

# ICES WKIZC Report 2005

ICES Oceanography Committee  
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## Report of the Workshop on the Impact of Zooplankton on Cod Abundance and Production (WKIZC)

7–9 June 2005

ICES Headquarters



International Council for the Exploration of the Sea  
Conseil International pour l'Exploration de la Mer

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## Executive summary

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Evidence of large scale changes in planktonic ecosystems and consequences of this for other trophic levels, including fish, has greatly improved. Relationships between indicators of plankton variability and fluctuations in recruitment or growth are in most cases supported by information about the underlying processes. The effects of physical and biological forcing on cod are not necessarily either linear or additive, and reductions in stock biomass due to intensive fisheries may have increased their sensitivity to climatic fluctuations.

Many research groups are currently engaged in efforts to build coupled biophysical models including the spatial and temporal interactions between zooplankton and larval cod, i.e. the integration of general circulation models with biological formulations of growth, feeding and behaviour of larval fish. These models are the main tools to integrate research from laboratory studies on sensory ecology, environmental effects on feeding and growth processes with large-scale fluctuations in oceanography and productivity of marine ecosystems driven by climatic forcing. The models are maturing, but still have important limitations, e.g. in the representation of small scale predator-prey interactions, the distribution of prey at a sub-grid scale and in realistic representation of larval behaviour and physiology.

Important results are also emerging from simpler models. For instance, comparisons between lab-derived growth models and field data suggest that surviving larvae grow near their physiological maximum (limited by temperature).

The preferred prey-size of larval cod seems to be proportional to larval length, deviations are due to absence of large prey items such as *Calanus*, and for cod 15-25 mm long the presence of large prey may be crucial. Both larvae and zooplankton appear to be concentrated in fronts. Although *Calanus finmarchicus* is a major component of the larval diet in most stocks, *Pseudocalanus* occupies this role at the warm end of the species range and particularly in the Baltic.

Recruitment to the Faroe Plateau cod stocks appears to be governed by a tightly coupled trophic chain, from nutrients through phytoplankton and zooplankton to forage species, such as sandeels. In other areas, such as the Baltic, the processes are considerably more complex, with large-scale, long-term changes in the physical and chemical environment causing inter-related fluctuations in the populations of cod and the two pelagic fish species.

It remains difficult to pull the detailed, process information which has emerged from large scale national and regional GLOBEC programmes into a form which finds a use in ICES fish stock assessments. The approach in such assessments is to use fixed stock-recruit relationships as a guide to short and long-term management, with some sensitivity analysis to explore the consequences of alternative stock-recruit relationships i.e. environmental variability is treated as noise.

## 1 Overview

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### 1.1 Introduction

Zooplankton are an important link in aquatic ecosystems, transferring primary production to fish. Recruitment of cod populations seems to be strongly influenced by spatio-temporal fluctuations in the availability of suitable food organisms. The sensitivity of certain key zooplankton species (e.g. *Calanus finmarchicus*, *Pseudocalanus* sp.) to climate-induced changes in the physical environment has been demonstrated and they thus mediate climate change effects on fish production. Recent changes in zooplankton standing stocks have, in some cases, resulted in a lowered carrying capacity of marine systems, and have contributed to fisheries induced collapses of cod stocks or hindered their recovery. Understanding of the processes and mechanisms influencing larval cod survival and eventually recruitment is critical to stock predictions.

Consequently, the ICES/GLOBEC Working Group on Cod and Climate Change held a Workshop on *The Impact of Zooplankton on Cod Abundance and Production* in June 2005, with the aim of reviewing and synthesizing the knowledge of cod-zooplankton interactions in the North Atlantic.

Early stages of zooplankton are important prey for larval and early juvenile stages of cod. For most cod stocks *Calanus* species are the main prey, while in some areas, e.g., the Baltic, other species dominate. Survival and growth through these early stages have been shown to be critical for establishing a strong cod year class in some cod stocks. The workshop was asked to examine relations between temporal and spatial dynamics of zooplankton and early stages of cod. The issues to be addressed included how timing of zooplankton production and spatial dynamics of nauplii relates to the spawning and distribution patterns of early stages of cod and ultimately cod recruitment. Links between later stages of cod and zooplankton were also investigated. A combination of statistical data analyses, process studies and a variety of modelling approaches were applied.

### 1.2 Terms of reference

2C08 **A Workshop on the Impact of Zooplankton on Cod Abundance and Production [WKIZC]** (Ø. Fiksen, Norway, and J. Runge, USA, and Christian Möllmann, Denmark) will meet at ICES, Headquarters from 7–9 June 2005 to:

- a) to determine the zooplankton species in the diets of cod, their temporal and spatial changes;
- b) to determine the variability in zooplankton populations and their relationships to cod;
- c) to examine the vital rates (growth, reproduction, mortality, recruitment) of zooplankton which are relevant to cod life histories ("stock assessment" of zooplankton);
- d) to determine how the timing of zooplankton production and spatial dynamics (including patchiness) of *nauplii* relates to the spawning, distribution and survival of early stages of cod;
- e) to establish the links between zooplankton and later stages of cod.

This will be carried out using a combination of statistical data analyses, process studies, and a variety of modelling approaches.

WKIZC will report by 1 July 2005 for the attention of the Oceanography Committee.



### 1.3 Preparation of the workshop

In preparation for the workshop the ICES/GLOBEC coordinator established a website ([www.ices.dk/globec/workshops/Zooplankton/WKIZC.htm](http://www.ices.dk/globec/workshops/Zooplankton/WKIZC.htm)) to facilitate communication among the participants before and after the workshop. Terms of references, circular letters, preliminary agendas and practical information were posted before the meeting. Participants were requested to provide working documents and discussion items prior to the workshop, for circulation via the website. These were grouped under three topics, which also served as the titles for the three main presentation sessions during the workshop:

- 1) Zooplankton dynamics in relation to larval fish
- 2) Larval cod feeding processes, diet and prey selection
- 3) Modelling the zooplankton – larval cod linkage.

The following working documents/abstracts were received before the meeting. Most were presented at the meeting and are included as abstracts in section 3 – the precise numbering is shown in the column headed Section. Titles which are underlined are included as longer papers in Annex 3–7. The final three columns refer to the above three topics and in many cases the presentations dealt with more than one topic.

#### Working documents provided before the meeting and still accessible on the website

AUTHOR	TITLE	SECTION	ZOO	FEED	MOD
Pierre Pepin	Early life history studies of predator-prey interactions: quantifying the stochastic individual responses to environmental variability			X	X
Myron Peck <i>et al.</i> ,	Scenario testing the effects of climate variability on match-mismatch of larval fish and their zooplankton prey: Coupling an IBM to an NPZD model	4.9	X		X
Jeff Runge	Effect of spatial and temporal variation in zooplankton concentrations on larval cod growth on Georges Bank: a comparison of two years based on modelling and observations	4.10	X		X
Øyvind Fiksen	(1) <u>Are larval fish limited by their prey availability? Yes – even at high prey abundance.</u> (2) Process-based models of feeding and prey selection in larval fish	4.13			X
Hans-Harald Hinrichsen	<u>The influence of circulation patterns on the interaction between Baltic larval cod and zooplankton as their prey</u>	4.11			X
Arild Folkvord	Evaluation of cod larval growth performance across several different experimental scales, environments and regions	4.12			X
Christian Möllmann <i>et al.</i> ,	<u>Eastern Baltic cod larvae and zooplankton</u>		X	X	
Ted Durbin	Annual and inter-annual trends in the zooplankton prey and growth of Atlantic cod and haddock larvae on Georges Bank		X	X	
Eilif Gaard	Plankton impact on the Faroe Plateau cod	4.2	X	X	
Peter Munk	<u>The role of physical features and spatial overlap on the interactions between zooplankton and larval fish</u>	4.7		X	
Howard Browman	Half-truths and myths surrounding feeding and escape behaviour in cod larvae. (1) Applications of sensory biology in marine ecology and aquaculture (2) Effect of turbulence on energetics of foraging in Atlantic cod larvae	4.8		X	

Stig Skreslet	(1) Abstract of “Switch from density dependent larval mortality in an accumulated cod stock caused by exploitation” and PPT presentation (2) <u>Some effects of ultra-violet radiation and climate on the reproduction of Calanus finmarchicus (Copepoda) and the year class formation in Arcto-Norwegian cod</u>	4.5	X		
Jeff Runge	Timing and magnitude of copepod production related to haddock recruitment on the Scotian Shelf and mackerel recruitment in the Gulf of St. Lawrence: recent results	4.6	X		
Erica Head	An exceptional haddock year class and unusual environmental conditions on the Scotian Shelf in 1999		X		
Keith Brander	Are we any closer to “strong, prediction” of fluctuations in recruitment and growth than we were in 1994?	4.14			
Jeff Runge	Discussion paper on zooplankton-fish interactions addressing the relation of zooplankton production cycles to recruitment processes				

## 1.4 Workshop structure and working procedure

The agenda for the workshop is given in Annex 2 and the participant list Annex 1. The workshop was basically divided into three activities: (i) presentations, (ii) break-out group discussions and (iii) report writing. After each session a round-up was made either through plenary discussions or by the co-conveners or group leaders presenting a summary. The final plenary session discussed the reports of the break-out groups and reviewed the conclusions in relation to the terms of reference.

## 2 Conclusions with regard to terms of reference

### 2.1 ToR a) to determine the zooplankton species in the diets of cod, their temporal and spatial changes

- Detailed information about zooplankton species in the diets of cod is presented in section 4.1, by region. The Workshop was also aware of a major synthesis and summary of this information, which had been produced by Dr M. Heath for the forthcoming book on Cod and Climate Change.

### 2.2 ToR b) to determine the variability in zooplankton populations and their relationships to cod

- Detailed information relevant to this ToR is presented in much of section 4.
- One of the main difficulties in coupled biophysical models is to include realistic prey-fields, both on the larger, regional scale, and also on the sub-grid scale.
- Our knowledge about zooplankton as predators on larval cod is very limited – although variations in predatory invertebrates do have the potential to affect recruitment success.

### 2.3 ToR c) to examine the vital rates (growth, reproduction, mortality, recruitment) of zooplankton which are relevant to cod life histories ("stock assessment" of zooplankton)

- Very little information on zooplankton life histories and population dynamics was presented at the workshop, but it is an underlying component of many of the regional studies which are summarised in section 4.1.

## **2.4 ToR d) to determine how the timing of zooplankton production and spatial dynamics (including patchiness) of nauplii relates to the spawning, distribution and survival of early stages of cod;**

- The distribution of zooplankton and larval cod overlaps mainly in fronts or other areas with above-average conditions for primary production. This may result from the size-dependent mortality schedules of larval fish, i.e. they will be consumed by predators in areas where they grow suboptimally. Alternatively, they may be physically aggregated in particular oceanographic regions. It is difficult to separate these processes.
- Spatial overlap between large-sized prey and larval cod varies between years, with consequences for the presence of large zooplankton prey (e.g. *Calanus*) in the diet.
- In some regions such as Georges Bank and the Barents Sea, the advection of prey into spawning- and nursery grounds of larvae appear to be quite variable. This suggests a connection between large scale oceanography, zooplankton distribution and cod recruitment.

## **2.5 ToR e) to establish the links between zooplankton and later stages of cod.**

- A number of strong interactions between larval cod and particular species of zooplankton were identified. In the North Sea interannual variability in abundance, seasonal timing and size composition of zooplankton appears to be responsible for a significant proportion of observed variability in survival of early life stages of cod (Beaugrand *et al.*, 2003). In the Baltic, cod recruitment is strongly influenced by interannual fluctuations in *Pseudocalanus*, and this species also affects growth of larval cod on Georges Bank, at least in some years. In the Barents Sea, *Calanus* is the main prey item. On the Faeroes, a strong relationship between general oceanography, primary production and the success of forage fish for juvenile cod has been revealed recently. Presumably, zooplankton is the link between the success of sandeel, which again is very important for juvenile cod.
- Some of the links between zooplankton and later stages of cod appear to be indirect. The lesson from the Faroes is that survival of juvenile cod is coupled to the availability of forage fish – and that the link from oceanography and zooplankton may act through the production of planktivores (sandeels in particular). In the North Sea and on Georges Bank, the absence of large prey has been documented in some years, and this may reduce growth rates and recruitment success.

## **3 Presentations given at the workshop**

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Presentations given by workshop participants are briefly summarized. Fuller versions are available either in Annex 3–7 (indicated by an \* after the authors name) or from the workshop website, where many are available in pdf and ppt formats. The presentations were originally grouped according to topic (see section 1.3), however as many of them cut across several topics they are not grouped here.

### **3.1 Prey availability and feeding of larval cod in coastal Newfoundland - *Pierre Pepin***

The feeding environment of larval cod in coastal waters of Newfoundland is numerically dominated by the nauplii of calanoid copepods as well as species of small copepods (*Oithona* spp., *Pseudocalanus* spp.). Although there is strong seasonality in the abundance of these species, with low numbers from December to April, their abundance is nearly constant throughout most of the period following the spring phytoplankton bloom. Data from an optical plankton counter towed between 5–70 m showed that the large scale structure in the distribution of

zooplankton prey, appropriate as food for cod larvae, did not show substantial seasonal variation. However, variations in the vertical structure represents a dominant source of differences in zooplankton abundance both within surveys and throughout the productive season. It is proposed that subtle changes in the vertical patterns of abundance may represent the most significant source of variation in the encounters between larvae and their prey. Feeding patterns in larval cod show an important shift from copepod nauplii to copepodites at approximately 8 mm SL. Calanoid nauplii dominate as prey in small larvae while *Oithona* spp and *Pseudocalanus* spp become increasingly important as larvae grow. The distribution of the number of prey in the stomach of fish larvae from Conception Bay, including cod, is well described by a Poisson distribution, one that is consistent with simple encounter models. The application of a simple model of encounters between prey and predators was used to estimate the effective volume swept by larvae based on the mean number of prey in the stomach and in the water column. It is proposed that this approach could be used to determine if larval cod form different stocks and ecosystems effectively have the same inherent “response” to prey encounters.

### **3.2 Plankton impact on the Faroe Plateau cod - Eilif Gaard**

The zooplankton community on the Faroe Plateau contains a mixture of oceanic species (mainly *Calanus finmarchicus*) and neritic zooplankton species (mainly *Temora longicornis* and *Acartia longiremis*). During spring there may also be high abundance of barnacle larvae on the shelf. In most years neritic species dominate by abundance, however, there is high interannual variability in advection and abundance of oceanic species on the shelf. The seasonal timing of zooplankton reproduction and abundance follows closely the timing of phytoplankton production and abundance. There is, however, also some significant pre-bloom egg production of the copepods, and these offsprings are important as food for cod larvae during the early spring.

Cod spawning takes place between February and May, however, peak spawning takes place in the second half of March. The eggs are advected clockwise and are then dispersed around the Shelf. On their way from the spawning grounds, the eggs hatch and the larvae start feeding. Many larvae may start feeding in April, which usually is in the pre-bloom phase.

The first feeding cod larvae predate mainly on copepod eggs. As they grow they progressively consume larger prey. First consuming copepod nauplii and small copepodites, followed by larger copepods, and they finally add decapod larvae and occasionally even fish larvae to their diet. In July, at lengths of about 4 cm, they migrate into the coastal areas.

Although feeding conditions for cod larvae obviously are important for survival and abundance of cod recruits, the final cod recruitment seems to be determined about one year later, apparently during their second winter, when they leave the coastal areas. There is a good relationship between sizes of one year old year classes, growth rates of demersal cod, food abundance (mainly sandeel, partly also Norway pout) and plankton production and abundance. Sandeel seems to be a key link between plankton and recruitment and growth of later stages of cod. The sandeel recruitment is highly variable between years, and in most years it follows plankton production. The knowledge on sandeel on the shelf is, unfortunately, scarce. However, sandeel larvae may, as cod larvae, depend on zooplankton abundance. Therefore the Faroe Plateau cod seems to be affected by zooplankton (re)production, not only directly during their larval phase but apparently more in their demersal phase, indirectly through sandeel.

### **3.3 Baltic cod and sprat recruitment in relation to zooplankton production - C. Möllmann, P. Grønkjær, H.-H. Hinrichsen, F.W. Köster, G. Kornilovs, G. Kraus and R. Voss\***

For the Central Baltic Sea the interactions between zooplankton and larvae of cod (*Gadus morhua*) and sprat (*Sprattus sprattus*) have been described. The early-life-stage dynamics of

both species take mainly place in the deep Baltic basins (Bornholm Basin, Gdansk Deep, Gotland Basin) where the adults spawn in the permanent halocline. The eggs dwell in the halocline region where they find sufficient salinity to be neutrally buoyant. Cod eggs are neutrally buoyant at higher salinities and thus are in danger to face oxygen deficiency, a risk which is lower for sprat. Consequently the egg stage of cod is assumed to be critical for recruitment success, which has also been shown by subsequent correlations of time-series on spawning stock abundance, egg and larval production as well a recruitment at age 0 (Köster *et al.*, 2003). Ambient hydrographic conditions in the deep Baltic basins are strongly dependent on lateral advection of highly saline and oxygenated water from the North Sea (major Baltic inflows, Matthäus and Franck, 1992). The frequency of these has been drastically reduced since the 1980s resulting in detrimental salinity and oxygen conditions (Matthäus and Nausch, 2003).

After an inflow event in 1993 high abundances of cod eggs have been observed, however larval abundance continued to be low, which raised the question of a possible food-limitation of cod larvae. Time-series analyses showed that due to the reduced inflow activity the formerly dominating copepod *Pseudocalanus* sp. decreased in abundance during the 1990s, while two other important copepods i.e. *Temora longicornis* and *Acartia* spp., increased (Möllmann *et al.*, 2000, 2003). Biomass of *Pseudocalanus* sp., which reproduces similar to cod in the halocline region, is correlated with salinity in the deep basins, demonstrating the dependence of this copepod on the renewal of the bottom water by inflow events. Process studies within GLOBEC-GERMANY showed *Pseudocalanus* sp. females to face during periods without inflows very low oxygen conditions while searching for high salinity for reproduction. This has obviously negative consequences for the survival of eggs and nauplii (Schmidt *et al.*, 2003). A mechanism behind the relationship between the *Acartia* spp. population and temperature (Möllmann *et al.*, 2000, 2003) seems to be increased hatching of resting eggs from sediments during the generally warmer 1990s (Dutz *et al.*, 2004).

As by diet analyses, *Pseudocalanus* sp. is the preferred food item of larval cod, while sprat relies to a large degree on *Acartia* sp. (Voss *et al.*, 2003). This difference is caused by differences in vertical positioning of the larvae. While peak cod larvae abundance were found in general below the thermocline where also early stages of *Pseudocalanus* sp. reside, sprat larvae dwell within the thermocline co-occurring with *Acartia* spp. (unpublished data).

As a consequence of the decadal trends in copepod abundance food supply for cod larvae was drastically reduced. In addition, the shift in cod peak spawning time from spring to summer brings the larvae in an environment with low nauplii abundances, as *Pseudocalanus* sp. reproduces mainly in spring (Renz and Hirche, 2004). Using a coupled individual-based/3-d hydrodynamics model run demonstrated that cod larvae were food-limited during the 1990s, but not in the years before (Hinrichsen *et al.*, 2002). In contrast to cod, for sprat the larval stage appeared to be the critical one (Köster *et al.*, 2003). Sprat larval survival has thus probably profited by the increase in *Acartia* spp. abundance. Indeed, there is a significant relationship among sprat recruitment and *Acartia* spp. abundance (unpublished data).

In consequence of the climate-related trends in dominating zooplankton species, the shift in peak spawning of cod, the differences in utilisation of copepods species, the carrying capacity of the ecosystem for larval survival switched from high for cod during the 1980s to high for sprat during the 1990s.

### **3.4 Annual and inter-annual trends in the zooplankton prey and growth of Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae on Georges Bank - L.J. Buckley and E.G. Durbin**

The dominant copepod taxa on Georges Bank were monitored between January and June of 1995 through 1999, using a pump sampler and a 1-M MOCNESS. Between March and May

of these years over 10 000 cod and haddock larvae were collected and recent growth of individual larvae estimated using RNA/DNA ratio analysis. Undertaken as part of the US GLOBEC NW Atlantic Georges Bank Program, the zooplankton sampling was completed on broadscale cruises covering much of the Bank, while most of the larval collections were made on process cruises concentrated on the southern flank. Together the two data sets afforded the opportunity to examine prey abundance and larval growth over extended spatial and temporal scales. Indices of prey abundance were estimated for different size-classes of larvae. Normalized prey counts ( $\# \cdot M^{-3}$ ) and prey biomass concentration ( $\mu\text{g dry weight} \cdot M^{-3}$ ) increased between February and May of each year. Following a similar trend, larval growth increased between March and May. Particularly strong correlations were observed between the biomass of *Pseudocalanus* spp. and larval growth. Residuals from models relating larval growth to larval size and photoperiod were highly correlated with normalized residual prey concentration. The spring of 1995 and to a lesser extent 1996 appeared to be periods of poor growth and low prey availability for cod and haddock larvae on Georges Bank. Although no large year-class of cod was produced during the study period, the 1998 year-class of haddock was among the largest produced over the previous 20 years on Georges Bank.

### **3.5 Switch from density dependent larval mortality in an accumulated cod stock caused by exploitation - Stig Skreslet\***

After World War II the Arcto-Norwegian cod stock was very large, probably being subject to density dependent larval mortality because of limitations in the carrying capacity of zooplankton. The spawning stock rapidly declined due to increasing exploitation through the 1950-ies. The break-down of a correlation with freshwater discharge and a survival index for cod larvae around 1960 may indicate that the population system switched from being density dependent to regulated by a variety of other environmental factors that are always present. Thus, recruitment to the present stock may not be forced by zooplankton abundance on the larval stage because the carrying capacity is larger than the demand from any larval stock.

### **3.6 Timing and magnitude of copepod production related to haddock recruitment on the Scotian Shelf and mackerel recruitment in the Gulf of St. Lawrence: recent results - Jeff Runge**

Head *et al.* (2005) report that the number of settled year-0 haddock on the eastern Scotian Shelf in July 1999 was the highest seen since record keeping began in 1970. The average length indicated most had hatched in late February, well before the historical peak spawning period. In the data record above average year-0 abundance leads to good recruitment, suggesting that early spawning incurs survivability advantages. Conditions may have been particularly favourable for haddock recruitment in 1999: (a) because an unusually large number of adults spawned early; and (b) because the earliest larval stages encountered an unusually plentiful supply of food, since the spring bloom and *C. finmarchicus* reproduction peaked in late February, 2–4 weeks earlier than usual.

Plourde and Castonguay (in prep: ESSAS conference, Victoria, May, 2005) update previous studies identifying relationships between RIVSUM, zooplankton biomass in early summer, and Atlantic mackerel recruitment between 1982 and 1991 in the southern GSL (Runge *et al.*, 1999; Ringuette *et al.*, 2002). Runge *et al.* found that an exceptional mackerel year-class produced in 1982 was significantly related to a spring with low RIVSUM and high zooplankton biomass (Runge *et al.*, 1999). Copepod egg production (especially female *Calanus finmarchicus*) was highest in 1982. Stomachs of mackerel larvae contained more prey biomass in 1982 than in other years, due to *Calanus* and *Pseudocalanus* naupliar prey (Ringuette *et al.*, 2002). The aim of this study is to add a second decade of data (1992–2003) to the previous studies (1982–1991). During this period a second mackerel boomer occurred in 1999, also

another year of low winter/spring RIVSUM and high zooplankton biomass. All relationships between climate, zooplankton, and fish recruitment identified in the previous decade held with a second decade of data, except for the mackerel recruitment / RIVSUM relationship. Other copepod species, notably *Temora longicornis*, contributed substantially to the prey field for larval mackerel in 1999. A greater contribution to the biomass (>1000  $\mu\text{m}$ ) of *C. hyperboreus* was observed during the period 1992–2003, which may explain the breakdown in the recruitment-RIVSUM relationship.

A highly significant relationship between copepod egg production and mackerel recruitment was also found, which brings further evidence of a strong link between interannual variation in copepod production and mackerel recruitment. Biophysical modelling will allow us to explore relationships between the physical environment, secondary production, and fish recruitment in greater depth.

### **3.7 The role of physical features and spatial overlap on the interactions between zooplankton and larval fish - Peter Munk\***

Recurrent observations have shown that both mesozoo- and ichthyoplankton in the North Sea are concentrated in restricted areas, either close to the shelf slope, nearshore, or in the vicinity of offshore banks. Comparison of distributions and hydrography indicates strong linkages between plankton and physical features, especially to horizontal/vertical stratification and the presence of hydrographic fronts.

In 2001, as part of the LIFECO programme, a field study was set up to investigate the physical-biological linkages in the plankton of the eastern North Sea. From this study (which include a long series of cruises) basic findings from two cruises are described in order to emphasize: 1) the influence of hydrography on distributional patterns of different plankton species, 2) the (seasonal) differences in distributions of cod larvae, and 3) the importance of the overlap between cod larval distribution and the distribution of prey of the appropriate size (which is to some extent related to copepod species composition).

The hydrographic variability was reflected in the plankton distribution with some species, such as *Calanus* sp and *Acartia* sp, being exclusively separated, while other species such as *Pseudocalanus* sp. and *Temora* sp. have intermediate distributions. There are distinct relationship between given copepod species and water mass characteristics. In April the cod are distributed in water masses where the bottom water density is below  $27.45 \text{ kg m}^{-3}$ , an area not inhabited by the larger copepod species *Calanus* sp, *Metridia* sp, *Microcalanus* sp, and a large part of the *Pseudocalanus* sp. In May, however, a part of the cod larvae has drifted to areas where they overlap the larger copepod species.

A spatial overlap to larger copepod species is important when cod larvae have grown to a certain size. When available, *Pseudocalanus* sp. and *Calanus* sp. contribute a major part of the preferred prey. In 2001 a large part of the cod population remained distributed in areas without large *Pseudocalanus* sp and *Calanus* sp. and consequently the mean size of prey items levelled off when they passed a size of  $\sim 20$  mm. This is in contrast to the larger mean sizes of prey for larvae  $>20$  mm in the study in 1994.

Cod larvae distributed in areas where they do not have all (large) prey sizes available ought to eat more of the smaller prey in order to fulfil their requirements. Comparison between the 1994 and the 2001 observations indicates that in 2001 a part of the population had suboptimal feeding conditions.

In conclusion, this part of the 2001 data presents additional examples of patterns described in earlier studies (e.g. Munk, 1995, 1997; Munk *et al.*, 1995, 1999), and it illustrate the strength and species-specificity of hydrographical influence. Hence the ontogenetic aspect is important

when evaluating cod growth and survival. 'Relevant' spatial overlap and interactions between larvae and zooplankton change during time, and we need to consider the full range of larval stages.

### **3.8 Half-truths and myths surrounding feeding and escape behaviour in cod larvae - Howard Browman**

Sensory perception links an organism's internal and external ecologies. It thereby also connects conspecifics to one another, and underlies many of the biological-ecological links between species in communities. It is demonstrated here how studying these perceptual links can help marine ecologists understand ichthyoplankton-zooplankton interactions. A case studies was used to underscore that some processes in marine ecology can only be addressed through the eyes (and/or other senses) of the organism(s) involved. Case Study 1. Turbulence and cod-zooplankton interactions; Case Study 2. "Operational" prey abundance and the myth of prey choice/prey selectivity by cod larvae; Case Study 3. Cod larvae lose in a match with almost any predator. In each case, it is emphasized how the answers that issue from the mechanistic sensory ecology approach can be of great practical advantage.

### **3.9 Scenario testing the effects of climate variability on match-mismatch of larval fish and their zooplankton prey: Coupling an IBM to an NPZD model - Myron A. Peck, Ute Hochbaum, Mike St.John, Corinna Schrum**

The impact of changing environmental conditions in the southern North Sea on the dynamics of zooplankton and larval fish is being investigated using four, inter-linked models: 1) a hydrodynamic model (HAMSOM) provides 3D fields of hydrographical properties, 2) a NPZD model (ECOSMO) generates local prey fields, 3) a Lagrangian transport model simulates temporal changes in larval fish cohort distribution, and 4) an IBM depicts foraging, growth and survival of larvae during early life. This inter-linked modeling approach will be discussed and an update provided on the progress of linking modelled prey fields (ECOSMO simulations) to vital rates of larval fish (IBM simulations).

Zooplankton prey fields – ECOSMO is a 3-D coupled biological-physical model developed to simulate ecosystem dynamics in the North and Baltic Seas. It includes three nutrient cycles, two phytoplankton groups (diatoms, flagellates) and two classes of zooplankton (omnivorous and herbivorous). Validation of zooplankton distributions was performed by comparison with observational data. Zooplankton distribution and biomass, as well as the timing of occurrence of biomass, were well described by ECOSMO. In contrast to earlier model approaches, ECOSMO identified frontal environments as zones of high primary productivity and simulations characterized the dynamics of different zooplankton feeding environments focusing on the role of frontal production. Historical changes in zooplankton production during a 25-year period (1980–2004) were estimated by numerical hind-casting and simulated fields were used to investigate the variability of plankton biomass and production in relation to changes in atmospheric forcing. Basic modes of variability were identified from production and biomass anomalies. In some instances, modes were related to physical forcing mechanisms including stratification-induced variability (1980–1998) or Atlantic inflow-induced variability (1996–2002). Within both periods, physical parameters such as the depth of the thermocline, turbulence and nutrient transport were found to be hydrodynamic indicators for ecosystem variability. Distinct spatial and temporal variability of zooplankton production and biomass was identified from the model output and will undoubtedly influence growth and survival of larval fish. A critical aspect of this modeling effort will be the conversion of bulk zooplankton biomass estimates into size-based prey fields.

Larval fish vital rates – The IBM includes an endogenously feeding stages (eggs, yolk sac larvae) and foraging and growth subroutines for exogenously feeding larvae. The IBM is cur-



rently parameterised for sprat using otolith-based growth rates and gut content analyses of field-caught larvae, new bioenergetics measurements of sprat post-larvae, and a general review of larval clupeid vital rates. The subroutines in the model are similar in structure to those used in a recent IBM for Georges Bank larval cod. Temperature-dependent parameters affect both energy gain (food consumption) and energy loss (metabolism) and will critically influence larval growth estimates and the dynamics of seasonal match-mismatch events. The structure, parameter estimates and potential shortcomings of these IBMs will be discussed.

The influence of varying climatic conditions and prey fields on vital rates of larval fish via scenario tests was estimated. Scenario tests included running these models during anomalously warm (e.g., 1992) and cold (e.g., 1986) years as well as within a year with average temperature conditions (e.g., 1993) in the southern North Sea.

### **3.10 The effect of spatial and temporal variation in zooplankton concentrations on larval cod growth on Georges Bank: a comparison of two years based on modelling and observations - Runge, J. A., L. Buckley, E. Durbin, L. Incze, G. Lough, M. Ohman, K. Pehrson Edwards, S. Plourde, J. Quinlan, and F. Werner**

The U.S. GLOBEC Georges Bank/NW Atlantic program has generated unprecedented data sets on vital rates, abundance and distribution of zooplankton and ichthyoplankton on Georges Bank. Concurrent with the observations has been the development and refinement of a coupled physical-trophodynamic model capable of describing the growth of cod larvae in a realistic three-dimensional description of the environment. Here we use both the trophodynamic model and measures of copepod abundance from the Georges Bank broadscale cruises in April, 1995 and April, 1998 to investigate the sensitivity of larval cod growth rates to spatial/temporal variation in abundance of three taxa of copepods that dominate the prey field of larval cod on the Bank. Model predicted larval cod growth rates were 2–3 times higher in April, 1998 than they were in April, 1995 and are attributable to changes in both the spatial distribution and abundance of the zooplanktonic prey (*Calanus finmarchicus*, *Pseudocalanus* spp. and *Oithona* spp.) The results suggest that interannual variations in copepod production and abundance on the northeast peak and southern flank can strongly influence growth and survival of larval cod on the Bank.

### **3.11 The influence of circulation patterns on the interaction between Baltic larval cod and zooplankton as their prey - H.-H. Hinrichsen, J.O. Schmidt, C. Möllmann, R. Voss, and A. Lehmann\***

A three-dimensional hydrodynamic model has been used to analyse circulation patterns in the Baltic Sea with special emphasis on drifting particles representing larval fish. Temporally and spatially resolved flow fields were used to investigate potential drift routes from the centre of the spawning ground of Baltic cod (*Gadus morhua*) during 1979–1998. The results suggest a general change in circulation pattern from retention during a first decade from 1979–1988 to dispersion in the following decade (1989–1998). As a consequence, differences in the location of potential nursery areas of Baltic cod could be identified. The increase in dispersion was related to an increase in the variability of the local wind forcing conditions over the Baltic. The more frequent occurrence of dispersion in spring of the second decade was accompanied by a strong decrease in biomass of one of the main larval fish feeding component, the calanoid copepod *Pseudocalanus* sp. This change in circulation patterns may have affected the spatial overlap and thus the contact rates between predators and their prey and may have resulted in a food limitation for early larval stages of Baltic cod and potentially contributed to the pronounced shift in cod spawning time from spring to late summer.

Temporal mis-match between the occurrence of larvae and their prey potentially may also affect the spatial overlap between predator and prey. A case study was performed investigating the influence of the circulation patterns on the spatial overlap of Baltic cod larvae with their prey, if a temporal mis-match between predators and prey was assumed. Generally, the overlap decreased since the mid 1980s, however, being maximally variable during the 1990s. Seasonally highest predator-prey overlap within the Baltic cod spawning ground occurred in summer months and lowest at the end of the cod spawning season. As obtained by a comparative analysis of spatial overlap and observed recruitment, temporal and their corresponding spatial mis-matches between predator and prey potentially have an impact on the survival of Baltic cod larvae. The simulations show that variations in physical forcing conditions, especially during the second half of the considered time period, have the potential to dramatically reduce the amount of food being available for larval cod.

### **3.12 Evaluation of cod larval growth performance across several different experimental scales, environments and regions - Arild Folkvord**

This study presents the first intra-specific evaluation of larval growth performance across several different experimental scales, environments and regions of a marine fish species. Size- and temperature-dependent growth models for larval and early juvenile cod (*Gadus morhua*) are developed based on selected laboratory experiments with cod fed in excess with live natural zooplankton. Observed size-at-age of cod from several experiments and stocks are compared with predictions from the models using initial size and ambient temperature history as inputs. Comparisons with results from other laboratory experiments reveal that the model predictions represent relatively high growth rates. Results from enclosure experiments under controlled semi-natural conditions generally provide similar growth rates to those predicted from the models. The models therefore produce suitable reference growth predictions against which field based growth estimates can be compared. These comparisons suggest that surviving cod larvae in the sea typically grow at rates close to their size- and temperature-dependent capacity. This suggests that climatic influences will strongly affect the year-to-year variations in growth of cod during their early life history due to their markedly temperature-dependent growth potential.

### **3.13 Are larval fish limited by their prey availability? Yes – even at high prey abundance - Øyvind Fiksen\***

To what extent are larval fishes limited by their zooplankton prey resources? This question has been asked a number of times in the literature on larval fish ecology. The most common approach to the question of food-limitation has been to evaluate effects of prey density, prey availability, size-structure of prey, spatial overlap etc. and correlate such measures with larval growth in field-, experimental- and modelling studies. The classical justification for taking this approach is that growth increases body size and therefore also survival, thus enhanced growth will reduce integrated mortality risk by decreasing the time with high vulnerability to predators (Houde, 1997). In oceanography, much attention has been devoted to temperature and how it relates to growth and larval fish survival. Numerous studies show clear correlation between temperature indices and recruitment success in fish. The links between zooplankton availability and growth or recruitment success are less clear and it seems to be difficult to establish clear responses between abundance of prey and larval growth in the field.

Fisheries ecologists are used to reason over growth and mortality rates, but may not be used to think in terms of behavioural ecology. In behavioural ecology, the main focus is on how organisms *respond* to their environment, i.e. how they change their behaviour as risk of predation, risk of starvation or growth potential varies. Often, such responses generate surprising (but logically) and highly ‘non-linear’ results. Here it is argued that larval fish are risk-

sensitive foragers, and that this implies survival effects of food abundance even beyond physiological satiation. The risk of starvation and the risk of predation are strongly connected, and they should not be treated separately.

### **3.14 Are we any closer to “strong, prediction” of fluctuations in recruitment and growth than we were in 1994? Keith Brander**

One of the principal aims of national and regional GLOBEC programmes was to provide better predictions of recruitment (and sometimes growth) but it is very difficult to tell from their results whether they have achieved this aim. In some cases it seems that they have either forgotten that this was an aim or have changed direction. In others (notably the Baltic) they have maintained their focus. A key question in this regard is whether there are strong, predictive relationships between physical/biological indicators of plankton variability and fluctuations in recruitment or in individual growth rates within fish and exploited invertebrate populations. A model of causal linkages goes from physics to plankton to fish and much of the science has been to explore the processes, which turn out to be exquisitely complex. The complexity is very interesting and professionally satisfying for biologists, but not directly helpful in providing predictive capability. Results from three recent papers were presented in order to raise some of the issue which I think are relevant in relation to prediction. Two questions to consider are: 1 What kinds of prediction do we need and how good do they have to be in order to be useful? 2 Does our partial, slowly improving understanding of processes give us a better basis for prediction and a greater degree of confidence, even though the models used for prediction do not explicitly include the processes?

## **4 Main scientific topics identified and discussed during the workshop**

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### **4.1 Zooplankton species in the diet of cod**

#### **4.1.1 Summary of regional diet studies**

##### **4.1.1.1 Baltic Sea**

The diet data of cod from the Baltic Sea is primarily related to first-feeding and younger larvae (Voss *et al.*, 2003). There has only been one published study on the feeding of juveniles and this relates to the late pelagic – early benthic stage of cod from the western Baltic (Hüssy *et al.*, 1997). Larvae in the size range of 4–6 mm almost exclusively feed on nauplii during the spring and summer period in the Baltic. The older copepod stages in the guts contribute approximately 5–10% to the number of prey items encountered. *Pseudocalanus* and *Temora* nauplii each make up approx. 40% of the number of nauplii found in the guts with a smaller contribution of *Acartia* and *Centrophages* nauplii. Contrary to other areas there is no indication of phytoplankton in the diets of the cod larvae. The larger larvae (5–10mm) still rely on nauplii but appear to switch to copepodite stages 1–3 during the late summer and autumn.

##### **4.1.1.2 Faroes**

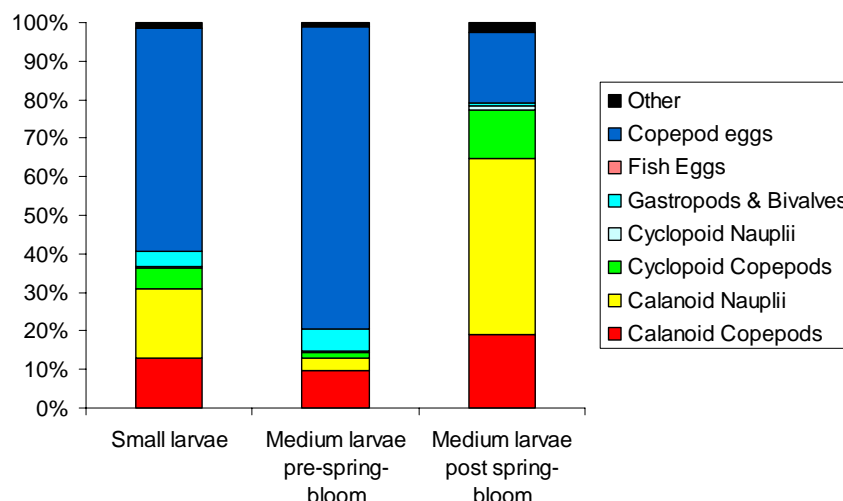
Cod larvae select their food largely based on sizes, combined with abundance of the prey. They start feeding in April, which in most years is in the pre-bloom phase. The first feeding larvae predate mainly on copepod eggs. In some years phytoplankton is commonly found in the guts. Copepod nauplii do not seem to be a dominant food item of the first feeding cod larvae on the Faroe shelf. As they grow they progressively consume larger prey. At sizes of about 12 mm they may feed small- to medium sized copepods. This may be copepod nauplii, young copepodite stages of *Calanus finmarchicus* and the neritic species *Temora* and *Acartia*. (Steingrund and Gaard, 2005). As they grow, they progressively select larger prey. Their

stomach contents are partly reflected by the *in situ* zooplankton composition and their size. At between 15–25 mm in length they may feed on *Temora* and *Calanus* (mainly large stages). At about 30–40 mm decapod larvae may be added to the diet, and cod larger than about 35 mm may take some fish larvae too (Gaard and Reinert, 2002). Food content of juveniles after settlement in July is not studied around the Faroes.

#### 4.1.1.3 North Sea

For the northern North Sea (e.g. north of the main spawning area at Dogger Bank), the number of studies on larval cod diets has been very limited and the data available often originates from studies focussing on other species or assemblages of fish larvae, not necessarily in the vicinity of known cod spawning aggregations. The available data indicates that cod larvae with established feeding (6–16mm) primarily feed on nauplii and copepodites of calanoid copepods. The key calanoid species in this region are *Calanus*, *Pseudocalanus* and *Paracalanus*. The proportion of copepodites will increase with body length of larvae although feeding on nauplii also continues. Cod appear to be able to consume copepodites relatively early (5–6mm), but primarily feeds on nauplii at this stage. The copepodites consumed are primarily the early stages C1–C3 of the key prey species. Prior to spring bloom conditions, first feeding (<6 mm) and larger cod have been observed to consume copepod eggs (most likely *Calanus* eggs – approx. 120 µm diameter), while they will switch to other prey as soon as it becomes available. In addition, cod larvae have been found to feed, to a more limited extent, on gastropod larvae, and cyclopoid copepods.

In the southern North Sea cod larvae start hatching in early March, and during the earliest stages the prey mostly consists of copepod eggs and nauplii. Already from larval lengths of 4–5 mm, the first copepodite stages are included in the diet, and soon these become the predominant prey type. The copepods constitute 70–80% by number, most of the remaining part is appendicularians and larval stages of *Bivalvia*, *Gastropoda* and *Polychaeta*. Of the copepods a restricted number of species is of primary importance. The following species (or genera) dominate: *Calanus finmarchicus*, *C. helgolandicus*, *Metridia lucens*, *Microcalanus pusillus*, *Paracalanus* sp. *Pseudocalanus elongatus*, *Oithona similis*, *Oithona plumifera*, *Acartia clausi*, *Temora longicornis*, *Microsetella norwegica* and *Centropages* spp. During ontogeny there is a gradual shift in the stage and species preference of cod larvae. The larger the larva, the older are the preferred stages, and the more preferred are the larger-sized copepod species (i.e. *Pseudocalanus* sp, *Calanus* sp and *Metridia* sp).



**Figure 4.1.1. Diet composition of first-feeding, and established feeding cod larvae from a 10-day survey in the North Sea in May 1996. All first-feeding larvae ('Small larvae' <6mm) during this study was caught prior to the onset of spring-bloom conditions, whereas larger larvae ('Medium larvae 6–12mm) are comprised by data before and during these conditions.**

The actual diet of cod is very variable, dependent on the site of living, and the availability of large sized prey. The prey size of maximal preference for larval cod are approximately 5% of larval length, hence at larval sizes above ca. 30 mm, the presence of *Calanus* and other large sized prey (e.g. amphipods) becomes crucial. Observations indicate that cod are not able to fulfil their needs (fill their stomachs to the same extent) when the sizes of available prey is far below the preferred. If other fish larvae are available and at appropriate sizes (e.g. sandeel larvae of 25 mm) they might be included in the diet of the cod larvae. Piscivory is seen to start at a cod size of 35 mm and might be an alternative strategy if the available copepod prey is not of the preferred (large) sizes.

**4.1.1.4 Norwegian coast (Barents Sea cod, local populations) and Norwegian Sea**

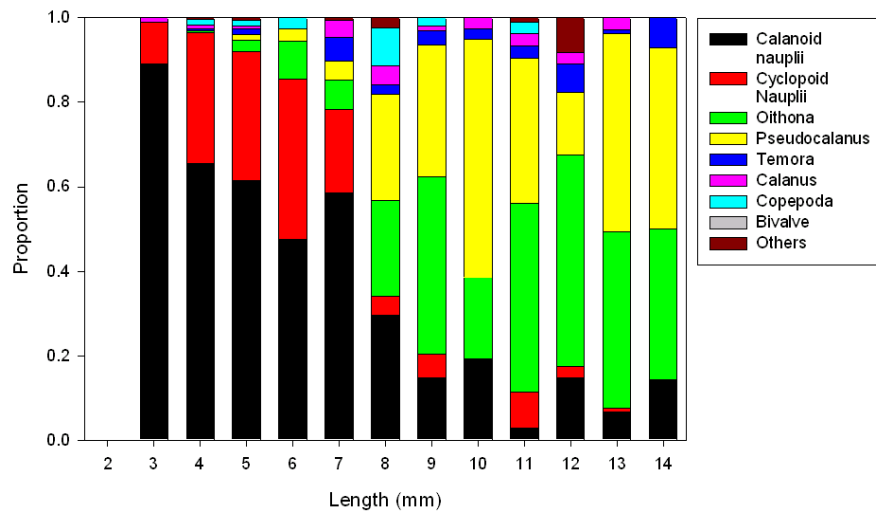
There exist a considerable body of literature on the feeding of cod larvae and juveniles from studies during 1970–80's in this area. However, there have not been new studies of the diets of cod larvae and juveniles in their natural environment during the last 10 year. On the other hand a lot of investigations have been made in mesocosms and other experimental designs.

From experiments the importance of phytoplankton/green water for the earliest larval stages has been emphasized. Similarly the experimental designs have shown that the early life stages can survive for a period on a diet of very small prey such as ciliates. In order to obtain substantial growth a diet consisting of nauplii was mandatory (van der Meeren *et al.*, 1994).

In the field, the studies during the 1970–80's identified the nauplii of *Calanus finmarchicus* as important prey of first-feeding and older larvae, and thereby confirmed the findings of Wiborg (1948). However, Wiborg (1948) also found that nauplii and copepodites of especially *Oithona helgolandica* may outnumber *Calanus* in the guts of larvae in the size range of 5–7 mm, which suggests that the diets in this area may be as diverse as in most other areas.

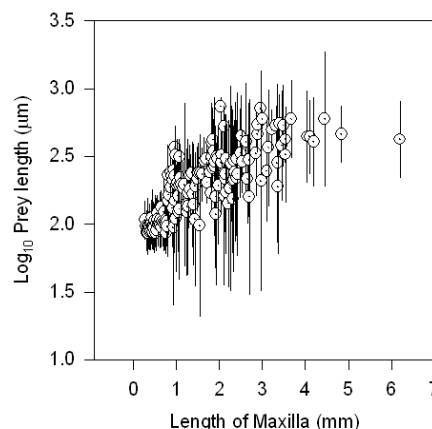
**4.1.1.5 Canada**

The diet data for cod from the Newfoundland Shelf is related to first-feeding and early larvae (<14 mm) from coastal waters, that are not necessarily representative of those found on the continental shelf. Although there are unpublished data on the prey of pelagic juveniles, the analysis is not currently available.



**Figure 4.1.2** Relative composition of the diet of cod from Conception Bay, Newfoundland, Canada, during the summer of 1986.

Newly hatched larvae up to 7 mm in length feed almost exclusively on the naupliar stages of calanoid and cyclopoid copepods. Beyond this stage copepodites of *Oithona* spp. and *Pseudocalanus* spp. become increasing (in about equal proportions) important, in terms of numerical importance (Figure 4.1.2).



**Figure 4.1.3.** Mean prey width and standard deviation in relation to maxilla length of cod larvae.

The size of prey increases with increasing size of larvae, as does niche breadth, measured as the standard deviation in log-transformed prey width (Figure 4.1.3) (Pepin and Penney, 1997). Based on prey abundance measured in the field, the effective volume swept by cod larvae for nauplii decreases with increasing larval size, possibly reflecting decreased response to this prey category, and increases with increasing larval size for both copepodite groups.

#### 4.1.1.6 US Georges Bank:

Potential prey of larval cod on Georges Bank is quite diverse with nauplii and copepodids of *Calanus finmarchicus*, *Pseudocalanus* spp, *Oithona* spp., *Centropages* spp, and *Metridia* sp. all being abundant during the March-May time period when cod larvae are present (Durbin and Casas, submitted). This is reflected in stomach content analyses (Kane, 1984; Lough *et al.*, 2005). Table 5.1.1 reflects the diversity of prey available to cod larvae on GB and indicates the changing size of prey taken by the different sizes of larvae. Despite the diversity of prey available, the various life stages of *Pseudocalanus* appear to make up the bulk of the diet

of both Atlantic cod and haddock through much of the larval period on Georges Bank (Lough *et al.*, 2005; Kane, 1984). While there is a potential issue about correct identification of N1-3 of *Calanus* and *Pseudocalanus*, this may also reflect temporal differences in abundance with *Calanus* nauplii becoming less abundant in May compared to *Pseudocalanus*, (Durbin and Casas, submitted), as well difference in vertical distribution. *Calanus* nauplii tend to be near the surface while *Pseudocalanus* is deeper and in the region where cod larvae are feeding.

**Table 4.1.1. Potential preferred prey stages (based on gut-content analysis of field-collected larval cod) of the four dominant copepods on Georges Bank for four size classes of larval cod (from Lough *et al.*, 2005)**

COPEPOD	5 MM COD (<5.5MM)	6 MM COD (5.5–6.4MM)	7 MM COD (6.5–8.4 MM)	8 MM COD (>8.5–MM)
<i>Calanus</i>	N1-3	N1-4	N1-6 C1-3	N1-6 C1-5 Adults
<i>Pseudocalanus</i> <i>spp.</i>	N1-6 C1-4	N1-6 C1-5	N1-6 C1-5 Adults	N1-6 C1-5 Adults
<i>Oithona</i>	N1-6 C1-4	N1-6 C1-5	N1-6 C1-5 Adults	N1-6 C1-5 Adults
<i>Centropages</i> <i>spp.</i>	N1-6 C1-2	N1-6 C1-3	N1-6 C1-5	N1-6 C1-5 Adults

#### 4.1.2 Temporal changes (interannual and seasonal)

The interannual changes in diets of larval cod have not been investigated in a systematic manner. Most studies have only focused on a couple of years and the differences between these years could be caused by the small-scale variation in the prey abundance rather than between years differences in prey availability and prey selection.

In the Baltic it is assumed that the delayed spawning of cod may lead to decreased availability of especially *Pseudocalanus* nauplii, however this trend is not obvious in the diet data collected in April, May and July 1994. When the seasonal changes are compared to the spatial differences observed these temporal changes appear small (Voss *et al.*, 2003; Grønkjær, unpublished). A case for seasonal differences may come from the northern North Sea where there appear to be significant differences between pre- and post-springbloom diets.

The size of cod larvae at first-feeding may influence their requirements with regard to prey size at this point. The size distribution of female spawners influence the size of eggs and larvae, and thus the demand for prey size for the larval stage may vary with time, e.g. due to exploitation. In stocks that mature at a young age, this may be more noticeable than in stock that mature at a higher age and larger size.

#### 4.1.3 Small-scale variation in the diets and patchiness

It appears that the early cod larvae are opportunistic feeders in which the main constraint in diet selection is related to the maximum prey size that can be ingested. The differences seen in the diets likely reflect the differences in encounter of potential prey. This is demonstrated in the Baltic Sea where the steep vertical gradients in prey and cod larvae abundance are clearly reflected in the diets. In areas with a pronounced vertical structure in the biotic and abiotic factors vertically integrating hauls may not represent the potential prey fauna.

Data from the Lofoten area (Skreslet, 1989) and the Baltic (Grønkjær and Wieland, 1997) suggest that the cod larvae may be able to locate and maintain themselves in patches and strata with high prey density.

There can be considerable differences in the diets of larger juveniles (>25mm) even on nearby stations. This is clearly illustrated by studies in the North Sea (Munk and Godiksen, unpublished). Although it has not been investigated this is probably related to the abundance of potential prey.

#### **4.1.4 What have we learned during the past decade?**

- Confirmation of opportunistic feeding – they appear to eat what is there within their size range.
- The quality of the diet is important for e.g. the organ development in the early life stages of cod. The quality of the diet is influenced by the individual components such as the essential fatty acids and free amino acids.
- Temporal changes in the diet composition do not seem to be large compared to the spatial differences.

#### **4.1.5 What are the critical issues or gaps in knowledge?**

- There is still a lack of direct small-scale coupling between prey field and diet.
- We do not know if the specific prey items/diets (e.g. *Calanus*) are essential to the development, growth and survival of cod at specific periods during their ontogenetic development.
- Are we too reliant on “conventional wisdom” when we make conclusions regarding the importance of specific species?
- How important is the size distribution of prey – can large larvae/juveniles survive on small prey?
- How are simple elements (e.g. phosphate, calcium) taken up by cod larvae – diets or gills.

#### **4.1.6 What are the future research directions/approaches?**

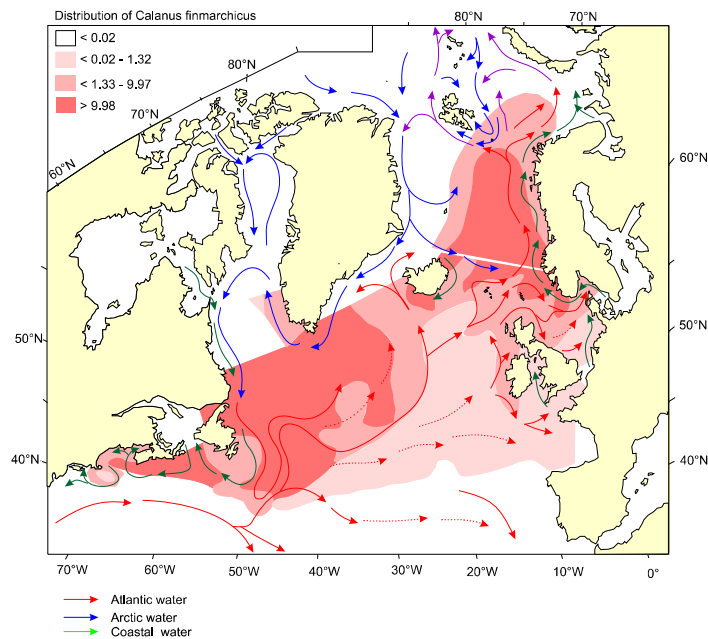
- A formal review of the diets of the early stages of cod must be undertaken in order to synthesize the large body of literature on the subject.
- Focus on ontogenetic diet shifts and try to isolate them from temporal and spatial influences.

## **4.2 The role of advection of zooplankton to larval and juvenile cod habitats**

The question of the effect of local production versus advection on the abundance of zooplankton and its availability as food for fish is an important issue. As the individual life cycle of the plankton increases the importance of the advection term increases. Phytoplankton blooms have a life span of weeks, while the life cycle of zooplankton, in general, is much longer. With a life cycle of several months, as for *Calanus finmarchicus*, the advection term may become very important. Aksnes *et al.* (1989) gave a prominent example of local zooplankton production *versus* import of zooplankton. As part of an extensive cod-rearing project, they investigated the carrying capacity for cod in Masfjorden in western Norway. Surprisingly, they found that 90 % of the zooplankton production was advected from the outside of the fjord.

On a larger scale Skjoldal *et al.* (1987) linked the variations in the zooplankton abundance in the western Barents Sea to the variations in the inflow of zooplankton-rich Atlantic water from the Norwegian Sea. Skjoldal and Rey (1989) showed that the large fluctuations in the zooplankton biomass in the Barents Sea in late spring during the period 1978–1985 were due to variations in the influx of Atlantic water from the Norwegian Sea.





**Figure 4.2.1. Large-scale features of *Calanus finmarchicus* distribution in the North Atlantic and relation the Subarctic Gyre (Sundby, 2000).**

The large-scale distribution of *C. finmarchicus* in the North Atlantic is strongly linked to the circulation system of the Subpolar Gyre (Sundby, 2000) (Figure 4.2.1). There are two core production areas of *C. finmarchicus*. One is located in the gyre system in the Northwest Atlantic, to the south of Greenland and east of Newfoundland. The other core production region is located in the gyre of the Nordic Seas. These two large-scale core production regions are deep-sea areas where also overwintering takes place. There is a large potential for advection of *C. finmarchicus* from these two core production areas onto the surrounding shelves where most of the larval and juvenile stages of fish are found. As appears from Figure 4.2.1 the horizontal gradient in concentration of *C. finmarchicus* from the deep-sea core production areas onto the shelves are large. This implies that relatively small change in the advection velocity,  $\mathbf{v}$ , may result in a large change in local concentration of *C. finmarchicus*,  $C$ , due to advection.

This can be seen from the continuity equation:

$$dC/dt = \nabla(K\nabla C) - \mathbf{v} \cdot \nabla C + \text{Production}(x,y,z,t) - \text{Mortality}(x,y,z,t)$$

where the local change in *C. finmarchicus* concentration  $dC/dt$  is a function of the 1) the diffusion term, 2) the advection term, 3) the production term and 4) the mortality term.

#### **4.2.1 Hypothesis on the link between cod recruitment, temperature and advection of copepods around the Nordic Seas**

Based on the above considerations it is of interest to explore in a general way the potential for the export of oceanic production of *C. finmarchicus* onto the surrounding shelves where it can be utilised for larval and juvenile growth of fish. The particular recruitment response of Atlantic cod stocks to temperature was described by Planque and Fredou (1999). They showed that the cod stocks located at the coldest habitats of the North Atlantic generally show an increasing recruitment with increasing temperature (e.g. the Barents Sea cod and the West Greenland cod), while those cod stocks located in the warmest habitats show increasing recruitment with decreasing temperature (e.g. the North Sea cod and the Celtic Sea cod). Those cod stocks located at intermediate temperatures show insignificant responses in recruitment to changes in temperature (e.g. the Icelandic cod). Based on the findings of Planque and Fredou (1999)

Sundby (2000) proposed a generic mechanism for the recruitment of cod stocks around the North Atlantic where the key issue was that the temperature is a proxy for the advection of water masses rich of *C. finmarchicus*. The Atlantic cod stocks are distributed around the fringes of the region of *C. finmarchicus* core abundance, as indicate in Figure 4.2.2. The cod stocks located at the upper fringe of *C. finmarchicus* distribution have a lower ambient temperature than in the core region. The cod stocks located at the lower fringe have a higher ambient temperature, while the cod stocks on the left-side fringe have an ambient temperature equal to that of the core region. An increased advection of water from the copepod rich core region to the fringes will result in improved food abundance for larval and juvenile cod resulting in better recruitment. If the increased advection is directed along a negative temperature gradient, i.e. towards the habitats of cod stocks at lower ambient temperature, the import of *C. finmarchicus* from the core region will be accompanied by an increased temperature, as for the Barents Sea cod (Figure 4.2.3A). If the increased advection is directed along a positive temperature gradient, i.e. towards the habitats of cod stocks at higher ambient temperatures than those at the core production regions for *C. finmarchicus*, the import of *C. finmarchicus* will be accompanied by a decrease in temperature, as for the North Sea cod (Figure 4.2.3C). For cod stocks located at temperature habitats approximately similar to the temperatures of the core production areas of *C. finmarchicus* the cod stocks will show no clear recruitment response to changes in temperature because the advection is occurring along the lines of equal temperatures, as for the Icelandic cod (Figure 4.2.3B).

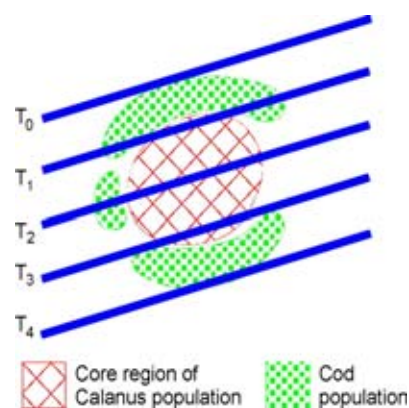


Figure 4.2.2. Principal spatial features of *Calanus finmarchicus*, cod and temperature in the Nordic Seas (Sundby, 2000).

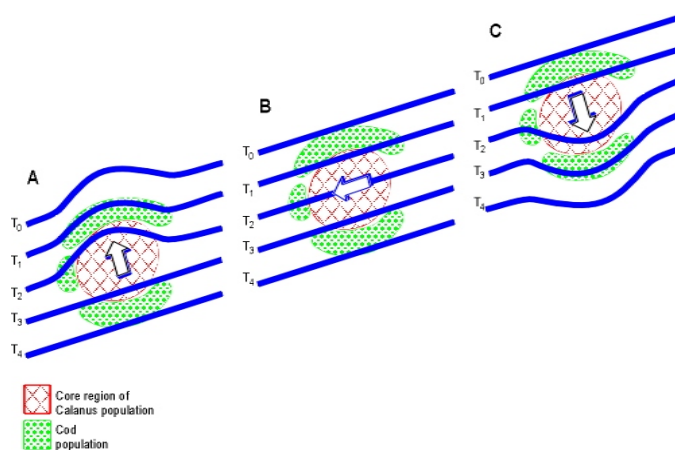


Figure 4.2.3. Conceptual model for the combined advection of heat and *C. finmarchicus* from the deep-sea core production areas onto the shelves.

#### 4.2.2 Advection of *C. finmarchicus* to the Norwegian shelf and the Barents Sea.

As described above Skjoldal *et al.*, (1987) and Skjoldal and Rey (1989) showed that the advection of Atlantic water from the Norwegian Sea into the Barents Sea is accompanied by increased abundance of *C. finmarchicus* in the Barents Sea. However, A Russian scientist indicated such relations earlier at an earlier stage (Ishevskii, 1961; Degtereva 1979). Helle and Pennington (1999) analysed a limited Norwegian time series of surveys on zooplankton in the western Barents Sea and Arcto-Norwegian early juvenile cod during the period 1978–1984. Using a model on volume flux of water into the Barents Sea developed by Ådlandsvik (1989) (see also Ådlandsvik and Loeng (1991) and Loeng *et al.*, (1997)), they found a significant positive correlation between zooplankton abundance and the influx of Atlantic water from the Norwegian Sea. They also found a positive correlation, although weaker, between the abundance of early juvenile cod and zooplankton abundance.

Ellertsen and Sundby (in prep.) study the distribution of *C. finmarchicus* in the Lofoten area at the main first feeding areas of Arcto-Norwegian cod larvae based on an extended zooplankton survey from 1987. They find that the copepods are not locally produced at the spawning areas but are advected in from the Trena Trough which is the gateway between the Norwegian Sea proper and the coastal spawning area. The Norwegian shelf contains a number of troughs that may act as gateways from the core production area of *C. finmarchicus* in the Norwegian Sea onto the Norwegian shelf. This might provide important supplies of food abundance also for other larval fish species that spawn along the Norwegian coast.

### 4.2.3 Advection of *C. finmarchicus* into the North Sea

Cushing (1984) pointed out that in certain periods there have been a weak positive correlations between North Sea haddock recruitment and abundance of *C. finmarchicus* ( $r^2 = 0.25$ ,  $p < 0.02$ ) and between North Sea cod recruitment and abundance of *C. finmarchicus*. In these cases he related the increase in *Calanus* abundance to increased inflow of water from the Norwegian Sea and the East Icelandic Current which is the region where *Calanus* is most abundant in the Northeast Atlantic. He also pointed out that during influxes of *Calanus*-rich water from the Norwegian Sea the temperatures decreased as shown by Dickson *et al.*, (1974). However, Cushing (1984) tended to focus on the effect of delayed *Calanus* production by the cooler water and hence a better temporal match in abundance between the early larval cod and zooplankton rather than the effect of increase in total zooplankton abundance as a result of increased advection. Brander (1992) reanalysed the relationships between *Calanus* and cod recruitment, including the effects of inflows, and concluded that they did not hold. Rothschild (1998) analysed the relationships between abundance of zooplankton and year-class strengths of North Sea cod and herring, including also the variations in fishing mortality. He found that large year classes of cod co-occurred with either high abundances of *Calanus* or *Paracalanus/Pseudocalanus*. He also found that high abundance of both *Calanus* and *Paracalanus/Pseudocalanus* rarely occurred. In years with low abundance of *Calanus* or *Paracalanus/Pseudocalanus* good recruitment of cod occurred only once while in all the other ten years with low zooplankton abundance bad cod recruitment occurred.

### 4.2.4 The relation between *C. finmarchicus* and recruitment of Icelandic cod

There is no direct evidence of advection of *C. finmarchicus* onto the Icelandic shelf. However, there are reports on the importance of abundance of *C. finmarchicus* for Icelandic cod recruitment. Astthorsson *et al.* (1994) showed that there was a positive correlation between zooplankton biomass in southwestern Icelandic waters (the region where the larval stages of cod are found) and the abundance of 0-group cod during 1971–1992. They did not find a significant correlation between mean length of 0-group cod and zooplankton abundance, but concluded that it is less likely that food conditions in the very early stages should be correlated with length at the 0-group stage.

### 4.2.5 Role of Advection of Zooplankton to larval cod habitats in the Western North Atlantic

#### 4.2.5.1 Gulf of St Lawrence

In the southern Gulf of St Lawrence advection of copepods onto shallow regions where mackerel are spawning appears to enhance their survival (Runge *et al.*, 1999).

#### 4.2.5.2 Scotian shelf

Head *et al.* (1999) suggest that the source of *Calanus finmarchicus* on the western shelf in the spring is from Slope Water. Runge and Plourde (1993) suggest that the Gulf of St Lawrence may also be a source of *Calanus* to the Scotian Shelf.

#### 4.2.5.3 Georges Bank

Water enters onto Georges Bank (GB) from the Gulf of Maine (GoM) in the region of the Northeast Peak and flows clockwise along the southern flank. Populations of *Calanus finmarchicus*, *Oithona*, *Pseudocalanus* and *Metridia* on GB are advected onto the bank from the Gulf of Maine (Durbin *et al.*, 1997; Durbin and Casas, submitted). Modeling (Hannah *et al.*, 1998; Lynch *et al.*, 1998; Miller *et al.*, 1998) supports a Gulf of Maine source of *Calanus* to Georges Bank. Other taxa on the Bank (*Centropages typicus*, *C. hamatus* and *Temora*) have

local populations on the shallow tidally mixed crest region of the bank and are less abundant on the flanks of the bank. Cod tend to spawn on the NE Peak of GB where water first enters onto the bank from the GoM (Smith, 1985) and are advected around the S flank as they grow. The NE peak is a region of high abundance of nauplii of off bank copepod taxa, particularly *Calanus*. As the cod larvae are advected along the southern Flank, the *Calanus* population is growing and abundance of older stages is higher. On an evolutionary time scale, cod may have adopted the NE Peak as a focal point for recurrent spawning because of the predictable supply of prey for their larvae, starting in mid-winter.

There is interannual variability in copepod abundance on GB (Durbin and Casas, submitted.). These differences are related to salinity with higher abundance when salinity was lower. The lower salinities result from shelf wide surface salinity waters being propagated down the shelf, perhaps from the Labrador Shelf/Sea. The mechanism by which salinity affects copepod populations is not clear. It may be an effect on timing of the winter/spring phytoplankton bloom in the Gulf of Maine enhancing production of copepods in this region (Durbin *et al.*, 2003; Pershing *et al.*, submitted.) that are subsequently advected onto Georges Bank.

#### **4.2.5.4 Larger scale advective linkages.**

A series of *Calanus* sub-populations are present in the western N Atlantic (Gulf of St Lawrence, Slope Sea, Gulf of Maine). These are linked through advection but the linkage is one way through westward flow along the shelf and in Slope water with no apparent recirculation occurring as in populations in the Labrador Sea and Norwegian Sea populations. There is a link between the Labrador Sea populations to the Slope Sea through transport in Labrador Current water, either at the surface, or at depth. Velocities at depth between the Flemish Cap region and the slope sea off the Scotian Shelf are short enough to transport resting *Calanus* (Luo *et al.*, submitted.).

### **4.3 Zooplankton and fish larval distributions at oceanographic discontinuities (fronts)**

Spawning of cod often takes place close to hydrographic discontinuities (fronts). Examples of cod spawning in the vicinity of frontal zones are seen at the flanks of Georges Bank, off the Faeroe Plateau and in the North Sea at the zones between coastal currents and central water masses of Atlantic influence. When hatching, cod larvae are still within the areas of fronts, and a number of observations suggest that the early life of cod is tightly linked to frontal processes.

The frontal processes lead to upwelling of nutrients, hence primary production is often enhanced, and moreover, surface convergent flow towards the centre of the frontal zone might lead to aggregation of plankton organisms across the zone. Hence, recurrent observations of cross-frontal variation in primary producers, meso-zooplankton and fish larvae, show peak abundances of these organisms in the area of the frontal zone. However, while being within the frontal zone, the exact positions of peak abundances are often displaced among species from the same group. For example the dominant copepod species in the (frontal) areas of cod spawning in the North Sea, differ in their patterns of distribution, smaller species, such as *Acartia* sp. and *Temora* sp. are distributed in the inshore areas of the front while larger species, such as *Pseudocalanus* sp. and *Calanus* sp. are distributed further offshore.

Observations in the North Sea indicate that the differences between spatial distributions of meso-zooplankton species have great consequences for the prey available to cod larvae. When newly hatched, cod larvae are found in the more inshore areas, overlapping distributions of smaller copepod species, such as *Acartia* sp., *Centropages* sp., *Oithona* sp. and *Temora* sp.. During ontogeny the larvae often will be distributed further offshore, where they meet larger prey of the species e.g. *Calanus* sp, *Pseudocalanus* sp. and *Metridia* sp. However, the spatial

overlap between late-stage cod larvae and the larger copepod species might vary extensively between regions and years. In the north-eastern North Sea, for example, significant overlap was seen between *Calanus* sp. and late stage cod larvae in 1992 (Munk *et al.*, 1995), while much less overlap was apparent during the same period in 2001 (Munk, unpublished).

The distributional patterns of both fish larvae and the meso-zooplankton prey are much connected to the specific hydrographic characteristics and the extent and position of frontal features. Hence the temporal variation in hydrography on a range of scales, for example daily (wind and tide), seasonal (weather) or annual (climate), have strong influence on patterns of distribution and the extent of overlap among species. These physical-biological linkages should be included in the understanding of zooplankton-fish larvae interaction

#### **4.4 Zooplankton predation on cod eggs and fish larvae**

The role of predation by zooplankton, nekton and small pelagic fish on population dynamics of cod eggs and larvae remains one of the most poorly studied elements of the life history. There have been relatively few detailed experiments conducted dealing with predation by zooplankton on ichthyoplankton in general, and those dealing with specifically with cod are in the minority.

General knowledge about the role of predation, the animals that are most likely to prey on the early life stages of cod, and the rate at which they will do so represent the greatest sources of uncertainty in models of egg and larval dynamics. The most common practice in models of egg and larval dynamics (e.g. individual-based models) is to apply some form of size-dependent mortality to represent predation, which is consistent with general principles from reviews (Bailey and Houde, 1989; Paradis *et al.*, 1996). Despite the possibility to apply basic principles such as size-dependency, there is no accepted approach to estimating the role of predation, let alone predict the effect of variations in the abundance and overlap between predators and egg/larval cod on survival potential.

Lack of the most basic knowledge about which groups of invertebrate carnivores prey on cod eggs and larvae represents a key area for research. Beyond the basic description of interactions, there is a strong need to develop tools and approaches that can be used to estimate the impact of predation on population dynamics, in both space and time. Because many crustacean species have unidentifiable gut contents, development of biochemical methods for the identification and quantification of prey-predator interactions (e.g. Theilacker *et al.*, 1993) are essential. Quantification and monitoring of the occurrence, abundance and overlap of a wide class of invertebrate predators (e.g., predatory copepods, euphausiids, medusa) with egg and larval cod must also be a priority, as is any research dealing with the potential role of predation (including the role of planktivorous fish), if process models are to achieve any predictive capability.

The following information has been extracted from ICES Cooperative Research Report No. 274 concerning the state of knowledge on the role of predation in cod stocks. It is notable that information is available for only three of the seventeen stocks reported on in the report.

##### **4.4.1 Arcto-Norwegian cod**

In some instances medusae, especially ephyra of *Aurelia aurita*, have been observed with cod eggs in their stomachs, in a few cases also with cod larvae (Melle and Ellertsen, 1984; Melle, 1985). Herring are found with large numbers of cod eggs in their gut (Melle, 1985).

##### **4.4.2 Baltic Sea**

Substantial predation by clupeids on cod eggs has been described for the Bornholm Basin, which is at present the only important spawning area of the eastern Baltic cod stock. Egg pre-

ation is most intense at the beginning of the cod spawning season, with sprat being the major predator (Köster and Schnack, 1994). At this time spring spawning herring concentrate in their coastal spawning areas and do not contribute to the predation-induced egg mortality of cod. Sprat spawn in the Bornholm Basin from March to July, thus concentrating in cod spawning areas at times of high cod egg abundance. After cessation of spawning, part of the sprat population leaves, resulting in reduced predation pressure on cod eggs. With the return of the herring from the coastal areas to their feeding grounds in the Bornholm Basin, the predation on cod eggs by herring increases to considerable levels (Köster and Möllmann, 2000).

#### **4.4.3 Gulf of Maine and Georges Bank**

Predation is considered to be an important source of pre-recruit mortality despite limited direct evidence. Mackerel and herring are likely predators of pelagic cod larvae and juveniles when their distributions overlap in the spring (Garrison *et al.*, 2000). Various invertebrate predators (e.g., amphipods, jellyfish, chaetognaths, crustacean, and squid) can have a potential impact and the quantification of these potential mortality rates will be made in the U.S. GLOBEC Georges Bank Study. Many piscivorous fish, such as dogfish, silver hake, larger cod, and sculpin, prey on juvenile cod (Edwards and Bowman, 1979).

Behavioural observations show that a suite of invertebrate predators will respond and attack fish larvae under laboratory settings. Large carnivorous copepods (e.g. *Eucheata* spp.) and euphausiids were shown to respond to the presence of larval cod (Browman, unpublished data). Gelatinous zooplankton may also be important predators of young cod, as they are for other species of fish, but the lack of observations and basic information remains a hindrance to understanding their influence on population dynamics. The degree to which this happens in nature is uncertain. Research in the Baltic Sea has demonstrated that the spatial overlap between cod eggs and adult sprat plays an important role in the interaction between these organisms (Köster and Möllmann, 2000).

### **4.5 Modelling the zooplankton/fish interaction**

There is a large literature on the efforts of relating zooplankton production to growth and survival of larval fish, including modelling. Now many research groups are engaged in efforts to build coupled biophysical models including the spatial and temporal interactions between zooplankton and larval cod, i.e. the integration of general circulation models with biological formulations of growth, feeding and behaviour of larval fish. These models are currently our main tool to integrate research from laboratory studies on sensory ecology, environmental effects on feeding and growth processes with large-scale fluctuations in oceanography and productivity of marine ecosystems driven by climatic forcing. The models are maturing, but still have important limitations, e.g. in the representation of small scale predator-prey interactions (see Section 3.8 and 4.5.3), the distribution of prey at a sub-grid scale (Pepin, 2004) and in realistic representation of larval behaviour and physiology.

Important results are also emerging from simpler models. For instance, the finding that larval cod in the field tend to grow near their temperature-limited growth rates (Folkvord, 2005) may suggest that food limitation plays a minor role in larval growth, and that changes in temperature are the main cause of growth variability. On the other hand, there are theoretical reasons to believe that higher food availability may lead to lower predation rates (see position paper by Fiksen in Annex 6), but this has not been explored in great detail for larval cod (but see Skajaa *et al.*, 2003).

#### **4.5.1 Coupled biophysical models**

Variations in marine fish egg and larval transport has been suggested as one of the important factors affecting recruitment variability in fish stocks (Iles and Sinclair, 1984; Fortier and

Leggett, 1985; Smith and Stoner, 1993; Lough *et al.*, 1994). Recent modelling efforts to understand the causes of mortality and survival of larval fish have focused on examining the effects of advective and trophodynamic processes (e.g. Werner *et al.*, 1996; Letcher *et al.*, 1996; Hinrichsen *et al.*, 2002). Motivation for this approach also stems from the observation that, in some cases, larval fish are dependent on circulation patterns for transport from the spawning ground to the nursery area. Local biological and physical events may explain fish early life stage growth and survival patterns, thus the development and utilization of coupled biophysical models became important for analysing these combined effects on fish recruitment. These models considered the spatial heterogeneity in environmental conditions by integrating larval trophodynamics (Figure 4.6.1.1.) into three-dimensional hydrodynamic models (see review in Runge *et al.*, 2005). Presently, several of these coupled biophysical models have been established, e.g. for walleye pollock (Hermann *et al.*, 1996, 2001; Hinckley *et al.*, 1996), haddock off Scotland (Heath and Gallego, 1998, 2000) and on Browns Bank (Brickman and Frank, 2000; Brickman *et al.*, 2001), bay anchovy from Chesapeake Bay (Rose *et al.*, 1999), and cod on Georges Bank (Werner *et al.*, 1996, Lynch *et al.*, 2001) and in the Baltic (Hinrichsen *et al.*, 2002).

Trophodynamic relationships are generally based on the contact rates and the interaction of larval fish as predators and zooplankton species/stages as their potential prey. The coupling of circulation models with trophodynamic relationships of larval or juvenile fish can be utilised to examine starvation mortality and growth rates at the level of individuals as well as estimating larval and juvenile losses from the system (e.g. Rose *et al.*, 1993, Hinckley *et al.*, 2001; Werner *et al.*, 1996). These coupled models allow examination of feeding success, growth, and starvation mortality of larvae and juveniles in the context of their transports by utilising trophodynamic relationships along their potential drift routes. Implementation of coupled models requires information on the distribution and abundance of zooplankton as well as light, turbulence and temperature fields as inputs to the larval and juvenile feeding. In addition, metabolic, and growth components must be accounted for.

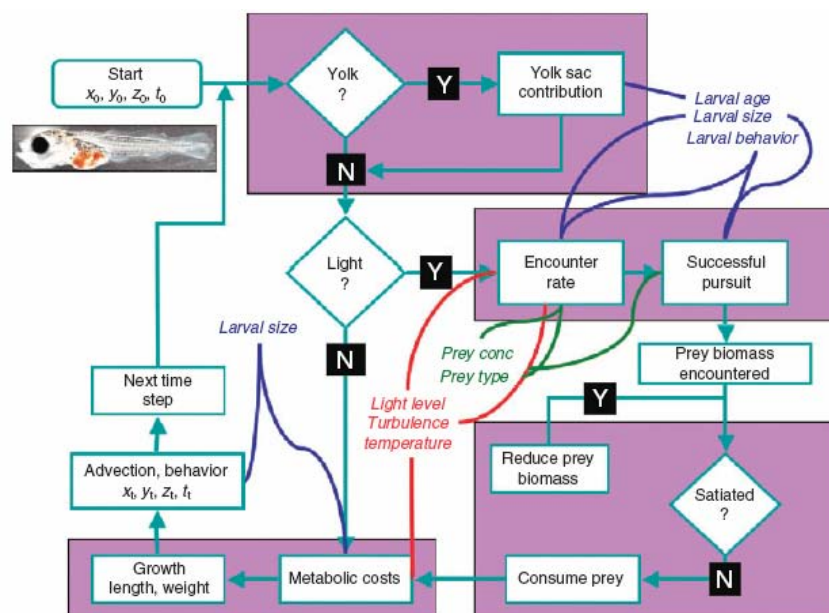
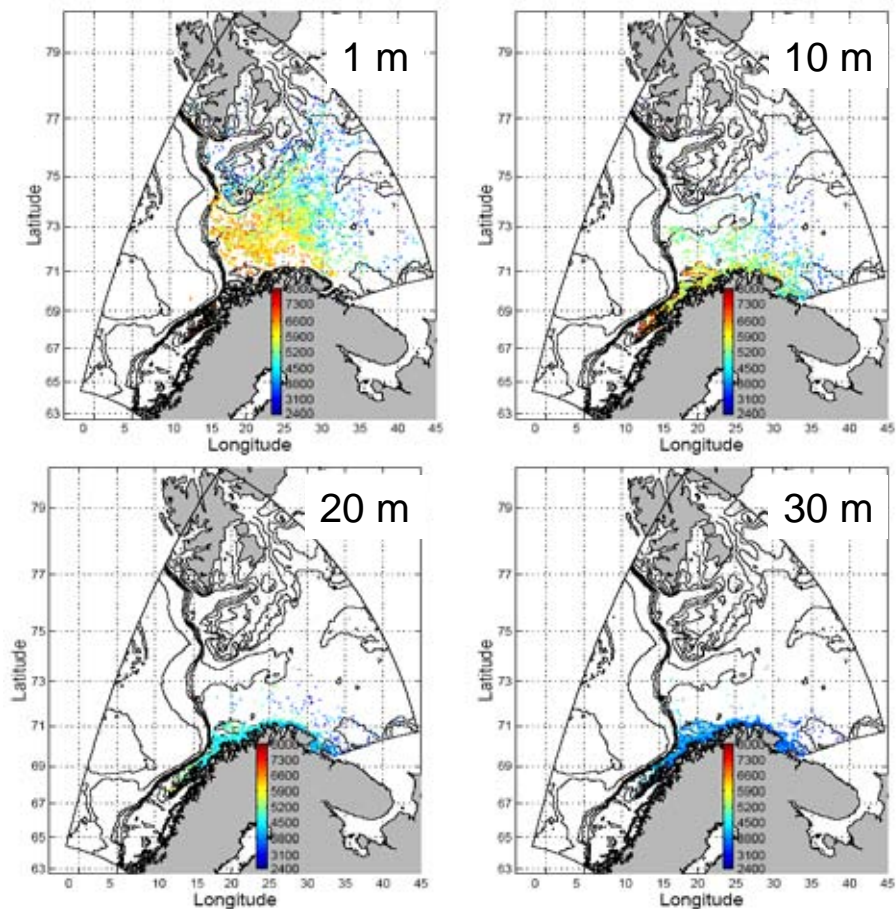


Figure 4.6.1.1. The general structure of trophodynamic models. Modified from Lough *et al.* (2005).

In general, the hydrodynamic models using either Lagrangian particle tracking (e.g. Werner *et al.*, 1993; Hinrichsen *et al.*, 1997) or advection-diffusion equation models (Lynch *et al.*, 1998) resolve the small-scale vertical and mesoscale horizontal variability of the hydrodynamics quite well. Although circulation patterns are relatively well known, validation of the results



from coupled biophysical models is difficult. The number of factors potentially influencing the effect on transport of larval fish is large. Variations in larval transport and hence horizontal distribution of pelagic and demersal stages of juvenile fish can be caused by intra- as well as interannual variations in meteorological forcing, temperature, light intensity, river runoffs, turbulence, frontal structure, sea level gradients, hydrographic property fields and surface heat fluxes. The dominant biological limitations to adequate modelling of transport of larvae are their vertical distribution and the timing and location of hatching. As an example, Vikebø *et al.* (in press) recently did a numerical analysis where particles (larvae) were released over some time from a fixed point in Vestfjorden (the spawning area of NEA cod) and then drifted at slightly different depths (1, 10, 20 and 30 m) over a few months. Both temperature-exposure (thus size-at-age) and spatial distribution were highly sensitive to the choice of depth for the particles (Figure 4.6.1.2). Deeper particles end up closer the coast and are exposed to lower temperatures than particles near the surface.



**Figure 4.6.1.2.** The sensitivity of spatial distribution and size at age for larval cod drifting from the Vestfjorden area into the Barents Sea. Modified from Vikebø *et al.*, (in press).

Trophodynamic processes are the most difficult to implement in models of larval growth and survival because of the difficulties in formulating, parameterising and validating such models experimentally or by data obtained during field programs. In general, coupled biophysical models examining the effects of larval feeding on growth and survival have to cope with a relatively sparse temporal and spatial resolution of prey fields.

Results of coupled biophysical models do not represent any new factual knowledge generated internally to the model itself, but are a reflection of the knowledge, insight, and assumptions that went into the model's formulation. Although, the biological part of those models often tend not to be very useful in a predictive sense, they are extremely useful components as intui-

tion building tools for scientific investigations, to identify data requirements and to test hypotheses. Furthermore, they may provide virtual environments that can be used to follow experimental designs and are a valuable tool to run controlled experiments and scenarios. The application of coupled biophysical models can potentially be very useful for aiding in the design of sampling programs and the determination of processes influencing the distribution of selected parameters. However, longer simulation runs will provide increasing uncertainties in the modelled property and current fields, and hence in the corresponding drift patterns. These uncertainties may arise from errors in the specified forcing, boundary and initial conditions, and subgrid scale physical processes not resolved by the model dynamics. To overcome at least some of these problems the utilisation of assimilation techniques to incorporate e.g. field observation may become important for long-term simulations.

As an additional tool, particle tracking techniques as part of coupled biophysical models also allow a backward projection of larval drift paths in order to trace larvae back to the sites where they were hatched and, moreover, can also give an estimate of the drift routes of larvae by starting recalculation from the different locations of the nursery areas of juvenile fish. Backward projection enables environmental reconstruction of larval fish to be contrasted with growth histories.

Recent IBM's for larval cod have added more biological realism by including functions describing the effects of physical processes on feeding (e.g., turbulence, light levels, e.g., Fiksen *et al.*, 1998; Fiksen and MacKenzie, 2002; Utne-Palm and Stiansen, 2002) as well as innate, physiological attributes (e.g., temperature- and size-specific metabolic rates, feeding satiation levels) (Lough *et al.*, 2005; Peck *et al.*, submitted). Thus, current parameterisations enable a more dynamic model response to concomitant changes in prey levels and temperature.

Another significant advancement in the use of IBMs as tools to understand the relationship between larval cod, their zooplankton prey and cod recruitment dynamics has been the inclusion of realistic prey fields based upon extensive field sampling (Georges Bank, Baltic Sea) (Hinrichsen *et al.*, 2002; Lough *et al.*, 2005) and larval cod gut content analyses (Lough *et al.*, 1997). Incorporation of prey field dynamics has included the role of microzooplankton on early cod survival (Quinlan *et al.*, 1997) as well as a 10-year retrospective analyses of the impact of changes in larval cod prey in the Baltic Sea (Hinrichsen *et al.*, 2002). Most recent modelling efforts include a detailed examination of the effect of changes in the copepod naupliar abundance (mean and variance) and species composition on first-feeding larval cod survival (Schmidt and Hinrichsen, submitted).

Sensitivity analyses of parameter estimates have been performed within a number of larval cod IBMs (Werner *et al.*, 2001; Hinrichsen *et al.*, 2002; Lough *et al.*, 2005). IBM growth estimates of larval cod are sensitive to both basic bioenergetic parameters (assimilation efficiency, metabolic costs) as well as to parameters associated with prey detection (visual field). In this light, one of the future challenges to cod modelling efforts will be to correctly parameterise the small-scale processes of prey detection, pursuit and capture. Recent studies suggest that previously used parameterisations for prey encounter by early stages of larval cod in IBMs may have dramatically overestimated the larval visual field causing overestimates of prey encounter and feeding (Galbraith *et al.*, 2004). If this is the case, offsetting errors must also exist within current model parameter estimates. In general, parameter estimates for these cod IBMs have been critically evaluated, corrected or updated (e.g., Buckley *et al.*, 2000; Peck and Buckley, submitted). A consensus exists that further laboratory studies on basic elements of physiology, behaviour and feeding of larval cod will improve IBM growth and survival estimates. Less mechanistic IBMs (e.g., Heath and Gallego, 1997) should also be employed to provide predictive capacity on targeted issues relating to larval cod – zooplankton interactions.

#### 4.5.2 Modelling small scale interactions between zooplankton and larval cod

Models of small scale processes of larval fish and zooplankton interactions have appeared frequently in the literature over the last decade. Most of the efforts have been related to feeding of larval fish, and how this is connected to environmental factors such as light and turbulence, to the actual feeding behaviour of larvae or other factors such as the escape ability of prey.

##### Feeding processes:

Feeding rates in larval cod are modelled in different ways, but all include a 'clearance rate' or the volume scanned for prey in a given time period. Considerable laboratory experiments have been allocated to quantify the feeding rate of larval cod the last decade. The most common equation that has been parameterised is:

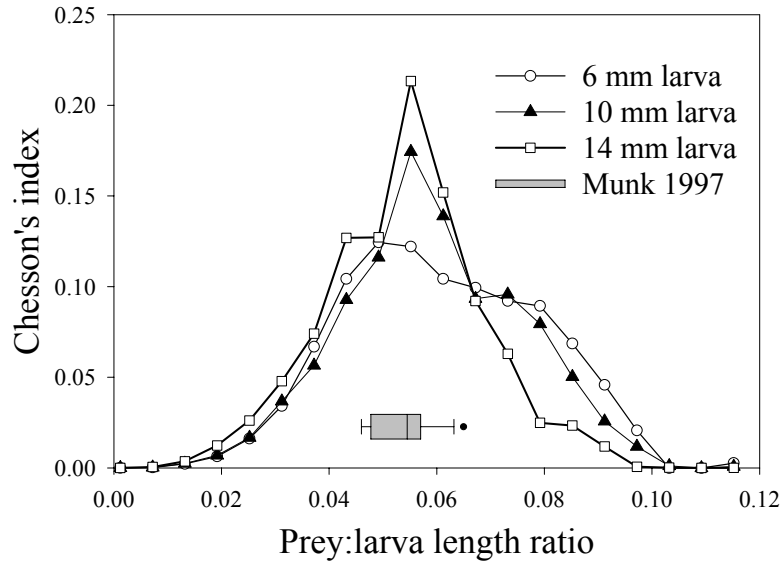
$$e = \frac{2}{3} \pi r^3 N f + \pi r^2 N \sqrt{(u^2 + 2\omega^2)} f \lambda$$

which describes the prey encounter rate for a pause-travel feeding mode, including contributions from prey movement and turbulence. This expression, first suggested for larval cod by Kiørboe and MacKenzie (1995) and MacKenzie and Kiørboe (1995) is applied in the US GLOBEC models, and by the group in Bergen. There are at least two critical parameters that are difficult to decide on in this formulation, and that is the prey detection distance ( $r$ ) and the pause duration ( $\lambda$ ). The prey detection distance is cubed in the expression and represents the most sensitive parameter. Prey detection distance have usually been fixed between 0.5 and 1 body length in the coupled models, but in Lough *et al.* (2005) this was also truncated to 0 at light levels below 0.1 lux, increasing linearly to 0.7 lux and then light is not limiting above this level. Fiksen *et al.* (1998) and Fiksen and MacKenzie (2002) applied a more general model of prey detection distance,

$$r \cong \sqrt{S_e C A_p \frac{E_b}{K_e + E_b}}$$

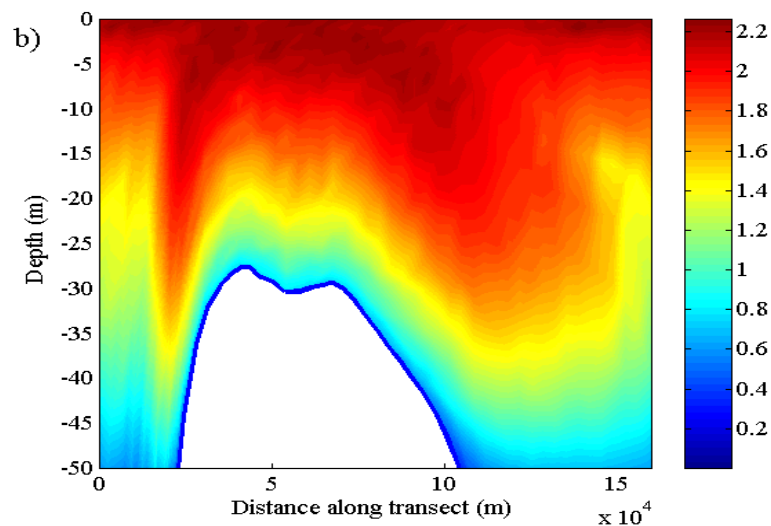
This model includes the effect of prey size and contrast, larval visual capabilities and ambient light level. This model is also difficult to parameterise, and the key parameter would be  $K_e$ , determining how prey detection distance drops with light. In addition, little is known about how prey can be detected with senses other than vision.

The actual shape of the visual field has also been questioned lately (Galbraith *et al.*, 2004). These issues will be very important for the actual levels of prey concentrations where larvae will be predicted to be food limited. Fiksen and MacKenzie (2002) formulated a very detailed model of larval cod feeding on zooplankton, including encounter processes and the subsequent prey capture successes determining the realised diet of the larvae. This included increasing encounter probability with prey size and a stochastic decrease in capture success with relative prey size, and generated results in line with the field data from Munk (1997) (Figure 4.5.2.1).



**Figure 4.5.2.1. Simulated prey selection (Chesson's index) of larval cod as predicted by the model by Fiksen and MacKenzie (2002), for three different larval sizes, compared with the field data from Munk (1997).**

Both this model and the one by Fiksen *et al.* (1998) emphasised the interaction between light and turbulence in the feeding process of larval fish. Turbulence may both increase and decrease the ingestion rate (Mackenzie *et al.*, 1994; MacKenzie and Kjørboe, 2000). In one simulation, Fiksen and MacKenzie (2002) showed how the prey encounter rates for larval cod would vary over one diel cycle across across the Georges Bank, including the natural light cycle and the tidal cycle (Figure 4.5.2.2).

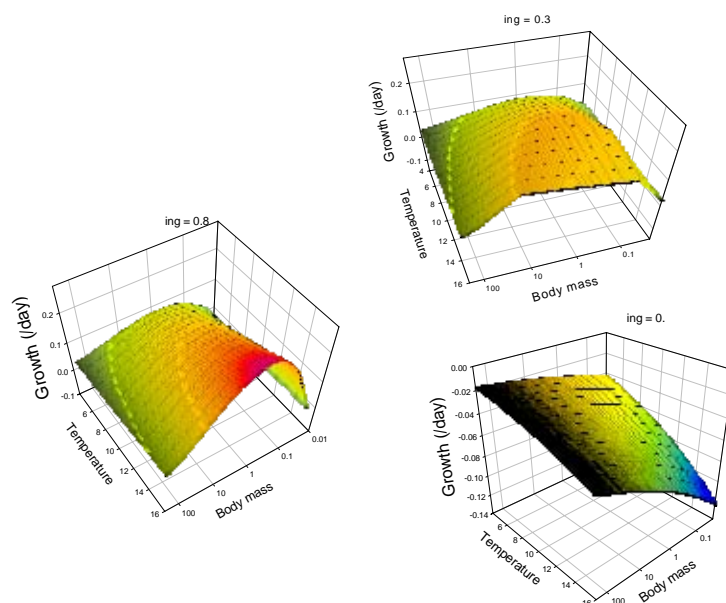


**Figure 4.5.2.2. Integrated prey encounters over a diel and a tidal cycle over Georges Bank. Predictions from the model by Fiksen and MacKenzie (2002).**

### **Modelling growth and food limitation.**

Food limitation occurs when ingestion rates are too low to sustain the maximum growth rates, determined in larval cod by size and temperature (Folkvord, 2005). This process has been modelled with bioenergetic sub-models (Werner *et al.*, 1996; Lough *et al.*, 2005), but in IBM's including stomach fullness as a state variable, this can be treated quite simply by com-

binations of models in Folkvord (2005) and Finn *et al.*, (2002). This is the approach taken by Kristiansen *et al.* (in prep.), as depicted in Figure 4.5.2.3.



**Figure 4.5.2.3 Food limitation in growth-model of larval cod:** As long as the food intake is high ( $ing = 0.8$ , ingestion per day is 80% of body mass), larvae grow near maximal rates as determined from lab experiments (Folkvord, 2005), at intermediate ingestion rates ( $ing = 0.3$ , ingestion per day is 30% of body mass) the highest growth rates can not be sustained, and at no food intake ( $ing = 0$ ), the larvae will loose mass according to Finn *et al.* (2002). From Kristiansen *et al.* (in prep).

### 4.5.3 Fine-scale mechanistic aspects of ichthyoplankton-zooplankon interaction

Sensory perception links an organism's internal and external ecologies. It thereby also connects conspecifics to one another, and underlies many of the biological-ecological links between species in communities (Weissburg and Browman, 2005). Studying these perceptual links can help marine ecologists understand the basis for the responses (or lack thereof) that they observe. Examples of direct relevance to the theme of this workshop follow.

#### Fish larvae as predators

Turbulence and predator-prey interactions in the plankton: Substantial effort has been applied in attempts to demonstrate that microscale turbulence can significantly increase the feeding rate of planktonic predators (reviewed in Dower *et al.*, 1997). This effort has been driven by the theoretically-derived conclusion that microscale turbulence increases the encounter rate between planktonic predators and their prey. The original theory assumed that the geometry of the water volume perceived (i.e., searched for prey) by a predator is spherical (Rothschild and Osborn, 1988). More recent theoretical formulations assume a forward-projecting hemispherical perceptual volume (reviewed in Dower *et al.*, 1997; Galbraith *et al.*, 2004). However, for all planktonic taxa for which such information exists, the geometry of the perceptual field is neither a sphere nor a hemisphere (see Lewis, 2003; Galbraith *et al.*, 2004). The manner in which a non-symmetrical perceptual field might affect the conclusions of turbulence encounter theory was recently examined by Lewis (2003) for cruise searching copepods. He concludes that, under turbulent conditions, the optimal swimming strategy (associated with prey search) for predators with non-symmetrical perceptual fields differs radically from what is otherwise predicted. Analogous work on larvae of Atlantic cod (*Gadus morhua*) produced a similar result: the advantage of turbulence is greatly reduced when the perceptual space is parameterized with a more realistic geometry (Galbraith *et al.*, 2004). Since virtually all models of predator-prey interactions in the plankton – zooplankton-phytoplankton; zooplankton-

zooplankton; ichthyoplankton-zooplankton – have at their heart a parameter for the distance at which prey can be located, this demonstrates how empirical knowledge of the perceptual abilities of marine organisms is essential. Without such information, we risk making large errors in prediction, which can lead to misleading and/or incorrect conclusions.

“Operational” prey abundance and the myth of prey choice/prey selectivity by small zooplanktivores: Although the abundance of prey that could be consumed by small zooplanktivores is temporally and spatially highly variable, it is reasonable to state that it most often ranges between 0 and  $10^1 \text{ l}^{-1}$ . The volume of water contained in the visual perceptual field (VPF) of a 6 to 10 mm fish larva is approximately 0.8 to 1.0 ml (see Browman and Skiftesvik, 1996; Galbraith *et al.*, 2004). Thus, at an *absolute* prey abundance (AA) of  $100 \text{ l}^{-1}$ , there would be only 0.08 to 0.1 prey items within the VPF at any given instant. The number of prey per VPF is the *visual* abundance (VA) and, from the perceptual perspective of the predator, VA, *not* AA, is the operational measure of prey availability. Thus, for this predator, AA would have to be  $> 2000 \text{ l}^{-1}$  in order for VA to be  $> 1$  (prey aggregations at thin boundary layers may be this dense: Gallager *et al.*, 2004). These VA numbers illustrate that small zooplanktivores – for example, carnivorous copepods or fish larvae - will only rarely have an opportunity to *actively* choose from amongst several simultaneously available prey items. While it is possible that these predators make choices from amongst prey encountered sequentially, under anything but the highest of prey abundances they must eat whatever and whenever they can, or risk starvation. Discussions of prey choice and/or active prey selectivity in these taxa must be undertaken within this context.

Conceptual and/or numerical models that attempt to define feeding rate, prey choice or prey selectivity in small zooplanktivores all use AA as an input variable. Since VA is three orders of magnitude less than AA, this represents another example of the need to accurately characterise the perceptual abilities of these organisms in order to realistically parameterise such models. Failure to do so leaves us at risk of making interpretive and predictive errors about predator-prey dynamics in marine food webs.

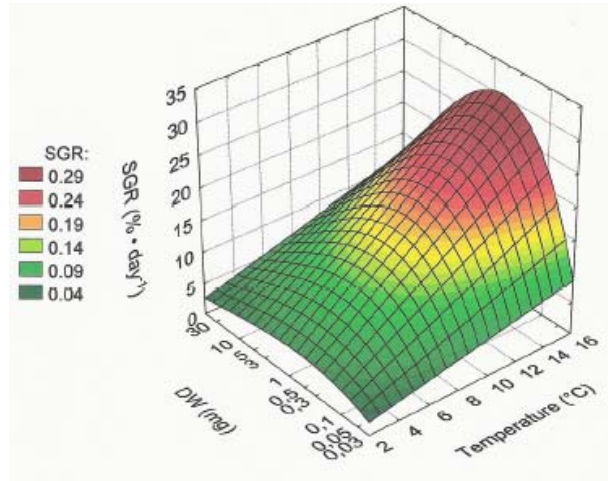
### **Fish larvae as prey**

Traditional aquatic food webs place plankton at the base of the food chain, often with fish as the top predator. However, during ontogeny, fish go through a phase as an important (albeit transient) member of the plankton. At this small size, fish larvae are subject to predation by other plankters: carnivorous copepods such as *Paraeuchaeta norvegica*, chaetognaths, gelatinous zooplankton, other ichthyoplankton, etc.

As early larvae, fish have only a limited capability to perceive and escape from predators. In contrast, many adult invertebrates, and/or older larval or juvenile fishes, are formidable predators against which early-stage fish larvae would have virtually no chance. There are almost no empirical observations of such interactions (although see Yen and Okubo, 2002; Browman *et al.*, in preparation).

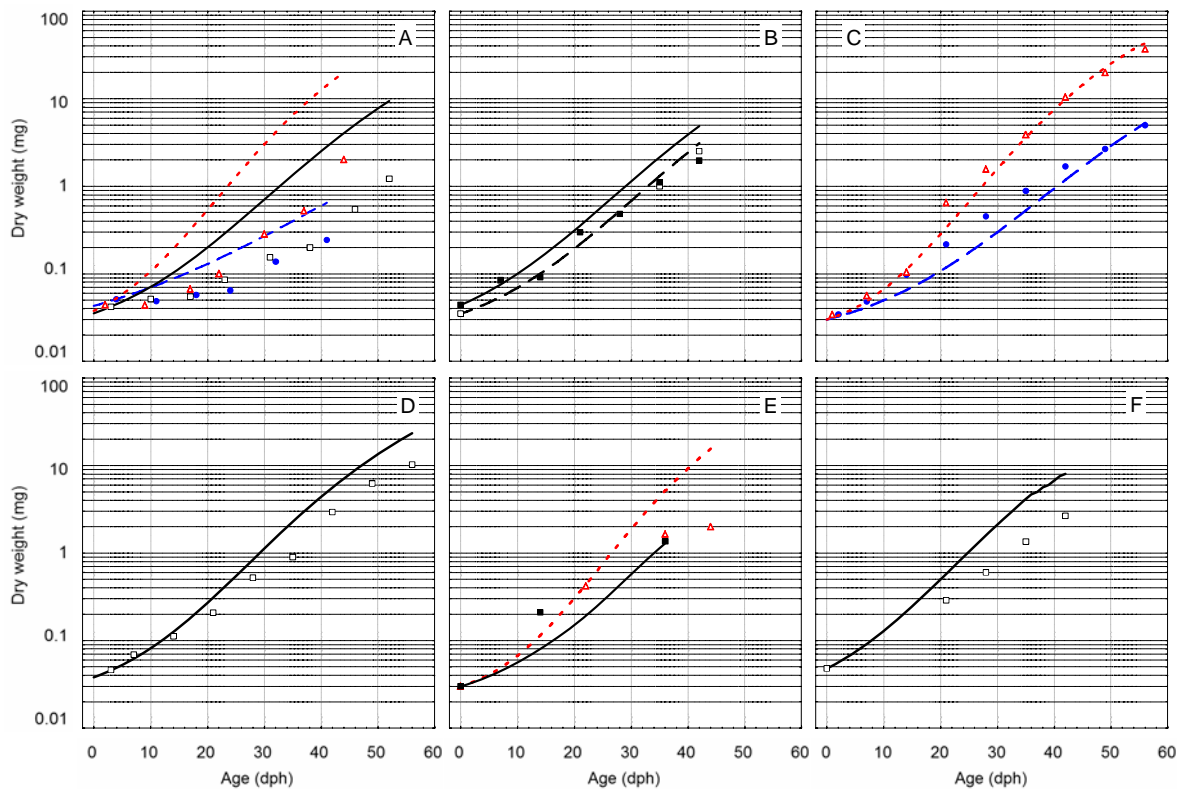
#### **4.5.4 Comparison of size-at-age of larval cod (*Gadus morhua*) from different populations based on size- and temperature-dependent growth models**

The motivation for the study was to review intra-specific larval growth performance across several different experimental scales, environments and regions of a marine fish species (Folkvord, 2005). Size- and temperature-dependent growth models for larval and early juvenile cod (*Gadus morhua*) are developed based on selected laboratory experiments with cod fed in excess (Figure 4.5.4.1).



**F4igure 5.5.4.1. Size- and temperature dependent growth model for Norwegian coastal cod.**

Observed size-at-age of cod from several experiments and stocks are compared with predictions from the models using initial size and ambient temperature history as inputs. Comparisons with results from other laboratory experiments reveal that the model predictions represent relatively high growth rates (Figure 4.5.4.2).



**Figure 4.5.4.2. Predicted size-at-age from different lab- studies (lines) versus observed size-at-age (points).**

Results from enclosure experiments under controlled semi-natural conditions generally provide similar growth rates to those predicted from the models. The models therefore produce suitable reference growth predictions against which field based growth estimates can be compared. A common statistic, growth ratio, is used to evaluate growth performance:

$$\text{Growth ratio} = \text{Average observed SGR} / \text{Average modeled SGR}$$

These comparisons suggest that surviving cod larvae in the sea typically grow at rates close to their size- and temperature-dependent capacity (Figure 4.5.4.3).

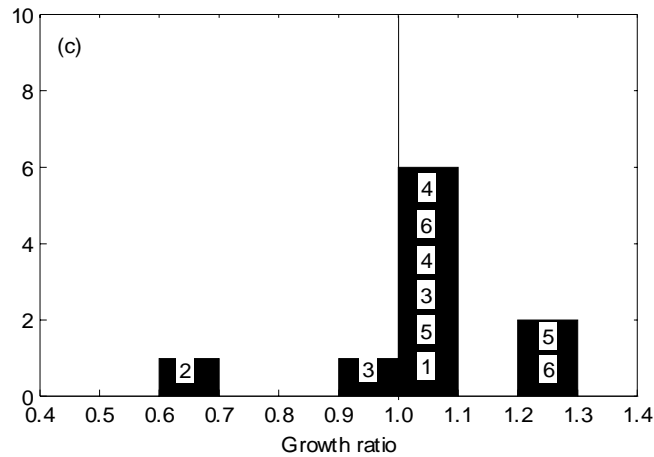


Figure 4.5.4.3. Average growth ratios of field-caught cod larvae from different studies. Numbers refer to study number (no. 2 is study by Campana and Hurley, 1989).

This suggests that climatic influences will strongly affect the year-to-year variations in growth of cod during their early life history due to their markedly temperature-dependent growth potential.

#### 4.6 Strong (i.e. statistically significant) relationships between physical/biological indicators of plankton variability and fluctuations in recruitment or individual growth rates within fish/invertebrate populations

The principal climate indicator for the N Atlantic, the NAO, has been rising over the past 30 years and the surface waters of the North Atlantic have been warming. This has caused extensive changes in the planktonic ecosystem. Although the precise mechanisms are not fully understood, we can detect consequences for plankton production, biodiversity, species distribution, and fisheries production.

Phytoplankton abundance in the NE Atlantic increased in cooler regions (north of 55°N) and decreased in warmer regions (south of 50°N). The effects propagate up through herbivores to carnivores in the plankton food web (bottom-up control), because of tight trophic coupling. Similar effects may be expected for other mid-latitude pelagic ecosystems, because the proposed mechanisms are general and the results for the NE Atlantic are consistent and based on very large scale, long-term sampling. (Richardson and Schoeman, 2004).

##### 4.6.1 Regional studies

###### 4.6.1.1 North Sea and other European shelf cod stocks south of 62°N

In the North Sea the population of the previously dominant copepod species, *Calanus finmarchicus* declined and was replaced by southern species. (Beare *et al.*, 2002). The seasonal timing of plankton production also altered in response to climate changes. This has consequences for plankton predator species, including fish, whose life cycles are timed in order to make use of seasonal production of particular prey species (Edwards and Richardson, 2004). The survival of young cod in the North Sea appears to depend on the abundance, seasonal timing and size composition of their prey. Changes in all of these since 1958 resulted in increased survival and good recruitment of cod throughout the 1960's and 70's and then a progressive decline over the past thirty years (Beaugrand *et al.*, 2003). Earlier work has also



noted correlations between temperature and cod recruitment in this and other areas (e.g. Ottersen *et al.*, 1994, Planque and Fredou, 1999; Brander, 2000; O'Brien *et al.*, 2000).

The decline of the European cod stocks due to overfishing has been exacerbated by climate induced changes in plankton production and these stocks are no longer able to provide as much surplus for the fishery as in the 1960's and 70's. As the stocks declined they have become more sensitive to the effects of the climate indicator (the NAO), due to shrinkage of the age distribution and geographic extent (Brander and Mohn, 2004; Brander 2005). This interaction between fishing and climate change effects has important implications for management policies.

To some extent the adverse effects of warming on fisheries production of the traditional "northern" species, such as cod, may be offset by increases in "southern" species, such as red mullet. There has been a northward shift in the distribution of many plankton and fish species by more than 10° latitude over the past thirty years (Beaugrand *et al.*, 2002, Brander *et al.*, 2003). This shift is particularly associated with the shelf edge current running north along the European continental margin and the northward shift does not apply across the whole Atlantic, because warming is not uniform across the whole basin.

#### **4.6.1.2 Baltic Sea**

In the Baltic Sea the continuously high period of the NAO has resulted during the 1990s in (i) warmer water temperatures, and (ii) decreasing salinities (Matthäus and Nausch, 2003; Fonselius and Valderrama, 2003). The latter is mediated by increased transport of humid air into the area by increased west winds resulting in increased runoff leading to freshening of the surface water. Furthermore, increased runoff may have prevented inflow activity (Matthäus and Schinke, 1998) leading to low salinity and oxygen conditions in the deep water of the Central Baltic basins (Hänninen *et al.*, 2000).

Low salinity and oxygen conditions since the late 1980s resulted in low egg survival in most of the cod spawning areas (Köster *et al.*, 2003). Additionally, during the 1990s cod larvae became obviously food limited due to the decreased population size of the copepod *Pseudocalanus* sp. (Möllmann *et al.*, 2000), being related to the high NAO-phase (Möllmann *et al.*, 2003a, 2005) and the shift in peak spawning from spring to summer, where nauplii supply is low. Consequently egg and larval mortality resulted in low recruitment levels during the 1990s (Köster *et al.*, 2005).

Contrary to cod, Baltic sprat recruitment was on an unprecedented high, although variable, level during the 1990s (Köster *et al.*, 2003). Recruitment has been related to climate, i.e. temperature variation, assuming warm temperatures as encountered during the 1990s being favourable for egg and larval survival (MacKenzie and Köster, 2004). Beside direct effects on egg and larval survival (Nissling, 2004), sprat larval survival is influenced by climate-induced changes in the food supply. Warmer temperatures during the 1990s have resulted in an increase in the population size of the copepod *Acartia* spp. (Möllmann *et al.*, 2000, 2003b), being the main food component of Baltic sprat (Voss *et al.*, 2003). Consequently sprat is significantly correlated with the abundance of *Acartia* spp. copepod stages (Möllmann, unpublished).

Beside effects on recruitment, variability in zooplankton populations influenced growth of pelagic fish in the Baltic. It has recently been shown that the climate-induced decrease in the *Pseudocalanus* sp. population since the 1980s has caused the decrease in growth and condition of herring in the Central and northern Baltic (Möllmann *et al.*, 2003a, 2005; Rönkkönen *et al.*, 2004). For sprat, intraspecific competition within the large stock during 1990s on the decreasing *Pseudocalanus* sp. population has contributed to their reduced growth and condition (Möllmann *et al.*, 2005). Because of multispecies interactions, the changes in pelagic fish species have consequences for different life history stages of cod.

#### 4.6.1.3 Faroes

There are large interannual fluctuations in plankton abundance, composition and productivity on the Faroe shelf (Gaard 2000, 2003). Zooplankton production, abundance and composition is related to phytoplankton timing and production and the zooplankton affects feeding conditions for fish larvae on the shelf during spring and summer.

The high interannual variability in primary production can be seen in higher trophic levels in the ecosystem, including important food items for demersal cod, such as sandeel and Norway pout.

There is a clear relationship between interannual variability in primary production and cod recruitment, growth rates and production and this relationship seems to be via zooplankton, and food for demersal, fish, mainly sandeel and Norway pout (Gaard *et al.*, 2002; Steingrund and Gaard, 2005).

The year-class strength of cod seems to be determined rather late in life, i.e. during the second winter, which coincides with the migration from coastal areas towards deeper habitats. The bottleneck seems to be food availability for demersal fish, determined by the phytoplankton production (about 6 months before) and also the abundance of older cod, i.e. competition.

Also the individual annual growth of Faroe Plateau cod fluctuates clearly with primary production (Steingrund and Gaard, 2005). Variations in annual growth rates of demersal cod by up to a factor of five are observed and these variations clearly follow primary production variability.

The links between primary production and cod recruitment and growth seem to go mainly through sandeel, and partly also Norway pout. Mainly sandeel abundance is highly variable on the shelf and when it is abundant it is the preferred food item for cod and haddock on the shelf. During larval stages sandeel larvae depend on small-sized food items (as the cod larvae) and plankton production during spring and summer therefore affects abundance of this food species.

#### 4.6.1.4 Iceland

Recruitment to this stock varies less than any other cod stock. The coefficient of variation (CV) of recruitment is 39%, which is less than the CV of the spawning stock biomass (56% - Brander, 2003). The relationship between recruitment (number of 3 year old) and abundance of 0-group cod is relatively weak but is improved by the addition of zooplankton biomass, strength of the coastal current and spawning stock biomass (Asthórsson *et al.*, 1994; Begg and Marteinsdóttir, 2002b).

Recruitment success derived from individual spawning components is dependent upon favourable environmental and stock effects that influence the dispersal and survival of early life-history stages. It has been hypothesized that the formation of large year classes will depend on successful production of eggs and larvae at the main spawning areas as well as successful transport from there to the northern located nursery grounds (Asthórsson *et al.*, 1994, Marteinsdóttir *et al.*, 2000; Begg and Marteinsdóttir, 2000, 2002b). Therefore, a potential important source of interannual variability in the relative contribution of the main spawning sites is hypothesized to be related to the strength and timing of the coastal current and Atlantic inflow from the main spawning grounds to the nursery sites in the north (Begg and Marteinsdóttir, 2002b). It is also demonstrated that the existence of multiple spawning components, each governed by distinct environmental and stock effects, is important for successful recruitment as the risk of mortality of early life history stages is spread both temporally and spatially (Marteinsdóttir *et al.*, 2000). It is therefore hypothesized that the population richness of the Icelandic cod stock may be responsible for the relative low fluctuations in recruitment in this

stock compared to many other cod stocks in the North Atlantic. Therefore, the production of the regional in-fjord units are thought to supplement the recruits derived from the main spawning grounds (Marteinsdóttir *et al.*, 2000; Begg and Marteinsdóttir, 2002b).

#### 4.6.1.5 Greenland

The cod stock at Greenland is strongly affected by changes in temperature, because it is at the extreme cold end of the range. It has appeared and increased its distribution during warm periods (e.g. 1925–1965) and has been reduced to small inshore populations during cold periods (Buch *et al.*, 1994; Brander, 2000). A variable but often very large proportion of the recruitment of cod at Greenland comes from the Icelandic spawning and returns there when mature.

Links have been investigated on the one hand between surface temperature, density stability of the water column and windstress and on the other hand between larval abundance or year-class strength at age 3 of cod in the West Greenland offshore area (Hermann *et al.*, 1965; Hansen and Buch, 1986; Stein and Lloret, 1995), but consistent and significant correlations were not detected. Pedersen and Rice (2002) found stronger association between cod larvae and zooplankton, or copepod, abundance than between cod larvae and hydrographic factors. Although the correlations were not significant, this may suggest that larval abundance was more strongly determined by system productivity than by hydrographic conditions, or that both cod larvae and zooplankton were aggregated and dispersed by the same mechanisms (Pedersen and Rice, 2002).

Considering that larval transport from Iceland to East and West Greenland is a major factor affecting the variability of year-class strength at age 3 off West Greenland, Borokov and Stein (2001) presented multiple linear regressions on the recruitment of West Greenland cod using SSB of Icelandic cod, sea surface and air temperatures around Greenland as well as zonal wind components between Iceland and Greenland. An extension of this analysis, which additionally includes meridional wind components off southwest Greenland, yielded a regression model that explains 79% of the variability in cod recruitment off West Greenland from the 1950s to the 1990s (Stein and Borokov, 2004). However, the final model considerably underestimates the strong 1984 and 1985 year classes and predicts much higher recruitment than was observed in the late 1990s.

#### 4.6.1.6 Georges Bank and Gulf of Maine

A strong relationship has been found between prey biomass concentration and recent growth of larval cod and haddock as measured by RNA:DNA ratio (Buckley and Durbin, submitted). The relationship between prey abundance and growth rate varied with larval size and the largest size class examined (SSL > ~12 mm) showed no significant relationship between prey biomass concentration and growth rate. Particularly strong correlations were observed between the biomass of *Pseudocalanus* spp. and larval growth, while indices based on *Calanus* alone were unrelated to larval growth rates. The spring of 1995 and to a lesser extent 1996 appeared to be periods of poor growth and low prey availability for cod and haddock larvae on Georges Bank. By contrast, 1997, 1998 and 1999 were years in which prey availability was at near, or at, saturating levels and no reduced growth was observed. This points to the need for multiple years to be studied in such an investigation; had the study been restricted to either of the two periods no relationship would have been observed.

Although no large year-class of cod was produced during the study period, the 1998 year-class of haddock was among the largest produced over the previous 20 years on Georges Bank.

The changes in prey abundance on Georges Bank were related to shelf-wide changes in surface salinity with higher abundance during years of lower salinity (Durbin and Casas, submitted).

#### **4.6.2 What have we learned in the past decade?**

Almost all of the material presented above was published in the past decade. The evidence on large scale changes in planktonic ecosystems and consequences of this for other trophic levels, including fish, has greatly improved. Relationships between indicators of plankton variability and fluctuations in recruitment or growth are in most cases supported by information about the underlying processes. For example the prey size requirements for cod larvae are an explicit part of the empirical relationship which has been developed relating plankton indicators to cod recruitment in the North Sea (Beaugrand *et al.*, 2003).

We have learned that the effects of physical and biological forcing factors is not necessarily either linear or additive, which should not be a surprise, but is nevertheless rarely a feature of models.

#### **4.6.3 Critical issues and gaps in knowledge**

It remains difficult to pull the detailed, process information which has emerged from large scale national and regional GLOBEC programme into a form which finds a use in ICES fish stock assessments. The approach in such assessments is to use fixed stock-recruit relationships as a guide to short and long-term management, with some sensitivity analysis to explore the consequences of alternative stock-recruit relationships i.e. environmental variability is treated as noise.

#### **4.6.4 New research directions and proposals**

Continuing effort is needed to make use of the increased process (generally small scale) understanding when looking at large scale (population) consequences, such as recruitment. Further relevant discussion of these issues can be found in the section on modelling.

A related issue concerns the development of application oriented science in relation to fisheries and marine ecosystem management. This requires cooperation with assessment scientist in order both to provide products which they are able to use in their existing methodologies (e.g. improvements to stock-recruit relationships, predictions of growth etc.) and to consider how to develop new methodologies, using a richer range of information than is found in current fisheries assessment. The ecosystem approach is in its infancy and the problems here are quite different. The possible information base here is very rich, and the need is to reduce it and to extract critical indicators of ecosystem performance.

### **4.7 Observing (monitoring) needs for effective analysis of long-term covariability of zooplankton and fish populations**

The current development and validation of zooplankton-fish interactions in a number of regions is being carried out as part of extensive short term observation programs that are designed to provide scientific understanding of processes. Such programs represent research initiatives of defined duration, not intended to serve as long term sources of information. The application of the models and relationships derived in such programs, either to hindcast population dynamics or to serve for the assessment of ongoing changes in environmental conditions, requires that key data be collected to provide long-term perspectives and advice. However, the maintenance of research levels of sampling is impracticable in the long-term, making less intensive, cheaper, monitoring programs essential for the continued application of new knowledge. Maintaining the flow of information to allow the interpretation of changes in population dynamics in relation to environmental fluctuations is a fundamental issue in the provision of advice in an ecosystem based approach to management.

Effective monitoring programs are based on the uninterrupted collection of information at sites that provide that data are representative over a broad spatial scale and that are collected

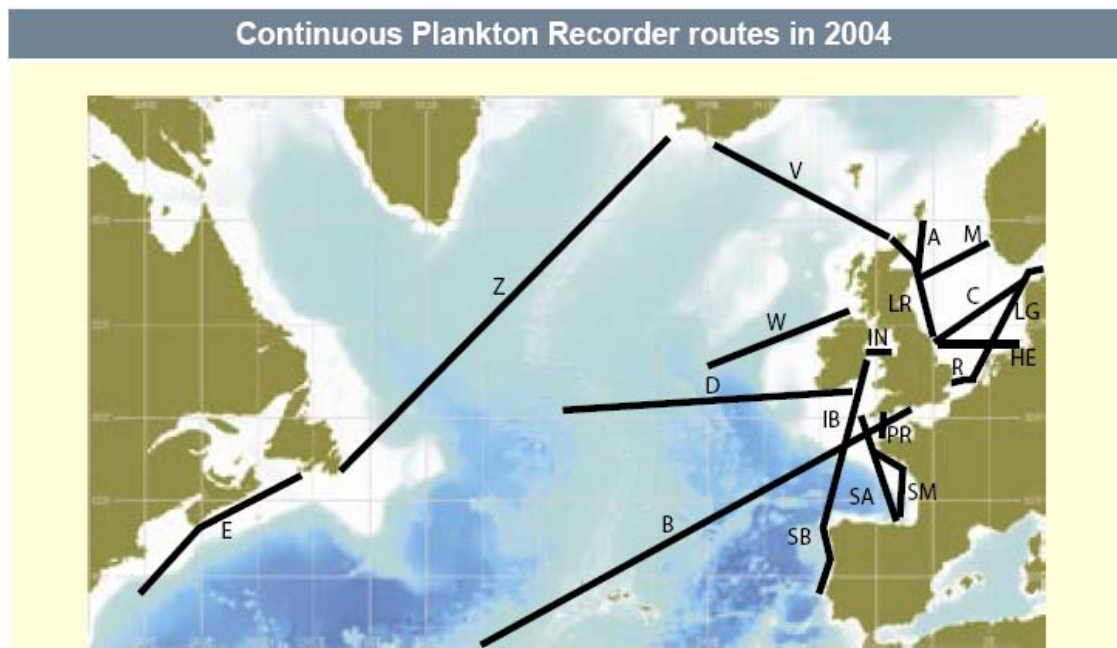
with a frequency sufficient to resolve the substantive changes in the populations on temporal scales appropriate to the key species. It is essential that such programs consist of multi-disciplinary collections that include hydrographic (e.g. temperature, salinity, density, oxygen), chemical (e.g., nutrients) and biological (e.g., phytoplankton, chlorophyll, zooplankton) variables. One approach to achieving these requirements to deal with zooplankton-cod interactions is to combine regional seasonal surveys, with a design appropriate to resolve inter-annual variations in the major regional features, along with representative fixed sites that are sampled at high frequency (< monthly) to better resolve the high frequency fluctuations in population abundance and dynamics as well as the interannual variations. Annual zooplankton surveys (only once a year) are likely to have severe limitations in forecasting and hind casting applications because of the potential for temporal aliasing. The goal of a monitoring program should be the development of lengthy time series that are more effective at resolving the long term changes characteristic of environmental or climate change.

There is an extensive (and growing) environmental monitoring system in many regions of the North Atlantic. There is substantial hydrographic sampling going on throughout the North Atlantic basin and on the continental shelves but the focus of this discussion involves those programs that include at least the monitoring of zooplankton populations since these are key to the application of dynamic process models. The Continuous Plankton Recorder program (CPR) is an extensive, widely based and long term program with an extensive set of routes around the UK and into the North Sea, and a more limited set of routes to Iceland and North America. The value of the CPR in monitoring long-term, large scale changes in the plankton ecosystem has been strongly established in a series of major papers and reports over many years (e.g. *Progress in Oceanography* 58(2–4) 2003, Special Issue on Achievements of the Continuous Plankton Recorder Survey and a Vision for its Future and other references below). Within the present workshop report it features regularly as the basis for time series analysis and geographic comparison. One of the major gaps in current coverage in the NE Atlantic is in the Norwegian EEZ, and another is located in the Labrador Sea.

There are also a number of long term coastal monitoring stations located off the coasts of the UK, Scotland, Germany and The Netherlands. However, there is no current coverage in areas off Norway, Greenland or in the Labrador Sea. Several monitoring sites (currently Gdansk and Gotland basins as well as the Gulf of Riga, and formerly in the Bornholm basin (pre-90s)) in the Baltic Sea have been sampled seasonally since the early 60s have been used to identify the long term changes in zooplankton community associated with changes in environmental forcing of the system (Möllmann *et al.*, 2000, 2003). A fixed station along with a series of seasonally sampled transects has been underway since 1989 in the Farøe Islands to provide advice on the state of the environment. A similar program is underway (1998-present) in the Atlantic zone off eastern Canada, which includes 6 fixed stations (3 sampled during ice free periods only) and 13 oceanographic transects sampled 2–3 time per year. In addition, sampling of the Norwegian and Barents Seas of oceanographic data, including zooplankton, along a number of oceanographic transects has been conducted seasonally by the Institute of Marine Research (1995–present).

Whether each monitoring program provides a representative view of the environmental conditions encountered during the early life stages of cod was not established during the course of the workshop. Decorrelation scales, in time and space, for a suite of oceanographic variables must be determined to assess the representativeness of monitoring sites or surveys relative to large scale patterns of variations in environmental conditions. The development of indices that capture the regional variations in environmental conditions could be used to drive current process models in order to provide forecasting skills with limited observation programs. Output from process models should also be used to guide the development or modification of monitoring activities that are most appropriate for the provision of advice about the impact of environmental variations on the dynamics of marine fish populations.

In addition to enhanced analyses of existing data sets, there is a need to enhance existing monitoring programs, such as hydrographic surveys, to include measurements of the lower trophic levels with sufficient detail that the information can be linked to ongoing process studies. There is considerably more hydrographic monitoring than there are observations of nutrients, phytoplankton and zooplankton. The addition of CPR routes in gap areas where there is regular commercial shipping activity (e.g., along the coast of Norway, in the Labrador Sea) should be a priority because these areas are key to the dynamics. Extension of CPR coverage to the Nordic Seas, particularly to the Norwegian Sea and the Barents Sea, would be extremely valuable for a number of reasons, particularly in the context of ecosystem-based advice and management of fish stocks. As one prominent example for such an extension of the CPR, *Calanus finmarchicus* is the most important zooplankton species in relation to fish recruitment and growth. There are two main core production regions in the North Atlantic for *C. finmarchicus*. One is located in the Northwest Atlantic, to the south of Greenland and to the east of Newfoundland and is partially sampled using existing routes. The other is located in the Norwegian Sea. The CPR has long time series for the spatial distribution of *C. finmarchicus* in the North Atlantic, but unfortunately, the important area of the Norwegian Sea is mainly missing in the CPR time series, except for a shorter period of time when the CPR was operated to and from OWS M. It is strongly recommended to re-open the transect to and from OWS M, and is also strongly recommended that establish a new transect in the northern part of the Norwegian Sea, possibly on the supply route between Tromsø and Longyearbyen.



**Figure 4.7.1. Continuous Plankton Recorder routes in the North Atlantic for 2004 (SM route not yet in operation). Letters refer to route identification.**

With the addition of enhanced CPR coverage, there would still be parts of the north Atlantic, particular in the north-east and in the northern Labrador sea, not covered by the CPR. To compensate for that, and to complement CPR data where they exist, observations on fixed monitoring stations should be secured or newly established to provide a broadly based coverage across most of the north Atlantic basin. Sampling of plankton, including larval and juvenile stages of fish and key food species, should be of principal importance. The resolution in time should be high and the sampling methods should be according to an international standard. Sampling at fixed stations should integrate or resolve the vertical structure of the water column to ensure representativeness of all oceanographic variables at those sites as well as establish correspondence with sampling programs with restricted sampling. For example, in Norwegian waters where areas for monitoring of biodiversity will be established in the near

future, zooplankton sampling would be of particular importance where fish reproduce (e.g. the spawning habitats of Arcto-Norwegian cod in Lofoten, and in the spawning habitat of capelin in Finnmark).

The implementation of process models as forecasting tools should be contrasted against representative (albeit limited) data for the populations of interest in order to validate model projections as well as detect departures that may indicate limitations of process models because previously stable elements were not included in the formulation. For example, the growth performance of larval cod is typically estimated by RNA/DNA analysis (Peck *et al.*, 2003) or otolith microstructure analysis (Meekan and Fortier, 1996), both which are labor intensive. This needs to be done, however, in order to determine the final outcome of the interaction between the zooplankton and the fish larvae. A multiple coverage of the populations at different time periods (and thus stages in development) would enable calculations of stage-dependent mortality and growth estimates (e.g. Sundby *et al.*, 1989). A specific benefit of a well planned sampling program could also be estimates of size selective mortality between sampling periods (Meekan and Fortier, 1996, Folkvord *et al.*, 1997) in addition to estimates of average growth and population abundance. Unlike other instantaneous growth measures, the otolith growth sequence holds information that can link the data obtained at the respective discrete sampling periods. Inclusion of otolith samples should thus be an integral part of studies estimating integrated growth responses of larvae.

## 5 Recommendations

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- a) The workshop strongly supports the proposal of the WG on Zooplankton Ecology for the 2 following Theme Sessions for the ICES ASCs 2006:
  - What zooplankton are fish really eating? Species and diets, availability and dependency. Conveners – Xabier Irigoien and Christian Möllmann
  - Biogeographical changes in zooplankton communities; consequences for marine ecosystems. Conveners - Luis Valdes and Peter Wiebe
- b) The workshop strongly supports initiatives by the WG on Zooplankton Ecology to maintain existing monitoring activities for zooplankton and to plan new ones.
- c) The workshop recommends the publication of the report in Cooperative Research Report – see Annex 8.

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## Annex 2: Workshop agenda

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### June 7

08:30-09:30 Welcome and Introduction - housekeeping, purpose, history  
(Jeff, Michala, Keith)

Presentations and Discussion in Plenary

09:30-10:45 Session on Regional Studies

Canada

Pierre Pepin

North Sea

Peter Munk

Faeroes

Eilif Gaard

10:45-11:00 Coffee

11:00-11:15 Cont. Session on Regional Studies

Baltic Sea

Christian Möllmann

Barents Sea

Svein Sundby

US

Ted Durbin

12:15-12:30 Common features and differences among regional studies

Summary by Jeff Runge

12:30-13:30 Lunch

13:30-15:00 Session on Zooplankton Dynamics in relation to larval fish

Introduction by Jeff Runge

Christian Möllmann et al.,	Eastern Baltic cod larvae and zooplankton
Ted Durbin	Annual and inter-annual trends in the zooplankton prey and growth of Atlantic cod and haddock larvae on Georges Bank
Eilif Gaard	Plankton impact on the Faroe Plateau cod
Stig Skreslet	Switch from density dependent larval mortality in an accumulated cod stock caused by exploitation
Jeff Runge	Timing and magnitude of copepod production related to haddock recruitment on the Scotian Shelf and mackerel recruitment in the Gulf of St. Lawrence: recent results

15:00-15:15 Break

15:15-16:45 Session on larval cod feeding processes, diet and prey selection

Introduction by Christian Möllmann

Christian Möllmann	Feeding of Baltic cod and sprat larvae
Pierre Pepin	Early life history studies of predator-prey interactions: quantifying the stochastic individual responses to environmental variability
Peter Munk	The role of physical features and spatial overlap on the interactions between zooplankton and larval fish
Howard Browman	Half-truths and myths surrounding feeding and escape behaviour in cod larvae.

16:45-17:00 Break

17:00-18:00 Break out groups discussing the following questions:

Q1: What is the evidence that zooplankton regulates recruitment success? Under which conditions do we expect zooplankton to be important for larval fish recruitment success?

Q2: What are the most pressing issues? How can we improve our understanding of zooplankton-larval fish linkages?

Q3: What have we learned? What are the emergent themes?

G1: Christian Möllmann, Svein Sundby, Pierre Pepin, Ted Durbin, Jens Rasmussen, Stig Skreslet

G2: Jeff Runge, Hans-Harald Hinrichsen, Arild Folkvord, Sophie Pitois, Peter Munk, Ken Drinkwater

G3: Øyvind Fiksen, Myron Peck, Howard Browman, Eilif Gaard, Keith Brander, Peter Grønkjær

18:00-18:30: Plenary - short summary of discussions within groups

### June 8

Session in plenary

8:30-10:00: Session on modelling the zooplankton – larval cod linkage

08:30-08:35 Introduction by Øyvind Fiksen

Myron Peck et al.,	Scenario testing the effects of climate variability on match-mismatch of larval fish and their zooplankton prey: Coupling an IBM to an NPZD model
Jeff Runge	Effect of spatial and temporal variation in zooplankton concentrations on larval cod growth on Geroges Bank: a comparison of two years based on modelling and observations
Hans-Harald Hinrichsen	The influence of circulation patterns on the interaction between Baltic larval cod and their prey
Arild Folkvord	Evaluation of cod larval growth performance across several different experimental scales, environments and regions
Øyvind Fiksen	Larval fish and food limitation

10:00-10:15 Break

10:15-12:30: Break out groups discussing to the following questions:

Q1: What advances have been made in modelling during the last decade?

Q2: What are strength and weaknesses of existing models and how can they be improved?

Q3: What are the future directions in modelling zooplankton-fish larvae interactions?

Each group should suggest at least 3 headlines synthesizing the discussions as a basis for writing groups

G1: Christian Möllmann, Myron Peck, Howard Browman, Eilif Gaard, Keith Brander, Peter Grønkjær

G2: Jeff Runge, Svein Sundby, Pierre Pepin, Jens Rasmussen, Stig Skreslet, Ken Drinkwater

G3: Øyvind Fiksen, Hans-Harald Hinrichsen, Arild Folkvord, Sophie Pitois, Peter Munk,

12:30-13:30 Lunch

13:30-15:00 Plenary - short summary of discussions within groups and general discussion on modelling issues

15:00-15:15 Break

15:15-16:45 Plenary –Application of research results and modelling in the context of fisheries management – How can it be useful?

Jeff Runge: “Coupled-physical biological models as an integrative tool for linking climate forcing to recruitment”

Keith Brander: “Are we any closer to strong predictions of fluctuations in recruitment and growth than we were in 1994”

– followed by general discussions.

16:45-17:15 Break

17:15-18:30 Further discussion and deciding on headlines we want to focus in writing groups. Organization into groups for writing about specific topics.

20:00 Workshop Dinner

### June 9

08:30-09:00 Plenary session to orient report writing. Discussion of potential for external publication (s) resulting from the meeting

09:00-10:30 Group work in parallel on headlines identified before.

10:30-10:45 Break

10:45-12:30 Writing continues

12:30-13:30 Lunch

13:30-14:00 Plenary Review of progress

14:00-16:30 Continue writing in groups

16:30-17:30 Review the state of the report and closing discussion

### **Annex 3: Working document - Long-term changes in zooplankton and shift in peak spawning time cause food-limitation of Central Baltic cod larvae**

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Christian Möllmann<sup>1</sup>, Hans-Harald Hinrichsen<sup>2</sup>, Friedrich W. Köster<sup>1</sup>, Rüdiger Voss<sup>2</sup> and Peter Grønkjær<sup>3</sup>

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#### Relationship to TORs of WKIZC

b) to determine the variability in zooplankton populations and their relationships to cod;

d) to determine how the timing of zooplankton production and spatial dynamics (including patchiness) of nauplii relates to the spawning, distribution and survival of early stages of cod.

*Due to recruitment failure and overfishing, Eastern Baltic cod (*Gadus morhua callarias* L.) decreased from a peak stock size during the early 1980s to a record low stock size during the 1990s. While in general high egg mortality due to adverse hydrographic conditions was considered to be the primary cause for low reproductive success, evidence accumulates that larval mortality due to starvation is as well of importance. Here we show that the decrease in the standing stock of the calanoid copepod *Pseudocalanus* and a spatio-temporal mismatch between *Pseudocalanus* production and cod peak spawning caused a food limitation for cod larvae. Our example shows the importance of a detailed understanding of seasonal as well as interannual production and distribution patterns of larval fish relative to their prey.*

In this contribution we evaluate the importance of the copepod *Pseudocalanus* for the survival of Eastern Baltic cod larvae. Stomach content analyses have shown that Baltic cod larvae rely mainly on nauplii of this copepod (Voss *et al.*, 2003; Grønkjær, unpublished). We first show the similarity in spatial distribution of cod larvae and their *Pseudocalanus* prey leading to the tight coupling between the two species. Further, we present two mechanisms that lead to the decrease in the ambient food supply for Baltic cod larvae, i.e. (i) a decrease in the standing stock of *Pseudocalanus*, and (ii) a seasonal and spatial mismatch between the production of cod larvae and suitable alternative prey. Finally, we evaluate evidence for food-limitation of cod larvae from time-series and modelling studies.

#### **SPATIAL DISTRIBUTION OF LIFE-STAGES OF COD AND PSEUDOCALANUS**

Cod and *Pseudocalanus* are primarily marine species which live in the Baltic Sea on the edge of their distribution with respect to salinity. Both species need high salinities for reproduction and thus produce their off-spring in the permanent halocline of the Central Baltic deep basins (Fig. 1). Cod eggs need a certain salinity level to be neutrally buoyant (>11psu), which exist only in the halocline in the deep center areas of the Baltic deep basins (Köster *et al.*, 2003). After hatching, cod larvae migrate to surface layers in the thermocline region (Grønkjær and Wieland, 1997, Fig. 1). Similarly, *Pseudocalanus* females (f) produce their eggs in the halocline region and the nauplii (N) migrate to surface waters and develop to copepodites (Fig. 1). In consequence, there is a vertical overlap between cod larvae and *Pseudocalanus* nauplii. Due to the production of cod larvae and nauplii in the centre of the basins and their parallel migration to shallower depth, there is also a large horizontal overlap between the two organisms (see mechanism 2, below).

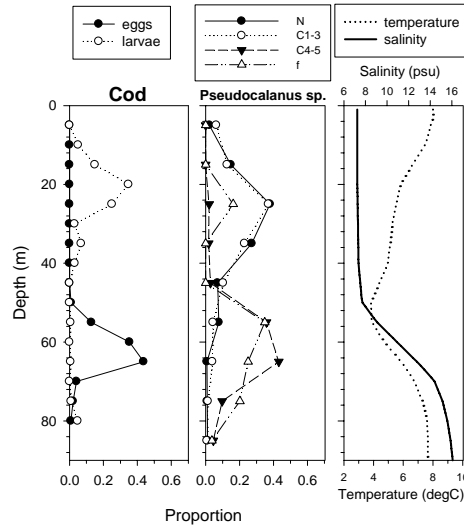


Fig. 1. Vertical distribution of cod eggs and larvae, *Pseudocalanus* life-stages, as well as temperature and salinity in May 1999 in the Bornholm Basin.

### MECHANISM 1: Long-term decrease in *Pseudocalanus* sp.

Long-term investigations on the mesozooplankton community demonstrated opposite trends in the development of the main copepod species in the Central Baltic Sea (Möllmann *et al.*, 2000, 2003a, 2003b). While *Acartia* spp. and *Temora longicornis* increased during the 1990s due to a general warming of the water, *Pseudocalanus* standing stocks decreased since the

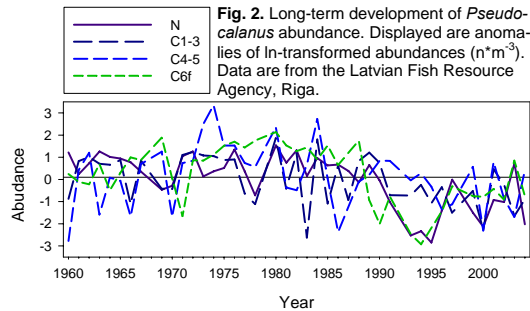


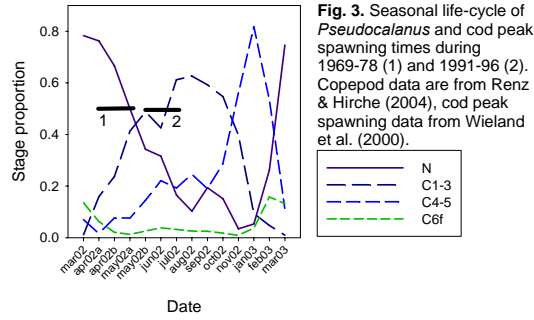
Fig. 2. Long-term development of *Pseudocalanus* abundance. Displayed are anomalies of ln-transformed abundances ( $n \cdot m^{-3}$ ). Data are from the Latvian Fish Resource Agency, Riga.

mid-1980s in parallel to a climate-induced decrease in salinity. Fig. 2 shows the development of the spring *Pseudocalanus* sp. abundance since 1960. Clearly during the 1990s the abundance of all stages was very much below average indicating a worsening of the food supply for cod larvae.

### MECHANISM 2: Seasonal and spatial mismatch between cod and prey production.

Fig. 3 displays the seasonal life-cycle of *Pseudocalanus* in the Bornholm Basin of the Central Baltic Sea from March 2002 to March 2003. Peak nauplii production occurs during March and April decreasing afterwards. During summer copepodites 1-3 dominate, while copepodites 4-5 dominate the overwintering stock. Assuming this seasonal pattern of *Pseudocalanus* sp. to be stationary, the change in cod peak spawning time from early spring to early summer

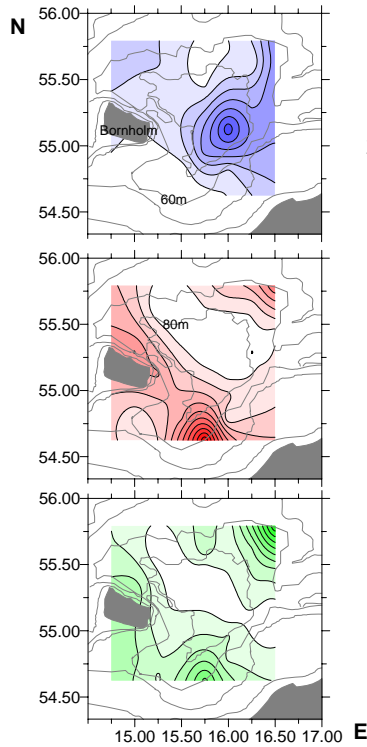




**Fig. 3.** Seasonal life-cycle of *Pseudocalanus* and cod peak spawning times during 1969-78 (1) and 1991-96 (2). Copepod data are from Renz & Hirche (2004), cod peak spawning data from Wieland et al. (2000).

(Wieland *et al.*, 2000) has resulted in a temporal mismatch between peak food and cod larval production (Fig. 3). During the “spring period” of cod peak spawning, production of cod larvae occurred in parallel with the peak nauplii production thus ensuring a sufficient nauplii supply. However, during the “summer period” most of the nauplii developed already to copepodites leading to a reduced food supply for cod larvae.

The general increase of the two other dominant food items of Baltic cod larvae, i.e. *Acartia* and *Temora* abundance (Möllmann *et al.*, 2000), suggests a replacement of *Pseudocalanus* as the main food source of cod larvae. However, this is prevented by distinct horizontal distribution patterns of the copepods. Both copepods produce in contrast to *Pseudocalanus* the first seasonal nauplii generation out of resting eggs which reside at the edges of the Baltic deep basins (Dutz *et al.*, 2003). Further their females reproduce in the halocline region where they were more prone to the clockwise circulation, advecting them to shallower areas. Both life-cycle traits result in a generally different distribution than *Pseudocalanus*. Fig. 4 shows examples of horizontal distributions of *Pseudocalanus* during May and *Acartia/Temora* during August in the Bornholm Basin.



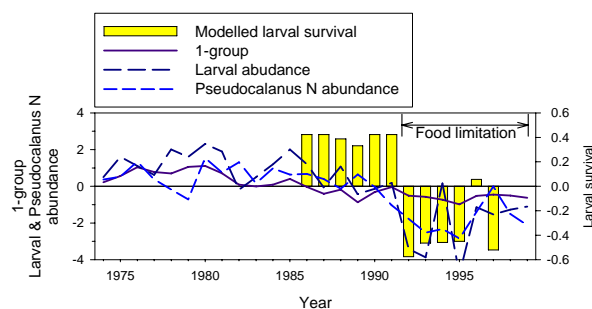
**Fig. 4.** Horizontal distribution of nauplii of *Pseudocalanus* in May (blue), *Acartia* (red) and *Temora* (green) in the Bornholm Basin. Data are proportions of the total abundance ( $n \cdot m^{-3}$ ) per station from sampling with 50um liner.

Clearly, *Pseudocalanus* nauplii concentrate in the deeper parts of the basins, while those of *Acartia/Temora* concentrate in shallower depth. This means for cod larvae, that when they are produced in summer (in center of the basin) during low *Pseudocalanus* nauplii production,

they find within the basin no alternative food. Only the larvae which are born close to the margins of the basin may have a high survival probability (Hinrichsen *et al.*, 2002).

### FOOD SUPPLY AND SURVIVAL OF COD LARVAE

Fig. 5 summarizes the effect of the reduced food supply on observed cod larval abundance, recruitment (age 1) from Multi-Species Virtual Population Analysis (MSVPA) and modelled larval survival. Clearly *Pseudocalanus* nauplii abundance, cod larval abundance and cod recruitment show parallel trends with relatively high anomalies during the 1970s and 1980s. During the early 1990s all time-series show mainly negative anomalies. Consequently nauplii abundance is significantly ( $p < 0.01$ ) correlated to larval abundance ( $r = 0.74$ ) and recruitment ( $r =$



**Fig. 5.** Time-series of *Pseudocalanus* nauplii abundance ( $\ln n \cdot m^{-3}$ , spring) cod recruitment ( $\ln n$  at age 1, 1st of January, shifted to year of origin) and cod larval abundance ( $\ln n \cdot m^{-3}$ , peak spawning), as well as modelled larval survival (%). All time-series are anomalies: *Pseudocalanus* data are from the Latvian Fish Resource Agency, Riga; cod recruitment from E. Teschner (Leibniz-Institute for Marine Research, Kiel).

0.64). Cod larval survival in dependence of the food supply and the timing of spawning as well as ambient temperatures was modelled using a coupled 3d-hydrodynamic/trophodynamic individual based model (Hinrichsen *et al.*, 2002). The model output shows generally low survival of Baltic cod larvae during the 1990s, being the result of a food-limitation.

### CONCLUSIONS

Our results give evidence for the importance of (climate-related) long-term trends in zooplankton populations for the food supply of fish larvae. Further, we have shown that the temporal and spatial timing between zooplankton and cod larval production is important for the survival of larvae. The case of Eastern Baltic cod demonstrates the importance of a detailed understanding of seasonal as well as interannual production and distribution patterns of larval fish relative to their major prey species.

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#### **Annex 4: Working Document – Some effects of ultra-violet radiation and climate on the reproduction of *Calanus finmarchicus* (Copepoda) and the year class formation in Arcto-Norwegian cod (*Gadus morhua*)**

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Stig Skreslet, Angel Borja, Luca Bugliaro, Georg Hansen, Ralf Meerkötter, Ketil Olsen and Jean Verdebout

Skreslet, S., Borja, A., Bugliaro, L., Hansen, G., Meerkötter, R., Olsen, K., and Verdebout, J. 2005. Some effects of ultra-violet radiation and climate on the reproduction of *Calanus finmarchicus* (Copepoda) and the year class formation in Arcto-Norwegian cod (*Gadus morhua*). - ICES Journal of Marine Science, XXX: 000-000.

Zooplankton sampling in 1997 identified the frontal zone of the Norwegian Coastal Current (NCC) as a reproduction habitat for *Calanus finmarchicus* in June-August. The abundance of nauplii in June-August 1997 was found to be negatively correlated with ambient salinity, i.e. positively related to precipitation, snow thaw and freshwater discharge in June-July which seems to be forced by North Atlantic Oscillation (NAO) in March-July. The summer reproduction habitat is subject to considerable ultra-violet radiation (UVR) as calculated from satellite observations of ozone and cloudiness. While *in situ* experiments indicated UVR-induced mortality in reproducing *C. finmarchicus*, monthly UVR doses during the actual reproduction period did not appear to affect the abundance of the resulting generation of adolescent copepodites (CIV-V) that accumulated in a fjord habitat during October 1983-2000. Local UVR in the spawning grounds of Arcto-Norwegian cod at the Lofoten Islands in March-May was positively correlated with the stock's 0-group index, which resulted in the rejection of the hypotheses that local UVR leads to high mortality of cod eggs or reduces the abundance of prey for cod larvae. Rather, the result suggests an indirect positive effect of UVR on the survival of cod eggs and larvae, possibly by controlling harmful microbes, if UVR is not a proxy for photosynthetic active radiation (PAR) that forces production of food for cod larvae by control of plankton production.

Keywords: climate, freshwater, Norwegian Coastal Current, radiation, recruitment, solar, trophodynamics, UV

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## **Annex 5: Working Document – The role of physical features and spatial overlap on the interactions between zooplankton and larval fish**

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### **Introduction**

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Recurrent observations have shown that both meso-zoo- and ichthyo-plankton in the North Sea are concentrated in restricted areas, either close to the shelf slope, nearshore, or in the vicinity of offshore banks. Comparison of distributions and hydrography indicates strong linkages between plankton and physical features, especially to horizontal/vertical stratification and the presence of hydrographic fronts.

In 2001, as part of the LIFEKO programme, a field study was set up to investigate the physical-biological linkages in the plankton of the eastern North Sea. From this study (which include a long series of cruises) I will shortly describe basic findings from two cruises in order to emphasize: 1) the influence of hydrography on distributional patterns of different plankton species, 2) the (seasonal) differences in distributions of cod larvae, and 3) the importance of the overlap between cod larval distribution and the distribution of prey of the appropriate size (which is to some extent related to copepod species composition).

### **Materials and Methods**

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Meso-zooplankton and fish larvae were sampled from 18 April to 02 May (4-01) and 22 May to 04 June (5-01). The sampling took place along transects, using 10 nm station distances along transects and 20 nm separations between transects. Sampling took place day and night during all cruises.

Meso-zooplankton was sampled by use of a submersible pump equipped with a conical net of 30  $\mu\text{m}$  mesh size. Meso-zooplankton was identified to the lowest taxonomic level, and the copepods were length measured (nauplii : total length, copepodites: cephalothorax length). Abundance (either in  $\text{no m}^{-3}$  or  $\text{no m}^{-2}$ ) was estimated from numbers, sampled volume filtered and sampling depth. Fish larvae and larger invertebrate plankton was sampled by a ring-net with an opening of 3.14  $\text{m}^2$  and a mesh size of 1000  $\mu\text{m}$ . The net was towed obliquely, integrating the water column. In the laboratory all larvae were identified, enumerated and length measured.

#### **Results and discussion**

The water masses in the area of investigation were strongly stratified, both vertically and horizontally. Figure 1 illustrates the horizontal stratification by the variation in bottom water density. The strong influence of the Jutland Coastal Current is obvious, and two frontal zones are indicated off the coast of Jutland. In the northern part of the investigation area the Atlantic inflow as well as the Norwegian Coastal current lead to stratification and formation of bottom and surface fronts.

In the area we identified a large number of plankton species. Of the meso-zooplankton the copepods constituted 70-80% by number, most of the remaining part was larval stages of Bivalvia, Gastropoda and Polychaeta. Of the copepods a restricted number of species was of primary importance. The following species (or genera) dominated: *Calanus finmarchicus* and *C. helgolandicus*, *Metridia lucens*, *Microcalanus pusillus*, *Paracalanus sp.* *Pseudocalanus*

*elongatus*, *Oithona similis* and *Oithona plumifera*, *Acartia clausi*, *Temora longicornis*, *Microsetella norvegica*, *Centropages* spp. Dominant fish larva/juveniles caught during the cruises were cod (*Gadus morhua*), whiting (*Merlangius merlangus*), sandeel (*Ammodytes marinus*) and flatfishes of the species plaice (*Pleuronectes platessa*) or dab (*Limanda limanda*).

The hydrographic variability was reflected in the plankton distribution. Figure 2 illustrates the distributional patterns of cod larvae and important copepod species. Obviously some species, such as *Calanus* sp and *Acartia* sp, are exclusively separated, while other species such as *Pseudocalanus* sp. and *Temora* sp. have intermediate distributions. The relationship between given copepod species and water mass characteristics is further illustrated in figures 3 and 4 where the abundance of each species is related to bottom water density at the site of sampling. The distinctness of the relationship is apparent from the recurrent patterns at the two cruises (and from other cruises as well).

In figures 2, 3 and 4 the distribution of cod larvae are compared to the distribution of copepods. In April the cod are distributed in water masses where the bottom water density is below  $27.45 \text{ kg m}^{-3}$ , an area not inhabited by the larger copepod species *Calanus* sp, *Metridia* sp, *Microcalanus* sp, and a large part of the *Pseudocalanus* sp. In May, however, a part of the cod larvae has drifted to areas where they overlap the larger copepod species.

A spatial overlap to larger copepod species is important when cod larvae have grown to a certain size. When available, the *Pseudocalanus* sp. and *Calanus* sp. contribute a major part of the preferred prey (example for 15-25 mm cod larva in Figure 5). In 2001 a large part of the cod population remained distributed in areas without large *Pseudocalanus* sp and *Calanus* sp. and consequently the mean size of prey items levelled off when they passed a size of ~20mm (Figure 6). This is in contrast to the larger mean sizes of prey for larvae >20mm in the study in 1994 (and a single observation at a station in 2001 where *Calanus* sp. was available to cod larvae, Figure 6).

Cod larvae distributed in areas where they do not have all (large) prey sizes available ought to eat more of the smaller prey in order to fulfil their requirements. Comparison between the 1994 and the 2001 observations indicates that in 2001 a part of the population had suboptimal feeding conditions. In figure 7 the stomach fullness is compared between cod larvae from the two stomach investigations, and to most of the larvae above ~20 mm the biomass of stomach contents is lower in the 2001 material than at the frontal stations investigated in 1994.

In conclusion, this part of the 2001 data presents additional examples of patterns described in earlier studies (e.g. Munk 1995, 1997; Munk et al 1995, 1999), and it illustrates the strength and species-specificity of hydrographical influence. Hence the ontogenetic aspect is important when evaluating cod growth and survival. 'Relevant' spatial overlap and interactions between larvae and zooplankton change during time, and we need to consider the full range of larval stages.

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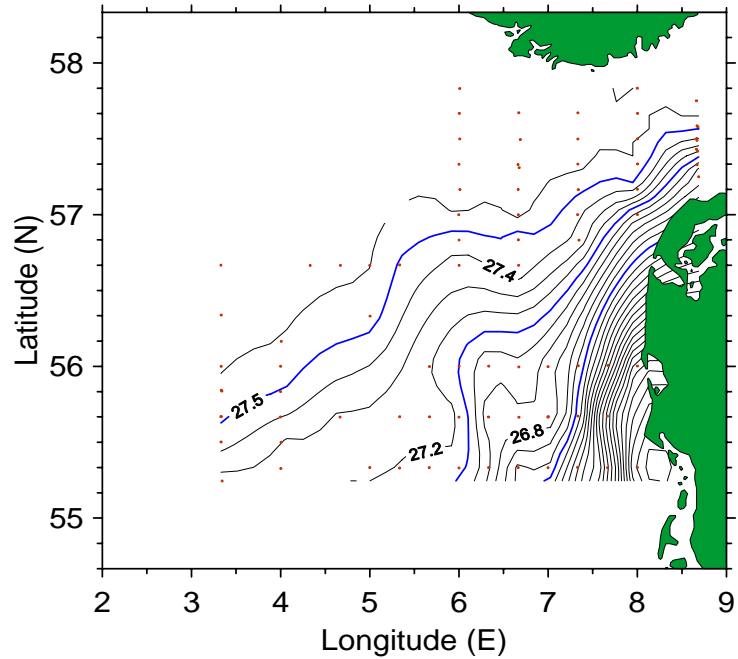
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April 2001 (DANA 4/01)

Bottom water density  
(Sigma-t, kg m<sup>-3</sup>)



May 2001 (DANA 5/01)

Bottom water density  
(Sigma-t, kg m<sup>-3</sup>)

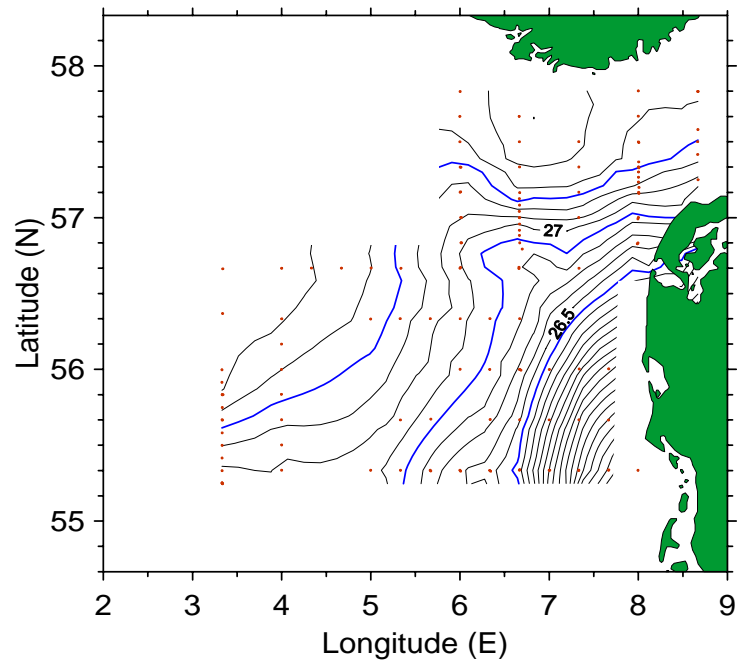


Figure 1.

Bottom water density (Sigma-t) contoured for each 0.1 kg m<sup>-3</sup> interval. Blue lines are reference lines for comparison to plankton distribution.



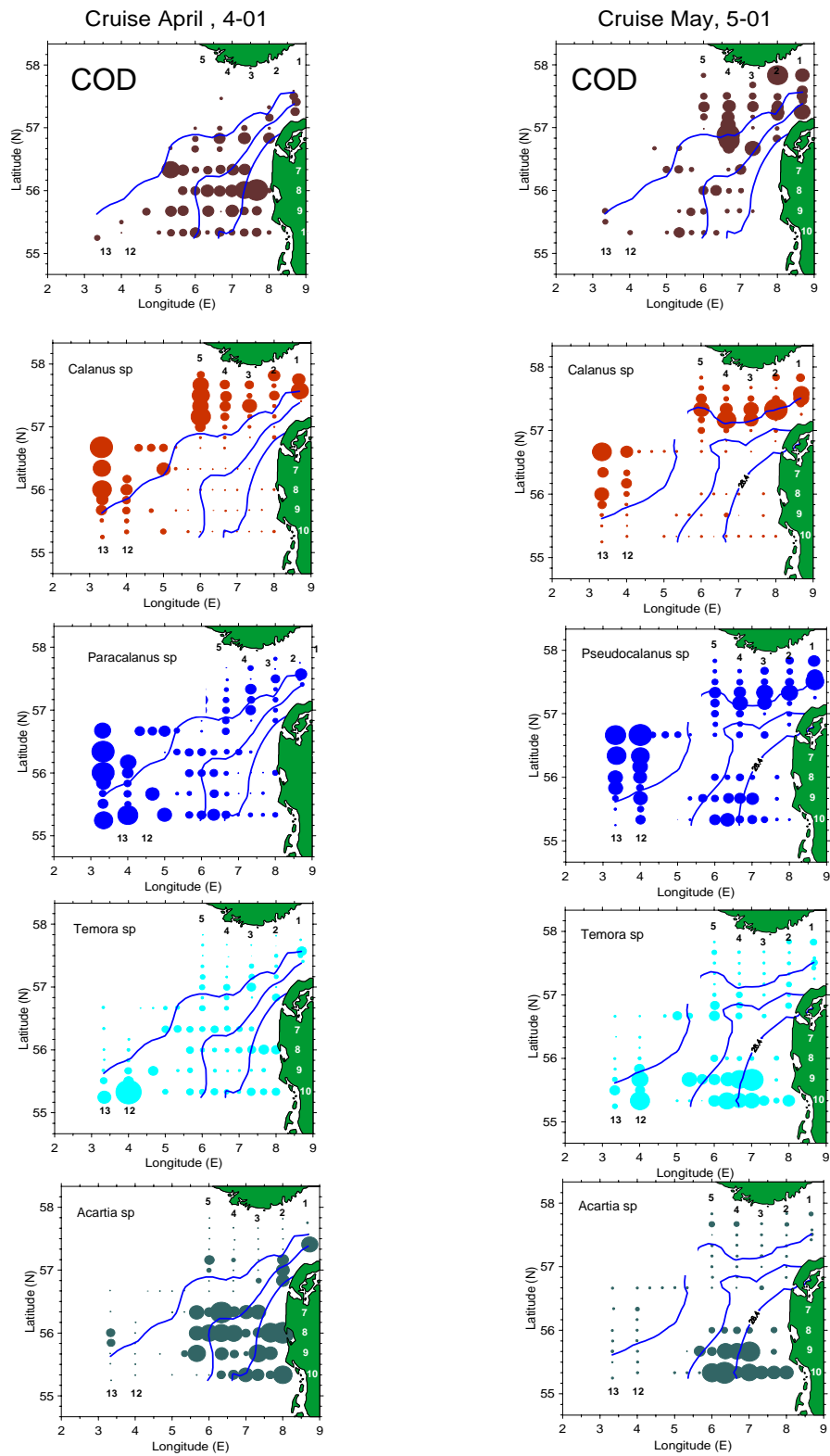


Figure 2

Relative distribution of cod larvae and dominant copepod species during April cruise (first row) and May cruise (second row)

Dana 4/01

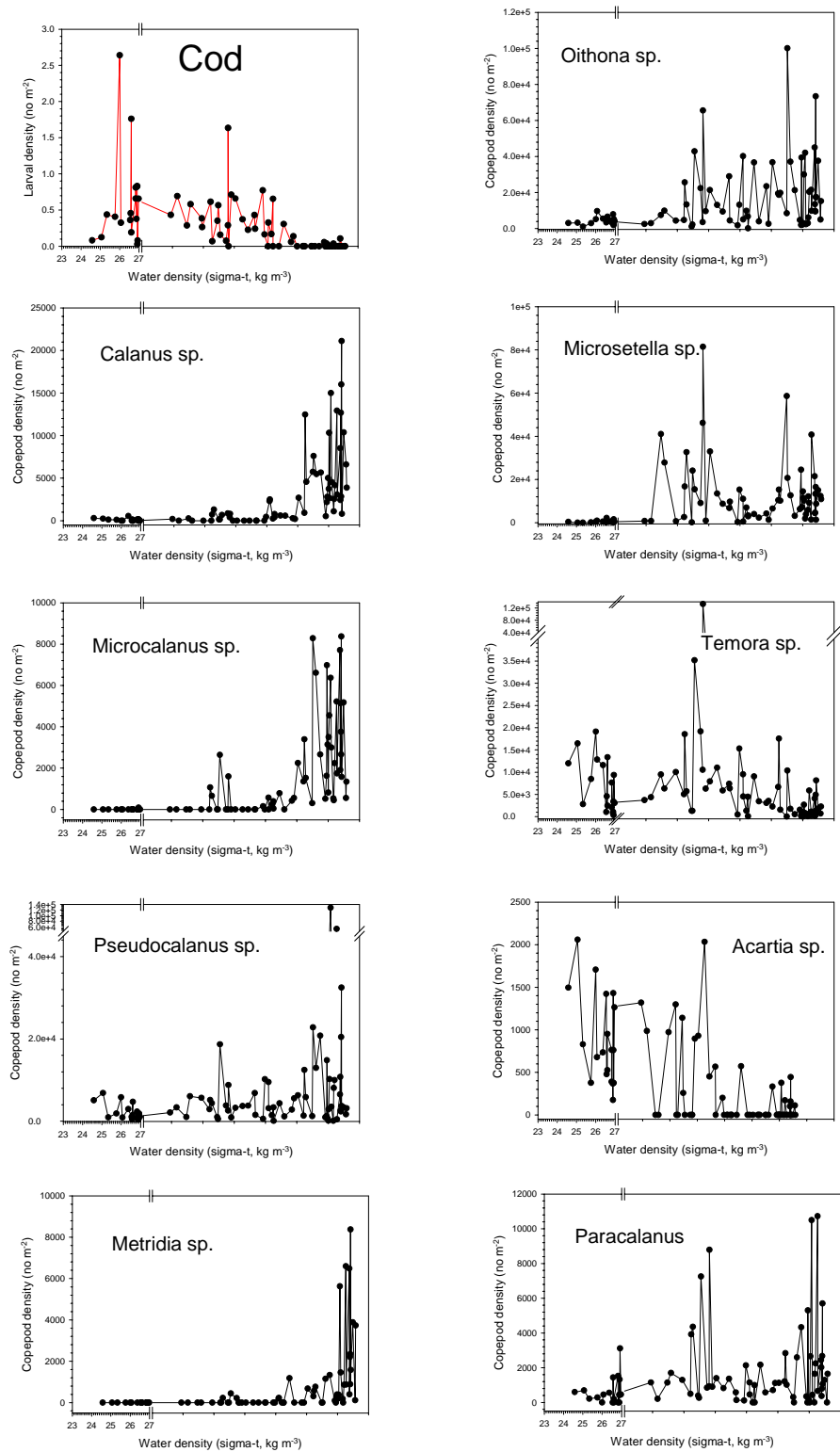


Figure 3.

April cruise. Abundance of cod larvae and important copepod species related to hydrographic characteristics (bottom water density) of the area. Note change of scale at 27.0 kg m<sup>-3</sup>

Dana 5/01

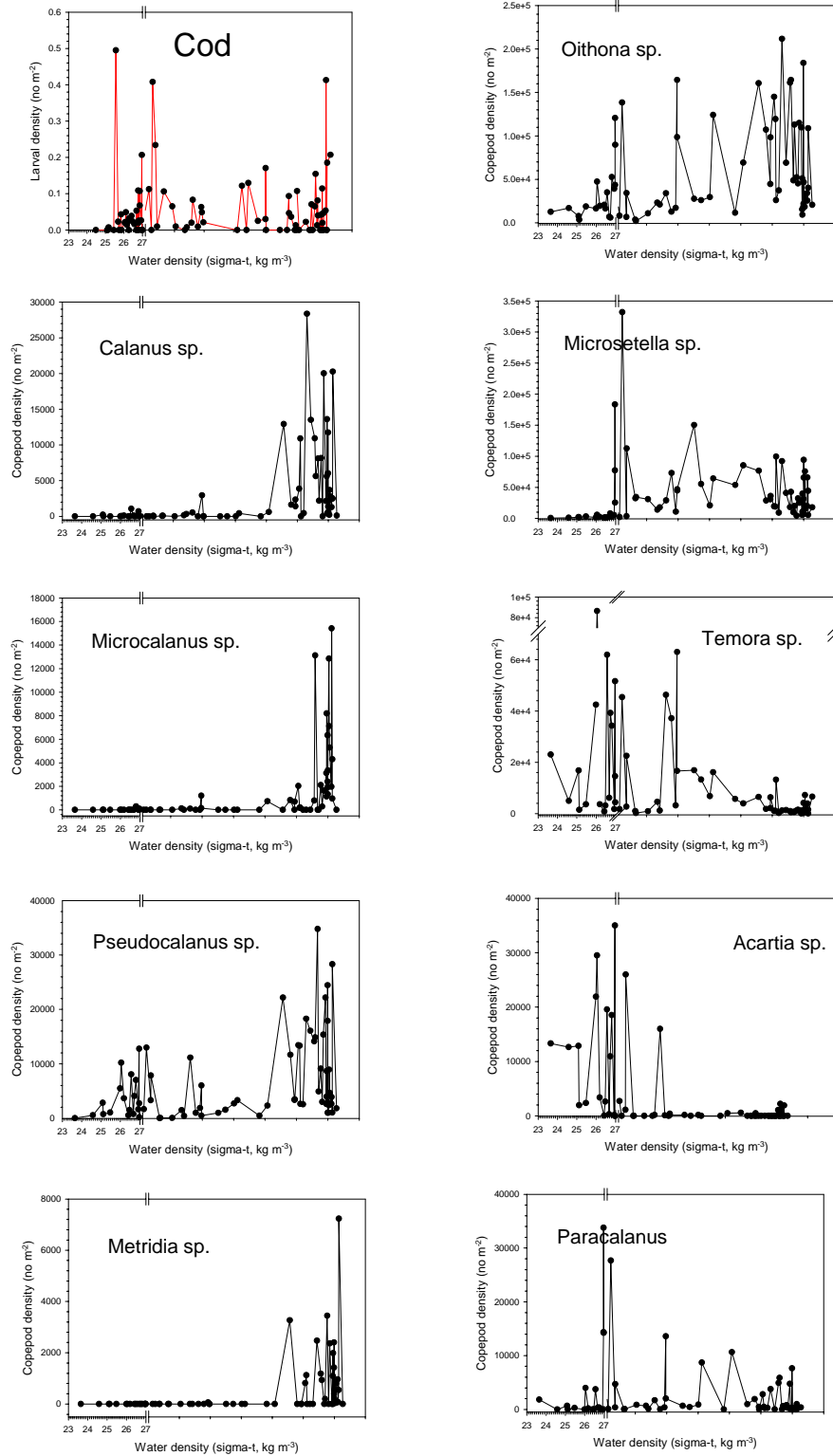


Figure 4.

May cruise. Abundance of cod larvae and important copepod species related to hydrographic characteristics (bottom water density) of the area. Note change of scale at 27.0 kg m<sup>-3</sup>

## Prey preference of cod 15-25 mm

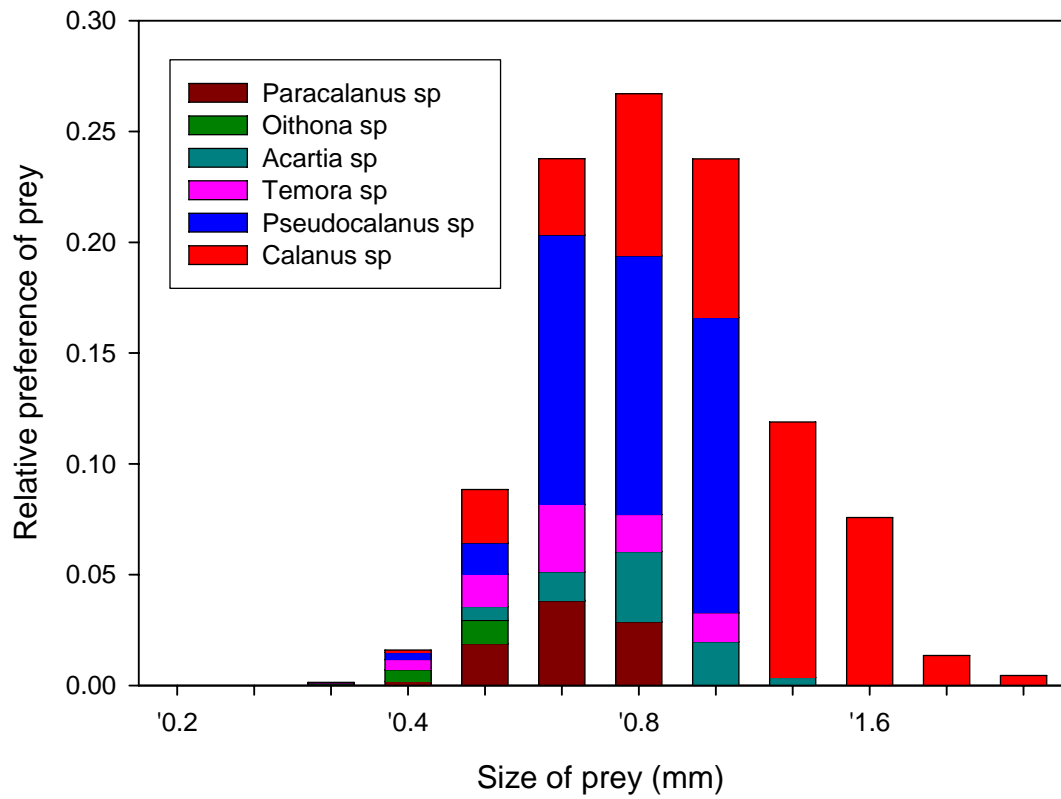


Figure 5

Example of prey species- and size- preference determined for cod larvae (sizes 15-25 mm) distributed in an area with mixed composition of prey species (investigations in 1994, Munk 1997).

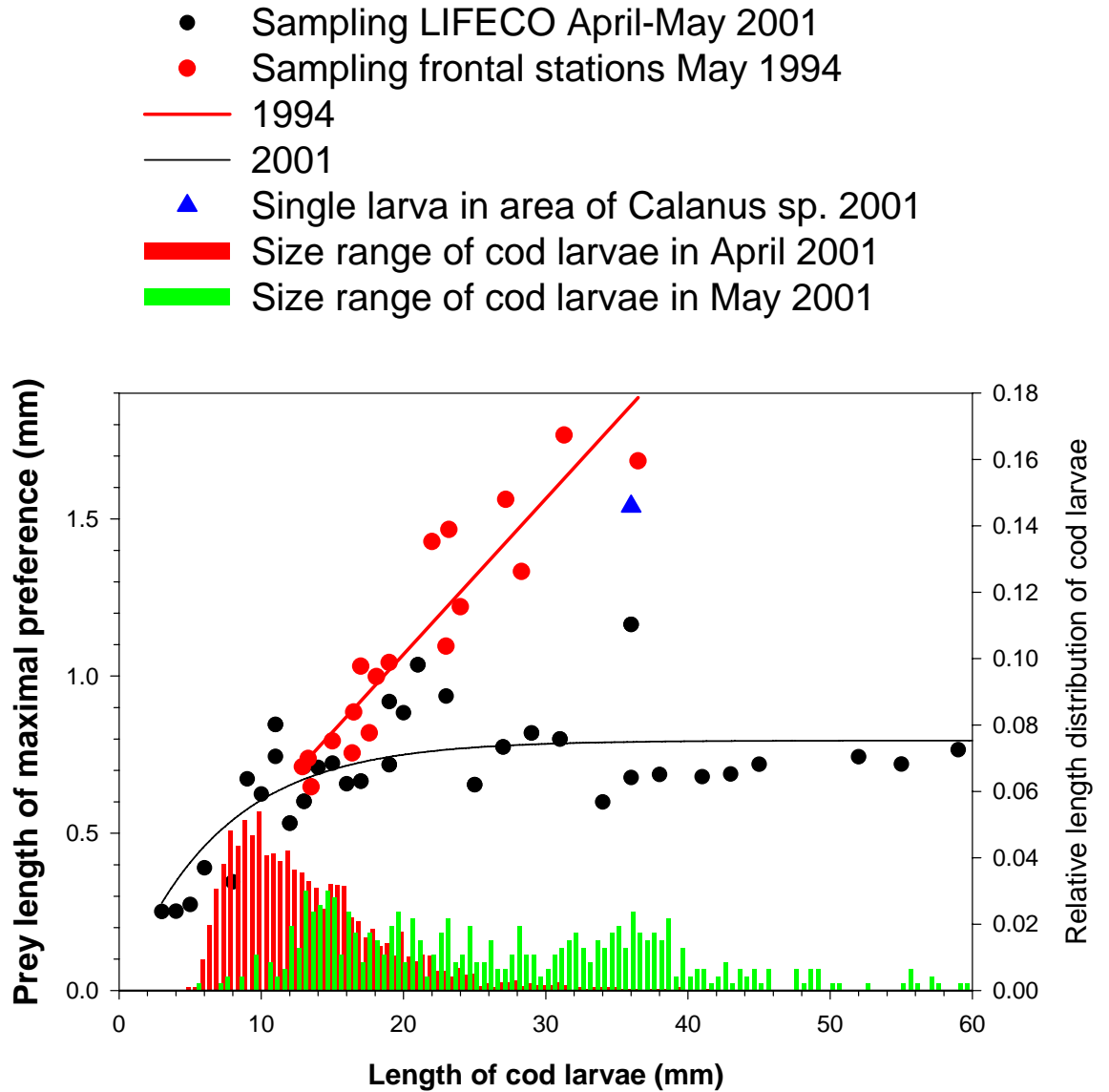


Figure 6

Comparison between prey size spectra from investigations in 1994 and 2001 (present LIFECO cruises). Black symbols and line illustrate the change in mean size of prey (maximal preference under the given conditions) as measured for the major part of the cod larval population in 2001. Red symbols and line illustrate the mean size of prey measured at frontal stations in 1994 (Munk 1997). Blue triangle illustrates observation from a frontal station in 2001 where *Calanus* sp. was present. Size ranges of cod larvae in April and May 2001 are illustrated by inserted histograms.

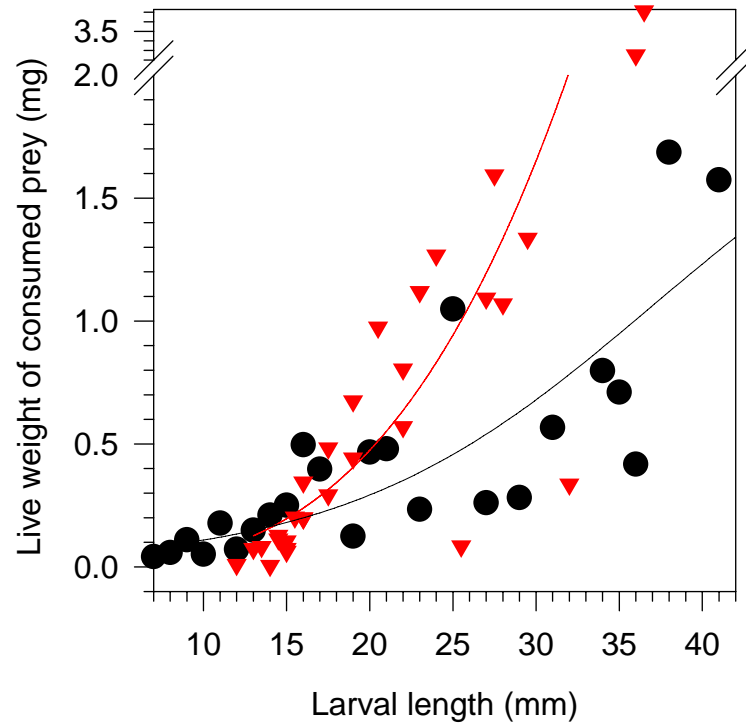


Figure 7.

Comparison between stomach contents of cod larvae sampled in an 1994 investigation (Munk 1997), red triangles, and stomach contents of larvae from the major area of distribution in 2001 (LIFECO March-April-May), black circles. Stomach contents are calculated from measured prey lengths and length-weight keys of copepod dry weights.

## **Annex 6: Working Document – The influence of circulation patterns on the interaction between Baltic larval cod and zooplankton as their prey**

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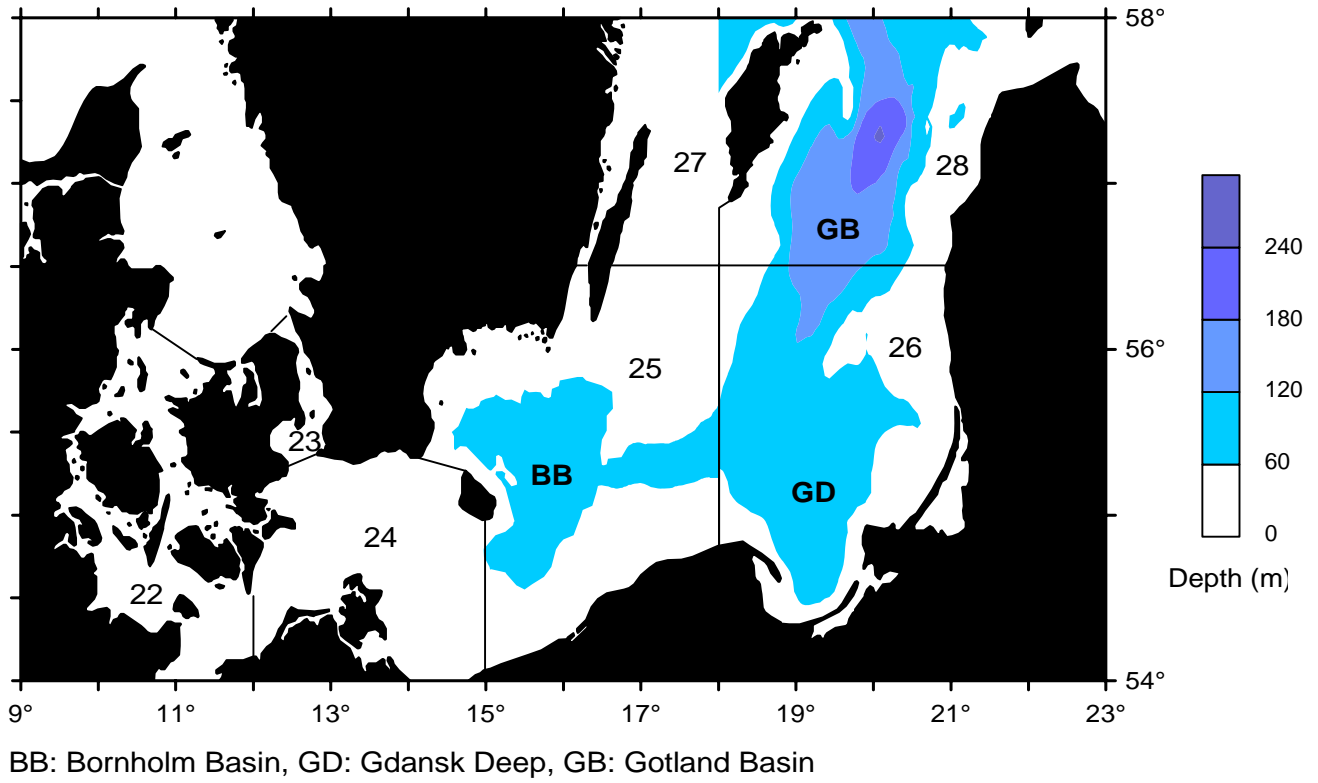
A three-dimensional hydrodynamic model has been used to analyse circulation patterns in the Baltic Sea with special emphasis on drifting particles representing larval fish. Temporally and spatially resolved flow fields were used to investigate potential drift routes from the centre of the spawning ground of Baltic cod (*Gadus morhua*) during 1979-1998 (Fig. 1). Retention and dispersal of larval fish were estimated by calculation of simple statistical parameters of larval drift patterns. Drift distances of larval cohorts from the centre of main spawning activity (Bornholm Basin) were ensemble averaged over a time period covering the duration of the pelagic larval phase of Baltic cod. Ensemble averaging over many individual trajectories enables calculation of dispersal scales in terms of variances of mean drift distances. The results suggest a general change in circulation pattern from retention during a first decade from 1979-1988 to dispersion in the following decade (1989-1998) (Fig. 2a,b). As a consequence, differences in the location of potential nursery areas of Baltic cod could be identified. The increase in dispersion was related to an increase in the variability of the local wind forcing conditions over the Baltic. The more frequent occurrence of dispersion in spring of the second decade was accompanied by a strong decrease in biomass of one of the main larval fish feeding component, the calanoid copepod *Pseudocalanus* sp. This change in circulation patterns may have affected the spatial overlap and thus the contact rates between predators and their prey. High contact rates between larval cod and *P. elongatus* as their preferred prey items occurred during retentive periods in spring and early summer until the end of the 1980s. In contrast, during the 1990s high encounter probability of predators and prey only results in late summer if the larvae were transported into more shallower coastal regions where other prey items than *P. elongatus* were more abundant.

Temporal mis-match between the occurrence of larvae and their prey potentially also affects the spatial overlap between predator and prey. A case study was performed investigating the influence of the circulation patterns on the spatial overlap of Baltic cod larvae with their prey, if a temporal mis-match between predators and prey was assumed. Generally, potential spatial overlap decreased since the mid 1980s, however, being maximally variable during the 1990s. Seasonally highest predator-prey overlap within the Baltic cod spawning ground occurred in summer months and lowest at the end of the cod spawning season (Fig. 3). As obtained by a comparative analysis of spatial overlap and observed recruitment, temporal and their corresponding spatial mis-matches between predator and prey potentially have an impact on the survival of Baltic cod larvae. The simulations show that variations in physical forcing conditions, especially during the second half of the considered time period, have the potential to dramatically reduce the amount of food being available for larval cod.

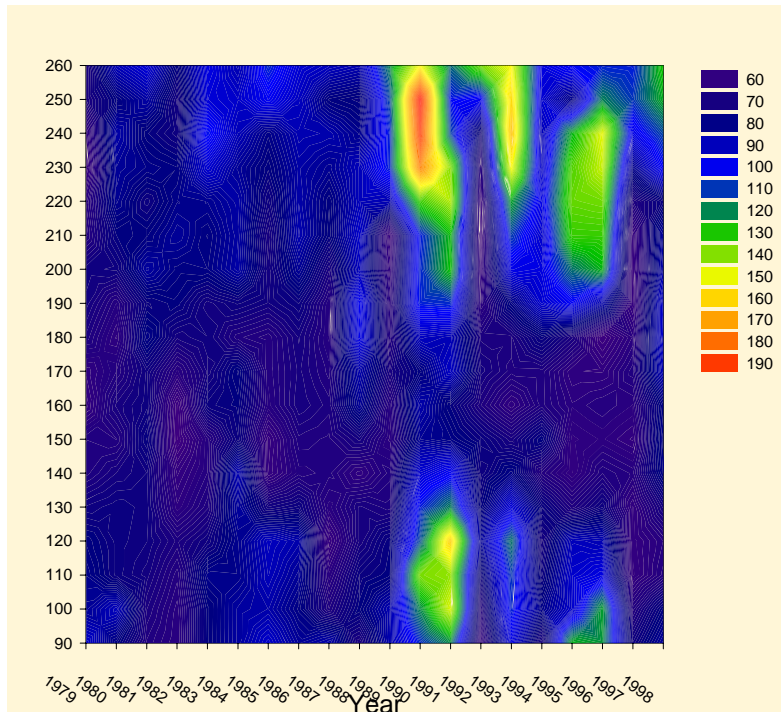
We have combined our three-dimensional eddy-resolving hydrodynamic model of the Baltic Sea with an IBM for larval cod. This IBM tracks individuals through the larval phase distinguishing four stages: yolk-sac larvae (< 4.5 mm), first feeding larvae (4.5 – 6 mm), well established feeding larvae (6 – 9 mm) and large larvae > 9 mm. Within the model the encounter of prey, foraging, growth and survival of individual cod larvae is simulated by specific sub-models in 6-hour time steps (Fig. 3). All larvae were initially defined to have equal length and weight at hatch. Along the drift trajectories within the coupled model the larval environment

consisted of the prey field, the ambient temperature and turbulence determining both their growth and survival. Yolk-sac larvae before reaching length at first-feeding ( $< 4.5$  mm) were considered as passive drift particles, with growth exclusively determined by ambient temperature. The results of the model runs indicate that the strong decay in abundance of calanoid copepod *P. elongatus* had a strong impact on cod larval survival (Fig. 4). The model predicts relatively high levels of larval survival from 1986 to 1991 as well as the strong decay in survival for spawners from 1993 onwards. Consequently, in the latter time period variability in the abundance of *P. elongatus* has had most likely only a limited impact on larval survival, depending to a higher extent on the availability of juvenile stages of other copepods. Comparing the ratio of observed recruitment and egg production at stage III of Baltic cod with the simulated larval survival potential revealed a similar trend. Although, e.g. late cod egg or early larval stages were highly abundant in the field, from 1993 onwards the recruitment remained on a relatively low level.





**Fig. 1. Spawning areas of cod**



**Fig. 2a. Mean larval cohort drift distance**

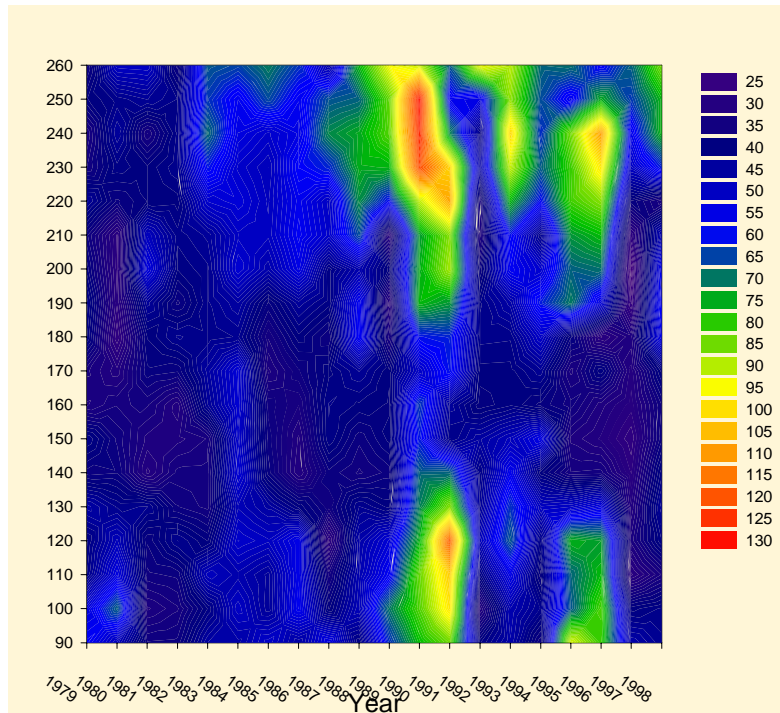


Fig. 2b. Variance of mean larval cohort drift-distance

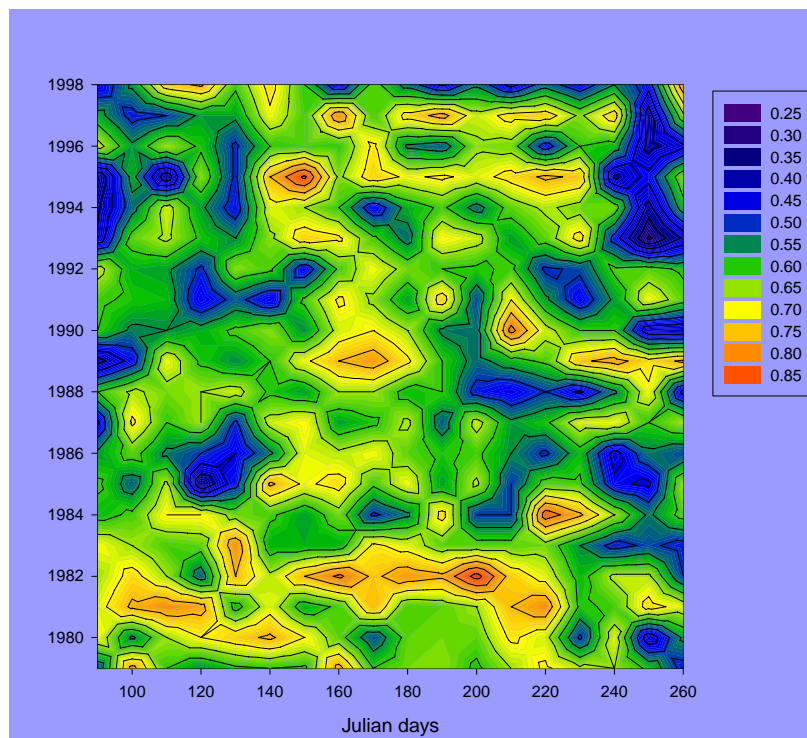
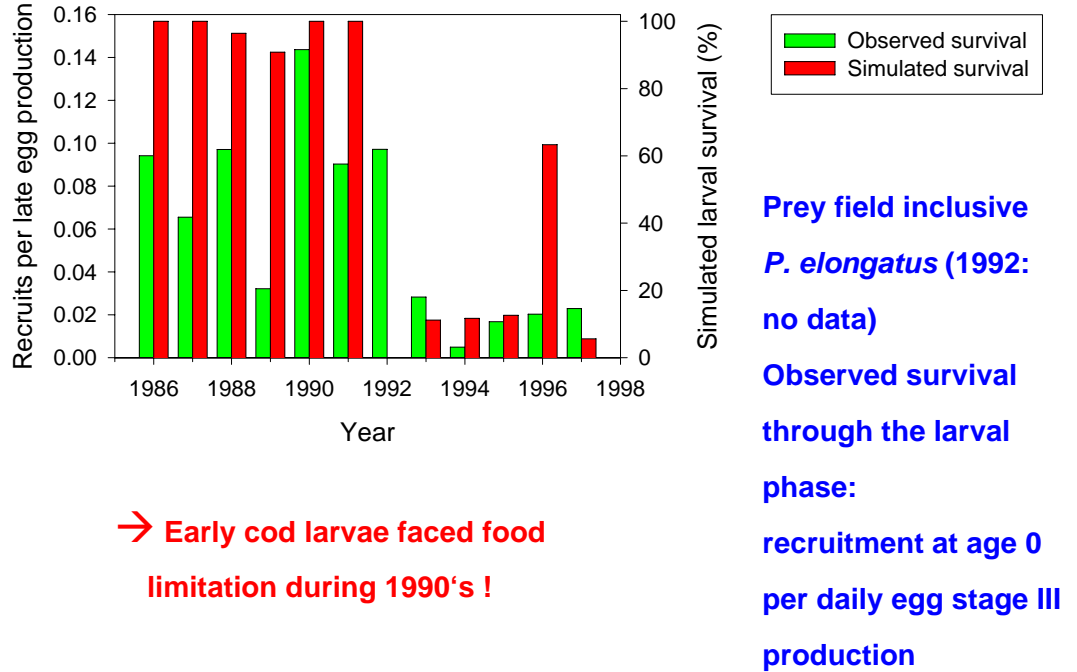


Fig. 3: Overlap between cod larvae and prey after 10 days of drift

**Output of coupled IBM and hydrodynamic model: interannual variability in larval survival in comparison to observations**



**Fig. 4. Larval survival.**

## **Annex 7: Working Document – Are larval fish limited by their prey availability? Yes – even at high prey abundance**

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### **Are larval fish limited by their prey availability? Yes – even at high prey abundance.**

*To what extent are larval fishes limited by their zooplankton prey resources? This question has been asked a number of times in the literature on larval fish ecology and it is a key question of our workshop in Copenhagen. Here I argue that larval fish are risk-sensitive foragers, and that this implies survival effects of food abundance even beyond physiological satiation. The risk of starvation and the risk of predation are strongly connected, and they should not be treated separately.*

The most common approach to the question of food-limitation has been to evaluate effects of prey density, prey availability, size-structure of prey, spatial overlap etc. and correlate such measures with larval growth in field-, experimental- and modelling studies. The classical justification for taking this approach is that growth increases body size and therefore also mortality risk, thus enhanced growth will reduce integrated mortality risk by decreasing the time with high vulnerability to predators (Houde, 1997).

In oceanography, much attention has been devoted to temperature how it relates to growth and larval fish survival. Numerous studies show clear correlation between temperature indices and recruitment success in fish. The links between zooplankton availability and growth or recruitment success are less clear. It seems to be difficult to establish clear responses between abundance of prey and larval growth in the field. In addition, rearing larval cod in land-locked fjords (e.g. Folkvord, Øiestad and Kvenseseth, 1994) have demonstrated the ability of cod to grow at maximum rates at quite low food abundances. Yet, the study by Beaugrand *et al.* (2003) suggest a connection between zooplankton abundance and recruitment success of North Sea cod, but the actual mechanisms remain unknown. Even less is known about predation rates, except that they must be very high and that both invertebrates and fish are involved (Bailey and Houde, 1989). Larval fish are generally more susceptible to predation than other planktonic organisms of comparable size (McGurk, 1986).

Fisheries ecologists are used to reason over growth and mortality rates, but may not be used to think in terms of behavioural ecology. I think there is an important lesson to be learned in the way behavioural ecologists think about predator-prey interactions to better understand the linkages between larval fish, their prey and their predators. In behavioural ecology, the main focus is on how organisms *respond* to their environment, i.e. how they change their behaviour as risk of predation, risk of starvation or growth potential varies. Often, such responses generate surprising (but logical) and highly ‘non-linear’ results. A textbook example of behavioural reasoning on the interaction between risk of starvation (the argument applies to growth as well) and risk of predation was presented by McNamara and Houston (1987), which I have outlined in Figure 1. The main message of their exercise was to demonstrate that for risk-sensitive foragers, that is organisms that allocate their behaviour between risky feeding habitats or activities and safe refuges in response to environmental (e.g. the presence of predators) or internal (e.g. stomach fullness) cues, an increase in feeding opportunities may not affect their risk of starvation (or growth). In fact, for some forms of  $P(\mu)$ , the risk of starvation may increase with higher food abundance. Similar arguments apply to prey selection (Giske and Salvanes, 1995).

To what extent is this relevant for larval fish feeding on zooplankton? I believe it is more important than we realise. First, larval fish live in strong vertical gradients of growth opportunities and predation risk. By moving up and down in the water column larvae can select among habitats with high temperatures and high feeding rates depending on light, turbulence, prey distribution etc. or habitats with lower growth rates, typically deeper down in the water column. Since larval fish are susceptible to predation from fish, which are raptorial, visual predators, risk of predation will often be higher in the best feeding and growth habitats near the surface, where starvation risk is less and growth rates are higher. If predation rate is proportional to ambient light, it may be an exponential gradient of risk.

Second, activity level, the swimming velocity or jump frequency of larval fish is proportional to clearance rate and therefore to prey ingestion rate, at least up to some prey concentration. It is also proportional to the probability of running into ambush or tactile predators, and thus involves a trade-off between risk of predation and growth. Fish larvae are known to adjust their feeding behaviour with stomach fullness (MacKenzie and Kiørboe, 1995; Munk, 1995), which can be interpreted both as a way of saving energy and to reduce risk of predation.

Third, larval fish may also adjust their behaviour in response to the presence of predators (Skajaa, Ferno and Folkvord, 2003, 2004) – which can also be interpreted in terms of Fig. 1. Increasing the density of predators means that  $P(\mu)$  is shifted up in the diagram, and it predicts no change in foraging intensity. This simple model is not realistic on this point, but more sophisticated treatments suggest that higher predator density should lead to reduced foraging effort (e.g. Fiksen and Giske, 1995; Fiksen, 1997; Fiksen, Eliassen and Titelman, in press). This would also interfere with interpretations of feeding, growth and survival of larvae in natural environments.

PS. I am working on a more complete analysis of larval cod in vertical gradients of feeding opportunities and predation risk. This is based on a detailed model of larval cod foraging and predation risk – and a state-variable optimisation model where body size and stomach fullness are the state variables. I would be interested in any data of larval cod where the vertical environment (light, temperature, prey distribution, turbulence, phytoplankton, predators etc.) has been sampled along with information on distribution and stomach fullness of larvae.

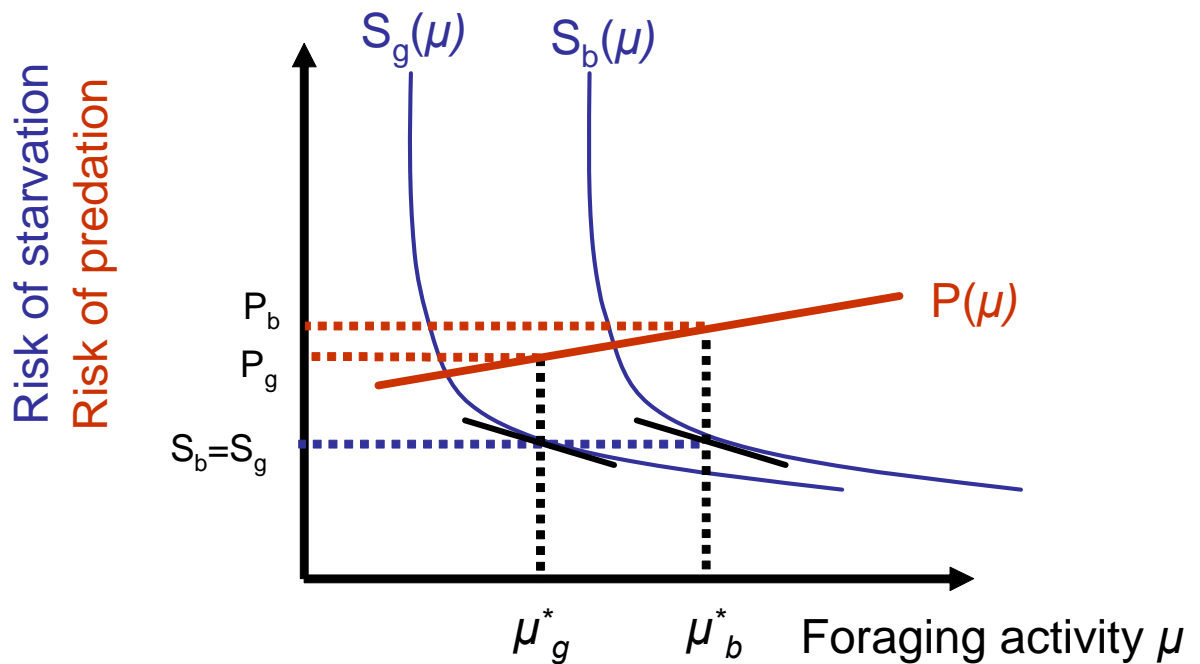


Fig. 1. This figure (modified from McNamara and Houston (1987), see also Krebs and Kacelnik 1991) illustrates what happens to an animal that can vary its foraging activity  $\mu$  (swimming, move to feeding areas from hiding areas, reduce vigilance etc.). Feeding is assumed to be linearly related to risk of predation  $P(\mu)$ , which is the case for a larval fish that increase its prey search in an area with ambush predators. The probability of starving during, say one day, is a decreasing function  $S(\mu)$  of foraging activity. This probability will depend on prey abundance, in situations with low food abundance  $S_b(\mu)$  more foraging effort is needed to maintain a given level of starvation risk. Improved feeding opportunities then means that the starvation risk curve is shifted to the left, to  $S_g(\mu)$ . Total mortality equals the sum of the two probabilities, the chance of death from either starvation or from predation, and the optimal compromise  $\mu^*$  between the two is then defined as  $S'(\mu^*) = -P'(\mu^*)$ , the point where the derivatives sum to zero. In Fig. 1, these are marked as  $\mu_b^*$  and  $\mu_g^*$  for the bad and the good environment, respectively. *The main lesson here is that for a risk-sensitive forager, an increase in the availability of food does not change the risk of starvation. Instead, it decreases the risk of predation.*

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## Annex 8: Resolution

The **Workshop** recommends that this report should be revised and edited by Dr Ø. Fiksen (Norway) Dr C. Möllmann (Denmark) and Dr J. Runge (USA), reviewed by the Chair of the Oceanography Committee and published in the *ICES Cooperative Research Report* series. The estimated number of pages is 100.

### Supporting Information

Priority:	This is an important scientific contribution to understanding processes of recruitment, growth and survival. It is relevant to current issues in developing long-term management strategies and recovery plans for cod and also to ecosystem based management. It requires high priority.
Scientific Justification and relation to Action Plan:	<p>Action Plan</p> <p>The report is part of the continuing commitment by ICES to act as the North Atlantic regional implementation body for GLOBEC (through the Cod and Climate Change Programme). It represents the culmination of a substantial effort by the ICES/GLOBEC Cod and Climate Change community. It will be of value in preparing and presenting scientific advice and information on the status and outlook for cod stocks and on the marine ecosystems within which they are often a major component.</p> <p>The drafts of the report have been available on the ICES/GLOBEC website and will continue to be updated there as an up-to-date data and information source. This will help to make the material on the biological status and trends in cod stocks available to a wide public.</p>
Resource Requirements:	Publication of this material as a CRR will cost ca 10 000 DKK. The material in the report is fairly straightforward, and therefore no specific additional costs are necessary
Secretariat Facilities:	The ICES/GLOBEC coordinator will assist with editing and preparing the report for publication.
Financial:	Publication costs. Staff costs for Dr Brander
Linkages To Advisory Committees:	There are no obvious direct linkages with the advisory committees, but the information will be useful in relation to long term advice on sustainable fisheries, recovery plans and ecosystem based management.
Linkages To other Committees or Groups:	This is a workshop of the WG on Cod and Climate Change. There is a close working relationship with the Working Group on Zooplankton Ecology.
Linkages to other Organisations:	The work of this group is closely aligned with similar work in national, regional and international GLOBEC programs.
Secretariat Marginal Cost Share:	100%