Effects of density dependence on diel vertical migration of populations of northern krill: a genetic algorithm model

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ABSTRACT: Net and acoustic studies of diel vertical migration (DVM) in krill often show a degree of dispersion around the mean population depth, which becomes greater during night-time. Trade-off models can predict optimum depths over diel cycles but rarely explain why there is vertical scatter and why aggregations disperse at certain times. We examined density-dependent factors as a potential explanation for these phenomena. A Genetic Algorithm model was developed that predicted DVM in a krill population based on internal state (i.e. levels of energy reserves), risk of predation and location of conspecifics. The modelling approach was designed to be dynamic in that optimal policies could respond to changing circumstances through time. Parameterisation of the model was achieved through measurements made in the Clyde Sea Area on northern krill *Meganyctiphanes norvegica* and its environment. Light intensity at depth was used to assess the level of risk of visual predation. Food provision was a mixture of vertically stratified phytoplankton and vertically migrating copepods. A negative exponential function was used to simulate density dependence in the food returns at each depth. Sensitivity analyses involved alterations to the level of density dependence and the metabolic rate. DVM was predicted in all sensitivity analyses and each correlated positively with net catch and acoustic observations. Increased density dependence in feeding success did not affect the mean depths chosen at night but did increase the spread of the population. The closest fit to observations was achieved when the metabolic rate was lowered and risk of mortality rate was assessed over a yearly rather than daily period. The model predicted that the population should spread more under low food conditions. We recommend that density-dependent factors be included in future state-dependent models predicting krill behaviour and life-cycle patterns.

KEY WORDS: Euphausiid · Zooplankton · Trade-off · Clyde Sea Area · Fjord · Diel vertical migration · DVM · *Meganyctiphanes norvegica*

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INTRODUCTION

Krill diel vertical migration (DVM) is believed to be the product of the classic trade-off of minimising predation risk whilst obtaining enough energy to fulfil energetic requirements (Alonzo & Mangel 2001). Both food availability and visual predation risk decline with depth so, whilst occupation of the deeper layers is safer, the necessary food to meet metabolic demands is not available at such depths. Venturing to the surface is a necessity and doing so under the cover of darkness incurs a low risk of visual predation. Such assumptions have been used successfully in many studies to predict optimum DVM patterns (e.g. Gliwicz 1986, Fiksen & Carlotti 1998, De Robertis 2002).

Net and acoustic studies are often used to validate the predictions of DVM models. Whilst the median depth of acoustic scattering layers frequently coincides with the predicted optimum, it is also apparent that there is considerable vertical scatter within the population, of orders of around 20 or 30 m (e.g. Kaartvedt 1996, Watkins & Murray 1998, Liljebladh & Thomasson

2001). This is especially seen at night when the population disperses, both horizontally and vertically (Buchholz et al. 1995, Tarling et al. 1998). This is not predicted by classic trade-off models, which are based on the premise that the most successful krill are those that maintain a vertical distribution as close as possible to the optimum. It appears that other factors must be involved in depth choice over diel cycles.

Krill typically occur as aggregations or swarms, from which they are believed to draw many benefits (Ritz 1994). Predation may be reduced by increasing the level of vigilance, and the probability of attack may be inhibited by confusing the senses of the predator. Evasion attempts are often co-ordinated and involve polarization of swimming direction, flash expansion, splitting and tail-flipping (O'Brien & Ritz 1988). Aggregating may increase foraging efficiency by enhancing the detection of new or richer patches of food (Pitcher 1993), decreasing per capita search time (Pulliam & Caraco 1984) and trapping food particles between individual krill to increase their probability of capture, thus enabling the grazing down of parcels of water to much lower concentrations than otherwise possible (Antezana & Ray 1984). Metabolic benefits may be obtained through slipstreaming in the wake of nearest neighbours, as was shown by Ritz (2000), who found that respiration rates of aggregated mysids were 10% of the rates in solitary individuals.

Foraging as an aggregation also has its costs, especially for organisms such as northern krill, which use their thoracic appendages to filter the water for phytoplankton, zooplankton and detritus. It is likely that the rate of filtering will be inhibited by (1) the rapid depletion of food sources; and (2) interference in filtering from near neighbours.

One would expect, therefore, that there is some degree of density dependence in feeding success. For example, Morris et al. (1983) found that the filtration rate of Antarctic krill *Euphausia superba* decayed exponentially with increasing krill density in laboratory experiments where between 1 and 11 individuals were maintained in either 1 or 2.4 l chambers. Although 11 krill do not make a school, a trend of decreasing reward with increasing krill density seems clear.

It is likely that the behaviour of conspecifics as well as predators and prey affect the decisions made by social aquatic invertebrates such as krill. In instances where abundances are large and resources are limited, a game situation occurs and individuals will choose patches of food according to the level of resource provisioning as well as its degree of exploitation by others in the aggregation. Over-exploitation of the optimal patch may make other patches, which are sub-optimal in terms of provisioning and risk, more profitable.

Fiksen (2000) incorporated these concepts in a genetic algorithm (GA) modelling technique that predicted evolutionary stable frequencies of different life-cycle phenologies in a population of *Calanus finmarchicus*.

GAs have been used for some time to determine optimal sets of behavioural and life history decisions as solutions to the complex problems faced by living organisms (Holland 1992). Behavioural and physiological responses to environmental variables are subject to the processes of evolution, and those that persist in present day populations of animals may represent long-term solutions to the problems they face. Optimisation models that mimic the process of evolution, like GAs, are thus a powerful approach to understanding why animals behave in particular ways. Giske et al. (1998) advocate individual-based neural network GA models to understand life history and behavioural strategies and responses, and further predict changes in the distribution and survival of important species. GAs have also been used successfully to predict spawning locations for Cape anchovy to ensure maximal survival after advective processes act to transport larvae to nursery grounds (Mullon et al. 2002).

The aim of the present study is to investigate the potential influence of density dependence on the DVM of northern krill. The study utilises the good level of parameterisation obtained for the Clyde Sea Area already published (Tarling et al. 2000, 2002, Lass et al. 2001, Saboroswki et al. 2002, Tarling 2003, Tarling & Cuzin-Roudy 2003). A GA modelling framework will predict vertical distribution of a population of individuals over the course of a diel cycle, as a function of internal state (i.e. the level of energy reserves), risk of predation and the location of conspecifics. The model is designed to be dynamic in that optimal policies can respond to changing circumstances as they evolve through time. The approach is the first attempt to model intra-specific competition as a means of predicting krill behaviour.

MATERIALS AND METHODS

Energy balance and mortality risk depth-time parameter matrices. The parameterisation of the model was the same as that of Tarling et al. (2000), with additional effects of density dependence on feeding. Surface light intensity measurements were combined with attenuation coefficients to give estimates of light intensity at depth. These were included in a visual feeding model for predatory fishes (Aksnes & Giske 1993) to predict the pattern of mortality risk as a function of depth (Fig. 1a). Metabolic rate was calculated for an average sized individual at the temperature encountered over the range of depths considered (Stuart 1986,
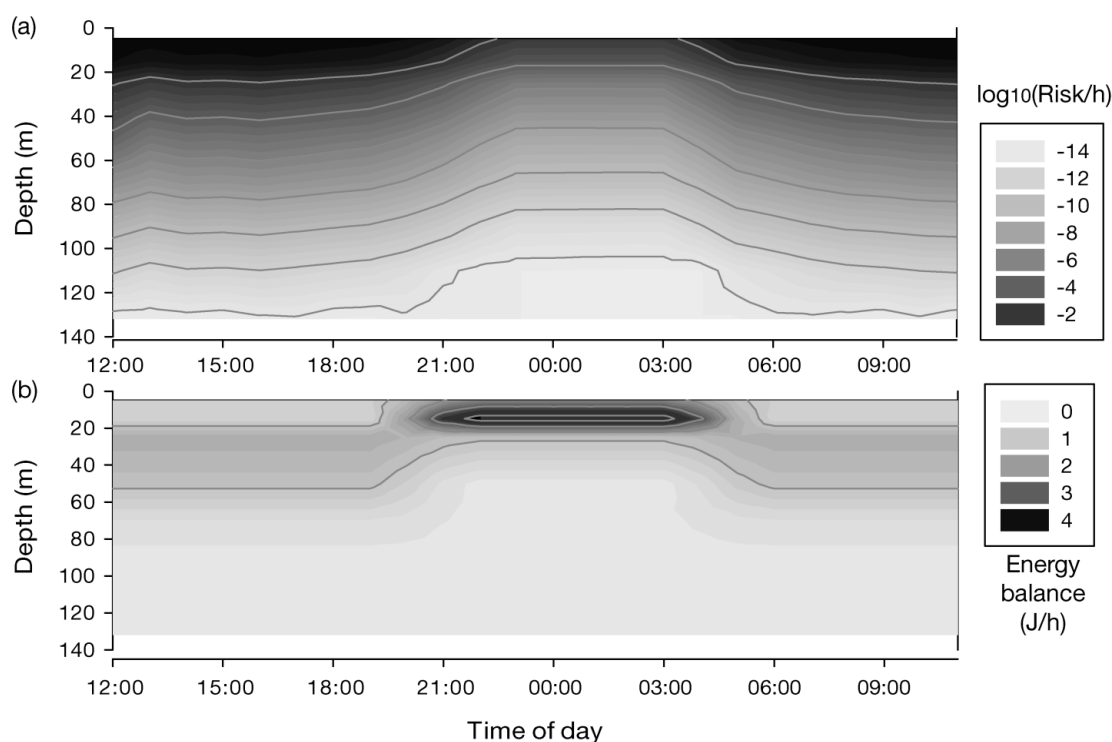
Fig. 1. Estimated depth-time parameter fields for (a) predation risk and (b) the balance of energy intake from food ingestion less the cost of metabolism

Saborowski et al. 2000). The rate of energy intake for the full range of depths in each hour of the day and night was calculated based on a mixed diet of vertically stratified phytoplankton and vertically migrating copepods (Tarling et al. 2000). In-water concentrations of phytoplankton and copepods were used to predict ingestion rates using the model of Tarling et al. (2000) modified from that of McClatchie (1985). Predicted ingestion less metabolic costs gave the depth-time matrix for energetic balance (Fig. 1b). Full details of parameter estimation for krill metabolism, feeding and predation risk are presented and discussed elsewhere (Tarling et al. 2000).

Formulation of the basic model. Various indices of evolutionary fitness that incorporate energy gain and mortality risk have been developed for use in optimal foraging models. Gilliam & Fraser's (1987) 'minimise μg^{-1}' rule, can be used by minimising mortality risk to attain a target energy intake or maximising energy intake for a given minimum acceptable risk (Tarling et al. 2000). While this is a powerful direct technique, it requires a decision as to required energy intake or minimum risk. In contrast, measures of fitness in state-dependent models (Mangel & Clark 1988, Fiksen & Carlotti 1998) do not need to set absolute values of energy gain or risk but do need a hypothetical function relating energetic status to fitness. Here, an index was developed that calculated a hypothetical fitness incre-

ment as a result of a day's worth of behavioural decisions. This was based on the cumulative exposure to mortality risk and cumulative energy intake over 24 h following the individual DVM policy. The long-term consequences for reproductive fitness of short-term changes in energy balance are extremely difficult to determine. It is reasonable to assume, however, that without energy reserves an animal would quickly die. Fitness should thus increase with the size of the energy reserve, perhaps reaching a maximum when a large store becomes too costly. A simple 1-parameter asymptotic function of the energy balance (e) was used, where a is the asymptotic fitness function parameter:

$$f(e) = \frac{e}{a+e} \qquad (1)$$

The fitness value (F) of a set of 24 chosen hourly depths was calculated as the product of the probability of survival through the period and the fitness value of the energy balance at the end of the day:

$$F(D_1, D_2, ..., D_{24}) = \prod_t (1-\beta_{it})^d \times f\left[\sum_t (Y_{it} - c_i)\right] \qquad (2)$$

where $D_1, D_2, ..., D_{24}$ were the depths occupied in each hour, t, of the 24 h cycle. Predation risk at each of the i depths adopted, β_{it}, was used to produce hourly survival values and thence daily survival from the product of the 24 values for each day. Survival over many days

was modelled by a power, d (the number of days), of daily survival. Daily energy balance was calculated as the sum of hourly energy values of ingested food at each depth and time, Y_{it}, less metabolic costs c_i.

Fitness was set to zero for negative cumulative energy balance at the end of the day. This can be seen as a consequence of the definition of this index. If negative fitness values were permitted, their impact would be lessened by the choice of high-risk depths. Since the DVM policy may be followed for many days before fitness could be realised as reproductive output, it is important to allow weighting of the survival term for periods of many days, d.

The density-dependent aspects of the model were parameterised through making the food returns at each depth dependent on the proportion of krill at that depth. Food intake per hour at depth i was weighted by negative exponential function of the proportion of the total krill population at that depth, P_i, adjusted to 100% for an even distribution of krill among the n depth zones. The rate of decline in food intake with density was determined by the parameter k.

$$Y_i' = Y_i e^{-kP_i} e^{k(1/n)} \qquad (3)$$

The individual fitness function was used in a much-simplified GA model. Populations of individuals, usually 5000, were generated with each individual having 24 'loci', representing each hour of the day, with 1 out of 7 preferred depths selected randomly. The fitness of each individual was calculated, depending on its own depth choice and the depth choice of all the other krill in the population. A new generation of krill was produced by selecting individuals randomly (with replacement) and producing 2 new individuals for every krill selected with above-average fitness until the new generation was as large as the old. Mutation in depth choice was allowed at a low frequency per locus (p = 0.02), where the offspring genotype was set at 1 zone below or 1 above the parental type.

Definitions of symbols used and the units of measurement for model parameters are summarised in Table 1.

Sensitivity analyses. The sensitivity of predictions was assessed by changes in mean and standard deviation of depth at 2 time periods representing midday and midnight. The relationship between energy balance after 24 h and future fitness as measured by growth and survival is relatively poorly known, but is likely to be an increasing asymptotic function. Sensi-

Table 1. Symbols and units of factors included in the model

Symbol	Description	Units
e	Energy balance	J
$f(e)$	Fitness value of energy balance	–
a	Asymptotic fitness function parameter	–
D_t	Depth adopted by krill at time t	m
$F(D_1, D_2, \ldots, D_{24})$	Fitness value of a particular DVM strategy	–
β_{it}	Predation risk at depth i and time t h^{-1}	h^{-1}
Y_{it}	Energy value of prey ingested at depth i and time t h^{-1}	J h^{-1}
c_i	Metabolic cost for krill at depth i	J h^{-1}
n	Number of depth zones	–
P_i	Proportion of krill population in depth zone i	–
k	Density dependence of food intake of krill	–

tivity to the shape of this function was determined by using 4 values of the parameter a in the function (Eq. 1) linking energy stored to future fitness. Values of a used were 1, 10, 100, and 1000. The first of these values gives a rapid asymptote while the last gives a form with a much more linear progression—energy added to the store yields an increment to fitness that declines slowly with an increase in the amount of energy stored.

The density-dependence parameter (k) in the model controlled energy returns as a function of population concentration. Four values of k (0, 1, 2 and 10) from no to high density dependence were used in sensitivity analyses, combined with the 4 values of the fitness value of energy.

The metabolic rates used were 100 and 10% of the values calculated for each depth (as Tarling et al. 2000). Predictions were made for 2 weightings for the number of days to be followed by the DVM: values of d of 1 and 365.

RESULTS

In each model simulation, predicted depths occupied by the population of model krill evolved rapidly towards a stable solution (Fig. 2). Every simulation began with krill evenly distributed throughout the water column by day and night. After 50 or so generations, depths occupied in each time period converged toward the optimal solution. With no or low density dependence (Fig. 2a), the average fitness of the krill population increased steadily with successive generations. The initial increase in average fitness was rapid. Progress slowed as the DVM for the population steadily approached an optimum. With the addition of significant negative density dependence (Fig. 2b), changes in depth distributions between successive generations reflected the negative density
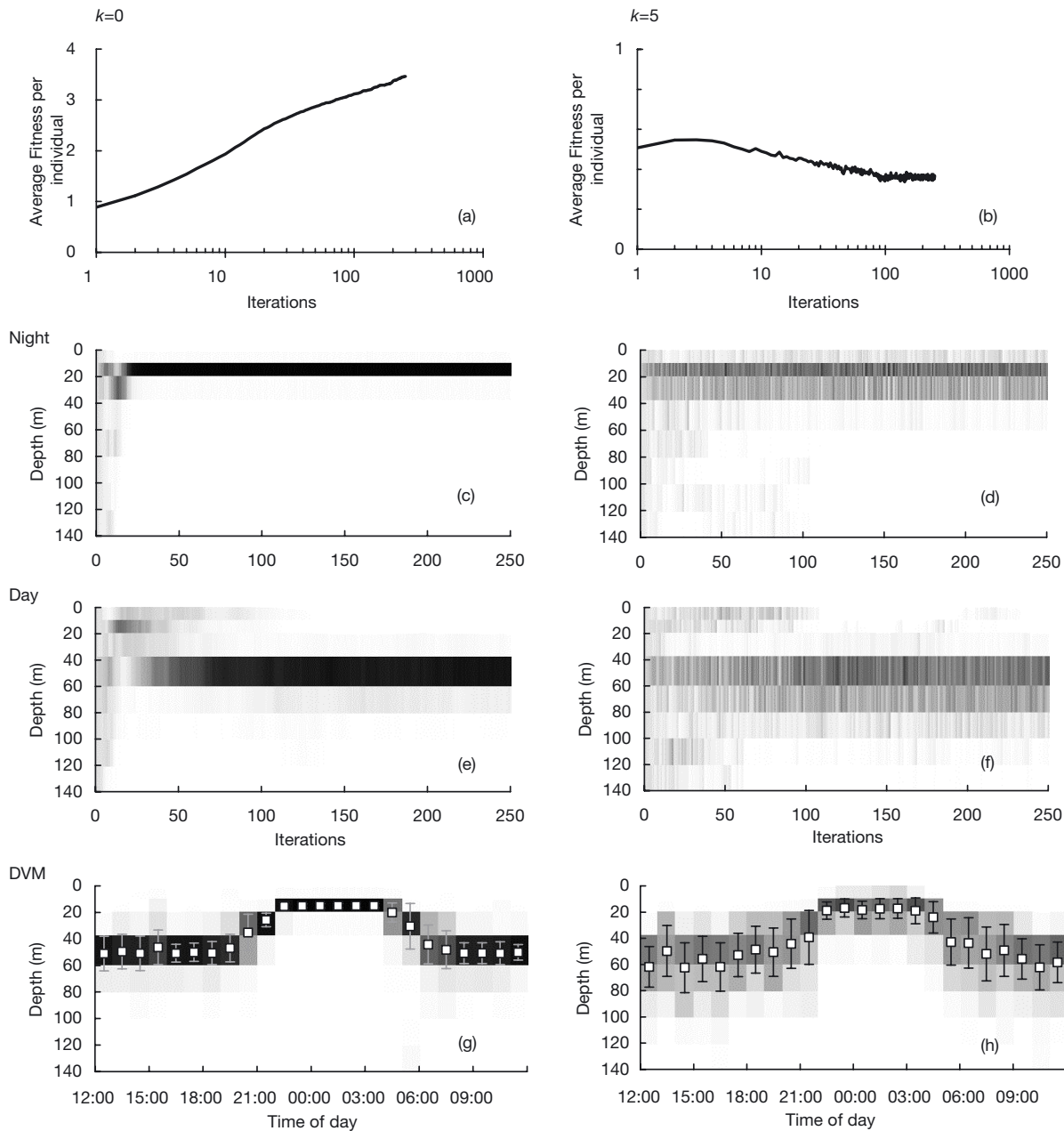
Fig. 2. Evolution of population diel vertical migration (DVM) strategies for 2 parameter sets representing (a,c,e,f) no density dependence of foraging returns ($k = 0$) and (b,d,f,g) high density dependence of foraging returns ($k = 5$). (a,b) Changes in average fitness value per individual; changes in depths adopted at (c,d) midnight and (e,f) midday; (g,h) DVM pattern after 250 generations

dependence of fitness. Concentration of the model population in a particular depth zone reduced the fitness of krill adopting that zone. These krill would be less likely to be selected to contribute to the next generation than those adopting adjacent zones where the negative influence of potentially increased mortality and lower food intake on fitness was outweighed by the positive influence of reduced krill density.

Sensitivity analyses

For all combinations of parameter values the model predicted the general pattern of DVM of ascent into the upper water column by night and descent into greater depths by day (Fig. 3). Model predictions were found to be insensitive to change in the function relating final energy balance to putative fitness (parameter *a*) in an initial analysis not presented
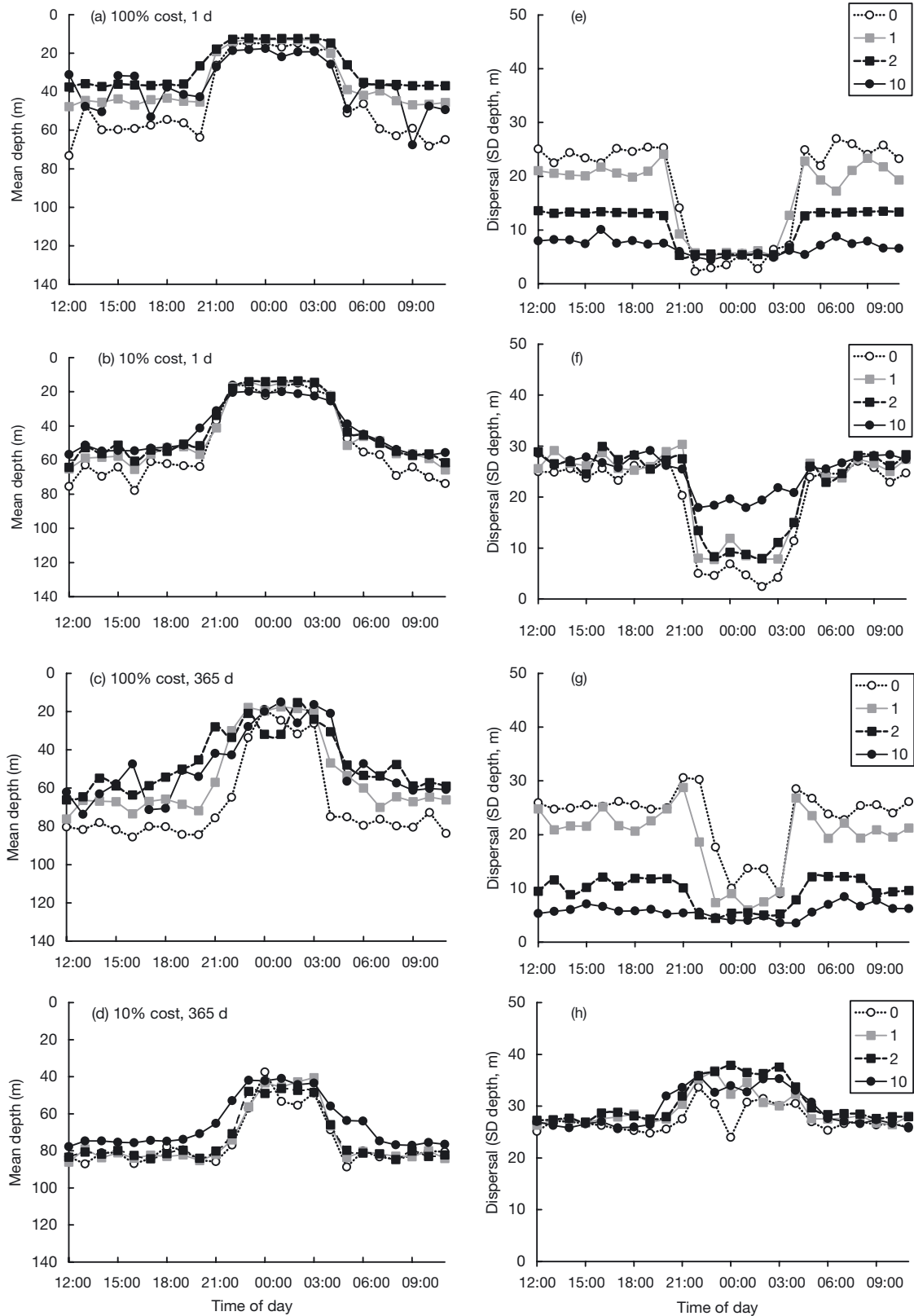
Fig. 3. Predicted diel vertical migration (DVM) patterns for different combinations of parameter values. (a–d) Mean depths h^{-1}; (e–h) SD of depths h^{-1}. Rows show DVMs and SDs respectively for (a,e) 100% metabolic cost and 1 d, (b,f) 10% cost, 1 d, (c,g) 100% cost, 365 d, and (d,h) 10% cost and 365 d. Values of k shown in the key

here. All further patterns presented use the value of $a = 10$.

The key process in the model was the effect of density dependence on the range of depths occupied through the day and night. At the higher level of metabolic cost (100%), density dependence (k) had no effect on the range of depths occupied at night: krill were predicted to occupy only the uppermost depths (Fig. 3a,b). Effects of density dependence on the range of depths occupied by day were the opposite of expectations, krill vertically dispersed more when k was low (Fig. 3a). For high values of k, krill were forced to adopt zones nearer the surface by day to avoid a much-reduced energy balance over the whole 24 h, since gains from foraging at night are low when krill are concentrated into narrow depth zones (reduced by high k, Eq. 3).

At a lower metabolic cost (10%), k had a similar unexpected effect on depth choice by day. Higher k-values led to reduced mean depths by day to offset the effects of reduced energetic returns at the shallowest depths by night (Fig. 3c). Increased density dependence did not affect the mean depths chosen at night, but did affect the range of depths chosen, as expected. With no density dependence ($k = 0$), model krill adopted a very narrow depth range by night. The range of depths chosen at night expanded as density dependence increased (Fig. 3b).

Prolonged exposure to risk of predation in simulations ($d = 365$, Fig. 3c,d) predicted generally deeper depths by day and night than for shorter exposure ($d = 1$, Fig. 3a,b) and a shorter period near the surface at night. Risk had little effect on predicted dispersal through the water column by day, but did affect dispersal at night at lower metabolic costs (10%, Fig. 3b,d). Krill were predicted to disperse less at night than by day for lower mortality risks (Fig. 3b), but to disperse more at night for higher risks (Fig. 3d). The latter pattern is more consistent with field observations (see below).

Comparison of model predictions with observed patterns of DVM and depth ranges

The DVM of krill *Meganyctiphanes norvegica* populations in the Clyde Sea Area has been measured using both acoustic and net sampling methods (Tarling et al. 2000, 2002). While visual inspection of the predictions (Fig. 3) gave some indication of the performance of the model, a quantitative assessment of goodness-of-fit revealed the ranges of parameter values that best reproduce the observed patterns. Pearson correlation between observed and predicted hourly values was used to measure the degree to which the model predicted temporal changes in mean depth and depth range. Sums of squared deviance

were used to assess differences between predictions and observations.

Three empirical DVM patterns were quantified for krill in the same area and time of year for which the model was parameterised. These patterns were compared with predicted DVMs for 24 combinations of parameters for density dependence, metabolic costs and weightings for the number of days for the DVM to be followed. The empirical patterns (Fig. 4) were (1) 1-d acoustic backscatter from 150 kHz acoustic Doppler current profiler (ADCP) (4–5 July 1996), (2) 6-d averaged 300 kHz ADCP acoustic backscatter (25 June–1 July 1999: Tarling et al. 2002), and (3) mul-
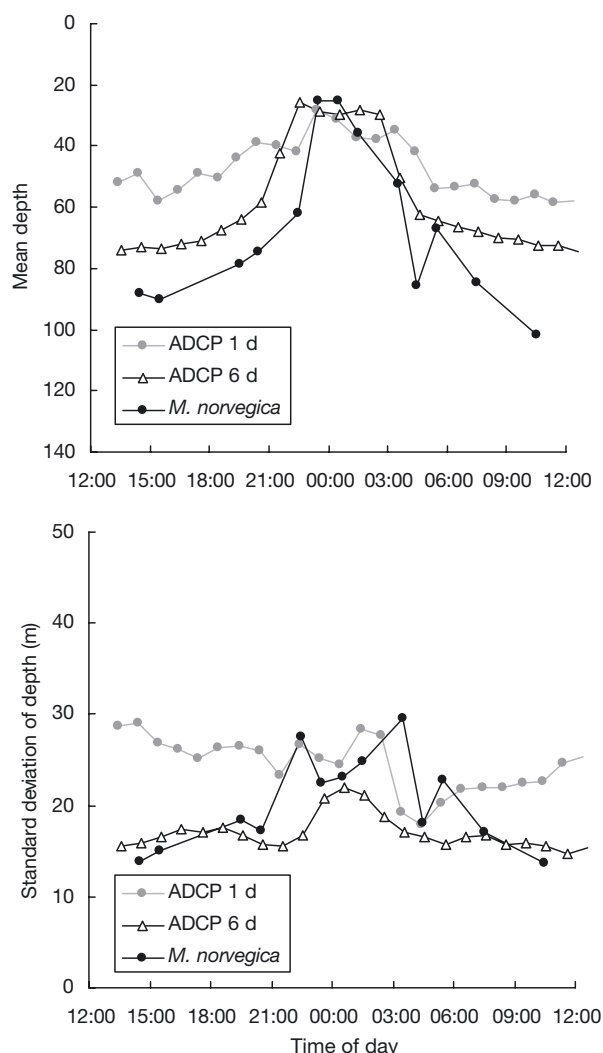

Fig. 4. Observed krill diel vertical migration (DVM) patterns from 2 moorings of acoustic instruments: 1 d acoustic backscatter from a 150 kHz acoustic Doppler current profiler (ADCP) (4–5 July 1996); 6 d averaged 300 kHz ADCP acoustic backscatter (25 June–1 July 1999: Tarling et al. 2002); and net catches with multiple opening and closing net samples (MOCNESS) to give depth-stratified abundance estimates of adult *Meganyctiphanes norvegica* (28 June–1 July 1999: Tarling et al. 2000, 2002)

Table 2. Goodness-of-fit of 24 h model predictions to 3 sets of empirically derived krill diel vertical migration (DVM) patterns as described by mean depth and SD of depth (1 d: 1 d 150 kHz ADCP backscatter; 6 d: 6 d average 300 kHz ADCP backscatter; Net: MOCNESS net samples). Fits of hourly changes in depth and spread of depths are measured by Pearson correlations, while small values of summed squared deviance give the absolute fit of predicted to observed depths and SDs. k: density dependence of food intake of krill; d: number of days; M: % of estimated metabolic rate

k	d	M	Pearson correlation						Summed squared deviance					
			Mean depth			SD			Mean depth			SD		
			6 d	1 d	Net	6 d	1 d	Net	6 d	1 d	Net	6 d	1 d	Net
0	1	10	0.89	0.88	0.78	−0.70	−0.17	−0.80	180	223	859	112	126	208
2	1	10	0.91	0.89	0.83	−0.77	−0.14	−0.75	336	140	1200	111	80	141
10	1	10	0.92	0.91	0.83	−0.72	−0.06	−0.75	331	80	1138	90	24	84
0	1	100	0.88	0.85	0.78	−0.68	−0.17	−0.75	285	189	990	113	143	229
2	1	100	0.91	0.92	0.80	−0.62	−0.17	−0.80	1029	395	2133	64	217	181
10	1	100	0.74	0.70	0.72	−0.45	0.08	−0.80	663	221	1512	109	322	232
0	365	10	0.73	0.74	0.80	0.24	0.03	0.57	418	875	246	116	22	75
2	365	10	0.82	0.78	0.87	0.73	0.13	0.83	318	768	187	195	58	142
10	365	10	0.89	0.86	0.90	0.47	0.07	0.85	108	375	220	167	44	115
0	365	100	0.81	0.74	0.88	−0.73	−0.33	−0.49	247	690	179	91	55	103
2	365	100	0.87	0.87	0.80	−0.63	−0.27	−0.65	228	70	904	76	252	192
10	365	100	0.77	0.83	0.74	−0.48	−0.18	−0.58	250	129	920	133	365	256

tiple opening and closing net samples (MOCNESS) giving depth-stratified abundance estimates of adult *Meganyctiphanes norvegica* (28 June–1 July 1999: Tarling et al. 2000, 2002). Tarling et al. (2002) showed that the majority of backscatter was caused by krill. All DVM patterns were expressed as mean and standard deviation of depth occupied per hour by weighting each depth by the estimated backscatter or proportional abundance at that depth (Fig. 4).

Goodness-of-fit of predicted to observed DVM patterns was measured by correlation and summed squared deviance (Table 2). All combinations of parameter values produced DVM mean depths that were positively correlated with observations (r > 0.7). Temporal patterns of DVM were better reproduced by simulations using 1 d as the baseline for calculated daily mortality (d = 1). Very few simulations, however, reproduced the increase in spread of depths at night compared with daytime. Only lowered metabolic costs (10%), and a longer mortality time base (d = 365) produced a positive correlation between observed and predicted standard deviation of depths occupied. This combination of low metabolic costs and longer mortality time also gave small sums of squared deviations of predictions from absolute values of both mean depths and standard deviations of depth (Table 2).

DISCUSSION

Modelling approach

In this model, we used the GA approach to include frequency dependence of optimal solutions where the fitness consequences of individual decisions depend on the decisions of all the other individuals in a population. Fiksen (2000) took a similar approach in determining optimal life-history phenologies in a population *Calanus finmarchicus*. Optimal policies, such as that to enter diapause or remain and graze at the end of summer, were dependent on both animal state and the decisions of others, since this affected the degree of resource available for exploitation. This approach shares many aspects with Game Theory approaches to predicting population distributions as a function of resource distributions, such as the Ideal Free Distribution (Fretwell & Lucas 1970).

Game Theory has been applied previously to understand DVM in aquatic organisms. In an early model by Iwasa (1982), DVM was considered as a game between predators and prey each with a choice of selecting upper or lower layers. Gabriel & Thomas (1988) extended this approach to include self-interacting populations in a model analogous to the approach adopted here, designed for migration of *Daphnia galeata* and *D. hyalina* in freshwater lakes. In their model, the density of zooplankton in surface layers impacted on the growth rate of algae. If the whole population moved into surface layers, the food intake per individual was reduced, in a similar way to the process proposed here for density-dependent food limitation. These 2 models both simplify the problem in order to make the solutions mathematically tractable. Iwasa (1982) considered only 2 time periods and 2 depth zones, while Gabriel & Thomas (1988) considered only the choice between 2 behavioural strategies: to migrate or not. While both these models give useful insights into the evolutionary consequences of DVM strategies for a

population, their emphasis was largely theoretical and the models hard, if not impossible, to implement for specific choices of depth ranges at hourly intervals. Our GA model was designed for comparison with empirical data and necessitated abandoning an analytical approach in favour of an iterative simulation of the evolutionary process.

An alternative approach to understanding DVM is the consideration of the effects of depth choice on the physiological and energetic state and the subsequent consequences, combined with exposure to mortality risk, for individual evolutionary fitness. Most directly, energy balance and mortality risk can be combined into a simple ratio of energy intake to mortality risk (Gilliam & Fraser 1987). Maximisation of this ratio can be used to determine optimal DVM patterns (Tarling et al. 2000). Other models make explicit the fitness consequences of levels of energy stores and gut contents and evaluate alternative choices in these terms, using techniques such as stochastic dynamic programming (Mangel & Clark 1988). Through stochastic outcomes to processes such as prey encounter and variability in reproductive status, these models can generate the variability in behaviour that could account for adoption of a range of depths by a population (Clark & Levy 1988, Burrows & Hughes 1991, Burrows 1994). Such models could well incorporate the effects of satiation as a potential cause of midnight sinking (Tarling et al. 2002).

Model results

DVM pattern

The GA model presented here predicted a plausible DVM in almost all circumstances, with generally a close prediction of migration timing and vertical amplitude. This is not surprising given the success of earlier models in predicting DVM in zooplankton and other pelagic organisms based on the shifting depth of the optimal trade-off between predation risk and feeding with changing light levels (Clark & Levy 1988, Burrows 1994, Fiksen & Carlotti 1998, Tarling et al. 2000, etc).

The response of the predictions of the model to changes in parameter values illustrates the relative importance of different processes in determining optimal depths. In particular, reducing metabolic costs to 10% of the originally predicted values made model animals spend less time at the surface: they ascended later and descended earlier than if they had higher metabolic costs. Ritz (2000) suggested that measurements of metabolic rate on individuals are probably overestimating *in situ* levels because aquatic animals that aggregate are able to gain metabolic savings

through various factors such as slipstreaming their nearest neighbours, exploiting favourable updrafts generated by the school to minimise sinking rate and minimising the energetic reactions to predatory attack (tail-flipping) by being part of a group (Ritz et al. 2001). The experiments of Ritz and colleagues were carried out on mysids, which are easier to handle and manipulate in the laboratory than krill. Obtaining empirical measurements of this parameter on krill is an essential step to increasing the accuracy of this and other modelling approaches (e.g. Hofmann & Lascara 2000) dealing with behaviour and life-cycles of krill.

Spreading of the population

The novel element in the model is the prediction that the krill population may occupy a range of depths throughout the diel cycle. Both acoustic and net catch observations of DVM in *Meganyctiphanes norvegica* in the Clyde Sea Area show spreading over a broad depth range, a pattern that is common to other areas (Simard et al. 1986, Buchholz et al. 1995, Kaartvedt 1996, Liljebladh & Thomasson 2001) and other krill species (*Euphausia superba*: Watkins & Murray 1998; *Euphausia pacifica* and *Nyctiphanes simplex*: Robinson & Gomez-Gutierrez 1998). The model predicted that the spread in the population would reduce at night if density dependence were not apparent in the population. This is because there is a high premium in occupying the most profitable depth zone at night when the majority of energy for the whole daily cycle must be consumed. Introducing density dependence into the model had the result of spreading the population to other depth zones. Spreading at night is apparent in many studies of euphausiid behaviour (Everson 1983, Buchholz et al. 1995, Robinson & Gomez-Gutierrez 1998).

The fact that spread in the population could only be predicted at night if density dependence was introduced suggests that aggregation behaviour could be affected by the level of resource. Under limited resource levels, competition through exploitation and interference leads to sub-optimal environments becoming more profitable. As a result, one would expect krill populations to spread more under low food conditions, all other factors, such as predation, being equal. In mysids, Ritz et al. (1997) showed that swarms of mysids expand in volume when individuals were hungry and condensed shortly after feeding. In krill, Lascara et al. (1999) found that aggregations of *Euphausia superba* close to the Antarctic Peninsula were more commonly found during the summer, when chlorophyll pigment concentrations were highest. However, at times of the year when resources are low, predation on

krill may also increase, which would encourage aggregation behaviour. This is because alternative prey items, such as copepods, are more likely than krill to starve when there is little food around. The predation pressure on krill, which are the main survivors in the planktonic community, correspondingly becomes greater. Daly & Macaulay (1991) found that krill aggregations in the marginal ice zone were equally as apparent in winter as in summer, which they believed resulted from the large number of air-breathing predators inhabiting this environment throughout the annual cycle. As yet there have been few studies examining aggregation behaviour of *Meganyctiphanes norvegica* under different conditions, both seasonal and spatial, which could validate the predictions of the present model.

The spreading of the population over a number of depth zones was apparent in the daytime even when density dependence was not introduced into the model. This was because there was little to separate depths below 50 m in terms of either their supply of resources or their risk to visual predators. Such a large spread is not observed in the Clyde Sea population during the daytime and the fact that the population remains aggregated, even when the pressures of predation and feeding are limited, implies that there may be other reasons for aggregating at these times. For instance, individuals may be aggregating to benefit from the metabolic saving of slipstreaming and other factors discussed earlier (Ritz 2000, Ritz et al. 2001).

Additional factors

Size of krill. The model assumed the population was made up of equally sized individuals with identical metabolic rates, functional responses to food and visibility to predators. Making this assumption allowed it to focus on the effect of density dependence as an agent for spreading a population over depth. In reality, the adult population of *Meganyctiphanes norvegica* during summertime observations was made up of a number of adult and juvenile size classes (Tarling 2003, Tarling & Cuzin-Roudy 2003), with different rates of respiration and feeding (Holm-Hansen & Huntley 1984, Ikeda 1985). Mauchline (1960) showed that different size classes of *M. norvegica* occupy different depth strata through the diel cycle, while De Robertis (2002) found size dependence in the timing of migration of *Euphausia pacifica*. It is likely that aggregations containing a range of age classes will spread in depth as a result of how each balances its trade-offs. Nevertheless, the fact that many aggregations spread even when they are made up of similarly sized individuals (Watkins et al. 1992, Lascara et al.

1999) indicates that size can only be a contributing factor to this phenomenon.

Reproduction and moulting. Moulting and reproduction influence the vertical positioning of adult *Meganyctiphanes norvegica* over diel cycles (Tarling et al. 1999). Moulting individuals tend to move away from the rest of the population, possibly to avoid cannibalism. Ready-to-spawn females frequently rise to the surface, above the rest of the aggregation, probably to increase the success of hatching and feeding in their offspring. Females are also more likely than males to ascend higher at night and feed in riskier habitats since they must fuel egg production (Tarling 2003). These factors may account for a degree of spreading in the reproductive season but cannot account for the fact that spreading is observed outside of this period (e.g. Tarling et al. 1998).

This study has shown that density dependence is an important mechanism in explaining the behaviour of krill in terms of depth choice and whether or not to aggregate. It has highlighted the possibility that individual krill make decisions based on the behaviour of conspecifics as well as their own internal state and the distribution of resources. Such factors prevent individuals converging on the same optimal depth or patch during feeding periods, mainly at night. As the level of resources and population density changes, this model would predict that the level of aggregation will alter, as has been frequently observed in the field. We recommend that future models incorporate density-dependent factors as well as state-dependent variables when predicting krill behaviour and life-cycle patterns.

LITERATURE CITED

Aksnes DL, Giske J (1993) A theoretical model of aquatic visual feeding. Ecol Model 67:233–250

Alonzo SH, Mangel M (2001) Survival strategies and growth of krill: avoiding predators in space and time Mar Ecol Prog Ser 209:203–217

Antezana T, Ray K (1984) Active feeding of *Euphausia superba* in a swarm north of elephant island. J Crustac Biol 4:142–155

Buchholz F, Buchholz C, Reppin J, Fisher J (1995) Diel vertical migrations of *Meganyctiphanes norvegica* in the Kattegat: comparison of net catches and measurements with acoustic doppler current profilers. Helgol Wiss Meeresunters 49:849–866

Burrows MT (1994) An optimal foraging and migration model for juvenile plaice. Evol Ecol 8:125–149

Burrows MT, Hughes RN (1991) Variation in foraging behavior among individuals and populations of dogwhelks, *Nucella lapillus*—natural constraints on energy-intake. J Anim Ecol 60:497–514

Clark CW, Levy DA (1988) Diel vertical migrations by juvenile sockeye salmon and the antipredation window. Am Nat 131:271–290

Daly KL, Macaulay MC (1991) Influence of physical and biological mesoscale dynamics on the seasonal distribution and behavior of *Euphausia superba* in the Antarctic marginal ice zone. Mar Ecol Prog Ser 79:37–66

De Robertis A (2002) Size-dependent visual predation risk and the timing of vertical migration: an optimization model. Limnol Oceanogr 47:925–933

Everson I (1983) Variations in vertical distribution and density of krill swarms in the vicinity of South Georgia. Mem Natl Inst Polar Res Spec Iss 27:84–92

Fiksen O (2000) The adaptive timing of diapause—a search for evolutionarily robust strategies in *Calanus finmarchicus*. ICES (Int Counc Explor Sea) J Mar Sci 57: 1825–1833

Fiksen O, Carlotti F (1998) A model of optimal life-history and diel vertical migration in *Calanus finmarchicus*. Sarsia 83: 129–147

Fretwell SD, Lucas HL (1970) On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheor 19:136–156

Gabriel W, Thomas B (1988) Vertical migration of zooplankton as an evolutionary stable strategy. Am Nat 132: 199–216

Gilliam JF, Fraser DF (1987) Habitat selection under predation hazard: test of a model with foraging minnows. Ecology 68:1856–1862

Giske J, Huse G, Fiksen O (1998) Modelling spatial dynamics of fish. Rev Fish Biol Fish 8:57–91

Gliwicz ZM (1986) Predation and the evolution of vertical migration behaviour in zooplankton. Nature 320:746–748

Hofmann EE, Lascara CM (2000) Modeling the growth dynamics of Antarctic krill *Euphausia superba*. Mar Ecol Prog Ser 194:219–231

Holland J (1992) Genetic algorithms. Sci Am 267:44–50

Holm-Hansen O, Huntley M (1984) Feeding requirements of krill in relation to food sources. J Crustac Biol 4:156–173

Ikeda T (1985) Metabolic rates of epipelagic marine zooplankton as a function of body mass and temperature. Mar Biol 85:1–11

Iwasa Y (1982) Vertical migration of zooplankton—a game between predator and prey. Am Nat 120:171–180

Kaartvedt S (1996) Habitat preference during overwintering and timing of seasonal vertical migration of *Calanus finmarchicus*. Ophelia 44:145–156

Lascara CM, Hofmann EE, Ross RM, Quetin LB (1999) Seasonal variability in the distribution of Antarctic krill, *Euphausia superba*, west of the Antarctic Peninsula. Deep-Sea Res I 46:951–984

Lass S, Tarling GA, Virtue P, Matthews JBL, Mayzaud P, Buchholz F (2001) On the food of northern krill *Meganyctiphanes norvegica* in relation to its vertical distribution. Mar Ecol Prog Ser 214:177–200

Liljebladh B, Thomasson MA (2001) Krill behaviour as recorded by acoustic Doppler current profilers in the Gullmarsfjord. J Mar Syst 27:301–313

Mangel M, Clark CW (1988) Dynamic modelling in behavioral ecology. Princeton Univesity Press, Princeton, NJ

Mauchline J (1960) The biology of the euphausiid crustacean, *Meganyctiphanes norvegica* Sars. Proc R Soc Edinb Sect B (Biol Sci) 67:141–179

McClatchie S (1985) Feeding behavior in *Meganyctiphanes norvegica* (M. Sars) (Crustacea: Euphausiacea). J Exp Mar Biol Ecol 86:271–284

Morris DJ, Ward P, Clarke A (1983) Some aspects of feeding in Antarctic krill, *Euphausia superba*. Polar Biol 2:21–26

Mullon C, Cury P, Penven P (2002) Evolutionary individual-based model for the recruitment of anchovy (*Engraulis capensis*) in the southern Benguela. Can J Fish Aquat Sci 59:910–922

O'Brien DP, Ritz DA (1988) Escape responses of gregarious mysids (Crustacea, Mysidacea)—towards a general classification of escape responses in aggregated crustaceans. J Exp Mar Biol Ecol 116:257–272

Pitcher TJ (1993) Behaviour of teleost fishes. Chapman & Hall, London

Pulliam HR, Caraco T (1984) Living in groups: is there an optimal group size? In: Krebs JR, Davies NB (eds) Behavioral ecology: an evolutionary approach, 2nd edn. Blackwell Scientific Publications, Oxford, p 122–147

Ritz DA (1994) Social aggregation in pelagic invertebrates. In: Blaxter JHS, Douglas B (eds) Advances in marine biology, Vol 30. Academic Press, London, p 155–216

Ritz DA (2000) Is social aggregation in aquatic crustaceans a strategy to conserve energy. Can J Fish Aquat Sci 57: 59–67

Ritz DA, Osborn JE, Ocken AEJ (1997) Influence of food and predatory attack on mysid swarm dynamics. J Mar Biol Assoc UK 77:31–42

Ritz DA, Foster EG, Swadling KM (2001) Benefits of swarming: mysids in larger swarms save energy. J Mar Biol Assoc UK 81:543–544

Robinson CJ, Gomez-Gutierrez J (1998) Daily vertical migration of dense deep scattering layers related to the shelf-break area along the northwest coast of Baja California, Mexico. J Plankton Res 20:1679–1697

Saborowski R, Salomon M, Buchholz F (2000) The physiological response of krill (*Meganyctiphanes norvegica*) to temperature gradients in the Kattegat. Hydrobiologia 426: 157–160

Saborowski R, Brohl S, Tarling GA, Buchholz F (2002) Metabolic properties of northern krill, *Meganyctiphanes norvegica*, from different climatic zones. I. Respiration and excretion. Mar Biol 140:547–556

Simard Y, de Ladurantaye R, Therriault JC (1986) Aggregation of euphausiids along a coastal shelf in an upwelling environment. Mar Ecol Prog Ser 32:203–215

Stuart V (1986) Feeding and metabolism of *Euphausia lucens* in the southern Benguela current. Mar Ecol Prog Ser 30: 117–125

Tarling GA (2003) Sex-dependent diel vertical migration in northern krill *Meganyctiphanes norvegia* and its consequences for population dynamics. Mar Ecol Prog Ser 260: 173–188

Tarling GA, Cuzin-Roudy J (2003) Evidence of synchronisation in the moulting activity of northern krill and its impact on recruitment. Limnol Oceanogr 48:2020–2033

Tarling GA, Matthews JBL, Sabarowski R, Buchholz F (1998) Vertical migratory behaviour of the euphausiid *Meganyctiphanes norvegica*, and its dispersion in the Kattegat Channel. Hydrobiologia 375/376:331–341

Tarling GA, Cuzin-Roudy J, Buchholz F (1999) Vertical migration behaviour in the northern krill *Meganyctiphanes norvegica* is influenced by moult and reproductive processes. Mar Ecol Prog Ser 190:253–262

Tarling GA, Matthews JBL, Burrows M, Saborowski R, Buchholz F, Bedo A, Mayzuad P (2000) An optimisation model of the diel vertical migration of 'Northern krill' (*Meganyctiphanes norvegica*) in the Clyde Sea and Kattegat. Can J Fish Aquat Sci 57(Suppl 3):38–50

Tarling GA, Jarvis T, Emsley SM, Matthews JBL (2002) Mid-night sinking behaviour in *Calanus finmarchicus*: a response to satiation or krill predation? Mar Ecol Prog Ser 240:183–194

Watkins JL, Murray AWA (1998) Layers of Antarctic krill, *Euphausia superba*: are they just long krill swarms? Mar Biol 131:237–247

Watkins JL, Buchholz F, Priddle J, Morris DJ, Ricketts C (1992) Variation in reproductive status of Antarctic krill swarms; evidence for a size-related sorting mechanism? Mar Ecol Prog Ser 82:163–174