

ICES WKMOR REPORT 2010

SCICOM STEERING GROUP ON ECOSYSTEMS FUNCTION

ICES CM 2010/SSGEF:13

REF. SSGEF, SCICOM

Report of the Workshop on Understanding and quantifying mortality in fish early-life stages: experiments, observations, and models (WKMOR)

22–24 March 2010

Aberdeen, United Kingdom



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Recommended format for purposes of citation:

ICES. 2010. Report of the Workshop on Understanding and quantifying mortality in fish early-life stages: experiments, observations, and models (WKMOR), 22-24 March 2010, Aberdeen, United Kingdom. ICES CM 2010/SSGEF:13. 30 pp.

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Executive summary

Variable mortality of fish early-life stages and zooplankton can be a dominant factor controlling their overall dynamics and abundance in marine ecosystems. Developing methods to estimate and model mortality has received considerable attention in recent decades, but the subject remains one of key importance because it is difficult to adequately sample organisms, determine ages or stages, and assign causes to mortality of planktonic animals in the sea. In addition, quantifying mortality is a critical component for understanding the factors that influence fisheries recruitment variability, including those due to climate variability and change. In this context, WKMOR was held to review and synthesize recent advances in modelling methodology and developments of new laboratory and field observational techniques to estimate and evaluate consequences of mortality. At the outset and during the workshop, it was clear that there has been considerable progress in quantifying mortality in the field (e.g., quantifying stage-specific abundances, estimating rates and causes of mortality, accounting for advection/diffusion effects) and for constructing process-based forecasting tools (models) that quantitatively link spawning stock biomass/egg production with post-juvenile stages. It also is clear that mortality experienced by ichthyoplankton and zooplankton is neither constant in time, invariant in space, or predictable by body size and developmental stage alone.

The workshop began with a review of the history of mortality estimation and present-day challenges, including a broad overview of sources of mortality. Topical sessions followed, emphasizing experimental (aquaculture, laboratory and mesocosms), observational (generally field investigations) and modelling methodologies. Contributions in a final session explored the links between mortality in early life and recruitment, revisiting the major theories that addressed recruitment variability in marine organisms while judging progress relative to theory.

In agreement with historical evaluations, workshop participants concurred that predation was the main likely source of mortality. But predation is highly variable in time and space, and differs among species and developmental stages. Except for certain "critical periods" in fish early-life stages and zooplankton stages, starvation generally seems unlikely to be the major direct cause of mortality. Nutritional state, and growth-rate and size-related variability in vulnerability to predation are mechanisms that link food supply to predation mortality. The importance of other factors, for example diseases, parasitism, and a suite of hydrographic and physical conditions, especially dispersal processes that result in unsuccessful transport to suitable nursery areas, remain difficult to quantify in the field but have decisive consequences on recruitment and population abundance based on experimental and theoretical research.

There was consensus among workshop participants that the way forward would rely on a combination of experimental, observational and modelling approaches. Increasing capability to conduct experimental research on early-life stages and zooplankton has opened the door to evaluate causes of mortality in more realistic ways than in the past. Additionally, experimental research can identify characteristics of survivors and non-survivors, and quantify levels and variability in parameters required for modelling mortality in the sea. Models have emerged as a powerful and essential tool to identify and evaluate important processes that directly or indirectly generate mortality. Mechanistic models of early-life dynamics, in which mortality is an emergent property, are proving to be valuable tools that require additional emphasis.

Two Breakout Discussion Groups (I. Laboratory-Experimental, II. Field-Scale) recommended a comprehensive review and summary of mortality estimation methods, with a careful articulation of their sensitivities and biases. The groups emphasized that the way forward should not only investigate fundamental mechanisms of the mortality process but also recommended development of suitable statistical tools to link mortality-estimating approaches to models for predicting and forecasting recruitment and abundance, with the appropriate caveats about their limitations. Recommendations included the development of cooperative field studies comparing ichthyoplankton and invertebrate zooplankton with respect to rates, patterns, and causes of mortality in the same field sites.

The workshop was held in Aberdeen, Scotland, UK, 22–24 March 2010. There were 32 participants from 13 nations, who presented 20 talks and 8 posters, followed by a day of breakout-group deliberations and discussions. WKMOR was co-chaired by Alejandro Gallego (UK), Elizabeth North (USA) and Ed Houde (USA). Alejandro Gallego served as local host. Workshop participants gratefully acknowledge the sponsorship and logistical support that was provided by Marine Scotland. The workshop web page (<http://northweb.hpl.umces.edu/WKMOR/WKMOR-home.htm>) was provided by University of Maryland Center for Environmental Science.

The workshop was a one-off event. There are proposed follow-up activities, e.g., journal publication of manuscripts derived from some presentations, but no additional meetings are proposed.

1 Opening of the meeting

The meeting was opened by co-chairs Alejandro Gallego (UK), Elizabeth North (USA) and Ed Houde (USA) at 09:30 on Monday, 22 March 2010. The meeting was held at the Inspire Conference Centre, Beach Boulevard, Aberdeen, UK.

2 Background and Terms of Reference

The plan to hold this workshop (WKMOR) evolved from recommendations identified during the “Workshop on advancements in modelling physical-biological interactions in fish early-life history: recommended practices and future directions (WKAMF)” (<http://northweb.hpl.umces.edu/wkamf/home.htm>), that was held in Nantes, France in 2006. Although extensively researched, accurate and precise estimates of mortality of planktonic organisms remain problematic to obtain. With the development of new laboratory and field observational techniques, and advances of modelling methodology, the time was right to review approaches for estimating, simulating, and improving our understanding of the processes that control mortality of zooplankton and meroplankton, with application to predicting recruitment variability of harvested fish and shellfish. WKMOR followed a Theme Session (Session T) on “Death in the Sea,” held at the ICES 2009 ASC in Berlin, Germany. The workshop’s aim was to review the state of knowledge and recommend approaches for quantifying mortality of fish larvae, zooplankton and meroplankton in the sea, and for constructing forecasting tools to quantitatively evaluate early-life processes. Such information can serve to link mortality processes in early life to abundance of recruited stages, which is critical for understanding fish recruitment variability and variability in abundance of zooplankton populations. The agenda of WKMOR emphasized presentations on technical and methodological issues, deliberations and discussion of important physical-biological processes, and on identification of future research needs.

Terms of Reference for the workshop were to:

- a) Review current and emerging laboratory, mesocosm, field and modelling methodology aimed at understanding the underlying mechanisms that control mortality during fish, shellfish, and zooplankton early-life stages;
- b) Summarize the state of our understanding of the mechanisms that control mortality of eggs, larvae and juveniles, identify information gaps, and list future research directions as proceedings from the workshop;
- c) Develop recommended techniques to quantify mortality in the sea and model its impact on subsequent recruitment.

3 Workshop structure and contributions

Summaries of the oral and poster contributions are appended in Annex 1. The workshop was organized into 6 sessions, as follows.

I – Introduction

Workshop co-Chairs opened the workshop, welcoming participants and introducing the workshop goals. In an opening presentation, the history of mortality estimation and present challenges were reviewed. The review included an overview of sources of mortality, a summary of approaches to estimate mortality, and discussion of the state of knowledge on mortality of early-life stages of fishes.

II - Laboratory studies: aquaculture, mesocosms, and small-scale interactions

The biological sources of mortality in planktonic organisms were presented and discussed, with emphasis on synthesis of previous research, new methodologies and findings, and information on, or application to, meroplankton. The aim was to learn from related disciplines (aquaculture) and experimental settings in which conditions can be carefully controlled (laboratory and mesocosms).

III - Detecting and partitioning mortality in the field from planktonic stages to juveniles

Speakers addressed the measurement and quantification of biological and physical sources of mortality in planktonic organisms in the sea, with emphasis on new methods, evaluation of losses to advection, and losses to other causes of mortality. Participants also discussed the larval-juvenile transition stage and young juvenile stage with respect to levels of mortality and how they related to overall survival, density-dependent processes, and recruitment potential.

IV - Quantifying mortality: assumptions and sensitivity analyses

The contributors considered the assumptions behind the algorithms and statistical models used to describe mortality as well as the sensitivity of these equations to input parameters. Sensitivity analyses related to larval physiology and three dimensional advection and diffusion also were explored.

V - Numerical models: procedures for incorporating mortality and validation techniques

The emphasis of this session was on the methods and challenges of incorporating mortality into coupled bio-physical models and possible methods for model validation. Contributors discussed the need for better information on juvenile stage dynamics, the sensitivity of model results to larval behaviour parameterization, and the reliance of successful model validation efforts on the methods used for model subsampling.

VI - Revisiting the paradigms: linking mortality to recruitment

Speakers presented their perspectives, revisiting the “big theories” such as match-mismatch, to understand the mortality process in early life. Density-dependent predation barriers, size-dependent regulatory processes, and the integration of multiple factors (including climate variability) were discussed and used to identify causes of recruitment variability.

Breakout Groups

On the final day of the workshop, participants divided into two breakout groups. One group deliberated on experimental (laboratory/mesocosm) approaches to estimate and quantify sources of mortality, while the second focused on approaches to conduct research on mortality in the sea. Each group included experts who conduct research using either empirical or modelling approaches. Notes prepared by each breakout group are attached as Annex 2. A summary of major recommendations follows.

4 Summary of breakout discussions

The breakout groups discussed **mechanisms** that control mortality processes and the **quantification** of mortality. They identified **knowledge gaps** and proposed **ways forward** to make further progress. The summary below highlights the most important points and recommendations that emerged from the breakout discussions.

Mechanisms

The consensus view among participants was that predation was likely the main mechanism controlling mortality. But predation pressure differs among species and, generally, is ontogenetically and spatio-temporally variable. Many potential sources of mortality (see below) are believed to act or impart variability by altering vulnerability to predation. Furthermore, and importantly, most mortality factors are likely to result from interacting causes that need to be integrated during the ontogeny of fish and invertebrates.

Starvation mortality is generally not thought to be the major, direct cause of mortality although it is significant at critical periods and possibly in certain ontogenetic stages. Nutritional deficiencies that lead to slow growth, long stage durations and size-specific vulnerability to mortality may govern the mortality process by interacting with predation.

Disease and parasitism, which are little understood and hardly quantified as causes of early-life mortality, are potential direct sources of mortality but also may act indirectly by interacting with starvation and predation mortality.

Advective losses and variable transport success of early-life stages to juvenile nursery are obvious and important causes of mortality and need to be taken into account when estimating mortality.

There is evidence of mortality in early life caused by unsuitable abiotic conditions (e.g. sharp salinity gradients, low dissolved oxygen, contaminant effects), although such mechanisms generally are poorly documented and understood. Unfavourable environmental or habitat conditions at the time of settlement could have particularly important impacts on recruitment and abundance.

Quantification

Mortality is estimated from observed changes in abundance and age/stage/size data, supplemented by estimates of other parameters (e.g. growth, development etc) that influence survival. Obtaining unbiased estimates of abundance (e.g. sampling) remains problematical. Errors in estimates of associated factors, for example growth rates and ages, or energetics parameters such as assimilation efficiency can be important. Otolith-aging is an advantage for estimating survival in fish larvae that is not available to plankton ecologists studying holozooplankton. Furthermore, quantifying dispersal losses through advection or other mechanisms is critical to accurately estimate mortality. Newer approaches to quantify or develop indices of potential mortality, including the use of gut contents/diet and nutritional condition data, were discussed. In the field, it is important to estimate abundances and mechanisms that generate mortality at relevant spatial and temporal scales, including evaluation of patchiness and the existence of "hot spots" where survival is enhanced or mortality elevated.

Knowledge gaps

The causes of mortality in early-life stages and in zooplankton generally remain unidentified, even when accurate estimates are obtained. Partitioning causes into components, for example predation, advective loss, nutrition-related, is a key need. The need to focus on regulatory processes (i.e., density dependence) in early life, including the juvenile stage, as well as accounting for environmental factors is apparent. Understanding how stage-specific and size-specific mortality processes operate is critical to advance our understanding of factors that regulate recruitment.

Disease might be an important source of mortality, but little is known about specific diseases or their effect in the sea. It is difficult at present to appreciate the relevance of laboratory research on diseases with respect to disease-caused mortality in the sea. Can we replicate in the laboratory the pathogen environment in the sea?

Mass mortality within a cohort in laboratory settings raises another unknown: the issue of developmental competence and possible variability in susceptibility to mortality. A related aspect is the heritability of different traits (on a stage-specific basis), including behavioural, that may make individual larvae more or less fit for survival. We know very little about genetics and heritability of physiological/behavioural traits in the field.

The way forward

It was the consensus recommendation of participants that a tripartite (experimental/observational/modelling) approach is required to interpret and guide investigations of mortality of early-life stages and factors that affect it. For example experimental/field research requires guidance from models to help identify processes and parameters that are most important in generating mortality (and variability in mortality), while modelling requires results of experimental and field research to parameterize and calibrate functional responses and validate model predictions.

Field research on mortality should be designed to account for geographical characteristics and circulation features and should be conducted at appropriate spatial scales large enough to avoid biases due to advection. Collection gears and methods should be capable of accurately sampling across ontogenetic stages and appropriate to the target species and stages. In addition to age- or stage-specific abundances, field estimates can benefit from tools and proxies that categorize and quantify individual nutritional condition and survival potential (e.g., RNA/DNA, biochemistry/stable isotope, and otolith-based approaches). Such techniques require calibration and validation when applied in the field.

Experimental research can be used to deduce the characteristics associated with survivors and non-survivors, and possibly can be applied to identify these characteristics in organisms in the sea. Experimental work can also quantify specific behaviours, their cost (e.g. energetic) and variability. Beyond the typical small-scale laboratory observations, mesocosms have proven to be of high value for experiments on predation and the predation process, including the nature of size-selective mortality when appropriate predators (kinds and sizes) are included in the experiments.

In modelling early-life dynamics, mechanistically-based simulations can be an important tool to develop understanding of processes that generate mortality, especially where mortality is an emergent property in the model, as opposed to being prescribed.

There was agreement that development of a comprehensive list of mortality estimation methods is needed, with a careful articulation of their strengths, weaknesses, sensitivities and biases.

In discussions of the breakout group recommendations, it was emphasised that providing guidance on the way forward (e.g. for fishery managers, modellers) was critical. The guidance can rely to an extent on models, statistical tools and correlation methodologies, with caveats regarding limitations for predictions. For exploited species, it is important to develop a list of predators and the early-life stages (ages, sizes) on which they prey. It would be useful to compile sets of standard functional response models and dependencies between trophic levels applicable to fish early-life stages and zooplankton, as a good starting point for modelling research on early-life mortality.

Specific recommendations are summarised in Annex 5.

5 Outcomes

The Journal of Marine Systems (JMS) has agreed to publish a dedicated group of papers based on presentations of WKMOR participants. It is anticipated that workshop participants will prepare 10–12 publishable manuscripts by 1 October 2010 for the JMS submission. The proposed JMS package will include a synopsis and foreword by the workshop co-chairs in addition to individual papers.

Annex 1: Abstracts of contributions (by section)

I - Introduction

Invited speaker: Edward D. Houde

What do we know about 'death in the sea?'

Mortality rates of small, planktonic organisms are high and variable, and small variability in mortality can lead to large differences in recruitment success. Environmental factors often act independently of density to rapidly reduce initial numbers of egg and larval cohorts while density-dependent mechanisms serve to stabilize and regulate numbers, allowing biomass to proliferate in the late larval and metamorphic stages. Temperature, prey availability, and predator abundances are major forcing variables. Predation, the primary, proximate cause of mortality is size-selective, growth rate-specific, and its effects are sensitive to stage duration. Accordingly, growth and mortality components of early-life dynamics cannot be decoupled and nutrition, if not starvation, is implicated prominently in death in the sea. Estimating mortality and separating it into constituent components remains a difficult endeavor. Confounding factors, such as dispersal losses, can only be accounted for with uncertainty. Experimental (lab and field) and modeling research are essential to advance the state of knowledge. Integration through coupled bio-physical modeling provides a promising approach to test hypotheses and validate observations on death in the sea.

II - Laboratory studies: aquaculture, mesocosms, and small-scale interactions

Invited speaker: Arild Folkvord

Growth and mortality patterns of fish larvae and juveniles under controlled experimental conditions - what can be learned from repeated samplings?

Experiments with fish larvae reared using live natural zooplankton as food have provided high growth and survival rates in the laboratory and in mesocosms. Large groups of larvae have repeatedly been sampled, and the obtained data have, among other things, provided the basis for estimation of size-dependent growth and size-selective mortality. Examples are provided from experiments with larval cod and herring, two species with notably different early life history dynamics. The cod larvae appear to have a higher prey concentration requirement in order to survive than cod, but the cod larvae also have a higher growth capacity at a given age and size than herring larvae when food is provided in excess. Daily mortality rates as low as 0.002 and 0.006 have been observed in absence of predators for herring and cod larvae fed in excess after the yolk sac stage. During periods of food limitation, groups of herring larvae exhibited no detectable weight increase over a 5 week period, while cod larvae typically did not survive such extended periods without net weight increase. The benefits of working with experimental closed populations of known ages are discussed as well as the limitations of extrapolating findings from experimental scale systems to field conditions.

Invited speaker: David Bengtson**What can aquaculture research tell us about causes of mortality in marine eggs and larvae?**

Hundreds of species of fish and shellfish are cultured around the world, requiring the routine rearing of larvae. Research in this area has evolved largely separate from research on causes of mortality in the sea. A survey of this research and industrial practice nevertheless provides some useful information on larval mortality: 1) embryo-larval survival is usually in the range of 5–50% (i.e., not 0.001%, but not 90–100% either); 2) interspecific variability in larval survival is considerable; 3) several causes of larval mortality are identifiable, including morphological problems, nutritional deficiencies, and diseases, that may or may not be relevant to populations in the wild. Broodstock nutrition and maternal provisioning of eggs are important factors in aquaculture, but it is assumed that wild fish feed optimally and problems only arise if toxic substances become incorporated. Reproduction in the hatchery rarely relies on natural spawning by the parents, so eggs may not be optimally ripe, whereas it is assumed that field spawning guarantees optimal ripeness. Hatched larvae are fed single feeds, like rotifers or brine shrimp, in the absence of predators, eliminating the needs of wild larvae to find food and avoid predation. The microbial environment of the tank can be managed to minimize disease under conditions of crowding, but we know little about disease impacts on wild larvae. Aquaculture has allowed us to examine food consumption by individual larvae in relation to growth and some of those data will be presented.

Invited speaker: Anne Berit Skiftesvik**Behavioural responses of fish larvae to pathogen challenges and starvation**

A series of experiments designed to assess changes in behaviour associated with exposure to pathogenic bacteria, and/or starvation, are presented. Eggs of Atlantic halibut and turbot were exposed to *Flexibacter ovolyticus* and pathogenic *Vibrio* sp. strains prior to and during hatching. Activity, buoyancy and mortality of yolk sac larvae were monitored from hatching until first feeding. Halibut larvae showed reduced activity, increased mortality and increased specific density in response to the challenge of bacteria compared to uninfected control groups. These responses were not found for turbot. However, turbot larvae infected with *Vibrio anguillarum* had lower activity than larvae infected with *F. ovolyticus*. The reduced activity of halibut larvae occurred 1–2 weeks prior to the increased mortality. The activity and swimming speed of fed and starved larvae of Atlantic cod and turbot were measured. The results indicate changes in behaviour over time, as well as differences between starved and fed larvae. The effect of food deprivation on the escape response of fish larvae will also be discussed.

Contributed (oral): Howard I. Browman, Jeannette Yen, David M. Fields, Jean-François St-Pierre, Anne Berit Skiftesvik**Predatory behaviour of the carnivorous copepod *Euchaeta norvegica* and escape responses of their ichthyoplankton prey (Atlantic cod, *Gadus morhua*)**

Free-swimming (and sometimes tethered) *Euchaeta norvegica* and Atlantic cod larvae were observed in small aquaria (6 l of water) using silhouette video photography. This allowed direct observations (and quantitative measurement) of predator-prey interactions between these two species. Even when tethered, *E. norvegica* (3 mm total length) can catch cod larvae (4 mm total length). Tail beats, used by cod larvae to propel themselves through the viscous fluid environment, also generate signals de-

tectable by mechanoreceptive copepod predators. The predatory copepod creates a feeding current and randomly entrains the fish larva. When the prey is close enough for detection and successful capture (approximately half a body-length), the copepod launches an extremely rapid high Reynolds number attack, grabbing the larva around its midsection. While capture itself takes place in milliseconds, minutes are required to subdue and completely ingest a cod larva. The behavioural observations are used to estimate the hydrodynamic signal strength of the cod larva's tail beats and the prey perceptive field of the copepod. The potential impact of *E. norvegica* on a population of cod larvae will eventually be assessed using estimates of predator-prey encounter probabilities at natural abundances.

Contributed (oral): Stefan Meyer, Myron A. Peck, Stephanie Borchardt, Arne Malzahn, Catriona Clemmesen, Helena Hauss, Christoph Petereit, Daniela Harrer, Josianne G. Støttrup, and Elaine Caldarone

On the edge of death: Impacts of temperature, species and body size on RNA-DNA ratios of starving marine fish larvae

In this study, we combined datasets from 50 laboratory trials examining the impact of food-deprivation on changes in RNA-DNA ratios of marine fish early life stages. The analysis included 3156 individuals of six temperate marine finfish species (*Gobius spec.*, *Clupea harengus*, *Coregonus oxyrinchus*, *Gadus morhua*, *Melanogrammus aeglefinus* and *Sprattus sprattus*) that spanned 3.5 orders of magnitude in body size from 20 µg dry mass larvae to 90 mg dry mass post-larvae. Changes in standard length, dry mass and individual-based standardized RNA-DNA-ratio (sRD) were assessed versus degree-days of starvation (dd_starv) to quantitatively compare and develop a conceptual model for the effects of temperature, species and/or body-size on starvation trajectories. During starvation, ln(sRD) of food-deprived individuals decreased linearly with time and slopes compared well (for all species at similar body sizes) among temperatures when time was expressed in dd. The largest differences in slopes were related to body size (-5.4 versus $-10.9 \cdot 10^3 \ln(\text{sRD}) \cdot \text{dd_starv}^{-1}$ for 35 mm post larvae and 5–10 mm larvae, respectively). Temporal resistance against food deprivation (i.e. time to death), was strongly impacted by initial condition and body mass but not by water temperature when expressed in dd. Changes in the 90% percentile of condition with dd_starv were compared across all trials to assess the potential highest magnitude of changes in sRD that could be expected from the highest ranking individuals within each trial. The conceptual model provides criteria to judge the risk of mortality of an individual due to starvation given measurements of sRD.

Contributed (poster): Elisa Ravagnan, Renée K. Bechmann, Ingrid C. Taban, Steinar Sanni, Bodil K. Larsen

Mortality of embryos and larvae of *Pandalus borealis* in control and oil exposed conditions

The purpose of this experiment was to study the effects of stress (oil exposure) during embryo development and/or during larval development of the Northern shrimp *Pandalus borealis*.

Three scenarios were considered, in addition to the control group:

- 1) Exposure of embryos followed by larvae development in clean water;
- 2) Embryo development in clean water followed by oil exposure of the larvae;
- 3) Both embryos and larvae exposed to oil.

The comparison of embryo exposed larvae with larvae exposed only after hatching indicated that shrimps exposed as embryos had the highest mortality. Mortality of larvae exposed both during embryonic development and after hatching was similar to mortality of those exposed only as embryos, indicating that there was no additive effect.

Contributed (poster): A. Ingvarsdóttir, C. Bjørkblom, E. Ravagnan, M. Arnberg, S. Sanni:

The effects of different levels of oil exposure on post yolk sac larvae of Atlantic herring (*Clupea harengus*) and can they recover from the exposure?

This study investigates the effects of different oil exposure concentrations on post yolk sack stage herring larvae from Norwegian Sea wild stock. The eggs were hatched in the laboratory and reared under laboratory conditions until feeding had been established. The larvae (40–100 individuals) were then transferred into flow through cylindrical containers and exposed to five different concentrations (0.015, 0.04, 0.06, 0.250 and 0.750 mg L⁻¹) of raw dispersed oil and control conditions for 12 days at local seawater temperatures (7–9°C). The aim was to identify the LOEC/NOEC for Atlantic herring larvae. The mortality rates of the larvae in the control and at different treatments were recorded. *C. harengus* was found to be affected by oil nominal concentrations as low as 0.015 mg L⁻¹ with significant difference in survival between control and all the exposed larvae concentrations ($p < 0.05$ – 0.01) and highly affected at 0.750 mg L⁻¹ ($p < 0.001$). After the oil exposure all the remaining larvae were transferred to clean seawater in 300 L tanks. All the larvae from oil concentrations 0.04, 0.06, 0.250 and 0.750 mg L⁻¹ raw dispersed oil were transferred to the same tank and larvae from control seawater and 0.015 mg L⁻¹ oil exposure were transferred to a separate tank of same size. In the recovery phase (60 days) no differences were found in larvae mortality rates among control and exposed groups.

III - Detecting and partitioning mortality in the field from planktonic stages to juveniles

Invited speaker: Mark Ohman

What is to be done?

It is challenging to arrive at a problem in evolutionary ecology, population dynamics, trophic dynamics, or climate change science that does not turn on understanding the rates of loss experienced by natural populations. Yet for scientific generations, people have eschewed the problem of quantifying such losses, in favour of potentially less important processes that happen to be convenient and experimentally tractable. Common objections raised to attempts to estimate mortality in situ for planktonic organisms include assertions that: it is impossible to sample the same population over time, advective losses predominate in all circumstances, patchiness generates poor precision of abundance measurements, unbiased sampling across the entire life history is unattainable, organism ages or stage durations are unknown, the models are biased and inappropriate, and numerical methods contain hidden assumptions and unmeasurable parameters to which they are unduly sensitive.

What is to be done? Beginning at the beginning, it is reasonable to infer that non-clonal organisms do die. It is also reasonable to infer that metazoans experience different risks and rates of loss at different points in the life history, since body mass can vary by 3 orders of magnitude or more from egg to adult. Hence it is reasonable to expect that the developmental stage composition of a natural population contains an

imprint of the points in the life history where higher or lower rates of mortality occur. The challenge becomes to find circumstances in the field where this imprint can be extracted or estimated, even if by indirect means. Some fjords, gyres, or regions of retentive circulation offer this potential. And while quantitative, unbiased sampling is rarely achieved in the plankton, some phases of the life history can be sampled in at least a consistent manner. Even if such abundance measures are biased, if there is a constant bias across successive stages the ratios of stage abundances contain useful information on patterns of loss, when appropriate models are applied. Absolute rates of loss remain strongly influenced by estimates of stage duration, which remain a key parameter requiring measurement or estimation in situ.

As an alternative, some have suggested that life (and death) are governed principally by body size, and therefore allometric scaling solves the problem. Of course, allometric scaling cannot be validated or parameterized until someone estimates mortality for organisms across a wide range of body sizes, so this hypothesis also remains dependent upon a body of empirical estimates.

This presentation will present results based on different field circumstances that illustrate the extent of comparability of mortality rates from disparate methods, the plausibility of rates and patterns of mortality estimated from imperfect methodologies, and the significance of understanding such rates for organisms that live in environments characterized by time and space-dependent risks.

Invited speaker: Claire B. Paris and Pierre Pepin

Fate of reef fish larvae through ontogeny: advection or true mortality?

A three-dimensional structure of the in-situ flow measured repeatedly for one month period during 2 consecutive years in the coastal region of Barbados and synoptic sampling of larval cohorts of the bicolor damselfish (*Stegastes partitus*) served to estimate larval transport within a small domain (15 km x 20 km x 100 m). Larval fluxes and observed declines in 3-d cohort densities were used to calculate age-specific instantaneous mortality rates throughout the entire pelagic duration. By tracking a total of 17 larval cohorts over station separation of 1 km x 2 km, we were able to separate advective losses from natural mortality, which mean rates were estimated 0.38 d⁻¹ and 0.20 d⁻¹, respectively. Both natural mortality rates and advective losses decreased with cohort age, the latter as a result of ontogenetic vertical migration (OVM). The passage of North Brazil Current (NBC) rings, bringing low salinity, high velocity bands, and changing the water column stratification, contributed in differential retention rates in the near field and caused variations in age-specific survival rates of local settlers. The impact of external forcing by the NBC rings on mortality of locally-spawned larvae was balanced by larval response as the centre of mass of post-flexion larval *S. partitus* cohorts moved deeper in the water column. The interactions between the occurrence of low salinity intrusions and timing of the production were critical to predictions of local recruitment, implying that physico-chemical factors that are significantly influencing the vertical distribution are also affecting larval survival in general.

Invited speaker: Richard D. M. Nash and Audrey J. Geffen

Surviving the transition from larva to juvenile and then on to the end of the first year of life; What can we learn from European plaice (*Pleuronectes platessa* L.)?

There are few estimations of natural mortality especially during the transition period from larvae to juveniles and then through to end of the following winter because the

appropriate data are scarce. In this contribution we will draw upon a range of species, life styles and habitats. Because many flatfish, and in particular, plaice (*Pleuronectes platessa*) have been extensively studied and much of the information and progress reported in a succession of international flatfish symposia we will utilize this species as a case study. The study of mortality rates in the juvenile phase is made easier because the nursery grounds are inshore and generally less than 5m deep. This contribution considers the factors affecting mortality rates from the end of the larvae phase, through metamorphosis to the end of the first winter period. The problems associated with estimating mortality rates, from experimental design to behavioural characteristics are highlighted. Examples include larvae residing close to the bottom in the latter stages of development, immigration to nursery areas confounding losses due to mortality and emigration of larger individuals off nursery grounds in the latter part of the annual cycle. The shifts in mortality schedules and the causes through the early life history are investigated along with how they fit with concepts such as 'nursery ground carrying capacity' etc. Finally, new techniques for estimating mortality and understanding processes, such as field manipulations or restocking and theoretical aspects of 'carrying capacities' such as dynamic thinning lines are also discussed.

Contributed (oral): Jun SHOJI, Yuji IWAMOTO and Masaru TANAKA

Cohort-specific mortality of larvae and juveniles of an estuarine-dependent fish, Japanese seabass: a comparison between artificial and natural habitats

Japanese seabass (*Lateolabrax japonicus*) immigrate from coastal waters to tidal zones of Ohta River estuary at a body length of about 15 mm (60 days after hatch). Larval and juvenile sea bass were collected with a seine net from February to May 2008 in an artificial habitat (AR: Ohta Diversion Channel) and a natural habitat (NR: Tenma River). Larval and juvenile fish abundance was adjusted based on the size-dependent catch efficiency. Abundance, growth and mortality coefficients of the seabass larvae and juveniles were compared between AR and NR. The larvae and juveniles were abundant from March to April. Approximately 90% of larvae and juveniles were collected at stations with salinity < 10. Larval growth rates and hatch dates were estimated using otolith microstructure. Growth rate ranged between 0.10–0.12mm/d, without significant difference between AR and NR. Thirteen hatch date cohorts (hatching from October 2007 to February 2008; 10 days for each hatch date period) were identified. Mortality coefficients of the larvae and juveniles, which were estimated from exponential decrease in abundance of each cohort, were significantly higher in AR than in NR. Seasonal fluctuation in abundance of major prey organisms (estuarine copepods and Cladocera) was suggested as an important determinant for survival of the sea bass larvae and juveniles in the Ohta River estuary.

Contributed (poster): Moshe Kiflawi

Tidal Current Power and the Settlement of Coral Reef Fishes in the North-Western Gulf of Aqaba (The Red Sea)

Data is presented which describes a previously undocumented pattern of variation in the intensity of settlement of coral reef fishes. Namely, in four years of observation in the north-western Gulf of Aqaba, settlement of several fish species was largely limited to periods in which the semi-diurnal long-shore tidal current was of relatively low power (i.e. derived from Fourier spectral analysis of consecutive week-long time series). The reason for the temporal variation in power, and for its relation with larval mortality and/or transport, is currently unknown. The puzzle is complicated further

by several additional observations. First, at least two of the species monitored reproduce continuously throughout the relevant period. Second, temporal variation in tidal current intensity was often decoupled from the lunar cycle. Third, on many occasions settlement commenced almost immediately with the drop in current intensity, and continued until the current intensified again (i.e. no time lags). Fourth, no other measured variable showed any association with tidal-current intensity (wind velocity, sea-surface temperature, chlorophyll concentration). Ideas are invited that may help resolve this puzzle.

Contributed (poster): Paula Alvarez, Marina Chifflet and Unai Cotano

The fate of eggs and larvae of three pelagic species, mackerel (*Scomber scombrus*), horse mackerel (*Trachurus trachurus*) and sardine (*Sardina pilchardus*) in relation to prevalent currents in the Bay of Biscay: Could does it affect larval mortality?

The spatial distribution of eggs and larvae of three pelagic species, mackerel, horse mackerel and sardine in the Bay of Biscay was studied in 2001 and 2004. This spatial distribution was clearly different between the studied years and it corresponds, quite precisely to current regime derived from the regional ocean model system applied to the region. Mackerel and horse mackerel larvae are more affected for these prevalent currents than sardine, since its spawning grounds are located a long way from the shelf break where the speeds of the currents are higher. The offshore larval transport derive from the current doesn't imply that dispersal will result in an increase of mortality rate but quite the opposite. Survival rates for mackerel and horse mackerel were statistically higher in 2001, when the offshore larval transport was stronger. For sardine, however, mortality rate hardly varied between years. The abundance of 25-day-old larvae, considered as an index of survival rate, seems to be a good recruitment indicator at least for 2001 and 2004. In the context of reproductive success, 2001 can be considered like a successful year for horse mackerel, positive for mackerel and neutral for sardine, ruling out the idea of the negative effect of offshore larval transport for the survival.

IV - Quantifying mortality: assumptions and sensitivity analyses

Invited speaker: Wendy C. Gentleman, Pierre Pepin, S. Doucette

Improving confidence in copepod mortality estimates: Choosing formulas and quantifying errors

Copepod mortality rates can be estimated from survey data using several methods, each comprising assumptions that are not always evident. To help ensure choices are appropriate and determine associated errors, we conducted a quantitative analysis of three vertical (single time point) methods. We review their foundation, as steady-state balances of recruitment and mortality, and explain how different formulae derive from different assumptions about physiological rates. We illustrate how the Basic method causes errors to propagate and amplify, the Ratio method smoothes true stage-to-stage variation, and the Alternative method is problematic when rates are constant and mortality is high. We also show that -- contrary to perception -- all three methods neglect the influence of advection, with corollary assumptions being more restrictive for the Basic and Ratio methods. Comparison of mortality estimates for *Calanus finmarchicus* in the Northwest Atlantic reveal significant differences among the methods. Assumptions of constant recruitment and transport are generally violated, such that all three methods can yield infinite and negative mortalities. Negative mortalities are most frequent for the Basic method, and smallest for the Alternative method. Simulations with an individual-based model reveal that errors caused by a dynamic environment are greater than those due to individual variability in all

methods, with both Ratio and Alternative methods being relatively robust. However, advection can lead to large errors in all methods, with Basic and Ratio exhibiting greater sensitivity. We conclude with specific recommendations for ways that empiricists and theoreticians can work to improve confidence in mortality estimates.

Contributed (oral): Myron A. Peck & Marc Hufnagl

Physiological-based biophysical modelling of North Sea larval fish: A sensitivity analysis of size- and starvation-based mortality estimates.

Different approaches have been used to incorporate mortality into 3-D biophysical individual-based models (IBMs) of larval marine fish and we show how spatially- and temporally-explicit estimates from some models are sensitive to the technique employed. We briefly review approaches used to implement mortality within IBMs constructed for the larvae of various fish species including plaice, Atlantic herring, sprat and Atlantic cod in the North Sea and European anchovy in the Bay of Biscay. The sensitivity of advection-based mortality estimates (to various parameterizations of behaviour and development) was examined by reviewing work on plaice drift modelling. Focus is then given on the results of a sensitivity analysis examining how different assumptions and parameterizations of mortality influence the mixing of herring from different spawning aggregations as well as larval feeding requirements. Using physiologically-based foraging and growth subroutines allows us to examine the impact of key abiotic (e.g., water currents, temperature, light, turbulence) and biotic (prey size and prey concentration) factors on the feeding, growth and survival of young larvae. It also may provide a useful tool to estimate the relative mortality stemming from bottom-up versus top-down factors and how the magnitude and relative contribution of these mortality sources changes spatially and or temporally within marine ecosystems.

Contributed (oral): Elizabeth North and Zachary Schlag

Advection and mortality: a collection of model sensitivity studies

One of the main strengths of three dimensional Lagrangian bio-physical models is their ability to simulate transport trajectories and estimate mortality due to the inability of larvae to reach suitable settlement habitats (i.e., advection-based mortality). Using oyster larvae in Chesapeake Bay as a model organism, we conducted model sensitivity studies to explore factors that influence the estimation of advection-based mortality and its relative contribution to total mortality when other factors are included. We show that the scale at which model results are aggregated influences the calculation of mortality, both in terms of the mean and the variance in model results. In addition, we explore the influence of spatial patterns in physical conditions on larval mortality due to physiological stress and its relative impact when compared to advection-based mortality. Finally, the interactive effects of larval behaviour, physiological stress, and advection-based mortality are assessed. Implications for estimating mortality in the field and on subpopulation connectivity will be discussed.

Contributed (poster): Elisa Ravagnan, Steinar Sanni, and Dag Ø. Hjermann

Population effects of reduced survival during larval development of shrimp *Pandalus borealis* using a population dynamic model

The Northern shrimp, *Pandalus borealis*, is widely distributed and highly important both for commercial purposes and as a relevant part of diet for numerous fish species, birds and some marine mammals.

Using a closed life cycle population model we simulated the shrimp population dynamic in the Barents Sea. Using abundance estimates for shrimps, we used statistical analyses to study how population size is affected by harvesting, predation and climate. The effects of harvesting and predation were found to be quite strong, while temperature also appeared to have a positive effect on recruitment. The best resulting model was then used to simulate the abundance of shrimp population in the Barents Sea in the period 1982–2007 with satisfactory results. Finally, we used the model to predict effects from a reduction in recruitment due to pollution. After having determined the best model parameters, and having found that the simulation ability of the model was quite adequate, simulations of recruitment loss was performed, as well as an analysis of sensitivity to uncertainty in parameter values.

V - Numerical models: procedures for incorporating mortality and validation techniques

Invited speaker: John Steele

Death and Resurrection: the after-life of larvae

For many, but not all, fish populations, the end of the larval phase is a transition from a planktonic, physically dominated, existence to adult life as part of a fish community.

The earlier part of the life cycle trades the advantages of dependence on physical processes - transport and retention - transports for the necessity of numerically large egg production and consequent high mortality (elasmobranchs have an alternative strategy). In the later period, competition for total available food is a limiting process for the community. This switch from predominantly physical control at the population level to biotic controls at the level of communities involves both the short term population dynamics and the longer term community structure. For these reasons, as Myers and others have shown, the processes involved in the transition from early to late life stages are critical for individual populations, but the dynamics of such populations cannot be determined solely by a combination of larval studies and stock assessments for each species. The challenge is to integrate the transitions between physical and biotic, early and late, population and community processes as integral parts of life strategies.

Contributed (oral): Geneviève Lacroix and Filip Volckaert

Sensitivity of the dispersal of sole larvae to hydrodynamics, vertical migration and mortality in the Southern North Sea: a modelling study

Sole (*Solea solea*) is one of the most valuable commercial species in the North Sea. The size of the spawning stock is above the level of sustainable exploitation, but fishing mortality is high. The stock is therefore at risk of being harvested unsustainably. Moreover, interannual recruitment variability is very high. It is crucial to understand the contribution of hydrodynamics, environment and biological parameters to recruitment variability in order to propose appropriate measures for the management of the North Sea stock. Here we use a particle-tracking model coupled to a 3D hydrodynamic model to study the relative effect of hydrodynamic variability, vertical migration and larval mortality on the dispersal of sole larvae in the Southern North Sea. The sole larvae transport model developed in the frame of the SOLEMOD project couples the 3D hydrodynamic model COHERENS with a particle-tracking transport model. It has been implemented in the area between 48.5°N-4°W and 57°N-10°E. The impact of the hydrodynamics is tested by simulating two spawning periods in two

different years. The sensitivity to active behaviour is assessed by adding an “active” component; we take into account diel and tidal vertical migration. The effect of mortality is tested by comparing model results obtained with and without larval mortality. Results are analysed in terms of final larvae distribution, larval retention in nurseries and connectivity.

Contributed (oral): Stéphane Thanassekos, D. Robert, L. Fortier

Individual based model of Arctic cod *Boreogadus saida* early life: testing a length- and growth-dependent mortality rate and validating simulations through controlled sub-sampling.

Focusing on the first days of life of Arctic cod, an individual-based model is used to test the two most accepted paradigms in fisheries science: that (1) larger and (2) faster growing individuals have a higher probability of survival. First, realistic numbers of survivors are determined using the constant mortality rate estimated from catch-at-age data in the Northeast Water and North Water polynyas. The intensity of length- and/or growth-dependent mortality rates is then adjusted in order to reach these realistic numbers at the end of simulations. Model results are compared to observations from both polynyas. A method of sub-sampling modelled individuals allows the application of sampling discontinuities in the model, and increases the quality of the validation of simulated mortality through frequency-at-age. The combined length- and growth-dependent mortality reveals the existence of several critical periods in the early life of Arctic cod: post-hatching, yolk exhaustion, and eventual starvation events. Taking account of both length and growth effects on survival results in an increased realism of modelled survivors and population dynamics, leading to an improved predictive power of the model.

Contributed (oral): Colleen M. Petrik, Rubao Ji, Cabell S. Davis

Optimal vertical behaviour of larval haddock larvae: trading the risk of starvation and predation mortality

Three-dimensional bio-physical models are used to study survival of larval fish. The larval environment has vertical gradients in light, prey, predation, turbulence, temperature, and currents that affect mortality. Larvae should position themselves in an environment that maximizes growth to reduce the time in the vulnerable larval stage. Many models use passive particles or assign depths, but fish larvae can change their vertical position in response to environmental conditions. It is necessary to know how larvae make vertical depth choice decisions for use in three-dimensional models. We constructed a one-dimensional idealized model of Georges Bank to test passive larvae and behaviours that traded off hunger and predation under different food concentration and predation risk conditions. The objective was to find the behaviour that lead to the shortest stage duration under these different conditions. This approach allowed the determination of the importance of predation mortality to the depth distribution of larval haddock. Including behaviour affected growth rate and stage duration. The optimal behavioural model will be used in a 3D model of larval haddock on Georges Bank.

Contributed (poster): Martin Huret , Pierre Petitgas and Caroline Struski

Quantifying the relative effect of spawning patterns and larval mortality on the survival at metamorphosis: a modelling analysis on the anchovy population of the Bay of Biscay.

Fish populations show complex life cycles with successive dependent life stages, the spatio-temporal patterns of distribution and mortality at one stage impacting distribution and abundance at the next stage. For example spawning distribution will de-

termine patterns of larval drift over the season, then larval drift and mortality will determine the distribution and abundance of juvenile and in turn the recruitment. Here we propose to assess the relative effect of spawning patterns (timing, duration, overall fecundity and spatial distribution) resulting from adult environmental conditions over the winter, and larval mortality, on the survival at the age of metamorphosis for anchovy in the Bay of Biscay. For that we combined sequentially different models of anchovy life stages. We used the outputs of a coupled physical-biogeochemical model to access to the environmental forcing fields. A bioenergetic model resolved individual fish growth and reproduction and determined the spawning time, duration and fecundity. A statistical habitat model determined the spawning locations depending on population length structure. These models provided the initial conditions for running a larval individual-based model to determine the drift and the survival of the passive larvae. Based on a 12 years realistic simulation, we quantify the relative contribution of spawning patterns and larval mortality on the variability of survivors abundance at metamorphosis.

VI - Revisiting the paradigms: linking mortality to recruitment

Invited speaker: Mike Heath

Many go in, few come out - competing for survival

Dynamical considerations demand that as the number of animals in a natural population increases so survival is eventually impaired, thereby limiting the maximum reproductive population. This relationship is usually referred to as 'density dependence'. In the context of marine populations, and in particular fish, this effect is most evident in the pattern of recruitment with respect to spawning biomass.

Often, recruitment seems to be independent of spawning biomass over the known range of abundances, which usually is interpreted as indicating no underlying relationship. However, such observations must in fact be symptomatic of a strong relationship between mortality rate and abundance. One interpretation would be that over the observed range of spawning biomass, the capacity of the system for recruits is always saturated at the point at which some resource becomes limiting, regardless of preceding variability in mortality rates. In the extreme case, variability in recruitment is driven entirely by variation in the capacity to support recruits. The drivers of such variation might be predation, habitat or food supply. Establishing where in the early life history the key regulating points occur is fundamental to generating an understanding of how the population dynamics work and developing dynamic models.

Mortality rates are notoriously difficult to measure in the field, even given data on abundance at age from otolith analyses. Hence, various surrogate measures have been devised. These include biochemical indices which respond to starvation, and correlates of survival such as parasite incidence. Simplifying theories such as size spectrum and size dependent mortality, attempt to infer survival from growth rate. However, the use of these approaches has almost exclusively focussed on resolving environmentally induced patterns in early life mortality which may be largely irrelevant to recruitment if they precede the stage where key density dependent processes take effect.

In conclusion, the review points to a need to focus on relating stage-specific mortality rates to abundance as well as to environmental factors. Without this it is hard to see how we can expose the key mechanisms regulating recruitment.

Invited speaker: Pierre Petitgas, Martin Huret, and Fabien Léger**Identifying the limiting factors of recruitment**

The controls of recruitment are conceptually multiple and potentially changeable over the years. In effect recruitment results from many processes during spawning, larval drift and the juvenile stage. Coupled physical biogeochemical models now provide realistic hindcasts that spatially resolve environmental conditions. Such information is useful to identify limiting conditions over the different habitats of the different life cycle stages. Environmental indices can be estimated and serve as indicators of processes favouring or limiting recruitment, allowing to revisit conceptual understanding such as the importance of retention or match-mismatch. The approach was applied on anchovy in the Bay of Biscay, for which a series of low recruitments occurred recently that previous understanding and regression models could not explain. Indices of physical features were estimated (river plumes, gyres, stratification, fronts) as well as indices of larval dispersal, primary production and temperature. Also estimated were indices of spawning aggregations derived from fisheries survey data. The indices were estimated in different areas and seasons corresponding to the habitats of spawning adults, larvae and juveniles. Limiting factors were searched for by evaluating the statistical significance of a quintile regression fit between the recruitment series and each index. Results showed that the larval period was where many indices responded, confirming that it is a critical period. The limiting factors changed across the series, confirming the multiple nature of the determinism of recruitment. The danger of spurious correlation when searching many indicators is discussed. Rather than predict recruitment, monitoring a suite of indicators is advised.

Contributed (oral): Tobias van Kooten, Andre M. de Roos, Lennart Persson, and Tim Schellekens**Size-dependent mortality: The need to be specific about population regulation**

In a recent series of papers we have developed a theoretical framework dealing with the population- and community implications of density dependent individual growth and size-selective mortality. The models show that size-dependent mortality can lead to an increased abundance in other size ranges, because mortality can reduce resource competition, promoting faster development of individuals. Under certain conditions it is even possible that higher mortality leads to higher abundance of the stage to which the mortality applies, a prediction which was recently confirmed experimentally. These results have important ramifications for exploited populations, which are often faced with selective mortality on large individuals (exploitation) and small individuals (higher natural mortality in early life stages). I will illustrate how different assumptions pertaining to the density- or resource-dependent growth in the different size classes lead to strongly different population responses to the different sources of mortality. I will also briefly touch upon the community-level effects of these results.

Annex 2: Breakout Group Notes

Group 1. Experimental, Laboratory Research

Notes contributed by Myron Peck and Arild Folkvord

Discussion centred around two main questions:

- 1) What are the main new ideas and approaches for understanding and estimating mortality that we find interesting and useful?
- 2) What are the major information gaps that we need to fill in order to move forward?

1) Understanding spatial and temporal scales that are most critical to examine

The spatial and temporal scale over which one conducts research is important to identify the important processes. At the individual level, growth physiology and its limitations are important but at the cohort and year-class scale, different (higher-order) processes and patterns are critical to understand.

2) Understanding Diseases and Competence

It is difficult to capture the impacts of diseases that act rapidly to kill early life stages. For example, when infected with parasites, individuals may die within hrs, days, months, etc. Also, risk may increase with age due to cumulative increase in exposure time. The pathogens can kill within a day and these will be difficult to detect in the field. The impacts of most diseases may not be easy to separate from general “starvation effects”. In other cases, the transmission of disease may or may not be related to density-dependent processes and may be different between the laboratory and the field settings due to microbial biodiversity. In some field cases, vertical transmission of disease will occur during spawning aggregations and transfer of pathogens / infestation. Quantification of the losses due to disease is a gap in our current understanding and how it will be detected and manifested. The mortality rates generated by these pathogens will be difficult to determine. The frequency of occurrence of terata or “cytological incompetence” is rarely examined in the field making it virtually impossible to estimate the contribution of “natural” or pathogen-based mortality in early life stages. Potential spatio-temporal differences in exposure and their causes (i.e. contaminants) need to be evaluated.

3) Understanding growth-mortality using mesocosms

It is important to recognize that larvae are growing through probabilities of being eaten by different predators. There are large mesocosm facilities at the spatial scale (water volume) necessary to design experiments to increase our understanding of how predation operates. Size-selective and growth-rate selective experiments in mesocosms should include more realistic depictions of the natural composition / assemblages of predators and prey. Sampling schemes from such experiments should be designed to identify the “losers” and “winners” (e.g., large numbers of individuals sampled at each interval”. Animal welfare issues need to be addressed in such experiments.

4) Calibration of Field-based Growth and Mortality Proxies

Laboratory calibration experiments are necessary to best utilize the various biochemical and/or molecular (DNA) and otolith-based tools that exist to estimate growth, condition and mortality of field fish. Standardization of techniques has progressed so

that comparisons can be made between and among systems/laboratories. The need to for validation will be particularly important with the development of new techniques and methods for estimating growth and mortality.

5) Feedback and Interaction between Experimentation and Modelling

Sensitivity analysis can identify key parameters for research in the laboratory and advances in knowledge on physiology / behaviour in the laboratory can help modelers include novel parametrizations that may be essential for specific modelling activities. Some specific example would include:

- a) Costs of transport (the respiratory costs at different levels of activity or swimming velocities) are currently unknown for small fish larvae swimming in a viscous environment. Therefore, models attempting to understand the energetic costs and tradeoffs of small-scale foraging in different feeding environments versus predation risk are now only possible based upon assumptions of functional forms derived for other life stages. These assumptions may be inappropriate.
- b) Behavioural measurements and understanding the mechanisms causing different activities will help transport and/or "fitness" modellers. Fitness modelling would require that inter-individual variability in behavioural traits be quantified. The extent of food searching behaviour in terms of predator avoidance and hunger has not been examined but can be in selected experiments. Vertical positions of larvae and cues (gradients in light, temperature, salinity) will be important for estimation of reliable drift trajectories. Experimentalists can also provide advice on the complexities of parameterizations required for temporal and spatial scale of modelling activities.
- c) The mean and variance (inter-individual) temperature- and prey level-dependent survival and growth of different species will help identify spatio-temporal "windows of opportunity" based upon temperature and food availability. The importance of different prey types / sizes to growth can be addressed.

In the laboratory we have the opportunity to assess the physiological and/or behavioural characteristics of both the survivors and the mortalities. Also, in aquaculture species, information exists on differences in offspring quality that lead to changes in mortality rates, as well as carry-over effects to later stages.

6) Genetics issues

Genetics issues may also be addressed through laboratory studies to tease out the relative importance of genetics and environment on key traits of species (e.g., growth). This may be critical to understand the behavioural / physiological plasticity of specific populations and how this is related to variability in the environment. For example, reductions in heterozygosity of cultured fish may lead to important consequences in terms of growth and / or behaviours that are maladaptive in the field. Other important traits may be metabolic (starvation resistance). Understanding which traits are most heritable and least heritable may provide information on key selective pressures acting on fish populations and that are associated with long-term trends in mortality acting on populations. It is also essential to evaluate the heritability of different traits on a stage-specific basis, and not only on a per generation basis to account for stage-specific selective mortality risks.

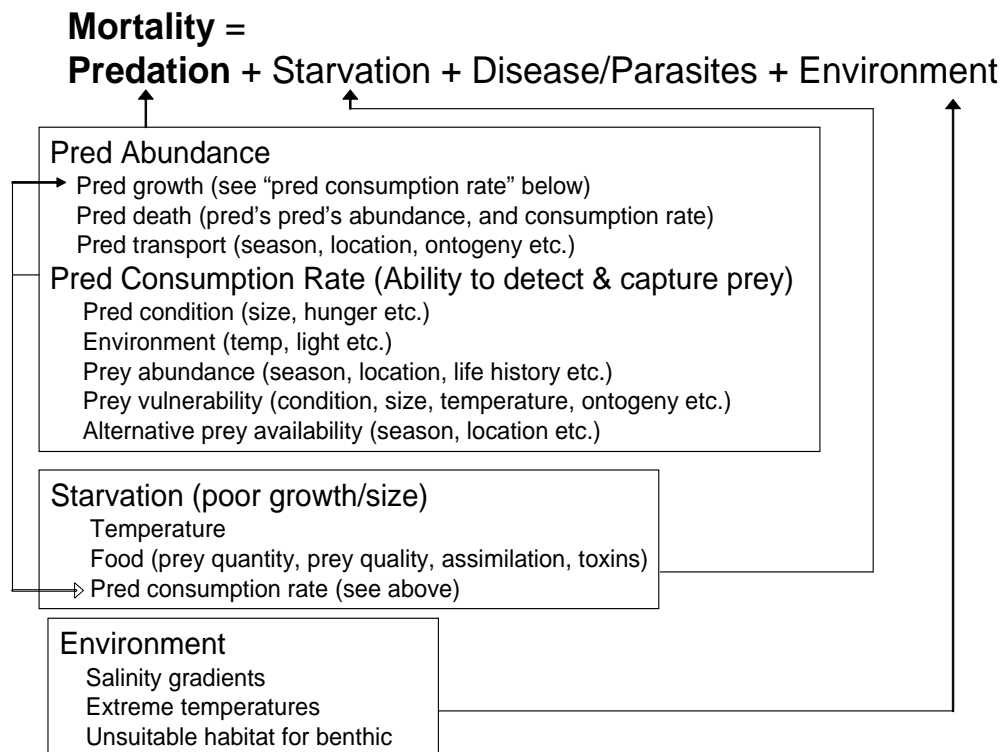
Group 2. Field Research

Notes contributed by Wendy Gentleman

Discussion centred on numerous issues, according to the following themes:

1) Why do they die?

The group recognized that predation is generally the principal mechanism leading to death of planktonic invertebrates and larval fishes in the ocean, although this can vary with species, ontogeny, geographic region and time-scale. Other mechanisms of mortality include disease, viruses/parasites, unsuitable environments and starvation. Present state of knowledge leads us to believe that starvation as a mechanism for death does not generally occur frequently, although it may be critical at certain periods or ontogenic phases. For example, the small sizes and limited energy reserves in copepod nauplii (and small fish larvae) mean they can be susceptible to low-food events. Examples of other types of lethal environmental factors include Mark Ohman's reference to abrupt salinity gradients that could lead to immediate death of copepods, and high rates of parasitic infestation of euphausiids in the California Current. In fishes, poor benthic conditions for settlement of larvae could cause mortality through elevated predation or poor feeding conditions. The group believed that food-limitation and poor-quality environment are two important controllers of vulnerability to mortality because they increase susceptibility to predation. The specific factors that contribute most to mortality depend on ontogeny, space, and time, and are typically interacting and integrative. We have tried to capture this with a conceptual model (see below).



2) How do we assess how many die?

The group discussed estimating mortality from observed changes in age/stage/size data and estimates of other parameters (e.g. growth, development etc). The discussion centred on the recognition that there are biases associated with assessing abundance (e.g. sampling) as well as issues related to estimating growth rates (e.g. assimilation efficiency) and errors due to advective loss/sources.

The group agreed that there is a need to develop lists of mortality estimation methods, and also a careful articulation of the sensitivities and biases associated with methods.

The group also discussed novel or unusual methods for potentially estimating mortality, including use of gut contents/diet.

3) What is best approach to use now?

The group felt that it is imperative to provide guidance on mortality estimation and prediction (e.g. for fishery managers, modellers etc). This includes recommending certain correlation tools, with caveats about their limitations with respect to predictions, as well as a listing of predators on specific taxa and their early-life stages/ages. The group believed it would be useful to summarize standard functional forms and dependencies so that modellers can identify a good starting point to incorporate the mortality modelling process into their research.

4) How do we improve our estimates of mortality?

In order to improve mechanistic understanding of mortality, the group agreed that we need to conduct:

- i) Field studies that are designed to account for geography, ontogeny and appropriate sampling methods associated, where possible, with each particular species.
- ii) Laboratory studies
- iii) Mechanistically-based model simulations, such that mortality is emergent as opposed to prescribed.

This tripartite approach could link lab-field-models in a way that each leg could be used to interpret and guide investigations for the others.

To establish priorities for these investigations we need to identify the sensitivities to processes (e.g. critical periods) and the methods, as well as gaps in our knowledge.

Annex 3: List of participants

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Annex 4: Agenda

Monday, 22 March 2010

8:30 - 9:30 Registration

I. Introduction

9:30 Welcome by workshop co-Chairs

9:40 What do we know about 'death in the sea'? Edward Houde.

II. Laboratory studies: aquaculture, mesocosms, and small-scale interactions

10:00 What can aquaculture research tell us about causes of mortality in marine eggs and larvae? David Bengston.

10:25 Coffee break

10:55 Growth and mortality patterns of fish larvae and juveniles under controlled experimental conditions - what can be learned from repeated samplings? Arild Folkvord.

11:20 On the edge of death: Impacts of temperature, species and body size on RNA-DNA ratios of starving marine fish larvae. Stefan Meyer, Stephanie Borchardt, Elaine Caldarone, Catriona Clemmesen, Daniela Harrer, Helena Hauss, Arne Malzahn, Christoph Petereit, Josianne G. Støttrup, and Myron A. Peck*

11:45 Behavioural responses of fish larvae to pathogen challenges and starvation. Anne Berit Skiftesvik.

12:10 Predatory behaviour of the carnivorous copepod *Euchaeta norvegica* and escape responses of their ichthyoplankton prey (Atlantic cod, *Gadus morhua*). Howard Browman, Jeannette Yen, David Fields, Jean-François St-Pierre, Anne Berit Skiftesvik.

12:35 Discussion

12:50 Lunch

III. Detecting and partitioning mortality in the field from planktonic stages to juveniles

13:50 What is to be done? Mark Ohman.

14:15 Fate of reef fish larvae through ontogeny: advection or true mortality? Claire B. Paris and Pierre Pepin.

14:40 Surviving the transition from larva to juvenile and then on to the end of the first year of life; What can we learn from European plaice (*Pleuronectes platessa* L.)? Richard D. M. Nash and Audrey J. Geffen.

15:05 Cohort-specific mortality of larvae and juveniles of an estuarine-dependent fish, Japanese seabass: a comparison between artificial and natural habitats. Jun Shoji, Yuji Iwamoto and Masaru Tanaka.

15:30 Discussion

15:45 Coffee break

16:15 Poster session and social

18:00 Adjourn

Tuesday, 23 March 2010

8:45 Welcome by workshop co-Chairs

IV. Quantifying mortality: assumptions and sensitivity analyses

9:00 Improving confidence in copepod mortality estimates: Choosing formulas and quantifying errors. Wendy C. Gentleman, Pierre Pepin, S. Doucette.

9:25 Physiological-based biophysical modelling of North Sea larval fish: A sensitivity analysis of size- and starvation-based mortality estimates. Marc Hufnagl and Myron Peck*.

9:50 Advection and mortality: a collection of model sensitivity studies. Elizabeth North and Zachary Schlag.

10:20 Discussion

10:35 Coffee Break

V. Numerical models: procedures for incorporating mortality and validation techniques

11:05 Death and Resurrection: the after-life of larvae. John Steele.

11:30 Sensitivity of the dispersal of sole larvae to hydrodynamics, vertical migration and mortality in the Southern North Sea: a modelling study. Geneviève Lacroix and Filip Volckaert.

11:55 Individual based model of Arctic cod *Boreogadus saida* early life: testing a length- and growth dependent mortality rate and validating simulations through controlled sub-sampling. Stéphane Thanassekos, D. Robert, and L. Fortier.

12:20 Lunch

13:20 Optimal vertical behaviour of larval haddock larvae: trading the risk of starvation and predation mortality. Colleen M. Petrik, Rubao Ji, Cabell S. Davis

13:45 Discussion

VI. Revisiting the paradigms: linking mortality to recruitment

14:15 Many go in, few come out - competing for survival. Mike Heath.

14:40 Size-dependent mortality: The need to be specific about population regulation. Tobias van Kooten, Andre M. de Roos, Lennart Persson, and Tim Schellekens.

15:05 Coffee break

15:35 Identifying the limiting factors of recruitment. Pierre Petitgas, Martin Huret, and Fabien Léger.

16:00 Discussion

- 16:15 Preliminary review and discussion of research recommendations
- 16:35 Identification of breakout groups
- 17:00 Adjourn
- 18:30 Workshop dinner

Wednesday, 24 March 2010

- 8:45 Welcome by workshop co-Chairs
- 9:00 Review and discussion of research recommendations
- 9:15 Breakout group meetings
- 10:15 Coffee Break
- 10:45 Breakout group meetings (cont.)
- 11:15 Breakout groups report (plenary)
- 11:45 Plenary discussion
- 12:15 Workshop conclusion and acknowledgements
- 12:30 Lunch and adjourn

Annex 5: Recommendations

RECOMMENDATION	FOR FOLLOW UP BY:
1. Mechanistic simulations of the early life stages of marine organisms should be developed where mortality is an emergent property, as opposed to being prescribed.	The scientific community within and outside ICES
2 Experimental research should identify the characteristics of survivors and non-survivors, and quantify levels and variability in parameters required for modelling mortality in the sea.	The scientific community within and outside ICES
3 Adequately controlled experiments should be carried out to quantify the importance of less well known sources of mortality, e.g. investigating the effect of disease by replicating the pathogen environment in the sea, and studying individual developmental competence and variability in intra-cohort survival	The scientific community within and outside ICES
4 A comprehensive listing of mortality estimation methods, with a careful articulation of their sensitivities and biases, should be compiled	The scientific community within and outside ICES
5. Providing guidance (e.g. for fishery managers and scientists) should also include recommending valid correlation tools, with relevant caveats about their limitations with respect to predictions.	The scientific community within and outside ICES
6. There is a need for coordinated research on fish early-life stages and on zooplankton to evaluate mortality, its magnitude, variability, and causes to further our understanding of how mortality operates in pelagic ecosystems	The scientific community within and outside ICES