

A probabilistic cellular automata approach for predator–prey interactions of arrowtooth flounder (*Atheresthes stomias*) and walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea

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Abstract: We developed a hybrid cellular automata (CA) modelling approach to explore the dynamics of a key predator–prey interaction in a marine system; our study is motivated by the quest for better understanding of the scale and heterogeneity-related effects on the arrowtooth flounder (*Atheresthes stomias*) and walleye pollock (*Theragra chalcogramma*) dynamics during the summer feeding season in the eastern Bering Sea (EBS), but can be readily extended to other systems. The spatially explicit and probabilistic CA model incorporates individual behaviours and strategies and local interactions among species, as well as spatial and temporal heterogeneity due to geographical and (or) environmental changes in the physical environment. The model is hybridized, with an individual-based model (IBM) approach for increasing its capacity and continuum and for balancing between computational efficiency and model validity, which makes it suitable for simulating predator–prey dynamics in a large, complex ecological environment. We focus on the functional and aggregative responses of predators to prey density at different spatial scales, the effects of individual behaviours, and the impacts of systematic heterogeneity. Simulations from the model with suitable parameter values share qualitatively similar features found in field observations, e.g., local aggregations around hydrographical features. Spatial heterogeneity is an important aspect of whether local-scale functional and aggregative responses reflect those operating over large, or global, scales.

Résumé : Nous avons mis au point une modélisation de type automate cellulaire (CA) hybride afin d'explorer la dynamique d'une interaction prédateur–proie essentielle dans un système marin; notre étude cherche à mieux comprendre l'échelle et les effets associés à l'hétérogénéité dans la dynamique de la plie à grande bouche (*Atheresthes stomias*) et de la goberge de l'Alaska (*Theragra chalcogramma*) durant la saison estivale d'alimentation dans l'est de la mer de Béring (EBS); notre méthodologie peut s'appliquer facilement à d'autres systèmes. Le modèle CA, qui est spatialement explicite et probabiliste, incorpore les comportements et les stratégies individuels, les interactions locales entre les espèces, de même que l'hétérogénéité spatiale et temporelle due aux changements géographiques et (ou) environnementaux dans le milieu physique. Le modèle est hybridé avec un modèle basé sur l'individu (IBM) afin d'augmenter sa capacité et son continuum et pour établir un équilibre entre l'efficacité informatique et la validité du modèle, ce qui le rend approprié pour simuler la dynamique prédateur–proie dans un milieu écologique complexe et de grande taille. Nous nous intéressons particulièrement aux réactions fonctionnelles et agrégatives des prédateurs en fonction de la densité des proies à différentes échelles spatiales, aux effets des comportements individuels et aux impacts de l'hétérogénéité systématique. Les simulations produites par le modèle avec des valeurs appropriées des paramètres présentent des caractéristiques communes qualitativement semblables à celles observées sur le terrain, par ex., les agrégations locales autour des structures hydrologiques. L'hétérogénéité spatiale est un aspect important à considérer lorsqu'on veut déterminer si les réactions fonctionnelles et agrégatives observées à l'échelle locale représentent bien celles qui agissent aux échelles plus larges ou globales.

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Introduction

There is a developing concern about the impact of predation by the increasing arrowtooth flounder (ATF; *Atheresthes stomias*) population (Wilderbuer et al. 2002; Duffy-Anderson et al. 2003) on the abundance of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea (EBS), which has recently experienced a declining trend (Ianelli et al. 2007). Most models used to assess the impact of predation such as tactical fishery statistical estimation models and strategic ecosystem simulation models (Sparre 1991, Jurado-Molina et al. 2005) require knowledge about the functional and numerical responses of predator populations to prey density. The functional response indicates how many prey are eaten by the predator in relation to prey abundance (Holling 1959). The numerical response links the predator abundance with its food availability (Holling 1959), which comprises two components: the reproductive response linking food availability to predator abundance from one generation to the next, and the aggregative response of predators around prey (Solomon 1949; Rindorf and Gislason 2005). In this paper, we consider the aggregative aspect of the numerical response. The characterizations of the functional–numerical responses have important consequences for the model-based management advice (Kinzey and Punt 2009). However, their estimation is generally based on annual data over a whole region of study, e.g., the EBS. A question arises as to how to relate these global responses to local processes (Walters and Martell 2004; Aydin 2004). A link back to local ecological processes is required for a comprehensive study of the ecological consequences of climate change and fishing, hence the need for understanding how spatial heterogeneity affects scaling-up and characterization of these important predator–prey relationships. In particular, our study is motivated by the need to better understand scale- and heterogeneity-related effects on the predation dynamics of age-1 pollock and ATF during the summer feeding season in the EBS.

Bottom-up simulation approaches, e.g., cellular automata (CA) (Ermentrout and Edelstein-Keshet 1993; Pekalski 2004) and individual-based models (IBM) (Grimm 1999; Breckling et al. 2005), have been proposed for refining our understanding of predator–prey problems. We construct a hybrid CA model for efficiently simulating and exploring the spatial-temporal dynamics of a spatially vast and heterogeneous predator–prey system. To increase the capacity and continuum of a modelling approach, we have incorporated some key features from the more complex IBM in a CA model. Thus our model lies between the two approaches, balancing between computational efficiency and model validity; in that sense, it is a hybrid-model.

Walleye pollock is one of the world's largest fisheries, and there is a growing concern about recruitment to the adult population. In the EBS, age-1 pollock are the major prey of ATF (Aydin and Mueter 2007), and recent assessments of the pollock fishery have highlighted the growing impact of this predator as a possible source of decreasing recruitment and fisheries yield (Ciannelli et al. 2005; Ianelli et al. 2007). Thus a pressing issue concerns the nature of the predator–prey relationship between these two species. Further, the field data collected over 30 years show that ATF in the EBS are pollock specialists (Aydin et al. 2007), making this an ideal

predator–prey pair to study in isolation while retaining a strong correspondence with the actual ecological system in question. We focus on studying the functional and aggregative responses at different spatial scales, the effects of individual behaviours and strategies, and the impact of systematic heterogeneity on the estimation of the functional and aggregative responses.

Model

Model structure

We consider a CA model comprising two species, a prey and a predator, on a lattice of size $L_1 \times L_2$. The model evolves in discrete time steps so that $t = 1, \dots, T$, with the basic time unit being, e.g., 1 day. In practice, the spatial scale could be determined by the unit-time mobility of the prey and the predator, so that the spatial and temporal scales are matching. To increase the capacity and continuum of the model, each cell on the lattice is occupied by multiple predators and prey. For each individual predator, there is one parameter indicating its reserve of energy, i.e., the reserve counter (t_r) (see Table 1 for a list of the parameters and symbols indexing the model developed herein); the counter is increased to the maximum value (T_r) after eating a prey and decreased by one after the completion of one time step. The predator dies when its reserve counter reaches zero. For each individual prey, there is one parameter indicating its status, i.e., life counter (t_l), which decreases by one after the completion of one time step. Each prey has a fixed lifetime (T_l) and dies when its life counter reaches 0.

It is well known that fish dynamics are affected by the geographical or environmental conditions, which are generally heterogeneous over space and time. Therefore our model accounts for the possible spatial and temporal heterogeneity. This is achieved in two ways. First, each cell s on the lattice is assigned a pair of numbers ($p_1(s), p_2(s)$), with $p_1(s)$ indicating the relative suitability of the cell for the predators and $p_2(s)$ that for the prey, i.e., how likely a predator or a prey will stay within or move to the cell. These numbers are referred to below as the background probabilities. These background probabilities allow flexible specification, that is, they can be functions of the cell location and may be prey- or predator-specific, e.g., they can be used to design the seascape or to restrict the overlapping area of the predator and prey. Second, we incorporate spatial heterogeneity in predator–prey interactions into the model by including a spatial function of predation efficiency in the cellular predation probability (see the section below).

Evolution rules

The evolution of the model is driven by random events. We start from N_1 predators and N_2 prey. The initial distribution of the prey and predators is determined based on the background probability matrices. Ruxton and Saravia (1998) suggested that when updating a CA model, the spatial-temporal ordering must be selected to match the biological characteristics of the target ecological system. In our analysis, we update each group of predators or prey one member at a time in each cell on the lattice in random order. Note that the updating of a CA is generally at the cell level, whereas the updating of an IBM is at the individual level.

Table 1. List of parameters and symbols.

Parameter	Meaning	Default	Range
L_1	Lattice dimension in latitude direction	100	
L_2	Lattice dimension in longitude direction	50	
N_1	Initial population size of predators	10 000	$\frac{N_2}{N_1} = 10 - 30$
N_2	Initial population size of prey	200 000	
T_r	Maximum reserve level of a predator	15 days	10–25
t_r	Reserve level of a predator		0– T_r
T_1	Maximum lifetime of a prey	365 days	
t_1	Life counter of a prey		0– T_1
$p_1(s)$	Habitat suitability index of cell s for predators		0–1
$p_2(s)$	Habitat suitability index of cell s for prey		0–1
h	Handling time	1 day	1–3
c_1	Predation efficiency parameter	1	1–3
c_2	Prey density threshold	$[N_2 / \sum_s p_2(s)]$	

Here, our approach again lies in between for balancing computational efficiency and model validity.

For two-dimensional lattice systems, a set of cells surrounding a given cell $s_0 = (x_0, y_0)$ may affect the evolution of the process in the cell. The Moore neighbourhood of range r , which is a square-shaped neighbourhood, is defined as

$$N^{(r)}(x_0, y_0) = \{(x, y) : |x - x_0| \leq r, |y - y_0| \leq r\}$$

where $N^{(r)}(x_0, y_0)$ denotes the collection of neighbouring cells of s_0 . In our simulation model, we use the Moore neighbourhood of range $r = 1$. We use reflective boundary conditions obtained by reflecting the lattice at the boundary. This type of boundary is commonly used if the system to be simulated also has a boundary and the values of the physical variables are not fixed.

The action of a predator depends on its own status and its neighbourhood. At each step, a predator first determines its next move, choosing between its current cell and the eight neighbouring cells. We consider two strategies: (1) random movement and (2) searching. For the first strategy, the predator chooses its next destination based purely on the background probabilities of the nine cells, i.e., the habitat suitability index $p_1(s)$ for the predators. For the second strategy, the probability of choosing a cell among the nine cells is proportional to the product of the number of prey and the background probability of the cell; thus the predator tends to move to a cell with high prey density and high habitat suitability. The search strategy does not necessarily mean that the prey are able to judge between the large neighbouring cells, but rather it is a rule that promotes the tracking of the prey by their predators as a result of local search and chase of prey by the predators over space and time. After the predator moves into a cell, the predation process immediately takes place.

Given the various sources of uncertainty in the predation process (Bailey and Houde 1989), we model an individual predator's feeding process probabilistically. We assume the predation probability P in general takes the following form:

$$(1) \quad P = I(t_r \leq T_r - h) \times f(t_r) \times g(n_2)$$

where t_r is the predator's current reserve level, n_2 is the number of alive prey in the cell at the time of predation, $f(\cdot)$ is a

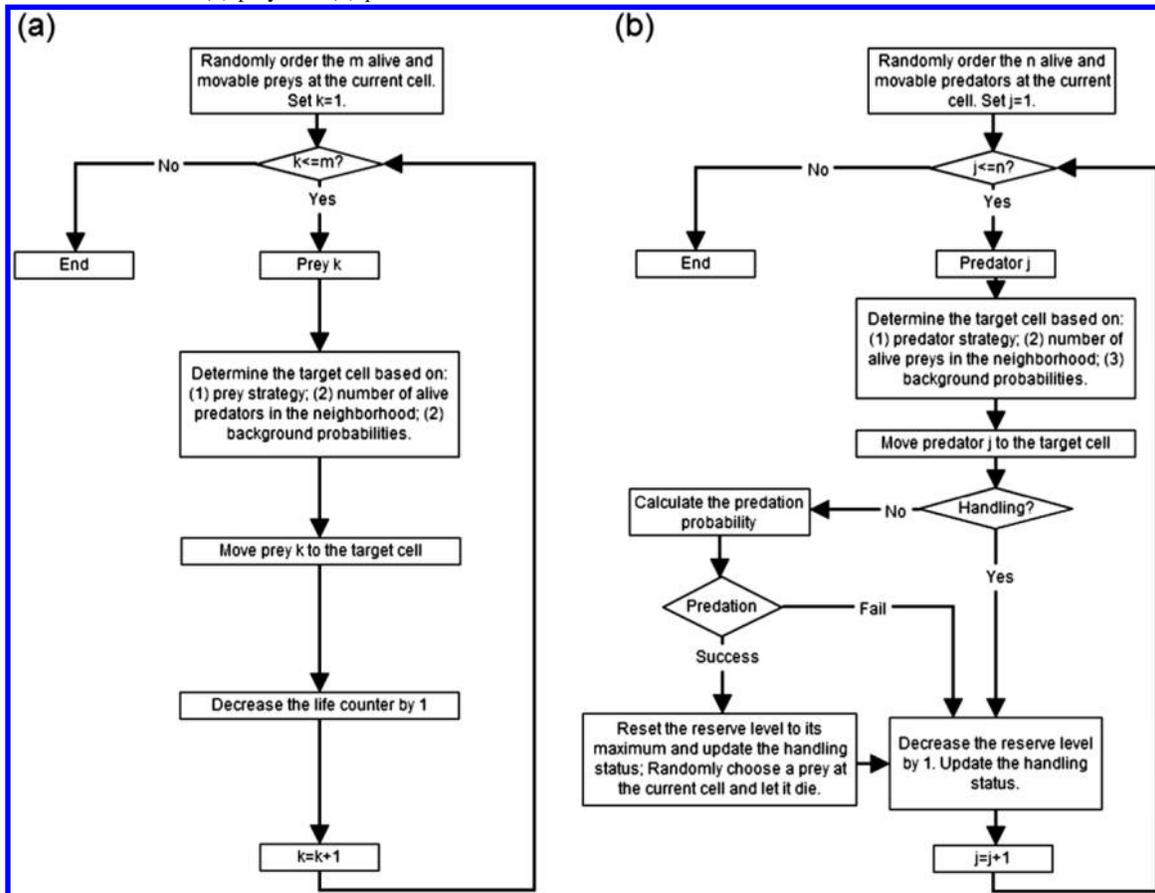
function of t_r , $g(\cdot)$ is a function of n_2 , and h is a constant. The predation probability consists of three multiplicative parts. The first part is an indicator function that equals 1 if the expression within the parentheses holds, which is used to model the digestion or rest processes, i.e., the predator is not allowed to hunt for h time steps after eating a prey. This setting plays the same role as the handling counter used in Yokoyama et al. (2008) with reduced implementation cost. The second part is generally a nonincreasing function of the reserve counter, which means that the hungrier the predator is, the more likely the predator is to succeed at predation. As predation success is limited by a number of factors, e.g., encounter rate, that can be affected by environmental conditions, the second part may be site-dependent. The third part is generally an increasing function of the prey density, possibly with a threshold, i.e., the more prey in the cell, the higher the chance for a predator to catch a prey. If the prey density exceeds some threshold value, then predation is no longer limited by the prey density. In this analysis, the predation probability P is specified as

$$(2) \quad P = I(t_r \leq T_r - h) \times \min\left(1, \frac{c_1}{t_r}\right) \times \min\left(1, \frac{n_2}{c_2}\right)$$

where h is the handling time, c_1 is a tuning parameter related to the environmental conditions of the cell that influence predation success, and c_2 is the prey density threshold over which a higher encounter rate is inconsequential to predation efficiency. Below, we refer to c_1 as the predation efficiency parameter. These tuning parameters are generally functions of environmental conditions. For example, the handling time, h , and c_2 are related to the gut evacuation time, which is generally temperature-dependent (Persson 1981). So far, the model accounts for saturation effects on predation due to high prey density. However, predation efficiency may be limited differently at low prey density, which is instrumental for type III functional response (Murdoch 1973).

Similarly, the action of a prey depends on its own status and its neighbourhood. We also consider two strategies: (1) random movement and (2) avoidance. For the first strategy, a prey chooses its next destination purely based on background probabilities of the nine cells, i.e., $p_2(s)$. For the second strategy, the probability of choosing a cell among the nine cells is proportional to the product of the inverse of the risk of being

Fig. 1. The evolution rules for (a) prey and (b) predators.



eaten and the background probability of the cell, where the risk is measured by the total number of potential hunters in the cell. Hence, a prey tends to move to a cell with low risk of being eaten and high habitat suitability. The avoidance rule does not necessarily mean that the prey can judge between the large neighbouring cells, but rather, it is a rule that promotes divergence of prey movement from predator tracking as a result of local elusion of prey from predators. (The individual evolution rules for both predators and prey are summarized in Fig. 1.)

Simulating the ATF-pollock interaction in the EBS

Background on the ATF-pollock interaction

Age-1 juvenile pollock are a major prey of adult ATF (Mito 1974; Livingston 1993; Aydin et al. 2007). The field data collected over 30 years show that ATF in the EBS are pollock specialists, consuming over 60% pollock by weight, with larger ATF consuming over 90% pollock by weight (Aydin et al. 2007). In summer, age-1 pollock are particularly vulnerable to predation by ATF because of their relatively close proximity to the sea floor compared with either age-0 or age-2 juvenile pollock (Duffy-Anderson et al. 2003).

During winter in the EBS, a cold pool of water $<2^{\circ}$ forms over the shelf (Fig. 2). The extent of the cold pool in the EBS is expected to be impacted by climate change. The distribution of the cold pool varies from year to year based on the overlaying winter sea ice, which depends on atmospheric

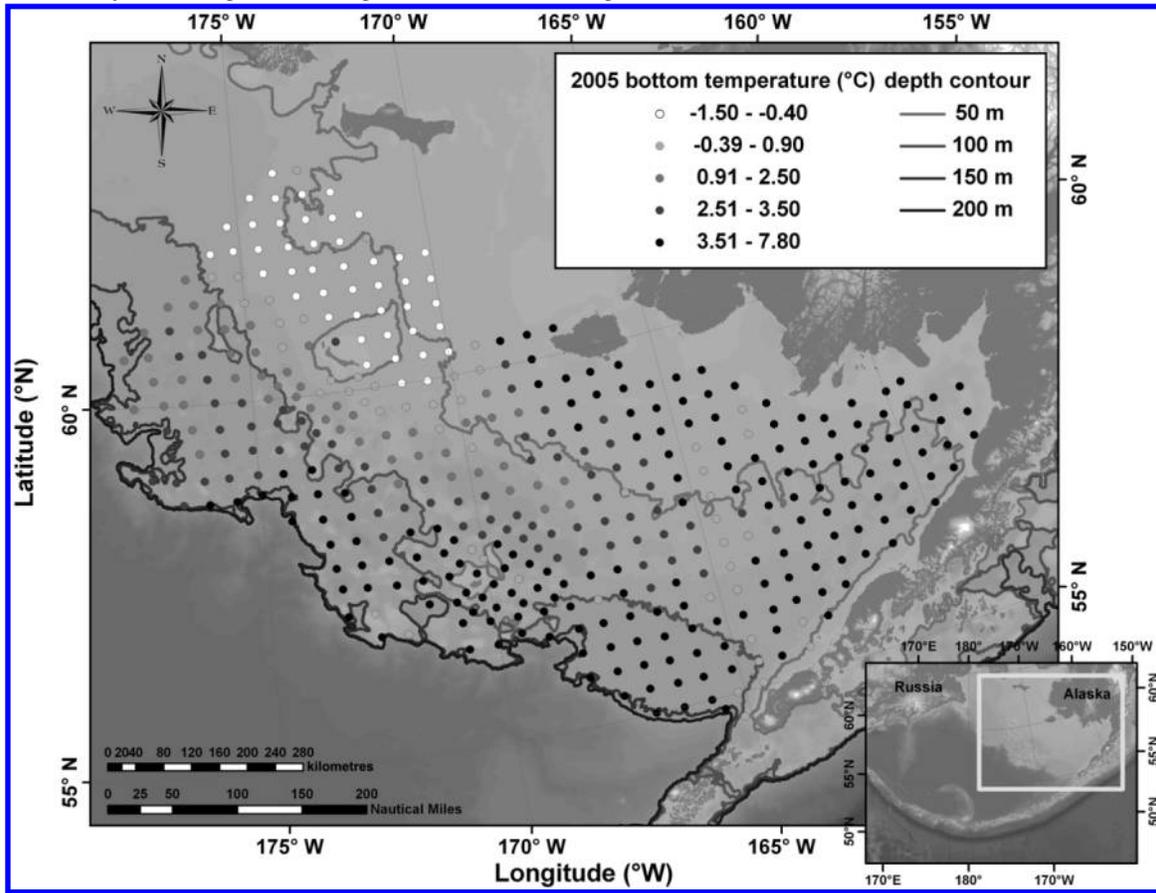
temperature and winter storm tracks. The cold pool persists in the bottom waters of the shelf until autumn when storms mix the water. The extent of the cold water influences the distribution of age-1 pollock (Wyllie-Echeverria and Wooster 1998), and there is an association of increasing water temperatures over the shelf with an increased overlap of juvenile pollock and ATF (Kihara and Shimada 1988).

A bottom trawl survey of the EBS shelf (Fig. 2) has been conducted annually since 1979. The sampling gear is a 83-112 eastern otter trawl with a 32 mm codend liner mesh. The sampling plan includes 356 stations from the 20 m isobath to 200 m on a regular grid pattern with 20 nm station spacing.

Simulation settings

When building the simulation model, we anticipated the trade-off between model parsimony and model validity. On one hand, the model is kept as simple as possible and yet can still capture the basic dynamics of the system. On the other hand, several parameters are built into the model to make it flexible enough for generalization. In our study, instead of performing extensive numerical analyses to explore the entire parameter space, we specify a set of parameter values based on our knowledge of juvenile pollock and ATF in the EBS. We choose the settings of the model to match the reality to a reasonable degree, so that the simulation results could potentially be used for comparing results from field experiments and making inferences on the ATF-pollock inter-

Fig. 2. Map of the eastern Bering Sea (EBS), with the bathymetry displayed in the contour plot. The dots mark the location of the sites where the summer trawl surveys were conducted in 2005. Dots have different grey levels according to the bottom temperature measured at the site during the trawl survey. Note the presence of a pool of cold water (cold pool) in the middle shelf of the EBS.



action in the EBS. Some implicit assumptions were made, and parameter values of the CA model were determined as follows.

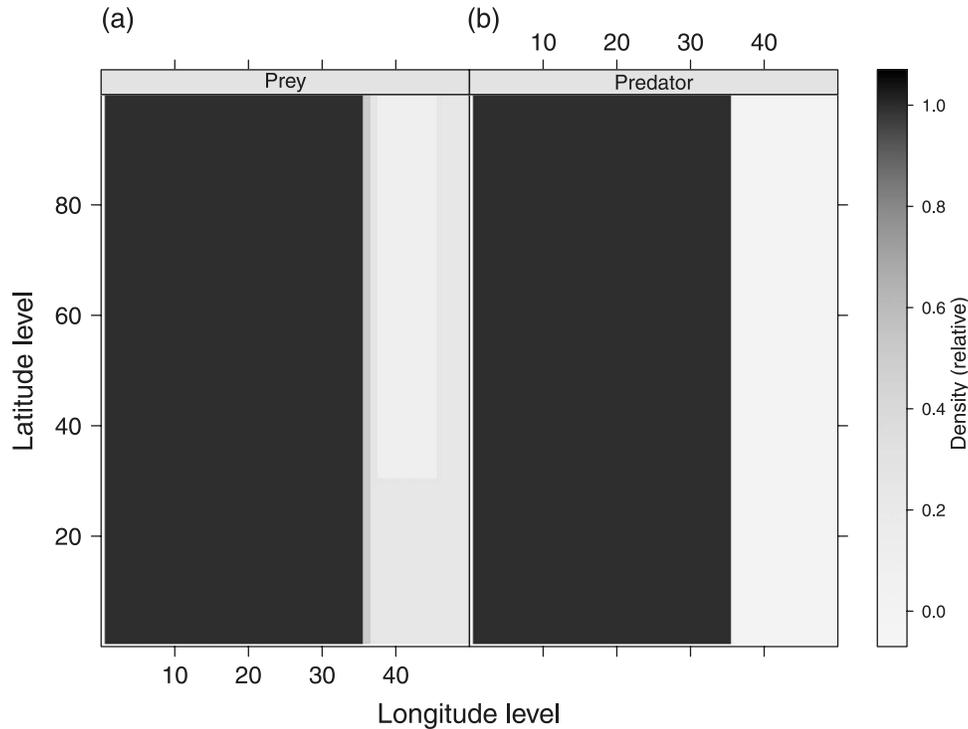
Because juvenile pollock is ATF's main food resource in the EBS, for our simulation purpose, we consider a single predator and single prey system. The spatial scale is roughly $10 \text{ km} \times 10 \text{ km}$ for a cell, and the temporal scale is 1 day. The spatial scale was determined by the daily potential mobility of ATF and pollock. As a consequence, the size of the lattice is approximately 100×50 cells, roughly the same as the actual size of the EBS shelf. Hence, the spatial and temporal scales of the model proportionally match those of the EBS. The entire depth of the system is considered as one layer for simplification. This is oversimplistic, but the effect of multiple layers can be captured by the encounter rate or predation probability, both of which are embedded in the tuning parameters as elaborated below.

The initial population size of predators N_1 is set to 10 000, and the initial population size of prey N_2 is set to 200 000. Larger population sizes in the model better resemble the ATF-pollock system in terms of real predator and prey population sizes, but at the cost of increasing computation time. Hence the magnitude of the population sizes was chosen as a compromise between model accuracy and computation cost. Actually, the relative ratio of the two population sizes is the most important factor here. The ratio was chosen to mimic the estimated population sizes of pollock and ATF in the

EBS published in stock assessment reports of the North Pacific Fisheries Management Council (North Pacific Fisheries Management Council 2008). The maximum value of the reserve counter T_r is set to 15 days, which means that a predator can live at most 15 days without eating any prey. The handling time h is set to 1 day. In reality, the reserve of each individual could vary due to numerous factors, e.g., prior feeding history. Therefore the initial level of reserve t_r for each individual is generated independently and randomly from the set of integers between 1 and T_r . The prey lifetime T_1 for each individual is set to 365. Note that we are only interested in the dynamics within a feeding season. This setting essentially assumes that predation is the main cause of the prey mortality. In the analysis, we use several different values of the predation efficiency parameter c_1 . We also consider c_1 as a function of location to create spatial heterogeneity in the predator-prey interactions. The prey density threshold c_2 is set to the expected number of prey in a cell, with $p_2(s)$ equal to 1 at time 0, i.e., $c_2 = [N_2 / \sum_s p_2(s)]$, where the $[\cdot]$ operation takes the integer part of a number.

We have experimented with several different combinations of N_1 , N_2 , and h values within their plausible ranges (Table 1), which all yielded qualitatively similar results. Hence, results reported below that are based on the above parameter setting are robust. The purpose of this simulation model is to reveal the basic dynamics rather than to numerically mimic reality.

Fig. 3. Background probabilities for cold pool setting 1 (CP₁). (a) The background probability for prey is set to 1 on the west side, 0.25 on the east side, and 0.1 in the cold pool area. The probabilities near the cold pool boundary are set to be gradually decreasing from 1 to 0.1. (b) The predators are allowed to move freely on the west side of the ocean but are not allowed to be on the east side of the ocean. The settings of CP₂ and CP₃ are similar except that they model an increasingly larger cold pool.



We consider four different combinations of strategies for the prey and predators, which are denoted by S_{11} (prey and predators both move randomly), S_{12} (prey move randomly, but predators search for prey), S_{21} (prey avoid predators and predators move randomly), and S_{22} (prey avoid predators, but predators search for prey). Three different pairs of background probability matrices are considered, corresponding to three different sizes of the cold pool, from small to large. We denote them as CP₁, CP₂, and CP₃. In the setting for CP₁ (Fig. 3), the background probability for prey is set to 1 on the west side of the ocean ($p_2(s) = 1$), whereas the suitability is less favourable on the east side of the ocean ($p_2(s) = 0.25$) and in the cold pool area ($p_2(s) = 0.1$). The probabilities near the cold pool boundary are set to be gradually decreasing from 1 to 0.1. The predators are allowed to move freely on the west side of the ocean ($p_1(s) = 1$) but are not allowed to be on the east side of the ocean ($p_1(s) = 0$). The R package *cappm* contains a function for doing the simulations reported below and can be downloaded and installed by R (<http://cran.r-project.org/>).

Results

Global-scale responses

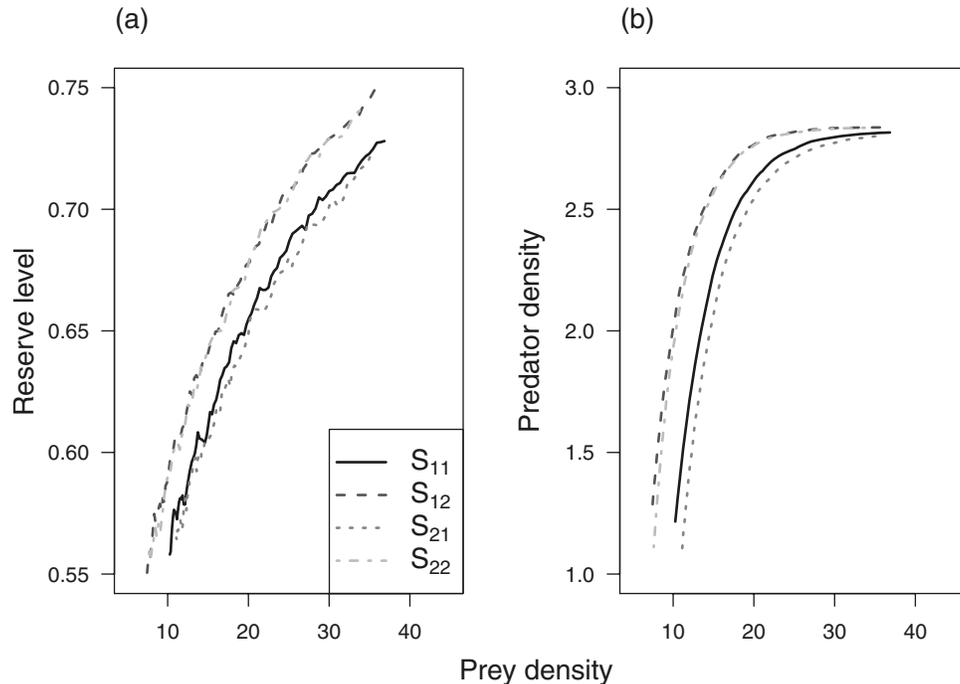
By global scale, we mean that the data are aggregated over the space at each time step ($t = 31, 32, \dots, 120$; $t \leq 30$ is discarded as burn-in, i.e., the period over which the dynamics is transient) where predators and prey overlap. The relationship between the average reserve level and the prey density serves as a proxy for the global-scale functional response, indicating

how many prey are eaten by the predator in relation to prey abundance. The relationship between the average predator density and prey density, both of which are computed over their overlapping habitat, serves as the aggregative response, linking the predator abundance with its food availability. We examined the effects of movement strategies, cold pool size, and predation efficiency on the functional and aggregative responses.

The simulation shows that the movement strategy of the predators is the dominating factor influencing both the functional and aggregative responses, regardless of the movement strategy adopted by the prey (Fig. 4). The combination of searching predators and randomly moving prey leads to the fastest reduction in prey density.

The cold pool size also influences both functional and aggregative responses of the predator-prey interaction (Fig. 5). Because all other parameters, including the initial population sizes are fixed, when the size of the cold pool increases, the predator habitat shrinks while that of the prey shrinks less because the cold pool acts as a soft boundary to the prey; hence the overlap between the habitat of the prey and that of the predator decreases as does the relative ratio of the (daily) prey density to the (daily) predatory density. The basic shape of the functional response seems unchanged, but rather it becomes uniformly lower as prey abundance decreases, which means that predators eat less on average under the conditions of increased competition and relatively reduced food availability. The consequence of the predator's reduced prey consumption is reflected in the aggregative response, i.e., the three scenarios initially have very different relative ratios of

Fig. 4. The effect of movement strategies (CP_1 , $c_1 = 3$, $t = 31, \dots, 120$): (a) functional response; (b) aggregative response. The predation efficiency index c_1 is set to 3. Solid black lines, prey and predators both move randomly (S_{11}); dashed black lines, prey move randomly but predators search for prey (S_{12}); dotted grey lines, prey avoid predators and predators move randomly (S_{21}); dotted–dashed grey lines, prey avoid predators but predators search for prey (S_{22}).



predator to prey density, but the differences gradually disappear over time. These results create a self-regulation phenomenon in the simulated predator–prey system.

Predation efficiency has a strong effect on functional and aggregative response (Fig. 6). Higher predation efficiency leads to faster extinction of prey.

Spatial patterns of predators and prey

When both predators and prey adopt random movement strategies, the distribution of the predators and that of the prey seem to be quite uniform over their overlapping area (Fig. 7). Note that all the cell densities are normalized to be between 0 and 1 (divided by the maximum cell density) for ease of comparison. The prey appear to have higher densities along the boundary of the cold pool, which may be caused by the partial absorption setting at the cold pool boundary. In contrast, we do not observe any marginal concentration behaviour of the predators.

Other “nonrandom” movement strategies such as when predators adopt a searching strategy and prey adopt an avoidance strategy could affect the spatial distribution patterns (Fig. 8). Compared with the random movement scenario, when the prey adopt a predator-avoidance strategy, they still appear to gather along the boundary of the cold pool. However, the scenario reveals a strong aggregation pattern, especially for the prey distribution, i.e., the prey tend to form large groups or clusters rather than distribute uniformly.

A quantitative way to examine the aggregation behaviour is to calculate the entropy of the spatial distribution. Generally speaking, entropy is a measure characterizing disorder and randomness, i.e., flatness of a distribution. It is speculated that organisms can collect energy and focus it on the

reduction of entropy in their environment (Gutowitz 1993). In the context of a predator–prey system, the entropy of the empirical prey distribution at time t , denoted as $E(t)$, is defined by the following formula:

$$E(t) = \sum_{s \in O} \left[-\log \left(\frac{X_{s,t}}{\sum_{s \in O} X_{s,t}} \right) \cdot \frac{X_{s,t}}{\sum_{s \in O} X_{s,t}} \right]$$

where $X_{s,t}$ denotes the number of prey in cell s at time t , and O denotes the collection of all cells in the overlapping area occupied by the predators and prey. Similarly, the entropy of the predator distribution can be calculated by replacing the prey counts with the predator counts in the formula. (Figure 9 shows the plot of entropy as a function of time for both predators and prey under various strategy combinations.)

Scaling-up and impact of heterogeneity

The local-scale response is simulated based on the trawl survey sampling scheme used in the EBS (Lauth and Acuna 2009). At each time step ($t = 31, 32, \dots, 120$), one cell on the lattice is sampled, and the prey density, predator density, and average reserve level of the predators in the sampled cells are recorded. In our simulation, we tried to mimic the same sampling scheme, i.e., the route of the sampled cells is similar to the route of the cruise track, proceeding from south to north. To reduce the variability of the samples, we repeated the simulation 20 times and computed temporal averages for each sampled cell. This is roughly equivalent to running the simulation model with the number of prey and predators 20 times larger than the default values.

Fig. 5. The effect of cold pool size (S_{11} , $c_1 = 3$, $t = 31, \dots, 120$): (a) functional response; (b) aggregative response. The predation efficiency index c_1 is set to 3, and prey and predators both move randomly (S_{11}). The settings of CP₂ and CP₃ are similar to those of CP₁ in Fig. 3, except with a larger and larger cold pool. Solid lines, cold pool setting 1 (CP₁); dashed lines, cold pool setting 2 (CP₂); dotted lines, cold pool setting 3 (CP₃).

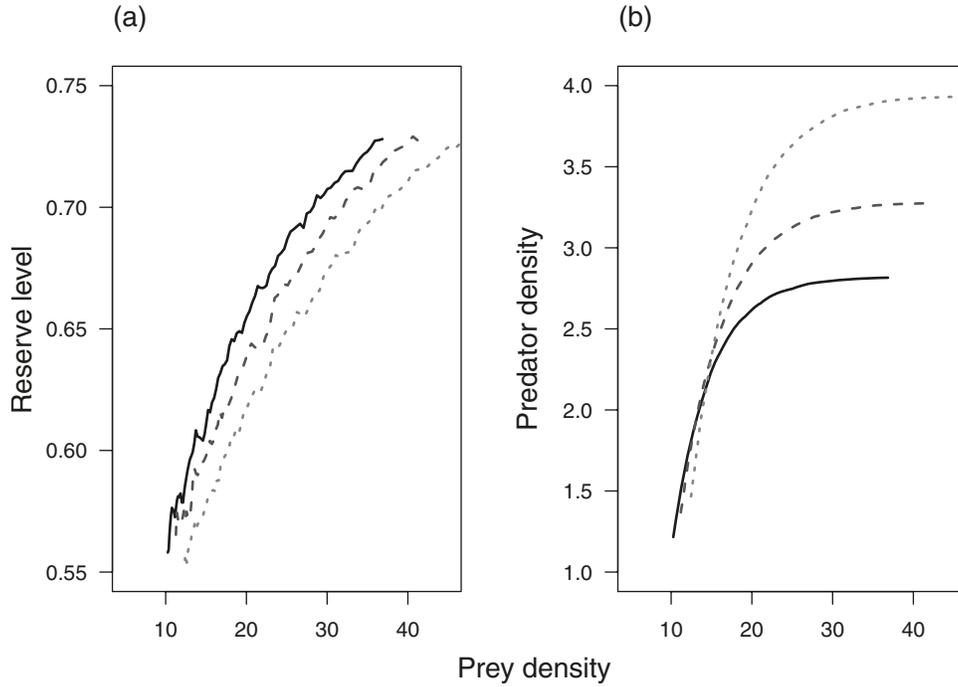
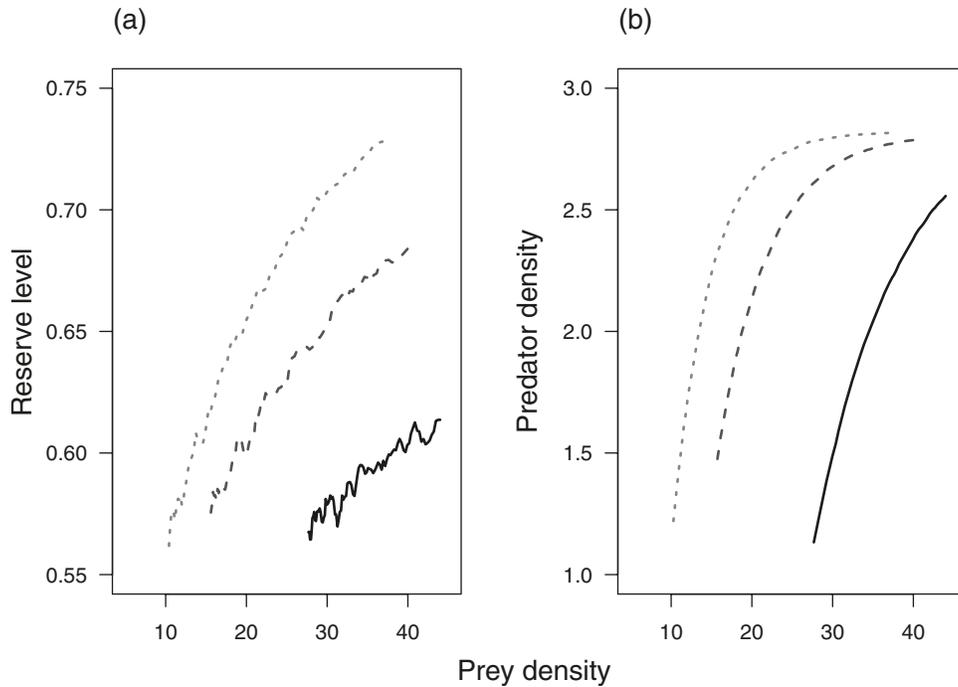


Fig. 6. The effect of predation efficiency (CP₁, S_{11} , $t = 31, \dots, 120$): (a) functional response; (b) aggregative response. Cold pool setting 1 (CP₁) is used, and prey and predators both move randomly (S_{11}). Solid lines, $c_1 = 1$; dashed lines, $c_1 = 2$; dotted lines, $c_1 = 3$.



In comparing the global responses and their local counterparts, it can be seen that under the homogeneous setting, the responses at the two extreme scales are quite similar to each other (Fig. 10, black lines versus shaded lines); this means that if the system is really homogeneous, then scale is relatively unimportant.

In reality, the geographical or environmental conditions of the ocean are heterogeneous over space and time, causing fish behaviour also to be heterogeneous over space and time. In this simulation, we examine the impact of habitat heterogeneity on fish dynamics and on the estimation of the functional and aggregative responses. In the homogeneous setting

Fig. 7. A snapshot of prey and predator distribution ($CP_1, S_{11}, t = 40$): (a) for prey; (b) for predator. Cold pool setting 1 (CP_1) is used, and prey and predators both move randomly (S_{11}).

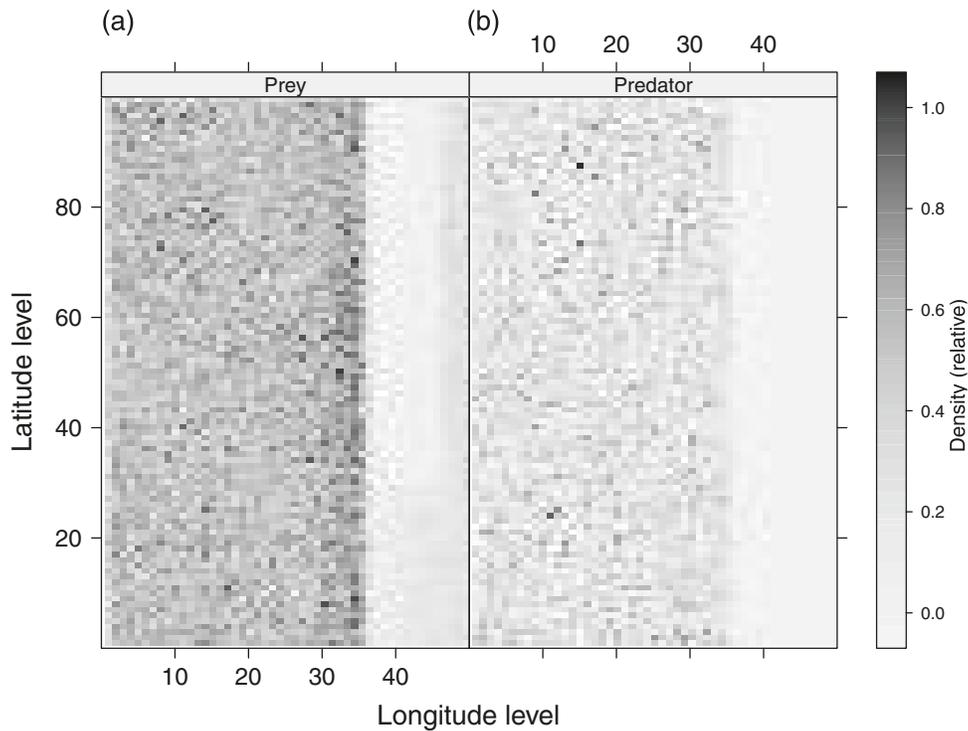
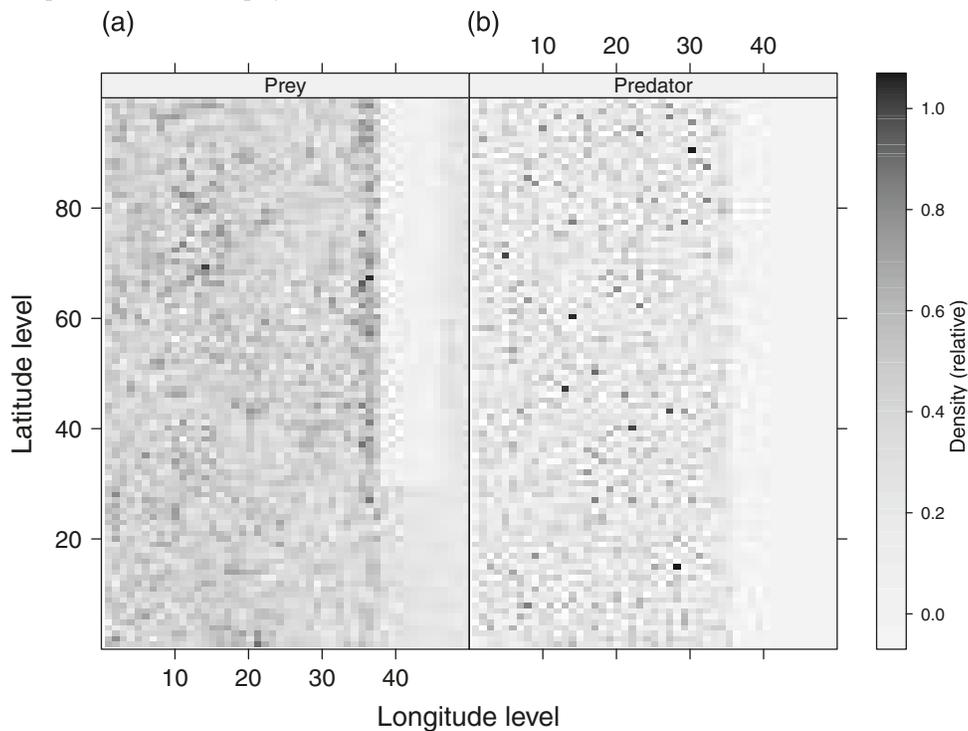


Fig. 8. A snapshot of prey and predator distribution ($CP_1, S_{22}, t = 40$): (a) for prey; (b) for predator. Cold pool setting 1 (CP_1) is used, and prey avoid predators but predators search for prey (S_{22}).



described above, we set c_1 as a constant, so that the predation efficiency was the same over the whole space. We considered two idealized heterogeneous scenarios in which the predation efficiency may vary spatially owing to environmental variation, e.g., higher encounter rate with warmer temperature

due to faster swimming speeds: (i) let c_1 be a smoothed function of the location, e.g., let c_1 follow a bowl-shaped curve along the south–north direction; and (ii) let c_1 be regionally different and distinguish the whole overlapping area to four subareas (Fig. 11).

Fig. 9. Entropy of prey and predator distribution (CP_1 , $c_1 = 3$): (a) for prey; (b) for predator. Cold pool setting 1 (CP_1) is used, and the predation efficiency index, c_1 , is set to 3.

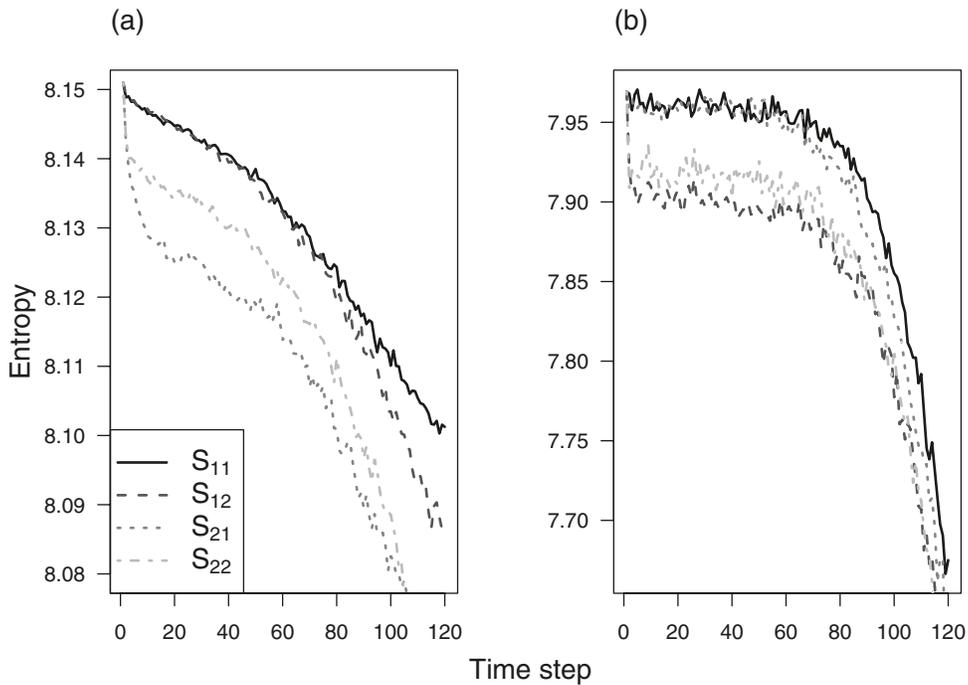
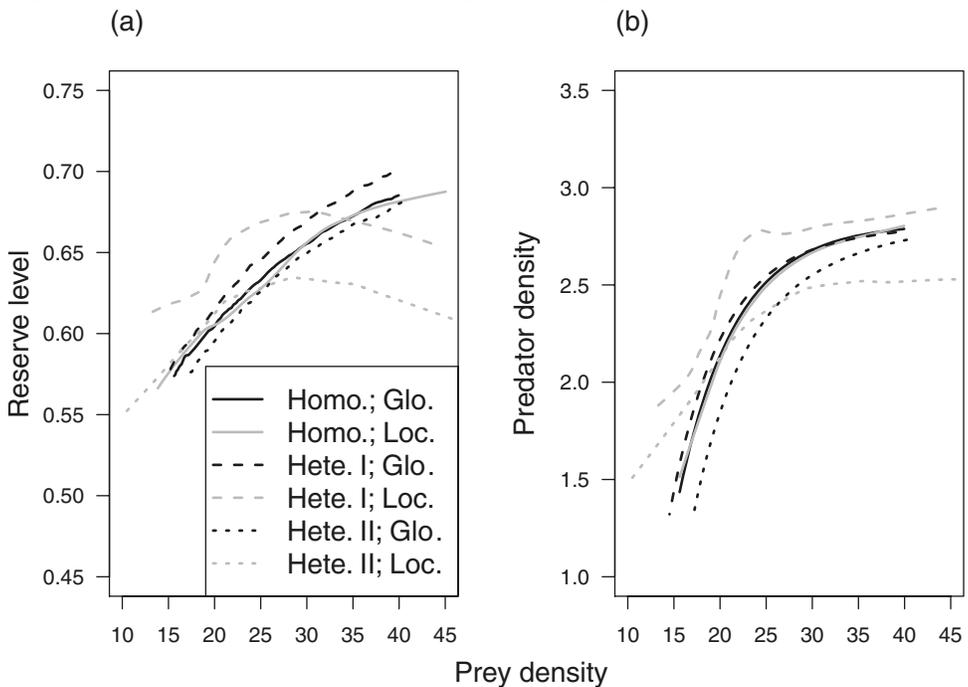


Fig. 10. Homogeneity setting vs. heterogeneity settings (CP_1 , S_{11} , $t = 31, \dots, 120$): (a) functional response; (b) aggregative response. Cold pool setting 1 (CP_1) is used, and prey and predators both move randomly (S_{11}). Solid black lines, global-scale response under homogeneous setting; solid grey lines, local-scale responses under homogeneous setting; dashed black lines, global-scale responses under heterogeneous setting 1; dashed grey lines, local-scale responses under heterogeneous setting 1; dotted black lines, global-scale responses under heterogeneous setting 2; dotted grey lines, local-scale responses under heterogeneous setting 2.



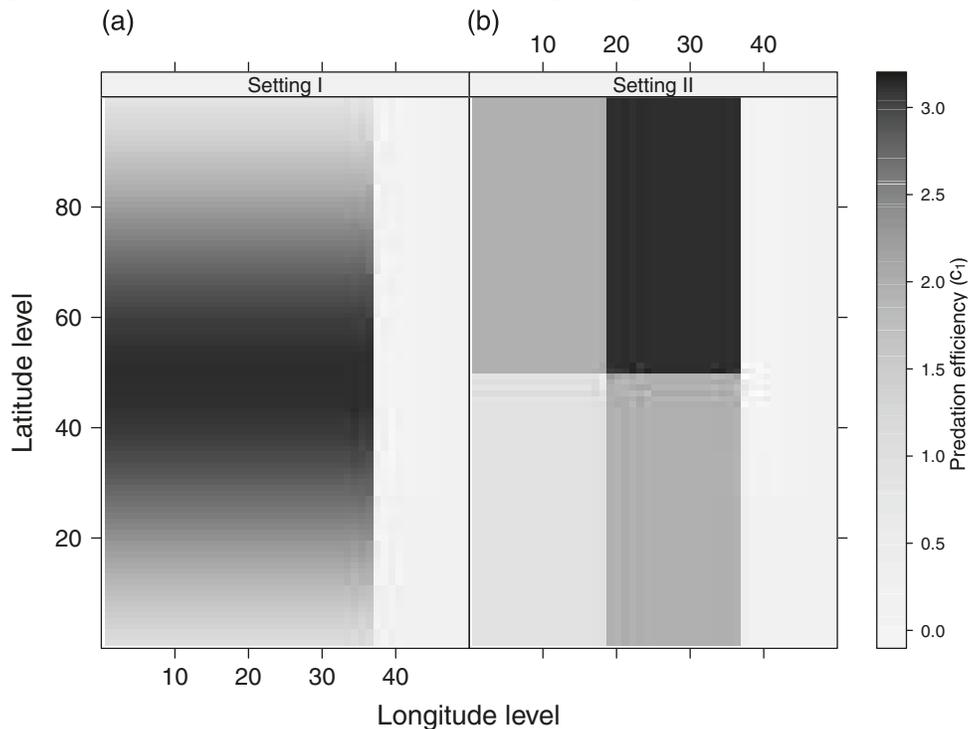
A comparison among the estimates of the functional and the aggregative response curves computed under the homogeneous and heterogeneous settings (Fig. 10) shows that spatial heterogeneity causes a discrepancy between the global responses and the local responses.

Discussion

We chose the CA approach as well suited for our study purpose: it allows the simulation of functional and aggregative responses at different scales of a predator–prey system

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Fig. 11. Two scenarios of heterogeneity induced by c_1 : (a) setting I: c_1 follows a bowl-shaped curve along the south–north direction (left); (b) setting II: c_1 is regionally different over four subareas indicated in the diagram (right).



with flexible specification of irregular heterogeneity in the predator–prey interactions that naturally occur in many marine systems. An advantage of CA over IBM is its simplicity and efficiency. A complex IBM model seems unnecessary as our main focus is the effect of spatial dynamics and scaling-up from local observations, rather than inherent individual heterogeneity. On the other hand, because the predator–prey system under study is spatially vast and not homogeneous, it may be too complex to be precisely quantified by an aggregated approach via a small number of mathematical equations (Lotka 1920; Volterra 1931).

We present a simulation model that describes the predator–prey interaction of age-1 juvenile pollock with an important predator, arrowtooth flounder, in the EBS. The model incorporates individual behaviours, local interactions among species, and spatial and temporal heterogeneity due to landscape effects. The model was used to explore several critical features needed for interpreting field observations of predation and their interplay with spatial scale. Most important, we found that spatial heterogeneity is an important aspect of whether local-scale functional and aggregative responses reflect those operating over large, or global, scales; this result reinforces previous studies (Bergström et al. 2006; Melbourne and Chesson 2006; Englund and Leonardsson 2008). We also included simulations of the effects of movement strategies, hunting efficiency, and the cold pool size on functional and aggregative responses at both local and global scales.

There is a rich literature on predator–prey systems related to scaling and heterogeneity issues (see Rose and Leggett (1990), Goodwin and Fahrig (1998), Melbourne and Chesson (2006), and many others). Spatial heterogeneity is generally

recognized as a critical aspect of predator–prey interactions (Kareiva et al. 1990). In homogeneous environmental conditions, the responses at the local and global scales are quite similar to each other, which indicates that if the system is homogeneous, then scale is relatively unimportant in the response. However, we found that when system heterogeneity is introduced, in this case by introducing spatial variation in predation efficiency, the responses on the local and global scales are quite different. This result indicates that representing global responses by local responses could be quite inaccurate under the more realistic condition of spatial heterogeneity. The relevance of these simulation results to the pollock–ATF system in the EBS may be assessed by estimating the empirical divergence of the local functional (aggregative) response from its global counterpart using trawl survey data. For example, stomach data from a significant portion of the fish caught in the trawl surveys are available, which can be used to estimate the functional response curve at different scales. To correctly scale up and estimate the global process characteristics from local characteristics, it is important to know the cause and the scale of the heterogeneity of the whole system. This result reinforces findings from other field and theoretical studies (Bergström et al. 2006; Melbourne and Chesson 2006; Englund and Leonardsson 2008). In reality, the global-scale responses are of primary interest, as they are used in the global-scale stock assessment. However, our results suggest that scaling up local-scale process characteristics (e.g., local functional or aggregative responses) in a heterogeneous system can be quite challenging.

Our simulation results also raise an interesting statistical modelling question of how to use local-scale data to estimate the baseline process functions and system heterogeneity si-

multaneously. One statistical approach consists of parameterizing the functional–aggregative response curves based on their ecological meanings, e.g., Holling’s disk equation, and then letting some parameters vary spatially or temporally to capture the underlying heterogeneity. This approach seems promising based on our preliminary modelling attempts on CA-simulated data (unpublished). Indeed, the CA approach provides a valuable tool for generating test data for building and validating new statistical methodologies for studying complex predator–prey interactions.

In our model, the movement strategy of predators dominates the predator–prey interaction in the sense of having a dominating influence on both the functional and aggregative responses compared with the prey-movement strategy. Our simulation results suggest that the predator–prey interaction is largely determined by whether the predator movement is search-oriented. A species such as ATF, which lives demersally, may have less ability to sight and determine where to hunt for prey due to a limited range of prey detection, as opposed to long-range visually oriented predators such as marine seabirds. However, ATF may be successful in finding prey indirectly by choosing areas to hunt that are historically suitable habitats for prey. From this point of view, the search strategy implemented in our model can be explained as a way to enforce positive correlation between predator movements and prey suitability.

On the other hand, both the prey and predator strategies have significant impacts on their own spatial distribution patterns. When prey adopt the avoidance strategy, their spatial entropy quickly declines on the first few days to a lower level, regardless of the predator movement strategy. Similarly, when the predators adopt the searching strategy, their spatial entropy also quickly declines to a lower level, regardless of the prey movement strategy. These results suggest that the searching or avoidance strategy can quickly alter the initial “random” spatial distribution of the prey and predators into configurations consistent with these movement strategies. The entropy of the prey distribution decreases over time, which may be partly caused by a declining prey population. Nevertheless, the entropy of the prey distribution is uniformly smaller when the prey adopt an avoidance strategy rather than when they move randomly. Similarly, the entropy of the predator distribution is uniformly smaller when the predators adopt a searching strategy than when they move randomly. Therefore, both the avoidance and the searching strategies promote aggregating behaviour of the fish and hence reduce the entropy of the spatial distribution. As an alternative to the search strategy, there may be another rule: predators tend to remain where they have just eaten and move (search) randomly when they have not eaten in a while. We have implemented this rule but found that it is not as effective as the search strategy in inducing aggregating behaviour of the fish.

The effect of a landscape feature such as the pool of cold water that forms annually over the Bering Sea shelf also was found to influence both functional and aggregative responses of the predator–prey interaction. When the cold pool is large (cold years), the functional response is lowered by a reduced availability of food and increased competition, as the predators are crowded into a smaller habitat that overlaps partly with that of the prey. Reciprocally, when the cold pool is less extensive (warm years), there is a higher aggregative re-

sponse due to a less crowded habitat for the predators with identical initial abundance, whereas the prey habitat is affected to a lesser degree owing to the design of our CA model. For the ATF in the EBS, part of their population may retreat to the slope of the continental shelf with an expanding cold pool, in which case the initial predator abundance may vary with the size of cold pool. Hence, the cold pool effect suggested by the reported CA outputs should be interpreted with caution as it applies to a closed predator–prey system. Our findings are consistent with earlier results of Kihara and Shimada (1988), who found a higher degree of overlap between ATF and juvenile pollock in warmer conditions in the EBS; see also Hunsicker et al. (2010) for recent related works. The cold pool has been shown to affect predator–prey interactions of other species as well, and complexities of the physical environment such as corridors in the cold pool are also important to consider, especially under the scenario of a shrinking cold pool during a warming climate (Ciannelli and Bailey 2005).

We have deliberately confined the time scale of our analysis to within one feeding season to avoid the complexity of the recruitment process of oceanic fish, which is not relevant to the main questions of our study (scale issues for the functional and aggregative responses and heterogeneity in the spatial distribution of the prey and predator). However, the omission of the recruitment process makes the model unsustainable as the predator will eventually be extinct. Nevertheless, we have balanced the time and abundance constraints of the model to ensure that there are plenty of predators and prey at the end of the season (120 days) so that the simulation results will not be affected by the transience of the model. How to extend the proposed model to incorporate recruitment of oceanic fish is an interesting future research problem.

As ATF mainly eat age-1 juvenile pollock (Mito 1974; Livingston 1993; Aydin et al. 2007), we have mainly viewed the interaction as a single predator–prey coupling. However, many marine systems are characterized by multispecies interactions, e.g., the cod–capelin–herring system in the Barents Sea (Hjermann et al. 2007). Thus, it is an interesting problem to extend the proposed model to include multiple species. Because our model is essentially agent-based, one direct extension is to include different prey species as different kinds of agents in the model. Each kind of prey can be defined by its own set of attributes or parameters such as cell suitability, lifetime, and so on. The movement and interaction rules of species can also be defined to better mimic reality. Interesting predator behaviours such as patchiness (Beyer and Nielsen 1996) and prey-switching can then be simulated. This having been said, it can be seen that the resulting model can be quite complex, and the efficiency of simulation may be dramatically reduced. Some simplifications may be made, for example, no competition between the prey species, and the predator dividing its time probabilistically between the different prey species, etc. However, there exist some issues that may prove difficult with which to contend, for example, the species in reality can interact with each other at varying spatial scales over different time intervals (Hjermann et al. 2007).

The CA models developed here may be useful for studying other biological systems and (or) contrasts between multiple

real systems. For example, although the EBS and the Gulf of Alaska (GOA) are neighbouring systems separated by the Alaska Peninsula, the pollock populations in the two regions appear to have different dynamics. For example, in the GOA ATF may have a greater impact on pollock due to the narrow shelf, which restricts the area of available habitat for both species. Interestingly in the GOA age-1 pollock are not predominantly associated with the bottom waters as in the Bering Sea (Duffy-Anderson et al. 2003), which may provide them with a vertically oriented spatial refugium. Hence, an interesting future problem concerns the use of CA models to test various hypotheses to explain the contrasting dynamics between the EBS and GOA systems. However, the setup of the CA model generally requires modification to reflect changes in the configuration and landscape of a studied system, as well as differences in animal behaviour that affect the dynamics. Such modification clearly requires in-depth knowledge about the real system.

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