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1 Preface

2 Understanding and quantifying mortality in pelagic, early life stages of marine
3 organisms — Old challenges and new perspectives

4
5 It is now appreciated that variable mortality is the most important factor controlling the population dynamics of marine organisms, while the survival of their early life stages has long been identified as a main determinant of the future abundance of adult populations, i.e., recruitment variability. Not surprisingly, the goal of understanding and quantifying mortality in pelagic, early life stages of marine organisms has been the focus of considerable attention since the birth of modern marine and fisheries ecology in the early 20th century (Houde, 2002). However, many uncertainties remain because of difficulties in accurately estimating abundance of predators and prey, the ageing of many invertebrate taxa, and a general lack of knowledge of the relative importance of the underlying causes of mortality and how to measure them in the field (e.g., Heath, 1992).

19 The need for improved knowledge of larval fish mortality in the field was identified as part of the terms of reference of the International Council for the Exploration of the Sea (ICES) Working Group on Modelling Physical-Biological Interactions (WGPBI), which emphasised the need to advance understanding of the ecology of early-life stages of fish (Gallego et al., 2007). Although research on zooplankton and ichthyoplankton ecology is usually conducted independently, the challenge of estimating mortality is common among these organisms. Accordingly, WGPBI sponsored a workshop with a broad taxonomic focus entitled “Understanding and Quantifying Mortality in Pelagic, Early Life Stages of Marine Organisms: Experiments, Observations and Models” (WKMOR), which was held under ICES sponsorship in Aberdeen, Scotland, 22–24 March 2010 (ICES, 2010). Objectives of the workshop were to review and synthesise recent advances in modelling methodology and developments of new laboratory and observational techniques to estimate and evaluate the causes and consequences of mortality of pelagic early-life stages of fish and zooplankton.

37 Both before and during the workshop, it was widely accepted within the scientific community that mortality experienced by ichthyoplankton and zooplankton is neither constant in time, invariant in space, nor predictable by body size and developmental stage alone (ICES, 2010). It also was clear that there has been considerable progress in quantifying mortality in the sea. These advances include quantifying stage-specific abundances, estimating rates and causes or mortality, accounting for advection/diffusion effects, and the development of process-based forecasting tools (models) that quantitatively link spawning stock biomass/egg production with post-juvenile stages.

48 The papers in this Special Issue of the *Journal of Marine Systems* are based on presentations made at WKMOR. Here, the workshop co-Chairs provide a brief introduction and overview of the Special Issue.

1. Quantification of mortality 51

52 Estimating mortality of planktonic organisms in the sea is challenging. As stated above, most of the difficulties are common to both zoo- and ichthyoplankton research. In reviewing the challenges facing quantification of zooplankton mortality rates, Ohman (this issue) addresses assertions that quantifying mortality is a largely intractable task. One assertion is that it is not possible to repeatedly sample the same population over time and that advective losses dominate other sources of loss (and gain). However, Ohman concluded that in cases of systems with closed or semi-closed circulation, sequential Eulerian sampling can be effective for quantifying mortality within a given population if spatial scales are defined explicitly and are large enough to ensure that residence time of the fluid is longer than the time scale of significant changes in abundance of the population. Similar conclusions have been derived from larval fish studies (e.g., Helbig and Pepin, 1998; Pepin et al., 1995). Ohman (this issue) also proposed Lagrangian approaches to address some issues, although these approaches are costly in vessel time and are difficult to sustain over longer timescales. Such methods have been applied successfully to estimate larval fish mortality rates (e.g., Heath and MacLachlan, 1987). Other challenges raised by Ohman (this issue) are the problems caused by patchiness of organisms in the sea, which leads to low precision in mortality estimates, and the difficulty in being able to sample relevant sizes and life history stages in an unbiased manner. This last point is especially important for fish early-life stages, where young fish can grow by orders of magnitude during their pelagic larval to juvenile transition period. In a modelling study, Thanassekos et al. (this issue) provide an example that demonstrates this type of bias. However, such challenges can be alleviated by proper sampling design (good coverage, replication, and awareness of physical features that may affect distribution) and careful analysis of abundance estimates obtained from multiple sampling instruments. Adequate replication and sampling effort are particularly important to account for patchiness when applying methods such as Vertical Life Tables (e.g. Aksnes and Ohman, 1996), which may otherwise result in negative mortality rates for some stages. 86

2. Sources of mortality 87

88 The effect of food-mediated mechanisms that control abundance of marine organisms was identified long ago, and formed the basis of classic recruitment hypotheses like the “critical period” (Hjort, 1914) and “match–mismatch” (Cushing, 1972, 1990). Meyer et al. (this issue) review laboratory studies, documenting nutritional condition and survival of fish larvae, and conclude that initiation of 93

exogenous feeding is a “critical period” when larvae are very sensitive to starvation, particularly at higher temperatures. They stress the importance of a match between larval phenology and prey availability, and the interaction with environmental conditions during this period (Meyer et al., this issue; Thanassekos and Fortier, this issue). However, sensitivity to starvation is not only influenced by external conditions; maternal characteristics affect egg quality (e.g. Marteinsdottir, and Steinarsson, 1998) which, in turn, can impact larval resistance to starvation. Quantifying the internal mechanisms controlling larval growth is no simple task, partly because bioenergetic models can suffer from lack of detailed knowledge of physiological parameters, although sensitivity analysis can be used to evaluate responsiveness and importance of individual parameters. Even though the direct contribution of starvation-induced mortality has been downgraded in recent decades (Bailey and Houde, 1989; Leggett and Deblois, 1994), the intuitive links between food, growth and mortality continue to be the focus of considerable research effort (Houde, 2008, 2009).

Beyond the direct effect of food on mortality (through starvation), recent emphasis has focused on length- and growth-dependent mortality (Takasuka et al., 2004). Thanassekos et al. (this issue) use a bioenergetic, individual-based model (IBM) to investigate the relative importance of length-dependent and growth-dependent mortality during the first 45 days in the life of Arctic cod (*Boreogadus saida*). Their results suggest the sequential occurrence of both types of mortality, i.e. a gradual increase in importance of growth-dependent mortality at the expense of length-dependent mortality, which decreases as larval length increases. The relationship often reported in the literature between mortality and temperature, in fact, could be the result of growth-dependent mortality, since lower temperatures often lead to slower growth and development and, consequently, longer stage duration. However, such relationships may mask a match-mismatch between larvae and their prey and/or predators (Nash and Geffen, this issue), particularly since predation is considered to be the main source of larval mortality (Hunter, 1981; Bailey and Houde, 1989), a view shared by WKMOR participants. Heath et al. (this issue) concluded that, in the absence of interannual trends in growth rates, the observed changes in loss rate of larval sandeel (*Ammodytes marinus*), sampled at a monitoring station off the Scottish east coast, must be attributed primarily to variable predation rates.

Contrary to the common perception that mortality of fish during early larval stages is largely density-independent, while density-dependence is generally observed in late larval/juvenile stages (Nash and Geffen, this issue), Heath et al. (this issue) proposed that the apparent dome-shaped relationship between mortality rate and larval abundance was indirect evidence of density-dependence, assuming a relatively constant abundance of predators throughout the time series. Notably, quadratic closure terms similar to the dome-shaped relationship above have been used in zooplankton models (Ohman, this issue). Furthermore, Nash and Geffen (this issue) propose a baseline level of density-independent mortality in early-stage plaice (*Pleuronectes platessa*), in addition to density-dependent factors that come into play when the numbers of late larvae/juveniles are sufficient to affect productivity of prey and/or predator behaviour in nursery areas. These observations and insights warn against over-simplistic approaches. Depending on circumstances, density-dependent and density-independent mortality can play a significant role at all stages in the early life of marine organisms.

There are other non-predatory sources of direct or indirect mortality in the sea, including parasitism, disease and toxicity, e.g. due to pollution (e.g. Heath and Nichol, 1991; Gallego et al., 1995; Khan, 2009; Nash and Geffen, this issue). These mechanisms of mortality can be rare, or rarely observed, and more research is needed to quantify their relative contribution to mortality through direct effects and indirect effects on growth and predation. Ingvarsdottir et al. (this issue) show how lethal and sublethal effects to larval herring could be caused by relatively low, ecologically relevant concentrations of

dispersed oil in the laboratory, even at a considerable time (2 months) after exposure.

3. The role of individual-based models in understanding mortality 162

The use of coupled physical-biological individual-based models (CPBM) has increased our understanding of the interacting factors that influence fish early life stages (North et al., 2009) and zooplankton. In the specific role of understanding and quantifying mortality, there are numerous examples in the literature where these CPBMs have made a valuable contribution. Peck and Hufnagl (this issue) review sensitivity analyses and scenario tests in published modelling research that provide estimates of sources of loss from populations of early life stages of marine fish. CPBMs are ideally suited to evaluate losses from a population resulting from physical processes (advection, diffusion), which can present serious obstacles to quantifying mortality in the sea (see above). The CPBMs can be used to distinguish “advective losses” from “true mortality” (e.g., Paris, 2009), if care is taken to account for factors such as swimming behaviour and movement of zooplankton and fish larvae (Peck and Hufnagl, this issue) which violate the common assumption of passive drift. Starvation, growth- and size-dependent mortality (“food-mediated mortality”) are also generally incorporated into CPBMs (Thanassekos and Fortier, this issue; Thanassekos et al., this issue), but such processes require numerous functions and parameters relating to intrinsic and extrinsic factors (Peck and Hufnagl, this issue). Such detailed and necessary information is often lacking and can only be obtained by dedicated observational research in the laboratory or at sea, and ideally is informed by sensitivity analysis (Thanassekos and Fortier, this issue) to assure that observational efforts target the most critical parameters.

Despite significant progress, the ultimate goal of modelling explicitly and mechanistically all relevant processes that control survival of zooplankton and early life stages of fish still has not been reached. For a truly mechanistic representation of growth, physiological parameters and functions, as well as foraging parameters such as estimates of larval visual field and predatory behaviour, must be quantified (Peck and Hufnagl, this issue). The difficulty of explicitly incorporating into models food- and predation-mediated mortality processes has led to imposed daily mortality rates that incorporate the outcome of those top-down and bottom-up processes implicitly. While this implicit approach may be valid, depending on the specific objective of the modelling exercise, it makes assumptions that may not incorporate temporal and spatial variability in mortality rates often observed in the sea (Peck and Hufnagl, this issue) and, accordingly, may bias results or limit their general applicability. Intermediate between implicit and mechanistic models are those that base food- and predation-mediated mortality relationships on the spatio-temporal overlap of fish larvae or zooplankton with their predators and prey, resulting from observational data or model outputs (lower trophic level models for prey, higher trophic level models for predators). Such an approach is promising but will present its own challenges (e.g. matching of spatial and temporal scales). Proliferation of modelling approaches and comparison of their performance have the potential to advance understanding and prediction of mortality in the sea.

4. Concluding thoughts 213

Participants of the WKMOR workshop agreed that the way forward relies on a combination of experimental, observational and modelling approaches (Table 1; ICES., 2010). Increasing capability to conduct experimental research on early-life stages and zooplankton and to understand physiology and disease have opened the door to evaluate causes of mortality in more realistic ways than in the past. Additionally, experimental research and otolith analysis from field samples can identify characteristics of survivors and non-survivors, and quantify parameters

t1.1

Table 1

Recommendations from "Understanding and Quantifying Mortality in Pelagic, Early Life Stages of Marine Organisms: Experiments, Observations and Models" (WKMOR) workshop (ICES 2010).

- t1.2
- t1.3
- t1.4
- t1.5
- t1.6
- t1.7
- t1.8
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.
 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.
 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.
 4. A comprehensive listing of mortality estimation methods, with a careful articulation of their sensitivities and biases, should be compiled.
 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.
 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.

222 required for modelling mortality in the sea. Models have emerged as
 223 powerful and essential tools to identify important processes that direct-
 224 ly or indirectly generate mortality. Integrated observational studies
 225 with physical measurements and models of drift show promise for separ-
 226 ating advective loss from natural mortality. Mechanistic models of
 227 early-life dynamics, in which mortality is an emergent property, are
 228 proving to be valuable tools. Targeted, process-oriented experimental
 229 and observational work is critical to support model development.

230 The WKMOR workshop (ICES, 2010) and the series of papers pub-
 231 lished herein constitute a timely review and status report on knowledge
 232 of mortality in pelagic, planktonic stages of fish and zooplankton. Peri-
 233 odic reviews of this critical topic in the future will be important to in-
 234 form the science community of advances in observational and
 235 modelling methods that can advance our understanding of mortality
 236 in the sea and the processes that govern zooplankton dynamics and
 237 fish recruitment variability.

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