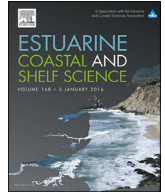




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Behavioral and physiological responses to prey match-mismatch in larval herring

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ABSTRACT

The year-class success of Atlantic herring (*Clupea harengus*) spawning in the autumn/winter in the North Sea (NSAS stock) and in the spring in the western Baltic Sea (WBSS) appears driven by prey match-mismatch dynamics affecting the survival of larvae during the first weeks of life. To better understand and model the consequences of prey match-mismatch from an individual-based perspective, we measured aspects of the physiology and behavior of NSAS and WBSS herring larvae foraging in markedly different prey concentrations. When matched with prey (*ad libitum* concentrations of the copepod *Acartia tonsa*) larval growth, swimming activity, nutritional condition and metabolic rates were relatively high. When prey was absent (mismatch), swimming and feeding behavior rapidly declined within 2 and 4 days, for WBSS and NSAS larvae, respectively, concomitant with reductions in nutritional (RNA-DNA ratio) and somatic (weight-at-length) condition. After several days without prey, respiration measurements made on WBSS larvae suggested metabolic down-regulation (8–34%). An individual-based model depicting the time course of these Behavioral and physiological responses suggested that 25-mm larvae experiencing a mismatch would survive 25–33% (10, 7 °C) longer than 12-mm larvae. Warmer temperatures exacerbate starvation-induced decrements in performance. Without Behavioral and metabolic adjustments, survival of 25-mm larvae would be reduced from 8 to 6 days at 7 °C. Our findings highlight how adaptive Behavioral and physiological responses are tightly linked to prey match-mismatch dynamics in larval herring and how these responses can be included in models to better explore how bottom-up processes regulate larval fish growth and survival.

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1. Introduction

In marine fish, young larvae are vulnerable to mortality through an amalgam of physical and biological (starvation, predation) processes (Bailey and Houde, 1989; Houde, 2008). The likelihood of mortality due to predation increases when fish larvae experience prolonged periods of poor feeding conditions which reduces growth rates (increasing the duration of the larval period) and the amounts of energy available for swimming activity (whether for foraging or predator escape response) (Houde, 1987; Leggett and Deblois, 1994; Cowan and Shaw, 2002). For temperate populations of marine fish, the spatio-temporal variability in spawning activity is often much lower than that in lower trophic level productivity (the spring bloom of phyto-, micro- and mesozooplankton). In the “match-mismatch hypothesis” (MMH),

Cushing (1969, 1990) suggested that the overlap of larvae and their prey was the most important factor affecting whether fish would have a strong or weak year class. In the following decades, evidence supporting the MMH and other, similar hypotheses has been reported (Ellertsen et al., 1987; Platt et al., 2003; Peck et al., 2012a,b) and, in recent years, this hypothesis has received renewed attention in the light of the potential for climate-induced warming and atmospheric forcing to alter the trophodynamic structure and function of marine ecosystems (Ji et al., 2010; Richardson et al., 2012; Durant et al., 2013).

Atlantic herring (*Clupea harengus*) is distributed along the shelf regions of the North Atlantic and in the northeastern Atlantic and Baltic Sea where it displays several discrete (meta-) populations separated by differences in spawning location and season (McQuinn, 1997; Geffen et al., 2011; Hufnagl et al., 2015). For the last decade, poor recruitment has been observed in both the Western Baltic Spring Spawning (WBSS) and North Sea Autumn Spawning (NSAS) stocks (ICES, 2013a; von Dorrien et al., 2013). The

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larvae of these two stocks experience contrasting environmental trajectories during their first months of life. The WBSS stock commence spawning after waters warm beyond 4–6 °C in the spring and spawning females continue to arrive for several weeks to a month when waters can reach 12–15 °C (Klinkhardt, 1996; Bekkevold et al., 2005). Larval cohorts produced relatively late (early) in the spring appear to contribute relatively more (fewer) survivors (Polte et al., 2014) likely due to a better match with suitable prey (calanoid copepods such as *Acartia spp.* and *Eurytemora affinis*) (Hesse, 2010). The recruitment of WBSS herring appears unrelated to hydrodynamics/larval drift (Bauer et al., 2013) and is not directly set by changes in predation (Kotterba et al., 2014). In contrast, NSAS herring initiate spawning at 9–11 °C in the autumn and larger, pre-metamorphic larvae experience the coldest temperatures of the year (5–6 °C; Röckmann et al., 2011). NSAS herring larvae also feed on copepods (various stages of *Calanus finmarchicus*) and poor recruitment stems from increased overwinter mortality (Nash and Dickey-Collas, 2005; Payne et al., 2009) ascribed to unfavorable drift, an increase in temperature, and/or prey mismatch (Dickey-Collas et al., 2009; Fässler et al., 2011; Corten, 2013). Reduced feeding frequencies and rates of growth in NSAS larvae in the last decade likely stem from changes in the quantity and/or quality of available prey (Payne et al., 2013; Lusseau et al., 2014).

Faster growth rate and larger body size enhance survival of marine fish larvae in some (but not all) year classes and/or cohorts (Takasuka et al., 2003; Robert et al., 2007). In both the NSAS and WBSS herring stocks, year-class strength appears to be largely established when larvae reach 20 mm in length (Oeberst et al., 2009a,b; Nash and Dickey-Collas, 2005; Hufnagl et al., 2015). Unlike the larvae of other fishes which must grow (increase in weight or length) to survive, herring larvae can survive at maintenance (zero growth) rations (Johannessen et al., 2000). At lower (sub-maintenance) prey rations or when completely deprived of food, various morphological and physiological changes occur (Catalán, 2003). Previous laboratory studies have examined maximum survival time and/or histo- and morphological changes in poorly fed or starved herring larvae (Blaxter and Hempel, 1963; Ehrlich et al., 1976; Skajaa et al., 2004). Malnourished and well-fed herring larvae can be distinguished based on nucleic acid ratios (RNA:DNA, RD) as a proxy for protein synthesis (Clemmesen, 1994; Mathers et al., 1994; Suneetha et al., 1999) as well as digestive enzymes such as the protease trypsin (Pedersen et al., 1987; Ueberschär and Clemmesen, 1992). In juvenile fish, swimming activity is often modified to minimize energy losses when individuals experience low food rations (Sogard and Olla, 1996). Finally, temperature is a key factor regulating metabolic rates of predators and prey as well as the phenology of productivity in temperate environments. When larvae experience a mismatch with prey, colder (but not lethal) temperatures may extend the time period when starving larvae are still strong enough to feed and survive if prey becomes available.

Given the potential for bottom-up regulation of herring productivity in some years, emphasis has been placed on developing and using mechanistic, individual-based models (IBMs) (Peck and Hufnagl, 2012). To examine the amalgam of bottom-up processes affecting the survival and growth of larval herring, physiological-based IBMs have been constructed which include energy losses due to activity as well as optimal foraging subroutines (Hufnagl and Peck, 2011; Hufnagl et al., 2015). A number of shortcomings and improvements to larval fish IBMs were suggested by Peck and Hufnagl (2012) including adding realism in larval fish behavior and studying and incorporating responses of larvae to changes in prey fields to better represent tradeoffs associated with foraging in optimal versus suboptimal prey fields.

This study conducted laboratory and modeling experiments to

better understand the Behavioral and physiological responses of larvae of NSAS and WBSS herring to different feeding conditions. Growth, condition (somatic, biochemical), behavior (swimming and foraging activity) and metabolism were examined in larvae experiencing a match and a mismatch in prey. These measurements were incorporated into a previously published IBM of larval foraging and growth (Hufnagl and Peck, 2011) which was then used to examine optimal responses and the potential survival of larvae within various prey field scenarios. We hypothesized that larvae are able to alter their swimming behavior and metabolism to either optimize feeding and growth during match situations or best endure prolonged mismatches with prey. Such adaptations would help explain how herring is able to exploit such different life history scheduling among regions.

2. Material and methods

2.1. Ethics

All procedures involving animals were conducted in accordance with the German law on experimental animals and were approved by the responsible ethical committee of the department for food safety and veterinary matters of the Hamburg Authority for Health and Consumer Protection (application nr. 95/11). Efforts were made to minimize suffering. For obtaining adult herring, no special permission was required since they were either collected during a routine survey (NSAS) or offered for sale by a commercial fisherman (WBSS).

2.2. Artificial spawning, egg incubation and rearing

Mature males and females from two Atlantic herring populations were used for artificial strip-spawning and fertilization. First, mature winter-spawning North Sea autumn spawning herring (NSAS) were caught using a trawl net on the RV Tridens in December 2011 in the English Channel, southwest North Sea (50.04°N, 00.50°E). Fish were strip-spawned and fertilized embryos were transported to the laboratory. Second, mature Western Baltic spring-spawning herring (WBSS) were obtained from gill nets in April 2012 in Kiel Fjord, southwest Baltic Sea (54.36°N, 10.16°E). Adults were transported on ice to the laboratory where they were strip-spawned. Eggs were incubated in the laboratory and larvae were provided microalgae (cryptophyte, *Rhodomonas baltica*), dinoflagellates (*Oxyrrhis marina*) and copepod (*Acartia tonsa*) nauplii and copepodite stages (depending on larval size) to allow *ad libitum* feeding (see Table 1 for incubation/rearing conditions).

2.3. Experimental design and sampling

Two experiments were conducted, one with NSAS and one with WBSS larvae, each consisting of two treatments: a fed (match with zooplankton) and an unfed (mismatch with zooplankton; see Table 1). The larvae within the match (fed) treatment were supplied *ad libitum* concentrations of *A. tonsa* nauplii, copepodites and adults (Fig. 1) every day in the morning (ca. 10:00). Larvae within the mismatch treatment were fed on day 0 and allowed to exhaust their prey resources. Daily changes in biochemical-based condition, as well as swimming and feeding activity were measured in both experiments and metabolism was measured on WBSS larvae.

The standard respiration (R_S) was measured in anaesthetized larvae placed within a commercially available micro-respiration system (OX-MR, Unisense, Aarhus, Denmark), using the same methods as described by Moyano et al. (2014). The vast majority (95%) of the larvae resumed normal behavior after recovering from anesthesia. Measurements were made between 10:00 and

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