Workshop on advancements in modelling physical-biological interactions in fish early-life history: 
*Recommended practices and future directions*

Nantes, France  •  3-5 April, 2006
Acknowledgements

This Workshop on advancements in modelling physical–biological interactions in fish early-life history: recommended practices and future directions (WKAMF) is held under the auspices of the International Council for the Exploration of the Sea (ICES) Working Group on Physical-Biological Interactions and Working Group on Recruitment Processes.

WKAMF Co-Chairs Alejandro Gallego, Elizabeth North, and Pierre Petitgas would like to thank the Director and staff of the French Research Institute for Exploitation of the Sea (IFREMER) Center in Nantes for hosting the workshop. We also appreciate the support of the US National Science Foundation, the UK Fisheries Research Services, the University of Maryland Center for Environmental Science (UMCES), and the NOAA National Marine Fisheries Service. We are grateful for the endorsement of the GLOBEC and Eur-Oceans programs.

This booklet was produced with the support of the US National Science Foundation, the clerical efforts of Zachary Schlag (UMCES Horn Point Laboratory) and the design and publication expertise of Joanna Woerner (UMCES Integration and Application Network).
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Workshop overview

The goal of this workshop is to evaluate the present state and next steps in the developing field of modelling physical-biological interactions in the early-life of fish. The workshop will focus on recent advances in coupled biological-physical models that incorporate predictions from three-dimensional circulation models to determine the transit of fish eggs and larvae from spawning to nursery areas. These coupled bio-physical models have been applied to gain new insight on how planktonic dispersal, growth and survival are mediated by physical and biological conditions and have contributed to enhanced understanding of fish population variability and stock structure.

The workshop is designed to survey major components of bio-physical models of fish early life, address numerical techniques and validation issues, define recommended modelling practices, and identify future research needs. The workshop will focus on aspects of modelling fish early-life history including: initial conditions (egg production, spawning location/time), small-scale processes (turbulence, feeding success), mesoscale transport processes (physics and larval behaviour), and biological processes (development, growth, mortality, juvenile recruitment, metamorphosis, settlement). A range of bio-physical modelling approaches will be addressed, including Lagrangian, Eulerian, and individually-based models (IBM). Workshop results will provide guidance and direction for integration of coupled bio-physical models with observing systems, operational models, monitoring programs, and ultimately to improve fisheries management recommendations. In addition to enhancing the field of physical-biological interactions, this workshop will foster information exchange and support collaborations between international workshop participants.

The workshop includes presentations, posters, general discussions, and writing sessions. Invited and contributed presentations, a poster session, and structured discussions will occur on April 3 and 4 to survey recent advances in the field, develop a list of recommended practices, and identify research needs. The final day of the workshop includes focused writing sessions devoted to identifying funding sources and developing teams for international collaborative proposals.

This workshop is being held under the auspices of the International Council for the Exploration of the Sea (ICES) Working Group on Physical-Biological Interactions and the ICES Working Group on Recruitment Processes. It is hosted by the French Research Institute for Exploitation of the Sea (IFREMER) Centre in Nantes, France with support from IFREMER, the United States National Marine Fisheries Service, the United States National Science Foundation, the UK Fisheries Research Services, and the University of Maryland Center for Environmental Science. It is endorsed by GLOBEC and Eur-Oceans.

ICES terms of reference

2005/2/OC05 — A Workshop on Advancements in modelling physical–biological interactions in fish early–life history: recommended practices and future directions [WKAMF] (Co-Chairs A. Gallego, UK, E. W. North, United States, and P. Petitgas, France) will be held in Nantes, France, from 3–5 April 2006 to:

a) summarize current state of the art in modelling physical–biological interactions in fish early–life history;

b) review important technical/methodological issues (including model sensitivity and validation), prioritise important processes to be included in the models, and identify knowledge gaps;

c) develop a manual of recommended practices and list of future research directions as proceedings from the workshop.

WKAMF will report by 1 May 2006 for the attention of the Oceanography Committee.
**Theme session descriptions**

**Session I — Initial conditions: Egg production, spawning location/time**
This session focuses on spawning and egg characteristics that can be regarded as the initial conditions for coupled bio-physical models of fish early life. Contributions should focus on techniques for parameterising, validating and conducting sensitivity analyses on initial conditions such as the location and timing of spawning, the duration of the spawning season, egg buoyancy and vertical distribution, and egg stage durations and mortality. Questions we plan to address include: What do we need to know about the distribution and characteristics of the adult population? How do we relate them to egg production? How do we distribute egg production in time and space? If egg production modelling is not feasible or required, how do we distribute larvae in space and time at the start of the simulations? Are there guidelines or criteria that are recommended for establishing initial conditions? In addition to papers focused on modelling techniques, contributions that include explicit connections between models and laboratory and field data are welcome.

**Session II — Small-scale processes: turbulence, feeding success**
This session concentrates on small-scale physical and biological processes relevant to eggs, larvae and early juveniles such as the effect of turbulence on vertical distributions, escape behaviours and feeding success. Questions we seek to address include: What are the small-scale processes that are critical to include in models of eggs, larvae and early juveniles? How are biological processes affected by small-scale physics? What is the best approach for modelling relevant physical processes at the right spatial and temporal resolutions? What are the components of the feeding sequence that are important to resolve? Should we consider other small-scale processes relevant to the ecology of larval fish (e.g., predation at the scale of individual larvae, encounter of conspecifics for the development of schooling behaviour)? Contributions should focus on theory development, links between models and laboratory/field data, and techniques for parameterising, validating and conducting sensitivity analyses on small-scale coupled physical and biological processes.

**Session III — Mesoscale transport processes I: Physics**
This session addresses the role of mesoscale physical processes for transport (or retention) of fish early life stages from spawning to nursery areas, in a wide sense of the term. Questions we plan to address include: What features of the physical environment (currents, eddies, fronts, salinity and temperature fields, internal waves, etc.) must be replicated by hydrodynamic models to capture processes that are critical for fish early-life stages? What is the appropriate spatial and temporal resolution of 3D hydrodynamic models, and how does model quality of hydrodynamic predictions influence biological predictions? Are 3D hydrodynamic models required in all circumstances, or are there other approaches that are valid for specific applications (e.g., using CTD or ADCP data or 1D/2D models)? How do Lagrangian and Eulerian approaches compare? What are the strengths and weaknesses of particle tracking algorithms and what are the recommended best practices for implementing them (i.e., on-line vs. off-line tracking, including sub-grid scale mixing or not)? Contributions should focus on identifying critical physical processes as well as techniques for parameterising, validating and conducting sensitivity analyses on the role of mesoscale physical processes in the early-life of fish.

**Session IV — Mesoscale transport processes II: Larval behaviour**
This session focuses on the role of larval behaviour in mesoscale transport processes. A suite of behaviours have been observed for larvae and early juveniles: diel vertical migration, tidally-timed vertical migration, phototaxis, rheotaxis, turbulence avoidance, and association with thermocline/halocline/pycnocline, as well as directed horizontal swimming and schooling. These behaviours can change or be accentuated as swimming abilities and buoyancy control improve with larval development, and may have important implications for the direction and speed of early-stage transport in waters with wind-, friction- or buoyancy-induced shear in current velocities. Contributions should focus on identifying critical behavioural processes as well as techniques for parameterising, validating, and conducting sensitivity analyses on the role of mesoscale transport processes in the early-life of fish.
What behavioural processes should be included in models, which should not? How can we replicate the patterns observed at the population level from the behavioural rules relevant to the individual? In addition to papers focused on modelling techniques, contributions that include explicit connections between models and laboratory and field data are welcome.

Session V — Biological processes I: Development, growth, and mortality
This session is centred on the biological processes that occur during egg and larval stages, and on the physical conditions that influence them. Current modelling approaches range from simple to complex; from constant stage-durations, to temperature-driven growth rates, to complex bioenergetics models that incorporate feeding dynamics (individual-based models). Questions we plan to address include: How much model complexity is necessary to accurately portray the development, growth and mortality processes that occur during egg and larval stages? Is it necessary to dynamically model prey and predator fields to capture spatial and temporal variability in growth and survival? Do we need explicit models of the various sources of mortality (e.g. predation, starvation, disease, etc.) or should we use a functional relationship between mortality and larval characteristics (e.g. size, condition)? What are the forcing data required to parameterise and validate models that include development, growth and mortality? How sensitive are these models to the predictions from hydrodynamic models? Contributions should focus on links between laboratory/field data and models on development, growth and mortality during egg and larval stages, and on recommended practices for parameterising, validating and conducting sensitivity analyses on them.

Session VI — Biological processes II: Juvenile recruitment, metamorphosis, settlement
This session focuses on the biological processes that occur during early juvenile stage, and on the physical conditions that influence them. There are a suite of developmental and ecological processes that take place at the end of the larval period such as metamorphosis, settlement, onset of schooling, changes in feeding/growth patterns, and different sources and/or levels of mortality. Questions we seek to address include: Are there quantitative/qualitative changes associated with ontogeny that should be reflected explicitly in the models at the end of the larval period? Should bio-physical models that extend into the early juvenile period be significantly different from larval fish models, or can this life history stage be modelled using the same tools? Is it feasible to model fish recruitment all the way from spawning? What are the data requirements for parameterising and validating models of early juveniles? How sensitive are these models to the predictions from hydrodynamic models? Can bio-physical modelling shed any practical light on ‘traditional’ stock-recruitment dynamics? Contributions should focus on links between laboratory/field data and models of the early juvenile stage, and on recommended practices for parameterising, validating, and conducting sensitivity analyses on them.

Session VII — Future directions: Integration with observing systems, operational models, monitoring programs, and management recommendations
This session anticipates future uses of fish early-life models to improve our ability to support fisheries and ecosystem management. We seek contributions that describe techniques used to incorporate observing system data into fish early life models, directly link monitoring programs with fish early life models, and support management recommendations with their predictions. Questions we plan to address include: What are the current limitations in hardware, software, and data availability needed to set up initial conditions and forcing data? How can we ‘operationalise’ larval fish modelling and in what circumstances is there a need to do this? What validation/calibration and sensitivity protocols are needed? Are the models necessarily site-specific? Can simplified operational models be designed? What data derived from the various monitoring programs (including GOOS-type initiatives) could be of use to larval fish models and how should it be incorporated? How can we best distil the output of larval fish models into products that could be used in fisheries and/or environmental management?

4 WKAMF Programme
Monday 3 April 2006

Registration
8:00 – 12:00

Introduction — Workshop goals
8:30 – 9:00  Alejandro Gallego, Elizabeth North, and Pierre Petitgas
9:00 – 9:30  Thomas Miller, University of Maryland Center for Environmental Science, United States

Session I — Initial conditions: Egg production, spawning location/time
9:30 – 9:55  Christian Mullon and Christophe Lett, IRD, France
9:55 – 10:20  Timothée Brochier and Christophe Lett, IRD, France
10:20 – 10:40  Discussion

Coffee break
10:40 – 11:00

Session II — Small-scale processes: turbulence and feeding success
11:00 – 11:25  Thomas Osborn, The Johns Hopkins University, United States
11:25 – 11:50  Howard Browman and Anne Berit Skiftesvik, IMR, Norway
11:50 – 12:15  Bernard Megrey, Sarah Hinckley, and Carolina Parada, NOAA/AFSC, United States
12:15 – 12:20  Presentation of posters
12:20 – 12:40  Discussion

Lunch
12:40 – 14:00

Session III — Mesoscale transport processes I: Physics
14:00 – 14:25  Bjørn Ådlandsvik, Institute of Marine Research, Norway
14:25 – 14:50  Joachim Bartsch, Consulting and Modeling of Marine Ecosystems, Germany
14:50 – 15:15  Albert Hermann, NOAA/PMEL, United States
15:15 – 15:20  Presentation of posters
15:20 – 15:40  Discussion

Coffee break
15:40 – 16:00

Session IV — Mesoscale transport processes II: Larval behaviour
16:00 – 16:25  Øyvind Fiksen, University of Bergen, Norway
16:25 – 16:50  Frode Vikebo and Øyvind Fiksen, University of Bergen, Norway
16:50 – 17:15  Jeffrey Leis, Australian Museum, Australia
17:15 – 17:20  Presentation of posters
17:20 – 17:40  Discussion

Poster session
17:40
Tuesday 4 April 2006

Introduction and announcements
8:20 – 8:35

Session V — Biological processes I: development, growth, and mortality
8:35 – 9:00  Edward Houde, University of Maryland Center for Environmental Science, United States
9:00 – 9:25  Geir Huse and Are Salthaug, Institute of Marine Research, Norway
9:25 – 9:50  Myron Peck, Ute Hochbaum, et al., University of Hamburg, Germany
9:50 – 10:15 Pierre Pepin, Fisheries and Oceans, Canada
10:15 – 10:20 Presentation of posters
10:20 – 10:40 Discussion

Coffee break
10:40 – 11:00

Session VI — Biological processes II: Juvenile recruitment, metamorphosis, and settlement
11:00 – 11:25  David Brickman, Bedford Institute of Oceanography, Canada
11:25 – 11:50 Hans-Harald Hinrichsen et al., Leibniz Institute of Marine Science, Germany
11:50 – 12:15 Asbjorn Christensen et al., DIFRES HFI, Denmark
12:15 – 12:20 Presentation of posters
12:20 – 12:40 Discussion

Lunch
12:40 – 14:00

Session VII — Future Directions: Integration with observing systems, operational models, monitoring programs, and management recommendations
14:00 – 14:25  Sarah Hinckley et al., NOAA/NMFS AFSC, United States
14:25 – 14:50  Gwenhael Allain, Pierre Petitgas, and Pascal Lazure, IFREMER, France
14:50 – 15:15  Charles Hannah and Mike St. John, Canada and Germany
15:15 – 15:20 Presentation of posters
15:25 – 15:40 Discussion

Consensus development: recommended practices and future directions
16:00 – 17:30  Discussion
17:30  Open-Session Wrap Up and Acknowledgements
20:00  Workshop dinner
**Wednesday**

**Introduction and review of research recommendations**
8:30 – 9:00

**Identification of writing teams**
9:00 – 9:30

**Writing session I**
9:30 – 12:00

**Coffee break**
10:40 – 11:00

**Lunch**
12:00 – 13:30

**Writing session II**
13:30 – 16:40

**Workshop wrap-up and acknowledgements**
16:40 – 17:00

**Adjourn**
17:00
List of Contributors

Note: ‘o’ indicates an oral contribution, ‘p’ indicates poster contribution

**Introduction — Workshop goals**

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<td>Contributions of coupled physical biological models to understanding fish recruitment: a review and prognosis</td>
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<td>Particle-based models of fish spawning: a review and methodological issues</td>
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<td>Biophysical models of anchovy and sardine early life stages in the Benguela and Humboldt upwelling systems</td>
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<td>Physical processes that affect early life stages</td>
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<td>Howard I. Browman and Anne Berit Skiftesvik</td>
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<td>Using IBM’s to compare two hypotheses for the effect of turbulence on feeding rates in larval fishes</td>
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<td>II.4.p</td>
<td>How should larval cod navigate in pelagic environmental gradients?</td>
<td>T. Kristiansen, Ø. Fiksen, and R.G. Lough</td>
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<td>Object-oriented approaches for biological-physical models of plankton</td>
<td>Patrizio Mariani, Brian R. MacKenzie, and André W. Visser</td>
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<td>II.6.p</td>
<td>The relative influence of advection, turbulence and larval behavior on particle dispersal</td>
<td>Elizabeth North, Zachary Schlag, Jeffery Biermann, Raleigh Hood, and Tom Gross</td>
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**Session III — Mesoscale transport processes I: Physics**

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<td>The particle-tracking method for transport modelling</td>
<td>Bjørn Ådlandsvik</td>
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<td>Relative merits of Eulerian vs. individual-based models of fish dynamics in patchy habitats</td>
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### Session V — Biological processes I: development, growth, and mortality

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### Session VII — *Future Directions: Integration with observing systems, operational models, monitoring programs, and management recommendations*

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<td>VII.4.p</td>
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<td>Modelling the dispersal of cod eggs and larvae in the North Sea</td>
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Abstracts

Abstracts for the oral presentations and posters presented at this workshop can be found under the session in which they appeared.

Introduction — Workshop goals

Contributions of coupled physical biological models to understanding fish recruitment: A review and prognosis (0.1.o)

Thomas Miller

Annual publications involving the application of coupled physical–biological models to understanding fish recruitment processes have increased over the last decade. Over sixty papers were reviewed to assess the contribution these models have made to recruitment prediction and understanding. The majority of models reviewed were 2- and 3D numerical simulation models, although a limited number of 1D analytical models were included. Most models used a Lagrangian tracking algorithm to advect and diffuse particles within the model domain. The vertical and horizontal resolutions and temporal durations of the models varied widely. The review identified three categories of paper. ‘Explanatory’ papers involved models that were used to explain an observed distribution of larvae in space, or with regard to a specific trait. This category dominated the reviewed papers. Assessment of the sensitivity of model predictions to the model parameters were rare, but not entirely absent in this group papers. A second group identified was termed ‘Inferential.’ In these papers, authors inferred the presence or role of a mechanism, based on the inability of a model to match empirical data in the absence of the mechanism. ‘Inferential’ papers made up a smaller proportion of the reviewed manuscripts, and are generally more recent publications. The final group identified was ‘hypothesis-generating’ publications. These publications either used models with different configurations to test specific hypotheses, or produced specific hypotheses that could be tested empirically by collecting new data. This group is the least common in the review, but perhaps has the most to contribute to a greater understanding of recruitment processes. An increase in the frequency of hypothesis-generating applications of coupled physical–biological models may be expected over time as the field matures and refinements to both the physical and biological processes included in the models are made.

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**Session I — Initial conditions: Egg production, spawning location/time**

Particle-based models of fish spawning: A review and methodological issues (I.1.o)

*Christian Mullon and Christophe Lett*

We review factors that influence spawning and egg production and discuss methodological issues related to modelling them. In addition to surveying the state of art in the spawning and egg production modelling, we will present insights gained from a Pattern Oriented Modelling approach (Grimm and Railsback 2005) as applied to the following questions:

- What are the spawning patterns that (1) emerge from observations, (2) can be modelled with Simple assumptions on individual behavior, and (3) could be related to different regimes of population dynamics?
- What is the null hypothesis when using a Lagrangian model? Are there generic simulations that could be applied to all systems to obtain reference values for more sophisticated simulations?
- Which inverse modelling approaches, that is from patterns to processes, could be applied to study first stages of fish populations?
- How can we utilize an experimental approach when modelling spawning and egg production?

*Christian Mullon*

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Biophysical models of anchovy and sardine early life stages in the Benguela and Humboldt upwelling systems (I.2.o)

Timothée Brochier and Christophe Lett

Coastal upwelling systems are major contributors to world fisheries, but face high levels of variability in fish abundance and catches. Small pelagic fishes, and particularly anchovy and sardine, represent the main part of catches in upwelling systems. Their early life stages, which are transported passively by ocean currents, are particularly sensitive to environmental conditions. Models of anchovy and sardine early life stages dynamics have been developed to investigate this sensitivity in the southern part of the Benguela Current system (South African coast) and the northern part of the Humboldt Current system (Peruvian coast).

The Regional Ocean Model System (ROMS) was used to provide simulations of the water circulation in the regions. These simulations served as inputs into individual-based models of ichthyoplankton dynamics. The influence of physical and biological processes on the transport/retention and survival of fish eggs and larvae were studied. We will present a review of the main results obtained, with a special emphasis on those concerning location, time and depth of spawning. We will also question the ability of such models to explain the variability and shifts observed in spawning patterns.

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The last 50 years has seen tremendous progress in oceanography. For physical oceanographers the developments in sampling technology have enabled measurements of the flow field in the ocean over a wide range of temporal and spatial scales. The direct measurement of turbulent velocity fluctuations in the ocean, at scales from 1 m to a few mm, is now routine. Detailed photographic and video observations of planktonic and larval organisms have shown fascinating behavior and feeding processes wherein the organisms interact with the local turbulent flow.

How do we combine the picture of oceanic turbulence with the information about predator and prey behavior and feeding to characterize the interaction between the physical and biological regimes for modelling purposes? What types of laboratory and oceanic measurements are necessary for progress?

The general picture of turbulence in the ocean is a thin surface (thickness of order the wave height) of enhanced dissipation due to the surface gravity waves. The upper layer is intermittently (in both time and space) the site of free and forced convection and Langmuir circulation. The thermocline is intermittently turbulent, deriving energy from internal gravity waves and inertial oscillations. Below the thermocline there are layers of turbulence of varying thickness and longevity. The bottom boundary layer is forced by the flow over the bottom and there is significant interaction with the surface wave field in shallow water. Below the upper layer and seasonal thermocline, the tide appears to be responsible for much of the mixing in both the shallow and deep ocean.

In deriving these results, the measurements are usually averaged in both time and space. Are the spatial and temporal time series and spectra, often used by the physical oceanographers, useful indicators of the variations apparent to planktonic organisms? How do we use the averaged information in the literature to derive the spatial and temporal variations sensed by the planktonic organisms?

This paper reviews our present understanding of small-scale turbulence (<1m) in the ocean and then relates the results to the scales appropriate for larval fish and their prey. Implications for oceanic and laboratory measurements are discussed.

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Session II — Small-scale processes: turbulence and feeding success

Half-truths and myths surrounding feeding and escape behaviour in marine fish larvae (II.2.o)
Howard I. Browman and Anne Berit Skiftesvik

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. Our goal here is to demonstrate how studying these perceptual links can help marine ecologists understand ichthyoplankton-zooplankton interactions. We will use case studies 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 active prey choice/prey selectivity by cod larvae; Case Study 3 – Early-stage cod larvae lose in a match with almost any predator. In each case, we will emphasize how the answers that issue from the mechanistic sensory ecology approach can (and must) be used to 1) assess the relative importance/weighting of the variables used in models, and 2) define their value ranges.

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Session II — continued

Using IBM’s to compare two hypotheses for the effect of turbulence on feeding rates in larval fishes (II.3.o)

*Bernard A. Megrey, Sarah Hinckley, and Carolina Parada*

Two of the main hypotheses that attempt to explain the impact of turbulence on larval fish feeding are based on completely different mechanisms. In one, fish larvae and their prey remain in the mixed layer and turbulence-enhanced ingestion takes place, reaching a maximum level of consumption at a specific level of turbulence. After that, increasing turbulence negatively impacts feeding. In the second, concentration changes induced by turbulence-avoidance behavior enhance feeding. Both assume that turbulence in the surface and mixed layer is a result of wind-driven mixing at the surface, rather than tidal mixing or other bottom sources of turbulence. We have included these different algorithms in alternate versions of an individual-based model of recruitment processes in larval walleye pollock (*Theragra chalcogramma*). We present the results of simulations comparing the output from the model to examine how feeding success and growth are affected and to determine the optimal wind speeds for feeding and the probability of starvation under the two different hypotheses. We compare these with information about wind speeds and recruitment success in the Shelikof Strait region of the Gulf of Alaska. Our goal is to explore which algorithm better explains the mechanistic relationship between wind speed, turbulence, feeding success, and recruitment.

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How should larval cod navigate in pelagic environmental gradients? Modelling the growth-predation risk trade-off for larval cod (II.4.p)  
*T. Kristiansen, Ø. Fiksen, and R.G. Lough*

The US-GLOBEC conducted cross-frontal time-series from 18-24th of May 1999 of zooplankton, hydrography, and fish larvae on the Georges Bank. Halfway through the time-series a storm swept by, stirring up the frontal zone and the stratified site, and reorganizing the distribution of prey (*Pseudocalanus, Oithona, Calanus finmar-chicus*). An individual-based model (IBM) parameterised for larval cod is used to generate temporal and spatial patterns of growth and predation rates across the front. This IBM is a composite of important processes that affect growth of larval cod larvae; both extrinsic factors (light, turbulence, temperature, prey abundance, etc.) and intrinsic factors (metabolism, growth, stomach fullness, etc.). A trade-off between feeding and survival emerge since both larval feeding and predation risk from fish predators increase with ambient light. Similarly, another trade-off exists between activity or prey search (swimming) and the risk of encountering ambush or tactile predators. Individual larvae with various attractions to risk (different behavioural rules) are tracked over time and assessed for success in different environmental gradients (mixed or stratified, deep and shallow regions). Model predictions are compared to observed vertical distribution of larval cod and optimal behaviour (depth and activity over a diel cycle) predicted from dynamic programming. In this work we focus on the local vertical gradient, and how larvae should select habitat to balance immediate growth and predation risk. Here, we ignore the risk of advection off the bank associated with different vertical behaviours, but this may also be an important aspect to fully understand selection pressures action on larvae.

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Object-oriented approaches for biological-physical models of plankton (II.5.p)

Patrizio Mariani, Brian R. MacKenzie, and André W. Visser

The ocean’s physical processes act on large variety of scales, some of which may be comparable to the characteristic scales of biological dynamics and can directly affect many important metabolic activities. It seems essential, therefore, to consider also the physics of the system when trying to understand the biotic dynamics of a marine ecosystem. This results in the so-called physical biological coupling.

It is generally believed that processes at a scale comparable to the individual organisms may play a major role in the above scenario. Marine organisms can either be dominated by effects of the local environment, or can somehow mediate such effects by active responses. The difference between these two situations lies largely in whether or not the organism can both obtain and use information about local environmental conditions. These capabilities in turn depend on both the characteristics of environmental variability and the sensory and response capabilities of the organism.

The aim of this talk is to investigate some of the physical and biological processes affecting the interactions between plankters and their resources. The analysis is conducted by attempting to model individually plankton organisms and their interaction with the surrounding environment, in order to obtain a description of the effects of the relative motion of plankton at small scale.

A survey of the individual-based models (IBM) developed to study such processes will be made, presenting some of the results obtained analyzing the zooplankton encounter processes with its food and the transport and survival of drifting fish early life-history stages. Particular attention will be devoted to describe the Object Oriented paradigm as a method naturally suited for the development of an IBM in marine system.

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The relative influence of advection, turbulence and larval behaviour on particle dispersal (II.6.p)

Elizabeth North, Zachary Schlag, Jeffery Biermann, and Raleigh Hood, and Tom Gross

Larval transport is influenced by advection, turbulence and larval behaviour. The relative influence of these factors on particle dispersal may differ between regions with different morphologies and stratification. We test this hypothesis with a particle tracking model implemented in Chesapeake Bay that includes vertical and horizontal sub-grid-scale turbulence as well as surface and bottom-oriented larval behaviors. Results suggest that stratification and estuary morphology influence the relative importance of vertical and horizontal turbulence on particle dispersal. In addition, particle dispersal was notably reduced in simulations with larval behaviour, even when vertical swimming speeds were as low as 0.5 mm s⁻¹. Particle dispersal estimates are compared with in-situ dye-release experiments and sensitivity of model results to turbulence parameterization is discussed.

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**Session III — Mesoscale transport processes I: Physics**

The particle-tracking method for transport modelling (III.1.o)

*Bjørn Ådlandsvik*

Lagrangian transport or particle tracking is an established method for modelling advection and diffusion of planktonic organisms in the ocean. A short description of the method is given. By consideration of the time development of the statistical momenta, the method is compared to the alternative approach of Eulerian transport. The particular case of vertical distribution of buoyant fish eggs is considered.

It is argued that a set of standard test cases for verification of particle tracking models is developed within the community. Some examples of such test cases are suggested.

The implementation of particle-tracking algorithms is described, including numerical schemes and practical issues such as time stepping, and land treatment. The sensitivity of these issues is examined both in the test cases and in a more realistic setting.

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On model system characteristics, data requirements and parameterisations for an individual-based model to predict the survival of early and post-larval stages of fish (III.2.o)

*Joachim Bartsch*

A state-of-the-art hydrodynamic model with realistic bottom topography forced by high resolution meteorological data, river run-off, tidal elevations at open boundaries and climatological temperature and salinity fields, treated in a prognostic manner, is required to provide an individual-based model (IBM) with appropriate physical input. The physical data required by a mesoscale IBM are the three-dimensional current, temperature and salinity fields at a daily rate. Biological data requirements for the IBM are larval vertical distribution data, for example as a function of light and length and initial horizontal and vertical egg distribution data over the whole spawning season. Furthermore, temporally and spatially variable prey distribution data for early and post-larvae over the whole spawning season at preferably a weekly rate are required. The importance of these datasets for the predictive capability of the IBM is discussed. In the context of model predictions of particle distributions it is important to consider that the duration of the IBM simulations are restricted by the “horizontal passivity” assumption for the particles and is determined by the time span for which this assumption is justifiable for any specific species. Larval and post-larval growth and mortality parameterisations as a function of length, temperature, prey distribution and absolute growth rate are discussed and the super-individual concept used for the treatment of mortality in the IBM is elucidated. Examples of field data required for the validation and for testing the predictive capability of the IBM are given.

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Session III — Mesoscale transport processes I: Physics

Relative merits of Eulerian vs. Individual-based models of fish dynamics in patchy habitats (III.3.o)

Albert J. Hermann

A fundamental equivalence was established by Taylor (1921) between Eulerian and Lagrangian approaches to turbulent diffusion; an ensemble of particles, each subjected to a random walk (the Lagrangian approach), can generate statistics equivalent to turbulent eddy diffusion (the Eulerian approach). This equivalence is relevant to the construction of statistically meaningful Individual-Based models of fish, and their Eulerian counterparts. Spatially explicit Individual-based models offer great flexibility in the specification of behaviours, especially those based on past history (e.g. gut fullness). However, when the circulation or prey fields are patchy in space and time, such models may require a large ensemble of realizations, to attain a statistically meaningful result. These patchy situations include eddy-rich circulation fields, as well as prey fields locked to a particular bathymetric feature. Eulerian models have less flexibility in the specification of history-dependent behaviours, but a single run may naturally integrate over some (yet not all) possible Lagrangian realizations of individuals in patchy environments. Here an attempt is made to determine which approach could be expected to be superior, based on the statistics of the circulation and prey fields, and given a finite computational resource to generate realisations of either type of model.

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Validation of lagrangian larvae drift trajectory (III.4.p)

Marina Chifflet, Pierre Petitgas, and Pascal Lazure

Individual based larval growth and survival models coupled to Lagrangian drifters in circulation models represent novel fisheries tools which allow to predict recruitment in fish populations under different scenarios of hydroclimate and fish spawning. Such biophysical models require that the velocity and turbulence fields be simulated realistically at a fine scale as well as over large areas and long periods. Uncertainty in the transport of biological particles need be assessed as a first step. The present work attempts to evaluate the variability in 2D lagrangian trajectories by comparing results of different model runs as well as differences between modelled trajectories and at sea deployed drogues trajectories. Tracking experiments of drogues released at sea showed the dominance of advective (deterministic) movement over diffusive (turbulent) movement. Can diffusion be omitted in estimating 2D larvae drift? The area studied is the French shelf of the Bay of Biscay for which a 3D circulation model has been developed.

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Session III — continued

From spawning grounds to nursery areas in the western Gulf of Maine: A modelling approach to define key processes for transport success. (III.5.p)

M. Huret, J.A. Runge, and C. Chen

We are investigating the transport of cod and herring larvae from major spawning grounds located in the western Gulf of Maine. Discrete spawning grounds and spawning periods are identified based on information meetings with local fishermen, egg and larva abundance maps and previously published studies. Nursery areas for juveniles are defined as nearshore according to bottom type from coastal substrate maps. The 3D FVCOM circulation model (Finite Volume Coastal Ocean Model) is used in an off-line version for passive particle tracking. The FVCOM was run with the actual tide, meteorological, and freshwater supply data from 1995 and 1999 to simulate flow fields for those years. We use a random walk model to simulate early stage larval vertical movement in the spatially variable turbulent field. Various vertical distribution scenarios are considered for the later larval stages.

In western Gulf of Maine, the success of larval fish transport is thought to be dependent on processes that move larvae out of the strong Western Maine Coastal Current (WMCC) to the inshore nursery areas, thereby retaining them in the western Gulf. In this context, we investigate mechanisms leading to the particle retention, such as the sources of the cross-shore component of the velocity field, or decreases or reversals of the coastal current, and the ability of the model in reproducing them.

Also, the seasonal and interannual variability of such mechanisms is investigated, along with the implications on larval transport for recruitment success.

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Session III — continued

Dynamics of SWODDIES in the Bay of Biscay (III.6.p)

Pantxika Otheguy, Xabier Irigoien, and Manuel Gonzalez

Slope Water Oceanic eddies (called SWODDIES by Pingree and Le Cann, Deep-Sea Res., 1992a) sometimes appear during the winter in the Bay of Biscay. These eddies have been widely observed by buoy measurements as well as by infrared satellite images. A recent observational programme (GIGOVI) provided high resolution observations, allowing to determine both the physical properties (García-Soto et al., 2002; Sánchez and Gil, 2004) and the biological properties (Fernández et al., 2004) of SWODDIES. Nevertheless, their physical understanding is not as far completely achieved as neither their birth nor their evolution can be forecasted. The present study aims at improving this understanding of their dynamics by determining the governing factors. Swoddies are created on the continental slope so that they can trap and transport biological material from the shelf and slope and therefore influence widely the pelagic ecosystem in their areas. In particular, they are believed to affect fish recruitment through two mechanisms. First, as they are anticyclonic, they generate an upward flow of nutrients in the photic layer, increasing primary and secondary production of the system. Second, SWODDIES can function as ‘safe heavens’ for fish larvae transporting them into oceanic areas with lower predation pressure, but at the same time maintaining a high enough food concentration.

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A random-walk Lagrangian particle-tracking model is applied to study horizontal mixing processes and larval transport in the ROFI system of the eastern English Channel. Our computations based on both the Lagrangian and Eulerian approaches show the existence of a classical coastal current along the French coast whose dynamics is strongly dominated by the freshwater runoff and modulated by the neap-spring tidal cycle. However, the Lagrangian and Eulerian residual velocity fields do not agree throughout the model domain.

We performed numerical Lagrangian tracking experiments with passive and active particles representing eggs and larvae of flounder (*Pleuronectes flesus*). Active particles are not neutrally buoyant and are able to exercise light dependent vertical migrations. The experiments reveal patchiness in the horizontal distribution of particles with the strongest accumulation observed on the margin of the ROFI. This happens because the interaction between the turbulence, freshwater buoyancy input, and tidal dynamics produces particle trapping and vertical spreading within the frontal convergence zone. Results of modelling are validated against observed concentrations of Flounder larvae. Spatial distribution of salinity and chlorophyll-a concentrations observed during the field experiments reveal similar variability in the high frequency range.

Tracking experiments with active particles indicate that the vertical migration might cause relatively significant departure from the passive particle transport pattern. The differences concern the rate of the northward migration of particles and the shape of the particle transport pattern. Vertically migrating particles could travel slower.

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Eulerian techniques for individual-based models (III.8.p)
Uffe Høgsbro Thygesen, Fredrik Nilsson, and Ken H. Andersen

Individual-based models appeal to marine ecologists because of the emphasis of the individual as the fundamental ecological unit, but their analysis often includes computationally demanding statistical exercises. Here we show that certain Individual-based models, those based on Markov additive processes, lend themselves to a simplified Eulerian analysis where for example the mean and variance over the population can be computed with relatively modest effort. Next, we discuss simplifications in the Eulerian model based on separation of time scales, and weak diffusion. We illustrate the framework with an example from larval transport, growth and survival, where the approach leads to partial differential equations for the mean larval length, as a function of position and time, and for the associated variance. We further discuss the generality of the framework as well as its applicability to marine ecological problems.

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Modelling of mesoscale transport and retention of early-life stages of fish in southern Brazil: Development and future directions (III.9.p)

Jose H. Muelbert

The coastal and shelf regions of southern Brazil (CSRSB) are among the most important fishery grounds for demersal species. Despite this importance, few initiatives have incorporated information on early-life stages to support fisheries and ecosystem management, which, in most cases just relate ichthyoplankton distribution to water mass and seasonal variability. My objective is to review past attempts to model larval fish transport and retention, and to discuss future needs and directions for these studies in the SBCSR. Only three studies, two in the continental shelf (CS) and one in Patos Lagoon estuary (PLE), have been conducted to model larval fish transport and retention. The methods employed were: simple use of physical and biological oceanographic data to calculate geostrophic velocities and estimate transport of larvae; use of a 2D hydrodynamic coupled to a Lagrangian transport model for buoyant passive particles representing fish eggs; and, the combined use of individual-based models (IBM) with two derived circulation patterns, Ekman drift and the output of a 3D hydrographic model. In general, the outputs obtained were able to replicate major circulation patterns and the observed fish eggs and larvae distribution. Increased complexity of model capability led to more detailed scenario of the relevant processes involved in transport and retention of early-life stages of fish. Future directions point to the need to pursue a better knowledge of the vertical distribution and life cycle parameters to enhance our understanding of mesoscale transport of early-stages of fish in the CSRSB.

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What can fisheries oceanography learn from behavioural ecology? (IV.1.o)

Øyvind Fiksen

Through the Darwinian process of natural selection, fish have evolved life histories and behaviours to a wide range of ecological challenges. Adults allocate energy and time between growth and reproduction such that the lifetime reproductive output is maximised, and spawn at times and places where their progeny have a high chance of survival including larval drift routes to favourable nursery grounds. Larval fish use their behavioural repertoire (e.g. vertical habitat selection and swimming activity) such that growth and predation rates are optimised given physical and physiological constraints. To predict how fish populations respond to changes in their environment, in terms of behaviour (location and timing of spawning, spatial distribution), life-history (e.g. egg production), and population dynamics, we need to combine two types of models: 1) mechanistic representations of ecological processes (growth, predation risk, density dependence, etc) and 2) the adaptive behavioural response to environmental signals. The latter can be modelled as a set of fixed pre-specified rules fish follow, such as ‘move randomly in upper 20 m,’ or as behaviours or ‘norms of reaction’ that emerge from a given ecological setting. One useful guideline is that, when applied locally and for each individual, the rules should be able to recreate observed patterns of e.g., size, age, or distribution in depth or space. If larvae can improve their success by modifying behaviour (within reasonable constraints) in a given environment then our models are not consistent. The behavioural schedule should be ‘evolutionarily stable’ or difficult to invade by alternative strategies, and evolutionarily robust, meaning that it works well in a range of typical scenarios. I will discuss methods and challenges in building consistent models of larval drift, behaviour, and recruitment success.

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How sensitive is drift and settlement patterns of Northeast Arctic cod eggs and larvae to vertical distribution? (IV.2.o)

Frode B. Vikebø and Øyvind Fiksen

Northeast Arctic (NEA) spawn at several locations along the Norwegian coast during March and April, with the Lofoten area as the major spawning ground. The offspring are subject to pelagic free drift from the spawning grounds to the nursery grounds in the Barents Sea, which is limited by the continental shelf edge in the south-west and the ice edge in north-east. The horizontal distribution of settling juveniles is highly affected by the circulation in the area and varies between years. Although the larvae are drifting passively with the currents, they are able to influence their drift route. The currents differ in the vertical and larvae can take advantage of this trough vertical positioning. We let larvae and juveniles evaluate potential growth rate and probability of survival in a limited part of the water column, and to select among them according to prescribed behavioural rules. We then investigate how this modifies the horizontal distribution achieved compared with advection at fixed depths as revealed in an earlier study. Adding different weights of preference for risk or growth to individual larvae, we also derive optimal vertical behaviours under given fitness criteria such as ‘maximise size at age times survival probability’. We search for behavioural rules that are robust at a range of spawning grounds and hatching dates.

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How larval fish behaviour influences dispersal – ontogeny, behaviour, physiology, phylogeny, hydrodynamics and biogeography meet hydrography (IV.3.o)

Jeffrey M. Leis

Both morphology and behaviour develop during the pelagic larval stage (PLS) of demersal teleost fishes. Perciform fishes begin the PLS as plankton but end it as nekton, with behavioural capabilities (including swimming, orientation, and sensory behaviours) that can influence, if not control, dispersal trajectories. The ontogeny of these behaviours, and the gradual transition from plankton to nekton is central to understanding how larval fishes can influence dispersal, and how to integrate behaviour into dispersal models. I review recent behavioural work showing that from about 5-8 mm SL, larvae of perciform fishes can directly influence dispersal because they: swim in an efficient inertial hydrodynamic environment; can swim for kilometres at speeds which heuristic models show will alter dispersal trajectories, and by settlement can swim faster than ambient currents; can orientate in the pelagic environment; and can detect sensory cues (light, sound, odour) that allow orientation. Fish larvae also control their vertical position (which may change temporally, spatially and ontogenetically), allowing indirect influence on dispersal. The hydrodynamic and physiological effects of temperature indicate that larvae in warm water should swim more efficiently and at smaller sizes than larvae in cool water. Limited evidence suggests that larvae of perciform fishes are more behaviourally competent and attain morphological and behavioural milestones when smaller (and younger?) than do larvae of clupeiform, gadiform and pleuronectiform (CGP) fishes. Perciform fishes dominate demersal fish communities in warm water, whereas CGP fishes dominate in cooler waters. These hydrodynamic, physiological, ontogenetic, phylogenetic and biogeographic factors imply that larval fish behaviour may have more influence on dispersal in warm seas than in cool seas.

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Lagrangian description of marine larval dispersal kernels (IV.4.p)

K. Pehrson Edwards, J.A. Hare, and F.E. Werner

Individual-based models (IBMs) track the characteristics of individual organisms over time and can be used to make global population-level statements. One natural application of spatially-explicit IBMs is the quantitative, Lagrangian, description of the post-spawn dispersal phase of individuals, where planktonic (or meroplanktonic) larvae are entrained in oceanic circulation fields with limited control over their trajectories (except perhaps for their vertical position in the water column, through diel migration, predator avoidance, etc.). The success of the larvae’s dispersal onto settlement sites, or nursery areas, is important in determining key population characteristics such as possible recruitment levels and population connectivity, among others. Quantitative measures of connectivity can be expressed through dispersal curves or dispersal kernels, the probability that a larva will settle at a given distance from its release location. As part of a larger effort in the development of Marine Protected Areas (MPAs) on the southeastern U.S. continental shelf, we use Lagrangian methods to construct dispersal kernels of target fishery species, black sea bass and bank sea bass. We discuss the effects of active individual larval behavior as well as interannual variability in ocean physics in the construction of the dispersal kernels.

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Influence of biophysical processes on coral reef fish population connectivity inferred by modelling (IV.5.p)


The distance and direction of larval dispersal largely influence the demography and genetic structure of marine fish species. Larvae may be diluted and carried away by currents while actively moving, which make their in situ study very difficult. Here we use various modelling approaches to examine the influence of physical and biological processes on larval trajectories and ultimately on population connectivity of coral reef fishes.

A biophysical off-line Lagrangian tracking system (BOLTS) designed for multiple processors and high throughput performance, estimates the spatial probability of successful dispersal (or dispersal kernel, DK) utilizing ocean general circulation models coupled off-line with a stochastic scheme tracking individual larvae within a GIS-based seascape. We examine the influences of time sampling, grid scale, and anisotropy of diffusivity due to submesoscale coastal features on the prediction of DKS from multiple sites throughout the Caribbean region. We further use sensitivity analysis to examine the impact of life history traits (e.g. spawning production, pelagic larval duration (PLD), ontogenetic vertical migration (OVM), larval mortality) on patterns of recruitment.

A hybrid model system operating on a smaller spatial scale and focusing on larval behavioural strategies in the pelagic environment (i.e. vertical and horizontal movements and feeding) serves to study the influence of behaviour in optimising larval survival and self-recruitment.

Our findings suggest that 1) including diffusivity anisotropy is critical in estimating dispersal distances; 2) DK patterns are mostly sensitive to seasonal reproduction and to OVM with increasing PLD; 3) larval behaviour has a strong influence on the degree of self-recruitment.

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Session IV — continued

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Quantifying and modelling dynamic biological processes in fish early-life stages (V.1.o)
Edward D. Houde

Eggs and larvae of fishes are small, numerous and patchily distributed. Rates of mortality and growth are high and variable, leading to variable stage-specific survival. Environmental factors act to rapidly reduce initial numbers of egg and larval cohorts while density-dependent, regulating mechanisms serve to stabilize numbers, allowing biomass proliferation in the late larval and metamorphic stages. Physical features and processes important for survival operate on micro- to ocean-basin scales. Temperature, prey availability, and predator abundances are major forcing variables. Body size and size-specific (or size-selective) predator-prey dynamics characterize early life. Factors that accelerate development and growth, thus compressing stage durations, usually increase survival potential of early life stages. Statistical and numerical modelling to evaluate and explain variability in recruitment has proliferated in recent decades. Technological advances in observational and experimental research have provided knowledge to parameterise and calibrate tropho-dynamic and coupled bio-physical models that describe cohort fates. Complexities of processes and constraints on sampling at relevant time and space scales necessitate modelling early-life dynamics, but also emphasize critical needs for observational data to validate models. Models restricted to egg and larval stages can explain their fates, but such restricted models rarely are sufficient to forecast recruitment.

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Predicting recruitment in Norway pout by combining ocean models with predators and prey distribution (V.2.o)

Geir Huse and Are Salthaug

Norway pout in the North Sea has experienced poor recruitment recently. Herring has been suggested to be a major predator on fish larvae in the North Sea. In order for predation to be an effective mechanism in impeding recruitment, there has to be substantial spatial overlap between larvae and their predators. There is potential for overlap between herring and larval Norway pout, but its magnitude remains unknown. Inflow of *Calanus finmarchicus* to the North Sea is another potentially important process for recruitment in North Sea fishes. Here we combine particle tracking of Norway pout larvae with observed distributions of herring and abundance/inflow of *Calanus* in the North Sea to investigate the causes behind variation in Norway pout recruitment.

Physical fields, including inflow of water to the North Sea will be taken from an archive generated by simulations using the Regional Ocean Model System. Data from the International Bottom trawl survey will be used to generate distribution of Norway pout spawning stock and herring. Particles will be released at the observed spawning grounds of Norway pout, and the particle tracking model will be used to calculate degree of overlap with the herring and the ambient temperature of larval Norway pout over the previous 20 years. We will also use *Calanus* data from the Continuous Plankton Recorder to give an index of food availability. The output of the spatial model will then be used in a statistical model to investigate the ability of the different variables in explaining Norway pout recruitment.

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All You Can Eat? Generating prey fields and limits to food consumption: Examples from a coupled NPZD-IBM approach for larval *Sprattus sprattus* in the North Sea (V.3.o)

*Myron A. Peck, Ute Hochbaum, Wilfried Kühn, Miriam Dickmann, Corinna Schrum, and Michael A. St.John*

Biophysical individual-based models (IBM’s) are widely used to help understand the factors affecting spatio-temporal differences in rates of survival and growth in early life stages of marine fishes. Depending upon the questions being asked, IBM’s have utilized a variety of different methods to 1) represent prey fields, and 2) depict larval fish foraging and growth. We provide a brief background of these two topics and explain recent developments in these areas within our modelling research focusing on larval sprat (*Sprattus sprattus*) in the North Sea. First, we discuss our approach of generating a size-based prey spectrum from bulk zooplankton carbon estimates obtained from an NPZD model. A sensitivity analysis of the impact of changes in the zooplankton size spectrum (e.g., via seasonal or spatial differences) for potential larval growth and survival is presented. Secondly, we discuss the pitfalls of using a threshold equation for food consumption (CMAX) (or growth, GMAX) within IBM’s having complex predator foraging subroutines. Specifically, that these non-mechanistic equations can dictate modelled larval growth dynamics, overriding growth estimates based upon mechanistic processes. To correct for this, we recommend a mechanistic (physiologically-based) alternative to limiting food consumption based on gut fullness, evacuation rates and the activity of digestive enzymes at different temperatures. The generation of realistic prey fields that vary both spatially and temporally and the establishment of foraging limits that are physiologically-based are active areas of development in larval fish biophysical modelling. Advancement made in these components should provide more biological realism within models and aid in our understanding of recruitment processes.

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Session V — continued

Modelling early life history losses to predators (V.4.o)

Pierre Pepin

Individual-based models (IBMs) of early life dynamics that incorporate potential losses to predators are often based on a very simple model of prey-predator dynamics and information on local predator densities. Although the predation process (encounter, attack, capture) is treated with a degree of stochasticity, other elements of the model, such as predator densities, drift history of the larvae, and sampling uncertainty, are not. Each of these elements can significantly affect the outcome of any comparison between observations and model projections. Using a hierarchical progression, based on what we have knowledge of and what we have to guess at, I investigate how uncertainty in each element affects the distribution of possible forecasted losses (i.e. mortality), using data from a field program with high resolution (in time and space), and a regional circulation model. The results show that our knowledge of uncertainty in our observations plays a critical role in our ability to model (and forecast) early life dynamics.

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An individual-based model of growth and survival along drift trajectories in the early life stages of anchovy (*Engraulis encrasicolus*) in the Bay of Biscay (NE Atlantic) (V.5.p)

Gwenhael Allain, Pierre Petitgas, Pascal Lazure, and Patrick Grellier

Fish recruitment is the result of the integration of small-scale processes affecting the survival of larvae and juveniles. A hydrodynamic model was used (a) to explore and model these physical-biological interaction mechanisms and then (b) to perform the integration from individual to population scale. This method was applied to the case of anchovy in the Bay of Biscay (NE Atlantic). (a) To tackle survival mechanisms, the main data available were past growth (otolith) records of larvae and juveniles collected at sea. The drift history of these individuals was reconstructed by a back-tracking procedure using hydrodynamic simulations. Along the individual trajectories obtained, the relationships between (real) growth variation and variations in physical parameters (estimated by hydrodynamic simulations) were explored and used to build and adjust an individual-based growth model. The origin of the individual trajectories in space and time was then examined in order to select larvae and juveniles supposedly belonging to the same sub-cohorts. The comparison of growth rates among these reconstructed sub-cohorts was used to set a growth-selective survival model. (b) Thousands of virtual buoys were released in the hydrodynamic model in order to reproduce the space-time spawning dynamics. The biophysical model was run along the buoy trajectories to simulate growth and survival as a function of the environment encountered. The survival rate after three months of drift was estimated for each micro-cohort. The sum of all these survival rates over the season constitutes an annual recruitment index. The modelling choices and model results are discussed.

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**Session V — continued**

Immersive visualization: A modern approach for the rapid exploration of Eulerian and individual-based models (V.6.p)

*Albert J. Hermann, Sarah Hinckley, Carolina Parada, Elizabeth Dobbins, Christopher W. Moore, and Dale B. Haidvogel*

Stereo-immersive visualization is a powerful and increasingly economical tool for the rapid exploration of 3D ecosystem and fish life history model output. By taking advantage of human binocular vision, this approach allows the user to experience and interact with model features as ‘virtually real’ objects in our three dimensional world. Here, a relatively new technology for immersive visualization (a portable ‘Geowall’) will be used to illustrate the 3D structure of output from a set of spatially nested physical and biological models of circulation, plankton, and fish in the Coastal Gulf of Alaska. Elements of this set include circulation and lower trophic level dynamics at ~3km resolution, and a spatially explicit Individual-Based Model of walleye pollock, *Theragra chacogramma*. Immersive techniques are especially powerful at revealing: 1) the structure of spatially patchy fields, such as phytoplankton (rendered as a ‘fog’ of concentration); 2) three-dimensional flows near topography (rendered as 3D vectors); 3) spatial tracks of individuals and the prey fields they experience along those paths (rendered as color-coded symbols moving through space). Participants will be given the opportunity to interactively ‘fly through’ and examine these and other fields of interest.

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Optimised biophysical model for Icelandic cod larvae (VI.1.o)

David Brickman

All biophysical models (BPM) contain parameters and algorithms that are poorly known or are known with some degree of uncertainty. The existence of appropriate data offers the opportunity to tune model parameters by minimizing the misfit between model prediction and data. This paper presents a highly efficient method to optimise biophysical models, applied to Icelandic cod larvae.

The method uses a probability density function approach to reduce the data from particle tracking experiments (particle position and attributes) from millions of pieces of information down to thousands. It is then shown how these probability transition matrices can be incorporated into a BPM, and how the problem of determining parameter values becomes translated into the solution of a bounded constrained optimization problem that minimizes the model-data misfit.

Icelandic cod spawn from numerous locations along the coast of Iceland, with the peak spawning times, spawning durations, and number of eggs released known with a degree of uncertainty. The model is used to determine optimal egg production model parameters for 15 spawning grounds, as well as the most likely egg/larval vertical migration algorithm. A simple larval settlement model is tested to see if it improves the result. This technique can be adapted to diverse BPM problems.

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Long-term recruitment variability of Baltic sprat and cod: the role of larval and juvenile transport from spawning to nursery grounds (VI.2.o)

Hans-Harald Hinrichsen, Rudi Voss, Gerd Kraus, Hannes Baumann, and Christian Möllmann

Sprat *Sprattus sprattus* L. and cod *Gadus morhua* L. are the major fish species in the Baltic Sea both in the fishery as well as from an ecological point of view. Both species spawn on the same spawning grounds where the eggs float in deep high salinity layers of the brackish Baltic Sea. Due to differences in specific gravity, sprat eggs generally are more buoyant and dwell higher in the water column than cod eggs. First feeding larvae of both species perform an active vertical feeding migration into upper water layers, with peak abundance of cod larvae below the thermocline between 20 and 40 m. The major fraction of feeding sprat larvae was observed in the upper 10 m of the water column. The current system in the Baltic Sea is mainly wind-driven, thus, larval/juvenile cod and sprat are exposed to completely different circulation patterns. Transport of larval/juvenile cod and sprat was investigated by detailed drift model simulations for the years 1979-2004. Simulated flow fields obtained from hydrodynamic modelling and data on spawning location, vertical distribution, the timing of spawning and settlement (only cod) were used as input to a particle tracking model. Results of this study enabled the identification of potential nursery grounds for sprat and cod.

For Baltic cod, a trophodynamic individual-based model of feeding was coupled to the particle tracking model in order to analyze the intra- and interannual variability of larval growth and survival. The potential drift of larval cod from the spawning grounds towards their nursery areas through temporally and spatially resolved three-dimensional prey fields indicate that larval cod changed from a non-food-limited to a food-limited stage during the last two decades. Lower survival rates are caused by the strong decrease in abundance of the calanoid copepod *Pseudocalanus acuspes* which has been identified as the preferred prey organism of larval and juvenile cod. Comparing the simulated larval survival potential with observed data on recruitment in relation late egg stage production revealed relatively high correlation (~ 60%), i.e. the model was able to predict high levels of recruits during the 1980s as well as the strong decay of recruitment during the 1990s. For sprat, from drift model simulations we derived the annual ‘bottom-depth anomaly’, an index that likely reflected the variable degree of annual larval transport from the central, deep spawning basins to the shallow coastal areas of the Baltic. This index is highly significantly correlated to sprat recruitment success and explained more than 75% of the overall variability for the time period under consideration.
Session VI — continued

Hydrographic simulation of Sandeel larvae dynamics in the North Sea (VI.3.o)
Ashbom Christensen, Ute Hochbaum, Irina Alekseeva, Henrik Jensen, Henrik Mosegaard, Mike St. John, and Corinna Schrum

The lesser sandeel (Ammodutes marinus) plays a pivotal role as a mid-trophic wasp-waist component in the North Sea ecosystem. The relatively short larval drift phase in February to May renders the sandeel recruitment rather sensitive to optimal hydrographic conditions and other timing issues. This fact also puts emphasis on appropriate representation of physical and biological processes influencing sandeel larval stages.

We have combined a 3D hydrodynamic model HAMSOM with an individual-based model for the early life-stages (egg/larvae) of the lesser sandeel to improve the understanding of the recruitment dynamics of the sandeel population, based on the underlying physical-biological processes.

We quantify the relative importance of biological and hydrographic key parameters for the survival success of sandeel larvae and test the sensitivity of our assumptions.

We discuss how to define robust larval transport and survival indices that may lead to improved population recruitment models.

Adult sandeel population survival and growth is regulated locally by spatial variability in mortality and zooplankton availability. We couple our transport model to a conceptual life-cycle model to estimate the influence of variability in transport, zooplankton and mortality on spatio-temporal patterns in the sandeel population dynamics.

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Potential biological mechanisms underlying the strong transport-recruitment relationships observed in Baltic sprat, *Sprattus sprattus* (VI.4.p)

Hannes Baumann and Hans-Harald Hinrichsen

Long-term Lagrangian simulations of larval and early juvenile sprat drift patterns in the Baltic Sea have shown that strong correlations exist between the annual degree of larval transport towards southern and south-eastern Baltic coasts and sprat recruitment variability. These relationships indicated that predominant retention of larvae and early juveniles within the deep spawning basins correspond to relative recruitment success, whereas large-scale coastal transport of larvae is associated to relative recruitment failure. For the most recent 25 years of observations (1979-2003), these patterns explained between 75%-80% of the overall recruitment variability. However, the exact biological processes underlying these transport-recruitment relationships have yet to be adequately understood. In this talk, we present the first study that detected starvation in the field in early juvenile sprat from the western Baltic Sea to propose that density-dependent food availability in Baltic coastal nursery areas may comprise a plausible mechanism regulating year class strength in Baltic sprat. We further used month- and depth-specific temperature data available from the ICES Oceanographic database between 1974-2003 to infer during which pre-recruit stages the influence of temperature is most important for recruitment variability. It was found that surface temperature in late summer (i.e. August/September) is most influential to Baltic sprat recruitment strength ($R^2=0.73$, 30 years), and that temperature- and thus growth-dependent mechanisms are likely to interact with transport-related recruitment determinants. Faster population growth of pre-recruit sprat due to higher temperatures may either result in lower cumulative predation mortalities or could lead to a better overall survival of 0-group sprat during the first winter. The general goal of this presentation is to instigate a discussion among workshop participants, which biological processes are ‘inherently’ modelled and which are currently neglected by long-term Lagrangian drift simulations.

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Session VI — continued

Metapopulation source-sink dynamics and connectivity of oyster reef networks (VI.5.p)
Rom Lipcius, Harry Wang, Mac Sisson, and Sebastian Schreiber

Various biophysical systems exhibit characteristics of metapopulation and network structure. The specific type of metapopulation or network structure can have substantially different effects on metapopulation dynamics of marine species with open populations displaying varying degrees of connectivity between subpopulations. We investigate the role of connectivity in metapopulation dynamics of the Eastern oyster, *Crassostrea virginica*, with a 3D hydrodynamic model simulating advection and diffusion between numerous oyster reefs (i.e., subpopulations) positioned according to historical observations. Model simulations produce estimates of the degree of connectivity between all pairs of oyster reefs, which subsequently permits assessment of the diversity of patterns in network connectivity. From these results we distinguish the major characteristic types of connectivity patterns among oyster reefs, and further discuss the means by which oyster reef networks, such as those occurring throughout Chesapeake Bay, may be restored successfully.

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An age structured population dynamics model of the Moroccan Atlantic coast sardine is presented. The model focuses essentially on the larval phase which is composed of two stages: endogenous and exogenous stages called respectively $S_1$ and $S_2$. The entrance in stage $S_2$ here called pre-recruitment is characterized by yolk resumption and mouth opening. At the beginning of stage $S_2$ there is a critical period when larvae have consumed their vitel-line reserves but are not yet able to move enough in quest of food. The recruitment in the juvenile phase occurs when the larva reaches a threshold size related to a certain amount of food it has to ingest during the whole stage $S_2$.

Larval mortality and feeding are density-dependent. A function $w(t,x)$ is introduced to take implicitly into account the impact of environmental and hydrographic conditions variability (upwelling, enrichment, retention, etc.) on pre-recruitment.

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Session VII — Future Directions: Integration with observing systems, operational models, monitoring programs, and management recommendations

Future directions in biophysical modelling of the early life history of marine fish at the Alaska Fisheries Science Center (AFSC): Incorporating management needs into modelling strategies (VII.1.0)
S. Hinckley, B.A. Megrey, A.J. Hermann, and C. Parada

The recruitment processes and early life history of several species of marine fish and invertebrates (walleye pollock, several species of flatfish, Tanner and snow crab) have been studied at the AFSC, with the goal of providing advice to fisheries managers. Alternative hypotheses exist to explain the impact of physical and biological interactions on recruitment success and stock structure for these different species. We describe some of these hypotheses, and how individual-based models, coupled with different generations of hydrodynamic models (and in some cases NPZ models) have been employed to investigate them through simulations. Towards the goal of operationalising these models in a management context, we discuss the roles of data assimilation for prediction, the monitoring necessary to support them, and the methods we have used for validating these models and testing their sensitivity. We also discuss types of output from these models that would be most useful to managers, productive avenues of research, strategies that resulted in unanticipated unproductive dead ends, and lessons learned.

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The applications of a ‘simple’ biophysical model: Recruitment prediction and investigation of recruitment mechanisms (environmental and stock effects) (VII.2.o)

Gwenhael Allain, Pierre Petitgas and Pascal Lazure

A growth and survival model in the early life stages was run along virtual drift trajectories tracked in a hydrodynamic model to simulate the annual recruitment process of anchovy (*Engraulis encrasicolus*) in the Bay of Biscay (NE Atlantic). The annual recruitment index obtained was compared to a series of ICES recruitment estimations (and to former recruitment predictions from a regression model). The biophysical simulations were then analysed in order to investigate the influence of environment and spawning dynamics on the survival of larvae and juveniles. The location of space-time survival windows revealed major environmental mechanisms involved in simulated recruitment variability at the different scales: retention of larvae and juveniles in favourable habitats over the shelf margins and turbulence effects. These mechanisms were related to the variations in wind direction and intensity during spring and summer. Survival was also variable according to the origin of the drift trajectories, i.e. spawning distribution in space and time. The spawning distribution that would maximise survival (according to the biophysical model) was compared with real spawning distribution (according to field surveys) on a seasonal scale, which revealed factors not considered in the biophysical model, including spawning behaviour of the different age classes. The variation of simulated survival according to spawning distribution was examined on a multi-annual scale, which revealed past and present stock structures. The interaction between population (influential on spawning) and environment (influential on survival) and its implications on recruitment and stock dynamics are discussed.

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Thoughts on future directions in modelling physical-biological interactions (VII.3.0)

Charles Hannah and Mike St. John

Reflection on 4 years of deliberations of the ICES Working Group on Modelling Physical-Biological Interactions and the discussions at the workshop on ‘Future Directions in Modelling Physical-Biological Interactions’ has lead to three broad themes concerning future work in the field. Firstly, model validation, the rigorous assessment of the level of confidence in the model predictions, is crucial for any model that will be used for practical applications. Secondly determining the level of model complexity required to capture the essential features of the problem being addressed is an open problem. Finally, all the problems are multidisciplinary and there is a need for more integration of physics, chemistry and biology on one hand and observationalists, experimentalists and modellers on the other. In this paper we argue that the process of model validation provides a framework for connecting these three themes.

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Modelling the dispersal of Plaice Eggs and Larvae in the North Sea (VII.4.p)

Johan van der Molen, Clive J. Fox, and Paul McCloghrie

A new Lagrangian model of the dispersal of Plaice eggs and larvae in the North Sea will be presented. The particle-tracking model uses hydrodynamics calculated by the three-dimensional General Estuarine Transport Model (GETM) (Burchard and Bolding, 2002), which we run on a parallel cluster. Following Wolk (2003), the particle-tracking model computes advective transport using an analytical technique and diffusive transport using a random-walk method. The magnitude of the diffusion is proportional to the local turbulence calculated within GETM. For this study, both development and active behaviour (mainly vertical movements) of the early life-history stages of Plaice were derived from literature and added to the model. First model test results will be presented. When finalised, observational data from recent egg and larvae surveys in the North Sea will be used to initialise and validate the model. Future plans include different implementations of vertical migratory behaviour to study the effect on larvae migration routes and final larvae destinations, and an operational on-board version to support day-to-day planning of plankton surveys at sea.


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Held under the auspices of

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

Working Group on Modelling Physical Biological Interactions and Working Group on Recruitment Processes

Supported by

French Research Institute for Exploitation of the Sea

University of Maryland Center for Environmental Science

Endorsed by

Programme designed and printed by

National Science Foundation

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