

Lagrangian modelling studies of Antarctic krill (*Euphausia superba*) swarm formation

Eileen E. Hofmann, A. G. Edward Haskell, John M. Klinck, and Cathy M. Lascara

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A two-dimensional Lagrangian particle model was developed to examine the spatial distribution of Antarctic krill (*Euphausia superba*). The time-dependent location of particles, which represent krill individuals, is determined by random diffusion, foraging activity, and movement induced by the presence of neighbours. Foraging activity is based on prescribed food conditions and is such that krill swim slower and turn more frequently in areas of high food concentration. The presence or absence of neighbours either disperses krill, if the local concentrations become too dense, or coalesces krill, if concentrations become too dilute, respectively. Predation on krill is included and affects swarm characteristics by removing individuals. Sensitivity studies indicate that the rate of krill swarm formation and the total number of swarms formed are determined primarily by foraging response and nearest neighbour sensing distance. Simulations using food distributions that are representative of those encountered at boundaries, such as fronts, mesoscale eddies, or the sea ice edge, show that foraging activity can produce rapid swarm formation. Results from other krill swarm models show that attraction between individuals is the primary mechanism producing krill swarms. However, the parameterizations for krill interactions used in those models and that used in this model differ, thereby implying different biological dynamics. Thus, parameterization of the basic interactions in krill swarm models remains to be defined.

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E. E. Hofmann and J. M. Klinck: Center for Coastal Physical Oceanography, Crittenton Hall, Old Dominion University, Norfolk, VA 23529, USA (e-mail: hofmann@ccpo.odu.edu). A. G. E. Haskell: Research Systems, Inc., 4990 Pearl East Circle, Boulder, CO 80301, USA. C. M. Lascara: 192 Ballard Court, Suite 300, Virginia Beach, VA 23462, USA. Correspondence to E. E. Hofmann: tel: +1 757 683 5334; fax: +1 757 683 5550; e-mail: hofmann@ccpo.odu.edu.

Introduction

Many species of marine animals form under-dispersed, non-random groupings that are termed schools, aggregations, and swarms. The mechanisms underlying the development of these formations have been the subject of many studies (see Okubo (1986) and Flierl *et al.* (1999) for reviews). Factors related to improved foraging and feeding ability, enhanced reproduction, protection from predators, social behaviour, and environmental conditions are cited as mechanisms that result in formation of animal groupings. The relative contribution of these processes has been examined primarily through mathematical modelling studies that make use of limited descriptive and experimental observations (e.g. Okubo, 1986; Flierl *et al.*, 1999).

Antarctic krill (*Euphausia superba*) is notable among marine crustaceans for its ability to form large aggregations (Hardy and Gunther, 1935; Marr, 1962). Descriptions of krill aggregations were limited to a few underwater (e.g.

Ragulin, 1969) and shipboard observations (e.g. Mauchline, 1980a) until the mid-1970s when hydroacoustic technology became available, and which provided the ability to classify euphausiid aggregations and to estimate approximate densities (Mauchline, 1980b; Kalinowski and Witek, 1985; Miller and Hampton, 1989; Hewitt and Demer, 2000). Awareness of the many forms of Antarctic krill aggregations resulted in development of a conceptual framework (Murphy *et al.*, 1988) that placed the range of space and time scales over which the different Antarctic krill aggregations interact in the context of the structure and function of the Antarctic marine ecosystem. A basic idea arising from this analysis is that krill swarms, which are aggregations with no parallel orientation that exist on time scales of hours to days and space scales of 10s to 100s of meters, form the basic unit of organization for this species.

Distinguishing between the factors that trigger a swarm (proximate causes) and those that are adaptive advantages of aggregation formation (ultimate effects) (Miller and

Hampton, 1989) is important in understanding how swarms form. The proximate causes put forward for the formation of krill swarms are response to light, proximity of phytoplankton (food), physiological stimuli, reproduction, and hydrographic mechanisms (Ritz, 1994; Siegel and Kalinowski, 1994). These factors involve an active response by the krill that in turn triggers the formation of a swarm.

The observational and experimental data available for defining the proximate causes causing swarm formation by Antarctic krill are from limited *in situ* (Hamner et al., 1983, 1989; Stretch et al., 1988), laboratory-based (Strand and Hamner, 1990), and correlative (Weber and El-Sayed, 1985; Weber et al., 1986; Levin et al., 1988; Morin et al., 1988) studies. The difficulties associated with observing krill swarms make mathematical models an important tool for investigating swarm processes. The existing models are largely based on reaction-diffusion equations that include parameterizations for krill growth and density-dependent attraction of krill (Morin et al., 1988; Grünbaum, 1994; Zhou and Huntley, 1996; Azzali et al., 1999). These studies show the importance of non-random forces, such as attractive forces between individuals, in triggering and maintaining a krill swarm.

This study presents a two-dimensional Lagrangian model designed to simulate Antarctic krill swarm formation in response to specific biological and physical processes that have been suggested as proximate causes for swarm formation. Random displacement, neighbour-to-neighbour interaction, and response to food gradients are included in the model and predation is externally imposed to remove individual krill (Figure 1). The equations and parameterizations used in the krill swarm model are described in the next section. The sensitivity of the simulation results to model parameters and the role of environmental structure in triggering krill swarm formation are examined. The discussion section places the model-derived results within the context of observations and other models developed to investigate krill swarm processes.

Model description

Governing equations

The time-dependent location of an individual Antarctic krill (i) in two horizontal spatial dimensions, X and Y, is assumed to be governed by:

$$\frac{dX_i}{dt} = D_i^x + F_i^x + N_i^x \quad (1)$$

$$\frac{dY_i}{dt} = D_i^y + F_i^y + N_i^y, \quad (2)$$

where the terms on the right side of Equations (1) and (2) represent physical diffusion, foraging motion, and motion induced by the presence of other individuals, respectively.

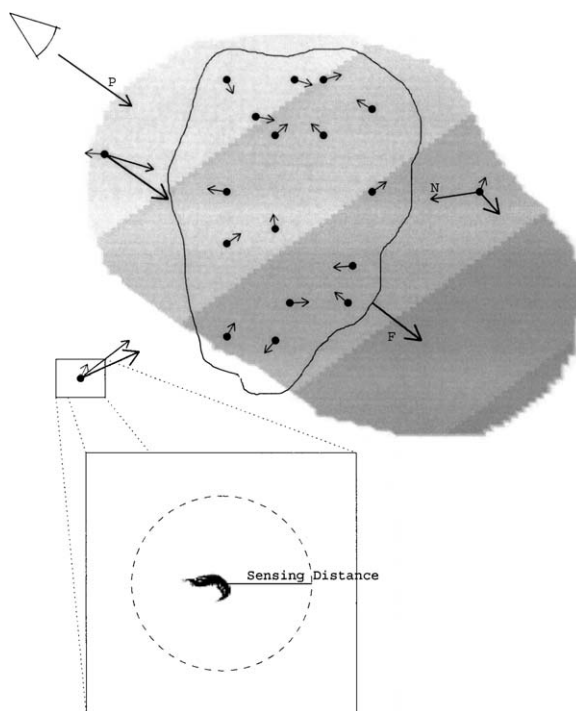


Figure 1. Schematic showing the processes included in the krill swarm model and the sensing ambit of the individual krill. Filled circles indicate individuals and the continuous thin line indicates a swarm. Forces acting on individual krill are neighbour-to-neighbour interactions (arrows designated by N), random diffusion (small arrows), proximity to food (arrows designated by F), and predation (P, upper left). The size of the arrow indicates the strength of force acting on an individual krill. Shading indicates a gradient in food concentration with darker shading representing higher concentrations.

Physical diffusion of krill individuals is a random process and is parameterized by a maximum diffusion speed, D^{\max} , and a random directional coefficient (β_i^x, β_i^y), as:

$$(D_i^x, D_i^y) = D^{\max} (\beta_i^x, \beta_i^y) \quad (3)$$

The range of values used for D^{\max} (Table 1) are representative of those used in other models of krill swarm formation (Morin et al., 1988). The random directional coefficient is determined for each krill individual at each time interval and is selected randomly from a distribution between -1 and 1 .

Foraging motion is represented in terms of a foraging speed, V^f (food, t), and direction of movement, α , as:

$$(F_i^x, F_i^y) = V^f(\text{food}, t) (\cos(\alpha_i), \sin(\alpha_i)) \quad (4)$$

where foraging speed is dependent on ambient food concentration and time and the direction of movement is measured as the angle from the x axis.

Krill swim slower in regions of high food concentration (Price, 1989) and the foraging speed (Table 1) is

Table 1. Definition, units, and values of the parameters used in the krill swarm model. For the parameters for which a range of values was used, the value used for the reference simulation is given in parentheses.

Parameter	Definition	Units	Value
D_i	Diffusion motion	m s^{-1}	Calculated
F_i	Foraging motion	m s^{-1}	Calculated
N_i	Neighbour-induced motion	m s^{-1}	Calculated
D^{\max}	Maximum diffusion speed	m s^{-1}	0.002–0.010 (0.005)
β	Direction coefficient	None	–1 to 1
$V^f(\text{food}, t)$	Foraging speed	m s^{-1}	0.02–0.30 (0.10)
α_i	Foraging angle	Radians	$-\pi/2$ to $\pi/2$
mFA	Minimum turning angle	Radians	$-\pi/4$
λ	Uniform random turning modifier	None	0 to 1
FR	Increased turning due to food	Radians	0 or $\pi/2$
δ	Turning potential	None	0.70–0.97 (0.90)
Ψ	Turning threshold	None	0 to 1
N^{\max}	Maximum neighbour-induced speed	m s^{-1}	0.010
κ_i	Neighbour-induced response coefficient	None	–1 to 1
ρ^{local}	Local swarm density	Number m^{-3}	Calculated
ρ^{target}	Target swarm density	Number m^{-3}	50–200 (100)
$\rho^{\text{repulsive}}$	Repulsive swarm density	Number m^{-3}	1 500
ζ	Sensing distance	m	0.20–0.35 (0.25)
P	Specific predation rate	d^{-1}	Calculated
P_0	Maximum specific predation rate	d^{-1}	0.0–0.2 (0.0)
γ	Predation rate constant	None	0.03

representative of measured values. Krill continue along a given path until they encounter food conditions that produce a change in direction and at high food concentrations tend to turn more frequently, presumably to stay within a food patch (Hamner *et al.*, 1983; Price, 1989). This behaviour is obtained by expressing the foraging angle, α_i , as:

$$\alpha_i^{\text{new}} = \alpha_i^{\text{old}} + \text{mFA} + \lambda \text{FR}, \quad (5)$$

where the new foraging angle for individual i is based on the old foraging angle and a random angle that is constructed from a minimum turning angle, mFA, and an additional turning due to the presence of food, FR. The uniform random variable, λ , is in the range of 0 to 1.

The additional turning that occurs in response to food, FR, is determined by comparisons of a turning threshold (δ) and turning potential (Ψ). The parameter δ is between 0.7 and 0.97 (Table 1) and controls the fraction of the krill population that does not turn in response to food. The value of δ used in the reference simulation (described below) is 0.9, which means that 10% of the krill will turn in response to food, i.e. their potential turning range is enhanced by the presence of food. The turning potential allows additional turning at specific times or locations, which serves as a proxy for food availability. If the value of Ψ is greater than δ , then the individual turns by the additional amount based on FR.

Theoretical arguments, which are based on limited observations, suggest that krill try to maintain a target swarm

density, but in doing so maintain a specified distance between individuals. Thus, there is a tendency for individuals to react to the presence of neighbours, as well as to the overall density of the swarm. This motion consists of an attractive/repulsive tendency between individuals and the swarm as:

$$(N_i^x, N_i^y) = N^{\max}(\kappa_i^x, \kappa_i^y) \quad (6)$$

where N^{\max} is the maximum neighbour-induced speed and κ_i is the response of individual krill to swarm density.

The value chosen for N^{\max} (Table 1) is consistent with observations of krill interactions (Hamner *et al.*, 1983, 1989; Strand and Hamner, 1990). The direction of motion, κ_i , is calculated from the local swarm density (ρ^{local}), a target swarm density (ρ^{target}), and a repulsive swarm density ($\rho^{\text{repulsive}}$) as:

$$\rho^{\text{local}} < \rho^{\text{target}}, \quad \text{up density gradient} \quad (7)$$

$$\rho^{\text{local}} > \rho^{\text{repulsive}}, \quad \text{down density gradient} \quad (8)$$

$$\rho^{\text{target}} < \rho^{\text{local}} < \rho^{\text{repulsive}}, \quad \text{random motion.} \quad (9)$$

The density gradient is determined by comparing values of local swarm density on either side of an individual, $\rho^{\text{local}+}$ and $\rho^{\text{local}-}$, and then assigning κ_i a value of either 1 or –1, depending on the gradient and direction. The direction of

krill movement is determined by the sensing distance (ζ), which specifies the ambit for detecting other individuals. Krill within the sensing distance move towards one another to satisfy the specified target swarm density, which is then maintained by interactions between the sensing distance, target swarm density, and repulsive swarm density. The values chosen for the sensing distance and target and repulsive densities (Table 1) are determined primarily from model sensitivity studies, but they are consistent with limited observational measurements (Hamner *et al.*, 1983; Strand and Hamner, 1990). At times when krill individuals are not following a gradient and are moving randomly, the values of κ_i^x and κ_i^y are set to zero.

Predation, such as from penguins or seals, removes individual krill, which reduces krill density. The assumption made in formulating predation is that krill predators are more effective on swarms than on solitary krill and that predation on an aggregation will maximize the number of krill caught. The potential advantages of a krill swarm in avoiding predation via increased surveillance capacity and the ability to respond with concerted motion (O'Brien, 1987a) are not included. The specific predation rate (P) is formulated as:

$$P = P_0(1 - e^{-\gamma\rho^{\text{local}}}), \quad (10)$$

where P_0 is the maximum predation rate (Table 1) and the rate at which this is approached is determined by γ and the local swarm density.

Model implementation

The two-dimensional Lagrangian model was solved numerically using an Eulerian integration scheme with a time step of 10 s. Sensitivity studies showed that this time step preserved the properties of the movement of individual krill and swarm integrity. The simulations were initialized with 10 000 individuals which were uniformly distributed in the 1000 m by 1000 m model domain.

The first set of simulations used the constant coefficient values that are given in Table 1. However, in subsequent simulations, the sensing distance, target swarm density, foraging speed, foraging angle, and specific predation rate were allowed to be time-dependent (Figure 2). The structure of the time dependency in these parameters is discussed with specific simulations, which are described in the following section.

Results

Reference simulation

The reference simulation used time-invariant parameters (Table 1) and an initial uniform distribution of individuals (Figure 3A). Initial swarm formation is rapid (Figures 3B, 4A), as the krill combine into many small swarms containing only a few individuals. By the end of day 1, the many small swarms have coalesced into a reduced number of larger swarms (Figures 3B, C, 4A). At the end of 2 days

(Figure 3D), the initial uniform distribution has evolved into 121 swarms, each containing an average of 81 individuals (Table 2).

The fraction of krill that are found in the swarms (Figure 4B) increases rapidly during the first day of the simulation as individuals move towards each other and towards regions of increased krill density. By the end of the simulation, most individuals are in swarms.

Sensitivity simulations

An important parameter in the krill swarm model is the distance over which the krill sense other individuals. The value used in the reference simulation (Table 1) is based on laboratory-based experiments that used few krill individuals (Hamner *et al.*, 1983) and this sensing distance may not be representative for all krill and times. Thus, the sensing distance was varied over a range that represents a 20% to 40% change from the value used for the reference simulation (Table 1).

Increasing the sensing distance, which makes krill individuals more aware of neighbours, results in rapid initial formation of many small krill swarms (Figure 4A), which then coalesce into larger swarms. The final number of swarms is slightly less than that obtained from the reference simulation (Table 2, Figure 4A). Entrainment of krill into swarms is rapid, with essentially all of the krill being associated with a swarm within one-half day (Figure 4B). As a comparison, decreasing the sensing distance, which reduces awareness of nearest neighbours, results in essentially no swarm formation and the krill remaining as individuals (Figure 4A). This scenario produces many small swarms with an average density of only 20 individuals per swarm.

Once krill begin to coalesce into swarms, the minimum number of krill m^{-3} needed to maintain a swarm determines the number of swarms that are formed over time. The value chosen for the reference simulation represents an average of many observations. Swarms with densities higher and lower than this value have been observed (Siegel and Kalinowski, 1994) and the consequence of different target densities on total number of swarms bears examination. Decreasing the target density of the swarm (Table 1) results in swarm formation over the first day that is similar to that obtained during the reference simulation (Figure 4C). However, decreasing the minimum of individuals needed for a swarm makes formation more difficult and results in many small swarms (Table 2). The total number of swarms stabilizes in the second day of the simulation at a value that is higher than obtained in the reference simulation (Figure 4C). In this case, 95% of the krill are in a swarm at the end of the 2-day simulation (Figure 4D).

Increasing the minimum target density makes swarm formation more difficult, which results in fewer swarms forming during the first day of the simulation (Figure 4C). These swarms continue to coalesce and by the end of the simulation the total number of swarms is less than that

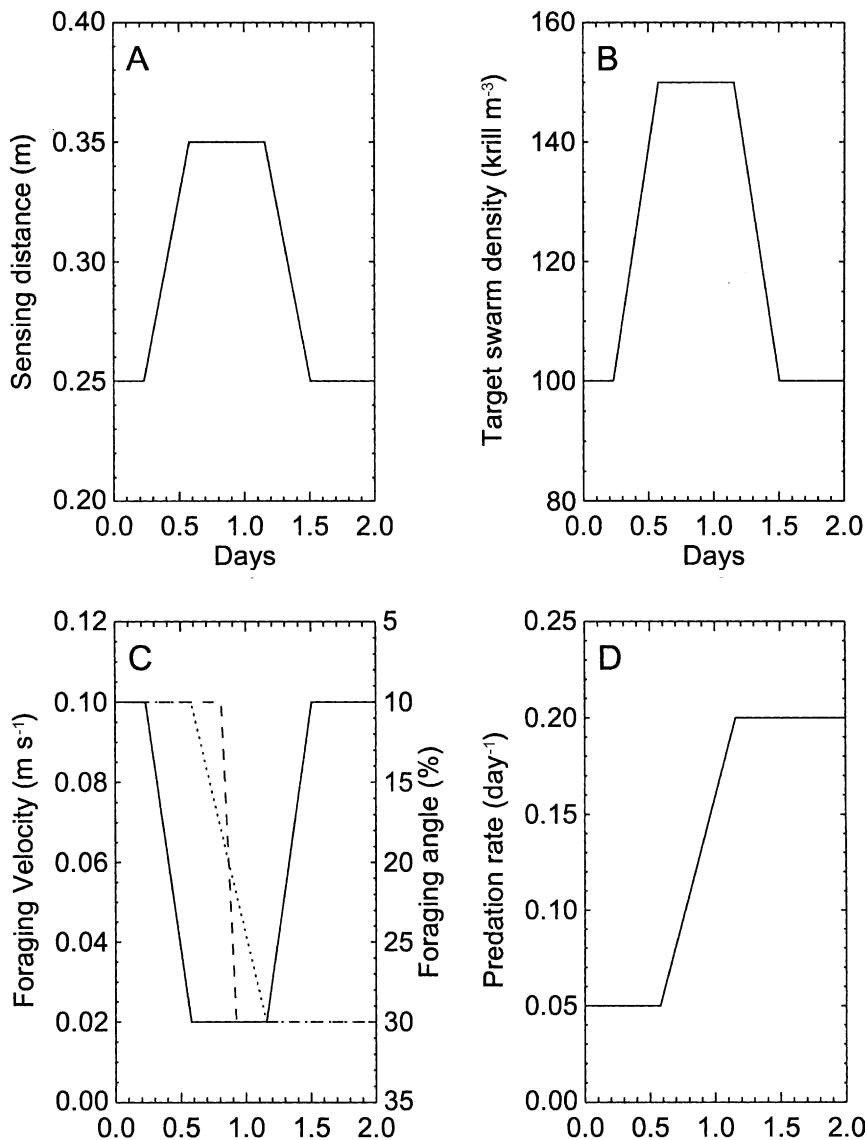


Figure 2. Idealized time dependence used to specify changes in krill (A) sensing distance, (B) target swarm density, (C) swimming velocity and turning rate, and (D) swarm predation. The time dependence of swimming velocity and turning rate are intended to represent encounters with food gradients that are abrupt (dashed line), gradual (dotted line), and temporary (continuous line).

obtained in the lower minimum density case, but more than obtained in the reference simulation (Table 2). Most of the krill individuals are in swarms by the end of 2 days (Figure 4D).

The role of random diffusion in krill swarm formation was examined by increasing and decreasing the maximum diffusion speed (Table 1). Increased diffusion prevents the formation of many little swarms during the first day of simulation (Figure 4E) and results in fewer swarms at the end of the simulation. Fewer individuals are included in swarms (Figure 4F) and by the end only 90% of the initial individuals are in a swarm. In contrast, reduced random diffusion allows for formation of many small swarms

initially (Figure 4E) and inclusion of most individuals in a swarm at the end of the 2-day simulation (Figure 4F).

Constant predation and constant food simulations

Predation rate was varied to determine its effect on swarm characteristics. High and low rates (Table 2) have more effect on the number of individuals found in a swarm rather than on the number of swarms formed (Figure 5A, B; Table 2). A high predation rate reduces the fraction of the animals found in a swarm.

Reduction in food concentration results in the formation of slightly fewer krill swarms in 2 days, relative to the

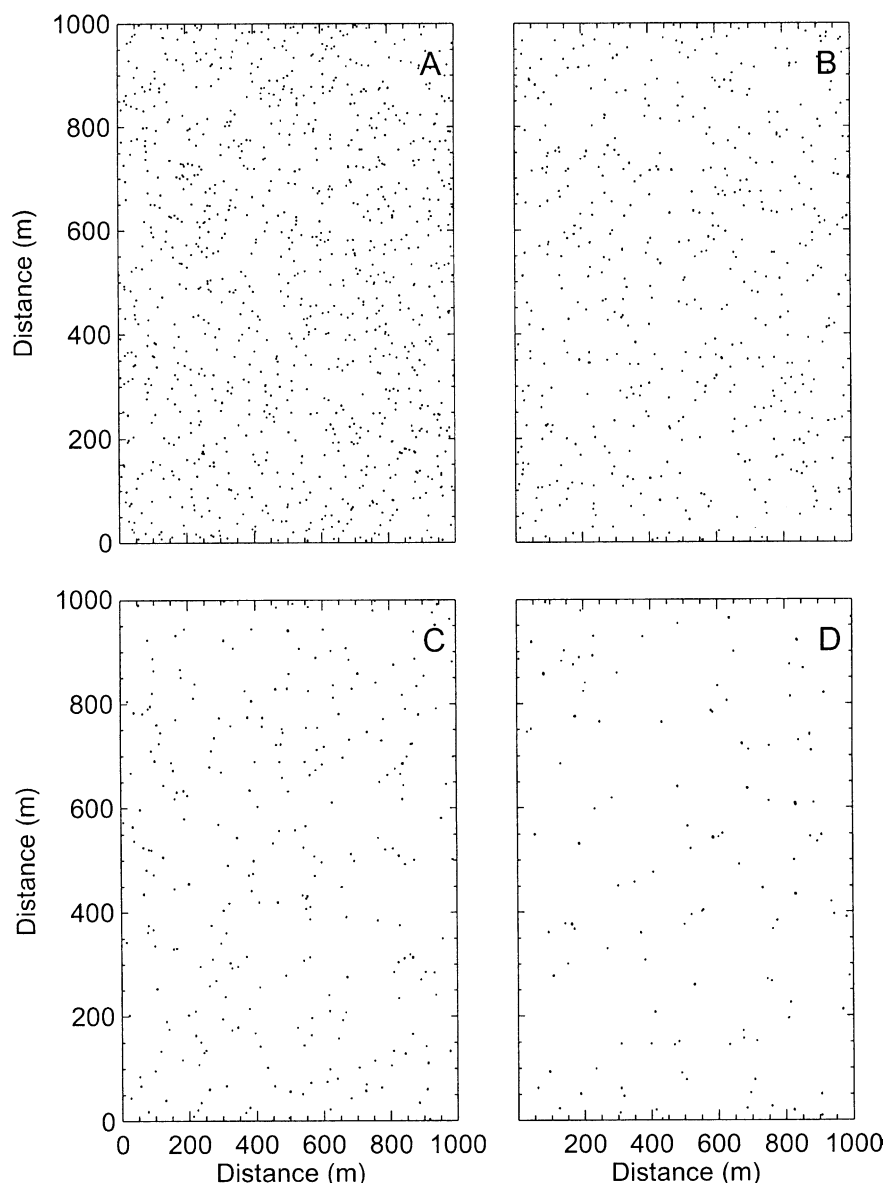


Figure 3. Simulated time evolution of krill swarm distribution in two dimensions arising from the (A) initial distribution after (B) 0.5 days, (C) 1 day, and (D) 2 days.

reference simulation (Figure 5C). Increased food concentration, in contrast, results in the formation of many additional swarms (Figure 5C) and reduction in the fraction of krill found in a swarm (Figure 5D). The occurrence of higher food affects the krill foraging speed and foraging angle such that the krill slow and remain in a given location longer. As a result, increased food produces many small swarms with few individuals per swarm (Table 2).

Time-dependent parameter simulations

Increasing the krill sensing distance over one day (Figure 2A) produces a transient increase in the number of krill

swarms (Figure 6A), which are small and contain few individuals. Most of the krill are in swarms by the end of one day (Figure 6B). However, this increase is followed by a reduction in the overall number of swarms as the small swarms coalesce into larger swarms. The number of swarms at the end of 2 days is similar to that obtained from the reference simulation (Table 2, Figure 6A).

A one-day increase in the desired swarm target density (Figure 2B) results in a small time offset in the peak value of the number of swarms (Figure 6C), relative to the reference simulation. The number of swarms after 2 days is higher than that obtained for the reference simulation,

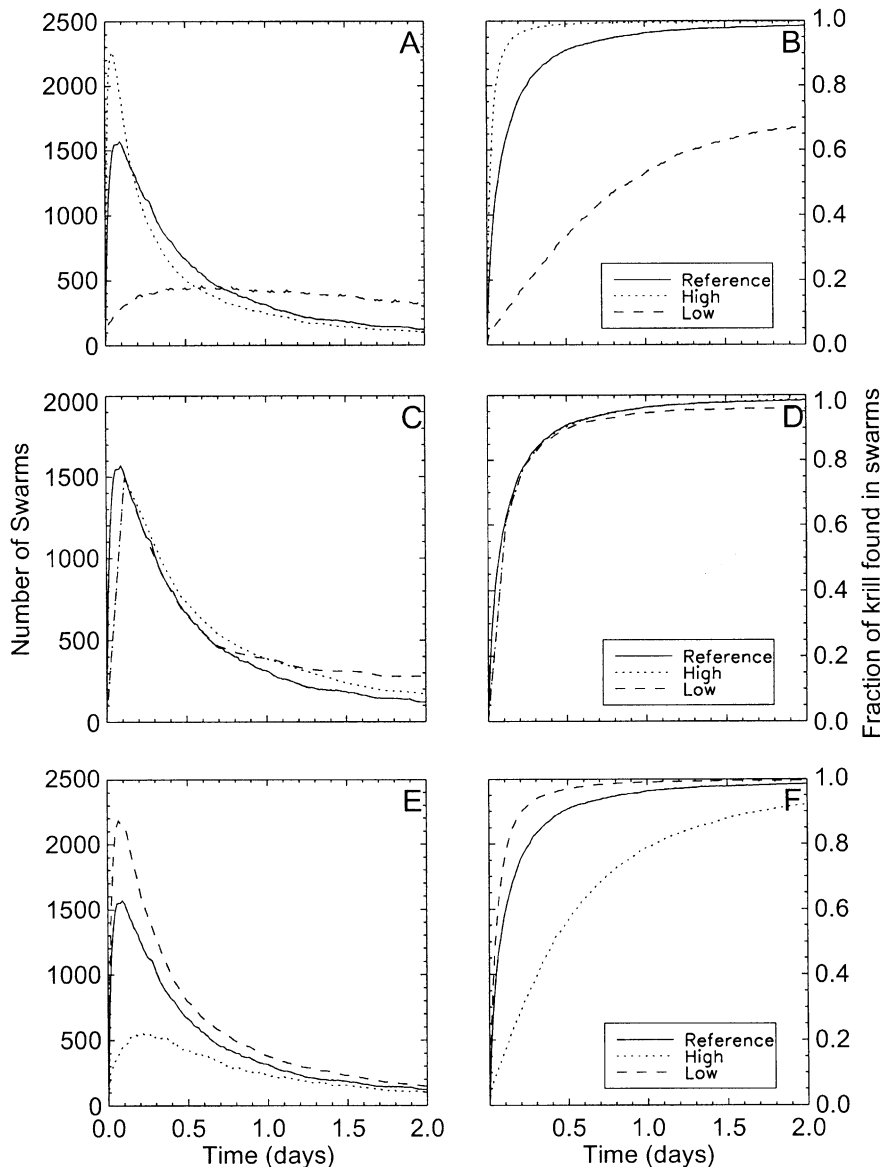


Figure 4. Simulated time development of krill swarm formation and the fraction of krill found in swarms that results from changes in the nearest neighbour sensing distance (A, B), changes in the density threshold of the krill swarm (C, D), and changes in the magnitude of the maximum random diffusion speed (E, F). The corresponding results from the reference simulation are shown for comparison.

but the number of animals per swarm is less (Table 2, Figure 6C). Essentially all krill are found in swarms after 2 days and the rate at which they enter swarms is similar to that obtained from the reference simulation (Figure 6D).

Time-varying food environment and predation simulations

The effect of a variable food environment on swarm formation was tested with simulations that included abrupt, gradual, and temporary changes in food concentration (Figure 2C). The first two scenarios represent conditions that may be encountered across a frontal boundary or when

moving into or out of a mesoscale eddy containing a different food concentration. The third scenario represents a transient event, such as a small patch of food.

Encountering abrupt or gradual increases in food concentration results in formation of more swarms relative to the reference simulation (Figure 7A). Increased food results in many small swarms with few individuals per swarm (Table 2). This pattern is reflected in the fraction of krill in swarms, with not quite 100% of the krill being in swarms (Figure 7B).

A one-day decrease in the foraging velocity and increase in turning angle produces more swarms than obtained with

Table 2. Comparison of the krill swarm simulations in terms of the final number of swarms formed, the percent change in number of swarms relative to the reference simulation, the average density of individuals per swarm, and the average swarm size. The figure number showing the individual simulation results is also indicated. The value of the coefficient that was varied for each simulation is shown in parentheses.

Simulation	Final number of swarms	% Change	Average density per swarm number (swarm) ⁻¹	Average swarm length (m)	Figure number
Reference	121	—	81	0.8	
High sensing distance (0.35 m)	103	−15	97	0.7	4A, B
Low sensing distance (0.20 m)	335	177	20	0.3	4A, B
High target swarm density (200 krill m ⁻³)	169	40	58	0.5	4C, D
Low target swarm density (50 krill m ⁻³)	279	131	34	0.9	4C, D
High random movement (0.010 m s ⁻¹)	103	−15	89	0.4	4E, F
Low random movement (0.002 m s ⁻¹)	149	23	67	0.4	4E, F
High predation (0.20 d ⁻¹)	125	3	68	0.6	5A, B
Low predation (0.05 d ⁻¹)	128	6	75	0.9	5A, B
High food (0.02 m s ⁻¹ , 30%)	495	309	19	0.3	5C, D
Low food (0.30 m s ⁻¹ , 3%)	83	−31	120	1.0	5C, D
Variable sensing distance (Figure 2A)	107	−12	93	0.5	6A, B
Variable target swarm density (Figure 2B)	134	11	74	1.1	6C, D
Gradual food increase (Figure 2C)	283	134	34	0.8	7A, B
Rapid food increase (Figure 2C)	304	151	32	0.8	7A, B
Temporary food increase (Figure 2C)	214	77	46	0.6	7C, D
Gradual food increase with predation (Figure 2C)	255	111	35	0.7	8A, B
Rapid food increase with predation (0.10 d ⁻¹ , Figure 2C)	272	125	33	0.7	8A, B
Predation with one food environment (Figure 2D)	137	13	64	0.6	8C, D
Predation with two food environments (Figure 2D)	671	455	12	0.2	8E, F

the reference simulation (Figure 7C), but not as many as produced by abrupt or gradual changes in these parameters (Table 2). However, once the foraging velocity and angle increase and decrease, respectively, the number of krill swarms decreases as the smaller swarms coalesce into larger swarms (Figure 7C). As a result, after 2 days, essentially all of the krill are found in swarms (Figure 7D).

The addition of a constant predation rate to the time-varying food environment results in the formation of more swarms than obtained in the reference simulation (Figure 8A). However, predation results in fewer swarms than in the food-only scenario (Table 2) and a smaller fraction of the total krill are in swarms at the end of 2 days (Figure 8B). A gradual increase in predation rate over one day results in swarm formation that is not substantially different from that obtained with the reference simulation (Figure 8C) because of the similar food environments used for the two simulations. However, the fraction of krill found in the swarms is reduced (Figure 8D) due to removal of individuals. In contrast, increased predation rate and a large gradient in food concentration produce many small swarms (Figure 8E) with few individuals (Table 2). The effect of predation is to reduce the fraction of krill in swarms (Figure 8F).

Discussion and summary

General characteristics

Sensing distance and response to the food environment, which is included in the model as changes in foraging velocity and foraging angle, are the dominant controls on the number of swarms formed and on the number of individuals in a swarm (Table 2). Low sensing rates and high food concentration have the largest effect on swarm formation. The neighbour-induced velocity (N^{\max}) is an order of magnitude less than the foraging velocity and consequently this process only becomes important for individual krill not found in a swarm. The effect of changing N^{\max} by $\pm 100\%$ produced no significant differences in the simulation results. Random diffusion and changes in target swarm density provide modifications to the overall swarm formation pattern. However, high diffusion rates can overcome the biological attraction and disperse swarms. Predation removes individuals, thereby reducing the average krill density per swarm and high rates of predation disrupt swarm formation, resulting in many small swarms.

For the majority of the simulations, the maximum number of swarms was reached within the first 0.25 days of the simulation. The initial coalescing into numerous small swarms is driven primarily by the krill sensing

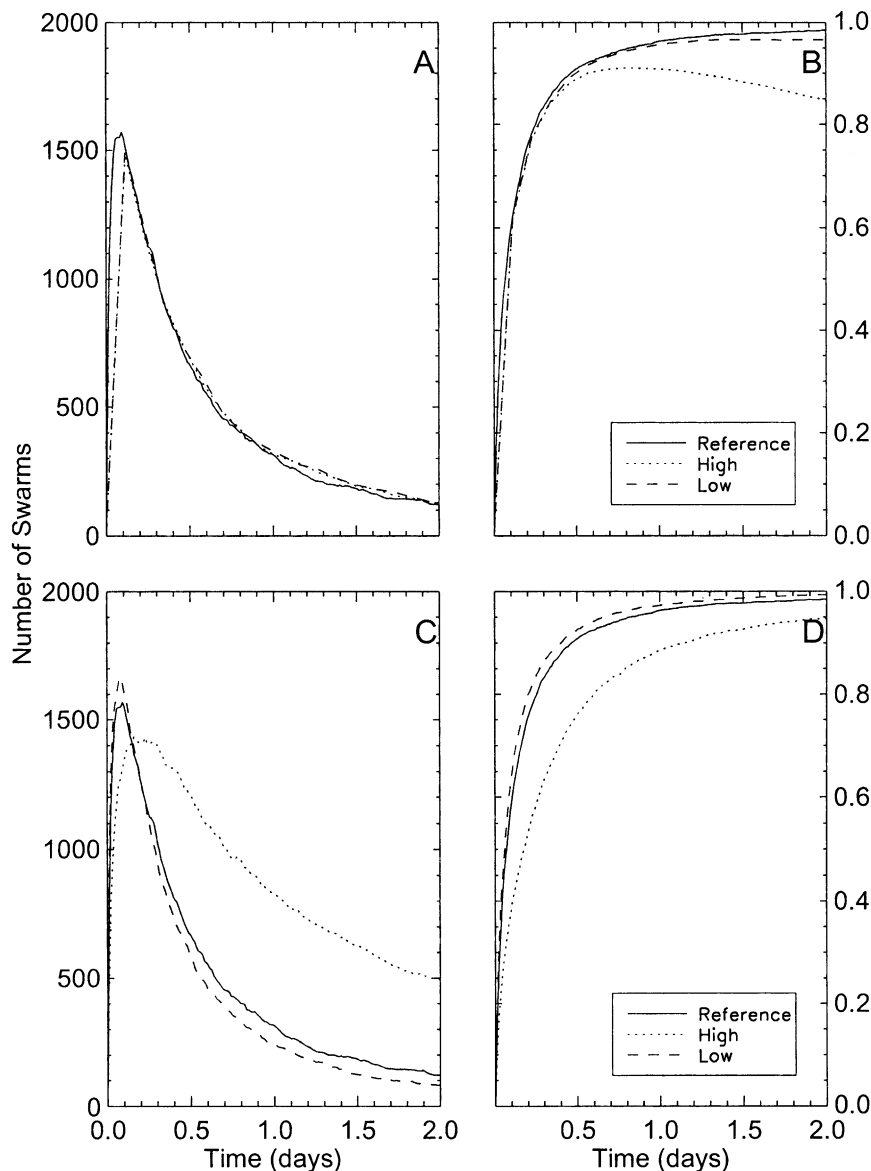


Figure 5. Simulated time development of krill swarm formation and the fraction of krill found in swarms that results from changes in the rate of predation (A, B) and changes in the ambient food concentration (C, D). The corresponding results from the reference simulation are shown for comparison.

distance and the desire to achieve a target swarm density. Once these conditions were satisfied, other factors, such as response to food or predation, became the primary determinants of swarm formation.

The relative effect of food and predation on swarm formation is illustrated by the two-environment simulation (Figure 8). In this case, predation removes krill primarily from the high food environment, which has more swarms. However, once stabilized, the ratio of the number of krill found in the high food environment to that of the number of krill found in the low food environment remained constant

throughout the simulation. The constant ratio is maintained by migration of krill across the food boundary. Many small swarms are produced as krill move in response to the food gradient and swarm density. The smaller swarms experience lower predation, which counteracts the predation effect that is causing the movement. The effect of uneven predation on large and small swarms in regions of a food gradient allows the swarms to stabilize at smaller size. Thus, small swarms may be a mechanism to counter predation.

The predation formulation used in the model is based on a density-dependent assumption, with predation increasing

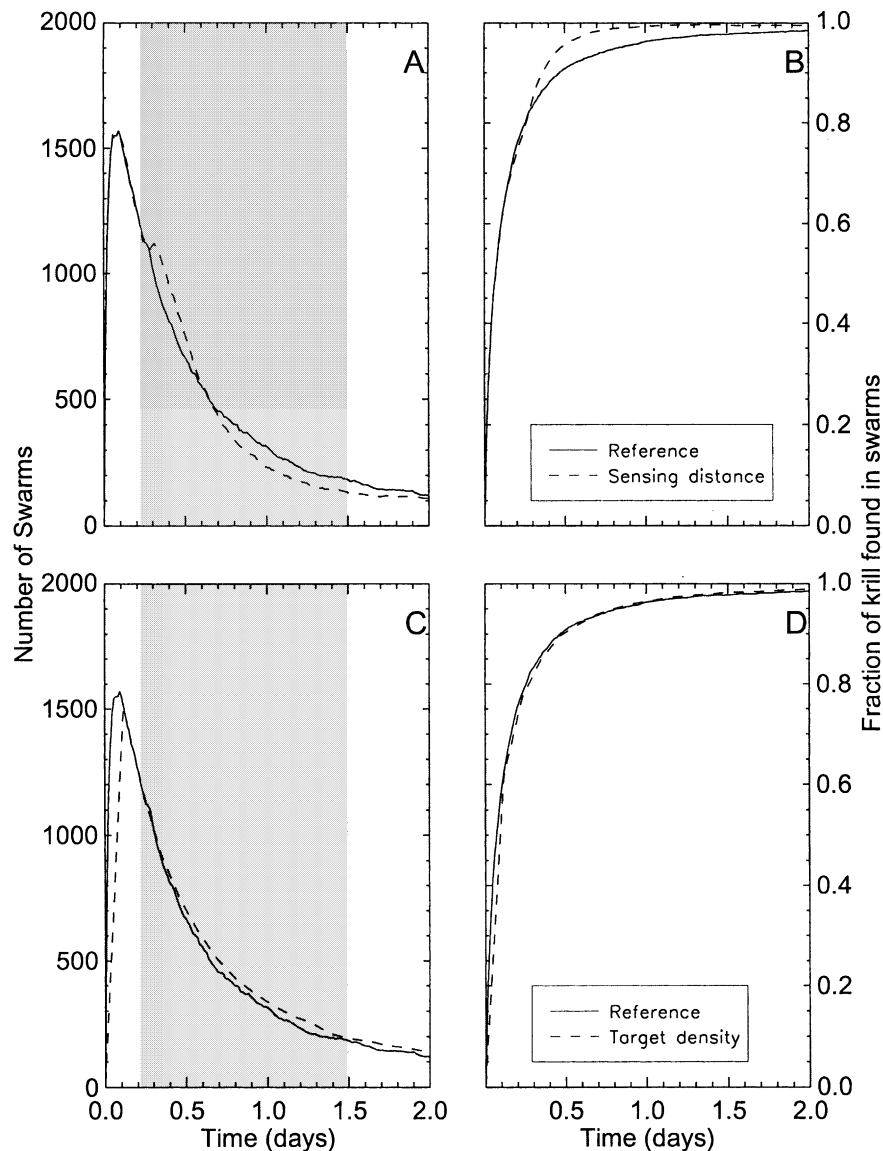


Figure 6. Simulated time development of krill swarm formation and the fraction of krill found in swarms that results when the nearest neighbour sensing distance is temporarily enhanced (A, B) and target swarm density is temporarily increased (C, D). The corresponding results from the reference simulation are shown for comparison. The shading indicates the period of the simulation when the model parameters are modified.

as local swarm density increases. However, the nature of the predator–prey relationship is likely more complex. For example, penguins and seals can feed on individual krill, which indicates that krill aggregations are not needed for predation to occur. Also, large dense aggregations may have a higher predation detection capacity and prey escape response, which is communicated via the swarm (e.g. O’Brien, 1987a; Daly and Macaulay, 1991). Some predators are not able to consume prey that is aggregated in high densities because of the distraction provided by many moving individuals (e.g. Ritz, 1994). Also, individuals that are highly

aggregated may have lower encounter rates with predators than those that are more homogeneously distributed. The role of these different predator–prey interactions in formation of krill swarms remains to be tested with models and observations.

Relationship to observations

Laboratory and *in situ* observations of krill behaviour are limited and observations of the time evolution of krill swarms are non-existent. Therefore, it is difficult to make

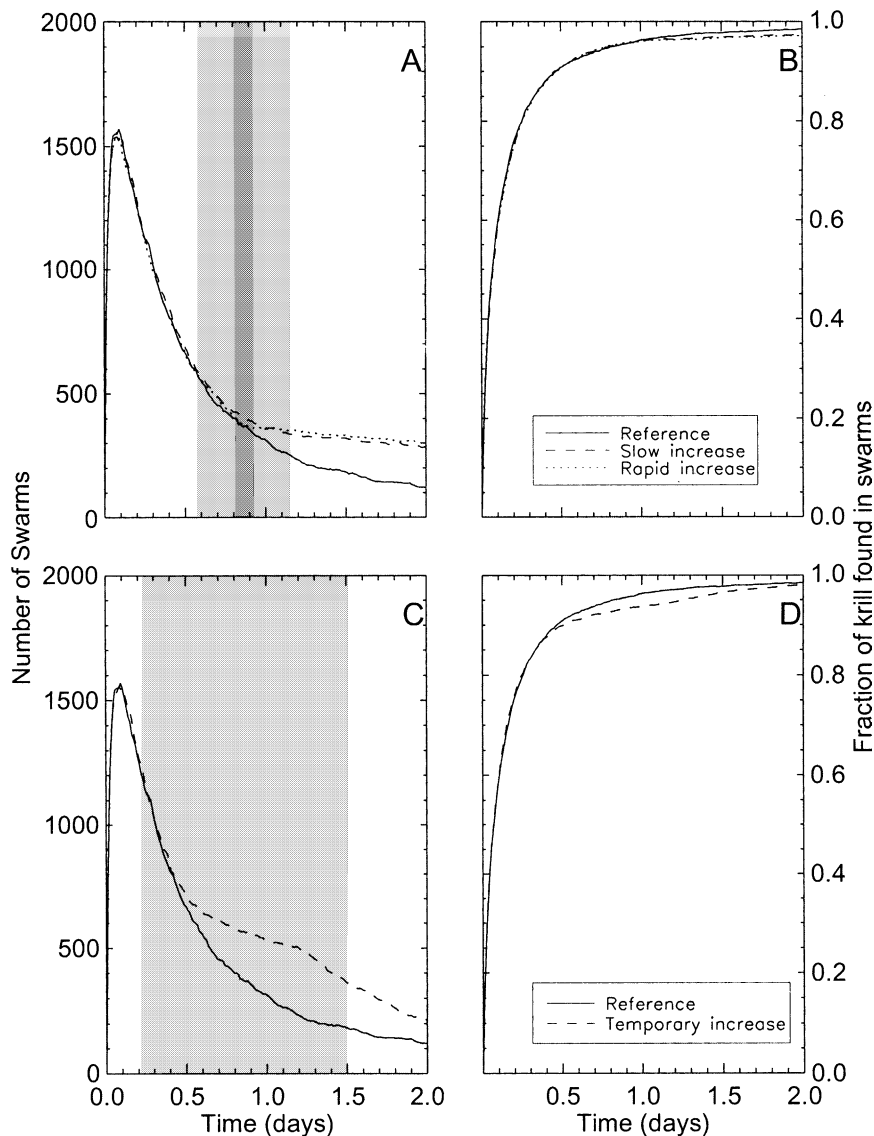


Figure 7. Simulated time development of krill swarm formation and the fraction of krill found in swarms that results when the krill experience rapid and slow increases in food concentration (A, B) and a temporary increase in food concentration (C, D). The corresponding results from the reference simulation are shown for comparison. The shading indicates the period of the simulation when the model parameters are modified, with the darker shading indicating the rapid change in krill swimming velocity and turning rate and the lighter shading indicating the gradual change in these parameters.

direct comparisons between the results of the various simulations and field observations. However, observations do exist from which general comments about krill swarms can be extracted and then compared to the simulation results.

Laboratory observations show that krill do modify their foraging velocity and foraging angle in response to food cues (Hamner *et al.*, 1983; Price, 1989; Strand and Hamner, 1990). Also, direct observations of krill feeding behaviour (Hamner *et al.*, 1983) show that krill do not feed by passive continuous filtration, but rather use area-intensive searching followed by rapid feeding. This behaviour is believed to be

an adaptation that allows krill to rapidly exploit regions of high food concentration. During periods when krill are rapidly swimming, the feeding basket is never opened (Hamner *et al.*, 1983), which suggests that slowing is needed for feeding to begin. The rapid turning that krill exhibit in areas of food increases the likelihood of finding concentrated and patchy food, but at the same time such behaviour is not conducive to remaining in an organized swarm with directed horizontal swimming. Hence, the process of feeding and that of maintaining a coherent swarm are incompatible. This trade-off is seen in the

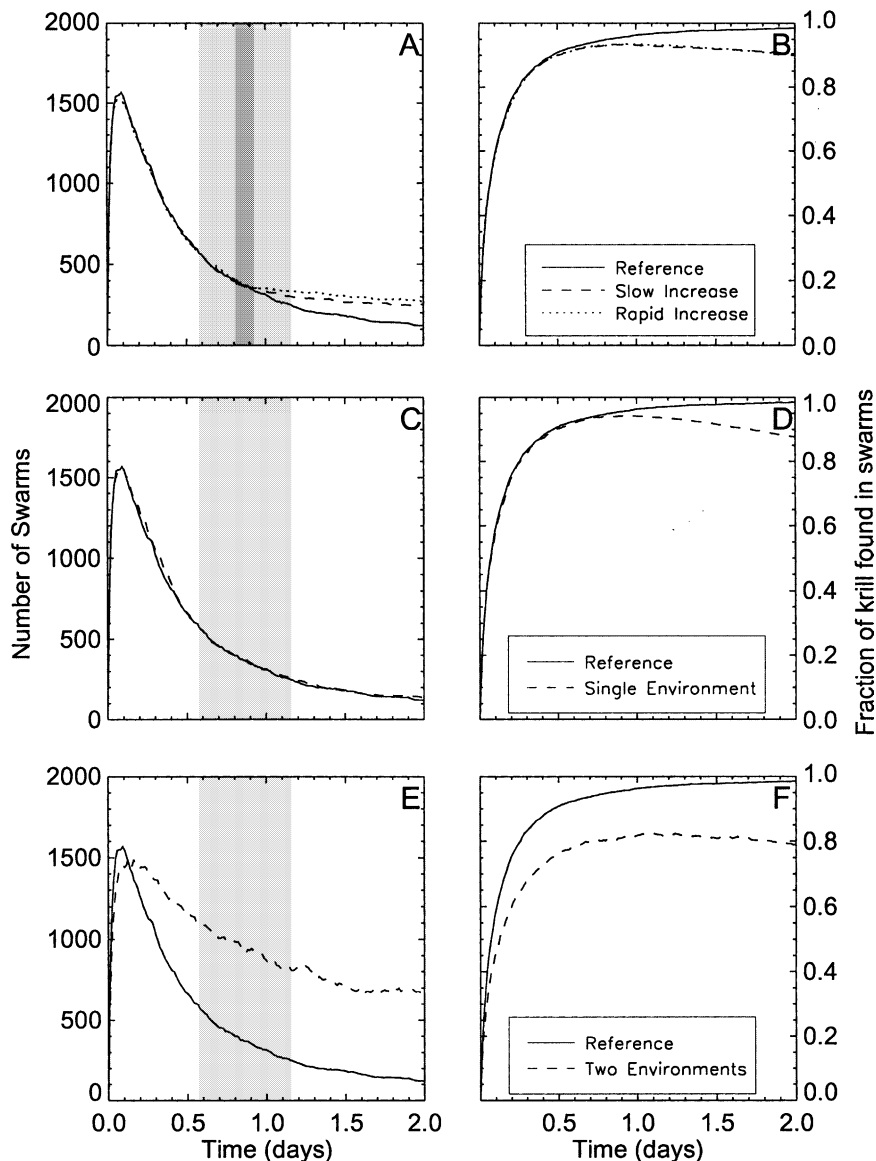


Figure 8. Simulated time development of krill swarm formation and the fraction of krill found in swarms that results when the krill experience slow and rapid increases in food concentration with constant predation (A, B), increased predation in a constant food environment (C, D), and increased predation in two food environments, with the left half of the model domain having normal food and the right half having elevated food (E, F). The corresponding results from the reference simulation are shown for comparison. The shading indicates the period of the simulation when the model parameters are modified. The darker shading in A indicates the period of rapid change in krill swimming velocity and turning rate and the lighter shading indicates the gradual change in these parameters.

simulated time evolution of krill swarms exposed to high versus low food concentrations, with the high food conditions resulting in the formation of small swarms with few individuals.

The simulations offer possible explanations for the processes that may trigger krill swarm formation. Individual krill try to move towards other individuals that are within their sensing distance resulting in formation of krill swarms. However, low sensing distance results in few

simulated swarms, which may be the case when krill are dispersed under sea ice. Observations of under-ice krill swarms (O'Brien, 1987b; Frazer *et al.*, 1997) indicate that these tend to be small with an average of 20–100 individuals. The average swarm density obtained from the low sensing distance simulation is at the lower range of these observations (Table 2).

Krill swarms have been observed at bathymetric boundaries, such as the shelf break (Witek *et al.*, 1988;

Ichii, 1990); at hydrographic boundaries, such as those associated with fronts (Makarov *et al.*, 1988; Witek *et al.*, 1988; Trathan *et al.*, 1993; Ichii *et al.*, 1998) and eddies (Witek *et al.*, 1988); and along ice edges (O'Brien, 1987b; Daly and Macaulay, 1988, 1991; Hamner *et al.*, 1989; Ichii, 1990; Azzali and Kalinowski, 1999). These boundaries are associated with gradients in properties, such as food. The simulations show that encountering a food gradient results in enhanced formation of swarms (cf. Figures 7, 8), with the result being formation of many small swarms. From analyses of hydroacoustic and environmental measurements, Hampton (1985) suggested that small krill swarms are associated with krill that are feeding or digesting. Hampton (1985) further suggested that large krill swarms are associated with animals that are actively migrating. The simulation that resulted in the largest swarm with the highest density of animals was the one that included low food (Table 2). The absence of an environmental cue for food may allow krill to actively form larger swarms that then become dispersed into smaller swarms once food is encountered.

In the krill swarm model, food concentration along a gradient is assumed to be the primary environmental variable to which krill respond. However, the possibility exists that other properties that change dramatically across boundaries, such as temperature, also have an effect on swarm formation. Observed krill distributions do not have a strong correlation with temperature (Weber and El-Sayed, 1985; Weber *et al.*, 1986). Attempts to correlate krill swarms with food concentrations produce significant results only at small spatial scales (Weber *et al.*, 1986; Priddle *et al.*, 1990). However, these studies strongly suggest that krill swarm formation and maintenance is associated with food concentrations. Gradients in other environmental properties, such as light (Strand and Hamner, 1990) and oxygen (Hampton, 1985), have been suggested as contributing factors to the formation of krill swarms. However, observations sufficient to allow quantification of these effects are lacking.

Krill swarm models

Zhou and Huntley (1996) developed a bio-continuum theory to describe the patch dynamics of marine zooplankton. This approach, which partitions animal motion into mean and random components, was used to examine the forces that act on an animal aggregation as a whole and those that act between individual animals. The analyses presented by Zhou and Huntley (1996) show that biological attraction, which acts at the level of individuals, is the primary factor maintaining animal aggregation coherence. Using the model with parameters derived from Acoustic Doppler Current Meter measurements of Antarctic krill distribution, Zhou and Huntley (1994) estimated a biological attraction for krill aggregations of the order of $7.8 \times 10^{-4} \text{ N m}^2 \text{ kg}^{-2}$.

In the development of the bio-continuum theory of patch dynamics, Zhou and Huntley (1996) used analogies to Newtonian gravity by assuming that the attractive force in animal aggregations is proportional to the inverse of the distance squared. This assumption results in a central conservative force that can be expressed in terms of a potential field. Specification of the attractive forces between individuals in this krill swarm model differs in that the attraction between individuals is specified as a velocity that is defined as a step function (an impulsive force), such that inward or outward movement depends only on the separation distance and the local density of individuals. This approach is not expressible in terms of a continuous force function, as was done by Zhou and Huntley (1996).

The bio-continuum approach and the one used in this study have different implications for biological dynamics of krill swarm formation. The bio-continuum approach assumes that there is a weak attractive effect at large distances, which becomes stronger as the distance is reduced. As a result, individuals experience a stronger attractive force the closer they get to one another, i.e. they accelerate towards one another. The impulsive approach assumes that there is a limit to the range of animal perception and that once the animal is inside this limit of perception, it will tend in a particular direction. Once the direction is determined, the animal then moves at a constant speed towards its neighbour.

The reaction-diffusion model developed by Azzali *et al.* (1999) assumes that krill individuals move toward the centre of a swarm with a constant speed that is independent of the distance from the centre of the swarm. Thus, an individual that is infinitely far from the centre of the swarm converges towards the swarm with the same speed as an individual that is near the centre of the swarm. The model used by Azzali *et al.* (1999) applies only within the sensory range of the krill, includes the implicit assumption that all organisms are already in the neighbourhood of the swarm, and does not include explicit dependencies for density-dependent effects, such as crowding or repulsive controls on swarm density. These processes are included via a general diffusive term that serves to disperse krill, and without this effect the krill swarm would become infinitely dense at the centre. Also, the parameter values used by Azzali *et al.* (1999) are representative of a migrating krill swarm and do not allow for variations in speed and behaviour that are associated with changes in the environment. The attractive force parameterization used by Azzali *et al.* (1999) is not directly comparable to that used in this krill swarm model because of differences in model structure and formulation. However, the comparison that can be made is that the biological attractive force in the two models is the dominant process that allows krill swarms to form.

The reaction-diffusion model developed by Morin *et al.* (1988) provides another approach for parameterization of the attractive force that is involved in krill swarm formation. In this model, the attractive speed is represented as a function of location and krill density distribution. The

spatial distribution of the attractive force is assumed to be an exponential function such that the strongest attractive force is at the centre of the swarm and decays exponentially away from the centre with a specified *e*-folding scale. The 10-m *e*-folding scale used by Morin *et al.* (1988) implies that the attractive force acts over large distances. Like Azzali *et al.* (1999), this model does not allow for variations in krill speed or behaviour that result from density-dependent processes or variations in the environment.

A clear message from the mathematical models developed to investigate animal aggregations is that a biological attractive force is an important part of the overall dynamics [see Okubo (1986) for a discussion]. However, the different approaches for parameterization of this force, while yielding plausible simulations, imply important differences in terms of the way in which an animal perceives its neighbours. Thus, the question is which approach for parameterization of the biological attractive force is the most biologically realistic? Answering this question will come only with detailed studies of animal behaviour in experimental and *in situ* environments.

Future directions

Continued exploration of krill swarm formation dynamics requires models that include biological processes such as swimming, variations in aggregation behaviour, variations in behaviour of different stages of krill, reproduction, and predator–prey interactions, and environmental factors such as light and oxygen (Naito *et al.*, 1986). Also, fuller exploitation of results from the extensive theoretical and observational work on patchiness in marine environments is needed. For example, considerable advances have been made on the interpretation of theoretical power spectra derived from models constructed for marine systems [see Powell and Okubo (1994) for a review]. These results provided a framework for the interpretation of spectra calculated from space and time measurements of such distributions as sea surface temperature and phytoplankton (e.g. Denman *et al.*, 1977).

Several studies have attempted to interpret spectra computed from hydroacoustic measurements of krill distributions in terms of biological and environmental processes (e.g. Weber *et al.*, 1986; Levin *et al.*, 1988), but the identification of processes controlling krill swarm formation and distribution was ambiguous or difficult. Hydroacoustics is a primary tool for measuring Antarctic krill distributions (Hewitt and Demer, 2000). Thus, krill swarm models that can be used to develop a theoretical basis for interpretation of krill spectra will provide a means for advancing and enhancing the interpretation of these data and allow better understanding of the factors affecting a species that is a primary link in the Antarctic marine foodweb.

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