sediment type from the analysis resulted in a significantly weaker fit to the data.

The basin theory predicts that the distribution of a fish species should expand during periods of high population abundance and contract during periods of low abundance (MacCall 1990), a phenomenon for which some evidence exists in flathead sole (McConnaughey 1995). If flathead sole distribution responds to overall abundance patterns in the Bering Sea, it would be

Table 3. Correlations (r values) among habitat variables in 1998 to 2000 Bering Sea survey data. *: linear regression of variables was significant at p < 0.05

Parameter	Depth	Temperature	Potential cover	Mud:sand ratio	Potential prey
Depth	1				
Temperature	0.07*	1			
Potential cover	0.02	0.02	1		
Mud:sand ratio	0.44*	0.25*	0.09*	1	
Potential prey	0.05	0.05	0.09*	0.06*	1

expected that the parameters of habitat relationships would change in concurrence with changes in abundance. For example, the most dramatic cold pool extension over the shelf during the period examined in this study occurred in 1999, when cool water was recorded throughout the middle domain and most of the outer domain above the Pribilof Islands. This should have resulted in cold pool avoidance by flathead sole and either higher catches over the outer shelf due to crowding of the population or higher catches in areas not typically utilized by flathead sole due to dispersal away from colder water. The residuals of the model fit in 1999 under-predict catches on the southern half of the Bering Shelf, especially inside the 100 m isobath (Fig. 7B), suggesting that the extensive cold pool in 1999 may have changed the distribution of flathead sole across the shelf.

Although this modeling approach was effective for predicting over half the variation in flathead sole CPUE, there was still considerable unexplained variability. The model fit could probably be improved by including more accurate measures of the variables that were indices of available resources. Sampling biases due to inaccurate measurement of important variables such as potential prey and potential cover are a problem in the analysis, and because we utilized only 1 sampling method (bottom trawl) probably contributed to the unexplained variance in the model. Another potential source of unexplained variation in the results could be variables that were missed by this study, such as competition with other species of fishes and invertebrates. The broad scale of this study (encompassing the entire Bering Sea shelf) would benefit from smaller-scale information that could more clearly develop mechanistic relationships between CPUE and habitat variables while controlling for confounding factors.

The modeling method demonstrated here is important in advancing fisheries science because predictive models can be utilized to forecast the effects of fishing activity and climate change on a population. One of the advantages of this modeling study over non-predictive models is that the relationship between flathead sole CPUE and the various habitat variables can be explored simultaneously. This is especially valuable in developing methods for ecosystem-based management and for describing essential fish habitats. Currently, there is an emerging discussion of the effects of fishing on essential habitats for fish species. Sheltering invertebrates are susceptible to trawling activity (McConnaughey et al. 2000, Freese 2001, Wassenberg et al. 2002), and were found to be important to flathead sole distribution in the current study. If the relationship between flathead sole and potential cover estimated in the current modeling analysis is robust, the effect of substrate removal on flathead sole distribution can

be easily predicted. For example, if there is an 80% reduction in the catch of invertebrates across the Bering Sea shelf, a reduction in flathead sole CPUE of <1% would be expected. Interestingly, a drop in temperature across the shelf of 1°C, would result in an estimated 25% reduction in flathead sole CPUE. The value of the method described here is in its potential for utilization by managers to make testable predictions about the distribution of flathead sole under varying environmental conditions. Models such as these should prove useful by allowing decision-makers to manage marine ecosystem components, and provide a framework for evaluating options in managing fish habitats.

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