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Can IBMs tell us why most larvae die in the sea? Model sensitivities and scenarios reveal research needs

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ABSTRACT

Biophysical individual-based models (IBMs) are the only tools that can provide estimates of spatial and temporal changes in mortality rates of marine fish early life stages as well as the various processes that contribute to those changes. Given the increasing use of these models, one must ask the question: How much faith can we have in their estimates? We briefly review mortality processes acting on marine fish early life stages and how IBMs have been used to estimate those processes. Next, we provide a summary of the sensitivity analyses and scenario results conducted in 50 studies that provided estimates of: 1) advection-based losses from drift modeling, 2) mortality due to starvation from foraging and growth modeling, and/or 3) modeled mortality due to predators. We illustrate how IBM estimates of larval distribution and survival can be sensitive to assumptions regarding the magnitude and timing of mortality by performing drift model simulations for Atlantic herring (*Clupea harengus*) larvae in the North Sea. Despite the growing number of studies applying IBMs, less than 25% reviewed here included formal sensitivity analyses of parameters. Our literature review indicated a need for biological research on 1) larval swimming behavior including cues for movements, 2) foraging parameters such as larval visual field estimates, and 3) parameters associated with growth physiology including assimilation efficiency and energy losses due to active metabolism. Ontogenetic changes in those factors are particularly relevant to examine for modeling activities. Methods also need to be developed for depicting predator encounter in a dynamic way (e.g., based upon predator–prey overlap). High priority should be given to developing (and funding) research programs that not only construct and apply IBMs but also that measure the aspects of larval behavior and physiology as well as aspects of the larval environment needed to parameterize them. Coupling these research activities will strengthen our confidence in IBM-derived estimates of mortality and the processes responsible for death of larvae in the sea.

1. Introduction

Individual-based models (IBMs) have attempted to disentangle the major factors that cause mortality in early life stages of marine fish for nearly three decades (Beyer and Laurence, 1980, 1981; Cowan et al., 1994; Laurence, 1985). The results of these early studies conform to those of life table analyses performed on a variety of marine fish species that indicated rapid declines in mortality rates with increasing larval size (e.g., see Houde, 1997). Early models also underscored the importance of attributes of both larvae (e.g., their size and growth rate) and predators in establishing the magnitude of early life stage survival. Nearly a decade after these seminal modeling efforts, IBMs were coupled to 3-D hydrodynamic and particle tracking models (Bartsch et al., 1989; Werner et al., 1993) and coupled modeling matured to include projections of larval foraging success and growth rates along drift routes (Hinrichsen et al., 2002; Lough et al., 2006; Werner et al., 1996). In recent years, biophysical IBMs have been coupled to lower trophic level models to include the effects of physical forcing on larval fish prey fields (Daewel et al., 2008 and 2011) and more complex, "End-to-End" models have been developed (Rose et al., 2010). In short, in the last decade, biophysical IBMs have become frequently used tools by marine scientists exploring the amalgam of abiotic and biotic factors affecting the mortality of marine fish early life stages (see reviews by Werner et al., 2001a, b; Miller, 2007; North et al., 2009).

Sensitivity analyses are recommended as part of the normal evaluation of the performance of models, particularly complex biophysical models (Gallego et al., 2007). Among other things, sensitivity analyses help modelers identify parameters that most influence model estimates, explore potential sources of uncertainty, and assess confidence in model estimates. Standard techniques exist to perform such tests including individual parameter perturbation (IPP) and Monte Carlo error analyses (Bartell et al., 1986). In some cases, the sensitivity of model estimates has been analyzed with respect to not only intrinsic (parameter estimates) but also extrinsic (environmental) factors (Daewel et al., 2008; Megrey et al., 2007; Megrey and Hinckley, 2001). In lieu of sensitivity analyses, model scenarios are often employed to reveal

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parameters/processes that most influence model outputs (Hufnagl and Peck, 2011). Larval survival, transport, and growth are the most common model outputs tested in sensitivity analyses and in scenarios.

In the present study, we briefly summarize the principal mortality agents acting during the early life stages of fishes (and invertebrates) and review how simulations using 0-D IBMs or coupled 3-D biophysical IBMs have explored those sources of mortality. Our primary objective was to discuss the results of sensitivity analyses and model scenarios in an attempt to identify common sources of uncertainty (key parameters and formulations). To this end, we also performed new simulations using a simple drift and growth model for Atlantic herring (*Clupea harengus*) larvae in the North Sea. These new simulations attempted to illustrate how seemingly subtle differences in assumptions regarding how mortality rates change during the larval period may have large consequences for model estimates.

Our review of previously published larval IBMs was not exhaustive but was comprehensive enough to allow assessment of current modeling approaches and recommendations to be made for future (biological) research. These future research efforts will strengthen our ability to utilize these models to understand mortality processes acting on early life stages of marine fish (and invertebrate) species.

2. Causes of mortality during the early life of marine fish

2.1. Unfavorable transport and lack of habitat connectivity

Connectivity among habitats that support growth and survival is a pre-requisite for life cycle closure and the persistence of populations of marine organisms (Rijnsdorp et al., 2009; Sinclair, 1988). For nearly a century, fisheries scientists have recognized the importance of the variability in drift of early life stages to inter-annual variability in recruitment (Hjort, 1914). Many marine fish species have planktonic eggs and/or larvae that are often transported via ocean currents and begin exogenous feeding along dispersal/drift pathways. Dispersal of early life stages is a key process in the life cycle of most marine populations since it has important implications for the structure and dynamics of populations, as well as the persistence, evolution, and distribution of species (Cowen and Sponaugle, 2009; Gaines et al., 2007). Moreover, understanding the factors influencing variability in transport and survival will have important consequences for effective spatial management (Fogarty and Botsford, 2007) and conservation (Jones et al., 2007).

Some marine fish have evolved complex life history strategies that help promote habitat connectivity, life cycle closure and population persistence in ecosystems exhibiting high spatiotemporal variability in key environmental factors (e.g., temperature, water currents, and prey production). For example, spawning site fidelity is an adaptive strategy that, on average, places progeny within environments providing favorable transport to areas promoting high rates of feeding, growth and survival during early life, increasing the probability of life cycle closure and recruitment success (e.g., Cushing, 1969; Ellertsen et al., 1989). Although flexibility in spawning times has been reported to occur in some temperate species in response to climate-driven changes in factors such as temperature (Sims et al., 2005), most populations exhibit peak spawning times that are rather constant. However, protracted spawning periods (in some cases more than several months) are common (Fox et al., 2000), during which egg batches are repeatedly produced by broadcast spawners as a "bet hedging" or "lottery" strategy that helps ensure recruitment success (for review, see Leggett and Frank, 2008).

Fish larvae are not necessarily passive particles, and they have the potential to influence their dispersal (see reviews by Leis, 2006 and 2007). For example, changes in the depth distribution of larvae via diel vertical migration (DVM) will impact dispersal trajectories impacting survival (Paris and Cowen, 2004). In some species of invertebrates (particularly crustaceans) and early life stages of demersal fish, changes in depth are associated with specific tidal phases (selective tidal stream transport, STST) that facilitate the ingress of early life stages to nursery habitats as reviewed by Forward and Tankersley (2001). Horizontal swimming appears to be particularly important in ecosystems such as coral reefs in which most fish larvae are relatively strong swimmers and can orientate to and find specific habitats by the time that they are competent to settle to demersal/juvenile habitats (Huebert and Sponaugle, 2009; Leis, 2006 and 2007). In comparison, the larvae of most temperate/sub-polar marine fish species are relatively poor swimmers (Fuiman and Batty, 1997; Peck et al., 2006). Furthermore, larvae may or may not display DVM and/or other swimming behaviors depending upon the prevailing physical and biological habitat characteristics (e.g., see Voss et al., 2007).

The broadcast spawning strategy utilized by many marine fish and invertebrates and the specialized larval swimming behaviors displayed in many species suggest the high magnitude of losses that can occur due to physical (hydrodynamic) factors. Within the context of habitat connectivity, the first source of losses during the early life of marine fish (and shellfish) that models hope to estimate is, therefore, "*advection-based losses*".

2.2. Inadequate prey fields and starvation

Even under favorable conditions of drift (e.g., transport to nursery areas), match–mismatch dynamics between larvae and their preferred prey may lead to further or complete losses of individuals in cohorts due to starvation. At ad libitum feeding conditions, the sizes of prey consumed by larvae increase with increasing larval size in accordance with optimal foraging theory (Barnes et al., 2010; Crowder, 1985; Krebs, 1978). Larvae often display a positive selection for specific life stages of certain copepod species in temperate areas (e.g., Heath and Lough, 2007) and a variety of other organisms in other areas, such as appendicularians by larval tunas in the tropical waters of the Western Atlantic (Llopiz et al., 2010). The rate and extent of ontogenetic changes in the larval fish prey field and prey requirements depend upon the rate and extent of changes in larval developmental characteristics including morphology (mouth size, digestive system function, swimming musculature) and energetics (rates of catabolism and assimilation efficiency), all of which are species-specific (Houde and Zastrow, 1993) .

It is very difficult to accurately assess prey concentrations that are needed for larval fish survival in the field because it is notoriously difficult to obtain accurate and precise estimates of the abundance of marine fish early life stages and their prey at the spatial scales appropriate for their interactions (Heath, 1992; Pepin, 2004). Young et al. (2009) highlighted the inherent problems associated with characterizing *in situ* larval fish prey fields due to high levels of variability within and among sampling sites. Most large-scale zooplankton sampling conducted for fisheries investigations (e.g., with nets) will not adequately describe the variability in prey fields experienced by foraging larvae. Small-scale, in situ sampling and digital imaging have helped characterize the distribution of plankton at relevant, small (e.g., 1 to 10 m) scales (Lough and Broughton, 2007; Owen, 1989; Young et al., 2009) allowing probability distributions to be calculated that describe prey patchiness in different water masses (Lough and Broughton, 2007; Young et al., 2009).

Given the complications associated with adequately estimating prey fields experienced by larvae, it is not surprising that quantitative estimates of prey concentrations required to support larval fish survival are generally not reported. Moreover, despite our ability to rapidly measure in situ larval condition using biochemical techniques (e.g., RNA–DNA ratio) which detect individuals in poor condition, quantifying the proportion of larvae in poor condition that will ultimately die due to starvation is nearly impossible (Meyer et al., this issue). Histological examination of gut tissues remains the most reliable index of the "point of no return" (irreversible starvation) in larval fish (e.g., see Bisbal and Bengtson, 1995) but is not utilized in large-scale, oceanographic research programs due to the relatively