

## Comparison of individual-based model output to data using a model of walleye pollock early life history in the Gulf of Alaska

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### Abstract :

Biophysical individual-based models (IBMs) have been used to study aspects of early life history of marine fishes such as recruitment, connectivity of spawning and nursery areas, and marine reserve design. However, there is no consistent approach to validating the spatial outputs of these models. In this study, we hope to rectify this gap. We document additions to an existing individual-based biophysical model for Alaska walleye pollock (*Gadus chalcogrammus*), some simulations made with this model and methods that were used to describe and compare spatial output of the model versus field data derived from ichthyoplankton surveys in the Gulf of Alaska. We used visual methods (e.g. distributional centroids with directional ellipses), several indices (such as a Normalized Difference Index (NDI), and an Overlap Coefficient (OC), and several statistical methods: the Syrjala method, the Getis-Ord  $G_i^*$  statistic, and a geostatistical method for comparing spatial indices. We assess the utility of these different methods in analyzing spatial output and comparing model output to data, and give recommendations for their appropriate use. Visual methods are useful for initial comparisons of model and data distributions. Metrics such as the NDI and OC give useful measures of co-location and overlap, but care must be taken in discretizing the fields into bins. The Getis-Ord  $G_i^*$  statistic is useful to determine the patchiness of the fields. The Syrjala method is an easily implemented statistical measure of the difference between the fields, but does not give information on the details of the distributions. Finally, the geostatistical comparison of spatial indices gives good information of details of the distributions and whether they differ significantly between the model and the data. We conclude that each technique gives quite different information about the model-data distribution comparison, and that some are easy to apply and some more complex. We also give recommendations for a multistep process to validate spatial output from IBMs.

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## 1.1 Introduction

Model validation (i.e. the comparison of model output to external, independently derived data) is a necessary part of the development and use of ecological models. Individual-based biophysical models (IBMs) of larval fish dispersal and early life history have been used in fisheries for several decades, but are often not well validated; there is much room for improvement (North et al, 2009). Depending on the purpose of the model, the type of validation will differ. In drift and connectivity studies, the emphasis is on validating spatial distributions and trajectories of larvae. Investigations examining growth, mortality and recruitment will need different types of validation; these are not discussed here. Spatial outputs of biophysical individual-based models are often compared to data by placing maps side-by-side for the reader, which is a good first step, but it is not quantitative. Several measures or indices have been used to compare individual-based model spatial outputs to empirical data, however there has been no consistent approach using multiple methods.

There are limited methods that can be used to validate model predictions of larval dispersal and transport of individuals. One method compares trajectories from model predictions to those from satellite-tracked drifters (North et al. 2009). This comparative method is usually based on a relatively limited number of drifters that were deployed at fixed depths, incorporate wind effects, and adds cost to the model validation. Characteristics of drifters predispose satellite-tracked drifter tracks to diverge from larval fish trajectories, such as the effect of wind on the drifter, or use of a constant depth of the drogue when individual fish often move vertically in the water column.

An alternative approach could be to use uniquely marked individual animals. Chemical marking has been attempted (North et al. 2009), and might be a useful validation technique but is only applicable when populations are small, mortality is low, and the likelihood of recapture is reasonable. Elemental fingerprinting has been used to infer natal origin of animals captured during distribution and abundance surveys (Thorrold et al. 2001, DiBacco and Levin 2000, Zacherl et al. 2003, Becker et al. 2007), and might be used to validate individual-based model (IBM) connectivity between spawning and nursery grounds, but detectable differences in seawater trace elemental composition between sites is required, and still, actual trajectories remain unknown. The

required gradient and resolution to detect change among sites may vary with factors other than seawater composition (e.g. temperature, salinity), and it adds cost to the validation. The use of otolith microchemistry enables assessment of larval fish natal origin (Campana, 1999; Thorrold et al., 2001), and seascape genetics or genetic fingerprinting may be used in some situations (Coscia et al., 2013, Selkoe et al., 2008, Galindo et al. 2010, Palumbi, 2003), but source populations must be known and characterized by detectable genetic differences (Hedgecock et al., 2007). Model error quantification techniques used for hydrodynamic models include cost functions (Delhez *et al.*, 2004; Radach and Moll, 2006), root-mean-square error of modeled vs. observed values, model skill scores (Warner et al., 2005), and Taylor diagrams (Taylor, 2001).

One of the most straightforward ways to validate dispersal and transport IBMs is by comparing modeled spatial distributions with empirical distributions of larvae and juveniles. Although it cannot be known if individuals from spawning sites are the same individuals that are caught during surveys, this comparative approach can be useful when the sources of individuals caught in the field are relatively well known. Several studies using IBMs have used several different measures to analyze spatial distributions (overlap index, Hinrichsen et al. 2005, Morisita's simplified overlap index, Utne and Huse, 2012, centroids (center of gravity), Vikebø et al. 2005, Castaño-Primo et al. 2014, (defined as convex hull), Petrik et al. 2014 and Utne and Huse 2012, Jaccard's Coefficient, Weidmann et al., 2012, a Correlation Index based on linear regression, Pedersen, et al. 2009, Root Mean Square Deviation (RMSD), Utne and Huse, 2012), the local index of collocation (Petrik et al, 2014), but no comparison of methods has been published.

We use walleye pollock (*Gadus chalcogrammus*) in the Gulf of Alaska (GOA) as a case study to validate the spatial output from an individual-based dispersal model. Walleye pollock has been studied intensively for several decades, and many lab studies and field surveys have been done. We used 1987 as our test year in this study, as there were several sequential surveys of different early life stages done in that year. Walleye pollock in the Gulf of Alaska have a life history where spawning and nursery habitat appear to be spatially disaggregated, and most of the currents in the region where pollock spawn are highly advective. Historically, a large part of the egg production of pollock has been located at the southwestern entrance to Shelikof Strait, an area between Kodiak

Island and the Alaska Peninsula (Fig. 1, Kendall et al., 1987; Schumacher and Kendall, 1991). Pollock eggs are spawned between mid-March and early May, with spawning peaking at the beginning of April (Doyle and Mier, This issue). By May, larvae are advected southwest by the Alaska Coastal Current (ACC) along the Alaska Peninsula. By summer and through early fall, juveniles arrive at their primary nursery area in the vicinity of the Shumagin Islands (Hinckley et al., 1991; Spring and Bailey 1991; Wilson et al., 1996; Hinckley et al., 2001). Other potential spawning and nursery areas have been reported in the literature (Wilson, 2000; Bailey et al., 1999; Mazur et al., 2007), but their relative contribution to the recruitment of pollock in the GOA is not known, nor is how their contributions may have changed over time. Spatial and temporal variability in spawning and the variability of current patterns may determine which locations function as pollock nursery habitats in the GOA, and explain some of the variability in pollock abundance. Connectivity between spawning and nursery areas is important to understanding recruitment, as differentiating between possible sub-populations is needed to clarify stock management areas.

A biophysical model, consisting of an IBM coupled with a hydrodynamic model, has been used to assess pollock spawning-nursery area connectivity in the GOA (Parada et al., This issue). The spatially-explicit features of biophysical models and the Lagrangian approach enable tracking of particles representing individuals from spawning area release locations to nursery destinations as juveniles. The work described here extends previous work that explored the life history of walleye pollock (Hinckley et al. 1996, Hinckley et al. 2001, Megrey and Hinckley, 2001, Hermann et al. 2001).

In this study, we update the IBM for pollock, and compare methods to validate modeled spatial distributions. Our goal is to see if this biophysical model can reproduce observed distributions of early life stages of walleye pollock between early larvae in the spring and juveniles in September. Spatial and temporal matches between model outputs and observed distributions will be compared using multiple methods. This will enable evaluation of various techniques which could be used to validate IBM outputs, and increase understanding of walleye pollock early life history.

## 2.1 Methods

The individual based biophysical model we use for walleye pollock has been described in detail elsewhere (Hinckley et al., 1996, Megrey and Hinckley, 2001). Here we give an overview of the model, and describe additions and updates to the model in detail.

### 2.1.1 The Walleye Pollock Individual-based Model

The pollock IBM, originally developed by S. Hinckley, B. Megrey and A. Hermann, simulates four developmental stages (eggs, yolk-sac larvae, feeding larvae, and juveniles) of 0-age pollock from spawning to the autumn of their spawning year. Processes in the model are stage-dependent (Hinckley et al., 1996; Megrey and Hinckley 2001). Egg development was driven by age and temperature (Blood et al., 1994). Yolk-sac larval growth depended on degree days which were accumulated for every day after hatch using temperature information from the physical model for each location and time step. A feeding probability for yolk-sac larvae was calculated prior to entering the feeding larval stage, unless they passed the point of no return without feeding, in which case they died. Dry weight of feeding larvae and juveniles depended on consumption (a function of individual weight and temperature, as described in Hinckley et al. 1996) and a bioenergetics formulation. The bioenergetics submodel for larvae included assimilation efficiency (Houde, 1989) and daily respiration rate (Yamashita and Bailey, 1989), and for juveniles, was estimated according to a modified version of Ciannelli et al.'s model (1998, see below) model. Net growth in weight (g) of larvae and juveniles was updated at each time step and converted to growth in length (mm).

Superindividual schemes (Scheffer et al., 1995, Megrey and Hinckley, 2001, Bartsch and Coombs, 2004) are approaches that allow the use of realistic mortality rates in IBMs by increasing the number of individuals represented by each particle (i.e. superindividual). In this way, we can simulate larger numbers of fish in a population without adding to computer processing time. The assumption behind this approach is that growth, feeding conditions, and the probability of mortality for each individual within a superindividual are the same (as they are at the same location). At the beginning of the simulation, each superindividual is assigned a “count”, indicating how many individual

fish the superindividual represents. This “count” is decreased by applying a random deviate from the daily mortality rate for that particular life stage. At any point in time, the total number of fish is the sum of the “count” variable over all superindividuals.

The daily probability of mortality for eggs, yolk-sac larvae, feeding larvae and juveniles in the pollock model was given by an exponential function dependent on the instantaneous daily mortality rate of the respective stage. We assumed that each particle represented a cohort of pollock eggs released in the spawning areas. The number of surviving superindividuals was assessed at each time step.

Each cohort of superindividuals was assigned to a particle that moved according to the directional ( $u, v$  and  $w$ ) components of velocity following a Lagrangian trajectory, plus behavioral subroutines that differed by life stage. Particle tracking was based on the Euler method, and we used a Java tool developed by Lett et al. (Ichthyop, 2008) which used the Regional Ocean Modeling System (ROMS, see below) native grid. The unique trajectories of the particles integrated environmental conditions experienced by each individual. Each trajectory resulted in a unique pattern of growth, distribution, and survival.

Algorithms for particle depth were stage dependent, as in Hinckley et al. (1996). The vertical position of each egg was calculated at each time step and depended on the terminal velocity (based on the density of the egg at each developmental stage) and the vertical component of water velocity,  $w$ , from the ROMS model. The terminal velocity was calculated based on Sundby (1983). Parameters for calculating changes in egg vertical location are described in Hinckley et al. (1996). Yolk-sac larvae were assumed to remain at the depth of hatch until first-feeding. Feeding larvae rose to the upper water column and began diel migrations at 6 mm with swimming speeds a function of length (Kendall et al., 1987; 1994). Larvae were found at the deepest level during midday and at the shallowest depth at dusk. They were found somewhat deeper at night than at dusk or at dawn. Vertical and horizontal movements of juveniles are described below.

### 2.1.2 Additions to the Pollock Model

The following are additions to the original pollock IBM of Hinckley et al (1996) and Megrey and Hinckley (2001).

### 2.1.2.1 Growth and Bioenergetics of 0-age Juveniles

A Gerritsen and Strickler (1977) encounter model as simplified by Evans (1989), was adapted for the juvenile stage of this model, and used to calculate the number of each prey type encountered by feeding juvenile pollock per hourly time interval (Eggers, 1977). We assumed the visual field of foraging juveniles was uniform within the search volume and did not attempt to account for microhabitat differences in the position of prey within the visual field (Mazur and Beauchamp 2006). Reaction distance was set at a constant distance for feeding during lighted periods; juvenile pollock were only allowed to feed during light periods of the diel cycle. Diel observations of juvenile pollock consumption *in situ* suggested little feeding occurs outside of lighted periods of the day (Mazur et al. 2007).

Prey consumption of juveniles was estimated using a bioenergetics-based foraging model for planktivorous fish (Tables 1, 2) developed by Bevelhimer and Adams (1993), evaluated by Stockwell and Johnson (1997), and subsequently field tested (Stockwell and Johnson 1999). For a full description of this modeling approach see Eggers (1977) and Stockwell and Johnson (1997, 1999). A similar approach was recently utilized to investigate pollock recruitment variability in the Eastern Bering Sea (Siddon et al. 2013). Estimates of prey consumption per hourly time step were generated using a single-species functional response that was modified to use prey encounters rather than weight (Bevelhimer and Adams 1993, Stockwell and Johnson 1997). The prey field used in the model was based on the horizontal distribution of euphausiids, large copepods and small copepods from an NPZ model described in Hinckley (1999), for the inner shelf, the mid and outer shelf, and the offshelf areas. Prey preferences were set following Wilson et al. (2006). Consumption of each prey type was partitioned based on juvenile pollock body size and prey size and summed to estimate the total number of each prey type potentially available for consumption per hour. Prey consumption was not allowed to exceed the theoretical maximum daily consumption ( $C_{max}$ ) for pollock of each size as estimated by the bioenergetics model (Ciannelli et al. 1998, Hansson et al. 1996). Consumption of prey during each hourly time step only occurred when space was available in the stomach following digestion and the daily maximum had not been



reached or exceeded. Daily maximum feeding rates were reset following the dark “no feeding” period of each diel cycle.

A new submodel for the bioenergetics of juvenile pollock was implemented in this IBM based on a modified version of Ciannelli et al.’s, (1998) model (Table 2). The energy consumed and subsequently digested (D) in the model was allocated between metabolism (R), egestion (F), excretion (U) and growth (G) (Hewett and Johnson, 1992):

$$G = D - R - F - U$$

Digestion was modeled hourly (Elliott and Pearson 1978) and used evacuation rates estimated for juvenile pollock (Merati and Brodeur 1996, Mazur et al. 2007). Numbers of each potential prey type were converted to weights and allowed to enter the diet based on available stomach capacity and prey preference. Growth of juvenile pollock was estimated using the bioenergetics model and the amount of available prey energy digested on an hourly time step (Stockwell and Johnson 1997). Prey energy density estimates for the Gulf of Alaska can be found in Mazur et al. (2007). Estimates of growth in weight (g) were updated each time step and converted to growth in length (mm) for use in subsequent foraging model time steps.

#### 2.1.2.2 Predation on Juveniles

Groundfish predation on 0-age juveniles was added to the juvenile subroutine. Other sources of predation (seabirds, marine mammals) on pollock can be important, however, comprehensive data with enough spatial and temporal resolution, plus consumption rates, do not exist. Predation rates were based on 8 years of groundfish predation data (K. Aydin, Alaska Fisheries Science Center, Seattle, WA, pers. comm., Table 3). For years where no data were available, an average rate over the 8 years was used. The predation rate was calculated using the total numbers of walleye pollock juveniles consumed by all groundfish predators in each year (Holsman and Aydin, 2015). We computed mortality rates assuming that the maximum number consumed was equivalent to a predation mortality rate of 0.3 per day (average). Predation rates for other years were standardized relative to this maximum.

#### 2.1.2.3 Movement of Juveniles

For vertical and horizontal movements of juveniles, new algorithms were incorporated into the original model of Hinckley et al. (1996). The vertical movement of juveniles is idealized, based on findings in Brodeur and Wilson (1996), who found that there is vertical migration in juvenile pollock. During the day, the distribution of juveniles is concentrated deeper in the water column, near 100 m or 30 m off the bottom, depending on water depth. During the night, distributions are higher in the water column, and more diffuse. Therefore, the migration algorithm added to this IBM is based on the time of day, where individuals are constrained to depth zones and within these depth zones, move up and down according to typical velocities of juveniles which are dependent on the length.

The vertical position of juveniles at each new time step,  $Z_{j,t+1}$  (m), was calculated as in equation (1) where  $Z_j$  is depth at last time step,  $w_j$  is the vertical mean velocity, and  $\Delta t$  is the time step.

$$Z_{j,t+1} = Z_j + w_j \Delta t \quad (1)$$

The mean magnitude of  $w_j$  depended on juvenile length and was inferred from Hurst (2007). The mean magnitude of  $w_j$  added to the deviance of  $w_j$  was sampled randomly from a triangular distribution with mode, minimum ( $0.05 w_j$ ) and maximum value ( $0.1 w_j$ ) was used to obtain the position at each time step. The direction of  $w_j$  (upward or downward) depended on a random deviate from a uniform distribution. The final depth in meters at each new time step was bounded with an upper and lower depth according to the hour (h) of the day in a 24 hour cycle (Equation 2 to 6).

$$h < 2 \text{ am} \quad 40 \text{ m} < Z_{j,t+1} < 60 \text{ m} \quad (2)$$

$$2 \text{ am} < h < 5 \text{ am} \quad 40 \text{ m} < Z_{j,t+1} < 110 \text{ m} \quad (3)$$

$$5 \text{ am} < h < 2 \text{ pm} \quad 90 \text{ m} < Z_{j,t+1} < 110 \text{ m} \quad (4)$$

$$2 \text{ pm} < h < 6 \text{ pm} \quad 40 \text{ m} < Z_{j,t+1} < 110 \text{ m} \quad (5)$$

$$h > 6 \text{ pm} \quad 40 \text{ m} < Z_{j,t+1} < 60 \text{ m} \quad (6)$$

When a particle is in an area of shallower water and the movement intervals are deeper than the bottom depth, then the particles are positioned 10 meters above the bottom plus a random deviation. Equations 2 and 6 show how pollock seek the euphotic

zone during the night, presumably to reduce predation risk (Brodeur et al., 2000, Schabetsberger et al., 2003). Equation 4 is based on a vertical migratory behavior which assumes that juvenile pollock seek deeper depths during the day to avoid visual predation risk (Schabetsberger et al., 2003, Lang et al., 2000). A transition period of broader dispersion through the water column at dawn and dusk is set in equations 3 and 5.

Horizontally, the position of the juveniles was determined using a correlated random walk based on Kareiva and Shigesada (1983). We modeled movement paths as a sequence of straight lines in which juvenile displacement depended on size class. The position of the juvenile at each new time step,  $X_{j,t+1}$  and  $Y_{j,t+1}$ , depended on the position in the previous time step,  $X_{j,t}$  and  $Y_{j,t}$ , the length of the juvenile  $L_j$ , and the turning angle at the time step,  $\alpha_{t+1}$ . Turning angles were measured relative to the previous direction of movement according to the following equation,

$$\alpha_{t+1} = \alpha_t + \theta_j \quad (7)$$

where  $\alpha_t$  was the turning angle at the previous time step,  $\alpha_{t+1}$  was the turning angle at time  $t + 1$  and  $\theta_j$  was chosen from a random normal probability distribution. Then, the new positions were,

$$X_{j,t+1} = X_{j,t} + L_j \cos(\alpha_{t+1}) \quad (8)$$

$$Y_{j,t+1} = Y_{j,t} + L_j \sin(\alpha_{t+1}) \quad (9)$$

### 2.1.2 The Hydrodynamic Model and Model Coupling

This modeling approach involved coupling the walleye pollock IBM to a circulation model, the Regional Ocean Modeling System (ROMS). ROMS is a free-surface, hydrostatic, primitive equation ocean circulation model that employs a nonlinear stretched vertical coordinate system that follows the bathymetry. The horizontal space is discretized using orthogonal curvilinear coordinates on an Arakawa C-grid (numerical details can be found in Haidvogel et al. 2000, Shchepetkin and McWilliams, 2005). The ROMS simulations for this study used a 10 km (horizontal) grid (Northeast Pacific, NEP) with 42 vertical layers. A finer resolution version of the ROMS model (CGOA) on a 3 km grid has been developed since this exercise was done, however it was not available at the time. The NEP grid includes the GOA and the Bering Sea (BS). For this study, we

used a subset of the output of a multi-decadal simulation of ROMS configured and run by Curchitser et al. (2005). Details of the physical model simulations and an assessment of the ROMS model's ability to reproduce observed modes of variability and their impact in the northeast Pacific can be found in Curchitser et al. (2005) and Parada et al. (This issue). The ROMS simulations were run with forcing scenarios (winds, freshwater and boundary conditions) appropriate for the year simulated. The hydrodynamic model produced daily averaged output consisting of salinity and temperature fields, 3D velocities and other variables. These were used to drive the IBM (offline) for 1987, the year used for this analysis.

A Java programming application (Ichthyop, Lett et al., 2008) was adapted to simulate the early life history of walleye pollock in the GOA. This application enabled us to calculate trajectories of particles representing individuals or groups of individual fish (superindividuals), and water properties (temperature, salinity) experienced by these particles during transport. The application used 3D fields of velocity, temperature, and salinity from simulations of ROMS to track particles within the model domain. The biological processes of the IBM are included as submodels within the modified Ichthyop application. The program stores information on the histories of individuals (e.g. time, longitude, latitude, depth, length, etc.). The Ichthyop application is distributed as a package that contains the program code and libraries. For this project, we used one of the early releases of the Ichthyops application and adapted it to our study requirements.

We used the Euler method as a particle tracking algorithm. We conducted a series of experiments comparing this method with the 4<sup>th</sup> order Runge-Kutta method. The Runge-Kutta method was more stable than the Euler method, and converged quickly, however the Euler method did converge properly when enough iterations were used, and was much simpler and faster to run, and was therefore chosen for this study.

### 2.1.3 Survey Data and Model Simulations

A simulation experiment was run to examine the spatial and temporal matching between modeled fields and observations of the distributions of successive life stages of walleye pollock in the GOA for 1987 (1987 was the only year where there were multiple surveys). The objective of the experiment was to use the coupled model to hindcast

distributions of larvae in May, early juveniles in June/July and later juveniles in August/September for the year 1987, and to compare these model outputs to survey distributions of young pollock for the periods 18-29 May, 1987, 18 June-16 July, 1987, and 12 August-20 September, 1987. Model output from the date nearest the midpoint of each survey was used to compare to survey data. A specific date was chosen to avoid blurring of features that we wanted to be able to distinguish, such as patchiness and current variability, blurring that would occur if we averaged over time. All tests were done within the survey boundaries, except for the centroid analysis and the hotspot analyses for the May time period. These analyses were done on both the very restricted May survey area, and the broader modeled area, to compare the results for both areal extents.

Methods for the May larval survey are described in Matarese et al. (2003). The survey area was restricted to the region between Shelikof Strait Sutwik Island (Fig. 1). The survey methods for the June/July and August/September cruises are covered in Hinckley et al. (1991). The June/July survey for early juveniles covered much of the western GOA on a regular grid, and used a Methot frame trawl (Methot 1986). The August/September survey for late juveniles in 1987 made transects from Unimak Pass to the eastern side of Kodiak Island, trawling with a 24-m high-opening shrimp trawl (Hinckley et al. 1991).

Eggs in the model were released in 14 areas (5000 in each) identified as potential spawning areas, on the 15<sup>th</sup> of each of 4 months (Feb, Mar, Apr, May), which covered the bulk of the known spawning areas and times of pollock in the GOA (Kendall et al. 1996; Matarese et al., 2003, Bailey et al., 2005, Doyle and Mier, This issue). The numbers of eggs released was proportional to the egg production estimates from the stock assessments for pollock, Dorn et al. 2005). The model was run using forcing for 1987, through September. Individual locations and other information were recorded once every five days.

In order to focus the study only on the simulated individuals derived from spawning areas and times where fish caught in the surveys most likely originated, we obtained information on both spatial and temporal distribution of eggs (derived from the Alaska Fisheries Science Center (AFSC) Ichthyoplankton database, Matarese et al,

2003), and on hatchdate distributions of larvae and juveniles caught in the surveys in 1987, derived from otolith analysis (Brown and Bailey, 1992).

Figure 2 shows the pollock egg spatial distribution from ichthyoplankton surveys in 1987. It can be seen that the majority of eggs were found in North Shelikof Strait and the Shelikof Strait exit region. The highest number of eggs was caught in the first half of April (Fig. 3) and catches of eggs were near zero by the end of May. Hatchdates computed for larvae from the May survey and juveniles from the June/July and August/September surveys are presented in Brown and Bailey, 1992 (their Figure 5). This figure shows that hatchdates for all surveys were between the beginning of April and the end of May. These pieces of information indicated that we should only follow individual particles in the model that were released in April and May, in the North Shelikof Strait and the Shelikof Strait Exit areas.

#### 2.1.4 Comparison Methods

Validation metrics included distributional centroids, their variance and directional ellipses, the Getis-Ord  $G_i^*$  statistic (Ord and Getis, 1995), a normalized difference index (NDI), an overlap coefficient (OC) index, the Syrjala test statistics (Syrjala, 1996) and various other geostatistical spatial indices. Comparisons were made within the survey domain for all validation metrics with the exception of analyses for May, which were computed over the whole model domain as well as the survey region (a subset of the model domain). This was done due to the very small region surveyed in May.

Units for the surveys are densities ( $\#/1000 \text{ m}^3$ ) for May and June/July. Units for the August/September survey were not normalized by area, but by time ( $\#$  per 10 minutes tow). Units for the modeled “individuals” are “superindividual number”, which is the number of individual fish represented by each individual particle in the model. These densities and numbers can be thought of as weighting factors for the spatial comparison methods, as they are not directly comparable, and in the case of the model, were not related to actual abundance of fish.

##### 2.1.4.1 Distributional Centroids

We have calculated centroids (centers of gravity) for the model output and the survey data for each time period, May, June/July and August/September. Each centroid was calculated from the model output using latitude, longitude and superindividual number for each particle, and by using latitude, longitude and density of fish (catch per 1000 m<sup>3</sup> for May and June/July surveys, and catch per 10 min tow for the August/September survey) for the survey data. In the May case, centroids were calculated over the smaller survey area as well as the whole model domain for comparison purposes. Variances around these centroids (inertia) were also calculated. Directional ellipses and the related isotropy (the square root ratio between the minimal and the maximal inertia associated with the main directions of the ellipse) of one standard deviation from the mean were calculated and plotted to indicate the directional trend of the data. The centroids and directional ellipses of the model and the data were plotted to give a visual indication of how they compared. These statistics also formed part of the geostatistical comparison of spatial indices described below.

#### 2.1.4.2 Hot/Coldspot Analysis

The Getis-Ord  $G_i^*$  (Getis and Ord, 1992, Ord and Getis, 1995) is a technique used to examine spatial clustering of georeferenced data. The Getis-Ord  $G_i^*$  statistic looks at each data point in the context of its neighbors. A data point with high values is only considered a statistically significant hotspot if it is surrounded by other points which also have high values, and the opposite for coldspots.

This statistic was calculated for each set of model output and survey data. Given a set of weighted points, this statistic identifies spatial clusters of high values (hotspots) and of low values (coldspots). The output of the analysis is Z scores and p-values for each feature, which represent the statistical significance of the spatial clustering of the values. Low or negative values of the Z score and low p-value indicate spatial clustering of low values, and the opposite for high or positive Z scores. The higher (or lower) the Z score, the more intense the clustering. A Z score near zero indicates no apparent spatial clustering. A low p-value indicates a high (low) Z score is significantly different from zero, and hence the clustering of high (low) values is significant. This analysis was implemented in ArcView Version 10.

Prior to the following two analyses, the distributions of early (May cruise) larvae, early juveniles (June/July cruise) and late juveniles (August/September cruise) and model results were discretized in three bin sizes:  $1/4^\circ$  (~25 k),  $1/2^\circ$  (~50 k), and  $3/4^\circ$  (~75 k) spatial resolution. Then two methods were tested to account for model and data discrepancies: a normalized difference index and an overlap coefficient.

#### 2.1.4.3 Normalized Difference Index (NDI)

A cost function was used to quantify the discrepancies between model and measurements, relating the difference to the variation of the measured variable. This was calculated by normalizing the difference between the mean field (by cell) from the model  $\bar{Y}_{o,i}$  and observations  $\bar{Y}_{m,i}$  respectively, with the standard deviation of observations by cell, following Berntsen et al. (1996) and S oiland and Skogen (2000). The cost function field  $NDI_i$  for each  $i$ -th cell for the modeled and data fields is defined by:

$$NDI_i = (\bar{Y}_{o,i} - \bar{Y}_{m,i}) / (sd(\bar{Y}_{o,i}) + 0.01) \quad (10)$$

The overall cost function NDI is the area average of the absolute values of the cost function field and was computed as the sum over all bins. NDI is always positive, while  $NDI_i$  has both negative and positive values. The overall NDI was calculated for each bin size for the modeled and data fields for the May, June/July and August/September time periods. The overall smaller the overall NDI value the smaller the difference between model and data.

#### 2.1.4.4 Overlap coefficient (OC)

This coefficient aims to estimate the spatial overlap between simulated and survey distributions of pollock and is based on Horn (1996) and Hinrichsen et al. (2005) studies. The overlap coefficient, OC, is 0 when no overlap is apparent and 1 when the two distributions are identical (Hinrichsen et al., 2005). Hinrichsen et al (2005) applied this coefficient to determine how many larvae and prey were simultaneously present in the specified subareas of the central Baltic Sea (Hinrichsen et al., 2005). However, our application of OC is focused on model and data comparison and is defined by:

$$OC_i = 2 \sum_{i=1}^{n_k} (x_i \cdot \hat{x}_i) / (\sum_{i=1}^{n_k} x_i^2 + \sum_{i=1}^{n_k} \hat{x}_i^2) \quad (11)$$



Where  $\hat{x}_i$  and  $x_i$  are modeled and observed cell values respectively (for each individual bin  $i$ , and where  $n_k$  is the number of bins in each of the three ( $k=1:3$ ) bin sizes.

#### 2.1.4.5 Syrjala Tests

Tests developed by Syrjala (1996) were applied to the model and survey distributions. Syrjala's test is a randomization test based on the Cramer von Mises statistic extended to bivariate distributions. These tests were developed to test the null hypothesis that there is no difference in the spatial distribution of two populations (here applied to the model and the survey distributions), versus the alternative hypothesis that the distributions are not the same. Two tests were applied: bivariate generalizations of 1) a Cramer-von Mises (CvM) type nonparametric test, and 2) a Kolmogirov-Smirnov (KS) type nonparametric test. For both tests, no specific distribution is assumed for either population. The data are normalized to the maximum densities for each distribution (model and data). These normalized values were then summed in  $1/2^\circ$  cells. The choice of cell size was based on balancing resolution with the number of cells occupied by modeled particles. The NDI and OC analyses showed that the  $1/4^\circ$  cells included very few particles, and the resolution of  $3/4^\circ$  was too coarse. The levels of abundance are not compared in these tests, just the spatial pattern. In these tests, the axes of the coordinate system describing the geographic locations which are being compared are rotated four times, once to each corner of the sampling grid, and an average of the test statistic for each rotation is calculated. This is to ameliorate the fact that the test statistic is not invariant with respect to the coordinate system used, although it does not vary by much (Syrjala, 1996). The significance of the test statistic is compared using a randomization test. Distributions were only compared for cells that were represented in both the surveys and the model output.

#### 2.1.4.6 Geostatistical Simulation of Spatial Indices

A hypothesis testing procedure was also used to compare spatial distributions observed during surveys to distributions from the model. The null hypothesis used in the comparison was that 95% confidence intervals for the values of spatial indices derived from the survey data contain the values of spatial indices from the IBM output.

To quantitatively describe walleye pollock spatial distributions, survey data and model output (June/July and August/September only) were characterized using spatial distribution indices developed by Woillez and colleagues (2007; 2009a). Spatial distribution indices included: center of gravity (i.e. weighted location or centroid, as above), inertia (variance of the spatial distribution), isotropy (evenness of dispersion), positive area (the area occupied by densities  $> 0$ ), spreading area (proportional area occupied per unit area), and equivalent area (area occupied if all data cells had the same density). Measures were compared within the survey region for all indices.

Confidence intervals for pollock spatial distribution indices derived from survey data were calculated using geostatistical conditional simulations (Lantuéjoul, 2002). The simulation of spatial distributions of young pollock was based on transformed Gaussian simulations and on a Gibbs sampler to treat zero densities (Woillez, 2007; Woillez et al., 2009b). The variogram of the Gaussian variable to be simulated was inferred using the normal-scored, fish density variable, which included a concentration of values corresponding to zero densities. Based on the inferred variogram model, Gibbs sampling was used to simulate missing Gaussian values corresponding to these zeros, which were lower than a threshold (determined from the proportion of zeros), and on the Gaussian values of all other data points. The transformation was modeled as 0 below the threshold, and by a linear interpolation above (corresponding to the non-zero values). This model was also used at the end of the simulation to back-transform the Gaussian realizations to raw data values. Multiple Gaussian realizations using observed or calculated Gaussian values were produced and then back-transformed. Multiple realizations of pollock spatial distributions were then used to compute spatial distribution index values. In this manner, survey uncertainty was propagated to spatial indices and 95% empirical confidence intervals were derived for each spatial index.

It is noteworthy that the support (i.e. set of locations with non-zero density values) helps define the resolution to be used for IBM simulations of pollock larvae and juvenile distributions. In this case the support is small, as the survey data are collected from vertical tows at station locations. First order distances from the survey data were computed, and the resolution of the simulation grid was set to 10 km, which was greater

than the support and below that of the sampling lag. Variability in neighboring samples within cells (i.e. below resolution) was considered measurement error.

The hypothesis test consisted of determining whether the survey confidence intervals contained the value of the IBM distribution index. Three combinations of spawning release areas (cf. Fig. 1: area 8 – North Shelikof Strait; area 11 – Shelikof Strait exit region, or the two areas combined, and spawning months: April, May or the two months combined, were two factors tested to identify the combination of factors for each distribution index value that provided the best match between the IBM output and the survey data.

### 3.1 Results

#### 3.1.1 General Features of Young Pollock Distributions

The survey area in May, 1987 was restricted to the area between Kodiak Island and Sutwik and Semidi Islands near the exit area of Shelikof Strait (Fig. 4). The distribution of early walleye pollock larvae in the May survey showed high densities east of Sutwik Islands and the Semidi Islands 130 km downstream of the observed spawning region in Shelikof Strait. The model output also showed a high density of early larvae in this area. An observed difference was that model showed a somewhat larger area of moderately high densities of early larvae in the broader region, to the northeast of the survey area in the exit region of Shelikof Strait, and to the southwest of the survey region, in areas which were not covered by the survey. We have no way of knowing whether pollock larvae would have been found in these regions outside the survey area. Note however, that centroids of pollock distribution from the model output and data centroids are in close proximity, near Sutwik Island, even given the larger model domain. This supports the choice of the survey area as being the center of the pollock larval distribution at this time.

The distribution of early juvenile walleye pollock in June/July in the survey data showed maximum densities between the Sutwik/Semidi Islands and the Shumagin Islands (Fig. 5). The model showed high density peaks located in the same area during the same time period. It can be seen in Figure 5 that the centroids of distribution are downstream of those seen in May for both the survey data and the modeled individuals (the Alaska

Coastal Current flows through Shelikof Strait from northeast to southwest) as described by Hinckley et al (1991), and that all centroids were clustered near the Shumagin Islands in close proximity to each other. The centroid for the survey was a slightly to the east, however, compared to the model.

The modeled distribution of later 0-age juvenile walleye pollock in August/September was located around the Shumagin Islands (Fig. 6). The highest densities of modeled individuals were somewhat to the east and inshore of the Shumagins. The survey data also showed maximum densities near the Shumagins (Fig 6). In the survey some juveniles were also found around Kodiak Island, which the model did not show, probably because individuals spawned outside Shelikof Strait were excluded. The survey did not cover the Bering Sea, however, the model showed juveniles transiting to this region (see Parada et al., This issue). The centroids of the modeled distributions (excluding the fish that transited to the Bering Sea) and the survey distributions were both located in the area to the inside of the Shumagin Islands, near to the Alaska Peninsula.

Figure 7 shows directional ellipses of one standard deviation from the mean locations and are plotted to indicate the directional trend of the data. The figure indicates that the directional trend of the survey and the model results were similar, both were oriented in the northeast/southwest directions. This is the main direction of currents in this area, although current strength in the region between Sutwik Island and the Shumagin Islands is not strong and can be somewhat variable in direction. The larger size of the model ellipses in May represents the fact that the survey area was much smaller than the modeled area. The relative size of the ellipses in June/July for model and data were similar. The survey data ellipse was larger in August/September because, although the regions compared were the same (ie. model and data were only compared within the survey area boundaries), the survey found juvenile pollock around Kodiak that were not present in the model output for reasons we will consider in the Discussion.

### 3.1.2 Hot/Coldspot Analysis

The Getis-Ord  $G_i^*$  statistic showed distinct hot and coldspots within the May survey distributions, indicating that the distribution was quite heterogeneous even within this small survey region (Fig. 8). Locations with high densities (hotspots) were located in

the northern part of the survey area, whereas locations with lower densities (coldspots) were more often found in the southern part of the distribution. The modeled distribution for May, on the other hand, showed no distinct hot or coldspots, with the exception of some weak hotspots just to the east of the Shumagin Islands, which was, of course, outside the May survey area. There were also no evident hot or coldspots in the modeled distribution when it was examined within the survey area

The June/July survey distribution showed distinct clusters of hotspots (Fig. 9), mostly located between Sutwik I. and the Shumagin Islands, near the coast of the Alaska Peninsula. The modeled distribution for this time period showed a few weak hotspots in this region, however several hotspots were also seen to the west of the Shumagins. Notable in the June/July modeled distribution was a large cluster of particles with low superindividual counts (coldspot) nearshore of the Shumagin Islands (seen in blue on Fig. 9). The data showed high catches in this region. An analysis of the particles found in this model coldspot showed that 58% were spawned in April, with the rest spawned in May. Also, 66% were spawned in the Shelikof Exit region, rather than North Shelikof Strait.

This analysis for the August/September time period shows more agreement between the model and the survey results. The August/September survey distribution showed hotspots in several regions: near the coast just to the west of Sutwik Island, and to the west of the Shumagin Islands (Fig. 10). The modeled distribution for this time period also showed several hotspots to the west and offshore of the Shumagin Islands, as well as the intense coldspot in the same location (nearshore of the Shumagin Islands) as in the June/July model output. Of the particles/individuals found in the coldspot area in August/September, 66% were spawned in May, and 63% came from the Shelikof exit region.

### 3.1.3 Normalized Difference Index

The cost function  $NDI_i$  field (Figure 11) was calculated for each bin size (columns in the figure) for the modeled and data fields for the three time periods (rows in the figure). Model and data were compared within the survey area for each time period. The overall NDI for the May time period showed minimum differences (132.4) at a bin

size of  $3/4^\circ$  and a maximum NDI at a bin size of  $1/4^\circ$  (3245.5). The  $NDI_i$  fields showed positive differences (observed values greater than the model) in several cells near Sutwik and the Semidi Islands (Fig. 1). At the  $1/4^\circ$  bin size during May, differences were seen in several cells on the northeast border of the survey area. Little difference between model and observations were seen for May at the  $3/4^\circ$  bin size. The overall NDI for the June/July time period again showed a maximum value at a bin size of  $1/4^\circ$  (7903.8), and a minimum NDI at a bin size of  $3/4^\circ$  (835.1). During this time period, positive differences in  $NDI_i$  (observed values greater than the model) were seen using the  $1/4^\circ$  and  $1/2^\circ$  bins at several scattered locations between Kodiak Island and the Shumagins, however the  $NDI_i$  fields were spatially quite uniform at the  $3/4^\circ$  bin sizes with only minor positive differences between model and data.

During the August/September time period, the overall NDI showed a large maximum (8843.0) at the  $1/4^\circ$  bin size, and a minimum at the  $3/4^\circ$  bin size (1620.5). At the smallest bin size, positive  $NDI_i$  values were seen in a cell near Sutwik Island, with several more just to the west of the Shumagin Islands. A positive  $NDI_i$  was seen near Sutwik also in the  $1/2^\circ$  bin at this time period, and also in several cells to the northeast of Kodiak Island and to the west of the Shumagins. At the  $3/4^\circ$  bin size during this period, differences were seen just offshore of the Shumagin Islands, and to the northeast of Kodiak Island, however there were more cells with no difference between model and data. Overall, the differences between model and data were always positive, ie. the observed values were greater than the model. The differences between model and data were smallest at the largest bin size. During the June/July period, large areas showed no differences between the model and data.

#### 3.1.4 Overlap coefficient:

The OC estimates the spatial overlap between simulated and data distributions, with higher values indicating more overlap. In May, the overall OC was the smallest at the smallest bin size, and largest at the largest bin size. At all three bin sizes, the  $OC_i$ s in May were highest near Sutwik Island. The local OC in May was highest at a bin size of  $1/4^\circ$  with values of 0.4 to 0.8, while the local OCs at bin sizes of  $1/2^\circ$  and  $3/4^\circ$  were on the order of 0.3 and 0.1 respectively (Fig.12). During the June/July time period, the

overall OC showed the highest value (0.2) seen at the  $1/4^\circ$  bin size, and the lowest OC (0.07) at the  $1/2^\circ$  bin size. Bins with higher local  $OC_i$  during June/July were seen around and to the east of the Shumagin Islands at all three bin sizes. During the August/September time period, the overall OC was the same (0.2) at the smallest and largest bin sizes, with smaller OC seen using the  $1/2^\circ$  bin size (0.1). At all three bin sizes, the highest local  $OC_i$  values were seen around the Shumagin Islands and somewhat to the west. In general the highest overlap between the model and data occurred during the June/July survey.

### 3.1.5 Syrjala Tests

Both of the Syrjala test statistics for the May distributions showed no significant difference between the modeled and survey distributions at  $p = 0.05$  (Table 4). The power of this test was relatively low, as only there were only 13 cells in common between the model and the survey (as the survey area represented a very small portion of the total area occupied by the modeled distribution). The Syrjala test statistics on the June/July distributions were different at the  $p = 0.05$  level. Neither test showed the August/September model and survey distributions to be significantly different.

### 3.1.6 Geostatistical Simulation of Spatial Indices

For both surveys (June/July and August/September), pollock density was highly skewed. A high (37.5%) proportion of zeros was observed in the 1987 June/July survey. In contrast, there were no zeros observed in the 1987 August/September survey, but there were low values in the data. To apply the simulation method to estimate confidence intervals (Woillez, et al. 2009b) for both surveys, values below a density of 17 per 10 min sample were considered zero values. The thresholded zero values represented 18.9% of the 1987 August/September survey data.

The first step when calculating confidence intervals around the survey data was the normal-score transformation of fish densities. As shown in Figure 13 a,b, this transformation was 0 below the threshold value of 17 per 10 min sample, and linearly interpolated above that threshold. As the Gaussian variable to be simulated was not known at all locations, the variogram model of the Gaussian variable was indirectly fit

using the variogram of the normal-scored variable (Woillez, 2007). The variogram model of the Gaussian variable was a nested structure with a nugget of 0.25, a Gaussian component of 0.45 with a range of 150 kilometers, and a spherical component of 0.80 with a range of 600 kilometers for the 1987 June/July survey (Fig. 13c). A nested structure with a nugget of 0.4, a spherical component of 0.6 with a range of 175 kilometers was the variogram model used for the 1987 August/September survey (Fig. 13d).

Gibbs sampling was used to simulate Gaussian values at locations corresponding to zeros. Then, a classical conditional simulation (i.e. a geostatistical simulation incorporating known data values) was performed to generate multiple realizations of the Gaussian variable, which were transformed to pollock densities values (Fig. 14). A total of 250 realizations of pollock spatial distributions were simulated over a 10 km x 10 km grid for the 1987 June/July (Fig. 14 a,b,c) and August/September (Fig. 14 d,e,f) survey areas. Highest pollock average densities were concentrated between the Semidi and Shumagin Island groups during June and July, as indicated by the center of gravity and inertia axes, shifting and extending southwest from the Shumagin Islands to Unalaska Island in the later survey.

Spatial distribution index values and 95% confidence intervals for survey data and IBM outputs are summarized in Table 5. For the June/July survey, all spatial indices computed from the survey data are contained within the confidence intervals generated by geostatistical conditional simulations from the survey data. The occurrence of index values calculated from model output occurring within confidence intervals depended on area and month. For the August/September survey, all spatial indices except inertia were contained within the confidence intervals. Inertia from 97.5% of the IBM simulated fields was higher than inertia index values computed from the survey data, and therefore this index wasn't used for the comparison between the survey data and the individual based model.

For both survey periods, the latitude of the center of gravity (i.e.  $y_{cg}$ ) was the model index most often included within the confidence intervals (Table 5) from the survey data, occurring within the confidence intervals for the June/July survey when particles were released in April area 11 (Shelikof Strait Exit region), and 8 (Shelikof



Strait North) and 11 combined. For particles released in May or when April and May releases were combined, the latitudinal component of the center of gravity occurred within confidence intervals in both release areas. For the August/September survey, the latitude component of the center of gravity occurred inside the confidence intervals regardless of where particles were released in April, and in area 8 for both release months (Table 5). The longitude of the center of gravity only occurred inside the confidence interval in the June/July survey when particles were released in April, and in area 8 for both release months (Table 5). The isotropy metric was contained within the confidence intervals when particles were released in April in area 8 for the period June/July, and in April in area 11 and 8 & 11 for the period August/September (Table 5). Inertia was included only in the August/September confidence interval when particles were released in May and area 11, however this case is not meaningful as the inertia from the survey data was not contained in the confidence interval. Finally, none of the occupation area indices were included in the confidence intervals. The IBM produced spatial distributions which always occupied smaller areas than those from the surveys.

To conclude this comparison, two (center of gravity and isotropy) of six spatial indices (inertia excluded) are included within survey data confidence intervals for each period independently or jointly. Particles from the IBM released in April in the Shelikof Strait exit region (Area 11) or when combined with the North Shelikof region (Area 8) produced spatial distributions that best matched spatial distributions from the two surveys. For the June/July survey data, the longitude and the latitude of the center of gravity were reproduced by the IBM output-derived indices. The latitude of the center of gravity and the isotropy indices from the IBM output data matched those in the August/September survey data.

#### 4.1 Discussion

We used several methods to visualize the difference between the model output and the survey data (methods summarized in Table 6, results summarized in Table 7). All of the methods applied in this study were useful in different ways. The plotting of centroids and their variance and isotropy enables visualization of similarities and differences in overall observed and predicted spatial distributions. The Getis-Ord  $G_i^*$  statistic provides an

index of spatial patchiness. The NDI and OC identified differences and overlaps between the model output and the survey data, both globally and locally, and the NDI had the added advantage of indicating whether model values were higher than the data or the opposite, as well as where the differences were located. The Syrjala statistics provide a statistical comparison of the two distributions, and were easy to apply, however they are not informative about the details of the distributions that cause agreement or differences. Despite its complexity of implementation, the geostatistical spatial indices comparison has the added advantage of identifying specific characteristics of survey spatial distributions that are reproduced by the IBM model. If the objective is to use IBMs to reproduce observed spatial distributions, then the extent of match or mismatch in geostatistical spatial indices can be used to identify properties of the IBM for refinement.

Visual inspection of the distributions, the centroids and their variance and directional ellipses, showed that the modeled distribution was consistent with the geostatistical comparison of spatial indices. These measures showed reasonable good fit between model and data. Centroid analysis has been used to compare spatial distributions (Alvares et al., 2000, Castaño-Primo et al., 2014, Ernst et al., 2005; Vikebø et al. 2005), even though one of the drawbacks of this approach is that it is a global statistic that does not tell you about local aggregations. This type of visual comparison can be a good first step in a model validation exercise. Although global indicators of spatial association indicate whether mapped data exhibits an organized pattern, care must be taken in interpreting the results. A global trend of spatial autocorrelation may mask the magnitude and direction of spatial heterogeneity.

The Getis-Ord  $G_i^*$  statistic, or hot/coldspot analysis (Getis and Ord, 1992, Ord and Getis, 1995) quantifies patchiness of the distributions. This statistic gives the sum of attribute values in a given region and the surrounding regions within a distance band relative to the sum of all values of the considered variable. Significant deviations of the Getis-Ord  $G_i^*$  values from the expected value indicate local clustering. If the deviation is significantly positive, the spatial cluster is called a hotspot (Kosfeld and Lauridsen, 2012). Care must be taken in deciding upon the size of the neighborhood (the distance band), as patterns may change with different size bands. The results of this analysis were

not consistent between model and data, probably due to the heterogeneity of currents in this area.

The Normalized Difference Index (NDI) and the Overlap Coefficient (OC) methodologies seem to be complementary, providing information in terms of the overlap between model and data, and the level of discrepancies between quantities assessed. However, the NDI and the OC analyses require binning survey data and the model information at a common resolution. The challenge is to determine an appropriate resolution that represents the information obtained from the model and the survey data. This is the “binning problem” that arises when comparing spatial model output and empirical data. In geography, this challenge is related to the modifiable areal unit problem (MAUP) arising from the imposition of artificial units of spatial reporting on continuous geographical phenomena, which may generate artificial spatial patterns (Heywood, 1988). When using these indices on output derived from a Lagrangian model, it is also important to consider that at the smallest bin size there will be a lower level of co-occurrence between survey stations and the occurrence of modelled particles. A balance must be found between resolution and the number of occupied cells. The binning problem and the selection of a given bin size may affect the outcomes of the analysis. Sensitivity analyses may be needed in order to make this choice. In the case of the model output, the hydrodynamics model resolution will be indicative of the lowest limit of the bin size, while the upper level is definition is less clear. These two indices showed local areas of differences which did vary with bin size. The smallest differences and highest overlap were seen during the June/July time period.

Syrjala’s statistics were used to analyze the spatial difference between predicted and observed distributions of young pollock. Results from the Syrjala tests showed agreement between the modeled and survey distributions for two of the three time periods. The KS statistic used in the Syrjala tests measures the greatest difference between the two cumulative distributions. It is therefore sensitive to small numbers of extreme values in the distributions (Syrjala, 1996). Extreme values can be a difficulty, although this did not appear to be an issue with our datasets, as the results for both statistics were the same. As noted by Syrjala, fish may be patchily distributed (due to concentration by currents, behavior, etc), yet fundamentally similar in overall

distribution. The Syrjala tests (Syrjala, 1996) provided a statistical means to test the difference between the modeled versus survey distributions, that is very easy to implement, as it has been coded into the R language (in the Ecespa package). However, this test is a global analysis while the Getis-Ord  $G_i^*$  analysis provide information in terms of local clustering.

Geostatistical simulation was used to derive confidence intervals for all spatial indices calculated using the survey data. Accuracy of the confidence intervals depends on the appropriate implementation of the geostatistical simulation used to evaluate survey uncertainty. Different approaches exist for validating geostatistical simulations. Each of these approaches is appropriate for a different component of the simulation: the stochastic model, the spatial domain, and the simulation algorithm. For instance, a cross-validation exercise can be performed to check the accuracy of the simulation against a set of empirical data (Deutsch, 1997) to evaluate the simulation algorithm and the stochastic model. Statistical tests also exist for validating the simulation algorithm (Emery, 2008). These methods check whether the mean value, the dispersion variance, or the variogram are reproduced, and indicate whether observed fluctuations in output values are consistent with the random field model and with the size of the domain where simulation is performed. In our simulation, the mean value was tested, the variogram was visually checked, and the multivariate distributions (i.e. the two first moments) of the simulated random field were compared to those of the model.

The comparison of spatial indices showed that the center of gravity (centroid) and to a lesser extent, isotropy (for specific release dates and areas), were the indices that were the most similar for the IBM and the survey data. Inertia, isotropy and measures of spatial coverage might not be expected to compare well in a region such as the GOA. The currents in this region are complex, and the hydrodynamic model cannot replicate this complexity to a high degree of accuracy, even though aggregate statistical comparisons of the modeled and observed currents do well. Since the larvae follow the currents for much of their early life, and these currents differ in detail from the real world, details of the distributions of particles would not be expected to do as well as aggregate measures such as centroids.

The purpose of the IBM was to generate realistic distributions and survival of young pollock over time. Spatial distributions produced from the two survey data sets analyzed in the geostatistical part of our study were treated as spatial point processes, where density or number weights were attributed to each point (i.e. the concept of superindividuals). Therefore, the predicted spatial distributions can only be considered as approximations of the true underlying spatial distribution. A potential modification to improve matches between survey data and model predictions would be to propagate the uncertainty of model-predicted spatial distributions to the IBM-based spatial indices. Then, the comparison of spatial distributions between IBM and survey could be based on the overlap between survey and model spatial index confidence intervals. Such uncertainty in model-based spatial distributions may be one reason why occupation area indices of the survey-model comparison performed poorly.

Differences in spatial distributions between IBM model output and data from surveys may be attributed to several factors. There may be differences between survey and model initial conditions (ie. the location and timing of spawning by fish caught in the survey compared to the initial distribution of particle releases in the model simulation). We addressed this possibility as best we could by examining only individuals released at times and locations of most of the known spawning for 1987 (Kendall et al. 1996). There may have been fish caught in the surveys that were spawned in other locations at other times, however only small amounts of spawning have been observed in other locations (Wilson, 2000). For example, it is thought that juvenile pollock found around Kodiak Island probably originated from spawning in areas around Kodiak other than Shelikof Strait (Bailey et al., 1999, Wilson, 2000). Since we only examined model output from individuals released in Shelikof Strait, these Kodiak fish would have been excluded. This issue may have influenced the mismatch of area-occupied indices between empirical and modeled data.

Differences between survey and model estimates may also be a result of using locally random initial conditions for this model simulation in spite of choosing individuals from specific areas and times. Individuals were released randomly within the North Shelikof and Shelikof Exit zones once per month. Pollock spawning occurs continuously in very dense aggregations in Shelikof Strait; spawning is highly localized

both in time and space, and is concentrated near line 8 (Fig. 1) in the first two weeks of April (Kendall, et al. 1996).

Differences between model output and survey data could also be related to the limitations of the hydrodynamic model. The ROMs output used in these simulation had a relatively coarse resolution in the coastal regions of 10 km compared with more recent configurations of ROMS, such as the 3 km resolution model now in use (Dobbins et al. 2009, Coyle et al. 2012). Physical processes with a higher spatial resolution are not resolved by simulations with the 10 km model. Also, bottom topography is smoothed significantly in some regions in the 10 km model. This has implications for flow patterns. Divergence between the real and the modeled flow fields is a common problem for all numerical ocean models due to small and mesoscale factors such as eddies, meanders, and the chaotic behavior of the real fields, which the models cannot replicate. This can be adjusted for if enough data exist which can be assimilated to correct the flow fields. This was not possible in our case due to the paucity of available data.

Another model condition that may result in different empirical and model-predicted juvenile fish distributions are the movement algorithms and the resulting interactions with the flow field (Hinckley et al. 1996, Werner et al. 1996, 2001, Hinrichsen et al. 2002, Fox et al. 2006, Staaterman and Paris, 2014). The vertical and horizontal movements of fish are affected by their life stage (Clark et al. 2005), and thus by their size, which in turn is affected by several factors from temperature to consumption rates. Inevitably, it is not possible, nor is it the goal, to replicate these patterns exactly in the models. The horizontal movement submodel incorporated for older juvenile pollock in this IBM is based on a correlated random walk (CRW). Since most animals have a tendency to move in a forward direction, CRWs have been used to model animal paths (Siniff and Jessen 1969, Skellam 1973, Kareiva and Shigesada 1983, Bovet and Benhamou 1988, Turchin 1998, Willis, 2011). As a caution, Codling et al. (2008) describe how CRWs can produce a local directional bias in which each step tends to point in the same direction as the previous one, although the influence of the initial direction of motion progressively diminishes over time, and step orientations are uniformly distributed in the long term (Benhamou 2006). The algorithm implemented in this model seemed to produce distributions of older juveniles which agreed with data

relatively well, in terms of several measures used (Table 7). However, distributions of juveniles which are more active later in the year may require refinements in the swimming algorithm, ie. consideration of factors such as more realistic modeling of directionality of swimming, such as movement towards food (Huebert and Sponaugle, 2009, see Staaterman and Paris, 2014 for a review).

The model presents some interesting results concerning the early life history of pollock in this region. For example, the concentration of modeled particles near the coast of the Alaska Peninsula, inshore of the Shumagin Islands, as shown by the Getis-Ord  $G_i^*$  statistic indicates that this may be a collection area for fish/particles. This result corresponds to observations that high densities of juveniles are found in this region (Hinckley et al. 1991, Brodeur et al., 1995, Wilson et al. 1996, our data). Also, the percentages of modeled particles found which had low superindividual numbers in June/July that were spawned in April indicates that the individuals had been in the water longer than those spawned in May and had therefore been exposed to higher mortality than those found elsewhere. This pattern was reversed in the August/September period, with more particles in this region having been released in May rather than April. This may reflect the addition of particles with time to this area. The majority of particles in the coldspot area were released in the Shelikof Strait Exit region rather than the more distant North Shelikof Strait, thus the trajectories of these individuals to the coldspot region were either less direct, or the individuals had remained in the coldspot area longer. The fact that this coldspot was present in both the June/July and the August/September time period indicates that the latter is more likely. The model indicates that this region near the Shumagin Islands concentrates juvenile fish and may function as a productive nursery area.

The walleye pollock model correctly predicted that the Shumagin Island area, especially the nearshore areas, is an important nursery area, and also that the origin of many of the Shumagin Island juveniles is most likely to have been eggs spawned in Shelikof Strait in April. This is consistent with the idea of the Shelikof-Shumagin spawning-nursery area pair (Hinckley et al., 1991). There is also evidence that the area near Sutwik Island may play a role as potential nursery areas (Mazur et al., 2007), which is consistent with the model predictions.

In conclusion, we recommend a multistep process for the validation of spatial output of biophysical IBMs, starting with visual comparisons and simple descriptive statistics, then calculation of indices showing features of interest, and finally, using hypothesis testing statistical and geostatistical approaches that can give measures of statistical significance to the differences/similarity between spatial model output and data. Model validation and model improvement is an iterative process where mismatches between model and data can be used to improve the model and the surveys (if they can be specifically designed to compare with model output). However, for some purposes such as management applications, “success” in validation must be defined. Some methods, such as visual inspections, the NDI and the OC require the user to define “success” in matching model and data, as this can be dependent on bin size. A new convention is needed to delineate success thresholds, perhaps from sensitivity analyses, for the validation process of biophysical IBMs.

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Table 1. Parameters and feeding model for juvenile walleye pollock.

Parameters and units	Symbol	Functions/Values	References.
Prey types	$k$	$k=1$ , euphausiids $k=2$ , large copepods $k=3$ , small copepods	
Density of prey $k$ (num $m^{-3}$ )	$N_k$		Hinckley, 1999
Offshelf area		Prey set to 0	
Inner shelf areas		1.17838 ( $k=1$ ) 66.6632 ( $k=2$ ) 486.277 ( $k=3$ )	
Mid and outer shelf $jd^{**} < 120$ )		0.29459 ( $k=1$ ) 16.6659 ( $k=2$ ) 121.569 ( $k=3$ )	
$120 \leq jd^{**} < 160$		Linear increase to inner shelf values	
Pollock size class (mm)	$j$	$j=1:3$	
Probability of preference for prey $k$ size $j$	$P_{kj}$	0.0000 ( $k=1, j=1^*$ ) 0.1429 ( $k=1, j=2^*$ ) 0.8571 ( $k=1, j=3^*$ ) 0.1270 ( $k=2, j=1^*$ ) 0.2381 ( $k=2, j=2^*$ ) 0.6349 ( $k=2, j=3^*$ ) 0.6481 ( $k=3, j=1^*$ ) 0.3242 ( $k=3, j=2^*$ ) 0.0278 ( $k=3, j=3^*$ )	Wilson et al. (2006)
Pollock mean swim speed ( $ms^{-1}$ )	$\bar{x}$	0.15	Sogard and Olla (2000)
Prey $k$ swim speed ( $ms^{-1}$ )	$v_k$	0.0285 ( $k=1$ ) 0.0100 ( $k=2$ ) 0.0020 ( $k=3$ )	De Robertis et al. (2003)
Conversion factor to hours	$A$	1/60	
Handling time (seconds prey $^{-1}$ )	$t_h$	0.33	Stockwell and Johnson (1997)
Reactive distance (m)	$d_c$	0.1	Link and Edsall (1996)

Mean weight of prey $k$ (g)	$\bar{W}_k$	0.0402 ( $k=1$ ) 5.674x10 <sup>-4</sup> ( $k=2$ ) 1.122x10 <sup>-4</sup> ( $k=3$ )	Winter et al. (2005), Dumont et al. (1975) Dumont et al. (1975)
Stomach capacity Initialization	$St_h$	0.2Cmax***	Mazur, M. Pers. Comm.
Number of prey $k$ eaten in $h$ hours	$E_{k,h}$	$E_{k,h} = \sum_j \left( \frac{S_k N_k P_{jk}}{1 + S_k t_h a} \right)$	Gerritsen and Strickler (1977), Stockwell and Johnson (1997)
Search volume of pollock searching for prey $k$	$S_k$	$S_k = \pi d^2 \sqrt{\bar{x}^2 + v_k^2}$	Evans (1989)
Total biomass eaten by hour	$G_h$	$G_h = \sum_k E_{k,h} \bar{W}_k$	Eggers (1977)
Digestion per hour	$D_h$	$D_h = St_h + G_h - St_h e^{d_c} + \frac{G_h}{d_c} (1 - e^{d_c})$	Elliott and Persson (1978), Bevelhimer and Adams (1993)

\*Corresponds to juvenile pollock size classes where  $j=1$ : 25mm <= length < 40,  $j=2$ : 40mm <= length < 120mm and  $j=3$ : length >= 120mm.

\*\*jd=Julian days

\*\*\*Cmax= maximum consumption based on Hinckley et al., (2002)

W=weight (g), T=temperature (°C)



Table 2. Parameters in the bioenergetics model for juvenile walleye pollock.

<b>Parameter description and units</b>	<b>Symbol</b>	<b>Values</b>	<b>Reference</b>
<b>Consumption (<math>\text{gg}^{-1} \text{day}^{-1}</math>)</b>	<i>C</i>		
Proportion of maximum consumption	<i>P</i>	0-2	1
Intercept of the allometric function	<i>Ac</i>	0.38	1
Slope of the allometric function	<i>Bc</i>	0.68	1
Temperature dependence coefficient	<i>Qc</i>	2.6	1
Optimum temperature for consumption ( $^{\circ}\text{C}$ )	<i>Tco</i>	10	1
Maximum temperature for consumption ( $^{\circ}\text{C}$ )	<i>Tcm</i>	15	1
<b>Respiration (<math>\text{gg}^{-1} \text{O}_2 \text{day}^{-1}</math>)</b>	<i>R</i>		
Intercept of the allometric function	<i>Ar</i>	0.0075	1
Slope of the allometric function	<i>Br</i>	0.251	1
Temperature dependence coefficient	<i>Qr</i>	2.6	1
Optimum temperature for respiration ( $^{\circ}\text{C}$ )	<i>Tro</i>	13	1
Maximum temperature for respiration ( $^{\circ}\text{C}$ )	<i>Trm</i>	18	1
Proportion of assimilated energy lost for Specific Dynamic Action	<i>Ds</i>	0.125	1
Multiplier for active metabolism	<i>Am</i>	1	1
Respiration in Joules	<i>Rj</i>		
Conversion from g of oxygen to joules	<i>convj</i>	13560	2
<b>Egestion</b>	<i>F</i>		
Proportion consumed energy	<i>Fa</i>	0.15	1
<b>Excretion</b>	<i>U</i>		
Proportion of assimilated energy	<i>Ua</i>	0.11	1

(1) Ciannelli et al. (1998), (2) Elliott and Davison (1975)

Table 3. Daily mortality rates for egg, larvae and juveniles of walleye pollock used for IBM experiments.

Year	Eggs*	Feeding larvae*	Juveniles**
1987	0.226	0.064	0.00005
1988	0.300	0.036	-
1989	0.170	0.157	-
1990	0.150	0.073	0.01400
1991	0.220	0.126	-
1992	0.184	0.049	-
1993	-	0.038	0.00607
1994	-	0.057	-
1996	-	0.037	0.01076
1999	-	-	0.00157
2001	-	-	0.00353
Other	0.205***	0.0200***	0.00509

\*For egg and larval daily mortality rates for pollock and methods of calculations, see Bailey et al. 1996.

\*\* Juvenile daily mortality was inferred from stomach contents from groundfish consumption and normalized to a maximum mortality, for missing values we used an average of the available data.

\*\*\* Average values for missing years (Bailey, pers. comm.)

Table 4. Results of the Syrjala tests on the three sets of model vs. survey information, based on 1000 permutations. Test uses normalized densities.

	May survey vs. model	June/July survey vs. model	August/September survey vs. model
Cramer-von Mises test			
Test statistic	0.591	1.232	1.399
P-value	0.417	0.023*	0.064
N	13	94	49
Kolmogorov-Smirnov test			
Test statistic	0.405	0.319	0.452
P-value	0.353	0.019*	0.058
N	13	94	49

\* Significant at  $p=0.05$  (Spatial distributions are different)

Table 6. Methods used in this study to compare modeled vs. survey distributions. Listed are attributes that are addressed, and considerations/constraints in using these methods.

<b>Method</b>	<b>Attribute Addressed</b>	<b>Constraints/Considerations</b>
Weighted Centroids	Center of gravity of a spatial distribution	Global measure. May be effected by sampling design (surveys) or initial conditions and modeling domain (IBM). Useful for initial visual comparison. May be effected by outliers.
Inertia	Variance of a spatial distribution	Global measure.
Directional Ellipses	Orientation of 1 standard deviation ellipse around center of gravity	Global measure. May be affected by directionality/heterogeneity of currents. Useful for visual comparison. May be effected by outliers.
Isotropy	Evenness of dispersion of a spatial distribution	May be affected by currents (and hydrodynamic model match/mismatch) and topography
Positive, Spreading and Equivalent Area	Area occupied by positive densities, proportional area occupied per unit area, area occupied if all cells had the same density	Affected by differences in measured vs. modeled currents. Affected by IBM initial conditions.
Getis-Ord $G_i^*$	Spatial clustering of georeferenced data, into clusters of high values (hotspots) and low values (coldspots)	Small scale features may be in different places in model output versus data because of hydrodynamics model mismatch. Results not reliable with too few values (<30). All features should have at least one neighbor. No feature should have all other features as neighbors. Chosen scale important. Spatial clustering may imply underlying spatial processes.
NDI	Normalized difference index	Strongly affected by bin size. Indicates where model values are greater than data and vs.
OC	Overlap coefficient	Strongly affected by bin size.
Syrjala	Nonparametric statistical tests of the null hypothesis that the spatial distribution of two populations is the same.	Global measure. May be affected by bin size. KS test is sensitive to small numbers of extreme values. Does not compare levels of abundance. Easy to implement.

<b>Method</b>	<b>Attribute Addressed</b>	<b>Constraints/Considerations</b>
Geostatistical Comparison of Spatial Indices	Allows tests of whether spatial indices from model/data are significantly different	Appropriate implementation and validation of simulation components important. If currents very heterogeneous, area occupied indices may not match. Initial conditions must be as accurate as possible.

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Table 7. Summary of results of methods used to compare IBM output and survey data.

<b>Method</b>	<b>Results</b>
Centroids	(May) Data: Centroid near of Sutwik I. Model: Centroid near Sutwik I. (June/July) Data: Centroid just east of Shumagins Is. Model: Centroids just east of Shumagin Is. (Aug/Sept) Data: Centroid shoreward of Shumagin Is. Model: Centroids shoreward of Shumagin Is. (Spatial Indices Test) June/July: 12 indices (of 18) within 95% CI Aug/Sept: (5 of 18) within 95% CI
Inertia	(May) Survey spread smaller than model due to reduced survey area (June/July) Spread similar (Aug/Sept) Survey spread larger than model spread due to exclusion of Kodiak area fish (Spatial Indices Test) June/July: 0 of 9 within 95% CI Aug/Sept: 1 of 9 within 95% CI
Directional Ellipses	All model and surveys oriented along Alaska Peninsula
Isotropy	(Spatial Indices Test) June/July: 1 of 9 within 95% CI Aug/Sept: 2 of 9 within 95% CI
Positive Area, Spreading Area, Equivalent Area	(Spatial Indices Test) June/July: 0 of 27 within 95% CI Aug/Sept: 0 of 27 within 95% CI
Getis-Ord Gi*	(May) Data: Hotspots present Model: Few hotspots present (June/July) Data: Hotspots between Sutwik-Shumagin Is., especially inshore of Shumagins Model: Coldspot inshore of Shumagins, hotspot just west of Shumagins (Aug/Sept) Data: Hotspots near Sutwik, inshore & west of Shumagins Model: Coldspot inshore of Shumagins, hotspots west of Shumagins
NDI	(May) Low coverage, some areas of difference (June/July) Low differences except in a few areas near Shumagins (Aug/Sept) Some differences near Shumagins (All time periods) Data values higher than model
OC	(May) Locally high areas of overlap (June/July) Higher overlap, esp. between Sutwik and Shumagins (Aug/Sept) Lowest overall overlap, high overlap near Shumagin Is.

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Syrjala	(May)	No significant difference between survey and model for both CvM and KS tests
	(June/July)	Significant differences for both tests at $p=0.05$
	(Aug/Sept)	No significant differences for both tests

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Figure 9. Distribution of Getis-Ord  $G_i^*$  statistics from the survey and the model output for June/July, 1987.

Figure 10. Distribution of Getis-Ord  $G_i^*$  statistics from the survey and the model output for August/September, 1987.

Figure 11. Normalized difference indices (NDI) for the three time periods (rows) and bin sizes (column). Small differences are indicated by hotter colors (lower numbers) and larger differences by cooler colors (higher numbers). Overall NDIs are shown in the lower right of each panel.

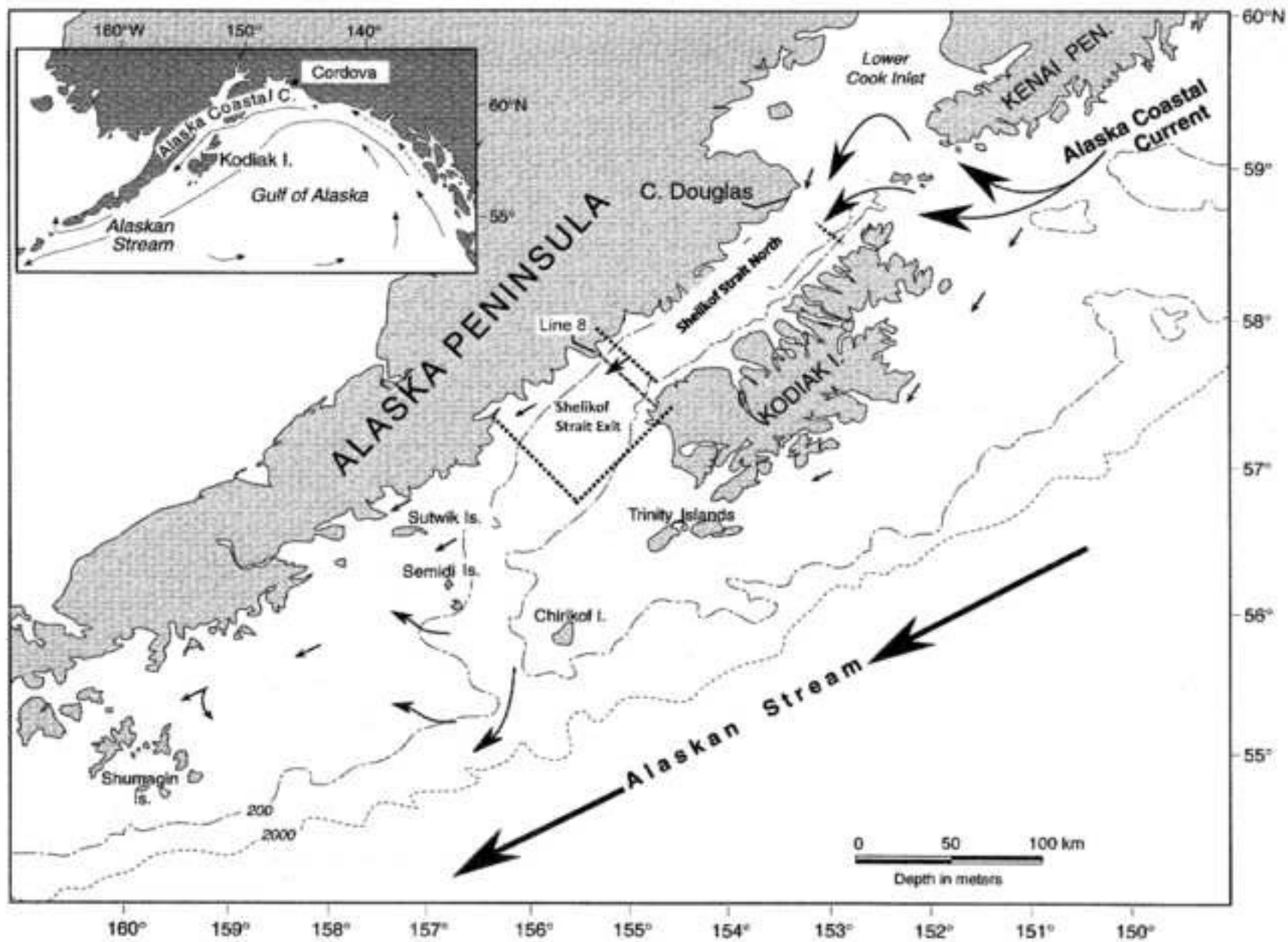
Figure 12. Overlap coefficient (OC) for three time periods (rows) and bin sizes (columns). Cooler colors (higher numbers) indicate higher overlap, while warmer colors (lower numbers) indicate lower overlap. Overall OCs (labeled C) are shown in the lower right corner of each panel.

Figure 13. (a) Linear interpolation model for the normal score transformation of the pollock densities sampled in June/July. (b) Idem for the August/ September survey. (c) The experimental variogram of the normal score variable for the June/July survey with circles proportional to number of data is shown in light grey. The model of the Gaussian variable and the corresponding expression for the normal score variable are represented, respectively, by a dashed and solid black line. The experimental variogram of the Gaussian variable with circles proportional to number of values, obtained after the Gibbs sampling, is represented in dark grey and is consistent with the Gaussian model. (d) Idem for the August/September survey.

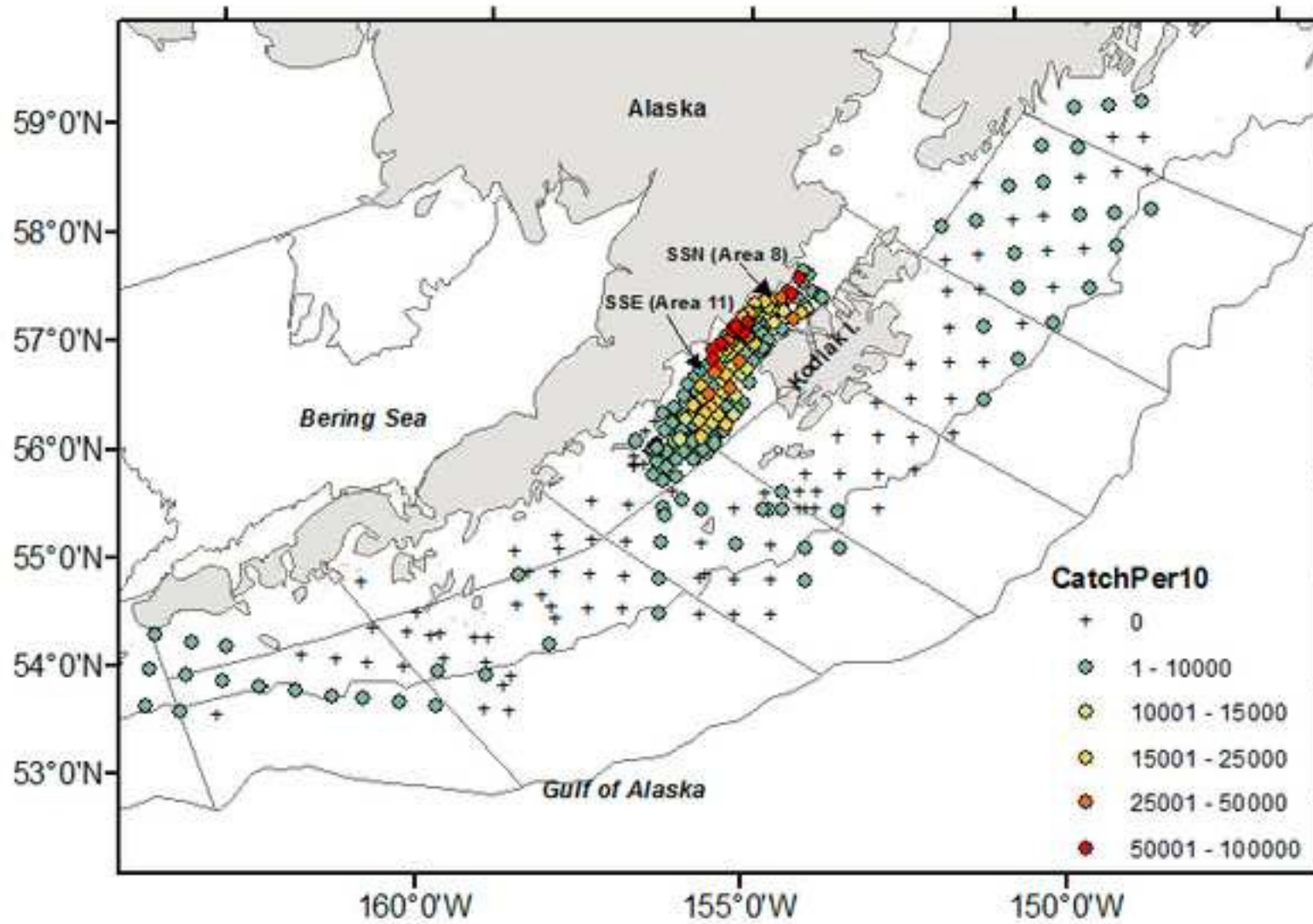
Figure 14. Top: three realizations (max., med., and min.) of spatial average density values, respectively a, b, and c) of the pollock densities in June/July. Bottom: three realizations (max., med. and min.) of spatial average density values, respectively d, e, and f) of young pollock densities in August/September. Only simulated values above zero have been colored. As examples of the computation of spatial indices from those simulated fields, the center of gravity and axes of inertia have been represented in white.

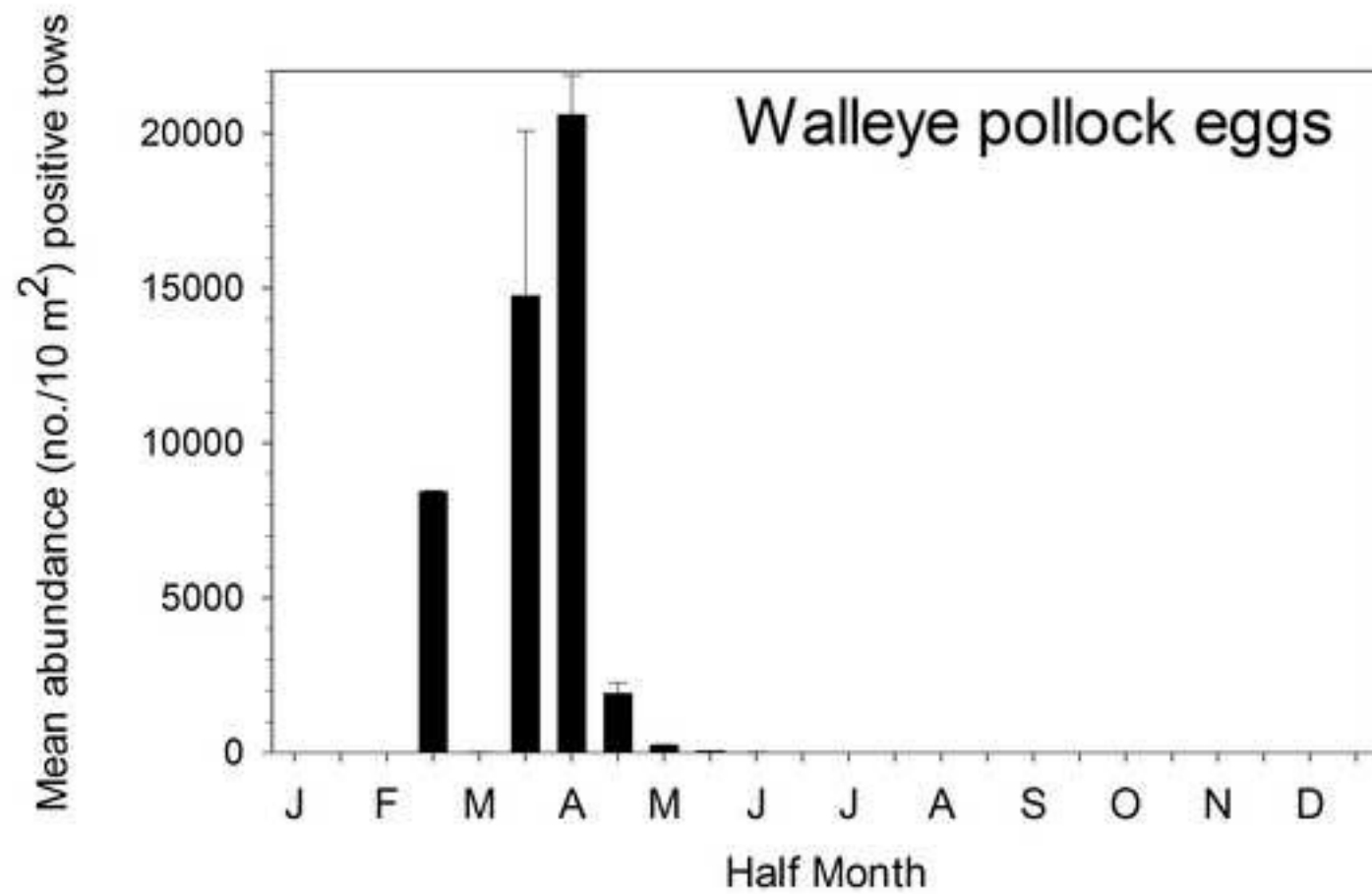


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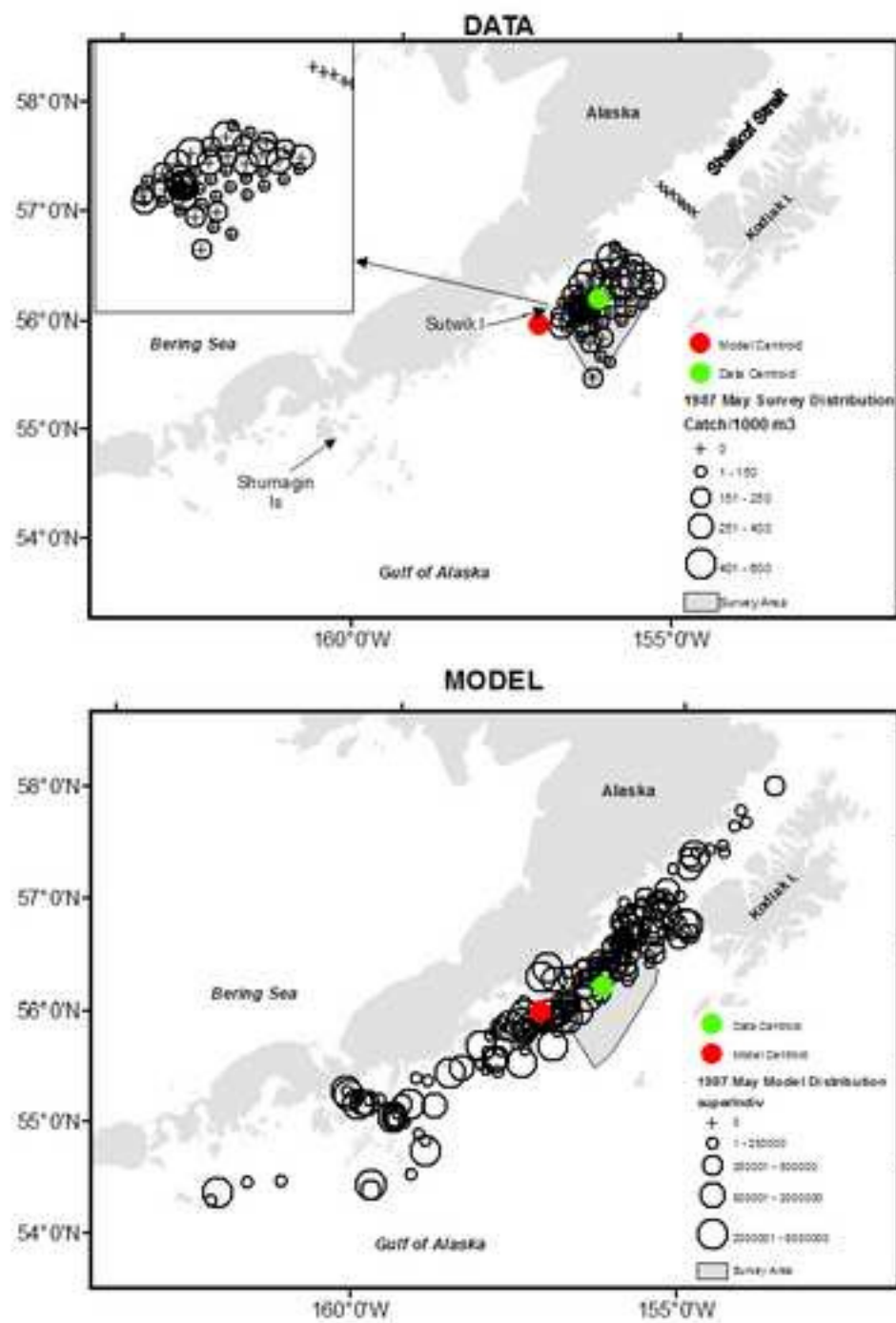


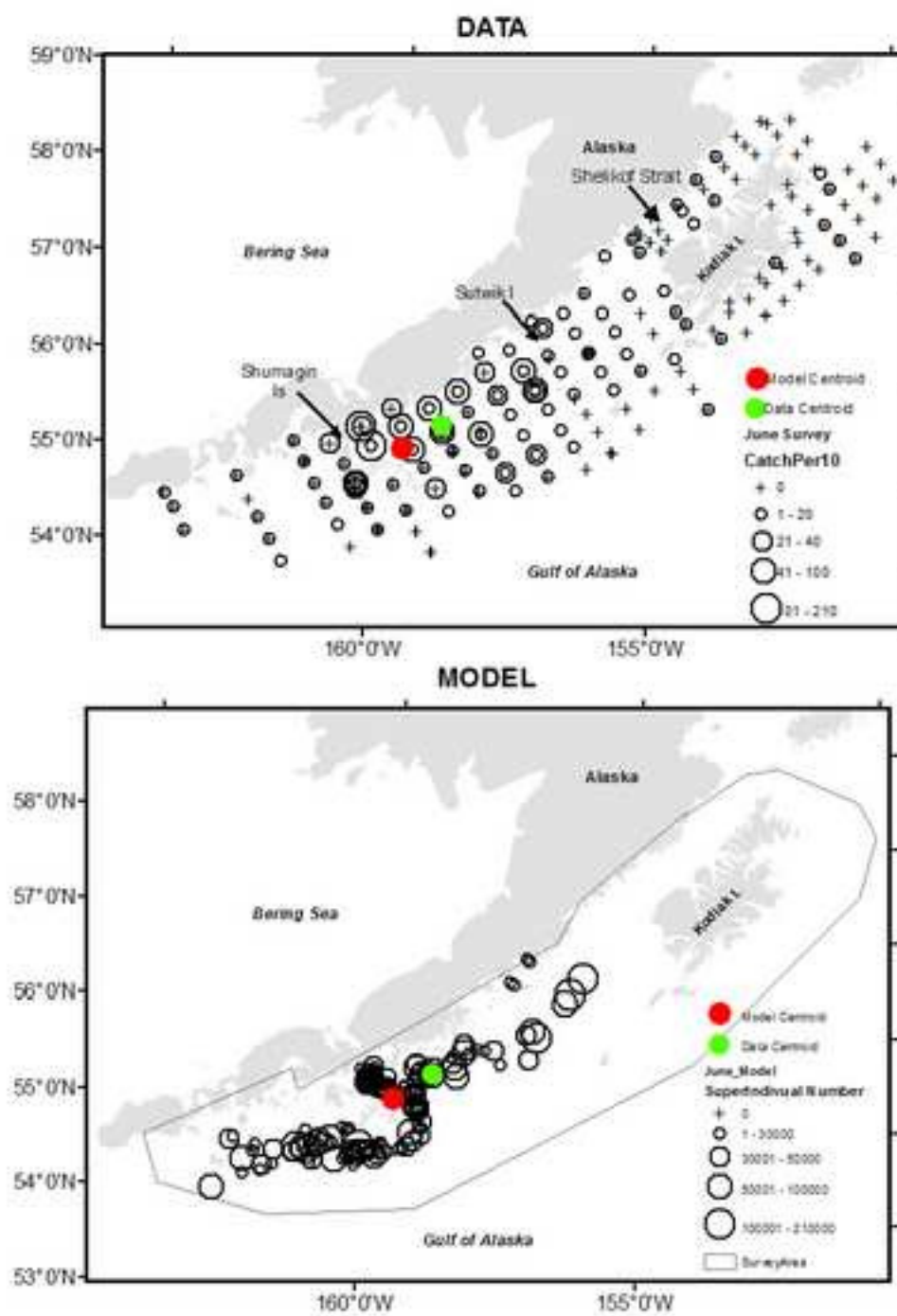
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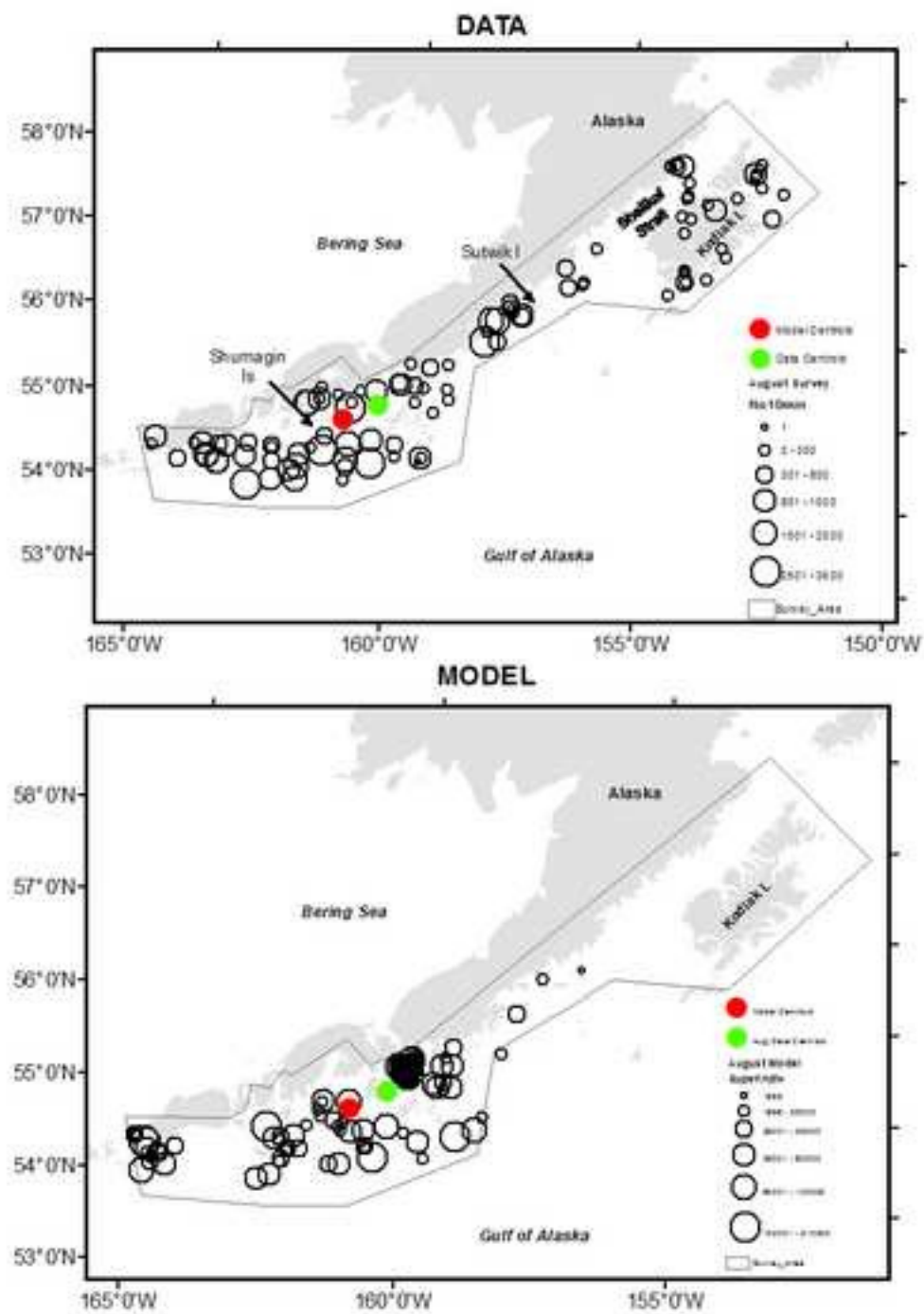


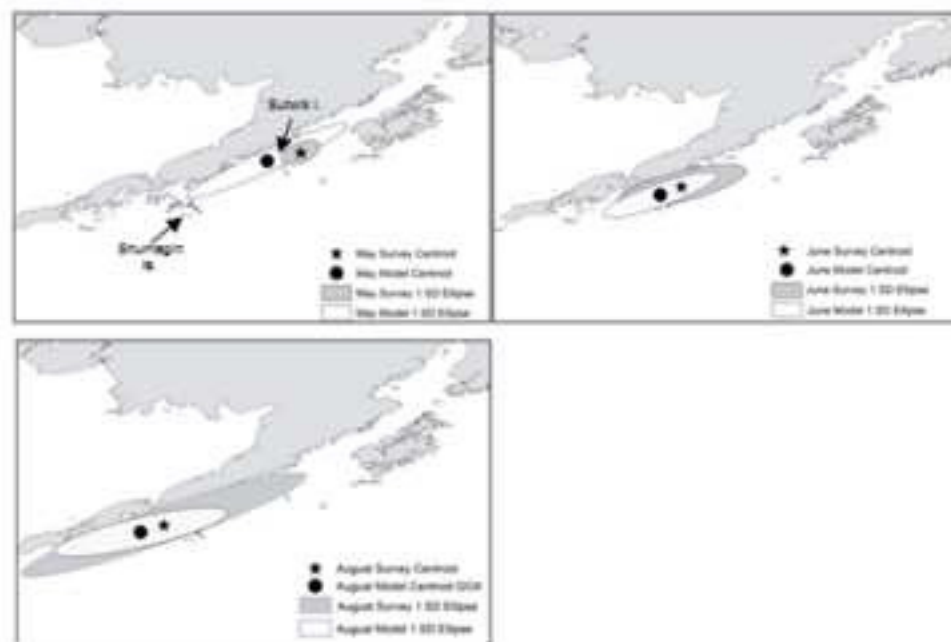


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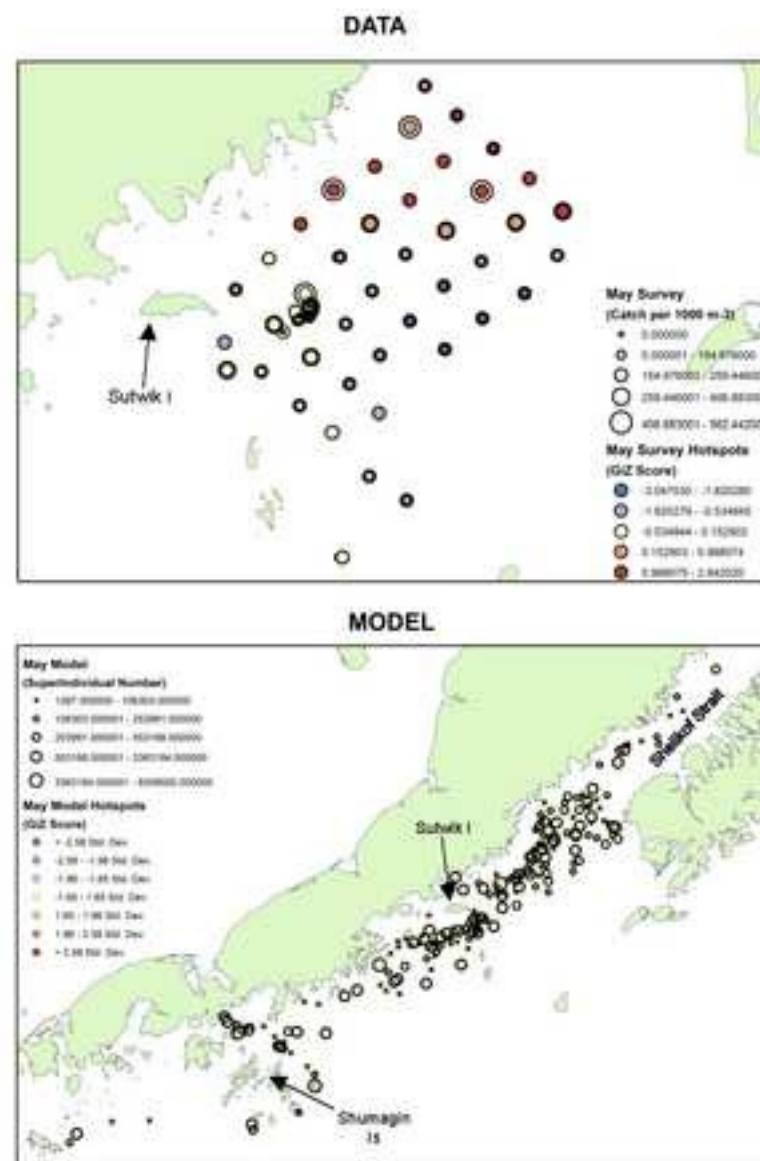




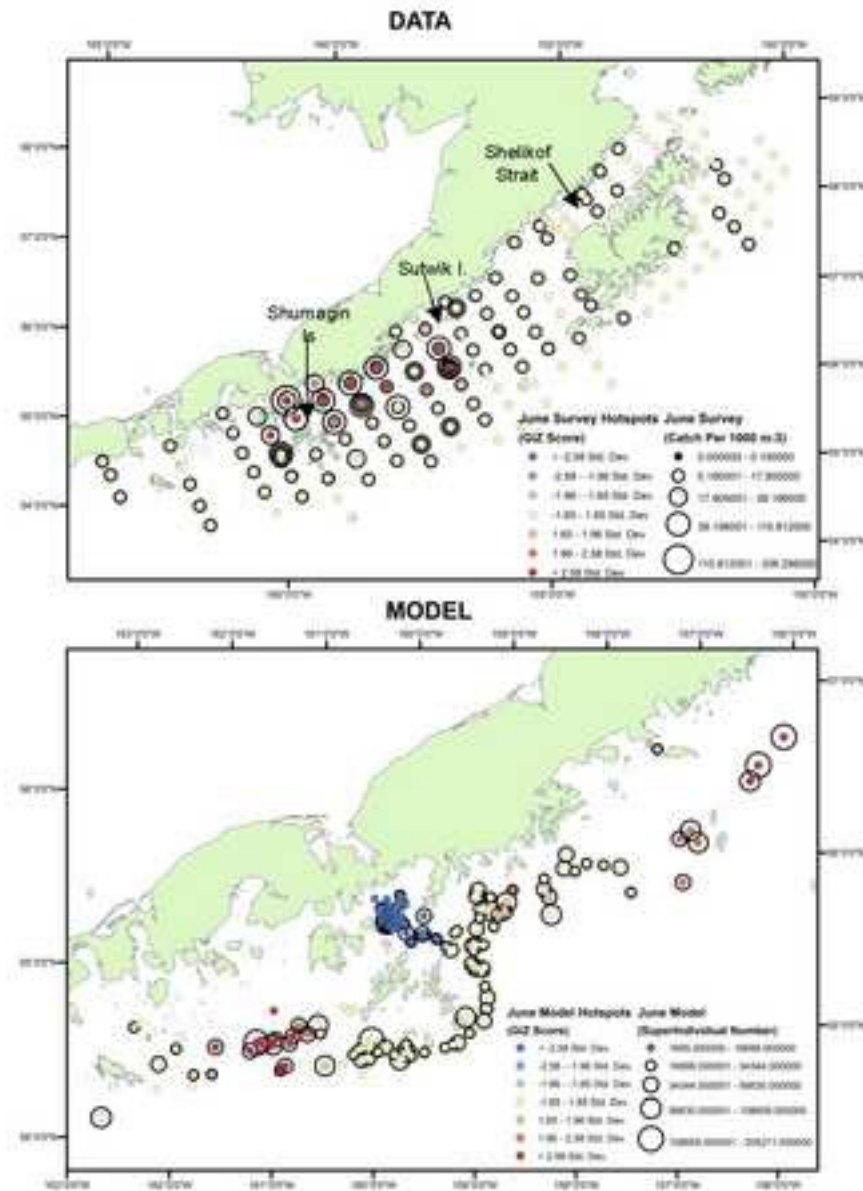


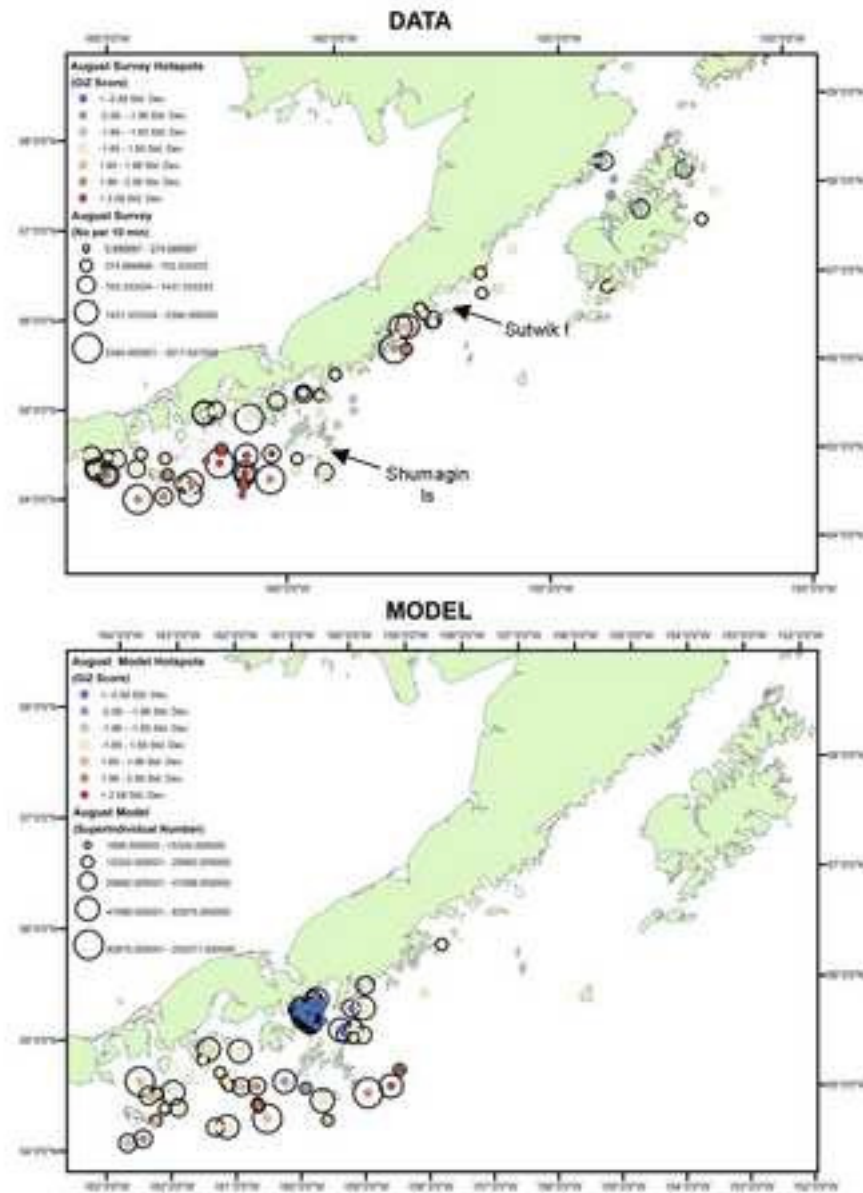


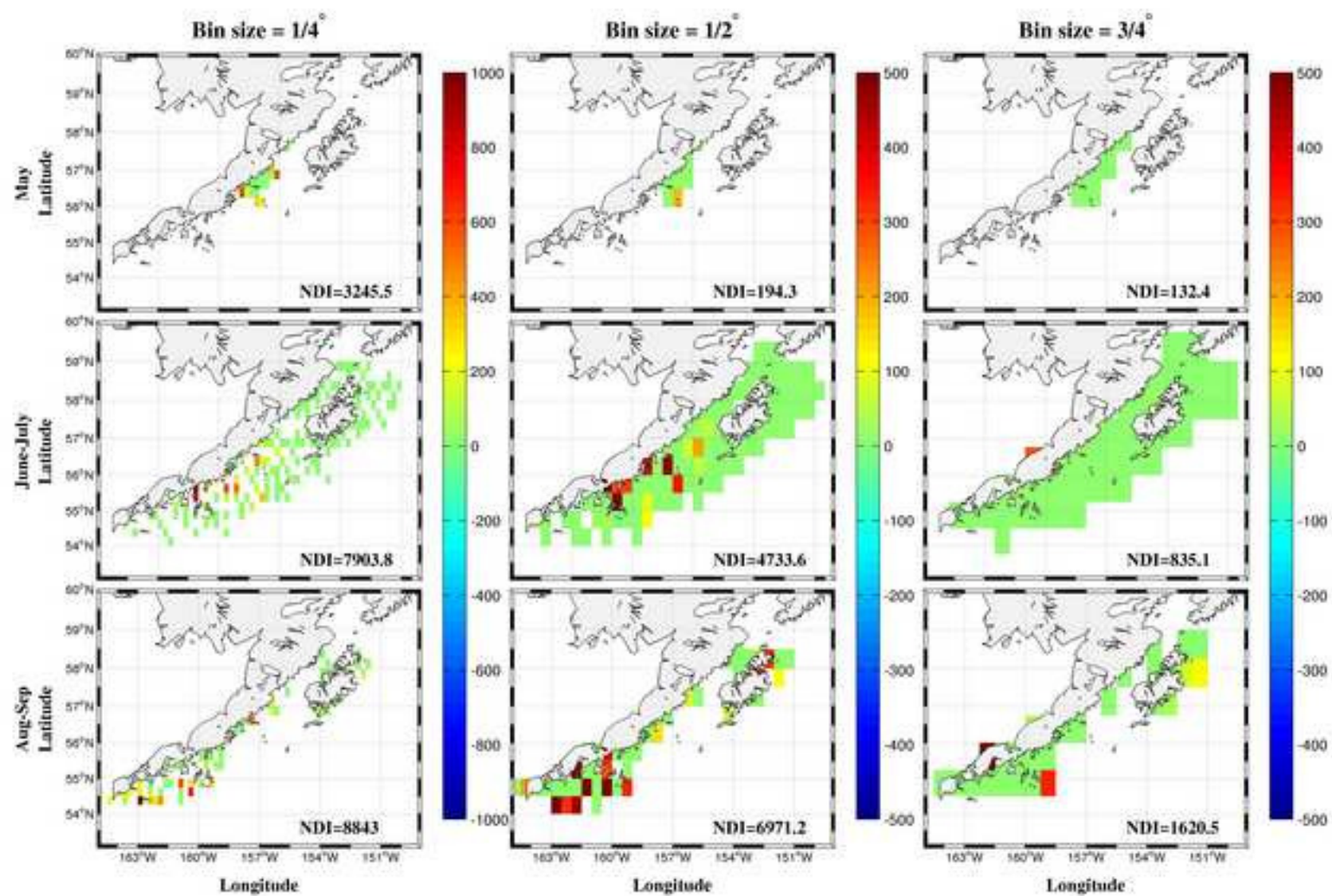


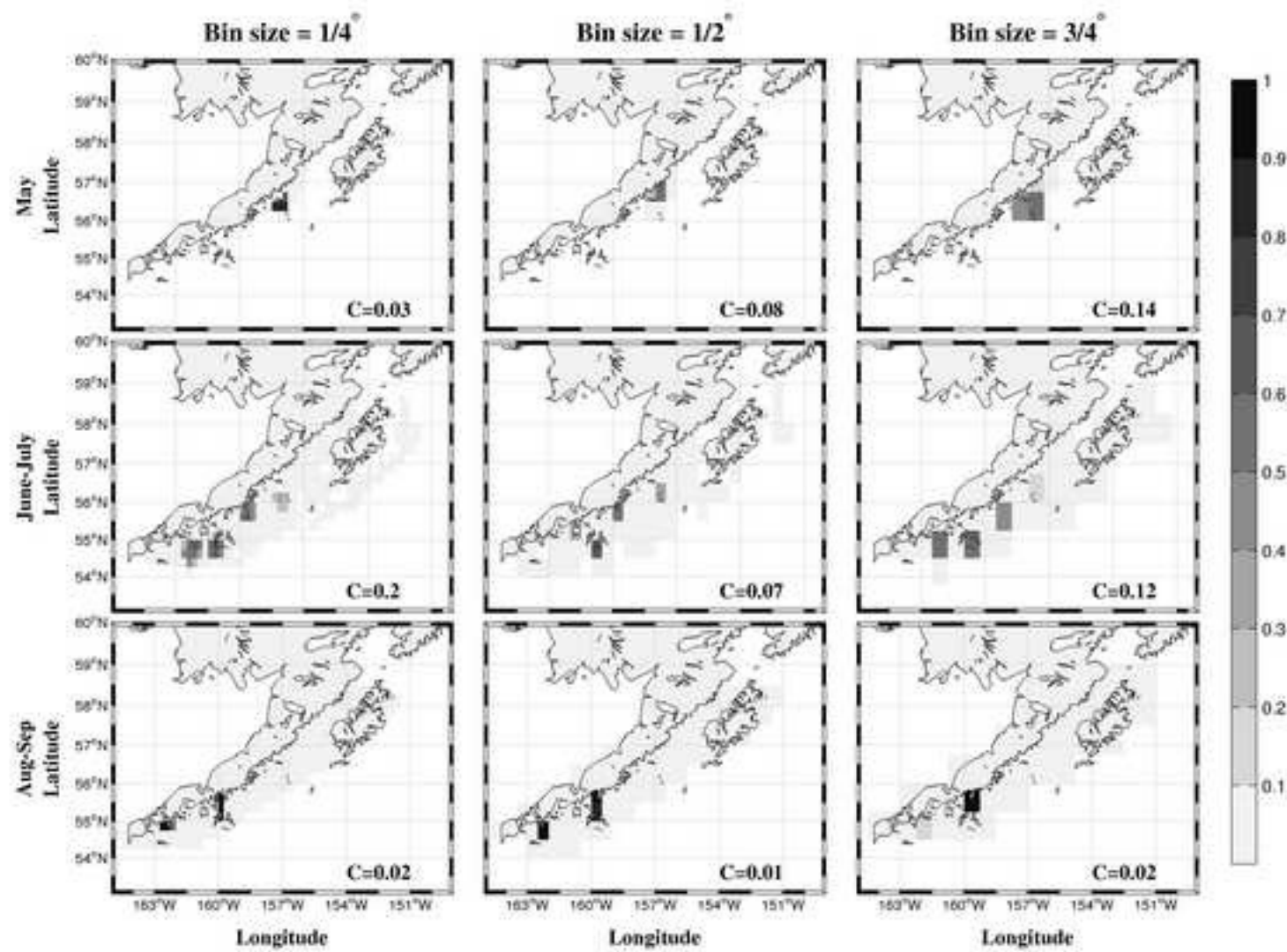


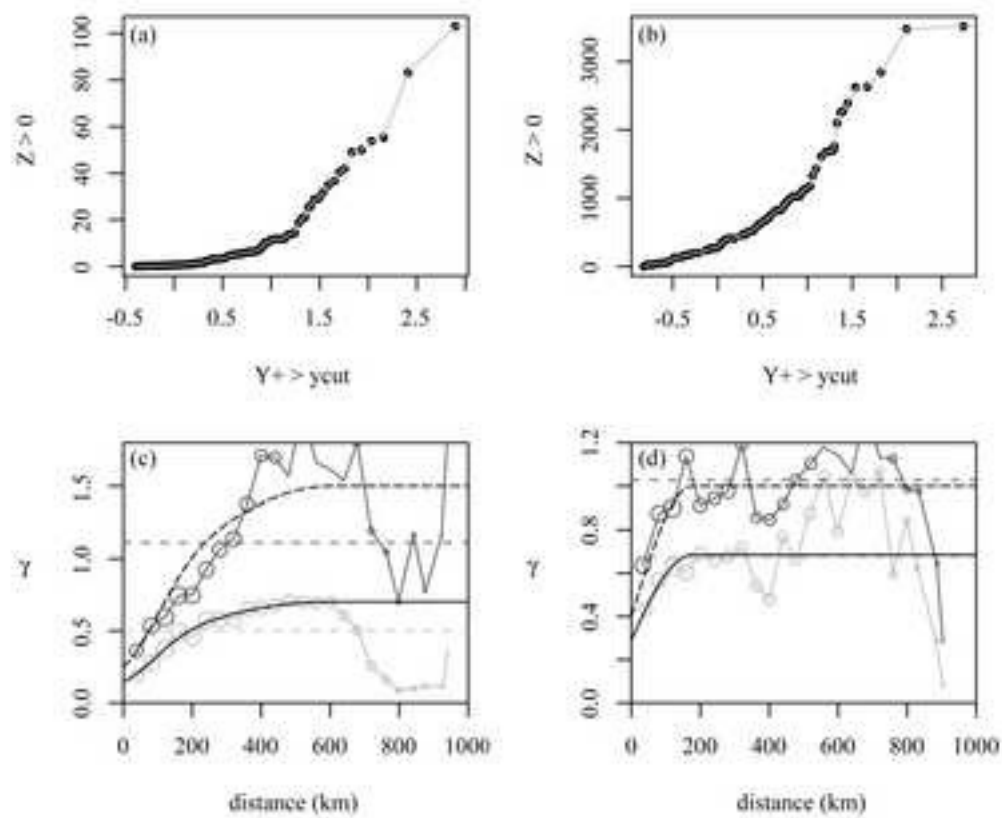






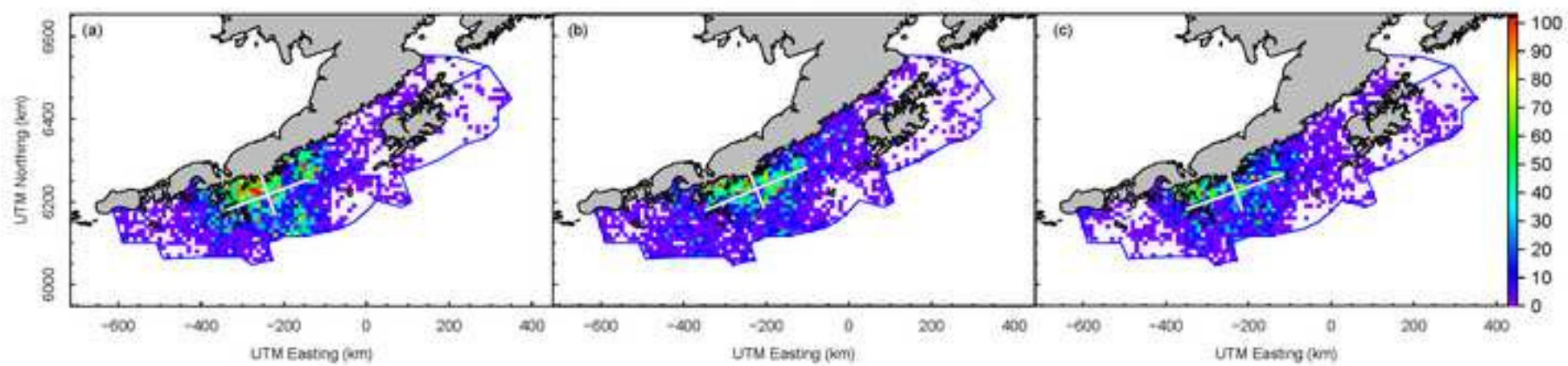








Simulated fields for June/July survey



Simulated field for August/September survey

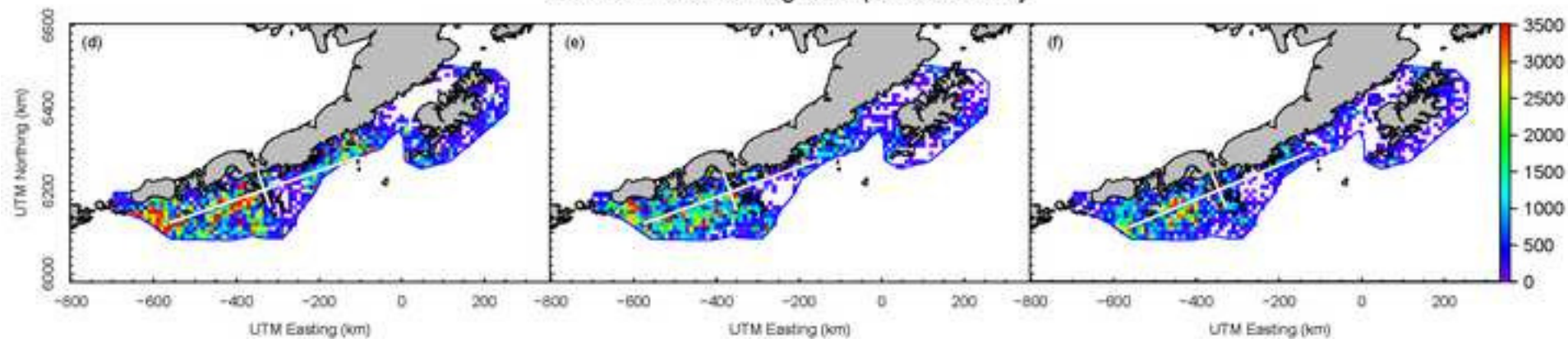


Table 5. Comparison of indices characterizing spatial distributions of pollock from the survey data and the IBM for June/July and August/September. Lower (lci: 2.5%) and upper (uci: 97.5%) confidence intervals associated with spatial indices computed from the survey data are shown. Values of spatial indices included within the confidence intervals appear shaded in grey. Longitude (in km, xcg) and latitude (in km, ycg) of the center of gravity, inertia (I), isotropy (Iso), positive area (pa), spreading area (sa) and equivalent area (ea) are the spatial indices used to describe each spatial distribution. Release spawning months (April, May) and areas (Area 8, North Shelikof Strait; Area 11, Shelikof Exit area) were tested.

Spatial Indices			xcg	ycg	I	Iso	pa	sa	ea
(June/July spatial distribution)									
Survey	lci		-383	6183	45146	0,149	75000	33744	34331
	uci		-289	6221	81629	0,218	90178	42528	43293
	data		-352	6199	53347	0,165	84789	38756	38437
Model	April	area 8	-338	6228	5319	0,186	1900	833	731
		area 11	-343	6212	7412	0,276	1900	1049	981
		areas 8 & 11	-342	6215	7136	0,273	3200	1183	1040
	May	area 8	-361	6193	8668	0,370	1800	1233	1313
		area 11	-444	6181	19914	0,245	2900	1849	1840
		areas 8 & 11	-423	6184	18452	0,255	4100	2393	2336
	April & May	area 8	-356	6201	8216	0,371	3200	1498	1557
		area 11	-408	6192	18042	0,252	4100	2238	2144
		areas 8 & 11	-397	6194	16413	0,264	6000	2692	2297

(August/September spatial distribution)

Survey	Ici		-261	6209	14504	0,297	101645	30191	27815
	uci		-218	6231	23930	0,426	120555	38365	37140
	data		-241	6221	13693	0,386	111506	32988	28490
Model	April	area 8	-342	6211	4553	0,243	1600	647	505
		area 11	-300	6215	6203	0,387	2500	1469	1166
		areas 8 & 11	-306	6214	6181	0,377	3600	1508	1062
	May	area 8	-268	6212	2032	0,460	2500	1840	2011
		area 11	-301	6192	15578	0,204	4900	3051	3147
		areas 8 & 11	-294	6196	12925	0,217	6200	3867	3989
	April & May	area 8	-282	6212	3295	0,429	3900	2091	2221
		area 11	-301	6198	13263	0,250	6700	3707	3050
		areas 8 & 11	-297	6201	11377	0,262	9000	4462	3474