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Dual impact of temperature on growth and mortality of marine fish larvae in a shallow estuarine habitat

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ABSTRACT

High individual growth and mortality rates of herring *Clupea harengus membras* and goby *Pomatoschistus* spp. larvae were observed in the estuarine habitat of the Gulf of Riga, Baltic Sea. Both instantaneous mortality (0.76–1.05) as well as growth rate (0.41–0.82 mm day^{-1}) of larval herring were amongst highest observed elsewhere previously. Mortality rates of goby larvae were also high (0.57–1.05), while first ever data on growth rates were provided in this study (0.23–0.35 mm day^{-1}). Our study also evidenced that higher growth rate of marine fish larvae did not result in lower mortalities. We suggest that high growth and mortality rates primarily resulted from a rapidly increasing and high (>18 °C) water temperature that masked potential food-web effects. The explanation for observed patterns lies in the interactive manner temperature contributed: i) facilitating prey production, which supported high growth rate and decreased mortalities; ii) exceeding physiological thermal optimum of larvae, which resulted in decreased growth rate and generally high mortalities. Our investigation suggests that the projected climate warming may have significant effect on early life history stages of the dominating marine fish species inhabiting shallow estuaries.

1. Introduction

Studies focusing on early life history stages of marine fish have been conducted since the early 20th century (Hjort, 1914) with an overall aim to establish a link between larval fish and variations in recruitment abundance (e.g. Cushing, 1990). A number of studies suggest that mortality rates are expected to decrease with increasing larval fish growth rates that is, in turn, related to habitat conditions (Houde, 1987 and references therein). There are several more recently conducted studies that provide further process-based evidences in this regard (Robert et al., 2009; Zenitani et al., 2009). However, it appears that mechanisms controlling growth and survival in early life history stages are relatively difficult to identify because of the potential change of dominant processes over time (Kneib, 1993).

Several hypotheses relate the size of marine fish population to growth and mortality in early life. Hjort (1914) proposed that the most critical stage for larvae is when they switch to prey external food, i.e. the "critical period hypothesis". Cushing (1975) suggests that larval growth and survival depends on the temporal overlap between the first feeding larvae and the availability of suitable prey. Prey abundance during this critical period influences larval survival (Cushing, 1990) as it depends on ingestion success that is "gape-limited". Therefore, larval growth and survival not only depends on the availability of prey species but also on prey size, which mean that larger individuals are able to forage on broader size range of prey (Mehner et al., 1998).

Only a few marine fish species can successfully reproduce in the northeastern Baltic Sea. Spring-spawning herring *Clupea harengus membras* and gobies *Pomatoschistus* spp. are adapted to spawn in low-salinity estuarine conditions and are therefore amongst a few marine fish able to reproduce in the NE Baltic Sea (Ojaveer and Kalejs, 2005). Thus, these taxa represent ecologically important marine fish throughout the Baltic Sea. The spring herring is a total spawner (Murua and Saborido-Rey, 2003) that mostly attain sexual maturity in the Baltic Sea at the age of 2 years (Ojaveer, 2003). Newly hatched larvae have a body size between 5 and 9 mm standard length, depending on temperature during embryonic development (Arrhenius and Hansson, 1996). Sheltered coastal habitats are used as retention areas, where larvae spend their most critical life stage and benefit on high production of prey species –

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copepod nauplii. External feeding of herring larvae mostly start at 8.0 mm, but never prior to complete utilization of yolk sac (e.g. Arula et al., 2012).

Pomatoschistus spp. is a small-sized short-living fish (Fonds, 1973) who is batch spawner with a relatively long spawning season (Waligóra-Borek and Sapota, 2005). Newly hatched larvae are approximately 2.5 mm long and in a remarkably advanced stage of development with almost no yolk (Borges et al., 2011). While herring is known to inhabit more temperate waters, *Pomatoschistus* spp. originate from warmer climate, but have well-adapted to the estuarine conditions (Bouchereau and Guelorget, 1998). In addition, prey spectrum of larval *Pomatoschistus* spp. is more diverse than that of herring and constitutes of several taxa such as the copepod *Eurytemora affinis*, and cladocerans *Evadne nordmanni, Bosmina* spp. and *Pleopis polyphemoides* (A. Lankov, unpubl. data, Estonian Marine Institute, Pärnu).

In the NE part of the Gulf of Riga (GoR) larval fish surveys have been performed since the 1950s. Large inter-annual and decadal variation in the abundance of the two most numerous fish taxa - herring and *Pomatoschistus* spp. have been observed (Arula et al., 2014a; Laur et al., 2014). Fluctuations have been related to winter air temperature that determines spawning and larval fish seasonal abundance dynamics together with temporal overlap by prey (Ojaveer et al., 2011; Laur et al., 2014). While for herring, the larval abundance is a good predictor of the year-class strength (Ojaveer et al., 2011); less is known about the importance of the non-commercial *Pomatoschistus* spp. larvae. Gobies serve as an important prey item for commercially harvested pike-perch (*Sander lucioperca*) and its recruitment fluctuations are strongly coupled to the abundance of gobies in Pärnu Bay (Müller-Karulis et al., 2013).

In this study, the vital rates of the Baltic spring herring and *Pomatoschistus* spp. larvae were examined in relation to remarkably warming estuarine habitat in the NE GoR. The current study was motivated by the fact that most of the related studies observed changes in vital rates in their optimal conditions (1–16 °C). However, those species experience in coastal habitats substantially higher temperatures (>17 °C). Aims of the study were to: i) identify daily growth rate and instantaneous mortality of the larval herring and *Pomatoschistus* spp.; ii) determine whether the vital rates vary at small spatial scales; iii) identify the impact of key environmental conditions on vital rates.

2. Material and methods

2.1. Study area

Pärnu Bay (PB), located in the northeastern Baltic Sea (Fig. 1) is a sheltered and shallow (maximum depth around 10 m) area covering 700 km^2 with a volume of 2 km^3. The average annual freshwater inflow from the Pärnu River is about 2 km^3 (Suursaar et al., 2002). In most years, the bay is fully ice-covered in winters. Sea surface temperature (SST) fluctuates seasonally from regular sub-zero degree Celsius in winter to >20 °C in summer. In the warm season, the water is generally well mixed down to the bottom. The currents are weak (velocity below 10 cm s^{-1}) and mainly determined by wind, but modified by coastline morphology and bottom topography (Suursaar et al., 2002). Because of the shallowness, changes in the air temperatures directly affect the water temperature. The hydrographic conditions are formed under the complex influence of ice conditions, freshwater inputs from the Pärnu River and the water exchange with the GoR (Kotta et al., 2008).

2.2. Data, sampling and laboratory analysis

Daily sampling of larvae was conducted in three stations (Fig. 1) from 1st to 14th of June in 2011 during daylight. The rationale behind the selection of stations lies on two pillars: i) high larval fish production in selected stations (Laur et al., 2014; Arula et al., 2014a); ii) sheltered from winds that cause the dispersal of fish larvae (Suursaar et al., 2002). Larvae were collected with Hensen net (mouth diameter 800 mm, mesh size 500 μm, mesh size in the cod-end sampler 170 μm). Net was towed near the water surface at a speed of ca. 2 knots for 10 min. To avoid the wake of the vessel, circulations were made so that the net was going in the inner circus. Larvae were preserved in a 4% buffered formaldehyde seawater solution. Larval fish abundances are expressed as the number of larvae per 100 m^3, calculated from the volume of water filtered during each haul (measured with flowmeter Hydro-Bios "Digital Flowmeter 483110").

Species composition in the samples was determined in the laboratory. Larval *Pomatoschistus* spp. were identified to the genus level (Table 1) as their identification to a species level is unreliable based on external morphology (Laur et al., 2014). Fish larvae were identified and counted at the species level (Table 1). All individuals were digitalized and notochord length was measured by LAS 4.1 (Leica Application Suite) from the images. Larvae were measured in three replicates to the nearest 0.1 mm SL. A maximum of 200 ind. were measured in each sample for both taxa. In total 11224 herring (including yolk-sac) and 2288 *Pomatoschistus* spp. larvae were analyzed. Herring larvae were divided into 18 length classes with 1 mm interval, from 5 mm to 22 mm, and *Pomatoschistus* spp. larvae to 22 length classes with 0.5 mm interval, from 2.5 mm to 13 mm. Shrinkage due to preservation in formalin was not considered.

Prey of larvae – mesozooplankton – was collected from all three stations along with larval fish sampling by vertical hauls with a Juday net (mouth opening area 0.1 m^2, mesh size 100 μm). Zooplankton sampling and analysis were carried out according to HELCOM (Helsinki Commission) recommendations (HELCOM, 1988). Four taxa (the copepod *E. affinis*, and cladocerans *Evadne nordmanni, Bosmina* spp. and *Pleopis polyphemoides*) were considered as preferred prey items for larval herring and *Pomatoschistus* spp. (Arula et al., 2012; Lankov., unpubl. data, Estonian Marine Institute, Pärnu). These four zooplankton taxa - *E. affinis* for herring and all four taxa for *Pomatoschistus* spp. larvae - were used to calculate suitable prey size for larvae (Fig. 2; zooplankton length from Simm, 1980; Põllupüü et al., 2010). Suitable prey size window was used in prey abundance calculations per day and per cohort identified (Daewel et al., 2011) considering the preferred prey concept (Robert et al., 2013).

On each sampling event, water temperature (°C), salinity (psu), oxygen (mg L^{-1}), turbidity (FTU) and chl a (μg L^{-1}) were measured by using hydrological CTD (model SAIV SD204). All the measurements were averaged across the water column from the surface to the bottom. Data on daily wind speed and wind direction were obtained from the Estonian Environment Agency.

2.3. Statistical analysis

Larval fish cohorts were identified by using the package "mixdist" (Macdonald, 2010) function "mix" in software R (R Development Core Team, 2012) to extract overlapping cohorts and their daily mean lengths. "Mix" analyzes histograms as a mixtures of statistical distributions, by finding a set of overlapping component distributions that gives the best fit to the histogram, using grouped-data maximum likelihood. The terms "start/beginning of the cohort" or "end of the cohort" used in the present work refers to the start or end of a growth cohort identified during the sampling period. We calculated the average daily growth rate (G, mm day^{-1}) of larvae for each cohort separately for three stations. G was calculated when the cohort could be followed in several