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Contributors: Geir Huse (IMR), Guillem Chust (AZTI)

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PP	Restricted to other programme participants (including the Commission)	
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Deliverable D3.7) Adaptive habitat models past and present geographical distribution
 is a contribution Task 3.5 Development of habitat models

Here we will use two approaches to resolve the oceanographic habitats utilized by key biogeochemical and ecosystem species. Firstly, we will draw the major part of the data together in synthesis using predictive habitat models. These statistical models relate present day geographical distribution of species and communities to their environmental conditions (Guisan and Zimmermann, 2000). When properly developed these models are extremely useful to produce accurate predictions of the distribution and abundances on the short medium term (non adaptive time scales). We will capitalize on the successfully use of these models in terrestrial ecology for conservation and management issues. Essential biological data will come from T3.1. Predictive habitat models will be established using the most adequate approach for each type of data, such as generalized additive models, Bayesian networks, ENFA (see Guisan and Zimmermann, 2000). In order to have a common basis a workshop/summer school will be carried out with introductions to the different statistical tools available, their advantages and their limitations. Predictive habit models produced will be made available in the project webpage. This work will feed to T6.3.

Secondly, another approach to habitat modelling in EURO-BASIN will be based on agent-based models; specifically targeted will be the Calanus complex. Work will be devoted to developing an individual based model for *C. helgolandicus* based on the existing *C. finmarchicus* model (Huse 2005, Huse & Fiksen, in press.). We will use the available literature and information on vital rates from WP4 to re-parameterize this model and validate it against historical data sets (T3.1) as well as from field observations in the basin and on the shelves (T3.3). The model system will then be integrated into the NORWECOM model along with the existing *C. finmarchicus* model and the species will be simulated together as competitors for resources over time in the Norwegian Sea. We will simulate the biogeography, population dynamics, and production of the two species under present day and a future climate scenario and evaluate how climatic variability and - change affects their interactions. This work will feed into T.6.1 and provide indicators for WP 8.3

Responsible: TecNALIA-AZTI; Participants: IMR; SAHFOS, BUC
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Research publications on which this report is based:

In Review:

Huse, G., Webjørn Melle, Morten D. Skogen, Solfrid Sætre Hjøllø, Einar Svendsen, Paul Budgell (in review). Modelling emergent life histories of *Calanus finmarchicus*, presented at the International workshop on Trait-based approaches to Ocean Life, 26-28 August 2013 the Centre for Ocean Life, Copenhagen, <http://www.trait-based-workshop.dk/upload/oceanlife/workshop-august2013/poster-geirhuse.pdf>

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Executive summary

This report contains EURO-BASIN Project Deliverable 3.7: *Adaptive habitat models past and present geographical distribution*. It is a contribution to Task 3.5. The purpose of this task is to use two approaches to resolve the oceanographic habitats utilized by key biogeochemical and ecosystem species. Firstly, we have drawn the major part of the data together in synthesis using predictive habitat models. These statistical models relate present day geographical distribution of species and communities to their environmental conditions. When properly developed these models are extremely useful to produce accurate predictions of the distribution and abundances on the short medium term (non adaptive time scales). Secondly, another approach to habitat modelling in EURO-BASIN will be based on a 3D individual based model with emergent life-history and behavior for *C. finmarchicus*. The objectives are to investigate the importance of spatial and inter-annual variability and different predator densities on the evolved life history traits and spatial distribution of *C. finmarchicus*. The results show that in most of the simulations the populations remain viable within the Norwegian Sea throughout the hundred years. Simulations with spatial-, but without inter-annual variability produced large differences in centre of mass, fitness and life history strategies between replicates. The model can be used for a range of different applications such as individual and population responses to climate change. The adapted trait values from this model are useful in parameterizing *C. finmarchicus* components of ecosystem models which is also shown below in the paper by Hjøllø et al. This will be pursued further in the coming year and also finalizing the modelling for *C. helgolandicus*.

Relevance to the project & potential policy impact

The report consists of two parts where the first part describes the adaptive modelling framework and a specific application for *C. finmarchicus*. The second part refers to a published paper (Hjøllø & al 2012) where output from the adaptive model has been applied to simulate the dynamics of *C. finmarchicus* in the Norwegian Sea in a fully coupled model system.

This work will feed into WP6 Basin-scale Modelling Task.6.1 and provide indicators for WP 8 Ocean Management Task.8.3.

Modelling emergent life histories of *Calanus finmarchicus*

Geir Huse, Webjørn Melle, Morten D. Skogen, Solfrid Sætre Hjøllø, Einar Svendsen, Paul Budgell

Institute of Marine Research, Box 1870 Nordnes, N-5817 Bergen, Norway; tel: +47 55236988; fax: +47 55238584; e-mail: geir.huse@imr.no.

Summary

The copepod *Calanus finmarchicus* is the dominant species of the meso-zooplankton in the Norwegian Sea ecosystem and is a key grazer of phytoplankton and prey for the abundant planktivorous fish stocks. Spatially explicit models are key tools for understanding spatial-temporal zooplankton dynamics as a function of currents, behaviour and selective growth, mortality and reproduction. Here, we present a 3D individual based model with emergent life-history and behavior for *C. finmarchicus*. The objectives are to investigate the importance of the simulated adaptive process on retention and fitness of *C. finmarchicus* and the importance of spatial and inter-annual variability and different predator densities on the evolved life history traits of *C. finmarchicus*. The results show that in most of the simulations the populations remain viable within the Norwegian Sea throughout the hundred years. In simulations with fixed spatial position there were small differences between the replicates. Inter-annual variability in forcing resulted in increased difference in fitness between years. Simulations with spatial-, but without inter-annual variability produced large differences in centre of mass, fitness and life history strategies between replicates. This was due to the repetition of a single year with a particular current pattern. In simulations with both spatial and inter-annual variability the replicates had small variability. Increased predator density resulted in increased day depth. The model can be used for a range of different applications such as individual and population responses to climate change. The adapted trait values from this model are useful in parameterizing *C. finmarchicus* components of ecosystem models.

1. Introduction

The copepod *Calanus finmarchicus* is the dominant species of the meso zooplankton in the Norwegian Sea (Melle et al., 2004). The species is largely herbivorous and constitutes an important link between the phytoplankton to the higher trophic levels in the Norwegian Sea food chain (Aksnes and Blindheim, 1996; Melle et al., 2004). The *C. finmarchicus* is vital to many of the planktivorous fish species including Norwegian spring spawning (NSS) herring (*Clupea harengus* L.), blue whiting (*Micromesistius poutassou*, Risso), and mackerel (*Scomber scombrus* L.), which enter the Norwegian Sea during summer to utilise the abundant zooplankton resources. In addition to these migrating predators, there are large standing stocks of invertebrates and mesopelagic fish that feed on different stages of *C. finmarchicus* (Dalpadado et al., 1998). Its life cycle consists of overwintering at depth mainly as copepodite stages 4 (C4) or 5 (C5), ascent towards the surface during early spring, maturation, and subsequent commencement of egg production prior to and during the spring phytoplankton bloom (Marshall and Orr, 1955; Hirche, 1996b). The new generation remain in the upper waters during summer and may mature and reproduce

within the season or build up fat reserves and descend to overwintering at stage C4 or C5 (Hirche, 1996a).

The shift between a deep, safe but unproductive habitat to a shallow, risky and productive habitat is important to the fitness of the *C. finmarchicus*. The timing of the spring bloom is important for the *Calanus* ascent (Hirche, 1996a), and the peak of the spring bloom is often associated with the first copepodite stage (C1) (Melle et al., 2004). Kaartvedt (2000) argue that predation from planktivorous fish is a key driver in the timing of the descent to overwintering, and causes the Norwegian Sea population of *C. finmarchicus* to descend in June at a time of relatively high phytoplankton production. Clearly the timing of ascent and descent is linked to a trade off between growth, survival and reproduction.

To organisms inhabiting the sea there are inherent problems in upholding life cycle closure due to the advective and diffusive forces that continuously act to disperse populations (Sinclair, 1988). While many marine fishes have solved this problem by counter current homing to distinct spawning areas (Harden Jones, 1968), planktonic organisms face greater difficulties in maintaining life cycle closure. Instead planktonic species need to utilize the vertical and horizontal differentiation in the current pattern to close their life cycle. This is a particular problem in areas of strong advective regimes such as those bordering the Nordic Seas. Bryant et al. (1998) studied the drift pattern resulting from different vertical positioning that mimicked the vertical distribution of *C. finmarchicus*. They found that some areas of the Norwegian Sea such as the Norwegian Basin and the area around the Faroese Islands were able to retain particles over more than 10 years. Such retention is maintained by the seasonal vertical migration pattern with a northward flow during summer in the upper waters and compensatory southward flow in deep waters (>600 m) during winter. The model applied by Bryant et al. (1998) did not include growth, mortality, reproduction, and inter-annual variability in drift pattern. These features are important to the long term retention of plankton populations.

Several approaches have been taken to simulate the spatial and population dynamics of *C. finmarchicus* both using 1D Individual Based Models (IBMs) (Carlotti and Nival, 1992; Carlotti et al., 1993; Carlotti and Radach, 1996; Carlotti and Wolf, 1998), 3D IBMs (Miller et al., 1998; Pedersen et al., 2001; Tittensor et al., 2003), and 3D Eulerian (Speirs et al., 2005; Speirs et al., 2006) models (reviewed by Gentleman, 2002). The different approaches have their pros and cons and the Eulerian models are in general numerically more efficient than IBMs, which on the other hand allow a more detailed biological description of individuals.

Due to the many interesting features in *C. finmarchicus* ecology and the broad impact this species has on other species in the ecosystem it is valuable to develop a flexible model for *C. finmarchicus* that can be used for a range of different purposes including analyses of *C. finmarchicus* ecology and behavioural strategies, population dynamics, advection trajectories, and to generate prey fields for fish larvae and planktivorous fish. We therefore chose to develop a 3D IBM for *C. finmarchicus* taking into account growth, mortality, and reproduction as well as adaptive traits, which control the interaction with the environment. The adaptive traits are evolved by a genetic algorithm (Holland, 1975). This concept involves equipping individuals in a population with “genes” and adapting these by simulating evolution by natural selection over many generations (Huse and Giske, 1998; Huse et al., 1999). This is parallel to the spin up time used in ocean circulation models.

Fiksen (2000) developed a 1D IBM for *C. finmarchicus* with three traits determining the time for ascent from diapause, the day for preparing for overwintering and the relative fat content to be obtained before descending to diapause. Here we use the same traits as Fiksen (2000), add three traits related to controlling vertical distribution, and extend the model to three spatial dimensions and with inter-annual variability. The *C. finmarchicus* model relies on input from a biophysical ocean model that generates temperature, advection and phytoplankton fields.

The objectives of the study are to investigate the importance of the simulated adaptive process on retention and fitness of *C. finmarchicus*, and the importance of inter-annual variability and different predator densities on the evolved life history traits of *C. finmarchicus* in the Norwegian Sea using a 3D individual-based model.

2. Material and methods

The model description is set in accordance with the protocol for describing IBMs proposed by Grimm et al. (2006). This entails an initial model overview in the subsequent paragraphs followed by a more detailed description of the model components under Submodels.

2.1 Purpose

The model is a 3D individual-based model taking into account growth, mortality, and reproduction of *C. finmarchicus* as well as adaptive traits (Huse, 2005; Samuelsen et al., 2009), which control the interaction with the environment. The model presented here addresses the entire life cycle of *C. finmarchicus*, and the main life history features and vertical movement are emergent properties resulting from many generations of evolution using a genetic algorithm (Fig. 1). The purpose of the model is to evolve behavioural and life history strategies of *C. finmarchicus* using an individual based model with a genetic algorithm, a physiological model, and a detailed description of the environment in order to improve understanding the *C. finmarchicus*' behavioural and life history strategies and their effect on population dynamics and retention. The model area is the Northeast Atlantic. Seven simulations were performed (Table 1), for a time period of 100 years. First two simulations (1 and 2) were performed without any spatial variability to study local adaptation with and without inter-annual variability. The rest of the simulations had spatial variability. Two simulations (3 and 4) without inter-annual variability were performed, with and without selection to illustrate the effect of selection. Then a simulation (5) was performed where the years 1981-2004 were repeated sequentially during the adaptation process to study the effect of inter-annual variability. Finally we investigate how differences in predation pressure affect the evolved strategies by varying the predation level by fish and tactile predators (6 and 7). For each simulation 4 replicate runs were made. This was done due the reliance on stochastic processes and initialisation where individuals differ with regards to initial position, composition of the strategy vectors, the sequence of mutations and movement diffusion. Since the simulated adaptation process depends on number of individuals in the population and is generally faster in smaller populations, four replicates of each simulation were made rather than one simulation with a four times greater number of individuals.

Table 1. Description of the different simulations. Trait indicates whether traits are inherited from "parents" or are initiated randomly from the initiation range. Predator density (N_v , N_t) is

given in Table 3. For all simulations 4 replicates runs over 100 years are performed.

Simulation number	Forcing period	Spatial location	Trait	Predator density
1	1983	Fixed	Evolved	N_v, N_t
2	1981-2004	Fixed	Evolved	N_v, N_t
3	1983	Variable	Random	N_v, N_t
4	1983	Variable	Evolved	N_v, N_t
5	1981-2004	Variable	Evolved	N_v, N_t
6	1983	Variable	Evolved	$N_v \cdot 0.8, N_t \cdot 0.8$
7	1983	Variable	Evolved	$N_v \cdot 1.2, N_t \cdot 1.2$

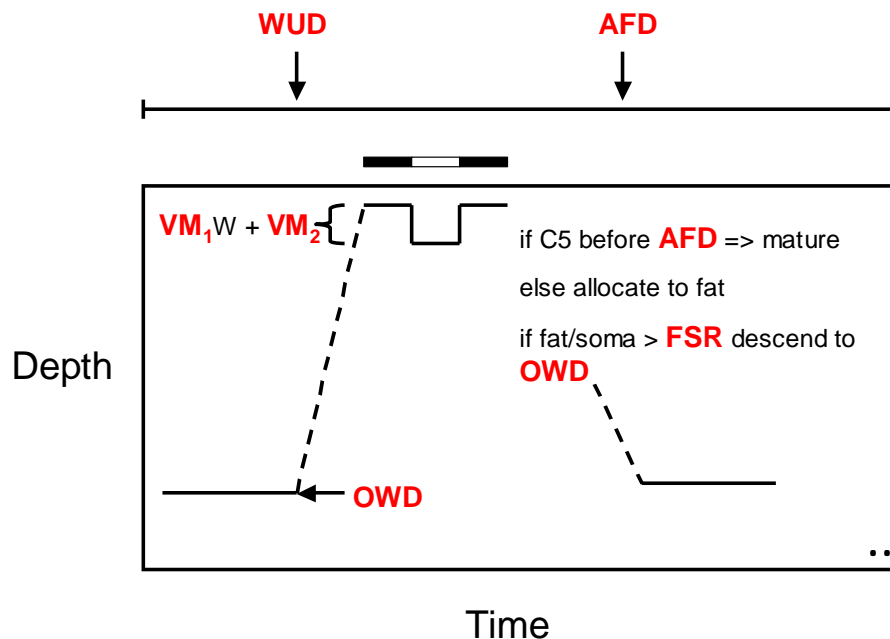


Fig. 1. The conceptual framework of the life history traits of the *Calanus* IBM. The strategy variables, whose values are evolved during the spin up simulation, are given in bold. OWD is the overwintering depth, WUD is the date at which the overwintering C5 starts ascent towards the surface, $VM_1(W)$ and VM_2 gives the deepening of the *Calanus* during day as a function of the weight of their total weight (W), AFD is the date after which an individual becoming C5 will prepare for overwintering, whereas before this date the individual will mature and reproduce in the same season, FSR gives the fat to soma ratio at which a C5 will descend to the OWD for overwintering in diapause.

2.2 State variables and scales

The model comprises individuals and their environment. The attribute vector (Chambers, 1993) of individuals consists of 13 different states including their stage, internal number, weight, fat level, age, depth (Table 2). The strategy vector (Huse et al., 1999), which is evolved, contains all the life history and behavioural strategies of individuals and comprises five behavioural and life history traits. The life history traits include the date for ascent from overwintering to the surface (WUD), the day for initiating fat allocation (AFD) in copepodite stage 5 (C5), fat/soma ratio needed before descending to overwintering (FSR), overwintering depth (OWD), and two genes (VM1 and VM2) that determine the day depth (DD) of non overwintering copepodites (Fig. 1). VM2 is multiplied by the size of the copepodite so that for values greater than 0, there will be size dependent vertical migration. In the results reporting here we refer to the day depth, which is the resulting “phenotype” of VM1 and VM2 which are rather difficult to interpret. The three former traits (WUD, AFD, FSR) were presented by Fiksen (2000), while the latter three are introduced here. Even though the individual-based structure is appealing, it is impossible to simulate copepod population dynamics on a truly individual basis due to the great abundances involved, and *C. finmarchicus* is therefore simulated using the super-individual approach (Scheffer et al., 1995). A super-individual represents many identical individuals and the number of such identical siblings is an attribute of the super-individual (Table 2).

Table 2. The attribute vector A_s of super-individual s .

Attribute	Explanation
0	dead=0, alive=1
1	stage, 0 is egg, 1-6 nauplia, 7-11 copepodits, 12 adult
2	internal number
3	structural weight in micrograms
4	age in days
5	fat energy level in KJ
6	moult cycle fraction of stages < N3
7	total number of eggs in a super individual
8	depth position
9	position along the x-axis
10	position along the y-axis
11	activity level: 0 diapause,1 active,2 allocating to fat, 3 move down,4 move up
12	net reproductive rate (R_0)

2.3 Process overview and scheduling

The processes governing the individuals are growth, mortality, movement and reproduction. *C. finmarchicus* has 13 different stages including an egg stage, six nauplia stages, five copepodite stages and an adult stage. *C. finmarchicus* does not commence feeding until the third nauplia stage (N3), and for stages below this, stage longevity was calculated as a function of temperature (Carlotti and Wolf, 1998). For stages N3 and above, growth is calculated as a function of phytoplankton density, temperature and size using a bioenergetics model (Carlotti and Wolf, 1998). The *C. finmarchicus* is assumed to change stage when a stage specific critical weight is achieved. Thus we did not utilise flexible critical weights. For the egg and nauplia stages, mortality consists of unspecified causes (taken from Ohman et al., 2004) and tactile predation. For the copepodite and adult stages mortality is attributed to predation from pelagic fish (herring, blue whiting, and mackerel), mesopelagic fish and tactile predators, starvation when the weight goes below the critical weight, and exhaustion if more than 800 eggs have been spawned. For individuals in diapause, no vertical movement is calculated, but for other individuals, movement is calculated either as a function of turbulence and sinking (stages < N3) or by adapted rules. A sex ratio of 50% is assumed, and males are removed from the population after one spawning event, as male *C. finmarchicus* have only a brief functioning after which they are expendable (Hirche, 1996b). Reproduction of adults can take place when their weight is above a threshold value and they have attained enough fat reserves to spawn a batch of eggs (Table 3). Spawning can only take place within the upper mixed layer (Table 3). If these conditions are met, the individual produces a new super-individual offspring whose internal number is a function of the batch size multiplied by the internal number of the mother. During reproduction, strategy vectors are passed on from parent to offspring.

The time step of the model is one hour, simulated on a day-to-day basis over the entire year repeated a hundred times in order to evolve robust life history and behavioural traits (Table 2). Fat is allocated to structural growth for immature individuals, but mature individuals and C5s preparing for overwintering allocate their surplus energy into fat

storage. During times of negative growth, the stored fat is depleted before the structural weight is reduced.

2.4 Design concepts

Emergence: Most of the features of the model are emergent properties including the individual traits, mortality, growth, reproduction and spatial dynamics.

Adaptation: The six life history traits are adapted and can be used to improve the fitness of individuals.

Fitness: During the year super individuals grow, survive and may reproduce. At the end of the year the product of the internal number and the weight of each super individual is calculated. At the start of each year, a fixed number of super individuals are then drawn randomly from the previous year's population and the probability of being chosen is proportional to the product of the internal number and the weight.

Sensing: Individuals are assumed to be able to sense the chlorophyll density and find the location of the depth with the highest chlorophyll density, they are also able to separate between day and night. They are also assumed to know which days are their inherited wake up and allocation to fat days respectively.

Interactions: Individuals interact indirectly through random cross over in the strategy vectors during reproduction.

Stochasticity: Mortality is determined by stochasticity at low internal numbers, but is otherwise deterministic. Mutations and movement of egg-N2 are stochastic. There is a random walk component in the movement of super individuals to represent sub grid "diffusion" processes. There is random initiation of the strategy variables within bounds as defined below.

Collectives: The individuals are super-individuals that each represents one or more identical individuals.

2.4 Initialisation

The model is initiated on January 1 with 500 individuals. The individuals are initiated as overwintering C5 at OWD or shallower if limited by bottom depth, at randomly chosen positions throughout the domain (Fig. 2) in areas with bottom depth greater than 100m. The weight of individuals is 120 $\mu\text{g C}$ and they have a fat reserve of 100 $\mu\text{g C}$ (Carlotti and Wolf, 1998). The life history and behavioural traits are initiated randomly within given boundaries. Test runs were used to determine that the end solutions were not found outside the initiation ranges. The strategy vectors were initiated randomly within the ranges: WUD [15,60], FSR [0.4,0.8], AFD [100,160], OWD [500,1000], VM₁ [20,60], VM₂ [1500,4500] for 500 individuals.

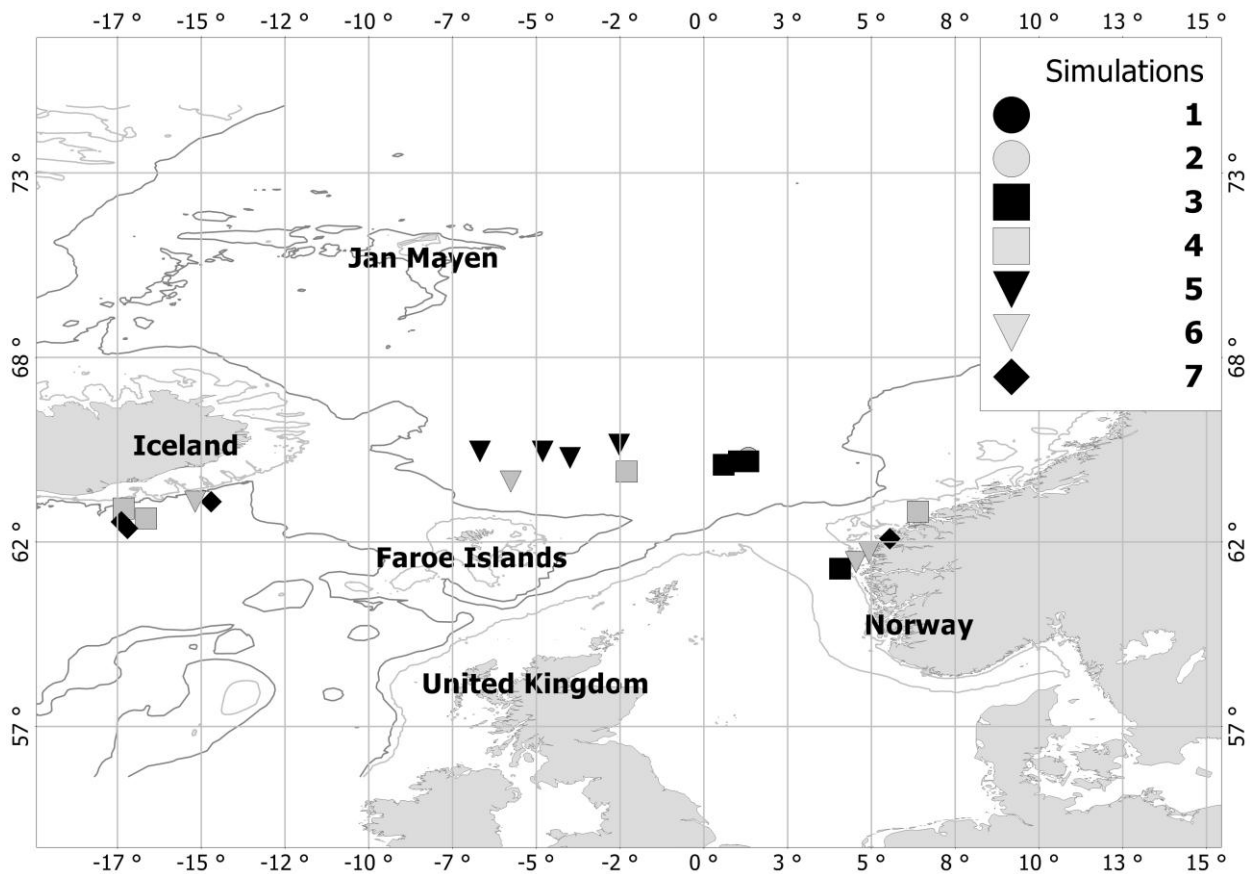


Fig . 2. The average centre of mass at the end of the year in the 30 last years in all four replicates of the simulations. The contours give the 200m and 500m depth. Note that simulation 1 and 2 are in the same location centrally in the Norwegian Sea, hidden behind the two black squares (simulation 3).

2.5 Input data

Input data on light, temperature and phytoplankton biomass were taken from a model system involving the Regional Ocean Model System (ROMS) (Haidvogel et al., 2000) and the NORWECOM phytoplankton model, initially presented by Aksnes et al. (1995) and further developed by Skogen et al. (2007). Three day fields were interpolated linearly to daily values. The model domain is the Nordic Seas (56 to 82N and 30E to 30W, Fig. 2). Each square is 1/3 longitude and 1/6 latitude which gives an approximate resolution of 20 km, and the total grid size was 181 by 153 squares. The NORWECOM model was run on a different grid as described in Skogen et al (2007), and the results were transferred to the present grid as done previously (Utne and Huse, 2012; Utne et al., 2012b). Hourly surface light was generated from a model giving hourly sun height above the horizon (Skartveit and Olseth, 1988). The visual predators that include mesopelagic and pelagic fish were assumed to be distributed homogeneously in the upper 500 m and the tactile predators were assumed to be distributed in the upper 1000 m.

2.6 Submodels

Adaptation: The adaptive traits are implemented on a strategy vector S_i (Huse, 2001; Huse et al., 2002). A genetic algorithm (GA, Holland, 1975) is then used to optimise the

strategy vector. The GA is a computational method that applies Darwin's principle of evolution by natural selection to search for optimal solutions to complex problems. For an introduction to GAs see (Goldberg, 1989) or (Mitchell, 1996). The population of individuals is adapted by repeated testing, selection and reproduction. Instead of using maximization of a utility measure, we used emergent fitness to evolve the strategy vectors (Mitchell and Forrest, 1995; Huse, 1998; Strand et al., 2002). This concept involves simulating survival of the fittest over hundreds of generations, and considering the strategies dominating at the end to be those best adapted to the simulated environment. Only individuals that fulfil certain criteria are allowed to reproduce (see below). The selection scheme is inspired by the way natural selection works in nature. By repeating the procedure over and over, the population will consist of increasingly fit members. This concept has been shown to be a useful concept beyond the realm of artificial life where it was initially conceived (Langton, 1989), and a validation for a biological case, namely vertical migration in fish, has proven successful (Strand et al., 2002). There is an inherent problem in individual based population models such as the present one in that the number of individuals may grow very large and thus increase computing time substantially. Since there was no density dependent feedback on the food resource, we implemented a direct density regulation. At the end of each year a fixed number of super individuals were selected from the population and passed on to the next year. This was done stochastically using Monte Carlo simulation and the probability for an individual being passed on to the next year was proportional to the product of its weight (structural + fat) and internal number. In this manner a fixed number of 500 super individuals with a fixed internal number were initiated on each January 1. The density regulation will thus have less effect on the selection of individuals and their strategies than if density regulation was to be imposed for example on the food availability during the feeding season. The net reproductive rate R_0 defined as the sum of the product of survival probability times the number of offspring produced is often used as a fitness proxy (e.g. Giske et al., 1993). Since R_0 is closely related to our selection criteria we used it to report and contrast the results in different simulations.

Mutations add variability to the solutions (Table 3). Offspring are initially clones of their mother, but the new strategy vectors are subject to probabilistic mutations where the trait values are change randomly by up to 20%. Each individual *C. finmarchicus* has a strategy vector that consists of:

$$SV = (wud, fsr, afd, owd, vm_1, vm_2) \quad (1)$$

Feeding and growth: It was assumed here that *C. finmarchicus* feed solely on phytoplankton, even though calanoid copepods, including *C. finmarchicus*, are known to be omnivorous and can also feed on microzooplankton. Ingestion (I) was calculated as a function of temperature, size, and phytoplankton level:

$$I = I_{max}(Q_{10})^{T/10} W^a \frac{b_1 phy}{b_2 + phy} \quad (2)$$

where I_{max} , Q_{10} , a , b_1 , and b_2 are constants (Table 3), phy is the phytoplankton concentration, W is the structural weight, and T is the temperature. The functional response parameters (b_1 and b_2) were scaled to resemble the relationships presented in Campbell et al. (2001). Respiration was calculated as a function of structural weight, temperature, and

ingestion:

$$R = r_1 W^a Q R_{10}^{MT/10} + r_2 I \quad (3)$$

where r_1 and r_2 are constants (Table 3) and MT is the mean temperature over the day. Egestion was calculated as a constant proportion of ingestion:

$$F = I \lambda \quad (4)$$

Finally growth emerges as the sum of the ingestion minus respiration and egestion:

$$G = I - R - F \quad (5)$$

Table 3. Parameters used in the model. Values in parenthesis indicate stages with 0 being the egg stage and 1:6 being nauplia stages one to six respectively. The parameters $critW$ $N3=minW$ $N4$ refers to the critical size for moulting into the next stage. For b_1 and b_2 the first values are for the nauplia stages and the latter for copepodite stages.

Symbol	Value	Unit	Source
l_{max}	0.86	day ⁻¹	(Carlotti and Wolf, 1998)
Q_{10}	2.1	wd	(Carlotti and Wolf, 1998)
a	0.80	wd	(Carlotti and Wolf, 1998)
t_{phy}	40	mg C m ⁻³	(Carlotti and Wolf, 1998)
f_{max}	100	mg C m ⁻³	(Carlotti and Wolf, 1998)
r_1	0.01	wd	(Carlotti and Wolf, 1998)
r_2	0.2	wd	(Carlotti and Wolf, 1998)
b_1	1.1, 1.12	wd	
b_2	15, 30	wd	
QR_{10}	3.4	wd	(Carlotti and Wolf, 1998)
$m_{0:2}$	0.3	day ⁻¹	(Ohman et al., 2004)
$m_{3:6}$	0.15	day ⁻¹	(Ohman et al., 2004)
$m_{7:12}$	0.05	day ⁻¹	(Ohman et al., 2004)
m_d	0.001	day ⁻¹	(Fiksen, 2000)
$critW$ $N3$	0.05	µg C	(Carlotti and Wolf, 1998)
$critW$ $N3=minW$	0.2	µg C	(Carlotti and Wolf, 1998)
$N4$			
$critW$ $N4=minW$	0.3	µg C	(Carlotti and Wolf, 1998)
$N5$			
$critW$ $N5=minW$	0.45	µg C	(Carlotti and Wolf, 1998)
$N6$			
$critW$ $N6=minW$	0.75	µg C	(Carlotti and Wolf, 1998)
$C1$			
$critW$ $C1=minW$	1.1	µg C	(Carlotti and Wolf, 1998)
$C2$			
$critW$ $C2=minW$	2.5	µg C	(Carlotti and Wolf, 1998)
$C2$			
$critW$ $C3=minW$	7	µg C	(Carlotti and Wolf, 1998)

C2			
critW	C4=minW 15	µg C	(Carlotti and Wolf, 1998)
C2			
critW	C5=minW 40	µg C	(Carlotti and Wolf, 1998)
ad			
critW Ad	90	µg C	(Carlotti and Wolf, 1998)
cmat	100	µg C	(Carlotti and Wolf, 1998)
c	0.2	m ⁻¹	(Aksnes and Utne, 1997)
k	0.05	m ⁻¹	(Aksnes and Utne, 1997)
C ₀	0.5	wd	(Aksnes and Utne, 1997)
E _{max}	50	µE m ⁻² S ⁻¹	(Aksnes and Utne, 1997)
K _e	5	µE m ⁻² S ⁻¹	(Aksnes and Utne, 1997)
ρ	0.5	wd	(Aksnes and Utne, 1997)
N _t	0.02	ind.m ⁻³	
V _t	0.05	m s ⁻¹	
N _v	0.0004	ind.m ⁻³	
V _v	0.8	m s ⁻¹	

Mortality: Mortality is assumed to result from visual and tactile predation, starvation, and spawning stress. In addition the egg and nauplia stages had an additional unspecified daily mortality rate of 0.06 adapted from Aksnes and Blindheim (1996).

The most important fish predators of *C. finmarchicus* are herring, mackerel, and mesopelagic fish. Predation risk from these visually feeding predators was calculated from irradiance at depth, predator visual capability, turbidity, and prey size. Surface light was calculated from The background light irradiance at depth (E_b) was calculated as a function of the surface light (E_0), light loss through the surface (ρ), and the vertical attenuation coefficient (k) (Aksnes and Giske, 1993):

$$E_b = E_0 \rho e^{(-kz)} \quad (6)$$

where z is depth. The visual range (r) of planktivorous fish was calculated using equation 9 in (Aksnes and Utne, 1997):

$$r^2 e^{(cr)} = |C_0| A_p E_{max} \Delta S_e^{-1} \frac{E_b}{K_e + E_b} \quad (7)$$

where c is beam attenuation constant, C_0 is inherent contrast of prey, A_p is the area of the *C. finmarchicus*, E_{max} is maximal retinal irradiance that can be processed by the predator, ΔS_e is sensitivity threshold for eye, K_e is an eye saturation parameter of the predator, and E_b is the background irradiance at depth (Eq. 2). The ΔS_e parameter was estimated to $4.88 \cdot 10^{-7}$ for a planktivorous fish of 30 cm based on the relationship given in Aksnes and Giske (1993).

The predation mortality from visual predators (P_v) is assumed to be a function of the predator density N_v , search area and swimming velocity (V_v):

$$P_v = \pi(r \sin \theta)^2 N_v V_v \quad (8)$$

Predation from tactile predators was calculated as a function of the predator density N_t , search area and swimming velocity (V_t):

$$P_t = \pi r_t^2 N_t V_t \quad (9)$$

In this case the search range of the predator is a constant, independent of light level. Implicitly, the predators are assumed to exert a linear functional response. The densities of visual and tactile predators are based on data for the Norwegian Sea provided by Skjoldal et al. (2004). The internal number of individuals was then updated each hour (h) by:

$$n_{ih} = n_{ih-1} e^{-\mu} \quad (10)$$

where $\mu = P_t + P_v$. When the internal number of a super individual becomes less than 1 the super-individual is removed from the population. When the structural weight of an individual falls below the minimum level ($minW$, Table 3), the super-individual is removed from the population. When the n_s gets below 10, the way that mortality rate operates is changed to probabilistic mortality using Monte Carlo techniques (Judson, 1994) for the remaining siblings.

Reproduction: Adult individuals can reproduce when their structural weight is above 100 μg , they have attained enough fat reserves to spawn a batch of eggs, and they are positioned within the upper mixed layer (<40 m). If these criteria are fulfilled new super-individuals are produced. An offspring inherits the strategy vector from its parent, but random changes take place with a probability of 0.06 per trait or weight on the strategy vector. Such mutations take place by changing the values randomly by $\pm 20\%$ of the value. The internal number of the new super-individual is a function of the batch size and the internal number of the parent individual. New super-individuals are initiated as eggs at the same depth as the parent. Following reproduction the weight reserve of the parent super-individual is reduced by an amount corresponding to the clutch size multiplied by the egg weight.

3. Results

3.1 Horizontal distribution

The centres of mass at the end of the final year of the four replicates of each simulation are shown in Fig. 2. In most cases the centre of mass is within the Norwegian Sea basin although there is some variation between simulations and replicates. In the two first simulations the spatial location was fixed at the centre of Norwegian Sea (Fig. 2). Simulation 3 was initiated randomly each year at the centre of the Norwegian Sea and the centre of mass also remained stationary. In simulation 4, the same forcing year was repeated, but with spatial variability. The replicates ended up in two different areas north of Iceland and northeast of Jan Mayen (Fig. 2). This is likely an adaptation to the peculiarities of the single forcing year. For simulation 5, with variable forcing years on the other hand, we see that the centres of mass are very close together at the centre of the Norwegian Sea. In simulation 6, with reduced predator density two different centres of mass are found,

one in the central Norwegian Sea and one further east on the 500m isobath. Finally in simulation 7, with increased predator density we find two different locations, with three replicates centred on the Icelandic shelf and one on the Norwegian shelf.

3.2 Simulation 1: Adaptation to a single forcing year and fixed position

The first two simulations were performed in a fixed location without any spatial variability and inter-annual variability, repeating the year 1983. Only the traits of the best replicate, defined as having the highest average fitness for the last 30 years, are shown here in panels a and b (Fig. 3). In simulation 1 the wake up day (WUD) was at around day 70 and AFD at 130 day (Fig. 3). This gives a surface period of about two months and allows time for producing two generations per year. The day depth was around 60m and the overwintering depth was at about 1000 m. The net reproductive rate R_0 was used here as a fitness proxy, and the fitness was between 2.5 to 3 indicating that the population was viable and growing (Fig. 3c). There was a clear increasing asymptotic trend in the fitness in all the replicates and there were only minor variation in fitness among them.

3.3 Simulation 2: Adaptation with inter-annual variability and fixed position

Adding inter-annual variability had only a minor effect on the life history trait (Figs. 4a and b) compared to the previous simulation. But there was an increase in the day depth to 75m and thus indicating a more risk averse strategy. There was a pronounced inter-annual variation in the fitness, but only a minor difference between the replicates (Fig. 4c). This shows that there is pronounced inter-annual variability in the “productivity” of the forcing data and that this is more important than the increase in fitness due to adaptation process.

3.4 Simulation 3: Random strategies

In the remaining simulations individuals were initiated over the entire spatial domain and transported with the currents. In simulation 3 individuals were selected randomly from the population at the end of the year before, to contrast the other simulations where the selection probability is proportional to the fitness. The strategies in this case reflected the initiation range in each year and the mean values remained stationary (Fig. 5). The fitness was also very low in this simulation and clearly did not reflect viable populations (Fig. 5c).

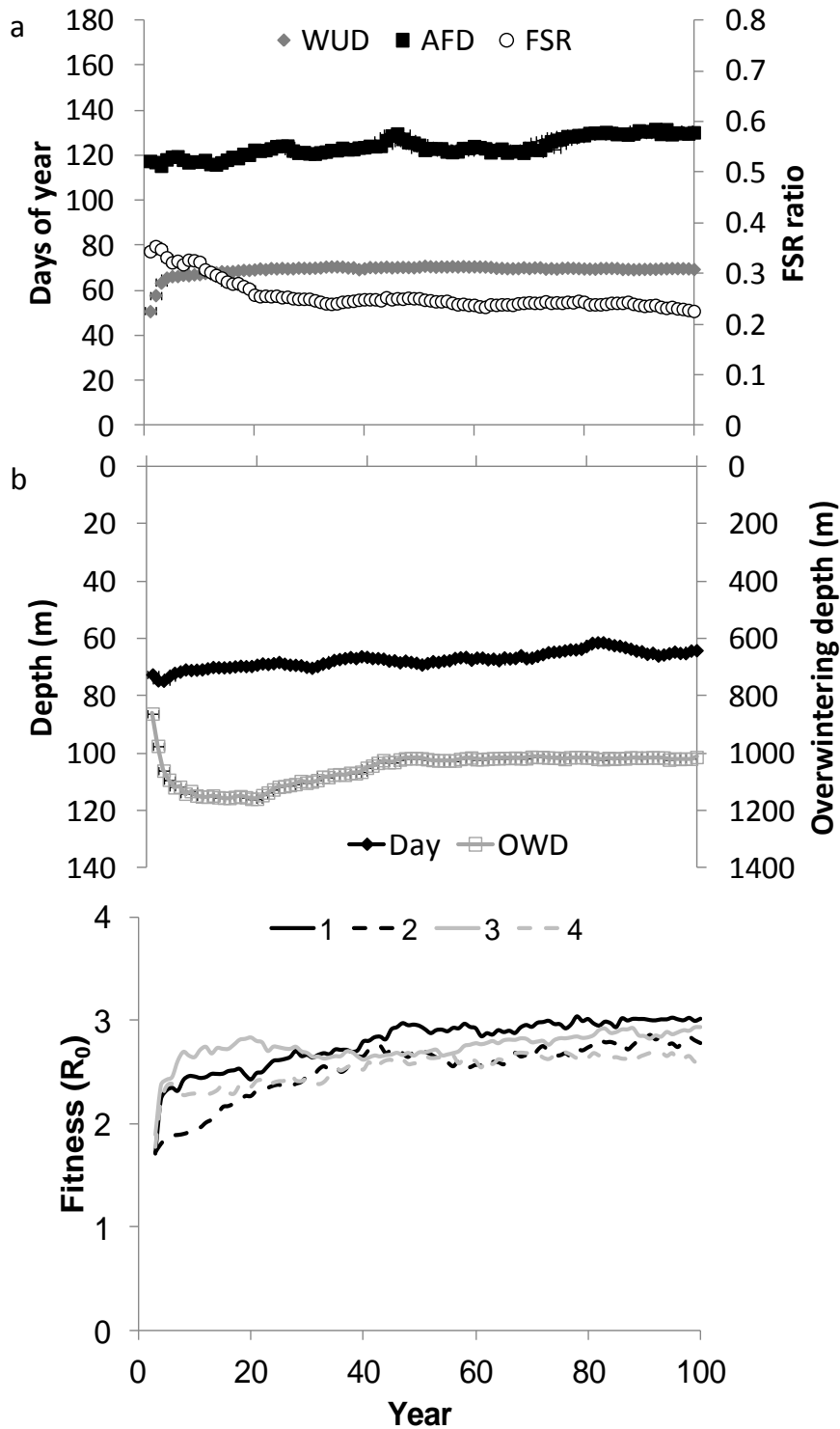


Fig. 3. The development over 100 years of the best replicate in simulation 1 in a) wake up day (WUD), allocation to fat day (AFD) and fat to soma ratio (FSR) traits, b) the day depth (DD) and overwintering depth (OWD), and c) fitness (the net reproductive rate, R_0) of all four replicates. Values are from end of each year.

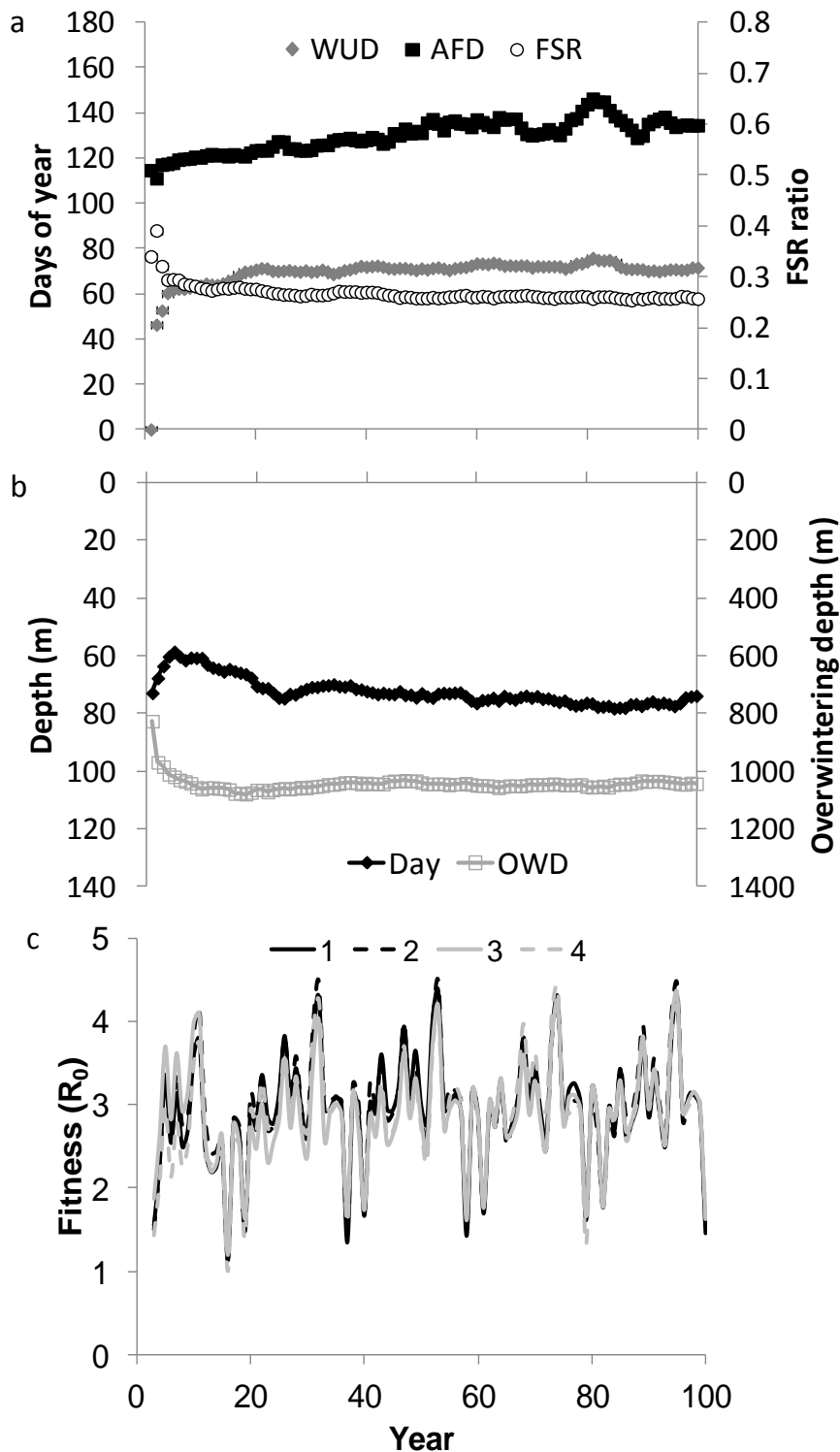


Fig. 4. The development over 100 years of the best replicate in simulation 2 in a) wake up day (WUD), allocation to fat day (AFD) and fat to soma ratio (FSR) traits, b) the day depth (DD) and overwintering depth (OWD), and c) fitness (the net reproductive rate, R_0) of all four replicates. Values are from end of each year.

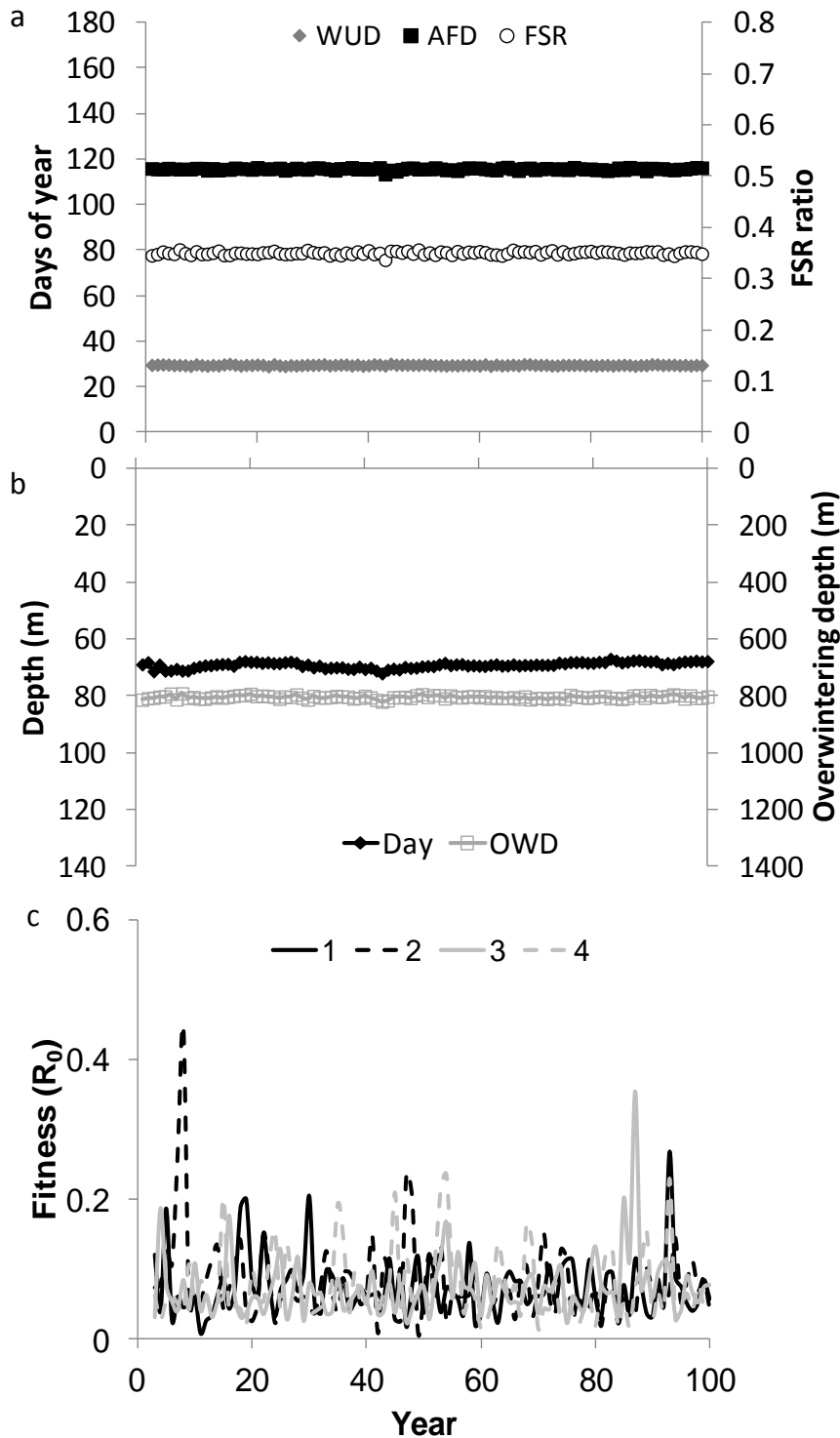


Fig. 5. The development over 100 years of the best replicate in simulation 3 in a) wake up day (WUD), allocation to fat day (AFD) and fat to soma ratio (FSR) traits, b) the day depth (DD) and overwintering depth (OWD), and c) fitness (the net reproductive rate, R_0) of all four replicates. Values are from end of each year.

3.5 Simulation 4: Adaptation to a single forcing year

In the fourth simulation the forcing in a single year (1983) was repeated over and over. In this case the best strategy had convergent wake up and allocation to fat days at day 100 (Fig. 6a).

6a).

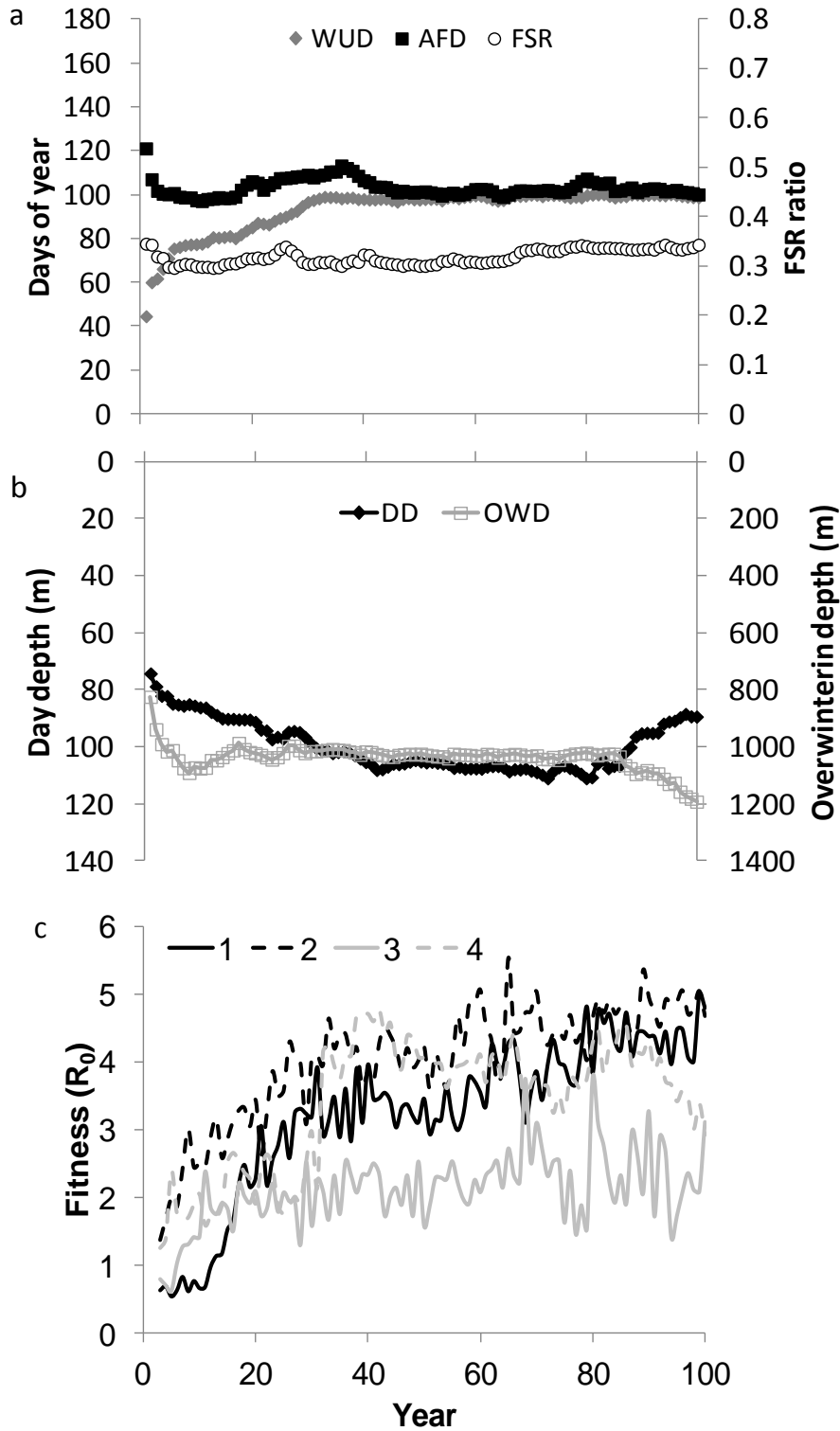
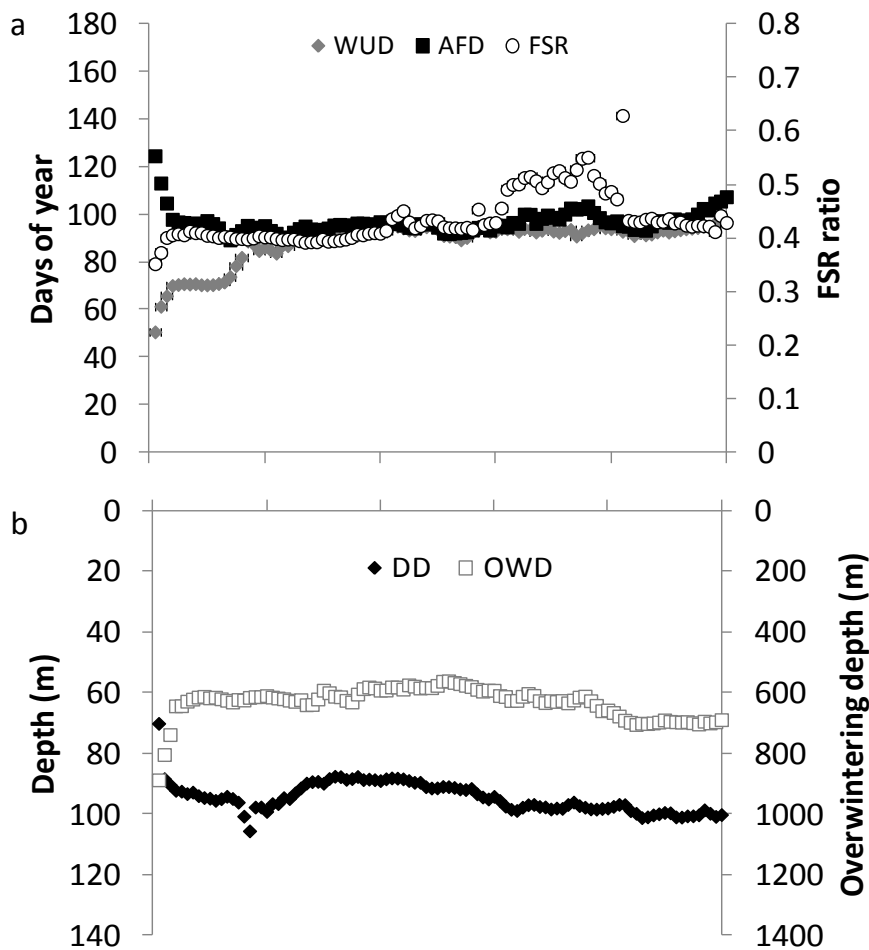


Fig. 6. The development over 100 years of the best replicate in simulation 4 in a) wake up day (WUD), allocation to fat day (AFD) and fat to soma ratio (FSR) traits, b) the day depth (DD) and overwintering depth (OWD), and c) fitness (the net reproductive rate, R_0) of all four replicates. Values are from end of each year.

The FSR ratio was slightly increased compared to simulation 1 which did not have the spatial variability. The day depth was at 90m, which is deeper than in the previous simulations. The four replicates developed slightly differently and the variation between them was more pronounced than in the previous simulations, illustrating the effect of spatial variability (Figs. 3 and 6). There is also great variation in centre of mass (Fig. 2) and fitness (Fig. 6c) between replicates.



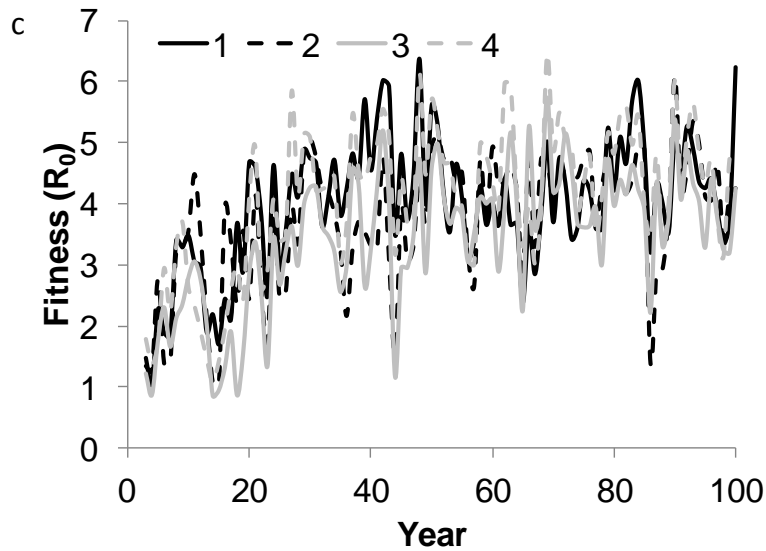
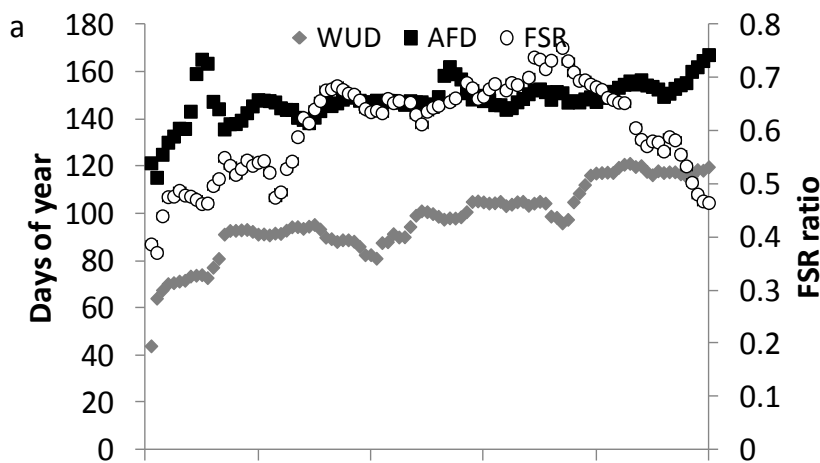


Fig. 7. The development over 100 years of the best replicate in simulation 5 in a) wake up day (WUD), allocation to fat day (AFD) and fat to soma ratio (FSR) traits, b) the day depth (DD) and overwintering depth (OWD), and c) fitness (the net reproductive rate, R_0) of all four replicates. Values are from end of each year.



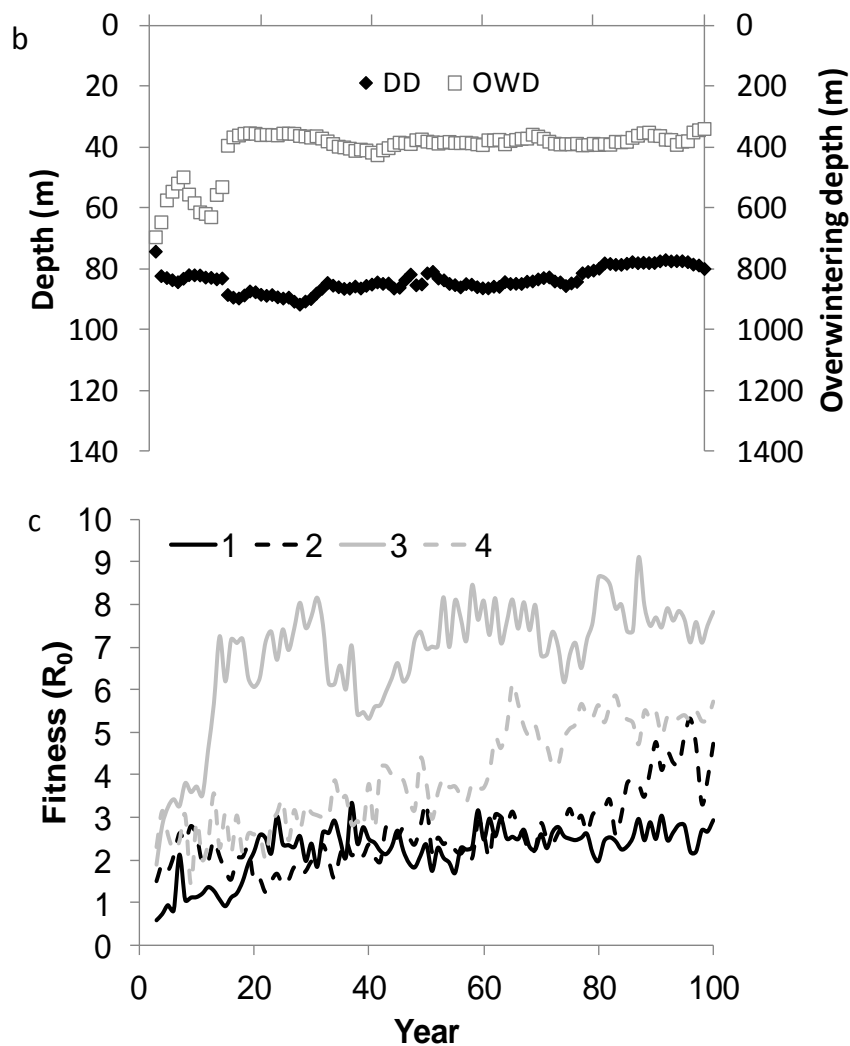


Fig. 8. The development over 100 years of the best replicate in simulation 6 in a) wake up day (WUD), allocation to fat day (AFD) and fat to soma ratio (FSR) traits, b) the day depth (DD) and overwintering depth (OWD), and c) fitness (the net reproductive rate, R_0) of all four replicates. Values are from end of each year.

3.6 Simulation 5: Multi-year forcing

In the next simulation the populations were adapted to inter-annual as well as spatial variability in forcing. This simulation (Fig. 7) produced a strategy with a slightly delayed ascent compared to the previous simulation and like in the previous simulation (Fig. 6), the AFD converged to the WUD value (Fig. 7). The day depth was slightly deeper than in the previous simulation. As expected, the fitness was more variable between years, but there was less variation between replicates than in simulation 4 (Fig. 6c vs. 7c).

3.7 Simulation 6: Reduced predator density

Reducing the predator density had a pronounced effect on the time that the simulated C.

finmarchicus spent at the surface. In this simulation the ascent from overwintering (WUD) was on day 120 and the AFD was at day 165, considerably later than for the other simulations. While the day depth was at around 80m, and similar to many previous simulations, the overwintering depth was at 400m, and substantially shallower than in all previous simulations (Fig. 8b). The peak in the fitness level was increased substantially compared to the previous simulations as expected with the lower predation risk, but there was considerable variation between the replicates (Fig. 8c). The highest fitness was associated with the replicate (number 3) that had a centre of mass in the central part of the Norwegian Sea, whereas the replicates close to the Norwegian Coast had substantially lower fitness (Figs. 2 and 8c).

3.8 Simulation 7: Increased predator density

When the predator density was increased on the other hand there was not a similar shift in life history (Fig. 9) and the WUD and AFD traits were to a large degree similar to simulations 4 and 6 (Figs. 6 and 8), except that the day depth was deeper than in these simulations. As expected the fitness level was lower in this simulation and about half the level in simulation 6 with decreased predator density. Again there were substantial variation in fitness between the replicates and the lowest fitness was associated with the location close to the Norwegian shore, where one of the replicates had its centre of mass (Figs. 2 and 8c). The other replicates ended up rather closely together to the south of Iceland, but still showed some variation in fitness.

3.9 Seasonal dynamics

The data on seasonal population dynamics were compared for the year 1983, due to the considerable inter-annual variability in the forcing. The seasonal population dynamics varied substantially between the simulations (Fig. 10). The highest peak in abundance was found in simulation 6 with reduced predator density. This simulation also had the latest peak, which took place in early September. Simulation 6 with an increased predator density on the other hand, had its peak in abundance two months prior, at the end of June. The second highest peak was seen in simulation 4, which was adapted to the year 1983 only. Simulation 5, adapted to inter-annual variability had a lower abundance. The seasonal dynamics of the two simulations without spatial variability (1 and 2) showed an almost identical pattern. The earliest and lowest peak in abundance was in simulation 3 without adaptation as could be expected (Fig. 10).

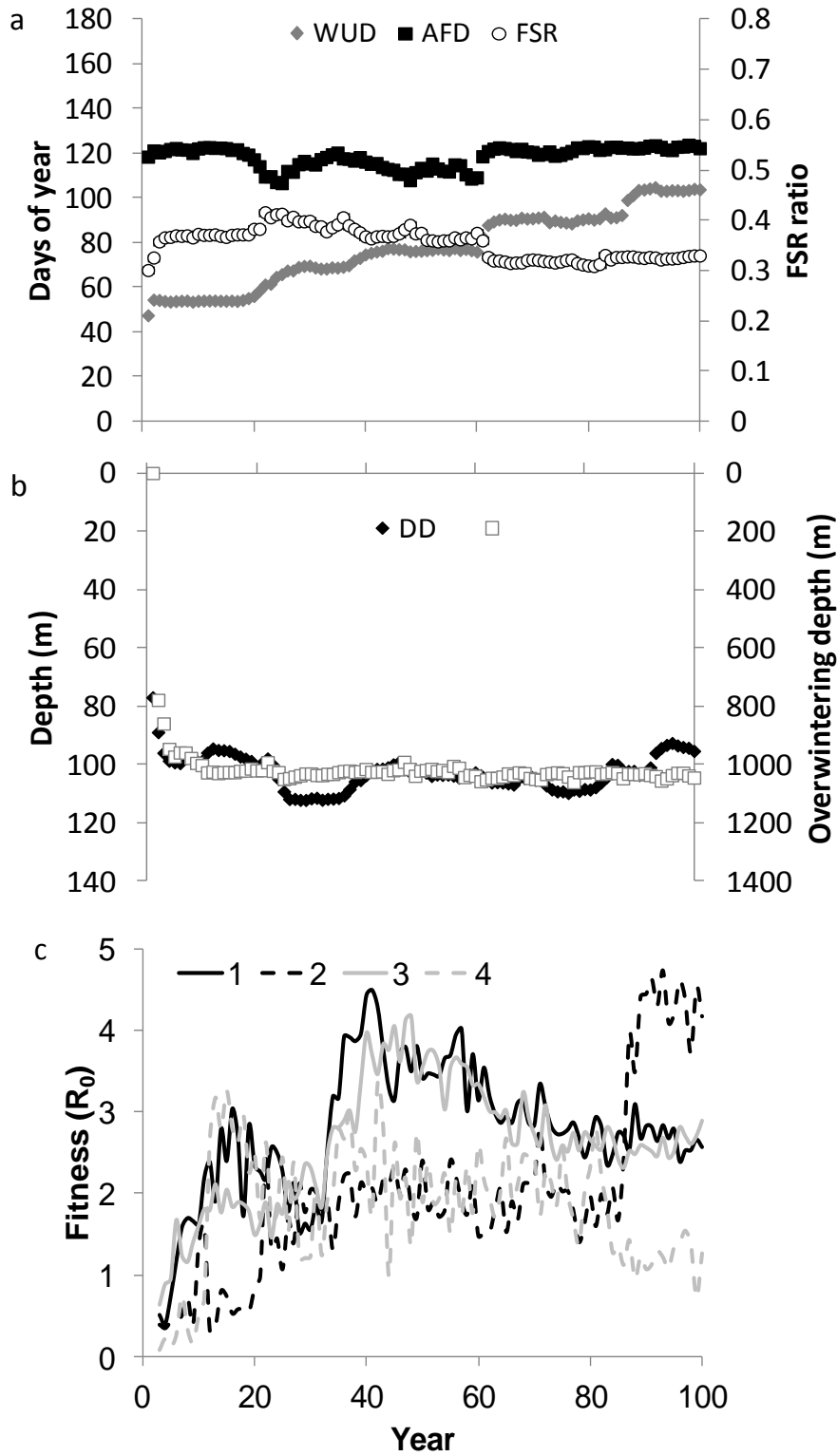


Fig. 9. The development over 100 years of the best replicate in simulation 7 in a) wake up day (WUD), allocation to fat day (AFD) and fat to soma ratio (FSR) traits, b) the day depth (DD) and overwintering depth (OWD), and c) fitness (the net reproductive rate, R_0) of all four replicates. Values are from end of each year.

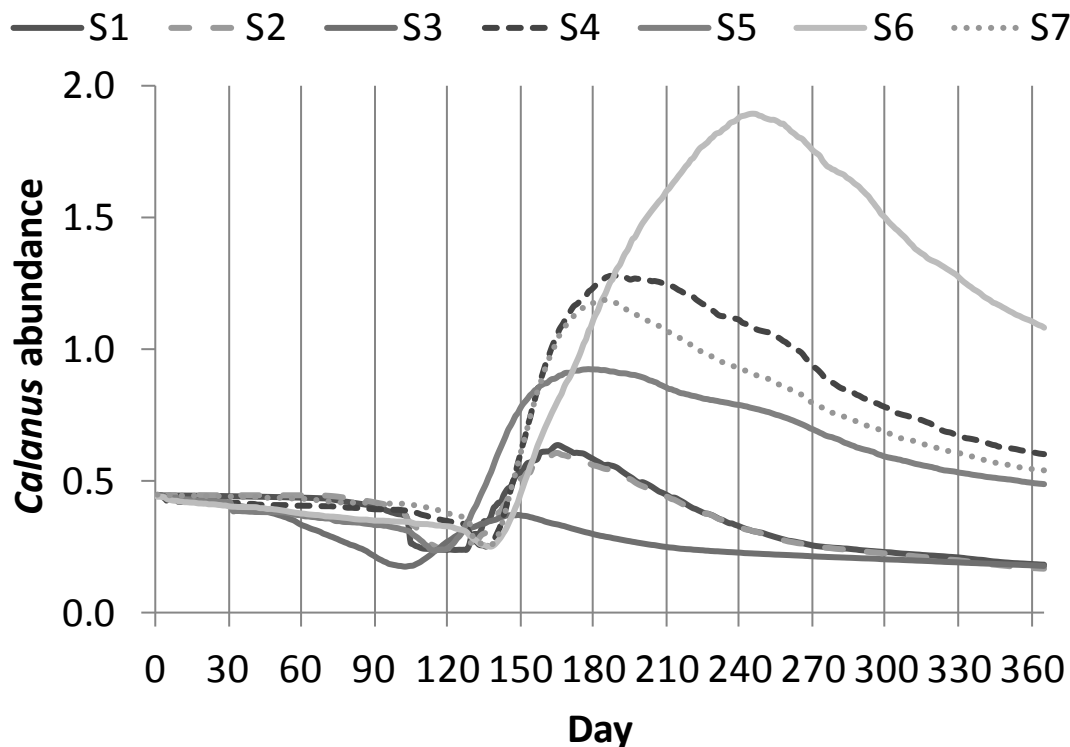


Fig. 10. The seasonal development in *Calanus finmarchicus* abundance in the 7 simulations (S1-7) for the year “1983” in the best replicate of each simulation.

4. Discussion

4.1 Effects of temporal variability

The simulations with inter-annual variability in forcing (2 and 5) resulted in a pronounced variation in fitness between years. This shows that although the populations adapt to the inter-annual variability, the adaptive process cannot make up for this variability. However, there was not a consistent effect on the trait values. The emergent wake up day was spread out over two months in the simulations from day 60 to day 120, with many simulations having an ascent initiated at day 90-100. In most of the simulations the peak in the *C. finmarchicus* abundance was at day 165-185 (Fig. 10). This corresponds well to the timing of the peak in *C. finmarchicus* abundance seen in the Norwegian Sea (Melle et al., 2004) and to previous model simulations with the NORWECOM.E2E system (Hjøllo et al., 2012). Observations from the Norwegian Sea show that the peak of the spring bloom varies by about one month (Rey, 2004), with April 16 (day 106) as the earliest peak day. There was a slight tendency for earlier wake up day in simulation 5 with inter-annual variation compared to simulation 4 without it. Early wake up day makes the copepodites exposed to predation for a longer time span compared to a later wake up. In line with this, simulation 5 had a greater day depth than simulation 4 indicating a more risk averse strategy with inter-annual variability. In the study by Hjøllo et al (2012) and Samuelsen et al (2009) it was found that changes in wake up day in spring had several effects on the subsequent population dynamics of the simulated *C. finmarchicus* population, manifested as changed

C. *finmarchicus* biomass values/timing and annual production.

4.2 Effects of spatial variability

In simulations without spatial variability, there were only minor differences between replicates (Figs. 3 and 4). However, spatial variability had a strong effect on the fitness variation between the replicates. These simulations produced rather different centres of mass, both between simulations and among replicates (Fig. 2). In particular it was shown that the simulations without inter-annual variability in forcing produced quite different centre of mass among replicates, whereas simulation 5 with inter-annual variation in the centre of mass was almost identical in the four replicates, and produced populations that remained in the centre of the Norwegian Sea. This indicates that there are current structures in some locations in some years that allow retention of plankton populations. In the model this resulted in local adaptation and widespread centres of mass in the simulations without inter-annual variability. This illustrates the importance of inter-annual variability in breaking down peculiarities in current patterns and thus varying the degree of retention in different areas. Plankton are at the “mercy” of this variability and consequently needs to be adapted to a range of different environmental situations. Bryant et al. (1998) found that only very restricted parts of the Norwegian Sea around the Faroese Islands and east of Iceland were able to retain simulated *C. finmarchicus* over more than 10 years. These areas correspond well to the areas where we found the centre of mass of most of the present simulations (Fig. 2). Torgersen and Huse (2005) found that there was a low degree of retention in the Norwegian Sea, and in particular for the eastern part of the sea. After 4 years the average retention was 10% of the particles initially released and mimicking a *C. finmarchicus* life cycle. Our model showed that long term persistence over 100 years is possible in the Norwegian Sea when the growth, mortality and reproduction are included. To our knowledge there are very few examples of similar long term model simulation with fine resolution in space, time and individual properties.

4.3 Effects of predator density

Predator density had a pronounced effect both on the population dynamics and behaviour of the *C. finmarchicus*. In particular the individuals adapted under the high predator density evolved a more risk averse strategy with a deeper day depth compared to the simulation with lower predator density. Bollens and Frost (1989) in a classic study found that *Calanus pacificus* increased the magnitude of their diurnal vertical migration when the density of predator fish was increased. The difference they observed was greater in magnitude than the increase that the present simulations produced which was about 20m. But the shallowest day depth in simulation 1 was 60m. The shift from simulation 1 to simulation 6 with increased predator density was 40m and thus about the same as the shift observed by Bollens and Frost.

Although the traits can be made more dynamic and dependent on local environmental factors, the present strategy vector with six traits works well in adapting the population to the prevailing conditions and shows clearly different adaptive trajectories under different environmental forcing. However, it is fairly easy to modify the day depth calculation so that it for example is related to the local predator density experience by the simulated *C. finmarchicus*.

Fiksen (2000) with a similar IBM as the present model found the wake up day to be at around day 75 and the allocation to fat day at around day 175. When density dependence

was added, the allocation to fat day decreased to around day 150, but nevertheless this span between wake up day and allocation to fat day is quite a bit longer than found in most of the present simulations. We found the span here to be dependent on the predator density and for the lowest predator density (simulation 6) the time span was much greater than in the high predator simulation (simulation 7). This resulted in a delayed peak in copepodite abundance in the low predator simulation compared to the other simulations (Fig. 10). This supports the hypothesis proposed by Kaartvedt (2000) that time spent at the surface is minimised to reduce predation risk from pelagic fish that enters the Norwegian Sea to feed in summer. The herring arrives early on the feeding grounds (Dragesund et al., 1997; Holst et al., 2002), but the mackerel arrives later on (Utne et al., 2012b), and avoiding this added predation level is beneficial to the *C. finmarchicus*.

4.4 Individual based population modelling of zooplankton

IBMs are valuable tools for addressing the consequences of different individual traits on for example population dynamics and trophic interactions (Grimm and Railsback, 2005; Neuheimer et al., 2010). The 3D individual based model with emergent life-history and behavior model presented here has been shown to be useful for investigating how different trait formulations affect the population dynamics and behaviour of plankton. There are a range of different hypotheses related to diapause initiation and termination in *C. finmarchicus* (Hirche, 1996a; Heath, 1999; Fiksen, 2000; Heath et al., 2000), and the present model system is ideal for investigating the consequences of such hypotheses for the spatial and population dynamics of plankton. We based our 3D model on the traits used by Fiksen (2000), who studied evolutionary robust strategies in a 1D model of *C. finmarchicus*. This approach has previously been used to study migrations (Huse and Giske, 1998; Huse, 2001; Strand et al., 2002) and life history traits (Huse and Ellingsen, 2008) in fish.

To model the demography of *C. finmarchicus* in the north-east Atlantic, Speirs et al. (2006) used a full *C. finmarchicus* life cycle model forced by phytoplankton through satellite observations and modelled weekly updated physical transport of individuals from one cell to another in two distinct layers (20 and 600m). They found that transport was generally not important to demography, but that there was a strong connectivity of *C. finmarchicus* within the entire distribution area of the species. This approach is computationally efficient and allows statistical parameter fitting, but lacks a fully resolved flow field and the feedback between the different trophic layers. The NORWECOM.E2E model takes into account feedbacks between the different trophic levels and driven by realistic physical forcing have been developed, and also extended to include pelagic fish. This fully coupled model has been used for experiments with diapause termination, overwintering *C. finmarchicus* stock size as well as fish consumption. The computer resource demanding NORWECOM.E2E model system benefits from testing and development of robust *C. finmarchicus* strategy vectors as in this study.

The simulations relied on a rather low initial population size. This makes the run time fast and allows multiple simulations and replicates. However there are potential downsides to this related to only finding local minima in the fitness landscape as well as covering only restricted geographic locations within the large simulation area. Hjøllø et al (2012) found that the aggregated variables such as production was sensitive to the number of super individuals simulated. They found a 10% lower production for a simulation with 23 000

individuals compared to the reference simulation with 200 000 individuals, but simulations with 47 000 and 120 000 super individuals have about the same cumulative production as in the reference run.

The resampling scheme introduced here with a fixed initial abundance at the start of each year, provides a simple approach to keep the number of super individuals simulated under control without constraining the ecological or evolutionary processes too much. This allows for rather long term simulations, over 100 years with a simulation time of a few hours on a laptop. Feedback on the phytoplankton is not included presently, but since this is known to be important in many areas, fully coupled model systems are developed. The models based on IBMs have much longer simulation time as more super individuals are needed to cover the geographical area and provide realistic forage feedback. An application of the present model is therefore to produce robust strategy vectors for use in fully coupled end to end models such as NORWECOM.E2E (Hjøllo et al., 2012; Utne et al., 2012a). Although the present offline version is valuable for providing a starting point for simulations, it is likely that the selection pressure will change slightly as a response to the density dependent food availability in the fully coupled model. This may create a “drift” in the strategy vectors that requires either to use some further adaptation or to use fixed strategy vectors for the population.

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Modelling secondary production in the Norwegian Sea with a fully coupled physical/primary production/individual-based *Calanus finmarchicus* model system

Solfrid Sætre Hjøllo ^a, Geir Huse ^a, Morten D. Skogen ^a & Webjørn Melle ^a

^a Institute of Marine Research, Bergen, Norway

***Calanus finmarchicus* abundance**

This figure shows the comparison of model predictions for calanus abundance with observations (Hjøllo et al., 2012). While there are some discrepancies between the model and observations, the model captures the key dynamics of the observations, particularly for the adult *Calanus* stages (C4-C6). For the younger stages there are likely some under sampling for the net applied (WP2 plankton net).

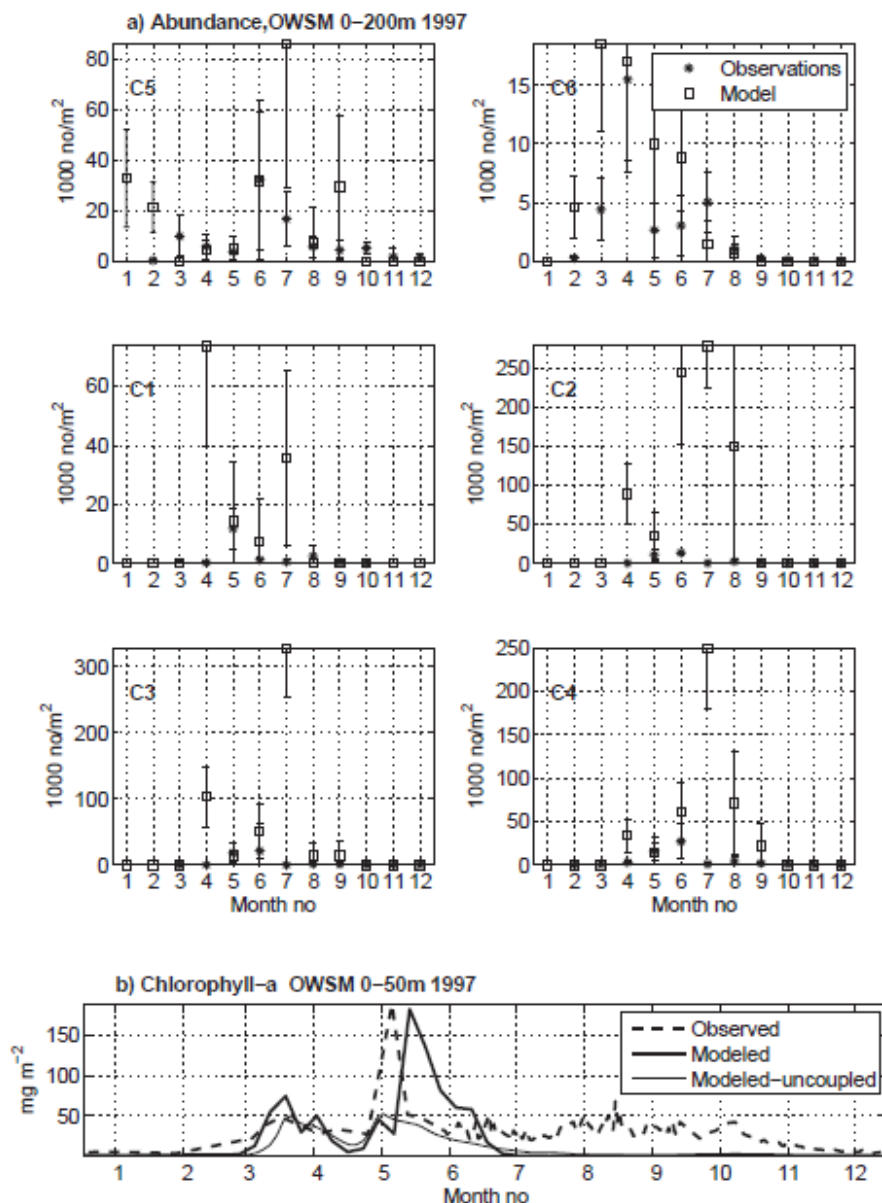


Figure 5. (a) Upper 200 m *Calanus* abundance at OWSM (66°N, 2°E), from observations and model for the year 1997. Data are sorted by stage C1–C6, and are grouped into monthly values. Vertical lines indicate 95% confidence interval. (b) Chlorophyll *a* observed (stippled line) and modelled (full line), and modelled from an earlier uncoupled simulation by (thin line). Observations from Rey (2004), uncoupled simulation from Skogen et al. (2007).

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