

Predation on larval Atlantic herring (*Clupea harengus*) in inshore waters of the Baltic Sea



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ABSTRACT

In fishery science, early life-stage survival and development are regarded as major factors driving the population dynamics of marine fishes. During the last century, the main research focus has been on the spatio-temporal match of larval fish and appropriate food (*bottom-up* processes). However, these field studies are often criticised for their limited capability to disentangle their results from mortality caused by predation since these *top-down* mechanisms are rarely studied. We examined the predation on herring (*Clupea harengus*) larvae in a Baltic inshore lagoon by investigating the spatio-temporal overlap of larval herring and their potential predators such as the dominant threespine stickleback (*Gasterosteus aculeatus*) in distinct habitats (sublittoral and littoral areas) using a set of different gears and sampling techniques. Despite significant spatial and temporal predator-prey overlap, stomach analyses suggested that very few larvae were consumed by sticklebacks, even if projected to the entire study area and season. Other well-known predators of clupeid larvae such as gelatinous plankton occur later in the year after young herring have migrated out of the system. The observed predation on herring larvae was much less than expected and appears being a minor factor in determining herring reproduction success in our study area, particularly if compared to other causes of mortality such as egg predation. Providing a relatively good shelter from predation might be a key element making transitional waters valuable nursery grounds for the offspring of migrating marine fish species.

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1. Introduction

Population dynamics of marine fishes and hence the capacity for their commercial exploitation are based on the production of offspring that recruit into the adult spawning stock thus replacing the losses caused by natural mortality and fishing pressure. Considerable research efforts have focused on understanding the recruitment dynamics of commercial fish and the processes behind large fluctuations in year class success in order to improve stock assessments and the predictive power of population models. Based on the seminal work by Johan Hjort who developed the *critical period* hypothesis (Hjort, 1914, 1926), bottom-up processes such as the availability of sufficient prey resources for larvae have been considered to be important for recruitment. Additional hypotheses

have been developed highlighting the importance of larval nutrition and the spatio-temporal match with adequate prey organisms (e.g. Cushing, 1974; Lasker, 1978). In comparison, top-down mechanisms have gained much less attention although predation has been demonstrated to act as an important driver of fish egg and larvae mortality (Bailey and Houde, 1989). Exemplarily for Atlantic herring in the Baltic Sea, Kotterba et al. (2014, 2017) have demonstrated a strong predation on herring eggs by the resident predators. But also for fish larvae, predation has been considered to be the ultimate agent of mortality (Houde, 2008). Indeed, predation on fish larvae by different fish species (Manzer, 1969; Fuiman and Gamble, 1988; Rankine and Morrison, 1989; Utne-Palm, 2000; Horbowa, 2001) including filial cannibalism (Karaseva et al., 2013) and invertebrates such as crustaceans and gelatinous plankton (Möller, 1980, 1984; Purcell et al., 1987; Purcell, 1989; Purcell and Grover, 1990; Lynam et al., 2005; Kumar et al., 2012) has been well documented. For several examples such as Capelin (*Mallotus villosus*; Gjosæter et al., 2016), and Atlantic herring (*Clupea harengus*) in Norwegian waters (Skaret et al., 2015), predation has been

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identified as a crucial driver of larval survival dynamics.

However, most research on top-down (predatory) control has been conducted in offshore habitats of marine ecosystems although estuaries and inshore lagoons are important retention and nursery areas for the larvae and juveniles of many marine fish species which, as larger juveniles and adults, inhabit offshore waters (Beck et al., 2001; Costa et al., 2002; Elliott, 2002). Therefore, it is surprising that the proportion of studies focusing on mortality processes of fish larvae within estuaries and shallow coastal areas is relatively small (Blaber, 2013).

In general, it is very challenging to study/quantify losses of larvae due to predation because of the often broad variety of potential predators, the diverse characteristics of individual estuaries (Elliott and Whitfield, 2011) and rapid digestion times of larvae in predator stomachs (Hunter et al., 2012). Nevertheless, Bailey and Houde (1989) emphasized the importance of increasing our knowledge on early life stage predation in order to explain the variability in fish recruitment.

Atlantic herring is a pelagic fish species of outstanding economic and ecological importance, particularly through its role linking zooplankton to higher trophic levels. In the highly productive coastal waters and marginal seas of the Atlantic Ocean the exceptional ecological role of herring thus appears similar to that of small pelagic fishes in the so-called *wasp-waist* marine ecosystems described by Bakun (2006). Herring is a litho-phytophilous spawner attaching its adhesive eggs on demersal spawning substrates (Balon, 1975) and several herring subpopulations migrate into coastal lagoons, estuaries and inshore waters for spawning.

To investigate the predation on larval herring in estuarine waters, we focused on a subpopulation of *C. harengus* that undergoes annual spawning migrations from marine feeding grounds in the western Baltic Sea and the adjacent North Sea into brackish lagoons at the southern coast of the Baltic Sea. We hypothesize that i) predation significantly affects the survival of herring larvae in these inshore waters, and ii) that this larvae predation is in a similar range as the predation on herring eggs demonstrated in earlier studies.

2. Methods and materials

2.1. Study area

Study area - Greifswald Bay (54°14'N, 013°33'E; Fig. 1) is an important reproduction area for spring-spawning herring in the Western Baltic Sea (Scabell, 1988). The semi-enclosed lagoon is a 514 km² non-tidal, mesohaline water body with salinities between 7 and 9 and a mean water depth of 5.8 m (Reinicke, 1989; Stigge, 1989). Water exchanges with the adjacent Baltic Sea as well as sea surface height within the lagoon are mainly wind-driven (Stigge, 1989). The system is highly eutrophic (Munkes, 2005) but the waterbody is well mixed with high concentrations of dissolved oxygen during spring. The fish community of the lagoon comprises more than 60 species including marine and freshwater species (Winkler, 1989a) with large seasonal changes in species composition. Among the resident fish species, the threespine stickleback (*Gasterosteus aculeatus*, L. 1758) is the most abundant and can display particularly high abundances in some years (Winkler, 1989a; Kotterba et al., 2014).

2.2. Investigations of larvae abundances

Since 1991, data on the abundance of herring larvae in the sublittoral of Greifswald Bay have been investigated each week during the entire reproduction season in spring (March–June) in the framework of the *Rügen Herring Larvae Survey* (RHLS) (Müller

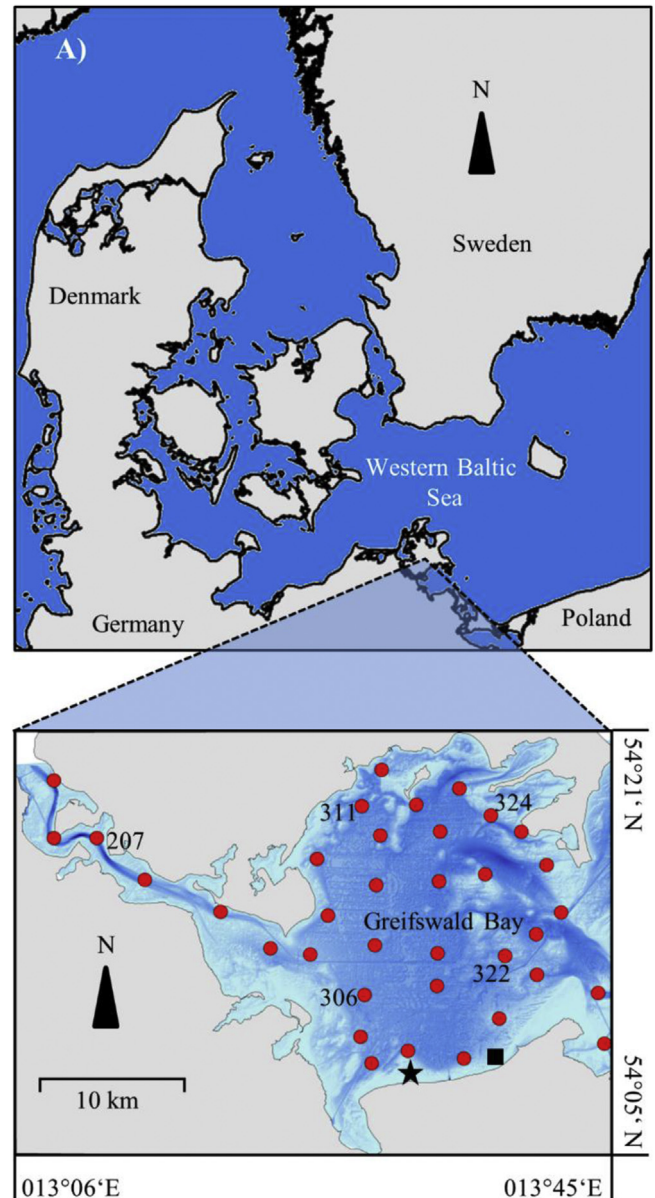


Fig. 1. Greifswald Bay and its location in the Western Baltic Sea. The solid circles represent the sublittoral stations sampled weekly during the Rügen Herring Larvae Survey (RHLS). Stations labelled with a number are locations which were sampled weekly (in 2011) with the BERND. The asterisk and the square indicate the littoral stations 'Gahlkow' and 'Lubmin', respectively. Elevation data was provided by the Federal Maritime and Hydrographic Agency of Germany (BSH).

and Klenz, 1994; Oeberst et al., 2009a). The RHLS covers a dense grid of 35 stations scattered within Greifswald Bay and the adjacent Strelasund (Fig. 1) and data of this survey feed into the Western Baltic herring stock assessment (Oeberst et al., 2009a). Herring larvae are sampled with a double Bongo (2 nets with mesh sizes of 335 μm and 780 μm), each with a net opening diameter of 60 cm. At every station, an oblique Bongo haul is conducted, i.e. the net is lowered stepwise (by 1 m water depth per step) from the surface down to 1 m above the sea floor. Each depth step is sampled horizontally for 30 s at a towing speed of approximately 2–3 knots ($\sim 3.7\text{--}5.6 \text{ km} \times \text{h}^{-1}$) before the net is lowered further with a speed of $1 \text{ m} \times \text{sec}^{-1}$ (Müller and Klenz, 1994). The volume of filtered seawater is measured using flowmeters mounted in the centre of both net openings. Macroscopically identifiable organisms such as

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