Physiology, phenology and behavioural strategies of forage fish
Studied by bioenergetic modeling

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Physiology, phenology and behavioural strategies of forage fish

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PhD thesis by

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Preface

My first introduction to ecosystems models was at my first semester during my engineering studies in environmental chemistry, where a group of us developed a simple box model of a Danish fjord system. A fundamental assumption to the model was: what enters a box exits the box as the same chemical compound. This assumption was difficult to accept and was later undermined, as I was introduced to microbiology and basic biology on the low trophic levels. I found it intriguing with the diversity of organisms which were found in the aquatic environment and wanted to explore this more. This wish was granted when I was accepted at a master programme in biological oceanography. Here my eyes were opened for the complex systems in the world’s oceans and the diversity seen in the organisms living there. Through the course of my PhD studies I was able to focus on the links between the individual to the environment – both the physical properties of the environment, its prey and predators. But I was also given the change to examine the drivers of the individual and how its life history and behaviour affects the individual. Today I am still fascinated by the diversity in life histories seen in the oceans on all trophic levels. But I have also, yet again, found out the more I seek answers, more questions are evolving.

My PhD has been made possible through collaboration with Axel Temming and Jens-Peter Herrmann (Institute for Hydrobiology and Fisheries, University of Hamburg, Germany), whom granted me access to the unique dataset on Baltic Sea sprat. I thank you very much for letting me use your data, and for welcoming me at you institute in 2009.

Also this work has been made possible through collaboration with Kristine S. Madsen (DMI, Centre of Ocean and Ice), whom supplied the temperature fields and climate scenarios for the Baltic Sea. Thank you very much for the help.

I am grateful to my supervisors, Ken Haste Andersen (DTU Aqua) and Gerd Kraus (Previously: DTU Aqua. Now: vTI, Institute of Sea Fisheries, Hamburg, Germany). I have never doubted your support and have always been met with an open door and a smile. Thank you very much for all of you help and patience. You have been the best supervisors.

To all my colleagues – past and present: Thank you very much for the discussions, both the scientific and the more informal talks over coffee. You have been indispensable through the ups and downs over the past years. You have all made my time at Aqua great.

To my family and friends: I could not have done this without you. You have always believed in me and encouragement has been unlimited. Your support is priceless and I cannot thank you enough. I am grateful to have all of you in my life.
Summary

Forage fish are small individuals, and are very abundant in numbers and can form dense schools. Forage fish are important within the food webs of the oceans, as they are at the lower trophic levels. Forage fish prey on zooplankton and they are themselves preyed on by piscivore fish. The individual forage fish and its growth dynamics are governed by an interplay between physiological rates, e.g. metabolism and consumption and the ambient environment as the rates are temperature dependent. The topic of this thesis is to describe the strong link between the individual and the environment through bioenergetic modeling. The bioenergetic model is based on the Wisconsin framework, and assumes that ingested energy is deducted losses to egestion, excretion, standard dynamic action and metabolic costs. Surplus energy, if available, is divided between growth in two structure pools; somatic tissue and reserves. The model includes an additional structure pool; gonads, to which energy is transferred during the spawning season. During periods of poor feeding, energy to cover metabolic costs are firstly taken from the reserve pool and secondly, if the reserves are depleted, from the somatic tissue pool. The model is forced by the ambient temperature experienced by the individual and prey. The bioenergetic model reveals how the physiology and the link to the environment are governing factors determining the growth dynamics of the individual. The model includes evaluation of the life history of an individual allowing study of individual behaviour, making the model a strong tool, for investigating hypotheses of life history and behavioural strategies in forage fish.

The model is parameterized for Baltic Sea sprat and was used for determination of the importance of temperature on physiology, growth and egg production of adult female sprat. Particular emphasis is placed on the allocation of energy inside the individual, whether energy is invested in growth or reproduction. The simulations reveal that a constant division of surplus energy between the lipid and soma pools leads to seasonal variations in growth and size matching observations. Also an increase in the soma growth potential as a function of temperature was observed, but that the maximum size will decrease with increasing temperature. Temperature is especially important for Baltic sprat as the Baltic Sea is at the species northernmost distribution limit with regard to temperature. Climate scenarios for the Baltic Sea predict a significant warming and the impact of predicted future climate changes and the prey phenology on growth, egg production and fitness was determined. We find the warmer future climate reduces egg production and fitness. The larger the temporal match of the prey with spawning season, the larger is the egg production and fitness. Therefore the effects of temperature on the sprat stock can be lowered if prey phenology responds to the climate. The bioenergetic framework is also used to investigate effects of individual behaviour on the fitness of an individual. Baltic Sea herring are observed to skip spawning when individuals have low condition. This phenomenon and its implications to individual fitness are quantified and are linked to the individual and environmental conditions as well as spawning season. Changes in the individual condition were affecting the number of skipped spawning events and age at first spawning. Spring spawning was found to be the better strategy compared to autumn spawning. Another behavioural strategy which was investigated was the burrowing strategy seen in
sandeel in the North Sea. The trade off by this strategy whereby the energy intake is lowered but the strategy also reduces potential predation is quantified. This revealed that the strongest trade off for the individual is to reduce mortality rather than to seek an opportunity to grow larger and thereby be able to produce more eggs.
Resume


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General introduction

The dissertation title ‘Physiology, phenology and behavioural strategies in forage fish’, reveal that this study includes processes which operate within the individual and exogenous influences affecting the individual and its life history traits and choices. The case has been on forage fish, which are an important functional group in the marine ecosystems, where they are essential for energy transfer from low to high trophic levels. The functioning of a forage fish, as every organism, includes a complex set of processes which governs growth and development: the physiology of the individual. The physiology is strongly linked to the surrounding environment as temperature play an important role in the physiological rates in iteparous organisms as forage fish. The link between the environment, including both seasonal and interannual variations, and the individual’s life history events are described by the phenology. Thus, the phenology is the relationship between returning biological phenomenon and its link to climate conditions, e.g. spring bloom timing and intensity as well as timing of the spawning event. The effects of the phenology can be affected by life history choices and individual behaviour. The life history choices are evolutionary encoded in the individual, such as spawning strategy and how energy is used for reproduction and anatomically characteristics. But the individual is able to optimize its life history traits according to the physiology and phenology through its behaviour. Therefore an individual is strongly linked to the environment but with regards to its physiology and the life history traits. These categories are the main focus of the work presented here and focus is on the interplay of all elements and their implications on the life of forage fish (figure 1).

Figure 1: Visualization of the main topics in the dissertation. The grey zones show the intersections between the main illustrating the strong interlink of the main topics. Some studies include two of the main topics and others include all three.

The dissertation consists of an introductory part, where the background to the project, according to the topics described above here, is presented and links to classical research and recent state-of-the-art studies are included to give the background to my work. General definitions and detailed background of specific details are given in text boxes. Following is a
perspective where I include the work I have performed during my study including summaries of research manuscripts. The manuscripts are enclosed as appendices to the dissertation.
Forage fish and their ecological role

Forage fish are small individuals, and are very abundant in numbers and can form dense schools. Forage fish are important within the food webs of the oceans, as they are at the lower trophic levels, and therefore channel energy to higher trophic levels. Forage fish is a broad grouping, which include several species that show a great variety of life histories and strategies. Important forage fish in the temperate zone includes sprat (Sprattus sprattus), herring (Clupea harengus), sardine (Sardina pilchardus), anchovy (Engraulis encrasicolus) and sandeel (Ammodytes spp.).

Ecosystem role
Within an ecosystem, which includes the entire food web including the abiotic environment, the links between all food web levels are dynamic and respond to changes in the web itself as well as direct changes in the abiotic environment. The changes in the food web can originate from anthropogenic stress, e.g. pollution and fishing, or it can be caused by inter-species dynamics, e.g. competition and predator-prey interactions. These implications on the ecosystem and how the different trophic levels are affected are a key research area which is also included in this study where focus is on the level of the forage fish. A quantification of the effects is described by the ecosystem functioning described by Cury et al. (2001) (box 1). I will here give examples of bottom-up, top-down and wasp-waist forcing of food webs and the consequences on the forage fish in the Baltic Sea.
Ecosystem dynamics – an example of the Baltic Sea

The Baltic Sea is an ecosystem which is dominated by three species, cod (*Gadhus morhua*), herring and sprat. These three species make up 90% of the total fish biomass (Thurow, 1993). In the recent three decades the overall functioning of the Baltic Sea ecosystem, according to the definition by Cury *et al.* (2001), has experienced periods when the forcing of the system has been altered by mechanisms related to both *bottom-up*, *top-down* and *wasp-waist*. This has changed the abundances in the different stocks and affected the dynamics within a stock e.g.
individual condition due to density dependence, but the combined biomass of the three species
has remained relatively stable.

In the beginning of the 1980’s the cod stock in the Baltic Proper was at its historically
highest level (ICES WGBFAS, 2011). Both herring and sprat had high condition (Casini et al.,
2011), and the stocks were exposed to a high predation pressure from the large cod stock.
During this period the two forage fish species were primarily top-down forced, that is their
biomass was not increasing, mainly due to the predation by cod, even though the feeding
conditions were good and recruitment was relatively high. During the 1980’s, the low intensity
of inflows of saline and oxygen rich water from the Kattegat lead to in a decline of the salinity in
the Baltic Sea (Fonselius & Valderrama, 2003). This lowering of the salinity reduced the
Pseudocalanus abundance (Renz & Hirche, 2006) which is the preferred prey for larval cod
(Möllmann et al., 2008). The situation with poor physical conditions for egg survival and the
poor feeding conditions for larvae resulted in a decrease of the cod recruitment (Köster et al.,
2005; Möllmann et al., 2008). At the same time the temperature increased due to changes in
the atmospheric forcing (Madsen, 2011). The rise in temperature changed the plankton
dynamics, increasing the biomass of dinoflagellates which led to an instantaneous response in
Acartia spp. (Möllmann et al., 2008). The Acartia spp. is preferred by sprat (Bernreuther, 2007;
Dickmann et al., 2007; Voss et al., 2006), which in combination with higher temperatures
increased recruitment in sprat (Köster et al., 2003; Nissling, 2004). Both the reduction in cod
recruitment and the increase in sprat recruitment are caused by bottom-up forcing. The sprat
biomass during this period increased dramatically both caused by the high recruitment but also
the reduction in predation mortality by cod. The bottom-up forcing can as seen in this period
affect different species in opposite ways, the change in the dominant prey specie is a benefit for
sprat whereas it is has a negative influence on cod recruitment, which is also worse off because
of the changes in the physical environment. In the following period from 1990 and onwards,
sprat had a role of a wasp-waist species, influencing both the biomass at lower and higher
trophic levels i.e. zooplankton and cod. The high sprat abundance is able to control the
zooplankton production (Möllmann & Köster, 1999) and density dependent processes operate
within the stock. The clearest effect of the density dependence is seen in reductions of the
weight at age. Especially in the oldest ages, the mean weight declined by approximately 40%
from 1992 to 1996 (ICES WGBFAS, 2011). The cod stock is at the same time affected by the large
sprat stock as sprat competes with larval cod for the available zooplankton resources (Voss et
al., 2003). Further, sprat is preying on cod eggs (Köster & Möllmann, 2000). The density
dependent effects also apply to the herring stock, even though the signal is not as strong as in
the sprat stock since the herring does not solely depend on zooplankton but also have other
prey options (Möllmann et al., 2008). In the most recent years the cod stock has increased due
to reduced catches and increased recruitment production (Eero et al., 2012).This has resulted in
re-establishment of the top-down effects on the sprat stock due to predation by cod. In the
recent years, only 5% of the cod stock is found in the northernmost ICES subdivisions of the
Baltic Proper, while the sprat is distributed mainly in these northerly subdivisions (Casnini et al.,
2011). The condition of the sprat in the south is higher than the individuals in the north (Casnini
et al., 2011). This is due to different processes acting in different areas, where the individuals in
the south experience abundant food resources but a high predation mortality, and are therefore top-down controlled. In contrast, the individuals in the north are more governed by density dependent processes. Thus, not only does the ecosystem function change dynamically over time, but also spatially within a relatively small area such as the Baltic Proper.

The examples given here illustrate the important role forage fish hold in the ecosystems. They can be a keystone species, as sprat in the Baltic Sea, where they either sustain a large cod stock and during other times they are the controlling factor within the food web.

**Biology of the forage fish**

The diet of forage fish consists of primarily zooplankton. Some species are strict zooplanktivorous preying on primarily copepods, e.g. sprat (e.g. Bernreuther, 2007; Voss *et al.* 2009) and sandeel (Macer, 1966; van Deurs *et al.*, in prep.), whereas others prey on larger zooplankton and small fish for the largest individuals, e.g. herring which also prey on the larger mysids and small fish (Blaxter, 1990; Bernreuther, 2007). But copepods are the most important prey throughout the lifespan of the forage fish. E.g. studies have showed for Baltic sprat and herring that the prey species is the same throughout the entire lifespan, but the size preference increase with increasing size of the forage fish (Bernreuther, 2007). Feeding is primarily by snatching the particles and feeding is therefore dependent on sufficient light levels. In high prey concentrations some forage fish are able to filter feed, e.g. herring which will swim with their mouth open allowing particle to be trapped by the gill rakers (Blaxter, 1990).

Forage fish compensate for their small size by forming large schools; hereby they try to avoid predation. The school is able to move as one unit, and thereby appear to be large and invincible to the predator. Their silvery skin functions as a distractor to the predators as it is nearly impossible to pin out a single individual from a dense silvery fish school, reducing the catch rate (e.g. Blaxter, 1990).

Forage fish are classically been described as r-strategist, that is they are fast growing, mature at an early age and produce many small off-spring hereby compensating for the strong mortality pressure (Pianka, 1970; Roff, 1992). The reproduction in forage fish can range from a total/determinate spawner as herring and sandeel which have a single spawning event to batch/indeterminate spawning as sprat which can produce up to 10 batches of eggs during the spawning season (Alekseeva *et al.*, 1997). The spawning effort can further be partitioned according to the energy expenditure patterns; capital breeding, which is solely dependent on stored energy and income breeder, which are able to allocate consumed energy to egg production. The mentioned strategies are all absolute endpoints within a range of observed strategies, and individual species are distributed throughout the range.
Physiology and bioenergetics

The physiology of an individual includes all the biological processes and functions which occur within the individual. Physiology includes both consumption, processing of the consumed energy, metabolism and growth. Growth can be either in biomass or as gonad production. The physiological processes may be represented by a mass balance where all energy consumed by the individual is allocated to the structures of the individual and/or the vital processes which can be both direct loss terms and energy expenditures (Winberg, 1960):

\[
growth = \text{consumption} - \text{metabolism} - \text{waste} = \text{consumption} - (\text{respiration} + \text{activity} + SDA) - (\text{egestion} + \text{excretion})
\]

Where the metabolic processes are costs to respiration, i.e. maintenance of the cells, and activity associated with swimming. The waste terms are egestion, i.e. fecal matter, excretion of nitrogenous waste over the gill surface and specific dynamic action which is the costs to food processing and assimilation.

Forage fish are poikilotherms and several of the physiological rates are temperature dependent. Increasing temperature raises the costs to metabolism, but it also increases the amount energy that possibly can be consumed. The biomass of an individual takes many forms, e.g. muscles, bone structures, lipids and organs (e.g. Love, 1970). Due to the indeterminate growth in forage fish the biomass fractions continuously grow, but some biomass fractions vary over season, e.g. muscle, lipids and the reproductive organs. During the periods of low feeding the individual can retract energy from the lipids and muscle, reversible biomass, e.g. as seen in sprat (Temming et al., in prep), or the gonads as seen in female herring (Kennedy et al., 2011; Bucholtz et al., in prep.). But some biomass is irreversible and energy cannot be retracted, e.g. bones, organs and some components of the muscles. The individual therefore needs to weigh growth investments respectively in the reversible and irreversible biomass fractions, as the reversible biomass can be used to cover metabolic costs during periods of poor feeding and thereby for survival.

In a seasonally varying environment the interplay between costs to metabolism and consumption will vary over seasons. This is due to both the seasonally resolved food availability and the seasonally varying temperature. In some parts of the year food will be plentiful. In the Baltic Sea the peak in food availability coincides with the period of highest temperatures, which raises possible ingestion but also raises the metabolic costs. During other seasons the habitat will not offer enough food to meet the costs to metabolism, and is therefore dependent on the biomass to cover the metabolic costs.

One method to elucidate the interplay of the physiology of an individual to the environment is through bioenergetic modeling. A bioenergetic model describes the governing energy pathways and the resolution is on the process level. Thus, a bioenergetic model supplies a dynamic and mechanistic description of individual growth.
A historical perspective of bioenergetic models and its applications

The Winberg (1960) formulation has been adapted by many over time. One of the most widely used models was developed by Kitchell et al. (1977). This model has later been denoted as the ‘Wisconsin model’ (Ney, 1990). The core of this bioenergetic model has been to address the question “how much did they eat in order to grow that way?” (Quote p. 217 from Hartman & Kitchell, 2008). The original paper by Kitchell et al. (1977) linked fish growth to the environmental forcing for Yellow Perch (Perca flavescens) and Walleye (Stizostedion vitreum vitreum). The authors used the model to determine the growth potential in the different seasons and to establish which was the most important: temperature or food quality. The model was requested by several others and the model was distributed as a software package named Fish bioenergetics (Hewett & Johnson, 1992; Hanson et al., 1997).

The original question of the Wisconsin model regarding the consumption potential have been posed to Baltic herring where the consumption was linked to observed growth dynamics (Rudstam, 1988) and the inclusion of the seasonally varying day length in the Baltic Sea were important during spring and autumn when comparing model to consumption data (Arrhenius, 1998). The physiological metabolic rate has also received attention. Investigations on varying metabolic costs according to season (Chipps et al., 2000) and the costs of activity in nature compared to in the laboratory have also been performed using the formulation from Kitchell et al. (1977) (Andersen & Riis-Vestergaard, 2004). The core of the Wisconsin model has been extended to include life history traits. The bioenergetic model used in these studies partitioned the biomass increments into two structure pools, soma and reserves, which in combination with dynamic modeling, were used to investigate how Atlantic cod should invest in growth in either the soma or reserve pool (Jørgensen & Fiksen, 2006). The reserves in the cod are used for either migration costs to the spawning ground or for reproduction. The evolution of the migration distance to the spawning ground was tested with the same model setup under different fishing regimes linking the migration distance to individual state (Jørgensen et al., 2008). Thus, the bioenergetic model has been used as a foundation for to study optimal behaviour in individuals based on life history traits. The original view of Kitchell et al. (1977) determining how the environment directly affects growth has been applied by others for testing further hypotheses including the response of growth and maturation to temperature (Harvey, 2009) and the climate effects on predation rates of juvenile Pacific salmonids (Oncorhynchus spp.) by its predators were quantified over a period of 60 years (Petersen & Kitchell, 2001). These examples of the application of the Wisconsin model shows the variety of physiological and growth dynamics that have been examined. In these studies the application of the bioenergetic model have clarified the governing physiological processes, and linked these to the environmental conditions. Also the effects of individual behaviour have been quantified.

The Wisconsin model has also been included as a core feature in a bioenergetic-based population dynamics model which is coupled to the nutrients-phytoplankton-zooplankton-detritus (NPZD) model. The model is named NEMURO.FISH and has been set up for Pacific herring (Clupea harengus pallasi) and the feed-back from the herring stock to on the environment was tested (Megrey et al., 2007). The model setup has been applied to test the growth dynamics according to both the phenology of spawning season (Ito et al., 2007; Mukai et
Pacific herring is a migratory species and the importance of the interannual variability in the different habitats, i.e. feeding - and spawning grounds, were investigated and was linked to the different growth dynamics observed in the population (Ito et al., 2007). This approach to combine the NPZD model to the bioenergetic fish model is essential to quantify the trophic effects which potentially can cascade through the food webs of the oceans, where the NEMURO.FISH model is a novel first step. Other models also use the link between models, e.g. Ecopath with Ecosym (Christensen & Pauly, 1992; Pauly et al., 2000) and Alantis (Fulton et al., 2011). These models are developed from the management models. Thus, the mechanistic and process oriented detail level obtained through the bioenergetic setup is not included in these models.

Concurrently to the developments by the Wisconsin model community another branch of bioenergetics modeling emerged: the Dynamic Energy Budget models (DEB) (Kooijman, 2000). The DEB model dates back to 1979 and originally focused on the effects of toxic stress on growth in daphinids. Today the DEB frame describes individual organisms as well as ecosystems as a whole (Nisbet et al., 2000). The main difference between the Wisconsin frame and the DEB model is the way energy is partitioned and the flow of energy within the individual. The DEB model assumes that surplus energy is first allocated to reserves, from where energy is used to cover costs of metabolic processes, i.e. maintenance, growth and reproduction (Kooijman, 2000), whereas the Wisconsin model subtracts all energy necessary for metabolism and activity before any investments can be performed. Besides this the DEB model per default partitions energy in reserves and soma. In contrast the Wisconsin model can operate by biomass alone. For the majority of studies both the Wisconsin model and the DEB model can be used. The fundamental assumptions in the two only leads to small differences and the output from each model will show the same tendencies. Thus, choice of the model is a question of tradition and appeal.

The bioenergetic models have been met by criticism. The paper by Ney (1993) posts several areas of concern. The forcing functions often used to drive the models, i.e. temperature schemes, diet composition and prey availability, are critical for the output of the model. But the functions are extremely difficult to determine and attempts demand extensive samplings. The physiological rates applied to the models are also an area which needs more attention, where Ney (1993) puts special focus on the costs of activity to be a central part of the model where errors are introduced. More generally concerns of the often many parameters needed to parameterize a bioenergetic model is pointed out and also the case where parameters are borrowed from other, believed to be similar, species. The latter two concerns have been raised in more recent times by Hartman & Kitchell (2008) and Chipps & Wahl (2008). Hartman & Kitchell (2008) further pick up on the recent usage of bioenergetic models for whole populations and wish better mortality estimates. Concern is posted on the applications and usage of the models (Chipps & Wahl, 2008). Caution is important when predictions are made based on bioenergetic models, as any uncertainties are channeled through to the model output, and thereby the predictions are dependent on more or less transparent uncertainties. Relative comparisons are therefore sounder ground, as the same uncertainties are likely to be eliminated when comparing. Despite the concerns posted regarding the use of bioenergetic models the
authors at the same time acknowledge the sound theoretical framework that bioenergetic models are founded in and thus do not fully reject the method but only raises concerns which should be addressed by the developers and should be kept in mind when using the model outputs.

This thesis is founded on the development of a bioenergetic model, and the points of criticism have been bared in mind in the development and usage of the model. The bioenergetic model has been adapted to understand the link to the habitat for the individual forage fish, and the decisions the individual undertake (figure 2). The bioenergetic model is based on the Wisconsin framework but elements from DEB model are also adopted. As in the Wisconsin model ingested energy is deducted losses to egestion, excretion, standard dynamic action and metabolic costs. Surplus energy, if available, is divided between growth in two structure pools; soma and lipids. The allocation between the two structure pools is implemented similarly to the DEB model, with a constant fraction to each pool. The model includes an additional structure pool; eggs, to which energy is transferred during the spawning season. During periods of poor feeding, energy needs to cover metabolic costs are firstly taken from the reserve pool and, if this is depleted, from the somatic tissue pool. The model is forced by a function of ambient temperature experienced by the individual and a prey availability function. The developed model allows for studies of the physiology and phenology of forage fish in environments with strong seasonal variation in environmental drivers. This model is used in MS1-3 includes an allometric description of consumption, whereas the model in MS4 includes a gastric evacuation model to describe consumption.

Figure 2: The model setup developed for the study of environmental influences on adult forage fish. Circles denote rates and squares are structure pools. The grey box arrows show the environmental drivers and the black line arrows show energy pathways.
Phenology and life history strategies

An individual has a particular life history strategy and behaviour associated to it. This life history strategy and the behaviour have evolved over several generations. For each generation the optimal strategy and behaviour have promoted these specific life history traits, and they have been carried on to the following generations and are refined in the process. Refinement to the most optimal life history is a continuous process through evolution.

The life history of a species can be described by numerous traits. The traits used in life history evolution are typically: birth, age and size at maturity, number and size of offspring, growth and reproductive investment, as well as length of life (Stearns, 1992). The traits are connected by constraining relationships: trade-offs. Central trade-offs in the life history are current reproduction versus survival as well as current reproduction versus future reproduction (Stearns, 1992). E.g. a trade-off can be to mature at a younger age to ensure reproduction under high mortality pressures, but at the cost of lower reproductive outcome. Thus, a trade-off exists when a benefit realized through a change in one trait is linked to a cost paid out through a change in another. The trade-off is implicitly included to the life history by a change in behaviour. The benefits and costs are reckoned in the currency of fitness, which determines the gain of a life history strategy to lifetime reproductive output. The effects on fitness can be estimated for the various traits which are affected by the trade-off. A general fitness measure is lifetime expected reproductive output, \( R_0 \) (box 2), which determines the total amount of eggs a female can produce in her life.

**Box 2: Lifetime expected reproductive output, \( R_0 \)**

The general formulation by Roff (1992):

\[
R_0 = \int_0^\infty l(t) m(t) dt
\]

Where \( l(t) \) is the probability to survive to age \( t \) and \( m(t) \) is the number of births at age \( t \). This formulation can be rephrased to forage fish which produce eggs rather than giving birth, and that can be numerically solved:

\[
R_0 = \sum_{t=1}^\infty \exp(-M \cdot t) \cdot G(t) \cdot \Delta t / w_{egg}
\]

Where \( M \) is the motality, \( t \) is age, \( G(t) \) is the total weight of eggs produced in the time interval \( \Delta t \) at age \( t \) and \( w_{egg} \) is the weight of a single egg. By the inclusion of the egg weight the \( R_0 \) gives the number of eggs the female will produce over a life time rather than the total weight of eggs.
Examples of trade-offs

As mentioned the trade-offs are given in behavioural strategies which promote one or more traits at the cost of others.

Sprat spends its entire life in the pelagic zone, where it experiences a large predation pressure. It has a strategy to avoid predation in periods where the food availability is low. Sprat has been observed to inhabit hypoxic waters in a Norwegian fjord during winters, with oxygen levels down to $\sim 7\%$ O$_2$ saturation (Kaartvedt et al., 2009). While in the hypoxic waters some sprat seized the opportunity to feed on dormant copepods, while others were not feeding. Thus, some individuals were able to both avoid predation but also to reduce the overall costs of the overwintering period. Some sprat were observed to swim to the surface to fill their swimbladder before immediately diving (Kaartvedt et al., 2009). This migration gave the gadoid predators their only chance to prey on sprat as they are not able to withstand oxygen levels below $\sim 15$-$20\%$ (Kaartvedt et al., 2009). In the Baltic Sea cod have been observed possibly to feed on zoobenthos in hypoxic waters with the lowest observed oxygen saturation of $\sim 10\%$ (Neuenfeldt et al., 2009). During the time spent in the hypoxic water the individual builds an oxygen debt, as the metabolism changes to an anaerobic energy production which is more costly for the individual. The individual therefore pays a greater price for the period spent in the hypoxic water compared to the metabolic costs during a similar period under high oxygen saturation levels. The oxygen debt was investigated in Baltic Sea cod at oxygen saturation level of 35% (Behrens et al., submitted), which has been observed to be an oxygen level frequently visited by the cod (Neuenfeldt et al., 2009). But at this oxygen level no additional costs to the oxygen debt was observed (Behrens et al., submitted). Baltic cod is observed to go to oxygen levels below 20% of saturation. At such low saturations an oxygen debt can evolve which was also suggested by Behrens et al. (submitted).

In other species, turbot and rainbow trout, an oxygen debt has been seen (Maxime et al., 2000; Svendsen et al., 2012). In both turbot (Scophthalmus maximus) and rainbow trout (Oncorhynchus mykiss) the metabolic recovery period lasted several hours. Therefore, when an individual chooses hypoxic waters for a period of time, the gain in the trade-off through better feeding conditions needs to compensate the additional metabolic costs. The trade-off as seen here can be predator avoidance or feeding. In sprat the strategy to overwinter in the hypoxic water lowers predation, but it is likely that they will have additional metabolic costs, an oxygen debt: even though it is believed that they are able to utilize the air in their swimbladder. Cod seek higher consumption in the hypoxic water, but at the cost of expenses to the metabolic oxygen debt.

As mentioned central trade-offs are current reproduction versus survival as well as current reproduction versus future reproduction. In iteroparous organisms, the mature individual needs to survive the spawning event to ensure future reproduction. The individual therefore needs to retain energy for future events, e.g. migration costs or reserves necessary to survive periods of poor feeding conditions. The latter is of special importance in seasonal environments. This is especially profound in sandeel which ascend from the sediment to spawn, after which overwintering is resumed. The same issue is valid for the autumn spawning individuals, e.g. the small population of autumn spawning herring in the Baltic Sea, who also face a period of poor feeding after the spawning event. The central trade-off is that the individual needs to weigh
today’s reproduction to the future reproduction. This is important as an individual has the possibility to gain extra fecundity with increasing size (Roff, 1992). This trade-off holds only under low predation pressures as the probability not to reach the coming reproductive season is too small. The interplay of the two central trade-offs to grow or to reproduce have been investigated in combination for Atlantic cod to determine the mechanism behind skipped spawning events (Jørgensen et al., 2006). The Atlantic cod has been observed to skip spawning frequently and the study investigated how several traits were affecting the skipped spawning events. The traits which influenced skipped spawning events in cod were: age, mortality risk, growth, migration costs. Several factors determined if an individual would skip spawning, including both mortality at the spawning and feeding grounds, natural mortality, prey availability as well as the size and condition of the individual. Two underlying mechanisms controlling the skipped spawning events in cod are: individual condition and future reproduction (Jørgensen et al., 2006). The individual will skip spawning if its stores are too small and the reproductive effort therefore will be low. Also if the individual has great likelihood to survive to the coming reproductive season, it is likely to skip spawning in the current reproductive season. Hereby the individual prioritizes growth and the gain in additional fecundity associated hereby. All traits operate simultaneously on the individual and the optimal strategy depends on each.

In the studies performed on forage fish, life history theory is included by a quantification of trade-offs. Investigated trade-offs have been linked to the phenology of the individual by running several scenarios. The scenarios does not include optimal life histories but are founded in observed behaviour of the individuals. The trade-offs are investigated through fitness calculations on overwintering and skipped spawning behaviour. The overwintering phenomenon is a mechanism where an individual responds to the low energy level available in the habitat by ceasing search for prey. This behaviour is especially profound in sandeel, which can remain buried in the sand up to 10 months (Winslade, 1974). This strategy allows the individual to reduce its energy expenditure to an absolute minimum and to avoid predation. The sandeel only ascent from the sand when the food availability is high enough to risk the additional predation associated with life as a pelagic forage fish, i.e. the energy/predation trade-off (Houston et al., 1993). This energy/predation trade-off is investigated at various scenarios of both prey availability and seasonality in prey availability as well as varying mortalities (van Deurs et al., 2010 – MS4). The skipped spawning strategy is a necessary precaution if an individual does not have the condition to undertake spawning. This has been observed in central Baltic herring (Bucholtz et al., submitted). The physiological constraints to spawning are tested through scenario runs and the phenology of the environment on the individual is investigated.
My work:

This study is centralised around the forage fish and how the habitat and behaviour affects the individual. The key focus areas have been to quantify some essential strategies and the implications on the forage fish:

- How is growth/behaviour determined by the surrounding environment?
  - MS1: How does growth in Baltic sprat respond to the environment?
  - MS2: How does future climate affect growth and egg production in Baltic sprat?
  - MS4: What is the optimal timing of the foraging window in sandeel?

- How does the individual invest energy?
  - MS1: Which allocation strategy does best describe the growth seen in Baltic sprat?
  - MS3: What is the condition level needed before herring will spawn?

- How does the individual change its behaviour seeking to increase fitness?
  - MS3: What forces Baltic herring to skip spawning?
  - MS4: How does sandeel weigh the trade-off between growth and predation?

Summary of MS 1: Model presentation and implications of seasons on the growth dynamics

*Status: Manuscript is ready to submit, but awaits publication of validation data. Intended for Ecological Modeling.*

The motivation of the study is to understand how the individual is affected by the surrounding environment which is an important determining factor for Baltic sprat stock. Recruitment in Baltic Sea sprat stocks has strong year-to-year variations due to fluctuations in the physical environment as a response to atmospheric forcing and longer term climate trends (MacKenzie & Köster, 2004). Previously focus has been on the temperature effects on the development of eggs and non-feeding larvae (Petereit *et al.*, 2008) and the stock with respect to the spawning stock biomass, recruitment and landings (MacKenzie *et al.*, 2008). But a mechanistic approach which examines the underlying physiological processes in the adult individual and its link to the seasonal environment has not been made. Thus, the objective is to describe growth and egg production in sprat and the links to the environmental forcing experienced by the individual.

The model presented in this manuscript has been calibrated for Baltic Sea sprat, but is generic and can be used for any forage fish, which feed on the same type of prey organisms throughout its life. We aimed at keeping the model as simple as possible and to keep the number of parameters low. This made it possible to estimate parameters either directly or indirectly from laboratory experiments or cross-species allometric scaling relationships. We have
been able to determine the governing processes of the growth dynamics on a seasonal level. This has been made possible based on the unique validation dataset, which has a rare temporal resolution and detail level (Temming et al., in prep.). The information of individual lipid content has made it possible to enhance our understanding of sprat life history trade-off; to grow or to reproduce. The high temporal resolution of the validation data allowed us to evaluate the allocation strategy used to determine the priority of growth in the two structure pools. We used two allocation schemes; constant and sigmoid allocation. The constant allocation scheme assumes that growth occurs simultaneously in both the soma and lipid structure pools with a fraction deciding the priority given to each. The sigmoid allocation scheme is based on the assumption that the early season is used for soma growth and later in the season priority is given to egg production (Iles, 1974). We implement this allocation with a sigmoid (s-shaped) curve ranging from 0 to 1, where 0 denotes full allocation of surplus energy to the soma structure pool and 1 is full allocation to the lipid pool. We find that the constant allocation scheme gives growth patterns which closely resemble the observed growth dynamics for sprat in the Bornholm Basin (figure 3). During the spawning period, consumed energy and stored energy are used for reproduction. After the spawning season, during the late summer growth season, both the soma and lipid pools are filled. The simulated total weight is representative for the observed weight at ages for Baltic sprat.
Figure 3: Growth dynamics and data of sprat caught in the Bornholm Basin (circles) and results of simulation for constant allocation scheme (solid lines) and sigmoid allocation (dotted lines). During periods with sampling intervals above three months, no line is added between the measurements. Time is given in years and denotes the age of the individuals in simulation and data which has been determined by otolith reading of captured sprat. Panel A is wet weight ($W_w = W_s + W_l$), panel B is weight of soma ($W_s$), panel C is lipid weight ($W_l$) and panel D is weight of produced eggs ($W_e$).

The influence of temperature on the physiology of sprat varies during the season. The feeding level determines the consumption over season, and is dependent on the available prey concentration and the temperature (figure 4). We found that for the environmental forcing applied to the model that an individual will gain energy during the summer season from ultimo February to mid-October. During this period the environment offers enough food so that the feeding level is higher than the critical feeding level, which is calculated as the energy needed to cover the metabolic costs and losses of ingested energy. The critical feeding level is nearly constant over the year (figure 4). This is due to the proportionality existing in the temperature functions for both consumption and metabolism. But a small lowering is observed during summer as the individual weight is reduced. The productive season is therefore 8 months with only the short winter period where the individual needs to sustain on build up lipids from the previous production season.
Summary of MS 2: Effects of future climate on Baltic sprat phenology

Status: Manuscript needs last round of comments from co-authors. Also need publication of validation data before submission. Intended for Fisheries Oceanography

The reasoning for MS1 was to evaluate the temperature effects on the adult life stages both with regards to growth dynamics and egg production, as this has not previously been established. We assume that temperature will be especially important for Baltic sprat as the stock is at its northerly distribution limit with regards to temperature (Muus & Nielsen, 1999) and therefore being sensitive to climate change (e.g. Myers, 1998; Rijnsdorp et al., 2009). Any changes in the physiology to changing temperature will possibly affect individual growth and egg production, which is also an important link to understand the temperature dynamics in all processes included in recruitment of Baltic sprat. Here we analyse the physiological responses of climate change on adult sprat in the Baltic Sea area based on reasonable climate predictions for the area. We aim at determining how this climatic change affects the fitness of the individuals and in particular their ability to reproduce. Also we use the model to test the importance of the lower trophic levels on growth and egg production, as the seasonality in the prey are also likely to change with a change in climate.

We use the bioenergetic model (figure 2) and force it with two different temperature functions based on climate scenarios covering the periods 1960-1990 and 2070-2100 (Madsen, 2011). Further for both climate scenarios we include three prey scenarios, which are described by bell-shaped functions which vary over time. For each scenario the peak time and width of the functions are altered but the integrated productivity is constant. The scenarios are current situation, which gives growth as seen today in Baltic sprat, earlier bloom, which has an earlier peak time in prey availability, and broader bloom, which has the same peak time as today but the function, is broader giving higher prey concentrations during spring and summer (for details on the background of the scenarios see MS2). The changes in the prey functions affect both the growth dynamics and the egg production. Growth is a function of the interplay of temperature
effects on the physiological rates, the prey availability and the overlap with the spawning season. Thus, the changes in growth curves are complex and each scenario combination reveal different growth dynamics. Generally, we conclude that the individuals reduce their total weights under future climate which is mainly caused by reductions in lipid weights. The egg production is especially dependent on the lipids which have been stored over winter, and only a small variability in egg production rates are seen with the changes in prey function (figure 5 – full lines). In the future climate scenarios the stored lipids are also of great importance. The egg production is reduced if the individual depletes the energy stores during winter (figure 5 – dashed lines). The lowest egg production under future climate is seen when applying the current situation prey scenario, as this scenario has the lowest temporal overlap with the spawning season.

Figure 5: Dependence of egg production with prey timing and climate scenario. Scenarios with recent climate are given in full lines and future climate with dashed line. The colour shading illustrates the three different prey scenarios; current situation in black, earlier bloom in dark grey and broader bloom in light grey.

The effects of system productivity are evaluated based on average weight-at-age (soma and lipids) and the fitness, as adult expected reproductive output. Higher system productivity increases both average weight-at-age (soma and lipids) (figure 6 – black lines) and the fitness (figure 6 – grey line). At a relative productivity of 1 and below the asymptotic size is reached already at age 2 or is even reduced at older ages compared to age 2. During these scenarios energy is used for survival and growth and reproduction is not possible. When increasing the relative system productivity the asymptotic size is reached at a higher age. The additional energy available to the individual is used both for reproduction and growth. Effects on reproduction are evaluated in the fitness measure. The fitness increase proportionally with increasing relative productivity. A decline in productivity shows a strong effect on the fitness, e.g. a reduction in system productivity by 20%, reduces fitness by 30%.
Figure 6: Effects of system productivity. The scenarios on system productivity are based on the same prey availability function, where the integrated productivity has been raised/reduced by 20% and 40%. Growth dynamics are described by the average weight-at-age for the ages 2-5 (black lines where width increase with age). Fitness is given for each productivity scenario, relative to the scenario with a productivity of 1 (grey line).

This study serves as a missing link in understanding climate effects for the entire life cycle of Baltic Sea sprat as other studies have focused on the egg, larval and young-of-the-year life stages (Köster et al., 2003; Baumann et al., 2004, 2006a, 2006b; Petereit et al., 2008). We tested the importance of climate and prey on growth, egg production and fitness. Future climate have been found to reduce both egg production and fitness for the current situation prey scenario. Comparing among prey scenarios we an increase in egg production and fitness with changes in the prey availability: The larger the temporal match with spawning season, the larger is the egg production and fitness. The system productivity test revealed large reductions in individual sizes and fitness with decreasing productivity. When increasing productivity additional energy was used both for reproduction. Thus, to keep the individual weight-at-age under future climate seen in sprat today, amount of produced eggs and fitness, the productivity of the system needs to increase or the phenology of the prey needs to change.

The manuscript further discusses the potential effects of future climate on all life stages in Baltic Sea sprat, herby addressing the entire stock.

**Summary of MS 3: Understanding skipped spawning events in Baltic herring**

*Status: Work in progress. Intended for Marine Ecology Progress Series, joint submission with Bucholtz et al. (in prep.)*

Baltic Sea herring have been seen to likely skip spawning and also show extensively down-regulation, where the individual reabsorb energy which has already been used in egg production
(Kennedy et al., 2008; Kjesbu, 2009, Bucholtz et al. submitted). When skipping spawning or down regulating the spawning effort, the individual has weighed the trade-off of today's spawning to the trade-off in other life-history traits, such as growth or survival (Roff, 1992). We wanted through this study to understand the life-history choices related to down-regulation and skipped spawning from a life-history perspective. Specifically we hypothesize that skipped spawning is determined by a threshold in condition, which the individual needs to be above to spawn. Also we determine the importance of the spawning type, according to choice of spawning season, on the spawning individual; linking the spawning type to growth, egg production and survival. Finally we quantify the effect of the environment has on the reproductive strategy in Baltic herring, through the food availability and thereby the condition of the individual.

We use the bioenergetic model (figure 2) which we parameterize for adult Baltic herring. Growth in the three structure pools depends on the time of year and condition of the individual (figure 7). Spawning occur at a specific day. The gonad production in the following year from a skipped spawning event is larger as the reserves have been able to grow through several years
Figure 7: Growth dynamics in the structure pools and agreement with observations. For all panels the model simulation is given in full line and validation data as data points. The simulation is based on a model run with a condition threshold CT of 0.05 to given an example of growth including skipped spawning events. The individual increase in wet weight over time (panel A), with decreases caused by spawning events. Wet weights from survey data from ICES (*) and the level of individual weight is in accordance with the observations made by Bucholtz et al (submitted) (diamonds with standard deviation) are displayed. The increase is occurring both in the soma (panel B) and the lipids (panel C). Spawning uses all available energy in the lipids. Absolute values of lipids in the simulation are in the range of the data reported by Bucholtz et al (submitted) (diamonds with standard deviation) but variations within ages occur as the simulation lipid pool is very dependent on the spawning events. The amount of produced eggs (given in grams and displayed as bars) is in good accordance with the observed gonad weights from Bucholtz et al (201X) (diamonds with standard deviation).

In the simulations the spawning frequency varied with varying CT. The spawning frequency was linked to the condition threshold applied and the age at maturity and number of spawning were reduced, at higher condition threshold values. As the spawning frequency reduces the maximal size of the individual is raised. This holds for all spawning types. But the autumn spawning individuals has lower spawning frequency, with maximal 5 spawning events over a life span of 10 year compared to maximal 10 spawning events in the spring spawning individual.

Fitness in closely linked to the number of spawning events and the age at maturity, as the fitness measure includes the mortality. But naturally also the actual egg production at a given
spawning event. But the egg production at the youngest stages proved most important for the fitness measure as the probability to be alive is reduced with age.

To better understand the implications on the stock and the implications for the stock assessment, we wanted to quantify a cut-off value at which skipped spawning can occur. We used the dynamics from both the scenario runs and the observed growth dynamics, to estimate a condition necessary for individuals to be spawning in spring. Based on this we state that Baltic herring should have a condition value of 0.08 or above to be able to have a successful spawning in the following spawning season.

**Summary of MS 4: Energy/predation trade-off in sandeel.**

*Status: Published in Marine Ecology Progress Series vol. 216, 201-214. 2010.*

We wanted through this study to investigate the overwintering strategy in sandeel ecotypes, and how this behavioural adaptation to the strong seasonal fluctuations affected the phenology. In the study, the overwintering behaviour is considered to be a strategy requiring two annual decisions: When to end overwintering and when to start overwintering, which combined comprise the timing and duration of the foraging window. The study is based on a bioenergetic model, which has a different frame compared to the other studies. The model assumes that the individual has reached its asymptotic size and all surplus energy is used for reproduction. Intake is based on stomach size and evacuation rates, and energy losses were determined by the assimilation efficiency, standard metabolism and activity costs related to swimming. Temperature dependencies were included in the stomach evacuation rate and the standard metabolic cost. The habitat was described as a 2-box system. The individual could either be in its refuge in the sediment, where predation mortality is low and food supply is zero, or in the pelagic zone (arena), where the individual can feed at the expense of higher predation mortality (including fishing mortality). During overwintering, the individual was permanently in its refuge. The model was used for demonstrating how the optimal timing of the foraging window involves a trade-off between energy gain and survival probability.

The optimal overwintering period was determined as the strategy which yielded the highest fitness. The prey dynamics influenced the optimal overwintering period by reducing the foraging window with reduced zooplankton spring burst duration (figure 8). Energetically the greater the burst intensity the shorter time is needed for the individual to gain energy for the overwintering period and for high reproduction success. Also the background food level was tested, to see if the individual would prolong the foraging window if the additional energy would get the individual to prolong feeding and thereby have a higher reproductive success. But this had only marginally influence on the duration of optimal foraging window, even when the background food level approached levels similar to the spring burst levels (figure 8).
Figure 8: Implications of the duration of the zooplankton burst duration and the background food level on the overwintering duration and timing. The date at which optimal overwintering should end is given in dashed lines and the onset time in full line. Grey lines in the left panel illustrate the intensity of the zooplankton burst.

We further tested the importance of the arena and refuge mortality on the optimal foraging window. We found that an increase in the mortality in the arena reduced the duration of the optimal foraging window. The trade-off between feeding and avoiding predation was tested by increasing the ratio between the refuge and arena mortalities. This only increased the duration of the foraging window slightly but moved the onset of the foraging window to be started earlier in the year. Thus, the individual is playing it safe, and weighs higher survivability over the chance for higher reproductive success.
Summary and perspectives

The model which has been developed was used for studies of several important questions regarding the life of forage fish and their link to their habitat. The studies investigated the purely physiological traits of the individual today and under future climate. Also specific behavioural strategies were examined and how a change in the behaviour would influence the life history of the individual. The model has proven a strong tool for hypothesis testing, where the importance of a given trait can be quantified. Further applications can be made for the models and the models can be used as a foundation for future investigations of behaviour in the forage fish.

The work presented here has focused in the individual and how the individual responds to physiology and the environment. The seasonality in environment has been kept constant and the scenarios are based on variations in integrated productivity. The environment is in reality not constant, and show large interannual variations. Interannual variations in temperature and prey availability can have great implications on individual growth and reproduction. Through the effects on growth the interannual variation can also influence the behavioural strategies of the individual, both the strategies examined here but also future investigations. To include the interannual variability in the prey availability a lot of validation data are needed. These need to be both on the model forcing but also on the growth dynamics in the individual. But it would enhance the understanding of population dynamics. Also a full description of the population can be made, hereby including the eggs and larval stage. This would be a strong model as the entire life cycle would be included. The main difficulty here is to estimate the mortality in the various life stages and to parameterize the governing processes describing the development. Whether any additions to the model are necessary depends on the aim of the study. Simple behavioural studies, e.g. MS3 and MS4, are able to reveal important insight to the mechanisms and processes describing the individual life history and behavioural strategies through rather simple models. Additional details in the model setup may not have improved the answer to the question raised in these studies. But had the question been different the additions mentioned here, or other driving properties to a given trait or trade-off, may be necessary.
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MS1: Physiological responses to temperature in Baltic Sea sprat (*Sprattus sprattus*) and the consequences for growth and egg production

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Abstract

Recruitment in Baltic Sea sprat stocks has strong year-to-year variations due to fluctuations in the physical environment as a response to atmospheric forcing and longer term climate trends. Even so sprat has managed to maintain an important role in the Baltic Sea ecosystem although the area represents the northernmost distribution limit for sprat with regards to temperature. To describe how growth and reproduction depends on temperature we constructed a dynamic, seasonally resolved, bioenergetic model for the stock component spawning in the Bornholm Basin. The model is forced by temperature and food availability. Particular emphasis is placed on the allocation of energy inside the individual, whether energy is invested in growth or reproduction. We show that a constant division of surplus energy between the lipid and soma pools leads to seasonal variations in growth and size matching observations. Further we hypothesise that the soma growth rate will increase as a function of temperature, but that the maximum size will decrease with increasing temperature.

Keywords: Bioenergetic model, allocation strategy, seasonal growth dynamics, environmental influences, physiology, phenology.

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1. Introduction

Forage fish play an important role in the ecosystem as they are the main link between plankton and higher trophic levels. Forage fish prey on zooplankton hereby transferring energy through the food web to larger piscivorous fish species which prey on forage fish. Classical examples of forage fish on the European continental shelf are sprat, anchovy and sardine. Anchovy and sardine share the similar oceanic habitats, often showing alternating biomass fluctuations (e.g. Barange et al., 2009). The spatial distribution of these species is not static. During several periods in the last century, sardine and anchovy have been recorded in the southern North Sea, which is more northerly than normal for the species, and the occurrence has been linked to long-term climate cycles and/or climate change (Kanstinger & Peck, 2009). Similarly, sprat is a small, pelagic schooling fish, with a wide geographical range; from the Black Sea and Mediterranean in south to the Norwegian coast and the Baltic Sea in north (e.g. Avsar, 1995; Shulman et al., 2005; Sirotenko & Sorokalit, 1979). With the Baltic Sea being the northernmost distribution limit with regards to temperature (Muus & Nielsen, 1999). Sprat is a batch-spawner, which can produce more than 10 batches of eggs in each spawning season (George & Alheit, 1987). Spawning is variable both temporally and spatially with regards to the time of peak spawning and fecundity (Alheit, 1987).

Baltic sprat is one of three dominating fish species in the Baltic Sea, constituting together with herring and cod 90% of the total fish biomass (Thurow, 1993). However, the observed distribution patterns of sprat are not well understood, although temperature is assumed to play a central role. How further warming of the Baltic Sea under future climate change will influence the role of the sprat in the Baltic Sea ecosystem remains unsolved, as well. A quantification of the temperature effect on the life strategies is needed to advance our understanding of sprat population dynamics. Attempts have been made to evaluate temperature effects on recruitment (MacKenzie & Köster, 2004), development in eggs and non-feeding larvae (Petereit et al., 2008) and development of the Baltic Sea sprat stock, i.e. spawning stock biomass, recruitment and landings (MacKenzie et al., 2008). Neither of these attempts has been mechanistic and/or dynamic in their approach. In order to achieve a full mechanistic understanding of the underlying processes we construct a seasonally resolved bioenergetic model of growth and reproduction in sprat which includes temperature influences on physiological rates. Particular attention is paid to individual investments of energy into growth in soma and lipids, i.e. energy stored for reproduction and metabolism during poor feeding periods. This allows us to determine the individual to growth and its allocation strategy and how this is interlinked with temperature.

Bioenergetic models of sprat have previously been used to estimate consumption in Baltic sprat (Arrhenius, 1998; Bernreuther, 2007), but these models are static, and do not resolve dynamic growth and reproduction. For North Sea sprat, an ecosystem model fully coupled to an individual based model for larval sprat was developed by Daewel et al. (2008) to determine potential survival and growth. However it did not include adult sprat. Compared to key species
in other ecosystems, only little effort has been devoted to understanding the entire life cycle of Baltic sprat. By the onset of the GLOBEC-Germany programme this was changed and focus in the Baltic Sea was targeted to understanding the trophic interactions between zooplankton and fish under influence of physical processes (www.globec-germany.de). During the programme, several physiological parameters were determined, allowing us to parameterize the model for sprat.

2. Model setup

We construct a general bioenergetic model for a forage fish parameterized for Baltic sprat, which for all life stages feed on the same resource. The model includes three structure pools; soma $S$ (e.g. muscle, bone, organs), lipids $L$ and eggs, all characterized by their energy content (Fig. 1). The energy density is 4 kJ g$_{WW}^{-1}$ and 40 kJ g$^{-1}$, respectively for soma and lipid (Jobling, 1994; Pedersen & Hislop, 2001). Flow of energy between the structure pools are determined by the surplus energy, the condition of the fish and season. The weight of the individual, which is used for allometric scaling relationships, is calculated on the basis of the somatic pool, $W = S/\rho_S$, where $\rho_S$ is the energy density of the somatic tissue in wet weight.

Ingested energy – consumption minus egestion, excretion and standard dynamic action (SDA) – is used to cover metabolic costs to standard metabolism, maintenance and activity. The remaining energy (from here on denoted surplus energy) is allocated to pools of either somatic tissue or lipids. In seasons where consumption cannot meet metabolic needs, energy is taken from the lipids and, if this is depleted, from the soma. Investment in reproduction (eggs) occurs in the spawning season if a threshold condition factor is exceeded. Eggs are produced from both protein from the soma and lipids. Only females are considered in the model.

This model setup allows us to quantify the seasonally resolved growth patterns in female sprat and to determine the reproductive effort possible under the given environmental conditions.

2.1 Consumption

Consumption is described by a food encounter model and a Holling type II functional response. Prey concentration $F(t)$ is a driving force in the model. An individual with soma weight, $W$, will be able to search a volume for prey per time $q_pW^4$ (Andersen and Ursin, 1977; Ware, 1978; Byström et al., 2004). Encountered prey is determined by accounting for the prey concentration $pW^4F(t)$. The functional response regulates the actual consumption, such that it is limited by the maximum consumption rate. On the short time scale, the feeding of sprat is a boom and bust dynamic determined by the exploitation of a patchy food resource. The temporal resolution of the model is coarser than the individual patch, and the maximal consumption rate therefore reflects the long term average maximum consumption rate, and not the instantaneous maximum consumption rate that can be high when an empty stomach is being filled. Maximal
consumption is an allometric function of weight: \( a_c W^{b_c} f_c(T) \) where \( f_c(T) \) is the temperature effect. The consumed food \( C \) then becomes:

\[
C = \frac{a_c W^{b_c} f_c(T) p W^q F}{a_c W^{b_c} f_c(T) + p W^q F} \quad \text{(Eq. 1)}
\]

The parameters related to the search rate, \( p W^q \), can be measured directly for small organisms like zooplankton (e.g. Kiørboe et al., 1985), but may only be measured indirectly (Byström et al., 2004) or using theoretical arguments (Ware, 1978) for large organisms like fish. Theoretical arguments based on allometric scaling of search radius and swimming velocity predicts that the exponent \( q \) is in the range \( \frac{3}{4} \) to 1 (Andersen & Beyer, 2006). We use \( q = 0.75 \). The factor for the search volume \( p \) scales the effective prey concentration, and is determined together with the prey concentration \( F(t) \) as part of the general calibration (section 3). The parameters related to the maximal consumption are the factor \( a_c \), the weight exponent \( b_c \) and the temperature correction \( f_c(T) \). The weight exponent is the “standard” metabolic exponent \( b_c = 0.75 \), which is generally to be expected for fish (Jobling, 1994; Peters, 1983). The factor \( a_c \) is determined as part of the calibration (section 3).

A proxy for the long-term average maximum consumption rate is the gut evacuation rate, and we therefore use the temperature dependence of the gut evacuation rate as a reasonable estimate of the temperature dependence of the maximum consumption. The temperature dependence of the gut evacuation rate has been determined experimentally by Bernreuther et al. (2009):

\[
f_c(T) = \exp(0.0775T) \left(1-\left(1+\exp(-0.659\left(T-23.989\right))\right)^{-1}\right) N^{-1},
\]

where \( T \) is the ambient temperature [°C]. \( N \) is a normalization factor which normalises the function to range between 0 and 1, by dividing the effect at all temperatures with the absolute maximum \( N = \max[f_c(T)] \).

2.2 Metabolism

Respiratory costs are determined from the weight of the individual, the water temperature and the activity level of the individual:

\[
R = a_R W^{b_R} f_R(T) \alpha_R
\]

where \( a_R \) is a constant, \( b_R \) is the exponent of the allometric mass function for standard metabolism, \( f_R(T) \) is a temperature function and \( \alpha_R \) denotes an activity multiplier.
Metabolic rates of Baltic sprat were measured experimentally by Meskendahl et al. (2010). This work includes both temperature and weight effects on metabolic costs. It was found that the weight effect is best described by an \( a_R \) factor of 8.5 \( \text{kJ} \, \text{g}^{-1} \, \text{yr}^{-1} \) and an exponent, \( b_R \), of 1.073. The factor \( a_R \) has been recalculated from the unit \( \text{mg} \, \text{O}_2 \, \text{ind}^{-1} \, \text{h}^{-1} \) to \( \text{kJ} \, \text{yr}^{-1} \) by assuming that the energy density of consumed food is 7 \( \text{kJ} \, \text{g}^{-1} \). The high activity level of sprat explains the higher exponent compared to the average suggested value of 0.86 by Jobling (1994).

The temperature effect on metabolic costs is included as an exponential relationship with a temperature coefficient \( c_R \) of 0.078 \( ^\circ \text{C}^{-1} \) (Meskendahl et al., 2010):

\[
f_R(T) = e^{c_R T}.
\]  

(Eq. 4)

Further we implement an activity multiplier \( \alpha \) of 1.25. The multiplier is included to account for energy demands other than those directly associated with the schooling behaviour of sprat, e.g. feeding and food searching, as suggested by Meskendahl et al. (2010).

### 2.3 Growth

Consumed food is assimilated with an efficiency \( \varepsilon_i \), which covers losses of energy to SDA, egestion and excretion. The surplus energy, \( E \) (measured in \( \text{kJ} \)) is the assimilated energy after respiratory costs have been accounted for:

\[
E = C - (1 - \varepsilon_i)C - R = \varepsilon_i C - R.
\]  

(Eq. 5)

The assimilation efficiency applied is 0.7 (Bernreuther, 2007). We assume that 10% of the energy uptake is lost to SDA, 10% to egestion and 10% excretion (Peters, 1983; Adams & Breck, 1990).

During periods when the energy balance is negative the individual will first use stored lipids, until these pools are depleted, but always assuring a minimum condition faction of 0.02. The condition factor is the ratio between the wet weights of the lipid and soma pools: \( (L/\rho_L)/(S/\rho_S) \). If the lipid pool is also depleted the individual will use the soma pool to cover the energy needs. Both energy transfers are associated with loss of energy described by a transfer efficiency, \( \varepsilon_M \) of 0.8.

As the energy budget during certain periods will be positive and during other periods negative, we define a measure termed the critical feeding level (CFL), at which consumed energy equal energy costs, which is when the available energy \( E = 0 \):

\[
\text{CFL} = \frac{R}{\varepsilon_i C_{\max}}.
\]  

(Eq. 6)
During periods with positive available energy the individual allocate surplus energy between the soma and lipid pools. Two allocation schemes \( f_A \) determining this allocation are tested: a variable fraction of the surplus energy according to season (sigmoid allocation) versus a constant fraction allocated to each pool at all times (constant allocation). \( f_A \) denotes the fraction of energy allocated to the lipid pool and \( 1 - f_A \) the fraction allocated to the soma pool.

The sigmoid allocation scheme is based on the assumption that the early season is used for soma growth and later in the season priority is given to egg production (Iles, 1974). We implement this allocation with a sigmoid (s-shaped) curve, representing \( f_A \), ranging from 0 to 1, where 0 denotes full allocation of surplus energy to the soma structure pool and 1 is full allocation to the lipid pool. The applied curve allows for minor growth in both pools, with minimum of 10% of available energy leaking into the non-prioritized structure pool:

\[
f_A = 0.5 - 0.3 \left(1 + \exp \left( \frac{t_s - t}{\sigma} \right) \right)^{-1}
\]

(Eq. 7)

where \( t_s \) is the day at which surplus energy is partitioned equally between the structure pools and is set to July 1\(^{st}\) by when Baltic sprat show increase in the reserve pool (Temming et al., in prep.). \( \sigma \) is the steepness of the s-shaped curve at the time when priority is changing between the two pools from high priority in soma growth to high priority in reserve growth. \( \sigma \) is 0.01 which gives full shift in priority of ~1 month. The constants ensure that the function ranges between 0.2 and 0.5 with allocation priority of 0.5 in the beginning of the year and 0.2 in the end of the year. The allocation to lipids varies from 0.5 to 0.8 over the year when applying the sigmoid allocation scheme.

The constant allocation scheme assumes available energy is divided between soma and lipids with \( f_A = 0.65 \).

2.4 Reproduction

The spawning season is constrained to range from March 1\(^{st}\) to May 31\(^{st}\) (e.g. Parmanne et al., 1994). Within this period eggs are produced if the individual has stored energy in the reserve pool so that the condition is above 0.02. Egg production requires both proteins and lipids (e.g. Love, 1970, Tyler & Sumpter, 1996 and Wiegand, 1996), but the size of the fraction from each pool is unclear. The fraction of energy taken from the lipid and soma pools is \( f_E \) and \( 1 - f_E \) respectively. \( f_E \) is determined based on the energy densities in the three structure pools measured in dry weights:

\[
f_E = \frac{\rho_{S,DW} - \rho_{E,DW}}{\rho_{S,DW} - \rho_L}
\]

(Eq. 8)
Where $\rho_{S,DW}$ and $\rho_{E,DW}$ are the energy density of dry weights of soma and eggs. $\rho_L$ is the energy density of the lipids. The energy needed to produce the eggs are determined in dry weight at the water content of the eggs vary during over the season and over the development process. We use an energy density of 30 kJ g$^{-1}$ dry weight of eggs (Hislop & Bell, 1987) and 20 kJ g$^{-1}$ for the energy content of dry soma, hereby assuming that the water content is 80% (Pedersen & Hislop, 2001). The function $f_E$ when using this parameterisation states that half of the energy needed to produce the eggs is lipids and the other half is protein from the soma pool.

The egg production rate is proportional to the total weight of the individual including both the soma and the lipid pool, and is determined based on $\rho_S$ and $\rho_L$:

$$\frac{\partial G}{\partial t} = r_{egg} W_{total} \varepsilon_G,$$

where $\varepsilon_G = 0.9$ is the efficiency of egg production and $r_{egg}$ is a rate constant. Produced eggs do not contribute to the total body weight in the model as it is assumed that the produced eggs are released immediately. The structure pool for the produced eggs is reset each year when the spawning season ends.

The rate constant, $r_{egg}$, can be approximated based on the observed fecundity of sprat. There are various reports on the fecundity: reported relative fecundities for North Sea sprat are 970.9 eggs per g female per year (Bailey & Pipe, 1977) and up to 400 eggs per g female per batch (Alheit, 1987), which recalculates to up to 4000 eggs per g female per year when assuming that they produce ten annual batches (Alekseeva et al., 1997) of equal size. For Baltic sprat the reported fecundity is 5,768 to 34,290 eggs per year for females per year in the length range 97-133 mm (Petrova 1960 from de Silva, 1973). When assuming that this fecundity applies for an individual of 10 g this gives a relative fecundity of 500 to 3400 eggs per g female. Therefore we can assume that the relative fecundity is in the range of 500 up to 4000 eggs per g female per year. The weight of an egg can be estimated from the mean gravity and mean diameter from Nissling et al. (2003) and by assuming that the eggs are perfect spheres, the wet weight of an egg can be determined to be 1.16 mg per egg. Using an energy density of egg of about 2.166 kJ g$_{WW}^{-1}$ (Riis-Vestergaard, 2002). Making the relative fecundity is 1.26 up to 8.54 kJ per g female per year. As the spawning season lasts for 3 months the rate at which eggs should be produced is four times higher, thus the egg production rate is in the range of 3.5 up to 34 kJ g$^{-1}$ yr$^{-1}$. We use a value of 30 kJ g$^{-1}$ yr$^{-1}$, which produce growth profiles in line with observed growth of sprat from the Bornholm Basin.
2.5 Summary of the model

The seasonal changes in the three structure pools are given in table 2. Eggs are only produced within the spawning season, thus the loss terms to egg production on soma and lipids are also only present then.

2.6 Forcing

The model is driven by food availability and the environment through temperature. Determining the ambient temperatures is complicated by the fact that sprat change position in the water column during the day and throughout the seasons. Applied temperature forcing is based on seasonal behavioral patterns, i.e. position in water column and seasonal habitat choice, as observed for Baltic sprat from the Bornholm Basin. Temporal and vertical positioning of sprat is coupled to information of observed temperature information.

The annual habitat choice in Baltic sprat is divided into a winter mode and a summer mode. During winter sprat concentrate in the deep basins below the halocline, where the water is warmer than at the surface, if the oxygen level is sufficient. Comparisons of sprat echograms, temperature and oxygen level revealed that the vertical depth distribution limit is at 4-5°C and an oxygen concentration of 1 mL L⁻¹ (Parmanne et al., 1994; Stepputtis, 2006). During spring sprat starts spawning in near-bottom waters. As temperature in the surface waters and in shallower areas increase during summer, sprat follow, while continuing to spawn (Grauman, 1975; Stepputtis, 2006). During summertime, both during and after the spawning period, diurnal vertical migrations (DVM) have been observed (e.g. Aro, 1989; Nilsson et al., 2003; Stepputtis, 2006). The observed depth range of the DVM in the Bornholm Basin is between 60-80 m depth during daytime and 10-20 m depth during nighttime (Stepputtis, 2006). Cold intermediate water layers or an exceptionally steep temperature gradient can inhibit DVM. This DVM behaviour optimizes energy intake and minimizes predation (Aro, 1989) and continues throughout the feeding period, after which sprat seek to the deeper, warmer waters again.

Observed temperatures from the BY5 station (Fig. 2) placed in the central Bornholm Basin (55° 15’ N, 15° 59’ E) are obtained from the SMHI database SHARK (Swedish maritime archives). Data are available on monthly basis at 10 m depth intervals. Here, data for year 2002-2006 have been averaged. The time period was selected to fit the GLOBEC programme duration (see section 3). In the surface layers, the maximum temperatures are seen in late summer (18±1°C at 10 m in August) and minimum temperatures are seen in early spring (2±1°C at 10 m in March), but the seasonal temperature cycle is dampened and delayed with depth, and at 70 m the maximum temperatures are seen in November (9±1°C) and minimum in May (5±1°C) (Fig. 3A).

We use observed temperatures at the deepest position of sprat in the water column (70 m) and at the surface (10 m) as a basis for estimating the ambient temperatures for sprat in the Bornholm Basin throughout the season. As the model does not resolve daily behavioural patterns, e.g. daily vertical migrations, the temperatures at the average depths at which sprat is located throughout the year is used. We have described the seasonal variation of the effective experienced temperature by a cosine function, which is adjusted such that it fits with the
bottom temperatures on March 1st where sprat is situated just below the halocline (around $5^\circ C$) and that it fits surface temperatures on September 1st (around $13^\circ C$) (Fig. 3A). In this manner we can use a simple temperature curve as a reasonable approximation of the experienced temperature.

2.7 Implementation and initial conditions

The model is implemented in MatLab 7.7.0 R2008b. Initial energy contents of soma and lipids are both 18 kJ, corresponding to an individual of age 1 with a wet weight of 4.5 g. Each time step is 3.65 days. Tests have been performed with time steps of 1 day which did not change the results.

3. Calibration and validation

The primary data used for tuning and evaluating the model are observations on age specific wet weight, dry weights and energy densities of individual sprat caught in the Bornholm Basin as a part of the German GLOBEC programme and continued in recent years. The spatial resolution of the data is high in the GLOBEC target years (2002 and 2003) with seven annual samplings and two annual sampling in 2004-2006. Data are presented in Temming et al. (in prep.).

An empirically determined relationship between the relative water content and the fat content is used to determine the fat fraction of the individual ($\rho$) Temming et al. (in prep.)

$$\rho = -0.84r + 0.71 \quad R^2 = 0.72$$

(Eq. 10)

where the relative water content $r = (W_w - W_D)/W_w$ is determined from the wet and dry weights, $W_w$ and $W_D$, of an individual. From the fat fraction and the wet weight of the individual we determine the lipid weight $W_R = \rho W_w$ and the remainder $W_s = (1-\rho)W_w$ is soma.

The observed temporal dynamics of the soma and lipid weights are used to calibrate the remaining constants in the model: the factors for the search volume and maximum consumption $p$ and $a_c$, and the prey concentration $F(T)$. The seasonal dynamics of the prey concentration is described as a bell-shaped curve with a zooplankton bloom during summer as observed in the Bornholm Basin (Fig. 3B). The factor of the search volume $p$ determines the product of the absolute values of the prey concentration and the foraging ability of sprat. The value of $p$, the factor for the maximum consumption $a_c$, and the exact time and width of the peak of prey concentration have been varied such that the predicted reserve weights fit the observed ones, leading to $p = 450 \text{ m}^3 \text{ g}^{-a} \text{ yr}^{-1}$ and $a_c = 350 \text{ kJ g}^{-1-bc} \text{ yr}^{-1}$.  

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4. Results

The results presented here spans six years starting on January 1\textsuperscript{st}. This time period has been chosen based on the availability data on wet weights and energy densities for year classes within this age range.

4.1 Seasonal growth and allocation dynamics

Growth is partitioned in three structure pools, of which two are evaluated against measured data; the lipid pool and the soma weight (Fig. 4B & C). The third structure pool is weight of produced eggs. Combining the lipid and the soma structure pools enables the model simulation to be evaluated against sprat weight at age data (Fig. 4A). Growth trajectories in each structure pool depend on the applied allocation scheme, and are examined separately in the following.

The constant allocation scheme (i.e. simultaneous growth of both structure pools) gives simulated growth patterns very close to observed patterns for sprat from the Bornholm Basin (Fig. 4A & B & C). Reproduction starts in spring and all consumed energy is used for reproduction as well as the energy available from the last growing season. After the spawning season, during the growth season, both the soma and lipid pools are restored. During the spawning season the decrease in the soma pool is lower in the validation data compared to the simulation. The individual will when spawning use lipids to produce eggs. The individual then compensates this weight loss by increasing its water content (Love, 1970 and eq. 10). Hereby the caloric value of the soma pool is reduced during this period. This reduction in the caloric value is not included in the simulation. The simulation assumes a constant value, and therefore the weight loss during the spawning season in the soma pool is greater in the simulation compared to the validation data. The individual is able to produce eggs from age 1 (Fig 4D). The egg production in the first year is low compared to the older ages, and from age 2 and onwards only shows a slight increase with age.

When applying the sigmoid allocation scheme (i.e. changing seasonal priority given to soma versus lipid growth) the total weight of the individual is in good agreement with the observations (Fig. 4A – dotted line). But the levels in the soma and lipid pools are not in agreement with the validation data, especially for the older ages (Fig. 4B & C). The soma pool is in the low range of the validation data and the lipids are overestimated. The reproductive effort is similar to the simulations with constant energy allocation (Fig. 4D).

4.2 Seasonal energy dynamics

The influence of temperature on the physiology of sprat varies during the season. The feeding level is dependent on the available prey concentration and the temperature. An individual will under the given temperature (Fig. 3A) and feeding regime (Fig. 3B) experience a gain of energy during the summer season from ultimo February to mid-October (Fig. 3C). During this period the environment offers enough food so that the realized feeding level is higher than the critical
feeding level, see eq. 6. During early summer a small decline in critical feeding level is seen (Fig. 3C), which is caused by the large change in the weight during the spawning season. The annual variation in critical feeding level is low which is due to the proportionality existing in the temperature functions for both consumption (Fig. 5A - solid line) and metabolism (Fig. 5A - dashed line) within the temperature ranges applied in the simulation. The productive season for sprat is approximately 8 months with only the short winter period where the individual needs to sustain on build up lipids from the previous production season.

4.3 Physiology and temperature

The temperature dependence of the growth potential at abundant food supply can be determined from the difference between assimilated energy and metabolism (Fig 5A). The maximal consumption, $a_c W^{\text{bc}} f_c(T)$, as a function of temperature for an individual of 5 g has a maximum at approximate 21°C (Fig 5A – thick line). At lower temperatures maximal consumption decreases, with a reduction to approximately a half at 5°C. At temperatures higher than optimum, a fast decrease is observed, reducing consumption to 10% at 28°C, and asymptotically reaching zero. Metabolic costs increase exponentially with temperature, exceeding the maximal consumption at 25.5°C for a 5 g individual (Fig. 5A – thin black line). Evaluation of the growth potential as a function of temperature, described by the energy balance, shows maximal possible surplus energy level at ca. 17.5°C (Fig 5A – grey line) and at a temperature of ca. 24°C growth is terminated even if fed ad libitum. This is due to the difference in exponents of the consumption and metabolism terms (0.75 and 1.005 respectively). An individual reaches its maximum size when all consumption is used for respiration. We have calculated the maximum size based on an average food concentration of $F = 0.3$, which turn out to be a decreasing function of temperature (Fig. 5B).

5. Discussion

We have been able to reproduce observed growth patterns in Baltic Sea sprat in our simulations, which includes three structure pools; soma, lipids and produced eggs. By resolving growth in the three structure pools we have obtained an understanding of the underlying processes governing the overall growth patterns and strategic decisions made by the individual. The decisions have been evaluated by testing two energy allocation schemes to describe observed growth patterns of sprat. Further direct temperature effects on the physiology of sprat were obtained by evaluating the energy balance under ad libitum feeding. This has been made possible due to an exceptionally high resolution of observations on sprat biology which helped to set up and calibrate our bioenergetic model in a very detailed way. Individuals used for energy density estimations, used for determination of fat content, were caught at stations in the Bornholm Basin at all sampling dates. It is difficult to determine for certain whether the sampled individuals are part of the same sub-population at all times of the year or whether they contain
a mix of fish from other basins in the Baltic Sea. Evidence from number of vertebrae indicates that migration between the basins is limited (Ojaveer & Kalejs, 2010). The calibration is based on the assumption that the data represent an average sprat in the central Baltic Sea.

The model presented here is based on the Wisconsin framework in its bioenergetic formulations (Hewett & Johnson, 1992), which recently have been applied in e.g. the NEMURO.FISH framework (Megrey et al., 2007). This framework assumes that growth occurs if the intake is higher than all losses due to egestion, excretion, specific dynamic action, respiration etc. and that growth is measured either in weight or length increments. We have extended this framework with an explicit structure pool for lipids as sprat is both a capital and income breeder (Stearns, 1992), dependent of the time within the spawning season. To implement this we included an allocation scheme, by which the growth strategy into either the lipids or the soma is specified. We tested two formulations of this energy partitioning; sigmoid and constant allocation. The constant allocation is equivalent the κ-rule from the dynamic energy budget (DEB) theory, stating that a fraction of the energy available for growth is used for soma growth and maintenance (κ) and the remaining energy (1 − κ) is used for maternal development and reproduction (Kooijman, 2000). Our equivalent to the κ parameter is $f_A$. The sigmoid scheme assumes that the allocation between soma and lipids are changing throughout the season.

When the sigmoid allocation scheme is applied an individual will prioritize investment into soma growth over investment in lipids in the beginning of the productive season. Therefore the individual will be able to consume more food as consumption is allometric, hereby raising potential fecundity. However it also risks that egg production is being limited by a lack of lipids, which are needed to produce eggs. This problem is avoided with the constant allocation scheme. Hereby the individual is able to allocate energy for growth and reproduction, as well as storing lipids after the spawning season for overwintering. Thus the simpler allocation strategy, constant allocation, is able to replicate the emergent growth seen in sprat from the Bornholm Basin. In both formulations the seasonality in the growth patterns of sprat is captured well although absolute values in the soma and lipid structure pools are in best accordance to validation data when applying the constant allocation scheme. This method also requires the fewest parameters of the two methods, and is thus less dependent on model fitting, and we have therefore used the constant allocation scheme in the calculations.

The fraction of surplus food which is allocated to soma and lipids will likely depend on the lipid content of the prey. Baltic sprat prey on older copepodite stages, adult copepods and cladocerans (e.g. Bernreuther et al., 2009; Diekmann et al., 2007). The total lipid content in Baltic *Pseudocalanus acuspes* copepodite stage V females, a preferred prey for sprat, ranges between 12-25% of dry mass (DW) according to season and for adult females between 10-15% of DW (Peters et al., 2006). Adult Baltic *Acartia* spp. females have a total lipid content of 4-8% of DW and adult Baltic *Temora* spp. females range from 5-12% of DW, both according to season (Peters, 2006). This indicates that the fraction of consumed food allocated to lipids, $f_A$, should be in the range of 4-25 %, which is the range of the lipids content in the prey of sprat. We use a $f_A$-value of 0.65, which was necessary to simulate realized growth in both the soma and lipid
structure pools (Fig. 4B+C). This value is higher than the lipid content in the prey species. We hereby assume that the individual will prioritize to store any consumed lipids and use other compounds to cover metabolic costs. The high caloric value of the lipids makes it a good compound to store, and is essential during the overwintering period as well as during spawning. With the constant allocation scheme, the seasonal variation in the lipid pool in sprat is an emerging result of the seasonal forcing of food concentration and the bioenergetic budget within the individuals, and not a product of a variable allocation.

Zooplankton production in the Bornholm basin relies on the establishment of a bloom of prey for the zooplankton, being both phytoplankton and protozooplankton (Renz & Hirche, 2006). The period of high copepod biomass in the Bornholm Basin is, in general, unimodal and is assumed to be similar to the neighbouring Arkona Basin (Zervoudaki et al., 2009). Over the year the nauplii stages dominate in abundance during April and May, these nauplii develop and the adults dominate from June and onwards (Dickmann, 2005). The nauplii are produced from adults who have stayed in dormancy during winter (Peters et al., 2006; Renz & Hirche, 2006). In July and August the most abundant zooplankton group is cladocerans (Dickmann, 2005). All stages of the copepods and the cladocerans are important prey organisms for sprat. The nauplii stages are prey for larval sprat and the adults are feeding on the copepodite stages, adults and cladocerans (Bernreuther, 2007). The zooplankton dynamics in the Bornholm Basin is implemented to the model in the food availability forcing function as a proportion of maximal consumption over the year. As we do not know the exact amount of consumed food, the function is calibrated against weight at age data and thus only the shape can be compared to field observations. The shape of the curve is in good accordance to concentrations observed in the adjacent Arkona Basin (Zervoudaki et al., 2009) and is thus assumed valid.

This method does not include interannual variability in the production rates in mesozooplankton, and thus in the sprat growth rate and reproductive potential. But the applied method is reasonable, as the size differences between year-classes, when tracking weight at age, are not substantial (Fig. 4A).

The model presented here has been calibrated for Baltic Sea sprat, but is generic and can be used for any forage fish, which feed on the same type of prey organisms throughout its life. We aimed at keeping the model as simple as possible and to keep the number of parameters low. This made it possible to estimate parameters either directly or indirectly from laboratory experiments or cross-species allometric scaling relationships. The model setup can be used for determining growth conditions for Baltic sprat under future climate simulations to analyse how this warm water species will grow and reproduce in a potential warmer climate. Further the model allows for elaboration to include population dynamics and thereby to quantify density-dependent processes and influences. The model provides a dynamic representation of the bioenergetics budget of adult sprat, and can be used as a module in a full life-cycle model of sprat in the Baltic Sea linking growth conditions for adults to egg production.
Acknowledgements

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<tr>
<td>Reproduction</td>
<td>Fraction of energy to eggs allocated from lipids</td>
<td>0.5</td>
<td>-</td>
</tr>
<tr>
<td>Energy densities</td>
<td>Energy density of the soma pool</td>
<td>4</td>
<td>kJ g^{-1}</td>
</tr>
<tr>
<td>Energy densities</td>
<td>Energy density of the soma pool in dry weight</td>
<td>20</td>
<td>kJ g^{-1}</td>
</tr>
<tr>
<td>Energy densities</td>
<td>Energy density of the lipid pool</td>
<td>40</td>
<td>kJ g^{-1}</td>
</tr>
<tr>
<td>Energy densities</td>
<td>Energy density of eggs</td>
<td>1.5</td>
<td>kJ g^{-1}</td>
</tr>
<tr>
<td>Energy densities</td>
<td>Energy density of the eggs in dry weight</td>
<td>30</td>
<td>kJ g^{-1}</td>
</tr>
</tbody>
</table>
Table 2: Summary of the model.

\[
\frac{\partial S}{\partial t} = \begin{cases} 
E > 0 & (1 - f_A) \left( \varepsilon_i \left( \frac{a_c W^{hc} f_c(T) p W^q F}{a_c W^{hc} f_c(T) + p W^q F} \right) - a_R W^{bs} f_R(T) \alpha_R \right) - \left( 1 - f_E \right) r_{e_{gg}} W_{total} \\
E < 0 & \begin{cases} 
\text{condition} \geq 0.05 & 0 \\
\text{condition} \leq 0.05 & \left( \varepsilon_i \left( \frac{a_c W^{hc} f_c(T) p W^q F}{a_c W^{hc} f_c(T) + p W^q F} \right) - a_R W^{bs} f_R(T) \alpha_R \right) \varepsilon_{M}^{-1} 
\end{cases}
\end{cases}
\]

\[
\frac{\partial L}{\partial t} = \begin{cases} 
E > 0 & f_A \left( \varepsilon_i \left( \frac{a_c W^{hc} f_c(T) p W^q F}{a_c W^{hc} f_c(T) + p W^q F} \right) - a_R W^{bs} f_R(T) \alpha_R \right) - \left( f_E r_{e_{gg}} W_{total} \right) \\
E < 0 & \begin{cases} 
\text{condition} \geq 0.05 & \left( \varepsilon_i \left( \frac{a_c W^{hc} f_c(T) p W^q F}{a_c W^{hc} f_c(T) + p W^q F} \right) - a_R W^{bs} f_R(T) \alpha_R \right) \varepsilon_{M}^{-1} \\
\text{condition} \leq 0.05 & 0 
\end{cases}
\end{cases}
\]

\[
\frac{\partial E}{\partial t} = r_{e_{gg}} W_{total} f_E
\]
Figure 1: Schematic of the bioenergetic model. Energy and structure pools are represented with circles and squares respectively. Arrows denote energy and structure pathways. Ingested energy – consumption deducted assimilation costs ($\varepsilon_I$) - is used to cover metabolic costs. Surplus energy is allocated to soma or to lipids. In periods where consumption cannot meet the metabolic needs, additional energy needs are covered firstly from the lipids and if these are empty, from the soma pool. Eggs are produced from both protein from the soma and lipids. All transfers are associated with losses ($\varepsilon_M$ and $\varepsilon_G$).

Figure 2: Map with temperature station.
Figure 3: Applied environmental forcing and seasonal consumption dynamics. Annual temperature (panel A) is implemented as a cosine function with minimum and maximum temperatures based on the behaviour of sprat and average water column temperature in the Bornholm Basin. Data points are bottom (crosses) and surface (diamonds) water temperatures with standard deviations. See section 2.5 for further details. Relative prey concentration (panel B) ranges over the season from 0.1 to 1. °C: The effects of temperature and prey concentration on the feeding of a 3 year old individual is shown in C. Solid line is the feeding level (consumption divided by the maximum consumption), dashed line is the critical feeding level which is the feeding level required to satisfy metabolic demands (CFL; Eq. 6).
Figure 4: Growth dynamics and data of sprat caught in the Bornholm Basin (circles) and results of simulation for constant allocation scheme (solid lines) and sigmoid allocation (dotted lines). During periods with sampling intervals above three months, no line is added between the measurements. Time is given in years and denotes the age of the individuals in simulation and data which has been determined by otolith reading of captured sprat. Panel A is wet weight ($W_W = W_S + W_L$), panel B is weight of soma ($W_S$), panel C is lipid weight ($W_L$) and panel D is weight of produced eggs ($W_E$).
Figure 5: Temperature effects on physiology. Panel A gives maximum consumption (thick black line), metabolism (black line) and surplus energy (grey line) for an individual weighing 5 g. For maximal consumption and metabolism the temperature range which is experimentally validated is given in full line. The dashed lines are extrapolations beyond the validated temperature ranges. Panel B gives the maximal size an individual can reach, due to the difference in exponent on consumption and metabolism. The maximal size is determined with average annual food concentration of 0.3, resembling the annual average in the simulation. The full line shows the temperature range for which both consumption and metabolism are experimentally validated and the dashed part the extrapolation in the temperature functions.
MS2: Effects of future climate on physiology and egg production in forage fish, exemplified by Baltic Sea sprat

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Abstract

Sprat in the Baltic Sea is a crucial link between lower and upper trophic levels. This link is however fragile as sprat in the Baltic Sea is at the species’ northernmost distribution limit. Temperature is therefore an important factor shaping the life history of sprat. Climate scenarios for the Baltic Sea predict a significant warming, thus our aim is to determine the impact of predicted future climate changes on growth, egg production and fitness of sprat. We use an existing physiological model for adult Baltic Sea sprat and force it using predicted sea-water temperature from a climate model. Further we examine the impact of future prey availability both in terms of seasonal variation and productivity changes. We find the warmer future climate reduces individual size as well as total adult reproductive output. The egg production today is the lowest even compared to the warmer future climate due to a mismatch of the spawning season and feeding season in the Baltic Sea today. Fitness is proportional to the system productivity with a stronger response in fitness to changes in system productivity.

Keywords: Climate change, egg production, Sprattus sprattus, spawning dynamics, fitness, phenology.

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Introduction

Sprat play an important role in the Baltic Sea ecosystem as the specie serves as a link between lower trophic levels (zooplankton) and higher trophic levels, mainly cod. Herrings and sprat compete for the same food resource as both species are zooplanktivorous but herring is also able to prey larger zooplankton species, i.e. mysids and small fish (Blaxter, 1990). In the Baltic Sea the main predator on sprat is cod, but also marine mammals feed on sprat (Lundström et al., 2007, 2010). But at the same time as sprat being the prey for cod, sprat is also a competitor to cod as larval cod prey on the same prey organisms as larval and adult sprat (Voss et al., 2003). Furthermore, sprat has been observed to prey on cod eggs (Köster & Möllmann, 2000). Based on this evidence sprat has been characterized as a wasp-waist species (e.g. Cury et al., 2001) as they have the potential to control both the biomass of the lower and higher trophic levels (Möllmann & Köster, 1999; Köster & Möllmann, 2000).

Recruitment of sprat has been variable both on the short and the long time scale. The long term variability has been linked to climate trends in all recruitment processes in the egg and larval phases both with regards to hydrodynamic influences (Baumann et al., 2004, 2006b) and the biological features, such as mortality, growth and development (e.g. Köster et al., 2003; Baumann et al., 2006a; Peteriet et al., 2008). It has been shown that especially temperature is the determining factor on the overall recruitment processes (MacKenzie & Köster, 2004). The reason for the sensitivity of sprat in the Baltic Sea to temperature is that it is at its northerly distribution limit with regards to temperature (Muus & Nielsen, 1999) and this makes is likely that the species will be impacted by climate change (e.g. Myers, 1998; Rijnsdorp et al., 2009).

As mentioned the influence of the temperature influences on the egg and larval stages and their impact of recruitment in the stock has been well described. However, the importance of changing temperatures on the adult physiology has received only little attention (Roessig et al., 2004; Pörtner & Peck, 2010). Any changes in the physiology to changing temperature will possibly affect individual growth and egg production, which will again link back to recruitment of Baltic sprat. Here we analyse the physiological responses of climate change on adult sprat in the Baltic Sea area based on reasonable climate scenarios for the area. We aim at determining how climate change affects the fitness of the individuals and in particular their ability to reproduce. Further we aim at describing the importance of the lower trophic levels on growth and egg production. We discuss the how the impact of climate change on individual physiology will influence the sprat stock in the Baltic Sea and how these changes will affect the ecosystem.

We use an existing bioenergetic model (Frisk et al., MS1) to determine effects of temperature and seasonal prey dynamics on growth patterns and egg production over season and life span of the individual. The model is driven by temperature and prey availability. We evaluate 10 scenarios which are aimed a examining the impacts of changes in temperature, bloom phenology and prey productivity in isolation: two temperature regimes drive the model and for each of these 3 scenarios of bloom phenology are evaluated: current situation, early bloom and broader bloom. The prey scenarios are theorized to describe the potential seasonality in the prey production under the future climate – current situation is a reference curve which is calibrated against observed growth patterns in Baltic sprat. We test the importance of the
system productivity by including additional four prey regimes in which we have reduced/raised
the consumption to mirror effects in potential changes in the productivity during the future
climate regime. For each scenario we evaluate growth dynamics, egg production and fitness.

**Methods**

Our study is based on a bioenergetic model which describes growth and egg production of Baltic
Sea sprat with a high temporal resolution (see Frisk et al. (MS1) for full description of the
model). The model includes two energy rates, i.e. intake and metabolism, and three structure
pools; soma S (e.g. muscle, bone, organs), lipids L and eggs, all characterized by their energy
content (Fig. 1). The model assumes that consumed energy is used for covering metabolic costs
to maintenance and activity. Surplus energy is used for simultaneous growth in the two
structure pools: soma and lipids. During periods with lower consumed energy than necessary to
cover the costs to metabolism, energy is taken from the lipids and, if this is depleted, from the
soma. The soma and lipids are also used to produce eggs. Egg production occurs within a fixed
time period, if the individual condition factor is above a threshold value. The model is validated
using data on lipid content and size of sprat with high temporal resolutions (Temming et al., in
prep), ensuring that the model is able to capture the seasonal dynamics in sprat growth.

**Climate scenarios**

We include two temperature schemes to simulate growth under recent and future climate. The
recent scenario covers the period 1960-1990 and the future scenario covers 2070-2100.

The climate scenarios are calculated by the DMI-BShCMOD regional ocean model. The
model is a 3-dimensional hydrodynamic model which covers the North Sea and the Baltic Sea.
For the present study area, the horizontal resolution is 11 km and the vertical resolution varies
from 2 m to 50 m depending on depth (She et al, 2007). The ocean model is forced with
atmospheric data from a downscaled global climate model and the future emission scenario
used is the IPCC medium- to upper range scenario (SRES A2; see Madsen, 2011).

We define the Bornholm Basin in this study by the 50 m bathymetry line and the
borderlines of ICES subdivision 25 (Fig. 2A - map). The model predicts temperatures for the
scenario periods (1960-1990 and 2070-2100), which are averaged spatially in the Bornholm
Basin and temporally over each month. We use two depths layers: bottom (60-80 m) (Fig. 2B,
crosses) and top (10-20 m) (Fig. 2B, diamonds). The depth layers and information of the
positioning of sprat in the water column during the day and year is used for constructing the
temperature forcing functions (Fig. 2B, lines) (See Frisk et al., (MS1) for further details). The
temperature forcing function is a sine-function based on a minimum temperature during winter
and a maximum temperature during summer. Under the future climate scenario we assume that
the vertical positioning of sprat is the same as in the recent climate scenario, and the
temperature forcing is calculated from the predictions from the hydrographic model. This give
an increase in temperature 2 °C at the winter minimum and an increase of 4 °C at the summer maximum compared to the recent scenario (Fig. 2B, lines).

**Prey scenarios**

Simulations include three prey scenarios to evaluate the effect of the timing and magnitude of the prey productivity over season on physiological response in sprat (Fig. 3A). The availability of prey is described by the consumption of an individual divided by the maximum consumption rate. Thus the prey scenarios $F(t)$ range from a minimum level of 0.1 to 1 during the season described by a bell-shaped function:

$$F(t) = F_p \exp \left( -\frac{(t-t_\mu)^2}{\sigma^2} \right) + F_0$$  \hspace{1cm} (Eq. 1)

Where $t$ is time, $F_p$ is the height, $t_\mu$ is the time of peak in function, $\sigma$ is the width term and $F_0$ is the minimum level the function can reach (table 1).

The three prey scenarios are based on the interplay of biological production in both primary and secondary producers and physical conditions, such as temperature and light. The current situation prey scenario (Fig. 3A – black line) has been simplified from the food availability function described and discussed in Frisk et al. (MS1), to be described by a bell-shaped function. The seasonal growth patterns observed with this simplification is not as accurate as for the original food availability function, but for the scope of this study the obtained level of details in seasonal growth is adequate. Here we aim at describing the trends in changes due to differences in prey availability and temperature in relative terms more than to predict the absolute egg production and fitness. The early bloom scenario (Fig. 3A – dark grey line) is based on the assumption that temperature influences copepod growth and therefore the timing of the peak prey availability. Temperature is an important determinant for the prey, i.e. copepods and cladocerans, and also affects their growth. Hansen et al. (1997) reviewed the temperature dependence and found $Q_{10}$ values in the range of 2.4-3.9 for copepod ingestion rate, 1.8-3.1 for copepod respiration and 3 for copepod maximal growth rate. For this scenario we therefore assume that the prey organisms for the copepods and cladocerans, i.e. the primary producers, are dependent on the temperature and will shift their peak production equally earlier in the season. Thus, we have shifted the peak value, $t_\mu$, of prey scenario earlier in the season to the date at which this prey-peak temperature occur in the climate scenario.

Temperature is just one of several factors governing future prey productivity. In the Baltic Sea the driver on the spring bloom in the primary producers is light, but the higher temperatures under future climate will increase the growth rates of the primary producers (Hansen et al., 1997). Thus the biomass will be higher earlier in the productive season. The earlier spring bloom will be channelled to the secondary producers, who also will benefit from the higher temperatures and thereby their growth rates are also higher (Hansen et al., 1997). This has been incorporated into the broader bloom scenario (Fig. 3A – light grey line), which has the overall shape as the current situation prey scenario to keep the light as the determining
factor, but the temperature relation broadens the production period, $\sigma$, because of the higher growth rates of the prey organisms. Under all three prey scenarios the integrated prey productivity is kept constant. Hereby we are able to see the responses to the timing of the prey dynamics on growth and egg production.

**System productivity**

To also account for the system productivity we included four prey regimes to the simulation. All prey regimes are based on the broader bloom scenario, which is believed to be the most likely scenario of the three for the future climate scenarios. The scenario with reduced productivity is implemented to reflect a regime where the Baltic Sea will have a stronger stratification, whereby the flux of nutrients to the surface layer is decreased. The regime with higher productivity simulates a situation in which more nutrients are introduced to the Baltic Sea, thereby raising primary production and also secondary production.

The importance of the future system productivity is tested including four scenarios: two which increase the productivity by 20% and 40%, and two which reduce the productivity by 20% and 40% (Fig. 3B). The scenarios are created by changing the height of the curve to obtain the integrated productivity aiming at. In the scenario with a 40% increase in system productivity the prey availability function is reaching values above one. As consumption is also physiologically restrained the function is lowered to 1 in the period where it is above; i.e. $F(t) = \min(F(t), 1)$. Hereby the individual is able to feed to $C_{max}$ for a longer period. In the scenario with a 40% increase this period is three months during summer. Applied parameters are given in table 2.

**Fitness**

As a fitness measure we use adult expected reproductive output, $R_0$:

$$R_0 = \sum_{t=1}^{\infty} \exp(-M \cdot t) \cdot \left( G(t)/\rho_{E,WW} \right) \cdot \Delta t / w_{egg,WW}$$

(Eq. 2)

Where $M$ is mortality, $t$ is age, $G$ is the flux to gonads calculated by the model and $w_{egg}$ is the weight of an egg. We use the average mortality estimates of age 2-7 Baltic Sea sprat from 2010 including both natural and fishing mortality; 0.83 yr$^{-1}$ (ICES, 2011). $W_{egg,WW}$ is 1.16 mg, which has been determined from the mean gravity and mean diameter (Nissling et al., 2003). The energy density $\rho_{E,WW}$ is 2.166 kJ g$^{-1}$.WW.
Results

Growth dynamics

The recent climate and the current situation prey scenario mirrors observed growth patterns in sprat fairly for both the soma and the lipids (Fig. 4A+C). The lipid dynamics are in good agreement with the observations and the seasonal variations are captured well by the model. The soma weight is underestimated at the oldest ages compared to the observations, but the soma weight in the younger ages is captured well by the model. The earlier bloom gives soma weights similar to the current situation simulation, but the lipids continue to grow with age – a trend not seen in the observed growth dynamics of sprat. This is caused by the high prey availability, and thereby consumption, within the spawning season. Hereby the stored lipids are not drained during spawning, and continuous growth in the pool occurs. The broader bloom scenario gives smaller individuals compared to the current situation scenario and the observations. The broadening of the prey availability function increases the growth period, but the feeding level is lower, hereby reducing both structure pools.

The scenarios with the future climate (Fig. 4B+D) generally give similar seasonal growth patterns, except for a single year in one scenario. The current situation prey scenario with the future climate give higher soma and lower lipid weights compared to the situation today. During the low feeding period between age 2 and 3 the individual depletes the lipids. This depletion forces the individual to grow within the spawning season, as the condition factor is below the limit which allows for spawning. Only a little energy is used for spawning that year resulting in a maximal soma weight of 18 g. The following winter the lipids are depleted yet again and the growth dynamics are repeated. The soma weights in the following years are higher than under the recent climate but lower than at age 3. In the earlier bloom scenario similar growth patterns evolve, but the absolute sizes in the structure pools are reduced. Here the individual also depletes the lipid pool during winter, which affects the growth and spawning dynamics. The broader bloom scenario has similar soma weights under the future climate as under the recent climate, but the lipid weights are reduced. This reduction gives lipid weights in the range of the observations. In this prey scenario the lipid pool is not depleted during winter leading to the highest average lipid weights of the scenario runs with future climate, and the winter levels are higher than the observations from the Bornholm Basin.

Egg production

The seasonal variability in prey availability determines the amount of energy that can be channelled to egg production. In the current climate the highest egg production is seen in the broader bloom scenario followed by the current situation scenario (Fig. 5). The lowest egg production under recent climate is seen in the earlier bloom scenario but the differences between all scenarios are minor. For all scenarios the smallest egg production is seen at age 1
and at age 2 and onwards the egg production is raised and nearly constant over ages. The small variability in the egg production under the three scenarios is caused by the changes in body size (total weight), as spawning in all scenarios is not limited by condition and/or available lipids for egg production.

Under the future climate scenario the broader bloom prey function have the highest egg production, and is in the same range as the current climate scenarios. Both the current situation and the earlier bloom have reduced egg productions compared to the other prey scenarios from age 3 and onwards. The reduction in egg production is caused by the usage of lipids to cover metabolism during the overwintering period, where food are scarce. The lowest total egg production under future climate is seen in the current situation prey scenario.

Fitness
The fitness estimate combines the reproductive outcome with the survival of an individual. The relative fitness estimates then compares the various scenarios to the reference scenario with recent climate and current situation prey scenario (Fig. 6).

In the recent climate scenarios the lowest fitness is observed in the current situation prey scenario. The larger temporal match in the feeding season and the spawning season, in both the earlier bloom and broader bloom scenarios, increase the fitness estimate up to 18%. The fitness estimate shows a consistent lower fitness for each prey scenario under future climate conditions. The reduction in fitness is largest for the broader bloom scenario where the fitness is reduced by 22%. Both the earlier bloom and broader bloom prey scenarios have similar fitness estimates as the current situation under the recent climate.

System productivity
Higher system productivity increases both average weight-at-age (soma and lipids) and the fitness (Fig. 7). At a relative productivity of 1 and below the asymptotic size is reached already at age 2 or is even reduced at older ages compared to age 2. During these scenarios energy is used for survival and growth and reproduction is not possible. When increasing the relative system productivity the asymptotic size is reached at a higher age. The additional energy available to the individual is used both for reproduction and growth. Effects on reproduction are evaluated in the fitness measure. The fitness increase proportionally with increasing relative productivity. A decline in productivity show strong effects on the fitness, e.g. a reduction in system productivity by 20%, reduces fitness by 30.
Discussion

Model setup

The model simulations are based on assumptions on the environmental forcing due to the predicted future climate, on the prey scenarios, and on the changed productivity regimes.

Projecting future climate change is challenging. Future emissions of greenhouse gases are unknown, there are uncertainties in our knowledge about nature’s response to the emissions, and climate models contain uncertainties themselves. Especially for regional studies such as the present, the uncertainty, or noise, can easily be larger than the climate change signal. In this study, we have looked at two time slices, 1960-1990 and 2070-2100, which are sufficiently far apart to give an acceptable signal-to-noise ratio. We have detected a temperature change in the sprat habitat of 2 °C in winter and 4 °C in winter, which is within the range of other climate studies for the Baltic Sea (The BACC Author Team, 2008). The difference between summer and winter is both due to larger changes in surface summer temperatures than surface winter temperatures, and due to larger change at the surface than at depth, presumably due to larger exchange with the North Atlantic with depth (Madsen 2011).

In the Baltic Sea it is expected that the warming of the water column will most likely result in an earlier stratification of the water column. This is further reinforced as the precipitation and river run-off is expected to increase (Frei et al., 2006). But at the same time the higher river run-off is likely to introduce more nutrients to the Baltic Sea especially since the Baltic Sea catchment area is heavily populated. Therefore the actual increase in the system productivity is very dependent on not only the oceanographic factors but also the anthropogenic pressure on the system and, thus, the policies taken by the countries in the catchment area. As we do not know the productivity changes in during the future climate scenario, and we do not know how the prey organisms will respond to both the biotic and abiotic conditions, we operate with scenario runs. Further we keep the prey scenarios applied in this work are as simple as possible. Hence, their shape is described by a bell-shaped function. The scenarios are designed to capture the trend in the plausible future changes in prey availability. This makes it possible to provide a qualified insight into how different future scenarios might influence sprat physiology.

Central to the individual life history is the trade-off between growth and reproduction (Stearns, 1976; Roff, 1992). An individual can by postponing maturity grow to a larger size and thereby increase future fecundity, but the choice to grow in size over maturing at an earlier age has to be weighed against the mortality. These effects are not included in the model as mortality is the same at all sizes. In nature the natural mortality varies with size, with the mortality risk decreasing with increasing size (Andersen et al. 2009). The reason for not including this effect is that the fishing mortality is very large for this specie, which when they are recruited to the fisheries will dominate over the effect of the natural size dependent mortality. The increase in fecundity with increasing size is included in the model as the egg production is a function of total weight. The egg production is also dependent on the lipids, i.e. the condition. Thus, the realized
egg production of the individual is both determined based on size and condition, which are the two most important proxies (Lambert et al., 2003).

Simulations of sprat growth and egg production

Prey scenarios affect both the duration of the growth season and the level of increase in the structure pools during a growth season. The timing of potential consumption is essential to growth of sprat. Besides the prey availability the growth of sprat is a function of temperature through the temperature dependence of metabolic costs and consumption. Therefore the growth dynamics for Baltic sprat is seasonally resolved. The winter season is long in the Baltic Sea compared to the other habitats of sprat. Thus, the individuals are very dependent on the energy gain during summer time, both for growth, overwintering and also the reproduction in the spawning season the following year. The model simulations of sprat growth are able to capture the seasonal variation in growth dynamics. We found that the prey scenarios are an important driver on egg production. The late peak in the current situation prey scenario results in the lowest egg production of the three prey scenarios, and thus the lowest fitness. In the current situation scenario the high prey availability is late in the season and the prey availability is low in the spawning season. Thus most of the eggs are produced from lipids from the previous feeding season. Both the earlier bloom and the broader bloom scenarios result in higher egg productions.

The warmer climate in the future climate scenarios leads to reduced lipid weight and lower egg production for all prey scenarios. This is mainly due to the higher winter temperatures which increase the metabolic costs. Also during summer the individuals will have higher metabolic costs. The increase in temperature also increases the possible consumption, hereby compensating for the additional metabolic costs. The effects of temperature on both consumption and metabolism have been evaluated (Frisk et al. (MS1). Up to a temperature of 17.5 °C under ad libitum feeding, the benefit of the increased temperatures is highest on consumption. But during winter when the habitat does not allow for ad libitum feeding the increase in winter temperature in the future climate scenario results in smaller individuals.

Management implications

When the effects of climate change of a stock are evaluated it is crucial to account for the effects on all life stages. For sprat several studies have been performed on the egg, larvae and juvenile stages (Nissling et al., 2003, 2004; Petereit et al., 2008) and with this study the entire life cycle have been covered. This makes it possible to review the effects on the population as a whole. The mechanisms which control how climate can affect fish populations are summarized by Rijnsdorp et al. (2009): (1) physiological responses, (2) behavioural responses, (3) population dynamics, (4) ecosystem level changes and (5) changes in exploitation patterns. Here we will evaluate the biological important mechanisms for Baltic sprat, i.e. 1-4.
The physiological responses to temperature affect all life stages of sprat. For eggs the most important factor for the development in the Bornholm Basin is temperature (Nissling et al., 2003; Nissling, 2004). The hatching success has been evaluated for a range of temperatures: at temperatures above 14.7 ºC no egg development was observed and below this temperature the stage duration increase with decreasing temperatures (Petereit et al., 2008). The stage duration is important as the lower the development time the lower is the predation pressure on the eggs (MacKenzie et al., 2008). But this argument only holds if there is a difference in the scaling between the temperature dependencies on egg development and on consumption in the predator. Today the temperature range at which sprat eggs are located is within the range of successful hatching suggested by Petereit et al. (2008). For the future climate the temperatures within the spawning season in the Bornholm Basin are also below the threshold temperature of 14.7 ºC. Thus within this area the egg development could be positively affected by the higher future temperature, due to the reduction in predation pressure because of the lower stage duration could ensure a higher hatching success. The physiological response of the yolk-sac larval stage is also strongly coupled to temperature as an optimum for survival is seen at 6.8 ºC (Petereit et al., 2008). Around this optimum a mismatch is seen in the time and temperature needed to successfully develop exogenic feeding, i.e. mouth opening and eye pigmentation, and the energy available in the yolk-sac. Therefore at this stage it is not simply a question of fast growth to minimize predation as it is a matter of also ensuring successful ontogenic development. For the feeding life stages the temperature effects on the physiology is an interplay between mainly metabolism and consumption. For the adult sprat we have previously shown that energy available for growth will increase until 24 ºC, but also that the individual sizes will decrease (Frisk et al., MS1). Small individuals can experience higher winter mortalities as the weight dependent scaling on metabolism is higher in small individuals. Thus, they exhaust their lipids faster than bigger individuals when accounting for the individual weight (Peters, 1983; Post & Evans, 1989; Shulter & Post, 1990). In this study we have shown that the future climate will result in lower total egg production because of the higher metabolic costs during winter. The egg production is greatly influenced by the seasonality in prey, and since this is likely to change with a warming of the Baltic Sea, we could observe unchanged egg production in the future.

The behavioural responses in sprat can evolve as the individuals will try to increase their fitness. This can be by seeking areas with optimal temperatures and/or better feeding conditions and/or to avoid predation (Charnov, 1976; Houston et al., 1993; Roessig et al., 2004). The behavioural response to fitness optimization can be to change the vertical positioning in the water column. The higher costs to metabolism in the future climate scenarios can be compensated if the individual seeks colder water layers if possible. Hereby the reduction in body size revealed in the future climate scenarios can be avoided, and also the egg production can be higher. The most important population-level response of temperature of sprat is through recruitment. Sprat recruitment is strongly linked to temperature and periods with higher temperatures, especially during late summer, give the strongest recruitment (MacKenzie & Köster, 2004; Baumann et al., 2006a). The year classes consist predominately of individuals born late in the spawning season (Baumann et al., 2006b). Also drift patterns of egg and larvae have
been linked to recruitment, where retention in the deep basins are linked with years of strong recruitment, whereas transport towards southeast lead to recruitment failure (Baumann et al., 2004, 2006b). The recruitment patterns summarized here is probably due to the lower stage duration in the egg phase and thus lower predation mortality, as well as the ambient temperatures in the deep basins late in the spawning season are close to the physiological optimum for the yolk-sac larvae combined with good feeding conditions. The higher future temperature can be beneficial to Baltic sprat as high temperatures have previously been linked to strong recruitment. On the ecosystem level the potential changes to sprat will propagate up the food chain to the predators. If the individual sizes are reduced predators will prey on smaller individuals, which most likely will have a lower condition as described by the broader bloom scenario. This will influence the predators and their population dynamics, as they also will have lower conditions whereby their egg production is also affected.

Conclusions

This study serves as a missing link in understanding climate effects for the entire life cycle of Baltic Sea sprat. We have tested the importance of climate and prey on growth, egg production and fitness. Future climate have been found to reduce both egg production and fitness for the current situation prey scenario. Comparing among prey scenarios we saw an increase in egg production and fitness with changes in the prey availability: The larger the temporal match with spawning season, the larger is the egg production and fitness. The system productivity test revealed reductions in individual sizes and fitness with decreasing productivity. When increasing productivity, additional energy was used both for growth and reproduction. The climate effects on all life stages were reviewed for physiological, behavioural, population and ecosystem implications.

Acknowledgement

We would like to thank Torkel Gissel Nielsen, DTU Aqua, for discussions on climate effects on copepod production. CF was funded by the ModRec project under the Marine Ecosystem Modelling Centre (MEMC). KHA was funded by the EU FP7 project FACTS.
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### Table 1: Overview of parameters and assigned values in the prey scenarios

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Current situation</th>
<th>Earlier bloom</th>
<th>Broader bloom</th>
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<tr>
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</tr>
<tr>
<td>$\sigma$</td>
<td>Width term</td>
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<td>0.09</td>
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<tr>
<td>$F_0$</td>
<td>Minimum level</td>
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<td>0.10</td>
</tr>
</tbody>
</table>

### Table 2: Overview of parameters and assigned values prey regimes

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<th>+20%</th>
<th>+20%</th>
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<tbody>
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<tr>
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<td>0.5</td>
</tr>
<tr>
<td>$\sigma$</td>
<td>Width term</td>
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<td>0.14</td>
<td>0.14</td>
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<tr>
<td>$F_0$</td>
<td>Minimum level</td>
<td>0.10</td>
<td>0.10</td>
<td>0.10</td>
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</tr>
</tbody>
</table>
Figure 1: Model setup. Circles display rates and squares are structure pools. Arrows show the energy pathways in the model. The grey boxes and arrows show the environmental drivers to the model and the rates they influence.

Figure 2: Temperature forcing. The study area (panel A) with the confined area marked in white, which is used to determine temperatures in the climate scenarios. The colour shading illustrates the depth. B: Average temperatures of bottom (diamonds) and top (crosses) layer for both the recent (black) and future (grey) model simulations. Temperature for both recent (black line) and future (grey line) scenarios used in the model is determined from the simulated habitat temperatures and the vertical position of sprat.
Figure 3: Scenarios for prey phenology (A) and productivity (B). The prey scenarios are described as a proportion of maximal consumption available for the individual. A: The phenology scenarios are: current situation (black), earlier bloom (dark grey) and broader bloom (light grey). B: Prey productivity scenarios are based on the “broader bloom” scenario and the system productivity is varied by +/- 40% in steps of 20%.

Figure 4: Effects of changed prey phenology on growth dynamics of sprat in recent climate (A + C) and future climate (B + D). A + B: Somatic weights C + D: Lipid weight. The different lines represent the prey scenarios; current situation (black), earlier bloom (dark grey) and broader bloom (light grey). The circles in A + C are observations on Baltic sprat.
Figure 5: Yearly egg production for the current (solid lines) and future temperature scenario (dashed lines). The line colour represent the different prey phenology; current situation (black), earlier bloom (dark grey) and broader bloom (light grey).

Figure 6: Fitness (adult reproductive effort) under recent and future climate for the current situation (black), earlier bloom (dark grey) and broader bloom (light grey) prey scenarios. The fitness is calculated relative to the simulation described by the conditions for sprat in the Baltic Sea today, i.e. recent climate and current situation prey scenario.
Figure 7: Effect of system productivity during future climate on the average weight at age 2-5 (black lines; width increasing with age) and fitness (grey). The productivities in the scenarios are calculated relative to the simulation with future climate and broader bloom.
MS3: Body condition may explain variability in life history decisions among individuals – exemplified by reproductive strategy in Baltic Sea herring

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Abstract

Down regulation of fecundity and skipped spawning are generally accepted phenomenon's among fish, where individuals choose to either reduce reproductive effort or completely sacrifice spawning to maximize growth or survival even though they are mature. A recent study indicated that skipped spawning is common among adult Central Baltic herring (Clupea harengus), and that this reproductive decision is related to the condition of the fish, although it was not possible to differentiate between “true” skipped spawning and delayed spawning (i.e. shifting from spring spawning to autumn spawning). The aim of the present study is to improve our understanding of these skip spawning events recently observed in Central Baltic herring. In order to achieve this aim, we construct a bioenergetic model of adult female herring, which explicitly quantify the annual reproductive output. We propose that spawning will only occur if the individual have reached a given condition threshold. We evaluate the lifetime reproductive output for various condition thresholds and quantify the resulting life history traits, such as, down-regulation of fecundity and events of skipped spawning. We found that fitness increased when the condition threshold was reduced. However, we suspect that in reality starvation mortality during winter will at some unknown point counteract this trend. Changes in the condition threshold were, furthermore, affecting down-regulation of fecundity, the number of skipped spawning events and age at first spawning. Spring spawning was found to be the better strategy compared to autumn spawning. Lastly, a comparison between model outputs and the life histories observed for this stock lead us to suggest that an individual Baltic Sea herring with a condition (lipid weight/soma weight) below 0.08 on the day of spawning is likely to skip spawning.

Keywords: Reproduction strategy, bioenergetic model, skipped spawning, condition, physiology, phenology, prey availability

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**Introduction**

Variation in life history decisions among populations can be ascribed to adaptations to local environmental conditions (Roff, 1992). However, when variation in life history decisions is observed to differ among individuals belonging to the same population (McQuinn, 1997), we often run out of explanations. In the present study we demonstrate how individual condition may determine the outcome of reproductive decision making. We use Central Baltic herring as an example. The environmental conditions of the Baltic Sea are stressful, which reflect upon the life history decisions taken by herring inhabiting this region. Especially the low fat prey types found in the Baltic Sea affects the Central Baltic herring by reducing body condition and size (Kändler & Dutt, 1958; Aro, 1989; Cardinale & Arrhenius, 2000; Möllmann et al., 2000; Casini et al., 2006). Low condition has been hypothesized to induce both down regulation of fecundity and skipped spawning. These are generally accepted life history decisions among fish. By skipping spawning or down-regulating fecundity, the individual has weighed the trade-off of today’s spawning to the trade-off in other life history traits, such as growth or survival (Roff, 1992). Down regulation is a mechanism where the individual is able to reabsorb already recruited oocytes (immature eggs) as the individual does not have enough energy to bring all recruited oocytes through to full maturation (Kennedy et al., 2008; Kjesbu, 2009). Further low condition has been hypothesized to be a general cause of skipped spawning in the Norwegian spring-spawning herring (Oskarsson et al., 2002; Kennedy et al., 2010; Kennedy et al., 2011a, 2011b; Bucholtz et al., submitted).

Down-regulation of fecundity and possibility of skipped spawning has recently been examined in the Central Baltic herring through analysis of oocytes at various stages of maturation (Bucholtz et al., submitted). They found a possible 73% reduction in potential fecundity and 68% reduction in relative potential fecundity during ovary maturation from the early developing ovary maturation stage (maturity stage II) to ovaries in the late development stage (maturity stage IV) due to atretia (degeneration and resorption) of developing oocytes. Furthermore, the developmental stages of oocytes prior to the spring spawning period indicated that 15% of the adult females would either truly skip spawning and not spawn until spring the following year, or catch up on oocyte maturation and spawn during summer or autumn. These females also had a substantially lower condition than the fish with progressed maturity stages, expected to spawn in the spring. These findings suggest that the low body condition of the Central Baltic herring, compared to other herring stocks, has great impact on the reproductive success of this stock.

Our aim is to understand the observations of down regulation of fecundity (hereafter referred to as down regulation) and apparent skipped spawning events in Central Baltic herring. We chose a life-history optimization approach and used a bioenergetic model of adult female herring which provide information about growth, energy stores, reproductive investment and the annual reproductive output. In the model spawning will only occur if the individual have reached a given condition threshold on a fixed annual spawning day (hereafter referred to as
the condition threshold). Additionally we were able to address the question of whether the skipped spawning events seen in the herring stock is due to different populations spawning at different seasons, or whether a more opportunistic approach exists in the stock, where spawning occur in either season when the individual has energy to do so. The study contains the following analyses: (i) Growth pattern of an individual with induced skipped spawning, (ii) patterns of down regulation for each of three different condition thresholds, (iii) fitness and skipped spawning patterns for a range of condition thresholds and for three different spawning types (spring spawners, opportunity spawners and autumn spawners), and (iv) effects of food availability.

The results presented here are based on a bioenergetic model of adult herring. We test the physiological constraints to spawning through a series of model runs on the minimum condition factor threshold needed for spawning. In the model, individual condition is the fraction of lipids to soma \( \frac{W_L}{W_S} \), where \( W_L \) is the weight of lipids and \( W_S \) is the weight of the somatic tissue. For each run we determine the degree of down regulation based on the total possible fecundity and the realized egg production in the model. These runs are tested for individuals spawning in only in spring or autumn and an opportunistic spawner, which spawn when the condition exceeds a threshold value. The model is also used for testing how the prey availability is affecting the spawning, but only for the spring spawning setup, as the majority of the Baltic herring are spring spawned. We discuss how this work is linked to work on skipped spawning events both for herring and other fish species.

**Method**

The model is based on a bioenergetic model made for Baltic Sea sprat (Frisk et al., MS1), but has been recalibrated to Baltic Sea herring. Since the development of the herring model by Rudstam (1988), experiments have been performed specifically on Central Baltic herring, which we use in the model setup presented here, e.g. temperature effects on metabolism. The model is dynamic and driven by consumed food. The ingested energy, which is consumption deducted egestion, excretion and specific dynamic action (SDA), to cover metabolic costs to standard metabolism activity and maintenance. The remaining energy is divided between three structure pools characterized by their energy content; soma (muscles, bone structures, organs etc.), lipids and eggs (Fig. 1). Flow of energy between the structure pools are determined by the surplus energy, condition of the fish and season. The weight of the individual, which is used for allometric scaling relationships, is calculated on the basis of the somatic pool, \( W = S/\rho_S \), where \( \rho_S \) is the energy density of the somatic tissue in wet weight and takes a value of. During periods with surplus energy, growth occurs simultaneously in both lipids and soma. During periods when ingested energy is not sufficient to cover the metabolic needs, the necessary energy is taken from the lipids, and if this is depleted, from the soma. The individual is allowed to spawn only on predefined spawning days and only if the condition exceeds a threshold, denoted \( CT \) from hereon. The spawning event removes energy from both the reserves and somatic tissue. Only
females are considered in the model. The model explicitly calculates adult expected reproductive output, which we use as a measure for fitness.

Consumption

Maximum consumption is described by an allometric function \( a_cW_s^{b_c} \), a clearance rate \( pW_s^q \), seasonal and a temperature effect function \( f_c(T) \). Realized consumption includes seasonally resolved prey concentration \( F \). Further the consumption term includes a Holling type II functional response:

\[
C = \frac{a_cW_s^{b_c}f_c(T)pW_s^qF}{a_cW_s^{b_c}f_c(T) + pW_s^qF}
\]

(Eq. 1)

The parameters for maximum consumption have been determined for Atlantic herring by de Silva and Balbontin (1974) and are also applied in the herring model by Rudstam (1988). The exponent \( b_c \) has a value of 0.744 \( \text{kJ g}^{-1}\text{yr}^{-1} \). The factor \( a_c \) is based on the same study but has been used for calibration of the model, see section hereon. The parameter \( q \) is 0.8 and the factor \( p \) is 900 \( \text{m}^3\text{g}^{-1}\text{yr}^{-1} \). The temperature dependence on maximum consumption is adopted the temperature dependence formulated by Thornton & Lessem (1978) and parameterized by Rudstam (1988). The function is a dome shaped-like curve, which is created from two sigmoid curves, where one describes the increase at increasing temperatures, and the other the decrease of consumption at temperatures above optimal.

The prey availability function \( F \) describes the seasonal variation in prey concentration in \( \text{kJ m}^{-3} \) and ranges from 0.1 \( \text{kJ m}^{-3} \) to 1 \( \text{kJ m}^{-3} \). The absolute values of the prey availability function cannot be linked to observed biomass of prey, as the seasonality in encountered prey has been calibrated through the \( p \) factor in the search volume function (see Frisk et al. (MS1) for details).

\[
F(t) = F_p \exp \left( \frac{-(t-t_p)^2}{\sigma} \right) + F_0
\]

(Eq. 2)

The shape of the function is a simplification for the prey availability function in Frisk et al. (MS1), and the parameters of the function have been determined as part of the calibration, see section hereon.

We test the importance of prey availability by varying the height of the prey function by a factor, \( PF \). I.e. \( F_{P,\text{scenario}} = PF \cdot F_p \). The scenarios with varying \( PF \) values are described later on.
Metabolism

Respiration is described by an allometric function \(a_r W^{b_R}\), a temperature effect function \(f_R(T)\) and an activity multiplier \(\alpha_R\):

\[
R = a_r W^{b_R} f_R(T)
\]

(Eq. 3)

The allometric exponent, \(b_R\), is adopted from Meskendahl et al. (2010) and is determined for sprat and takes a value of 1.073. It is believed that herring are as active as sprat, and therefore the large value describes this activity level. The allometric constant \(a_r\) is 5.2 kJ g\(^{-1}\) \(b_R\) yr\(^{-1}\) and \(\alpha_R\) has been fitted as part of the model calibration. The temperature effect on metabolism is described by an exponential relationship (Bernreuther, 2007):

\[
f_R(T) = \exp(d_R T)
\]

(Eq. 4)

Where \(d_R\) is 0.087.

Growth

Growth is determined by the surplus energy (measured in kJ):

\[
E = C - (1 - \varepsilon_i)C - R = \varepsilon_i C - R
\]

(Eq. 5)

Where \(\varepsilon_i\) denotes the losses to egestion, excretion and SDA, and takes a value of 0.7. During periods with a negative energy balance, e.g. during winter when the food availability is low, the individual use stored reserves until these pools are depleted to a minimum condition of 0.02. The condition factor is the ratio between the wet weights of the lipid and soma pools: \((L/\rho_L)/(S/\rho_S)\). If the reserve pool is also depleted the individual will use soma pool to cover the energy needs. Both energy transfers are associated with loss of energy, here described by a transfer efficiency, \(\varepsilon_{st}\), of 0.8. The individual allocates surplus energy simultaneously to the somatic and reserve structure pools. Priority to reserve growth is described by the fraction, \(f_A\), which is 0.65 and growth in the soma is \(1 - f_A\) (see Frisk et al., MS1 for further details).

Reproduction

The spawning event is simplified so that egg production and spawning occur simultaneously. Spawning occur at two predefined days, May 1\textsuperscript{st} or October 1\textsuperscript{st}. The specific dates are in the middle of the two observed spawning periods in Central Baltic herring (spring and autumn spawning) (Aro, 1989). Also we test a more opportunistic spawning approach, where the individual can either spawn in spring or autumn. Spawning can occur in either season if the condition threshold \(CT\) is exceeded. Spawning is restricted to only occur once a year by including a switch to the simulation which determines whether spawning has occurred or not. The switch
is reset at the beginning of a new year. Thus indirectly priority is given to spring spawning over autumn spawning in the opportunity spawner scenarios. Eggs are produced from both the reserves and the somatic tissue. The fraction from the reserves are described by $\psi$.

Maximal potential fecundity, in kJ, has been determined in central Baltic herring based on individuals in maturity stage II to be (Bucholtz et al., in prep.):

$$G_{\text{MAX}} = (a_G \cdot W_{\text{TOTAL}} - b_G) \cdot W_{\text{EGG,WW}} \cdot \rho_{\text{E,WW}}$$  \hspace{1cm} (Eq. 6)

Where $a_G$ and $b_G$ are factors, $W_{\text{TOTAL}}$ is determined as the weight of the reserves and somatic tissue as $W_S \cdot \rho_S + W_L \cdot \rho_L$, and $W_{\text{EGG,WW}}$ is the weight of an egg. $W_{\text{EGG,DW}}$ is 1 mg and $\rho_{\text{E,DW}}$ is 20 kJ g$^{-1}$. The eggs are at this stage not fully developed, and we therefore assume that the water content is low, as we apply a higher energy density than for spawned eggs. The applied value is within the range for observed energy densities for spawned eggs of 2.1 kJ g$^{-1}$ (Riis-Vestergaard, 2002) and dry weights of eggs which have an energy density of 30 kJ g$^{-1}$ (Hislop & Bell, 1987).

The individual is not able to utilize the maximal potential fecundity, as the lipid pool is not large enough to produce $G_{\text{MAX}}$. Therefore we implement a description, which uses the entire lipid pool for egg production, measured in kJ:

$$G = \psi \cdot L + (1-\psi) \cdot S$$ \hspace{1cm} (Eq. 7)

Where $\psi$ is 0.75. G is measured in kJ. The spawning effort can be determined in weight by accounting for the energy content in eggs, $\rho_{\text{E,WW}}$, measured as wet weight. The model is validated against observed gonad weights from Baltic Sea herring. The eggs in these gonads are not fully hydrated and therefore have a higher energy density than spawned eggs. To account for this when comparing the simulated eggs we apply a higher energy density than for spawned eggs. We use $\rho_{\text{E,WW}}$ of 20 kJ g$^{-1}$ which give simulated total weight of the eggs which are in accordance to the measured gonads.

As mentioned, the egg production in the simulation is always smaller than the maximal potential fecundity seen in Central Baltic herring. This is due to the down regulation of individual potential fecundity during maturation caused by atresia (Bucholtz et al., submitted; in prep.). The percentage of actual egg production to the maximal egg production is determined from the following equation:

$$G_a = \frac{G}{G_{\text{MAX}}} \times 100\%$$ \hspace{1cm} (Eq. 8)

The degree of down regulation is therefore $1 - G_a$. 

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Fitness
As a fitness measure we use adult expected reproductive output, $R_0$:

$$R_0 = \sum_{t=-\infty}^{\infty} \exp\left(-M \cdot t\right) \cdot \left(G(t) / \rho_{E,WW}\right) \cdot \Delta t / w_{E,WW}$$

(Eq. 9)

Where $M$ is mortality, $t$ is age, $\Delta G$ is the flux to gonads, and $w_{E,WW}$ is the weight of an egg. We use the average mortality estimates of age 2-7 Baltic Sea herring including both natural and fishing mortality; 0.524 yr$^{-1}$ (ICES, 2011). $w_{E,WW}$ is 1 mg and $\rho_{E,WW}$ is 20 kJ g$^{-1}$ with the same argument as above. The specific values of $w_{E,WW}$ and $\rho_{E,WW}$ applied are of lesser importance, as the fitness measure is only used to compare the effects of the scenarios. The values only scale the R0 estimate and therefore their importance is insignificant when making the comparison.

Calibration and validation of the model

The model is tuned against observations on age specific wet weight, total lipid content $\omega$ and gonad weights of herring caught in ICES subdivision 25 in March 2008. The data are presented in Bucholtz et al. (submitted & in prep.). Lipid weight in the data is determined as $W_L = W_w \cdot \omega$ and soma is determined as the remainder, i.e. $W_s = W_w - W_L$. Further weight at age data from the BITS survey is included to include seasonal variations (ICES WGBFAS 2009). The data are based on herring catches in ICES subdivision 25 during 2008. The quarterly data are plotted with Q1 at time 1.25, Q2 at 1.5, Q3 at 1.75 and Q4 at 2.0 (Fig. 2A).

The tuning of the model is done by varying three parameters: the factors in the allometric weight functions $a_c$ and $a_w$ and the fraction of lipids in eggs $\psi$. The factor in the allometric function is used to determine the shape of the growth curves. The parameter is used for tuning the asymptotic size in the simulation and also the seasonality in the growth dynamics. $a_c$ is based on the study of de Silva and Balbontin (1974), but is reduced to 20% of their original value. The factor is also converted from $g^{1-k} \cdot yr^{-1}$ to kJ yr$^{-1}$ by assuming an average energy density of 7kJ g$^{-1}$ The value of $a_c$ in the model is therefore 107 kJ yr$^{-1}$. Consumption is further controlled by the search volume and the food concentration, i.e. $pW^q \cdot F(t)$. The search volume parameters are 900 m$^3$ g$^{-q} \cdot yr^{-1}$ and 0.8, for respectively $p$ and $q$. The prey concentration is tuned to match observed growth by tuning the following parameters; $F_p$, $\sigma$ and $F_\sigma$ to take the values of 1, 0.16 and 0.4 respectively. $\psi$ is 0.75. All parameters used in the model is summarized in table 1.
Simulations

The model is based on the assumption that both the environment and the physiology affect the reproductive decision-making, i.e. skipped spawning, down regulation and spawning time. Spawning occurs only if the individual have reached a certain condition threshold on the spawning day (the physiological mechanism). The decision not to spawn in situations where body condition is below the condition threshold (CT) is defined as a skipped spawning event. As a simplification the spawning period is reduced a single day. Since food availability will affect body condition, it will indirectly affect reproductive decision-making (the environmental mechanism).

We aim at determining the link between condition and reproductive decision making. The model runs which tests the physiological threshold for spawning and implications for growth are based on the condition of the individual in combination with the maturity stage. Individuals caught in March are grouped according to maturity stage to evaluate, at which condition the individuals were able to spawn. The condition in the different maturity stages are overlapping, with average condition values of 0.036 (range 0.02-0.08) and 0.046 (range 0.01-0.07) for individuals in respectively maturity stage II and maturity stage III. The overlap is caused by the investments in gonad development (and growth) which in herring already initiates during autumn the previous year, whereby the reserves are reduced (Ma et al., 1998; Kurita et al., 2009). Thus the condition of the individual must have been higher at the time of initiation of the gonad investments. In our starting point we accept that we have no knowledge of the exact value of CT. Instead we evaluate $R_0$, patterns of skipped spawning events and down regulation for a whole range of CTs. Furthermore, growth patterns and age at first spawning is also analyzed in the mode. The lowest CT applied in our simulations is 0.04, as we are sure that this fall below the actual value.

The tests which determines the importance of the prey availability on the skipped spawning events covers a wide range of PF values, from 0.6 to 1.5. As consumption is also physiologically restrained the function is lowered to 1 in the period where it is above; i.e. $F(t) = \min(F(t).1)$. Hereby the individual is able to feed at $C_{max}$ for a longer period.

Lastly, we decided not to restrict the study to the assumption that Central Baltic herring only spawn in spring. We therefore repeated the CT simulations three times, one for spring spawners only, one for opportunity spawners (i.e. the individual can choose to spawn in autumn provided it did not already spawn in spring), and one for autumn spawners only.

Results

Growth dynamics and down regulation
The growth dynamics are here exemplified by the model run with CT of 0.05, to illustrate the effects of skipped spawning (Fig. 2). The model is able to reproduce convincing growth
trajectories compared to the data from Bucholtz et al (submitted; in prep.), which are resolved in total wet weight (Fig. 2A), soma (Fig. 2B), lipids (Fig. 2C) and eggs (Fig. 2D). Also the seasonal variation in the wet weights from ICES WGBFAS (2009) is captured. Growth in the three structure pools depends on the time of year and condition of the individual. Spawning occur at a specific day of spawning as described previously, and the spawning events and gonad weights are displayed here as ‘histograms’ (Fig. 2D). Model runs without skipped spawning events give maximal egg production at age 2 and then decreasing with age (data not shown). The gonad production the following year from a skipped spawning event is larger as the lipids are carried over from the year before, e.g. the spawning at age 7.

The gonad weights observed in Baltic herring by Bucholtz et al. (in prep.) show large standard deviations, which is likely caused by variations in individual condition. As mentioned previously Central Baltic herring show a possible reduction in the mean relative potential fecundity of 68% (Bucholtz et al., submitted). These estimations are based on the same individuals used here for validation. Thus the gonad weights here are already subject to down regulation. We are able to quantify the degree of down regulation in the model runs, based on the maximal fecundity as a function of individual weight and the actual egg production in the simulation (Fig. 3). The degree of down regulation in the simulation is determined as the remainder between the actual egg production and the maximal oocyte production. Here we present three simulations of varying CT values: CT of 0.02 (Fig. 3A), 0.05 (Fig. 3B) and 0.08 (Fig. 3C). In the run with CT of 0.02 spawning occur each year, with actual egg production ranging from 5-25% of the potential oocyte production, which means that the individual has down regulated the spawning effort by 75-95%. In the other CT scenarios given in figure 3B and 3C the down regulation is in the same range. For all model runs the greatest down regulation occur in the oldest individuals which is due to the higher living expenses in the larger the individual (Frisk et al., MS1). The actual relative egg production is higher in years in subsequent years to skipped spawning events, e.g. at age 7 in the model run with CT of 0.05. Also the fewer spawning events leads to lesser down regulation, which is caused by larger reserves pools available for spawning, as the reserve pool is not completely depleted during winter, cf. fig. 2C. The level of down regulation in the model is larger than observed in the field. This is caused by the precautionary approach used when determining the energy needed to produce \( G_{\text{max}} \). The parameters used here on the egg weight and egg energy density are in the conservative range, and had the values been chosen differently the down regulation would seem smaller in the simulation.

**Implications of spawning type**

The effect of spawning type, i.e. spring, autumn and opportunistic spawning, on spawning frequency (Fig. 4ABC), growth (Fig. 4DEF – crosses on an arbitrary axis and fitness (Fig. 4DEF – black line) is evaluated as a function of the condition threshold, CT, for spawning. General for all spawning types we see an increase in age at maturity with increasing CT values, as the individual needs some years before the individual acquires a sufficient condition to undertake spawning. Also with increased CT value the frequency of skipped spawning events increase which is accompanied in an increase in maximal size. Meanwhile the fitness is reduced as the egg production is reduced.
In the spring spawning simulations the number of spawning events decreases when CT increases. (Fig. 4A). The first response is seen by skipped spawning events occurring at the highest ages in the simulation. Also the age at maturity increase from scenarios with CT values of 0.08 or above. The maximal total weight also increases for increasing CT (Fig. 4D). This is caused by the simultaneous allocation of energy to both the somatic tissue and reserves. In years where spawning is skipped there is no loss of energy from the pools. The somatic tissue will when spawning does occur have increased more than the losses caused by the spawning event. All the CT runs yield realistic maximal weight of Baltic herring. Fitness decrease with increasing value of CT, and the trajectory of the fitness curve is determined by the spawning frequency. If the frequency is reduced, the fitness estimate is also reduced, and similarly in periods with constant spawning frequencies the fitness estimate is constant.

For the opportunity spawner the same patterns evolve as for the spring spawner. The spawning frequency is reduced with increasing CT value. The spawning frequencies are similar to the spring spawners, except at the run with CT of 0.09 and 0.10, where the autumn spawning possibility allows for an additional spawning event compared to the strict spring spawner. By being able to spawn in both seasons, the individual gains fitness. This is both because of the higher spawning frequency, but also because of higher egg productions at the spawning events. The dip in fitness for the scenario with CT of 0.10 is caused by a much lower egg production at age 1 compared to the egg productions at age 2 in the following CT scenarios. The maximal weight, winter weight losses and fitness show identical patterns as for the spring spawner.

The autumn spawner also shows reducing spawning frequency with increasing CT value. But the number of spawning is reduced with maximal five spawning compared to ten in the other spawning types. Besides the reduction in number of spawning the spawning patterns are similar, with Increasing age at maturity for increasing CT scenario and lowering of spawning frequencies. Fitness is reduced when spawning during autumn compared to during spring. This is due to the reduction in number of spawning in each model run. But the number of spawning events increases the egg production at each spawning event, which raises fitness.

**Discussion**

*Assumptions and fundamentals of the model setup*

The model is based on parameters taken from various studies on herring We have not been able to solely parameterize the model with data on Central Baltic herring, but the setup have been able to describe the growth dynamics observed in the stock. We were able to reproduce the growth dynamics seen in Central Baltic herring, based on both seasonal variations in total weight (ICES WGBFAS, 2009) and age variations in the composition of soma, reserves and gonad weight (Bucholtz et al., in prep.). Further, the model presented here give realistic maximal weights compared to observed maximal weights of Central Baltic herring. As our objective is to compare the relative effects of various model runs and scenarios to improve the understanding of reproductive strategies in herring the model and interplay of the parameters are satisfactory.
The individual face a decision to spawn or to skip reproduction. In the model this decision is determined on the day of spawning and is based on individual condition. This is a strong simplification of the reproduction cycle in herring as oocyte production and development initiates up to 9 months before spawning. The process of oocyte development, from oogonies (the pre-stage of oocytes) to eggs that are ready for spawning, is very complex involving several processes, which are impossible to parameterize and describe in the model. The simplification applied here benefits the individual as it have had a period of feeding prior to spawning. In nature the Fulton condition factor seen in central Baltic herring is also believed to increase as the development progresses, as the individuals have increased their weights (Bucholtz et al., submitted). Bucholtz et al. (submitted) therefore argues that central Baltic herring are not strict capital breeders but has an intermediate strategy, not being capital nor income breeders, which allows them to channel ingested energy to oocyte production. We have made some general assumptions regarding the energy densities of the different structures described in the model. These are difficult to validate, but we have tried to be precautionary in the parameter choices made. This is e.g. the case with the maximal possible fecundity where we assume that the energy density $20 \text{ kJ g}_{\text{ww}}^{-1}$. This real value is likely below this value, as the individuals in maturity stage II are still growing the oocytes. Had the value been lower the down regulation determined based on the simulation would have been in better agreement to the observations made by Bucholtz et al. (in prep.). But for now the precautionary approach taken is believed to be the better choice.

Effects of physiology on spring spawning dynamics

The importance of the physiological limit, the CT value, to the skipped spawning events has been tested. The physiological limit is an energy storage buffer for the individual to ensure survival after the spawning event. In the central Baltic Sea strong seasonal variation in prey availability is observed with little prey available during the winter time. Therefore the individual are dependent on the stored energy during winter to survive. This is included in the model by the CT value, which describe how the individual is able to foresee the necessity of storing energy for survival during poor feeding periods and thereby ensuring its own survival.

The runs with variable CT values reveal that the individual has the highest fitness at the lowest CT values. This leads to spawning occurring at the youngest ages and without skip spawning event. This is caused by the mortality component of the fitness measure, which is high for the central Baltic herring stock, making the spawning at the youngest ages disproportionally more important for the fitness compared to subsequent ages. The model is not forced by a specific age at maturity or size at maturity, but age at first spawning is dynamic and is based on the condition, which determines if spawning occur or not. In a fish stock the age/size of maturity is plastic and is dependent of individual growth dynamics and predation pressure (Roff, 1992). This is included in a maturity ogive, which gives the proportion of mature individuals of each age group. For central Baltic herring gives that maturity is seen first at age 2 at which the ogive is 0.7, at age 3 the ogive is 0.9 and at age 4 all individuals are mature (ICES WGBFAS, 2011).
Further, the data from Bucholtz et al. (in prep. B), which are also used in this study, show that the youngest spawning individuals are age 3, thus older than the maturity ogive adapted by ICES WGBFAS. The age at maturity seen in the field, is in the CT runs suboptimal. However, in the model, where age at maturity was kept as an emergent property, age at first spawning occurred at the age of 1 in simulations using low CT. Such early reproduction has not been observed in the field. Hence, more processes besides individual body condition governs the age/size at maturity in Central Baltic herring. These processes could involve mortality associated with the spawning event and prolonged physiological changes associated with sexual maturation before the first spawning event, as the gonads are developing before the actual maturation of the oogonies can start. These effects are not included in the model but will also contribute to higher age/size at maturity.

The skipped spawning events in the simulations presented were strongest in the oldest individuals. This finding is contradictory to another study which suggests frequent skipped spawning in Norwegian spring spawning herring at the year following the first spawning event (Engelhard & Heino, 2006). This skipped spawning was linked to the size and condition of the individual which resulted from climatic factors, where food availability is mentioned as the likely determinant. Another study has on the other hand argued that there is no evidence of the high frequency in skipped spawning at the second spawning event proposed by Engelhard and Heino (2006) but only found a small proportion of the Norwegian spring spawning herring that were likely to skip spawning (Kennedy et al., 2011a). This study investigated the development stages of the ovaries throughout the seasons. The oocyte production was investigated and the spawning effort was linked to the prey availability (Kennedy et al., 2011b). The nutritional status of an individual may be so poor that skipped spawning events are observed, both in the model presented here but also in the field (e.g. McQuinn 1997; Rideout & Tomkiewicz, 2011).

**Effects of spawning type**

The opportunity spawning simulation is included as Central Baltic herring are flexible with respect to spawning time (Rajasilta, 1992), whom argues that the timing of spawning is primarily determined by the feeding conditions prior to spawning. The shifts in spawning type were observed both to occur at the oldest and the youngest ages. Further we saw several changes over the life span of the individual. This is contradictory to another study showing that the spawning time is determined during the first spawning and remain the same throughout its life (McQuinn, 1997). Energetically in the model this tendency is caused by the rebuilding of the lipid pool, which takes at least one feeding season dependent on prey availability. However, also the development and growth of the oogonies to oocytes takes several months, thus two annual spawnings are not possible in herring.

The evaluation of the influence of spawning type on fitness revealed lower fitness for autumn spawners compared to spring spawners. As mentioned, this is caused by the reduction in spawning events at age, and skipped spawning is seen even in the lowest CT values. Other dynamics potentially making autumn spawning inferior include larger overwintering mortality in
adults and larger mortality in the offspring during the first period of its life. The spawning event leaves the adult individual with depleted lipid reserves, both for the spring and autumn spawning individuals, but the consequence is different in the two spawning types given here. A spring spawning individual has a period of good feeding in prospect. Here it will be able to refill its lipid pool which can be necessary for survival during the low feeding period during winter. The autumn spawning individual will after spawning also have depleted its lipid pool, but it will face a period of poor feeding conditions. Thus, the individual will enter the winter period with low lipid reserves and therefore is likely to experience a larger starvation mortality compared to the spring spawning individual. A central assumption is that the individual will use all available energy in the lipid pool for reproduction and thereby it does not earmark a fraction of the lipid pool as an insurance to minimize starvation mortality during winter. If the individual chooses to do so the egg production will be smaller, leading to a further reduction in fitness for the autumn spawning individuals, thereby making the autumn spawning strategy even more inferior to spring spawning.

For the offspring spawned in autumn experience lower temperatures compared to the spring spawned individuals. This prolongs the stage duration allowing the individual to sustain on the energy in the yolk-sac for a longer period, but at the same time the longer period spent in the very vulnerable life stage potentially increase the mortality. Also at the onset of the feeding period for the herring larvae sufficient prey is scarce. This additional mortality, caused by predation and the mismatch with prey availability for the larvae (Kosior and Strzyewska, 1979), is not included in the fitness estimate for the autumn spawning individuals. But the fitness will be further reduced by also including these effects.

The model simulations revealed based on individual physiology, that autumn spawning was inferior to spring spawning. Also the offspring is worse off when spawned during autumn compared to spring spawned. These effects are not included in the fitness estimate, thus the autumn spawning strategy is even worse that revealed by the fitness estimates given here.

Condition threshold for spawning and assessment implications

To better understand the implications on the stock and the stock assessment, it is desirable to quantify a cut-off value at which skipped spawning can occur in the stock. In Norwegian spring spawning herring Kennedy et al. (2010) found that individuals, who were not able to reach a Fulton condition factor above 0.7 during the feeding season, were not likely to begin ovary maturation. As Baltic herring are not able to prey on the same high fat organisms as the fellow specimen off the Norwegian coast, this condition factor can be different in Baltic herring caused by necessary adaptations to the poor feeding habitat. We are not able to directly give a Fulton condition factor for central Baltic herring, as the model setup is based on individual energy levels and biomass, and not length. Based on the simulations presented here and observed growth dynamics we are able to give an estimate of the condition necessary for individuals to be spawning in spring. The age at maturity which reports the youngest spawning individuals to be age 2 (ICES WGBFAS, 2011) and in 2008 the youngest spawning individuals were 3 years of age
To obtain this age at maturity in the CT simulation the condition should be 0.08 or above at the spawning time. This value is also the maximal value seen in maturity stage II individuals caught in March of 2008 (Bucholtz et al., in prep.), i.e. the individuals which are not able to spawn during the coming spring spawning period. But at the same time the value of 0.08 is higher than the value observed in individuals at MSIII, which therefore should not be able to spawn based on the argumentation given here. But the individuals caught in March have, as mentioned, made the decision to mature long before the actual analyses were performed on them. Based on the model setup which does not include this prolonged maturation period, we can displace this condition threshold to also count at the time of the actual decision making which for Baltic spring spawning herring is in autumn. Thus, based on the simulations here a central Baltic herring should have a condition value of 0.08 or above to be able to have a successful spawning in the following spawning season.

The skipped spawning events can have great importance for the stock assessment. If potentially not all individuals in the stock the total egg production and recruitment could be reduced compared a situation where all mature individuals are spawning. Skipped spawning events are not included in classical stock-recruitment relationships. The implications hereof have been investigated in the Northeast Arctic stock of Atlantic cod (Jørgensen et al., 2006). This study was also founded in a bioenergetic description of growth and reproduction. Further the model is based on dynamic programming which determines the optimal strategy in allocation and thereby also spawning events (Jørgensen & Fiksen, 2006). Hereby they found that up to 30% of the sexually mature biomass skips spawning. A similar estimate has been made for central Baltic herring based on the individual maturity stage in March (Bucholtz et al., submitted). Individuals in maturity stage II are assumed not to catch up with the oocyte development to spawn during the spring spawning season. Based on this the Bucholtz et al. (submitted) found that potentially 15% of the sexual mature population are not spawning, and thus the SSB applied in the assessment could be overestimated by 15%.

As shown in this study and the cod study (Jørgensen et al., 2006) the skipped spawning is closely linked to the prey availability and thus the condition. Therefore is would be desired to determine if a large proportion of the stock would skip spawning or not. This would as mentioned overestimate the spawning stock biomass and recruitment is potentially smaller that assessed. This could have great implications in a stock which could be harvested unsustainable. An indicator of the condition is therefore important to give a better estimate of spawning stock biomass. We here state that the condition of central Baltic herring should be above 0.08 in autumn to be able to have a successful spawning the following year.
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Table 1: Overview of the parameters and assigned values used in the model.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Value</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>$a_C$</td>
<td>Factor of the allometric mass function</td>
<td>107</td>
<td>kJ g$^{-1}$ yr$^{-1}$</td>
</tr>
<tr>
<td>$b_C$</td>
<td>Exponent of the allometric mass function</td>
<td>0.744</td>
<td>-</td>
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<td>$q$</td>
<td>Exponent on the search volume</td>
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<td>-</td>
</tr>
<tr>
<td>$p$</td>
<td>Factor on the search volume</td>
<td>900</td>
<td>m$^3$ g$^{-q}$ yr$^{-1}$</td>
</tr>
<tr>
<td>$F_p$</td>
<td>Height of prey function</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>$t_\mu$</td>
<td>Time of peak value</td>
<td>0.58</td>
<td>yr</td>
</tr>
<tr>
<td>$\sigma$</td>
<td>Width term</td>
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<td>-</td>
</tr>
<tr>
<td>$F_0$</td>
<td>Minimum level</td>
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<td>-</td>
</tr>
<tr>
<td>$\tau_1$</td>
<td>Temperature for $f_c(T)$</td>
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<td>°C</td>
</tr>
<tr>
<td>$\tau_2$</td>
<td>Temperature for $f_c(T)$</td>
<td>13</td>
<td>°C</td>
</tr>
<tr>
<td>$\tau_3$</td>
<td>Temperature for $f_c(T)$</td>
<td>15</td>
<td>°C</td>
</tr>
<tr>
<td>$\tau_4$</td>
<td>Temperature for $f_c(T)$</td>
<td>23</td>
<td>°C</td>
</tr>
<tr>
<td>$K_1$</td>
<td>Proportion to $C_{\max}$ in $f_c(T)$</td>
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<td>-</td>
</tr>
<tr>
<td>$K_2$</td>
<td>Proportion to $C_{\max}$ in $f_c(T)$</td>
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<td>-</td>
</tr>
<tr>
<td>$K_3$</td>
<td>Proportion to $C_{\max}$ in $f_c(T)$</td>
<td>0.98</td>
<td>-</td>
</tr>
<tr>
<td>$K_4$</td>
<td>Proportion to $C_{\max}$ in $f_c(T)$</td>
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<tr>
<td>$\alpha$</td>
<td>Activity multiplier</td>
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<td>-</td>
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<tr>
<td>$\epsilon_I$</td>
<td>Assimilation efficiency</td>
<td>0.7</td>
<td>-</td>
</tr>
<tr>
<td>$\epsilon_G$</td>
<td>Transfer efficiency; growth of gonads</td>
<td>0.9</td>
<td>-</td>
</tr>
<tr>
<td>$\epsilon_M$</td>
<td>Transfer efficiency; reserves/somatic tissue to metabolism (surplus energy is negative)</td>
<td>0.8</td>
<td>-</td>
</tr>
<tr>
<td>$f_A$</td>
<td>Allocation priority to lipid growth</td>
<td>0.65</td>
<td>-</td>
</tr>
<tr>
<td>$\rho_S$</td>
<td>Energy density of the soma pool in wet weight</td>
<td>4</td>
<td>kJ g$^{-1}$</td>
</tr>
<tr>
<td>$\rho_{S,DW}$</td>
<td>Energy density of the soma pool in dry weight</td>
<td>20</td>
<td>kJ g$^{-1}$</td>
</tr>
<tr>
<td>$\rho_L$</td>
<td>Energy density of the lipid pool</td>
<td>40</td>
<td>kJ g$^{-1}$</td>
</tr>
<tr>
<td>$\rho_{E,WW}$</td>
<td>Energy density of eggs in wet weight</td>
<td>20</td>
<td>kJ g$^{-1}$</td>
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<tr>
<td>$\rho_{E,DW}$</td>
<td>Energy density of the eggs in dry weight</td>
<td>30</td>
<td>kJ g$^{-1}$</td>
</tr>
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</table>
Figure 1: Processes, energy flow and structure pools in the bioenergetic model. The energy rate: consumption and metabolism, are given in circles, and the structure pools: soma, lipids and eggs, are displayed in squares. Arrows displays the possible pathways of energy transfers in the model. Energy intake is used to cover the metabolic costs, and any surplus energy is allocated to both the soma and lipid pools. In periods where consumption cannot meet the metabolic needs, additional energy needs are covered firstly from the reserve pool and if these are empty, from the somatic tissue, which is displayed with decreasing arrow shades. Eggs are produced from both protein from the soma and lipids and are spawned immediately in the model.

Figure 2: Growth dynamics in the structure pools and agreement with observations. For all panels the model simulation is given in full line and validation data as data points. The simulation is based on a model run with a condition threshold CT of 0.05 to given an example of growth including skipped spawning events. The individual increase in wet weight over time (panel A), with decreases caused by spawning events. Wet weights from survey data from ICES (*) and the level of individual weight is in accordance with
the observations made by Bucholtz et al (submitted) (diamonds with standard deviation) are displayed. The increase is occurring both in the soma (panel B) and the lipids (panel C). Spawning uses all available energy in the lipids. Absolute values of lipids in the simulation are in the range of the data reported by Bucholtz et al (submitted) (diamonds with standard deviation) but variations within ages occur as the simulation lipid pool is very dependent on the spawning events. The amount of produced eggs (given in grams and displayed as bars) is in good accordance with the observed gonad weights from Bucholtz et al (201X) (diamonds with standard deviation).

Figure 3: Relative actual and potential oocyte production and down-regulation. Panel A is for a simulation with CT of 0.02, panel B for CT of 0.05 and panel C is for CT of 0.08. The bars give the potential egg production which is determined based on the total weight of the individual on the day of spawning for each age. The actual egg production is shown in black, and is lower that potential oocyte production, as the reserve pool does not allow for full reproduction.
Figure 4: Effects of spawning type on growth, fitness and survival as a function of condition threshold for spawning for spring spawners (panel A+D), opportunity spawners (panel B+E) and autumn spawners (panel C+F). Each spawning event is displayed with a letter according to the spawning season; S for spring and A for autumn. The age at first spawning is highlighted by the grey line in each panel. The lower set of panels show the maximal weight (crosses on arbitrary axis) and fitness (black line for the spring spawners (panel D), opportunity spawners (panel E) and autumn spawners (panel F).
MS4: Overwintering strategy of sandeel ecotypes from an energy/predation trade-off perspective (and supplementary)

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Overwintering strategy of sandeel ecotypes from an energy/predation trade-off perspective

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ABSTRACT: The overwintering strategy is widespread among planktivorous fish from temperate to sub-polar regions, and is particularly pronounced in sandeel ecotypes. This adaptation is presumably a behavioural adaptation to strong seasonal fluctuation in prey availability, day length and temperature. Yet so far, insight into the evolutionary and ecological mechanisms involved has remained elusive. In the present study, the overwintering behaviour is considered to be a strategy requiring 2 annual decisions: When to end overwintering and when to start overwintering, which combined comprise the timing and duration of the foraging window. We present a model framework for sandeel that demonstrates how the optimal timing of the foraging window involves a trade-off between energy gain and survival probability. Physiological components of the model are based on laboratory experiments with sandeel, some of which are presented as part of this study. The major findings were that optimisation of individual fitness is strictly dependent on the temporal match between the foraging window and the peak period of the spring burst of zooplankton. In contrast, fitness is only marginally reduced in individuals that fail to optimise the foraging window in relation to the level of mortality and prey availability experienced during the zooplankton spring burst. Lastly, overwintering remained the optimal strategy, even in scenarios where winter prey abundances approached abundances near that of the peak abundance in spring.

KEY WORDS: Ammodytes · Life history optimization · Fitness · Bioenergetics · Foraging window · Mismatch

INTRODUCTION

Many zooplanktivorous fish species in temperate and sub-polar regions experience strong seasonal fluctuations in prey availability, and often rely on a transient zooplankton production fuelled by the exponential primary production in late spring, which is triggered by temperature-induced stratification and increasing day length. As a life cycle adaptation to the harsh conditions, many species build energy reserves to avoid starvation (Schultz & Conover 1997, 1999, Biro et al. 2005, Hurst 2007) and some even overwinter in a state of passiveness and stop actively searching for food. Such an overwintering strategy has been reported for a number of species of high commercial and ecological value (e.g. Winslade 1974a, Huse & Ona 1996, Kaartvedt et al. 2009), and is particularly pronounced in sandeel ecotypes. The archetypical example of this ecotype is the Ammodytes genus. Species of this genus can remain buried in the sediment for up to 10 mo (Winslade 1974a). However, insight into the evolutionary and ecological mechanisms underlying the overwintering strategy in fish has so far remained largely elusive.

The consequence of high mortality due to predation is that many individuals will not live long enough to reproduce. In this case foraging decisions become a trade-off between predation mortality and energy gain maximisation, also referred to as the energy/predation trade-off (Houston & McNamara 1999). The discovery of the energy/predation trade-off (e.g. Mittelbach 1981, Werner et al. 1983) led to a bloom of theoretical and empirical research suggesting that this trade-off impacts not only on the level of the individual but also
at the level of populations and entire ecosystems (e.g. Werner & Anholt 1993, Lima 1998). Sub-maximal
growth, temporal and spatial variation in distribution of prey organisms and their predators, and climate
change-induced compensatory foraging activity are just some of the consequences of the energy/predation

In the present study, we adopt the principles of the energy/predation trade-off in order to shed light on
the evolutionary and ecological processes underlying the overwintering strategy. We consider the
overwintering strategy as a plastic behaviour involving 2 annual decisions: When to end overwintering and
when to start overwintering. The combination of these 2 decisions comprises the timing of the foraging
window during which the individual exploits the food regime of the habitat. The optimal foraging win-
dow is defined as the one that maximises fitness (lifetime reproductive index; R0). In this context we
ask the following questions: (1) Is overwintering also the optimal strategy even when winter prey abun-
dance (background food level) is high enough to support a positive surplus energy budget? (2) What is
the optimal timing of the foraging window, and how is it influenced by predation mortality (including fish-
ing mortality) and food regime (for example the intensity and timing of the zooplankton spring burst)?
(3) What is the fitness-related incentive of adapting to changes in mortality and food regime? In order to
answer these questions, we developed a simple (few parameters) generic model framework that linked
mortality, bioenergetics, physiology and behaviour of the lesser sandeel Ammodytes marinus. Parameteri-
sation of the model was based on values from the literature and our own recently performed ex-
periments. In these experiments, stomach evacuation rate, stomach capacity and metabolism were mea-
sured (see Supplement 1 at www.int-res.com/articles/ suppl/m416p201_supp.pdf for details). The overwin-
tering behaviour and annual life cycle of lesser sandeels is well documented and relatively simple to
model as dispersal of lesser sandeel larvae is limited (Christensen et al. 2008) and adults are highly resi-
dential (Gauld 1990, Pedersen et al. 1999, van der Kooij et al. 2008). Lesser sandeels reach sexual matur-
ity around the age of 2 yr and subsequently spawn in December/January (Macer 1966, Bergstad et al.
2001). They are a commercially valuable, short-lived, trophic key species (e.g. Furness 1990, Hain et al.
ecosystems worldwide (e.g. Sherman et al. 1981, Bréthes et al. 1992, Van Pelt et al. 1997, Yamada
2009).

MATERIALS AND METHODS

Overview of the model. We developed an individual-
based bioenergetics model (an adaptation from Fish
The model in the present study employs an adult indi-
vidual that has reached its asymptotic size, so that all sur-
plus energy goes to reproduction. The simulation period
was 1 yr and addressed the optimal overwintering stra-
tegy in relation to investing foraging effort at the cost of
mortality. The spawning date was fixed to January 1
(Macer 1966, Bergstad et al. 2001).

Energy gain was based on stomach size and evacua-
tion rates, and energy losses were determined by the
assimilation efficiency, standard metabolism and activity
costs related to swimming. Temperature dependenc-
ies were included in the stomach evacuation rate and
the standard metabolic cost.

The habitat was described as a 2-box system. The
individual could either be in its refuge (which for a
sandeel means being buried in the sediment), where
predation mortality is low and food supply is zero, or in
the pelagic zone (arena), where the individual can feed
at the expense of higher predation mortality (including
fishing mortality). During overwintering, the individ-
ual was permanently in its refuge. As sandeels also
burrow in the seabed within the foraging window, dur-
ing night time as well as during parts of the day
(Winslade 1971), we resolved the model on daily time
steps. However, physiology and diel behavioural pat-
terns were related to hourly time scales after each
daily time step, such that the individual in the model
only spent time in the arena during daylight hours
starting at sunrise and whilst the stomach was not
full. Gut filling dynamics were therefore a function of
prey availability, day length and gut evacuation. The
energy uptake, energy expenditure and mortality that
accumulated over the course of the year, as a result of
a given foraging window, were combined into the life-
time reproductive index R0 (an index for the numbers
of offspring produced per lifetime; see Stearns 1992).
The foraging window which gave the highest R0
was considered the optimal foraging window. Individuals
that chose an overwintering behaviour that would
not let them accumulate enough energy to cover the
energy costs during the simulation year died from star-
vation. Model parameters are summarised in Table 1.

Details of the model. Consumption: Within the forag-
ing window, consumption (C) on a given day t was
described as assimilated energy (kJ):

\[ C(t) = N(t) \cdot \epsilon \]  

(1)

where N(t) is the number of encountered (and in-
gested) prey items on day t (see Eq. 5) and \( \epsilon \) is the
caloric value (kJ) of each prey item after accounting
for assimilation efficiency and the metabolic cost associated with digestion, absorption and storage of nutrients. The number of prey that could potentially be encountered by the individual on day \( t \) was determined by the availability of prey and the day length:

\[
N_{\text{enc}}(t) = f(t) \tau(t)
\]  

(2)

where \( \tau(t) \) is day length (h), and \( f(t) \) is the food regime, and describes encounter rate on day \( t \) (number of suitable prey encountered per hour). As a simplification, swimming velocity was assumed to be constant and is therefore not included in Eq. (2). The upper limit on the number of encountered prey per day was determined by available stomach volume at sunrise:

\[
N_{\text{max}}(t) = V - S(t - 1) + E
\]  

(3)

where \( V \) is volume or capacity of an empty stomach (numbers of prey items), \( S(t - 1) \) is the stomach fullness on day \( t - 1 \) (numbers of prey items), and \( E \) is what has been evacuated (numbers of prey items) since the previous day. As simulations in the present study were carried out for only a single size, the same \( V \) was used in all simulations. In order to keep the computation simple, \( E \) was estimated in the following way at sunrise:

\[
E(h) = S(t - 1) - \exp[\ln[S(t - 1)] + [a + b T(t)] h]
\]  

(4)

To avoid introducing a non-systematic bias to \( E \), the extent of the time period during which the stomach was filling up on day \( t - 1 \) was accounted for. Evacuation time \( h \) is therefore the time (h) since the midpoint of the foraging period on day \( t - 1 \), which was calculated here as \( 24 - H(t - 1)/2 \), where \( H(t - 1) \) is time spent foraging on day \( t - 1 \), calculated using Eq. (6). By using this approach only a small systematic bias was introduced to \( E \). \( T(t) \) is a forcing function describing seasonality in water temperature, and \( a \) and \( b \) are fitted coefficients describing the temperature effect on stomach evacuation. Both \( N_{\text{max}} \) and \( N_{\text{enc}} \) are upper boundaries on the number of encountered prey. In our model, the actual number of encountered prey was therefore:

\[
N(t) = \min[N_{\text{enc}}(t), N_{\text{max}}(t)]
\]  

(5)

**Behaviour:** On a given day \( t \), the individual was allowed to be in 1 of 2 states: foraging (daily shifts between arena and refuge) or overwintering (permanently in the refuge). Furthermore, the individual could only shift state twice during the year. In this way, behaviour on the annual time scale was condensed into 2 annual decisions, when to end overwintering and when to start overwintering, which when combined, comprised the timing and duration of the foraging window. A given overwintering scenario is described in the model by \( \sigma \), which is a binary vector of length 365 corresponding to the 365 d of the year. \( \sigma(t) = 1 \) if the individual, on day \( t \), is foraging in the arena and \( \sigma(t) = 0 \) if the individual is overwintering in the refuge.

To ensure that the individual did not spend unnecessary time in the arena (where mortality was high), but instead went to the refuge during the hours after sunset and when its stomach was full, the time in hours spent on day \( t \) in the arena was:

\[
H(t) = \tau(t) \frac{N(t)}{N_{\text{enc}}(t)}
\]  

(6)

**Energetic cost:** The daily metabolic cost \( (R) \) is a function of the combined costs of standard metabolism and activity:

\[
R(t) = \begin{cases} 
R_S(t) \cdot 24w + w[R_A \cdot H(t)] & \text{for } \sigma(t) = 1 \\
R_S(t) \cdot 24w & \text{for } \sigma(t) = 0 
\end{cases}
\]  

(7)

where \( R_S \) and \( R_A \) are the hourly standard metabolism and the activity metabolism, respectively, for 1 g of fish (kJ), and \( w \) is the weight of the fish (g). \( R_A \) is constant, whereas \( R_S \) depends on temperature:

\[
R_S(t) = c T(t) - d
\]  

(8)

where \( c \) and \( d \) are fitted coefficients.
**Mortality:** The daily mortality \( (Z_t) \) was described by the time spent in the arena and the refuge:

\[
Z_t(t) = \begin{cases} 
\sum_i H(t) \cdot Z_A + [24 - H(t)] Z_R & \text{for } \sigma(t) = 1 \\
\sum_i [24 - H(t)] Z_R & \text{for } \sigma(t) = 0
\end{cases}
\]  

(9)

where \( Z_A \) and \( Z_R \) are hourly predation mortality in the arena and refuge, respectively \((Z_A \text{ could also include fishing mortality)}\). From the daily mortality and the overwintering scenario \( \sigma \), the probability of surviving 1 yr is:

\[
P(\sigma) = \exp\left( -\sum_{t=1}^{365} Z_t(t) \right)
\]  

(10)

**Fitness:** If results of the equations for consumption (Eq. 1), energetic cost (Eq. 7) and mortality (Eq. 9) are summed over the entire year for a given overwintering scenario \( \sigma \), the lifetime reproductive index \( R_0 \) can be calculated in the following way:

\[
R_0[\sigma] = \omega \frac{P}{1 - P} \sum_{t=1}^{365} [C(t) - R(t)]
\]  

(11)

where \( \omega \) is the probability of surviving the larval and juvenile stage. As juvenile and adult life-stages are temporally separated, the juvenile and adult contribution to \( R_0 \) factorises in Eq. (11), and the influence of juvenile and adult life strategies on \( R_0 \) can be investigated independently. The sum of \( C - R \) over the entire year is the annual surplus energy gain \( (G) \) and is assumed to be proportional to individual fecundity. When the inter-annual variability in abiotic conditions is neglected, the reproductive output can explicitly be summed over the entire life span as in Eq. (11). It was assumed that population density affects the individual either by increased larval/juvenile mortality \( (\omega) \) or by reducing annual surplus energy gain \( (\text{competition}) \). This corresponds to population density effects of class 1 and/or class 3 respectively in the classification of Mylius & Diekmann (1995), and thereby optimisation of \( R_0 \) rigorously finds the overwintering scenario \( \sigma \) that corresponds to the evolutionary stable strategy. This is a considerable simplification compared to explicitly including population density effects in the model. In the present study, \( R_0 \) is simply optimised with respect to \( \sigma \) in order to predict the overwintering scenario that contains the optimal timing of the foraging window.

**Forcing functions:** The temperature forcing function applied to the model was a stylistic and general representation of the temperature cycle in the North Sea. The function is a cosine function:

\[
T(t) = T_{\text{min}} + 0.5(T_{\text{max}} - T_{\text{min}})[1 - \cos(2\pi(t + t_{\text{min}}))]
\]  

(12)

with minimum temperature of 5°C \((T_{\text{min}})\) on January 31 \((t_{\text{min}})\) and a maximum temperature of 20°C \((T_{\text{max}})\) on July 31. Values of day lengths \( t(t) \) correspond to the annual cycle on Dogger bank, North Sea.

The main time window for copepod production in the North Sea lasts for only a couple of months, with a steep increase in abundance peaking in late spring, at annual median temperatures, followed by a steep decline in abundance (Carlotti & Radach 1996). A Gaussian distribution and a constant background food level was used to make a schematic representation of the food regime contained in the forcing function \( f(t) \). The unit of \( f(t) \) is number of prey encountered per hour. As a simplification, all suitable prey encountered were of uniform size (see Supplement 1). Unless stated otherwise, the background food level in the model \( (\text{the food level that the fish experience in the model outside the zooplankton bloom in spring}) \) provide the fish with just enough energy to sustain the energetic cost of foraging, i.e. even if the fish choose to forage in the arena during winter the daily energy budget will not become negative. The mean of the Gaussian distribution defines the timing of the peak in the zooplankton spring burst, the standard deviation \( (\text{SD}) \) defines the duration and increase/decrease, and the space under the curve defines the intensity of the burst.

**Model simulations:** Eq. (11) was optimised with respect to \( \sigma \) for various scenarios of predation mortality and food regimes. In order to investigate how food regime affects the optimal foraging window, \( f(t) \) was manipulated either by changing the intensity or duration of the zooplankton spring burst, or the background food level. In order to investigate how predation mortality affects the optimal foraging window, Eq. (11) was optimised with respect to \( \sigma \) for a range of \( Z_t \) \((\text{at 2 different } Z_t: Z_A \text{ ratios})\). Alternative mortality scenarios were also explored, in which daily mortality during the foraging period was either constant, i.e. not dependent on number of hours spent in the arena, or correlated with temperature, i.e. \( Z_t \cdot (T_{\text{max}} - T_{\text{mean}}) \).

As the model was solved numerically, \( R_0 \) was calculated for all combinations of timing and duration of the foraging window. This made it possible to compare \( R_0 \) from suboptimal foraging windows with those from the optimal foraging window. This comparison was used to explore the fitness buffer capacity of an adaptive foraging window as opposed to a mal-adaptive or fixed foraging window.

**Parameterisation:** Model parameterisation was carried out for an adult female of length 13 cm and weight 6 g, and was based on a combination of values from the literature and experimental studies conducted on *Ammodites tobianus* as part of this study. A detailed description of the parameterisation and experimental measurements of stomach evacuation rate, stomach capacity, and swimming metabolism is given in Supplement 1, and Table 1 provides an overview of selected parameter values.
RESULTS

The model was analysed both numerically and analytically. The sections below contain the numerical exploration with application to lesser sandeels. By imposing certain simplifications on the model, it was also possible to perform analytical exploration of the model; the highlights are presented here and the detailed analytical results are provided in Supplement 2 at www.int-res.com/articles/suppl/m416p201_supp.pdf. The aim of the analytical approach was to verify that the findings were not just the result of the chosen parameterisation but were valid in general, and to obtain a deeper insight into life strategy trade-offs.

General patterns and the effect of elevating winter prey abundance (background food-level)

The model predicted that the optimal foraging window was more or less symmetrically distributed around the Gaussian zooplankton spring burst curve, albeit considerably narrower (Figs. 1 to 3). The timing of the optimal foraging window remained more or less the same when winter prey abundance (background food level) supported a daily consumption of one third of the consumption during the zooplankton spring burst (Fig. 1C). The end and beginning of the overwintering period depended on a combination of the entire annual foraging history (including accumulation of mortality), and not on a threshold daily surplus energy gain. For example, when the zooplankton spring burst was spread out over a longer period, by increasing the standard deviation, the model predicted that sandeels will initiate the foraging window earlier (and end it later), and at lower daily surplus energy gain (Fig. 2).

Exactly how the optimal trade-off was determined between feeding- and mortality-related aspects was elucidated by mathematical analysis of Eq. (11). The analysis confirmed that the optimal foraging window was distributed symmetrically around the zooplankton spring burst (and the minor asymmetry explained by the phase lag between temperature and zooplankton productivity). Further, the analysis revealed that 2 fit-

Fig. 1. Ammodytes marinus. Optimal foraging window in relation to food regime. (A) Daily total prey encounter (given in hundreds of prey items per day) for 3 different zooplankton spring burst intensities as a function of time of the year. (B) Onset (dotted) and offset (solid) of the optimal foraging window as a function of relative spring burst intensity. The vertical lines refer to the graphs in (A). (C) Onset (dotted) and offset (solid) of the optimal foraging window as a function of background food-level (values on the x-axis are the winter prey abundance relative to spring burst peak abundance, as %). (D) Annual survival probability (P, solid) (%) and annual surplus energy gain (G, dashed) (kJ) as a function of spring burst intensity. In all simulations an hourly arena mortality and refuge mortality of 1 × 10⁻³ and 1 × 10⁻⁵, respectively, were used.
ness regimes were possible. In Type 1 situations, $R_0$ always exhibits a single optimal overwintering period. Type 1 situations are characterised by a seasonal pattern, where consumption minus energetic cost of foraging is negative in a period during the winter. If consumption minus energetic cost of foraging is positive all year round, it is a Type 2 situation, where it is possible that overwintering is skipped if the arena mortality $Z_A$ is sufficiently low. We have not found Type 2 situations in biologically relevant parameter regimes for lesser sandeels in the North Sea, but they may exist for other species resembling the sandeel ecotype. Even though the model always predicts a single optimal overwintering period, the mathematical analysis also reveals a range of mortalities so high that fitness in the demographic equilibrium falls below 1. This is due to the fish size-determined upper limits on fecundity; see Supplement 2 for technical details of the mathematical analysis.

Effect of the intensity and duration of the zooplankton spring burst

Reducing the duration or increasing the intensity of the zooplankton spring burst resulted in reduced duration of the optimal foraging window (Figs. 1B & 2). However, there was a maximum level of spring burst intensity above which the optimal foraging window remained at a constant duration despite further increase in spring burst intensity (Fig. 1B). This maximum level was determined by daily total consumption shifting from being limited by prey encounter rate to being limited by stomach capacity and evacuation rate.

At low intensities of zooplankton spring bursts the distribution of daily prey encounters followed the
Gaussian spring burst curve, and hourly prey encounters was the limiting factor on consumption. However, at high burst intensities consumption became limited by stomach evacuation (E) and day length (τ), thus the full potential of the spring burst was not utilised (note the flat top on the upper 2 curves in Fig. 1A).

Increased intensity of the zooplankton spring burst resulted in increased surplus energy gain (G) and survival probability (P) values. However, G levelled off when daily total consumption became limited by stomach capacity (Fig. 1D,B). In the lower range of spring burst intensities, the increase in P was due to the reduction in the duration of the optimal foraging window. In contrast, in the upper range of spring burst intensities, an increase in P was caused by the high prey abundance leading to a reduction in the number of hours spent in the arena per day (Fig. 4B; note the dip in hours spent foraging per day; black dash-dotted line).

Effect of mortality

The duration of the optimal foraging window depended on mortality in both the arena and refuge. An increase in Zₐ resulted in a decrease in the duration of the optimal foraging window. In contrast, the duration of the optimal foraging window increased slightly when Zₐ/Zₐ was increased from 0.01 to 0.1 (Fig. 3A), and the onset and offset shifted to earlier in the year, by approximately 1 wk, when Zₐ was scaled with temperature (Fig. 3B). The reduction in P following elevated arena mortality was highest in the lower range of arena mortality and levelled off toward the upper range (Fig. 3C). In contrast, G decreased more or less steadily as arena mortality increased.

Daily processes of importance

When the zooplankton spring burst intensity was high, the top of the distribution of daily surplus energy uptake became flat and slightly tilted (Fig. 1A). The daily processes involved were explored more thoroughly in a scenario of a long lasting, high intensity spring burst. The foraging window was centred symmetrically on the zooplankton spring burst and was considerably narrower than the flat tilted top of daily surplus energy uptake (Fig. 4A).

Warmer water increased metabolism as well as stomach evacuation rate (Fig. 4B), and in combination with increasing day length, the daily energy uptake more than outweighed the expense of increased metabolism. Based on this, one may expect that the optimal foraging window should be shifted to later in the year. However, the individual also spent more hours foraging in the arena as days became longer (Fig. 4B, grey dashed line), which in turn increased the daily accumulated mortality and, therefore, shifted the optimal foraging window to earlier in the year. This is illustrated by comparing the default scenario (Fig. 4A, black line) to a scenario where daily mortality is constant instead of being dependent on the hours spent foraging (Fig. 4A, grey line).

Fitness buffer capacity and mismatch between foraging window and zooplankton spring burst

We calculated R₀ for the optimal foraging window for both a high and a low zooplankton spring burst intensity (using intermediate Zₐ). We then either shifted timing of the foraging window (Fig. 5A) or reduced/expanded it (Fig. 5B) and calculated the associated values of R₀. We found that a 14 d mismatch between the centre of the foraging window and the peak of a

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Fig. 4. *Ammodytes marinus*. Behavioural and physiological control of the optimal foraging window during a high intensity and long-lasting zooplankton spring burst. (A) Onset (dotted lines) and offset (solid lines) of the optimal foraging window as a function of hourly mortality in the arena (Zₐ) for the default scenario (black) and a scenario in which daily mortality is constant (12 × Zₐ) and is thereby independent of the number of hours spent foraging in the arena (grey). Hourly arena mortality = 1 × 10⁻³; hourly refuge mortality = 1 × 10⁻⁵. (B) Water temperature (°C) (solid grey); time spent in the arena per day (h) (grey dashed); daily surplus energy uptake (kJ) (black dashed); daily metabolic cost of foraging including standard metabolic cost (kJ) (black dash-dotted)
low intensity spring burst (in either direction) resulted in ~20% reduction in $R_0$, and a 25 d mismatch resulted in ~50% reduction in $R_0$ (Fig. 5A). The fitness loss of a temporal mismatch was lower for the high burst intensity (Fig. 5A). Both contraction and expansion relative to the optimal foraging window also resulted in notable reduction of $R_0$. High contraction of the foraging window eventually lead to negative fitness, which means that the metabolic cost of overwintering exceeded surplus energy gain during the foraging period.

**DISCUSSION**

To facilitate an investigation of the energy/predation trade-off in the context of the overwintering strategy of sandeel ecotypes, we developed a simple model framework that linked behaviour, mortality and bioenergetics. We demonstrated that the optimal solution to these 2 decisions was determined by an energy/predation trade-off, and found that the overwintering strategy remained the optimal strategy even when winter prey availability supported the energetic cost of foraging many times. We also found that food regime and hourly mortality affected the timing of the optimal foraging window.

In the present work, we did not include interannual variability in abiotic conditions, as we wished to understand the link between regimes of abiotic conditions and differences in the optimal overwintering period, with the aim of understanding local adaptations as well as expected responses to anthropogenic and climate changes. Furthermore, timing of the spawning window was fixed at January 1 in the present work assuming it to be determined solely by hydrographical properties ensuring maximal larval retention rates. A complete life history investigation should also consider optimisation of the spawning window and inter-annual variability in abiotic conditions; because an optimal life strategy corresponding to an average regime of abiotic conditions may become suboptimal when facing inter-annual fluctuations. Our model can certainly be extended to include stochastic fluctuations, thereby addressing a stochastic optimisation problem, but this is beyond the scope of the present work.
Lesser sandeels make both seasonal and diurnal shifts between the pelagic feeding arena and being buried in the sandy sediments. Commercial landing data strongly suggest that the seasonal foraging window for adults lasts for only 2 to 4 mo during spring, with a peak in activity around May. This distinct pattern is reflected in both the fishery and in the diets of their predators (Macer 1966, Winslade 1974a, Reeves 1994, MacLeod et al. 2007). The timing and extent of the foraging window seem to vary slightly from year to year and from region to region (Macer 1966, Winslade 1974a, Reeves 1994, Sharples et al. 2009). Furthermore, lesser sandeel juveniles (mainly age-0 and age-1) have a prolonged feeding period compared to adults (Macer 1966, Reeves 1994, Hamer et al. 2000, Kvist et al. 2001). This pattern finds further support in a study of the sandeel-eating shag Phalacrocorax aristotelis, which showed that intense feasting on sandeel continued until at least October in years where juvenile sandeels were the most abundant item in the diet, whereas in years where adult sandeel dominated the diet, feeding activity concentrated around April (Harris & Wanless 1991). It has been suggested that prey concentrations, light intensity, day length and temperature determine the shifts between overwintering period and foraging period (Winslade 1974a,b,c).

In agreement with the published data, the general trends that emerged from the present model simulations predicted that adult lesser sandeels should only forage during the peak period of the zooplankton spring burst and spend the rest of the year overwintering submerged in the seabed. Simulations were based on general and schematic representations of temperature and prey availability, as the main aim of the study was to understand the generic links between the seasonal environment and overwintering from an energy/predation perspective, rather than attempting to forecast geographical patterns in the North Sea. However, Winslade (1974a) presented data for the southern North Sea of monthly prey availability, sea temperature and commercial sandeel landings from before the sandeel fishery became strictly regulated by quotas and seasonal constraints. When these environ-

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**Fig. 6. Ammodytes marinus.** Fitness buffer capacity in relation to changes in predation mortality and zooplankton spring burst intensity. Fitness (plotted as relative values) as a function of (A) hourly mortality in the arena and (B,C) spring burst intensity for an adaptive case where the foraging window is adapted optimally (grey) and for a fixed case where the foraging window is held fixed while spring burst intensity or mortality is varied (black). The vertical dashed line is the starting point at which the foraging window of the fixed case is optimal. This starting point is the only difference between (B) and (C). In (A), the exercise was carried out for low spring burst intensity (thin black line) (corresponding to the lowest daily prey encounter graph in Fig. 1A) and high spring burst intensity (thick black line) (corresponding to the highest daily prey encounter graph in Fig. 1A). The ranges of spring burst intensities in (B) and (C) correspond to the range used in Fig. 1B. An hourly arena mortality ($Z_A$) of $1 \times 10^{-3}$ was used in (B) and (C) and an hourly refuge mortality of $1 \times 10^{-5}$ was used in (A), (B) and (C). Note: $Z_A = 1 \times 10^{-3}$ results in an annual mortality that roughly corresponds to the annual mortality applied in the North Sea sandeel assessment (ICES 2007).
mental data were used in the model the predicted foraging window enveloped 70% of total sandeel landings (Fig. 7).

In the present study a constant hourly arena mortality of approximately $1 \times 10^{-3}$ (and a refuge mortality vs. arena mortality ratio of $1 \times 10^{-2}$) was used in all analyses where mortality was kept constant. At this level of hourly mortality, the model estimated annual survival probability to be roughly 50%, which resembles the annual mortality of 0.6 estimated for lesser sandeels in the North Sea for age 2 and older (ICES 2007). In reality, daily predation risk presumably fluctuates over the year. Firm measures of intra-annual fluctuations in mortality were not available, and inclusion of a sub-model of seasonal variation in mortality would involve a detailed analysis of the evolutionary processes related to the close interactions and multiple feedback pathways between prey and predator(s) as well as the assemblage of alternative prey from which the predators can choose at a given time of the year. This was therefore not considered to be within the scope of the present study. However, as roughly 90% of the predators on lesser sandeels in the North Sea are poikilotherms (Furness 2002), a first step towards introducing seasonal variation in mortality to the model would be to assume that mortality due to consumption of sandeel by fish predators is limited by the temperature-dependent stomach evacuation rate of the predator. Results presented here suggest that scaling mortality with temperature has a slight effect on the outcome of the model as it moves the foraging window to slightly earlier in the year.

The total energy content of a 13 cm lesser sandeel in July–August is approximately 50 kJ, and 85 kJ for a 15 cm lesser sandeel (Hislop et al. 1991, Pedersen & Hislop 2001). Assuming that 60% of this energy can be mobilised (Hislop et al. 1991), these values conform to the values of annual surplus energy gain predicted for sandeel at the lower range of zooplankton spring burst intensities (or high population densities leading to intra-specific competition for food).

### Energy/predation trade-off in general

The majority of previous studies of the energy/predation trade-off in fish, and animals in general, have focused on short-term processes (daily or hourly timescales, as opposed to the annual time-scale addressed in the present study) such as diel vertical migration, and ontogenetic or state-dependent diurnal decisions regarding habitat choice and foraging activity (e.g. Lima & Dill 1990, Houston et al. 1993, Burrows 1994, Railsback et al. 1999, Biro et al. 2003, 2006). Those studies show that the optimal behavioural response to increased predation mortality is to reduce foraging activity, given that foraging activity is proportional to the mortality and a critical minimum energy uptake is not compromised. This agrees with our predictions, despite the difference in the time-scale at which the trade-off was addressed. Fish studies investigating the energy/predation trade-off on an annual time-scale are much rarer. A field study utilising data from passive integrated transponder (PIT)-tagged roach *Rutilus rutilus* and their main predators (*Esox lucius* and *Perca fluviatilis*) indicated that roach make seasonal migrations between habitats in order to minimise the ratio between predation mortality and growth rate (Brönmark et al. 2008). Related model studies have focussed on diel vertical migration of copepods using a state-dependent approach and dynamic programming framework to identify the optimal annual behavioural and reproductive strategy (e.g. Fiksen & Carlotti 1998). Dynamic programming techniques are, in many ways, a more advanced approach to solving complex optimality problems. However, it is also far more difficult to interpret the results from such models, and a comparison of the fitness from the optimal strategy to that of sub-optimal strategies is difficult if not impossible to conduct. Furthermore, by imposing certain simplifications, it was possible to solve the present type of model conceptually and analytically. This helps to identify which features and properties of the results are generic and whether other types of results are possible.

![Fig. 7. Ammodytes marinus. Onset and offset (vertical grey lines) of the optimal foraging window compared to monthly North Sea sandeel catches from before the fishery became strictly regulated. Catch data (black solid line; percentage of total annual catch), temperature (grey solid line; °C) and copepod index (dashed line; number of copepods per sample) reported by Winslade (1974a) were used to force the model (the original copepod data are from Colebrook & Robinson 1961). Before using the copepod index in the model, values were raised so that peak abundance in June corresponded to a daily total prey encounter of 700. Annual survival probability was 50%, which resembles the mortality applied by ICES for adult sandeels](image-url)
Daily processes

Using a mechanistic model of the ingestion rate of Norwegian spring-spawning herring *Clupea harengus*, Varpe & Fiksen (2010) show that high latitude seasonality in day length and light regimes may be more important in determining the onset of the foraging window than the exact timing of the zooplankton spring burst. A similar pattern arose from the present model. Here, hourly prey encounters reached their seasonal maximum when the spring burst peaked. However, water temperature and stomach evacuation rate were still low and day length still relatively short. Maximum daily total consumption was therefore reached later than the peak in the zooplankton spring burst. The question of whether it is better to forage during times when total daily consumption is maximised or during times when the hourly prey encounters are maximised therefore depends on whether daily mortality is constant or proportional to hours spent foraging. If daily mortality is proportional to the number of hours spent foraging (which is how the model here implemented mortality in the default settings), then the daily mortality becomes inversely proportional to the hourly prey encounters as long as maximum stomach capacity is not reached. However, when consumption shifted from being limited by prey encounter rate to being limited by stomach evacuation rate, daily mortality became dependent upon day length. It seems reasonable to assume that daily mortality is proportional to hours spent foraging. It could however be speculated that sandeels are more vulnerable during the emerging and burying phases, and during the vertical migration in the morning and afternoon/evening, as indicated by some field observations (Hobson 1986, Darbyson et al. 2003, Temming et al. 2004, Engelhard et al. 2008).

Behavioural plasticity and fitness benefits of adapting to environmental changes

Behavioural plasticity can be a result of adaptations to local environmental conditions driven by natural selection of genotypes in the population (adaptations on the population level) or can be a result of phenotypic plasticity (adaptations on the individual level) (e.g. Via & Lande 1985, Kawecki & Ebert 2004). In contrast, when the individual perceives its surroundings, processes the information, and acts accordingly and momentarily, we often use the term adaptive decision-making instead (e.g. Lima 1998).

We know that a range of behaviours may have fitness comparable to that of the optimal behaviour (Mangel 1991). In the present study, we found that the fitness-related advantage of adapting the timing of the foraging window to differences in predation mortality (and/or fishing mortality) is very small, even when mortality during the foraging period increases or decreases many-fold. The minor fitness advantage of adapting indicates that, at the population level, adaptations to local environmental conditions are possible only if mortality rate is relatively stable on an evolutionary time-scale.

The fitness-related incentive for an adaptive response to differences in zooplankton spring burst intensities (or intra-specific competition for food) was not entirely clear. Even though there seemed to be a considerable fitness-related advantage of adapting overwintering behaviour according to a decrease in spring burst intensity, the relative advantage of adapting to an increase in spring burst intensity was very small. It therefore seems reasonable to assume that the optimal behaviour during low spring burst intensities is a stable optimal strategy. However, it may be that with very high consumption, reserves and growth become saturated and sandeels would benefit, in terms of fitness, from starting the overwintering phase earlier than predicted by the model.

The present study showed that inability to adjust the timing of the foraging window to variation in the timing of the zooplankton spring burst would have a large negative effect on fitness. Expanding the foraging window to increase the probability of capturing the spring burst and thereby avoid mismatch is not an optimal solution to the problem, since fitness decreased rapidly when the foraging window covered periods outside the spring burst, including its tail end. Considering this large fitness-related incentive of adapting the foraging window to the spring burst timing, it seems possible that local adaptations or phenotype plasticity could have evolved. For adaptive decision-making to have evolved, the individual needs ways to perceive the advancement of the spring burst and its fading out. The existence of such abilities remains an open question.

Perspectives

The lethal aspects of predator–prey interactions, and their implications for population dynamics and ecosystems, are indisputably crucial and relatively well understood. However, the implications and quantitative importance of behaviourally mediated population responses of predator–prey interactions, the non-lethal aspects, are still poorly understood (Lima & Dill 1990, Lima 1998, Dill et al. 2003). From this perspective, the simple type of model framework presented here offers an analytical tool to interpret observations and formu-
late testable hypotheses regarding the overwintering strategy and zooplankton burst-directed foraging activity. The model produced general patterns of behaviour, bioenergetics and mortality related to lesser sandeels in the North Sea, while at the same time illustrating how sandeels trade off energy gain maximisation for mortality reduction on an annual time-scale.

An important finding was that the precise level of mortality and energy gain rates had little influence on the foraging activity level. However, this does not imply that predation mortality and anticipated energy gain do not influence the behaviour of lesser sandeels. On the contrary: the cost of predation related to foraging activity is what led to the predictions that all foraging activity should strictly coincide with the peak period of the zooplankton spring burst. Inter-annual shifts in the timing of the spring burst could therefore cause the size of succeeding year-classes and spawning stock size to fluctuate, in particular when the population is below carrying capacity.

The notion that timing and intensity of the zooplankton spring burst have substantial effects on population dynamics of lesser sandeels has recently been proposed in a study on the timing of reproductive allocation in this species (Boulcott & Wright 2008). It is also known that spring burst timing exhibits regional differences, inter-annual fluctuations and climate-induced long-term shifts within ecosystems populated by sandeels (e.g. Brander 1994, Edwards & Richardson 2004, Greenstreet et al. 2006, Sharples et al. 2006). Understanding how sandeels, as a key mid-trophic species and an important commercial resource, cope with this variability is essential for understanding population dynamics both in the present time and in projections of climate change scenarios. We propose that the type of model presented here can play a role in this context, although we admit that focused field studies are required to confirm for example the adaptive capabilities of sandeel.

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Overwintering strategy of sandeel ecotypes from an energy/predation trade-off perspective

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Supplement 1. Parameterization of the model

Consumption (ε: Eq. (1), V: Eq. (3), and a, b: Eq. (4))

Specimens of small sandeel *Ammodytes tobianus*, a close relative of lesser sandeel *A. marinus*, were caught by seine and held in a 300 l tank with a 5 cm layer of sand on the bottom. Fish were starved for at least 72 h prior to each experiment. On the day of the experiment, fish (ranging from 10 to 13 cm in total length) were fed a number of meals consisting of thawed *Artemia salina* over a period of 1.5 h to ensure that the fish had reached satiation. This was necessary, since it turned out that the oesophagus constituted a bottleneck, which expressed itself as a reduction in willingness to take food after each meal. The time halfway through this feeding period was defined as the time zero of the experiment. After feeding the fish to satiation, 8 fish were removed every 3 to 4 h for the subsequent 48 h and killed by a blow to the head. All sampled fish were cut open and the stomach was removed and weighed (wet weight, WW) and the total fish length was measured. This experimental procedure was carried out at 5, 10 and 17°C. Fish were acclimatized to the temperature for at least 3 wk prior to each temperature experiment.

At the beginning of the experiment (just after feeding to satiation), the 2 fullest stomachs from each half-centimetre group (fish of length 10 to 13 cm) were selected, and the weights of these were plotted against total fish length. The relationship was best described with a linear regression model of the form:

\[ \text{Maximum stomach content (g, WW)} = 0.17 \times \text{total fish length (cm)} - 1.28 \left( R^2 = 0.74 \right). \]

Relative stomach fullness was calculated by dividing the weight of the stomach content with the length-specific maximum stomach content, as derived from the above linear relationship. A multiple linear regression model of the form: \( \ln(\text{relative stomach fullness}) = \text{time since feeding (h)} \times \text{temperature (ºC)} \) was fitted to the data (estimated coefficients were highly significant, \( p > 0.001 \)). From this fit, we derived coefficients \( a \) and \( b \) for Eq. (4): \( a = -2.7 \times 10^{-2} \) and \( b = -3.6 \times 10^{-3} \).

During a previous study (authors’ unpubl. data) more than 1000 sandeel stomachs from various locations in the North Sea were analysed, and the stomach content was found to consist predominately of copepods (at a few locations Larvacea were the dominant prey items). Based on this observation, a homogenous diet consisting of adult copepods was assumed in the model. Comita et al. (1966) reported that the
caloric content of adult *Calanus finmarchicus* ranged from 21 to 35.2 kJ g\(^{-1}\) of ash-free dry weight (DW). Using the midpoint of this range, 28.35 kJ g\(^{-1}\), a WW:DW ratio of 5 (Yamaguchi & Ikeda 2000) and a weight of 500 µg (WW) for an adult copepod (Gentleman et al. 2008), the energy content of 1 prey item was calculated to be 33.5 \(10^{-4}\) kJ. Consequently, assuming that 30% of the energy of ingested food is lost to excretion, egestion and specific dynamic action (SDA) (e.g. Ciannelli et al. 1998), \(\varepsilon\) in Eq. (1) was set to 23.5 \(10^{-4}\) kJ.

Using the above derived model for maximum stomach content and a weight of 500 µg for an adult copepod, stomach capacity \(V\) in Eq. (3), for a 13 cm sandeel, was estimated to be 1860.

**Energetic cost (\(R_A\): Eq. (7) and \(c, d\): Eq. (8))**

Specimens of small sandeel were caught by seine and held in a 1500 l circular holding tank with fully oxygenated and recirculated seawater. A tube was placed in the centre of the tank. Fish in the tank emerged from the sand when light came on in the morning and swam unidirectionally as a school around the tube during all active hours of the day, until they once again buried into the sediment in the afternoon. Swimming speed was frequently measured at various times of the day at 5 and 10\(^{\circ}\)C. The observed swimming velocity was assumed to resemble routine or preferred swimming velocity during foraging. With the exception of the late afternoon, just before burying, the fish swam at a velocity of \(~1.5\) body lengths per second, and there was no significant temperature effect.

In order to measure the energetic cost of routine swimming velocity, fish were swum, 10 at a time, in a circular respirometer, at 10\(^{\circ}\)C and without sand. Water in the circular swimming lane (height: 9 cm; width: 7.5 cm; average diameter: 32.5 cm) was pumped around to create a current within the respirometer. The water velocity was carefully measured (flowmeter from Höntzsch) at 9 different positions in each of 14 equally spaced cross sections of the swimming lane, to account for the velocity gradient. Fish maintained their position in the respirometer, except when they occasionally stopped swimming momentarily and drifted down-current to a new position. The flow velocity was therefore assumed to approximate the swimming velocity of the individual fish. The pump generating the water current was adjusted so that the fish approached the routine swimming velocity (\(\pm 0.1\) body lengths per second) measured in the holding tanks. The experiment was replicated 4 times at 10\(^{\circ}\)C, each time using 10 new fish that were starved for at least 48 h prior to each experiment. The measuring procedure and energy cost calculations were adopted from Behrens & Steffensen (2007), except this time the measuring period lasted 24 h and consisted of 20 min of flushing and 30 min of continuous measuring.

The energetic cost explicitly related to swimming was derived by subtracting the standard metabolic cost for buried sandeels at 10\(^{\circ}\)C from the energetic cost measured for swimming fish at the same temperature. This resulted in \(R_A = 33.9 \times 10^{-4}\) kJ g\(^{-1}\) h\(^{-1}\) (the average of the experimentally measured values). We made the assumption that the energetic cost of swimming at routine velocity was independent of temperature (as long as velocity is independent of temperature) as reported by, for example, William & Beamish (1990).

The fitted coefficients \(c\) and \(d\) in Eq. (8) (standard metabolic cost for 1 g of buried sandeel as a function of temperature) were provided by M. van Deurs (pers. obs.): \(c = 0.08\) and \(d = 0.25\).
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Supplement 2. Analytic solution and properties of the model

By imposing certain simplifications on the model, it is possible to solve it conceptually and analytically, which aids understanding of the patterns in the simulations. For example, it helps to identify which features and properties of the results are generic for the ecotype described by the model, and which ones are associated with the particular parameterization for the North Sea sandeel, and whether other types of results are possible for this ecotype or not.

The key approximation is averaging intake and consumption over the innermost time scale, i.e. the intraday cycle, which covers the day–night cycle and the detailed stomach evacuation dynamics. By doing this, the daily bioenergetic budget becomes dependent on the external conditions, and the state variables (e.g. instantaneous stomach fullness) associated with stomach evacuation dynamics become hidden and replaced by the average expected bioenergetic response to external conditions. In this approximation, the energy assimilation rate $\gamma$ (if foraging) is:

$$\gamma(r, T) = S(r, T) - m_A \left( \frac{1}{r} \right)$$

$$\gamma(t) = S(r(t), T(t)) - m_A \left( \frac{1}{r(t)} \right)$$

$$r(t) = \frac{v_{swim} f(t) \tau(t)}{n_o(T)}$$
where $S$ is the functional response-modulated uptake function effectively associated with this bioenergetic model, and $m_A$ is the cost of movement per time in relation to foraging (and temperature $T$). The key variable is $r = \frac{v_{swim}}{\tau/n_0}$, which is the potential food intake rate (the average total number of encountered prey) divided by the food intake index $n_0$ (which can be thought of as the cost of resting metabolism recalculated to number of prey per day), so that $r > 1$ means the fish is in a consumption-limited regime, whereas $r < 1$ means the fish is in a feeding rate-limited regime. Conversely, the ratio $1/r$ is a proxy for the activity level of the fish (if still foraging), and when $1/r \gg 1$, the fish is expected to be active with a high $v_{swim}$ for all of the daylight window $\tau$, saturating $m_A$ expenses, whereas $1/r < 1$ reduces $m_A$. Eq. (S1b) shows how the time-dependent function $\gamma(t)$ is constructed, and when and how much the actual forcing functions affect assimilation. The function $\gamma(t)$ will be a sinusoidal-like function with maximum in the summer time (in the Northern hemisphere). The function $\gamma(t)$ will have a trough in the winter time, where $\gamma(t)$ may become negative, in which case there is no energetic incentive for feeding in this period.

When averaging over the daily time scale, we can also apply an integral formulation of the energy budget, which simplifies the analysis. If the yearly active period is $[t_0; t_1]$ we obtain the total yearly energy surplus:

$$F(t_0, t_1) = \int_{t_0}^{t_1} \gamma(t) dt - M_0$$

(S2)

where $M_0$ is the yearly total resting metabolic cost. The energy surplus $F$ is invested in reproduction and contributes to the net lifetime reproduction. As shown in the introduction, the question about optimal overwintering strategy is now reduced to a relative simple optimization problem of the function:

$$R(t_0, t_1) = \omega \frac{FP}{1-P}$$

(S3)

where $\omega$ aggregates survival to adulthood and adult competition (food/habitat) effects, and $P$ is the probability of surviving 1 yr with the given foraging strategy. Straightforward optimization ($\partial R = 0$) of Eq. (S3) gives the result:

$$\begin{align*}
\gamma(t_0) &= \gamma(t_1) \\
\phi(t_0) &= \alpha(t_0)
\end{align*}$$

(S4)

where:

$$\begin{align*}
\phi(t_0) &= \frac{\gamma(t_0)}{F(t_0, t_1(t_0))} \\
\alpha(t_0) &= \frac{\Delta Z}{1-P(t_0, t_1(t_0))}
\end{align*}$$

(S5)

Eq. (S4) is a neat result: it tells us that the active period is $[t_0; t_1]$ is bounded by time points with the same assimilation potential $\gamma$; so if we know the starting point $t_0$, from a diagram of $\gamma(t)$, we can also find the ending point of the active period, indicated by $t_1 = t_1(t_0)$ in the following equation. The second equation is also neat: it tells exactly how the optimal trade-off is determined between feeding-related aspects ($\phi$) and
mortality-related aspects ($\alpha$). A little further algebra (following the second derivative of $R$) gives the condition for a maximum as:

$$\frac{\partial \phi}{\partial t_0} > \frac{\partial \alpha}{\partial t_0}$$

(S6)

at the maximum of $R$. This constitutes the basic analysis of the bioenergetic model.

**Fig. S1** Graphical illustration and interpretation of solving Eq. (S4) for the optimal overwintering strategy. The abscissa $t_0$ shows the starting point of the active period. The point OLS indicates the optimal life strategy solution.

Fig. S1 illustrates the solution of Eq. (S4). The analysis splits into 2, depending on whether the assimilation potential $\gamma(t)$ is positive (right column) or negative (left column) at some time in the winter period. The upper row shows how the feeding-related function $\varphi(t)$ is constructed in both cases. If the active period starts very late (large $t_0$) the function $F$ becomes negative: the fish is simply not able to cover the resting metabolic costs. When $t_0$ is moved back (i.e. longer feeding period), $F$ increases. At a certain point—the ‘break-even point’ ($t_0^*$), $F = 0$ and the fish is just able to cover basic metabolic costs, but without energy for reproduction. Moving $t_0$ further back makes $F$ positive. The lower row shows $\varphi(t)$ constructed from $\gamma$ and $F$ in the upper row for both types. The major difference between Type 1 and 2 is that the root of $\gamma$ leads to a root for $\varphi$ for Type 1, whereas $\varphi$ for Type 2 ends at a positive
value at point A (lower left, where the active period covers all year). Simple arguments show that $\alpha(t_0)$ is a monotonously increasing function of $t_0$, as sketched in the figure. This implies that Type 1 always has a single optimal overwintering strategy, for any mortality and feeding level. For Type 2 there is only an overwintering period if $\alpha(t)$ crosses $\varphi(t)$ (solid curve $\alpha$). If $\alpha(t)$ creeps below $\varphi(t)$ (dashed curve $\alpha$), no overwintering period is predicted at all. This happens, if the arena mortality is very low (i.e. very low $\Delta Z$). The transition happens, when $\alpha(t)$ crosses the point A in the lower right figure.

When the analysis above gives a true maximum of Eq. (S3), $R(t_0, t_1)$, one further condition must be assured, namely that $R(t_0, t_1) > 1$; in that case population density effects will downregulate $\omega$ by increasing the population size, so that eventually $R(t_0, t_1) \sim 1$, and the population is stable (or quasistable). $\omega$ is a decreasing function of the population density; this means that it has an upper bound $\omega_0$. Therefore, if a (quasi)stable population should be attainable by self regulation, the following condition must also be fulfilled:

$$\omega_0 > \frac{1 - P}{FP} = \eta(t_0) \quad \text{(S7)}$$

at the maximum of $R$; otherwise the population will eventually become extinct. This will be the case in Fig. S1 (lower left) with sufficiently high fishing pressure (large $\alpha$). Thus Eq. (S7) introduces the extinction function $\eta(t_0)$, where $t_1 = t_1(t_0)$ has been applied again. The biological interpretation of Eq. (S7) is also clear: if the surplus on the bioenergetic budget is low ($F$ small or negative) or if the yearly survival chance is low ($P$ low), population density effects are not able to reinstate the population level. The resilience capacity $\omega_0$ of the ecotype is given by the biology of the species and the ecosystem hosting the ecotype.

**Fig. S2** The generic form of the extinction function $\eta(t_0)$, which can take either of the 2 curve forms indicated
Based on Fig. S1, the generic form of the extinction function $\eta(t_0)$ can be sketched, as shown in Fig. S2 above. The sketch applies to both Types 1 and 2 introduced in Fig. S1. Generally, $\eta(t_0)$ diverges as $t_0$ approaches the bioenergetic ‘break even point’ $t_0^*$ (because $F$ approaches zero), where feeding just balances basic metabolic costs; this means Eq. (S7) always lowers the actual ‘break even point’. Depending on the actual curve shape in Fig. S2 and the actual resilience capacity $\omega_\alpha$ of the ecotype, Eq. (S7) may also make very long active periods unsustainable on the long term (even though they correspond to a maximum of $R$).

Finally, it is of interest to understand the potential impact of changed fishing mortality. Change in fishing mortality will influence the predicted optimal overwintering strategy by shifting $\alpha(t)$ up or down in Fig. S1. Simple differentiation and Fig. S1 show that

$$\text{sign}(\frac{\partial t}{\partial \Delta Z}) = \text{sign}(\frac{\partial \alpha}{\partial \Delta Z}) = \text{sign}(1 - P - \Delta Z(t_0 - t_1)P)$$

(S8)

In the biologically relevant parameter regime we always find that $\partial \alpha / \partial \Delta Z > 0$, so that isolated increased fishing mortality (increasing $\Delta Z$) always reduces the active foraging period by Eq. (S8) (and may further cause stock collapse, if Eq. S7 becomes violated). In fishery management contexts, Eq. (S7) can also be used as a device to estimate the proximity to stock collapse for this ecotype.