WKMOR

Workshop on understanding and quantifying mortality in pelagic, early life stages of marine organisms: experiments, observations and models (WKMOR)

Programme Book

This workshop is sponsored by Marine Scotland and the University of Maryland Center for Environmental Science and held under the auspices of ICES Working Group on Modelling Physical-Biological Interactions and Working Group on Recruitment Processes.

International GLOBEC and EUR-OCEANS have endorsed this workshop.

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

Welcome to the 'Workshop on understanding and quantifying mortality in pelagic, early life stages of marine organisms: experiments, observations and models (WKMOR)'

On behalf of the WKMOR co-chairs, welcome to Aberdeen, the 'Granite City'. We hope you will enjoy not only the workshop but the time you spend here in the northeast of Scotland. There is much to see and do in Aberdeen and surrounding area so we hope you find time to relax and have fun, and not just to WorK MORe!

A bit of history: In 2004, the informal 'larval fish sub-group' of the ICES Working Group on modelling Physical-Biological Interactions (WGPBI) was formed and outlined a 'plan' to advance knowledge of early-life ecology of fish. The first steps involved a Theme Session at the ICES Annual Science Conference (ASC) in preparation for 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). The workshop was held in Nantes in 2006 and produced a 'Manual of Recommended Practices, published as ICES Cooperative Research Report No. 295, and a Theme Section in Mar. Ecol. Prog. Ser. (MEPS 347:121-306). During WKAMF and subsequently, we identified the topic 'mortality' as one requiring particular attention. Although it has been extensively researched, there remain many problems that deter obtaining accurate and precise estimates of mortality of planktonic organisms. With the development of new laboratory and field observational techniques, and the advance of modelling methodology, it is a good time 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.

This workshop (WKMOR) aims to develop recommended practices for quantifying mortality in the field and for constructing process-based forecasting tools that quantitatively link spawning stock biomass/egg production and post-juvenile stages, critical to understanding fish recruitment variability for fisheries management. In the next three days we will focus on technical and methodological issues, discuss important physical-biological processes, and identify future research needs.

We have a formidable task in front of us but a great pool of knowledge and expertise among the participants. We are confident that the outcome will be valuable and the process enjoyable.

Thanks for joining us!

Alejandro Gallego, Elizabeth North and Ed Houde

WKMOR Co-Chairs

The objectives of the Workshop on understanding and quantifying mortality in pelagic, early life stages of marine organisms: experiments, observations and models (WKMOR) are:

a) **Review current and emerging laboratory, mesocosm, field and modelling methodology aimed at understanding the underlying mechanisms that control mortality during fish and shellfish 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 field and model its impact on subsequent recruitment.**

I. Introduction

Workshop co-Chairs will introduce the workshop goals and logistics. In addition, Dr. Edward Houde will review the history of mortality estimation and present challenges. His talk also will include a broad overview of the sources of mortality (for example, disease, parasitism, starvation, predation, advective loss).

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

Three to four speakers will discuss the biological sources of mortality in planktonic organisms, with emphasis on synthesis of previous studies, new methodologies and findings, and information on, or application to, meroplankton.

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

Three to four speakers will address measuring biological and physical sources of mortality in planktonic organisms in the field, with emphasis on new methods, advection, and meroplankton, and discuss the larval-juvenile transition stage and young juvenile stage with respect to levels of mortality and how it relates to overall survival and recruitment potential, density dependence, etc.

IV. Quantifying mortality: assumptions and sensitivity analyses

Three to four speakers will be asked to examine the assumptions behind the algorithms and equations we use to describe mortality as well as the sensitivity of these equations to input parameters.

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

Three to four speakers will address the methods and challenges of incorporating mortality into coupled bio-physical models and possible methods for model validation.

VI. Revisiting the paradigms: linking mortality to recruitment

Three to four speakers will present their perspectives on the links between mortality and recruitment (in a general ecological, not fisheries, sense), perhaps revisiting the 'big theories' like match-mismatch, etc. in the light of what we know in the 21 century.

MONDAY, MARCH 22, 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 trough 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, MARCH 23, 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 t he 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, MARCH 24, 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***

WKMOR POSTERS

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?
Paula Alvarez, Marina Chifflet* and Unai Cotano

Tidal current power and the settlement of coral reef fishes in the North-Western Gulf of Aqaba (The Red Sea)
Moshe Kiflawi

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.
Martin Huret , Pierre Petitgas and Caroline Struski

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?
A. Ingvarsdóttir, C. Bjørkblom, E. Ravagnan*, M. Arnberg, S. Sanni

Population effects of reduced survival during larval development of shrimp *Pandalus borealis* using a population dynamic model
Elisa Ravagnan, Steinar Sanni, and Dag Ø. Hjermann

Mortality of embryos and larvae of Pandalus borealis in control and oil exposed conditions
Elisa Ravagnan, Renée K. Bechmann, Ingrid C. Taban, Steinar Sanni, Bodil K. Larsen

Biotechnology applications on sustainable marine fish reproduction and larval rearing aquaculture development: effects of using probiotics (bacteria and algae) as aquaculture disinfectants on Gilthead Sea Bream embryonic and newly hatched larval rearing development.
Ahmed. Md. Salem, H. S. El-Sayed, M. A. Essa, H. A. El-Sharkawy, A. M. Nour, M. I. Zaki, and T. M. Srour

Impact of hatching date, vertical distribution and inter-annual variation in physical forcing on northward displacement, temperature exposure and survival of Norwegian spring spawning herring larvae (*Clupea harengus*)
Frode Vikebø, Åse Husebø, Aril Slotte, Erling Kåre Stenevik and Vidar Lien

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 endeavour. Confounding factors, such as dispersal losses, can only be accounted for with uncertainty. Experimental (lab and field) and modelling research are essential to advance the state of knowledge. Integration through coupled bio-physical modelling provides a promising approach to test hypotheses and validate observations on death in the sea.

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II. LABORATORY STUDIES: AQUACULTURE, MESOCOSMS, & SMALL-SCALE INTERACTIONS

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.

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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 detectable 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.

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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 sea water 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.

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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.

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

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 oxyrhynchus, 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*10^3 ln(sRD)*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.

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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.

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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.

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III. DETECTING AND PARTITIONING MORTALITY IN THE FIELD FROM PLANKTONIC STAGES TO JUVENILES

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.

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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.

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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 drawn 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.

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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 unmeasureable 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 three 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 trough ontogeny: advection or true mortality?

A three-dimensional structure of the *in situ* flow measured repeatedly for one month period during two 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.

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Contributed (poster) : Ahmed. Md. Salem, H. S. El-Sayed, M. A. Essa, H. A. El-Sharkawy, A. M. Nour, M. I. Zaki, and T. M. Srour

Biotechnology applications on sustainable marine fish reproduction and larval rearing aquaculture development: effects of using probiotics (bacteria and algae) as aquaculture disinfectants on gilthead sea bream embryonic and newly hatched larval rearing development.

Marine hatcheries are marine aquaculture development backbone. Probiotics are different kinds of microorganisms (bacteria, fungi and algae) used in fish nutrition in different stages, invading its digestive canals receptors and inhibit the other organisms coming through culture environment, feeds and that already in fish digestive canal, thereby improves fish immunity and producing vitamins and enzymes inside fish digestive canals. Thus far, few global studies had done to study the effects of using probiotics on fish embryonic stages and newly hatched larvae development. For that in this study, an applicable method of gilthead sea bream (*Spaurs aurata*) sustainable embryonic stages and newly hatched larval rearing development by adding probiotics directly to culture water. Twenty experimental tanks (30L each) were stocked with 225 fertilized eggs (1st day post fertilization) (1st DPF). Tanks were supplied with 20L/tank aerated filtered sea water. The ten treatments in duplicate were Control (C), Formalin (F), Iodine (I), Bacteria (*Bacillus subtilis*) (B), Algae Nanochlorpsis sp. (N), (B+N), Algae chlorella (Ch), (B+Ch), (N+Ch), and (B+N+Ch). Embryonic stages development were investigated daily (2nd DPF-4th DPF), newly hatched larvae (2nd day post hatching (2nd DPH)-3rd DPH) and microbiologically B. subtilis CFU/ml were done in the beginning and in the end of the study. The results of this study demonstrated that (B+N+Ch), (Ch) and (B) were possessed the best results for growth in length .Other treatments were also showed a good trend in total length gain. This applicable method of new biotechnology applications could be utilized for gilthead sea bream (*Spaurs aurata*) sustainable embryonic stages and newly hatched larval rearing development by using probiotics directly in culture water.

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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.

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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.

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Contributed (oral) : **Marc Hufnagl and Myron A. Peck***

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 physiologically-based IBMs created for the larvae of clupeid fish such as Atlantic herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the North Sea. 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 the North Sea.

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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.

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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.

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V. NUMERICAL MODELS: PROCEDURES FOR INCORPORATING MORTALITY AND VALIDATION TECHN IQUES

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 determine 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.

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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.

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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.

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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.

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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.

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Contributed (poster) : Frode Vikebø, Åse Husebø, Aril Slotte, Erling Kåre Stenevik and Vidar Lien

Impact of hatching date, vertical distribution and inter-annual variation in physical forcing on northward displacement, temperature exposure and survival of Norwegian spring spawning herring larvae (*Clupea harengus*)

It has previously been demonstrated that early hatching is associated with increased survival of Norwegian spring spawning herring (*Clupea harengus* L.) larvae. The present study investigates whether the process behind is related to larval drift and ambient temperature. A 3D hydrodynamic model was used to simulate the impact of hatching date on northward displacement and ambient temperature of larvae from spawning grounds off western Norway during the period 1989-2008. The simulations demonstrated that northward displacement of larvae during a period of 60 days was highest if hatching occurred early in the season and the larvae were located near the surface. There was a negative relationship between northward drift speed and ambient temperature of the larvae, though it became less significant later in the season as the coastal current became progressively warmer. However, results from the simulated inter-annual variations in larval

drift compared to observed survival suggest that a rapid northward displacement to the main nursery area in the Barents Sea is more important for larval survival than ambient temperature. The significant impact of northward displacement on survival may be explained by reduced overlap with predators and/or higher prey densities, but these are processes that remain to be investigated.

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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 by 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.

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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 favoring 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 quantile 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 adviced.

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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.

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