

Modeling early life history of cod

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Scientific environment

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A handwritten signature in blue ink, appearing to read 'Trond Kristiansen', with a stylized, cursive script.

Trond Kristiansen

Summary

Newly hatched Atlantic cod (*Gadus morhua*) larvae face an uncertain future when they first enter their marine pelagic habitat. Prior to complete yolk absorption, the larvae will have to find food. This process includes the visual encounter, pursuit and attack, and capture and digestion of the prey item for utilization to meet energetic demands for metabolism and growth. However, food is not always easy to find and it is essential for larval survival that they encounter habitats where prey are abundant, and that the prey are of edible size. Fast growth ensures short time as small vulnerable larvae in a marine habitat consisting of numerous predators.

This thesis emphasizes the use of individual-based models to explore and understand the various mechanisms that determine successful growth and survival through the early pelagic life stages of cod (*Gadus morhua*). We model larval feeding, growth, behavior, and survival, under various environmental settings at the spawning and nursery grounds along the coast of northern Norway and at Georges Bank located on the eastern coast of USA.

Paper 1 focuses on the assemblage of a mechanistic individual-based model (IBM) for larval and early juvenile cod, and the validation of the model by comparing observed and modeled data. Validation and forcing data consisted of biological and environmental data from a controlled environment (macrocosm). Larval cod are able to move up and down in the water column in a prescribed manner by following rules of behavior. Vertical behavior elevates larval growth rates, compared to growth achieved under random behavior. Maximum growth rates are achieved for larvae in environments where prey density exceeded $10 \text{ nauplii} \cdot \text{L}^{-1}$.

The implementation of vertical behavior in IBMs of larval fish was elaborated in Paper 2. Strong gradients in pelagic horizontal currents create different dispersal patterns of larval fish at different depths. This will in turn have strong effects on the integrated survival, growth, and dispersal of larval fish. Adaptive traits differ between individuals, are subject to selection, and have implications for the life history success of individuals, and emergent properties at the population level. Adaptive behavior in coupled IBMs and general ocean models can have significant impact on our understanding of life history traits of fish.

In Paper 3 we test various strategies for vertical behavioral in IBMs. We implemented vertical behavior as a property that emerges from the trade off between individual state (stomach fullness and size) and the local environment (prey and predators). A number of strategies were tested and all proved to increase survival probability drastically compared to individuals that moved randomly.

By implementing the vertical behavior as described in Paper 3 in an IBM, we are able to compare observations, and modeled feeding of cod larvae on zooplankton on Georges Bank, as described in Paper 4. The model predicts *Pseudocalanus* spp. to be the main prey item for larval cod because of its visibility of in the water column and its abundance. The preference for *Pseudocalanus* agrees with stomach observations.

The model also predicts *Centropages* to be an important prey item. However, with the exception of nauplii stages, *Centropages* is seldom found in stomach samples. *Centropages* may be inaccessible as a prey item because of their behavior or morphology.

In Paper 5 we couple an IBM with a three-dimensional ocean model (ROMS). Individual larval cod are allowed to migrate vertically following simple rules while being advected horizontally by the simulated currents. Larvae that differ in behavioral strategy are released at two major spawning grounds of Northeast Arctic cod, Vestfjorden and Moskenesgrunnen in Northern Norway (68°N) and tracked until size 18 mm. Behavior increased larval probability of survival compared to larvae passively drifting at fixed depths. Behavior influenced both the local depth distribution and the long-term horizontal distribution of larvae.

The coupled biophysical model is used in Paper 6 to explore the effect of light, prey density, temperature, and turbulence on larval growth of Northeast Arctic cod through the spawning season. Light has a severe impact on growth of small (5-7mm) larvae. Prior to mid April, larval growth is low because of the limited hours of light sufficient for feeding. After mid-April, the increase in day length enables high growth rates for both 5 and 7mm larvae as long as prey density exceeds $5 \text{ nauplii} \cdot \text{L}^{-1}$. This suggests that peak spawning time of Northeast Arctic cod occurs when light conditions are optimal for larval feeding and growth.

This thesis advocates the use of adaptive behavior as part of individual-based models for understanding the mechanisms that drive the dynamics and interactions between the ecosystem and its inhabitants. An IBM represents a practical and reliable tool to bridge the gap between physical oceanography and biology across a wide range of scales. Observations of the biological and physical structure of ecosystems provide data necessary for model validation, a requirement for making general ecological conclusions based on model results. In light of my work, I believe that this approach can reveal new information of life history traits of individuals and their consequences on population level, thereby increasing our understanding of ecosystems.

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List of papers

Paper 1

Trond Kristiansen, Øyvind Fiksen, and Arild Folkvord.

Modelling feeding, growth and habitat selection in larval cod (*Gadus morhua*): observations and model predictions in a macrocosm environment.

Accepted for publication in *Canadian Journal of Fisheries and Aquatic Sciences*.

Paper 2

Øyvind Fiksen, Christian Jørgensen, Trond Kristiansen, Frode Vikebø, and Geir Huse.

Linking behavioural ecology and oceanography: larval behaviour determines growth, mortality, and dispersal.

In revision.

Paper 3

Trond Kristiansen, Christian Jørgensen, R. Gregory Lough, Frode Vikebø, and Øyvind Fiksen.

Trading risk and growth: exploring behavioral rules of larval cod on Georges Bank. Manuscript.

Paper 4

Trond Kristiansen, R. Gregory Lough, Francisco E. Werner, Elisabeth Broughton, and Larry J. Buckley.

Modeling prey selection and growth of larval cod on Georges Bank.

Manuscript.

Paper 5

Frode Vikebø, Christian Jørgensen, Trond Kristiansen, and Øyvind Fiksen.

Drift, growth and survival of larval Northeast Arctic cod with simple rules of behaviour.

In revision.

Paper 6

Trond Kristiansen, Frode Vikebø, Svein Sundby, Geir Huse, and Øyvind Fiksen.

Growth and feeding of larval cod (*Gadus morhua*) in large-scale latitudinal environmental gradients.

Manuscript.

Introduction

”Nogen løsning av spørsmålet om fiskeriernes vekslinger engang for alle – ved en eller anden formel – lar seg ikke oppnaa, og enhver paastand om at ha naadd en slik løsning, vil ved nærmere prøvelse vise sig at tilhøre fantasiens verden.”

”Any solution to the variability in the fisheries once and for all – by some formula – is not achievable, and any assertion that a solution has been found, will by closer inspection, prove to belong in a world of phantasy.” (free translation)

Hjort (1914b)

For hundreds of years, fishermen have noted the large variability in the annual abundance of fish. Scientists have tried to explain why species of fish may explode in numbers one year, and be close to depleted the next year. So far, no single explanation has been found that solves the enigma of the variance in recruitment, however the problem is very much alive in scientific environments.

The ability to predict recruitment can have major implications for fisheries management and exploitation of commercial species, such as Atlantic cod (*Gadus morhua*). Spawning stock biomass was early on regarded as an indicator for the year-class strength, however with varying degree of success (Bradford & Cabana 1997). The spawner-recruit relationship assumes a correlation between recruitment biomass and the spawning stock biomass (SSB) or the biomass of eggs (E) (Marshall et al. 1998, Jennings et al. 2001). MacKenzie et al. (2003) examined the relationship between several decades of empirical data of SSB and recruitment of 20 different North Atlantic cod stocks. The authors revealed large inter-annual variability of SSB and recruitment that occurs within stocks and among stocks of different sizes. The variability that makes prediction difficult is due to mechanisms that act at the pre (*i*) and post-spawn (*ii*) stages:

i) Spawning stock biomass is not necessarily proportional to egg production since individual fecundity of females is proportional to length and condition (Marshall et al. 1998). The quality and number of eggs spawned increases with female condition and age (Kjesbu et al. 1992, Kjesbu et al. 1998), hence a population of mainly first-time spawners have less recruitment potential compared to a wide age and size structured population (Marshall et al. 1998). Spawner-recruit models try to reduce a multi-dimensional problem to 2 dimensions (SSB and recruitment), and tend to ignore variability in pre-recruit mortality. Consequently, the spawner-recruit approach fails to explain the large inter-annul variation that is caused by biological and environmental mechanisms and their interaction (Ulltang 1996).

ii) Egg quality (Marteinsdottir & Steinarsson 1998) and numbers (Marshall et al. 1998) combined with density-independent abiotic processes (e.g. Pepin et al. 1997) has consequences for larval hatching success and larval condition (Marteinsdottir & Steinarsson 1998). In addition, the environmental and biological conditions of the larval habitat may be of crucial importance for larval survival through the early life stages. In fact, the variety of processes that affect larval survival probability from the egg to the early juvenile stage is so important that the number of survivors is believed to have prognostic value for recruitment (Sundby et al. 1989). Predicting recruitment therefore requires an understanding of the early life stages of fish. What identifies survivors and what life history they have, may differ between ecosystems, between years, and between fish species.

Survival through the early life stages

Studies of the early life history of fish focus on ontogenetic changes and the interaction between the individual and the environment (Hunter 1981, Chambers & Trippel 1997). Many important biotic and abiotic mechanisms (e.g. temperature (Otterlei et al. 1999, Ottersen & Loeng 2000), light (Blaxter 1986), turbulence (e.g. Sundby et al. 1994, MacKenzie & Kiørboe 1995), prey abundance (e.g. Hjort 1914a, Cushing 1990), predation (e.g. Øiestad 1985, Bailey & Houde 1989) of importance

for survival and growth of larval and juvenile fish have been identified (ICES 1994, 2005). Still, only limited knowledge of their interaction exists (Nakken 1994, Ulltang 1996). For nearly 100 years, the early life stages of fish have received much attention from fisheries biologist that have explored possible correlations between early life stage abundance and recruitment strength and variability (Bailey & Houde 1989, Leggett & Deblois 1994, Nakken 1994). A range of hypotheses exist on explaining sources of mortality during early life stages and possible variability in survival to recruitment, and most are not mutually exclusive. Starvation was proposed by Hjort (1914a) to be the main source of mortality for first-feeding larval fish. Cushing (1990) (and references therein) extended the ideas of Hjort in his match-mismatch hypothesis, and proposed starvation as a significant mortality source for the entire pelagic phase of larval and juvenile fish. In addition to the hypothesis of Hjort (1914a) and Cushing (1990, 1996), several other theories exist that describe sources of mortality through the early life stages of fish. Physical conditions that retain early life fish in nursery habitats was highlighted by Iles and Sinclair (1982) in their member-vagrant hypothesis as a key element for survival. Physical properties of varying scale also modify the properties of a habitat such as aggregation of prey patches during calm wind events (Lasker 1975). Patches of prey increases the feeding incident while simultaneously decreases the activity level of larval and juvenile fish needed to obtain food. Reduced activity level is also believed to reduce larval conspicuousness to predators (Munk 1995, Skajaa et al. 2003). Encounter rate between predator and prey (Rothschild & Osborn 1988, MacKenzie & Kiørboe 1995) has also been recognized to increase in a dome-shape fashion (MacKenzie & Kiørboe 2000) with small-scale turbulence both in the laboratory (Kiørboe & MacKenzie 1995, MacKenzie & Kiørboe 1995) and in natural environments (Sundby & Fossum 1990, Sundby et al. 1994, Sundby 1995).

Despite good feeding conditions through the early life stages, survival is modified by mortality rates from predation (Øiestad 1985). Predation pressure varies between ecological systems both temporally and spatially (Garrison et al. 2000), and decreases with size (Folkvord & Hunter 1986, Miller et al. 1988, Bailey & Houde 1989,

Leggett & Deblois 1994, Houde 1997). Thus, the probability of survival through ontogenetic stages is closely related to growth rate (Hare & Cowen 1997), size (“bigger is better hypothesis”, e.g. Leggett & Deblois 1994), and consequently the duration of ontogenetic stages (Houde 1987). When grouped this is usually termed the “growth-mortality hypothesis” (Hare & Cowen 1997).

The mechanisms that regulate recruitment of fish are many and can vary within seasons, and between years among ecosystems and among their inhabitants. By incorporating currently identified mechanisms important to early life history of fish in individual-based models (IBMs), forced by realistic environmental conditions, we are able to study their relative importance and their interaction. Individual-based models relate the individuals to the environment so that properties and dynamics on population level emerge (Grimm & Railsback 2005). This thesis focuses on modeling the early life history of cod (*Gadus morhua*) during the transition from newly hatched larva to early juvenile with the intention of increasing our understanding on how processes at various scales may operate and differentiate larval cod growth and survival.

Fish species and stocks

Cod is a highly commercial fish species that lives in discrete stock units along the European coast from the Bay of Biscay to the Barents Sea, around Iceland, on the east and west coast of Greenland, and from Cape Hatteras to Ungava Bay along the east coast of USA (ICES 2005). This thesis focuses on two cod populations: the Northeast Arctic (or the Arcto-Norwegian) and the Georges Bank cod stocks. The Northeast Arctic cod (NA) is distributed throughout the Barents Sea. Mature individuals migrate to the Norwegian coastal areas as far down as 62°N to spawn (Fig. 1 **Paper 5**). The majority of eggs are found in the Lofoten areas (~68 °N) in the period from late February to early May (Pedersen 1984, Ellertsen et al. 1989). Eggs and larvae are then transported northwards with the ocean currents, away from the

spawning areas and into the nursery grounds in the Barents Sea. Pelagic juveniles settle to the bottom after 5-6 months (40-70-mm) (ICES 2005).

The Georges Bank cod stock is primarily resident (ICES 2005). Spawning takes place at the Northeast Peak on Georges Bank (Fig. 1 **Paper 3**) during November to May, with peak spawning during February and March (ICES 2005). Eggs and larvae drift southwesterly with the currents towards the Great South Channel, before they enter the nursery grounds on Georges Bank sometime during summer (Lough & Bolz 1989). Bottom settlement occurs at the size of 40-mm (Lough & Potter 1993).

Objectives

Modeling early life history of cod from the Georges Bank and Barents Sea dominates the main *objectives* of this thesis:

- Develop a mechanistic individual-based model for the early life history of cod based on first-principle physics and biology. Use empirical biological and environmental data to validate and force the model. Can the model reproduce observable patterns in real systems? How does larval behavior affect feeding, growth, survival, and interaction with the environment?
- Integrate the IBM with a general circulation model covering the habitat for the Northeast Arctic cod. How does the coupled model system predict larval growth under various environmental settings through the spawning season? What is the effect of behavior on survival and drift of larval cod?

Background

Computer models provide researchers with a convenient tool for exploring and understanding the processes of an ecosystem. Or as stated by Peck (2004); “*When a researcher builds a simulation model, they have created a world in which they have access to all of the laws and components of that world, and the relationships among those components.*” However, how can we model complex ecosystems?

Modeling individuals and populations

A population is a system of individuals that differ in genetics and environmental histories (Heath & Gallego 1997, Fuiman et al. 2005). Consequently, variations in phenotypical traits such as behavior, growth, size, condition, and survival arise (**Paper 2**, Grimm & Railsback 2005). An important step towards understanding properties at the population level is therefore to recognize that individuals have different traits. The integrated interactions and properties at the individual level, defines the dynamics and properties at the population level (Grimm & Railsback 2005). These properties are not present at the individual level, but emerge from interactions among individuals and the environment (Breckling et al. 2005, Grimm et al. 2005). Further, the differences in genetic coding between spawners of the population ensure a large gene pool and thereby genetic differences between their offspring, and consequently a wide range of life history strategies. The range of strategies between individuals may dampen variability in populations in a fluctuating environment and the best strategy may differ between years. Considering the differences that exist between individuals it therefore seems logical to model ecosystems as a collection of individuals that differ in traits using an individual-based model. Information on individual traits is obtainable from measurements, which is a major advantage for individual-based models compared to population models (Huston et al. 1988).

Individual-based models

Complex systems are classically approached by reductionism; i.e. the system can be described by sub-elements or mechanisms (Chalmers 1978). Each mechanism represents a process (e.g. metabolic rate, gut evacuation, prey encounter) studied experimentally. The general properties of the system can be described when the elements of the system are understood. The introduction of computers greatly increased the possibilities of understanding complex systems and made it possible to perform model analyses difficult to achieve in real life (Getz 1998, Peck 2004). Models evaluated against observations may therefore represent a scientific tool that can be used to test hypothesis (Peck 2004). The use of individual-based models (Huston et al. 1988) as an experimental system in evolutionary and ecological studies has drastically

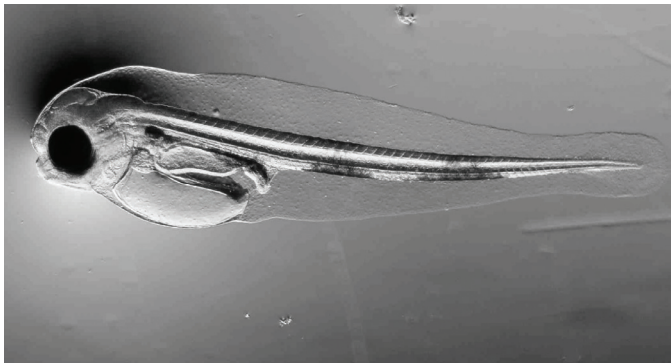


Figure 2 *Image of a newly hatched, 2 days post hatch, larva of size 4mm. Photo: Arild Folkvord.*

increased since the 1990's (DeAngelis & Rose 1992, Grimm & Railsback 2005). Individuals are represented by their state variables, e.g. weight, length, stomach fullness, (i-state, DeAngelis & Rose 1992), while the environment is described theoretically or from observations. This approach is contrary to the classical population models (p-state, Caswell & John 1990) where size classes defines the structure of the population. This implies that individuals of the population are considered equal in traits. An early attempt to use IBM as a tool in ecology was DeAngelis et al. (1979) who explored the development of the size-structure of a largemouth bass cohort over a period of 50 days. The size-structure of the population was revealed from the state of the individuals, and provided results not accessible by the standard structured population

models (Grimm 1999). The DeAngelis et al. model has had extreme influence on the development and use of IBMs in ecology and started a whole new family of fish population models (Grimm 1999). IBMs have since been used to explore a variety of ecological problems, such as the selection of anchovy spawning grounds in Southern Benguela (Mullon et al. 2002, Huggett et al. 2003, Parada et al. 2003), the recruitment variability of bay anchovy in Chesapeake Bay (Wang et al. 1997), growth-dependent mortality of herring (Gallego & Heath 1997), the drift and growth of Northeast Arctic cod from the spawning grounds in Lofoten to the nursery grounds in Barents Sea (Vikebø et al. 2005), how size-dependent predation controls size-distribution of larval/juvenile bloater (*Coregonus hoyi*) in Lake Michigan (Rice et al. 1993), artificial evolution of behavior and life history traits of Müller's pearlside (*Maurolicus muelleri*) (Strand et al. 2002), and in many other applications.

An IBM represents organisms and ecosystems that can be manipulated in ways difficult to achieve in real life (Peck 2004). Still, model reliability depends on the underlying assumptions of the model and the models' ability to reproduce observable patterns. Laboratory experiments where scientists have identified and explored the properties of a single, or a multitude of processes, provide information on relevant parts of an IBM. As the number of processes included in the model grows, the complexity and the room for error increases as well. Elements of a model should therefore be limited to the ones thoroughly studied and well documented.

This thesis presents new approaches on modeling early life stages of cod, which can be distinguished into three main components; (i) mechanistic understanding of feeding and predation, (ii) the use of environmental and biological data to run and validate the IBM, (iii) how individual behavior influences growth, and survival.

Mechanistic modeling of feeding

The IBM

The IBMs presented in this thesis is a blend of earlier model components (Fiksen et al. 1998, Fiksen & Folkvord 1999, Fiksen et al. 2002, Fiksen & MacKenzie 2002)

combined with a new physiology (**Paper 1**) and behavioral component (**Paper 1, 3, 4, 5, 6**). The IBM contains a mechanistic feeding module, and the tight integration with high-resolution environmental data allows for detailed modeling of early life history of cod. The IBM is based on physical and biological parameters from observations on encounter, pursuit and attack, capture success, ingestion, assimilation, metabolism, and growth (**Paper 1, 3, 4, 5, and 6**). Feeding is estimated in a mechanistic fashion (Caparroy et al. 2000, Fiksen & MacKenzie 2002) where light (Skartveit & Olseth 1988), visual perception (Aksnes & Giske 1993, Aksnes & Utne 1997), and larval size are key mechanisms together with the physical and biological characteristics of the prey (contrast, visibility, size, jump angle, and escape speed) (Fiksen & MacKenzie 2002).

Modeling larval foraging

In most IBMs, capture success of larval fish is a deterministic relation between the size of the larvae and the prey, based on empirical stomach content data (Werner et al. 1996, Werner et al. 2001, Lough et al. 2005). This implies that capture of a given prey item is either a success or a failure, while the mechanistic model estimates capture success as a larval-prey size-dependent probability function. Leising and Franks (1999) modeled growth and feeding of cod and haddock on Georges Bank using an IBM based on work by Laurence (1985). In the model of Leising and Franks (1999), larval fish successfully captured prey items when the ratio of prey and predator length was above 1/70 and less than 1/10. These values are comparable to the ratio between prey and larval cod length observed in gut samples by Munk (1997). The model described here was parameterized for cod by Fiksen and MacKenzie (2002), and modeled capture success (**Paper 4**) agree with the observed values of Munk (1997).

The distance a predator is able to perceive and encounter prey items increases with prey size (image area), and varies with light intensity, the clarity of the water, and the eye sensitivity of the predator. Encounter between prey and predator is then followed by pursuit. The pursuit time necessary to reach attack position increases with

increasing prey size (Walton et al. 1992). Small predators may therefore visually see prey items far away, but pursuit success may fail if pursuit time is long and the prey has moved out of perception area.

Combined, pursuit and capture success varies with depth, light intensity, and with the relative length ratio between prey and predator, and the result is a dynamic interaction between predator, prey, and the environment (**Paper 1-6**). When we compared the mechanistic model with observations of prey items larval cod were able to capture (Lough et al. 2005), only small differences were revealed (**Paper 4**). This suggests that the most important physical and biological characteristics of both prey and predator is included in the mechanistic model. Luo et al. (1996) modeled prey selectivity of bay anchovy in Chesapeake Bay using a mechanistic model. The model setup estimated prey-predator encounter rates in a 3D setting. The visual ability of the anchovy, light intensity, water quality, and the size of the prey determined the rate of encounter, while a size-dependent function determined prey capture. Modeled prey selectivity corresponded with stomach samples. Luo et al. (1996) conclude that understanding of fish feeding ecology is best understood by observing the environment as seen by the fish.

Turbulence has long been considered important for encounter rates between prey and predator (Rothschild & Osborn 1988, Sundby et al. 1994, MacKenzie & Kiørboe 1995, Sundby 1995), however most IBM models have ignored light (Fiksen et al. 1998). In the pelagic realm, light and water quality (turbidity level) shows large latitudinal and seasonal variations among ecosystems that influence feeding and growth of larval fish (**Paper 6**, Suthers & Sundby 1996). Newly hatched Northeast Arctic cod have a short growth season, but almost continuous light conditions (Pedersen et al. 1989), that enable continuous feeding and potentially high growth rates. Mechanistic models represent a method for modeling first-principle physics and biology of ecosystems as close to the real world as possible, and gives the researcher the opportunity to understand how components interact on a detailed level. Of course, our ability to correctly parameterize the model (see Fiksen and MacKenzie (2002) for

discussion on uncertainty in parameter values) are critical for model reliability and validation. New laboratory experiments on visual perception of larval cod would help increase the general validity of simulation results.

Mechanistic modeling of predation on larval cod

Rice et al. (1993) modeled size-dependent mortality of bloater fish in Lake Michigan using an IBM model. The probability of being eaten by the predator alewife (*Alosa pseudoharengus*) decreased with larval size, and survivors were the largest and fastest growing individuals. Similarly, Ottersen and Loeng (2000) found significant correlation between mean individual length and year-class strength of Northeast Arctic cod at the stage of 5 month-old pelagic juveniles, indicating that rapid larval and juvenile growth favors high survival. In **Paper 3, 4, and 5** encounter between larval cod and predators were simulated mechanistically as a function of the visual perception of the predator, the light conditions, and the predator density (Fiksen et al. 2002). Visibility of larvae to fish predator increases with size, still, the probability of the larvae being eaten decreases as larger larvae are able to migrate deeper in the water column where predation is minimized (**Paper 3-5**). Many individual-based models include mortality, although the implementation differs. Some models include mortality on egg stages (Mullon et al. 2003), starvation (Letcher et al. 1996, Leising & Franks 1999, Hinrichsen et al. 2002), size-dependent functions (mortality decreases with larval size) (Bartsch & Coombs 2004, Bartsch 2005), as a growth-related function (faster growing individuals have a higher probability of survival) (Gallego & Heath 1997), or as a random function (Gallego & Heath 1997). Modeling predation is not an easy task as predation pressure varies spatially and temporally within and among ecosystems. On Georges Bank, Garrison et al. (2000) observed increased predation pressure from mackerel and herring on cod and haddock larvae in years when temperature was high. The predators followed the temperature gradient and occasionally overlapped with the distribution of larval cod and haddock and caused high predation pressure. Such mortality events may be difficult to model

correctly; still, predation is of crucial importance for larval fish survival and should be included in IBMs in order to resemble real life history traits. By splitting mortality into three components (**Papers 3-6**), the scientists can explore how predation from invertebrates and piscivores, and starvation influences survival in size-structured populations. Explicit mechanistic simulations of predation from piscivores on larval fish enable us to understand how physical properties of the environment (e.g. phytoplankton production decreases visibility in the water column) may influence predation rates.

Modeling the environment in IBMs

The environment (larval habitat) describes the theater where the early life histories are played out, and represents a key element of an IBM. The fluctuating and changing environment is challenging to model in a reliable way, which can result in differences between the modeled and the actual habitat of interest. Studies of advection, dispersal, and distribution of larval fish (e.g. Hare et al. 1999, Fox et al. 2006) may not require a detailed description of the prey fields, but is required when modeling feeding ecology (**Paper 1, 4**). In most models the habitat is an assemblage of the ocean currents, temperature, turbulence, and prey fields, where variables are theoretically based (e.g. **Paper 5**, Hinckley et al. 1996, Werner et al. 2001), or a combination of theoretical and observed values (**Paper 1, 3, 4, 6**, Lough et al. 2005). An excellent example of the latter approach is the model of Bartsch et al. (2004, 2005). Bartsch et al. (2004, 2005) derived monthly egg production of *Calanus finmarchicus* based on the long-term observations of the number of females from Continuous Plankton Recorder (CPR) data, and satellite data of sea surface temperature and chlorophyll *a* concentration. The result was weekly average spatial distribution of prey suitable for mackerel in the North Atlantic. Zooplankton models provide an efficient way of to estimate larval prey abundance in time and space (**Paper 6**, Huse 2005). However, such models may be difficult to validate, as observations over large areas are needed. Still, oceanographic models encounter the

same problem, but model results have been verified by testing modeled data at specific stations where sampling is conducted (e.g. Vikebø et al. 2005). Most model experiments use data to validate the model (Wang et al. 1997, Voss et al. 1999), but environmental and biological observations are seldom used to force the model (**Paper 1, 3, 4**). The re-simulation of the macrocosm experiment (Folkvord et al. 1994) used observed values of zooplankton, temperature, wind speed, and modeled light to epitomize the habitat, and enabled a direct comparison between modeled and observed stomach content and growth (**Paper 1**). **Paper 4** modeled growth and prey selectivity of larval cod on the Georges Bank using data on the distribution and daily variation of four species, 13 stages each, of prey. This allowed for a detailed comparison between observed and modeled stomach content, and in my opinion, extensive use of data increases the validity and viability of a model.

Scientific sampling procedures, e.g. 10m strata MOCNESS samples 6 times a day (e.g. Lough et al. 2005), do not necessarily resemble the fine scale details of the water column as experienced by larval fish (Pepin 2004). The data used in **Paper 3 and 4** were obtained by following a drifter deployed at 13 m depth for several days (Lough et al. 2005). The idea was that the trajectory of the drifter and the larval cohort corresponded, and consequently water samples along the drift trajectory would resemble the environment as experienced by the members of the cohort (Lough et al. 2005). Horizontal currents differ with depth, and the drift at 13 m may not have been appropriate to describe the drift of the larval cohort. Pepin (2004) warns about the relatively low probability of sampling the same water parcel twice, thereby deducing assumptions of growth and predation by using samples from different parcels containing both zooplankton and larvae, but which essentially have experienced different ecological settings. Video plankton recorder (VPR) based studies may open up new possibilities for modeling the habitat of larval fish correctly (Davis et al. 1992, Gallager et al. 2004). The VPR is moved through the water column at the speed of larval fish and digitally records plankton composition of the water column, as experienced by larval fish. A computer scans the digital pictures of the water and automatically recognizes prey species and sizes. VPR increases our ability to

understand the environmental composition as seen through the eyes of larval fish. VPR data can enforce a new, efficient method for modeling the environment more correctly, and perhaps increase our knowledge of small-scale processes effect on larval feeding and growth.

Implementing behavior in individual-based models

Coupled bio-physical models (**Paper 6**) generate dispersal patterns of individual members of populations in realistic flow fields. This opens up possibilities for bridging the gap between oceanography and biology (**Paper 2**, Vikebø et al. 2005). Spatial and temporal variability in the distribution of prey, light, turbulence, and other environmental cues, enforce larval fish to locate habitats for feeding while simultaneously avoiding predators. During the last few years, coupled models have been used extensively to model the effect of large-scale ocean currents on population dynamics of fish species around the world. Much effort has been put into model efforts to investigate how eggs and larvae drift passively with the prevailing currents from spawning grounds to nursery habitats, and how variability in current systems may affect egg and larval survival and recruitment (e.g. Werner et al. 1993, Hare et al. 1999). Huggett et al. (2003) modeled passive drift of anchovy eggs and larvae in the southern Benguela. Based on model results, the authors concluded the eggs and larval products that reach the nursery habitats successfully originate from the areas where the majority of spawning occurs. However, they also concluded that the model reproduced observable patterns when active swimming of the larvae was included. The same conclusion was reached by Werner et al. (1993) when they modeled drift of cod and haddock larvae on Georges Bank. Number of individuals to reach the nursery grounds on Georges Bank increased when directional swimming was included. Anchovy eggs and larvae in the southern Benguela was also explored by Parada et al. (2003). Here, the authors included buoyancy of the eggs and larvae, and tested for differential transport success of eggs and larvae from the spawning grounds to the nursery habitats. Parada et al. (2003) concluded that density played a significant role

in transport success. Studies like Huggett et al. (2003), Werner et al. (1993), and Parada et al. (2003) are fascinating and may help researchers understand underlying strategies of choice of spawning grounds and timing of the spawning. Still, larval fish do exhibit vertical behavior (Ellertsen et al. 1984, Lough & Potter 1993, Leis et al. 2006) which could be included in coupled bio-physical models (**Paper 2, 5**) and increase our understanding of dispersal and drift of eggs, larvae, and early juvenile fish. Vikebø et al. (2005) showed that large variation arise in transport trajectories of particles located just a few meters away in the vertical. Strong gradients of horizontal ocean currents can have significant impact on the drift of particles. This was illustrated by modeling efforts by Fox et al. (2006). The spawning grounds of plaice in the eastern Irish Sea are close to the nursery habitats and settlement grounds. Fox et al. (2006) revealed that when larval and juvenile plaice exhibited vertical behavior synchronized to the tides, the number of individuals to reach the nursery grounds increased. **Paper 2** and **3** suggests that environmental (e.g. light, prey, predators) and physiological (e.g. size, stomach fullness) cues could be used as mechanisms to drive the behavior of larval fish. This thesis shows that flexible behavior of larval fish significantly increases the probability of larval fish survival (**Paper 3, 5**), growth (**Paper 1, 3, 4**), and dispersal (**Paper 5**), and represents an important element of IBMs that needs further research.

Main findings and future perspectives

- Modeled foraging of first-feeding larval cod suggests that prey density of $10 \text{ nauplii} \cdot \text{L}^{-1}$ is sufficient for the larvae to grow at their physiologic maximum rate at temperatures 6-10°C in early May (**Paper 1, 6**). The implementation of stomach as a larval state variable in the IBM improved the model bioenergetics, and proved important as an energy reserve during the early hours of the night (**Paper 1**).
- Larval cod on Georges Bank favors *Pseudocalanus* spp. as prey item because of its visibility and abundance in the water column. *Centropages*

was modeled as a potentially preferred prey item, however *Centropages* spp. is seldom found in stomach samples with the exception of nauplius stages (**Paper 4**). This indicates a negative selection for this prey item

- Flexible individual behavior motivated through environmental cues and individual states (**Paper 2, 3**) have significant impact on growth (**Paper 1, 3, 5**), and survival (**Paper 3, 5**), and on dispersal patterns (**Paper 5**).
- Day-length limit feeding and growth for newly hatched larval cod in Lofoten in Northern Norway prior to mid-April. By mid-April, day-length has increased considerably and the IBM suggests high growth at prey densities above $5 \text{ nauplii} \cdot \text{L}^{-1}$ (**Paper 6**). Time of season, day-length, and water temperature have major impact on growth and survival of larval cod in northern Norway (**Paper 6**).
- Modeling early life history of cod using a mechanistic individual-based model in combination with detailed environmental data revealed information on the interactions between biotic and abiotic processes important for larval growth and survival. Models allow us to explore how processes and mechanisms influence larval growth and survival in an ethical, reliable, and affordable way. Virtual experiments can be repeated, and each single process can be turned on and off, thereby revealing its true effect on the system as a whole.

In conclusion, understanding the functional relationships between physical and biological properties of ecosystems is a challenging task where individual-based models can suffice as a valuable tool. However, the strength of an IBM rests on our knowledge on the mechanisms and processes that compose the model in the first place. Experiments and observations provide valuable information that modelers may utilize. In future perspectives, it is tempting to hope that models, such as IBMs, can be used to predict recruitment strength of fish populations. If we understand what causes variability in year-class strength, we can take measures and precautions to

manage and sustain the populations and the fisheries. The study of early life history may prove to be a viable way to understand ecosystem dynamics and for preservation and management of marine habitats. Such knowledge seems ever more important when faced with climatologic changes and increasing interest in exploration for oil in marine habitats. It is therefore necessary to strive for knowledge of marine ecosystems, not only for exploitation of resources but also for the sake of preservation.

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