Marine Environmental Research 113 (2016) 164–173

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

Projected habitat loss for Atlantic herring in the Baltic Sea

Björn Illing*, Marta Moyano, Marc Hufnagl, Myron A. Peck

Institute of Hydrobiology and Fisheries Science, University of Hamburg, Olbersweg 24, Hamburg, D-22767, Germany

ARTICLE INFO

Article history:
Received 29 September 2015
Received in revised form
11 December 2015
Accepted 12 December 2015
Available online 15 December 2015

Keywords:
Climate change
Baltic Sea
Salinity
Adaptation
Atlantic herring
Clupea harengus

ABSTRACT

Projected, climate-driven changes in rainfall patterns are expected to alter the salinity (S) of estuaries and larger brackish water bodies, such as the Baltic Sea. Some marine fish larvae are potentially more sensitive to low salinity than older stages, hence we compared the low salinity tolerance of Atlantic herring (*Clupea harengus*) larvae at the individual and population levels including four populations in the North and Baltic Seas. Acute low salinity tolerance was similar (S = 1.9–2.7) across populations and increased with increasing body size. Based on this physiological threshold and a regionally down-scaled climate model, spawning habitats in the northern and eastern Baltic Sea are projected to be largely unsuitable for herring by 2100. Although adaptive mechanisms may attenuate the effect in some species, the limited physiological tolerance of fish larvae will remain an important bottleneck for the persistence of marine fish populations in brackish waters undergoing climate-driven freshening.

1. Introduction

Climate-driven changes in marine habitats will be multi-facetted and a plethora of research has examined the influence of either warming or ocean acidification (OA) on the survival, productivity or distribution of marine animals (Hollowed et al., 2013; Doney et al., 2012; Hollowed and Sundby, 2014). Most of the research summarizing climate change impacts on fishes has focused on changes in distribution due to warming (Pörtner et al., 2014) or changes in growth and survival due to OA (Kroeker et al., 2013). In some brackish habitats, climate-driven changes in rainfall and wind patterns will alter physicochemical features of catchments and estuaries such as turbidity, nutrient load and especially water salinity. Very few studies have examined the potential ecological impacts of the projected freshening of brackish waters. This is surprising given the importance of gradients in water salinity to structuring the spatial and temporal dynamics of fish assemblages in estuaries (Marshall and Elliott, 1998; Martino and Able, 2003) and the important role that brackish waters play as nursery grounds for early life stages of both freshwater and marine species (Able, 2005; Vuorinen et al., 2015).

The Baltic Sea is one of the largest semi-enclosed brackish water bodies in the world. It has a relatively simple food web containing a few dominant marine fishes such as Atlantic herring (*Clupea harengus*), Atlantic cod, (*Gadus morhua*), European sprat (*Sprattus sprattus*) and flounders (*Pleuronectes spp.*) and a few dominant groups of zooplankton (calanoid copepods, cladocerans and rotifers) (Schulz et al., 2012). The region has a strong gradient in salinity (S) (Janssen et al., 1999) from the southwest in the Kattegat and Danish Straits (S = 30 to 20) to the northeast in the Gulf of Finland and Bothnian Bay (S = 4 to 1) (Fig. 1). Inter-annual and decadal shifts in prevailing atmospheric conditions across the Northeast Atlantic have caused changes in the salinity and temperature of Baltic Sea waters (Hänninen et al., 2000). A sharp reduction in the frequency and strength of inflow events of marine water from the North Sea since the early 1990s has caused a freshening of Baltic waters and increased hypoxia in deep basins (BACC, 2015). Within deep basins, historical changes in the biomass and productivity of marine fish, zooplankton and phytoplankton have been correlated with changes in temperature and salinity (Alheit et al., 2005; Möllmann et al., 2009) and losses in biodiversity in a variety of habitats is envisioned with further freshening and warming (Mackenzie et al., 2007).

At sub-optimal salinities, fish and other osmoregulators incur added costs which can reduce the energy available for other important processes such as swimming, feeding and growth, effectively narrowing the range of tolerable temperatures (Pörtner and Peck, 2010). Moreover, marine fish larvae are poorly equipped with osmoregulatory organs (i.e. fully functional guts or gills) and are expected to be particularly sensitive to changes in salinity as

---

* Corresponding author.
E-mail address: Bjoern.Illing@uni-hamburg.de (B. Illing).

http://dx.doi.org/10.1016/j.marenvres.2015.12.007
0141-1136/

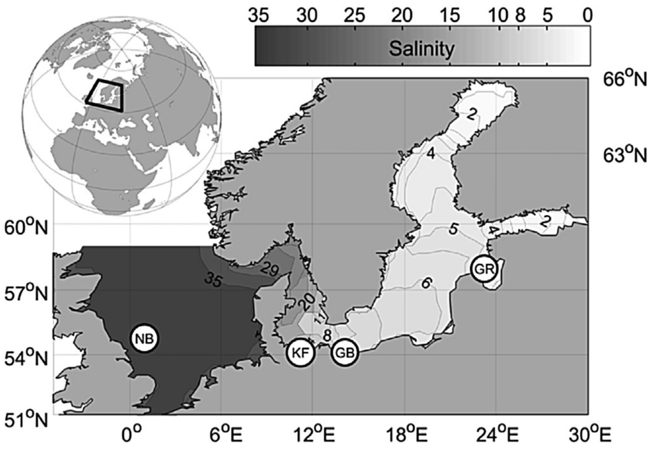

Fig. 1. Mean annual salinity (1980–2004) of the North and Baltic Sea (grid resolution S = 0.1, ICES WGOOFE data, see Janssen et al., 1999). Symbols denote the location of spawning areas of Atlantic herring examined in the present study given: Gulf of Riga (GR); Greifswalder Bodden (GB); Kiel Fjord (KF); and North Sea Banks (NB). Isohaline lines differ by 0.5 (S = 1 to 8) and 3 units (S = 8 to 35), respectively.

well as other climate-driven changes such as OA and/or warming (Llopiz et al., 2014). Climate change impacts on a species are likely to be strongest (either positive or negative) in populations existing at the edges of tolerable conditions. Identifying physiological optima and tolerance thresholds via controlled laboratory experiments is a prerequisite to gaining a mechanistic understanding of the sensitivity of a species to climate-driven changes in environmental factors (Hollowed et al., 2013). Moreover, the physiological tolerance to factors affected by climate can differ among populations of a species and may display a high amount of local adaptation as reviewed by Crozier and Hutchings (2014). For example populations of chinook salmon (*Oncorhynchus tshawytscha*) in the Pacific Northwest of the United States are predicted to have differences in their adaptive capacity to climate change based on heritable differences in thermal tolerance (Muñoz et al., 2015).

We examined the tolerance of the larvae of Atlantic herring from four populations (three stocks) reared at the same salinity (S = 6). The four populations spawn in either marine (S = 34) or brackish (S = 16, 7 or 5) waters. A first objective was to assess whether larvae display any adaptation to local salinity conditions that would, in this case, make larvae from brackish water populations more tolerant to low salinity. These and previously published data on the salinity tolerance of early life stages (eggs, larvae and juveniles) of herring and other fishes were reviewed in this study. Furthermore, we tested whether the knowledge base is sufficient to make physiological-based projections of how climate-driven changes in the salinity of the Baltic Sea and other areas may affect the suitability of these areas as nurseries for marine fishes.

2. Material and methods

2.1. Ethical statement

All experimental work involving animals has been performed in accordance to the German animal welfare laws and efforts were made to minimize suffering. The work was approved by the responsible Ethical Committee of the department for food safety and veterinary matters as part of the Hamburg Authority for Health and Consumer protection (application no. 95/11). For obtaining adult herring, no special permissions were necessary.

2.2. Adult fish spawning and egg and larval rearing

Larvae used in this study originated from eggs collected in the North Sea (Banks area, NB), Kiel Fjord (KF), Greifswalder Bay (GB) and Gulf of Riga (GR) corresponding to (mean ± SD) natal salinities of 34.9 ± 0.1 (autumn-spawned), 16.0 ± 1.4 (spring), 7.3 ± 0.2 (spring) and 5.3 ± 0.1 (late summer/early fall), respectively (Fig. 1). These herring belong to three stocks (North Sea Fall Spawning (NB), Western Baltic Spring Spawning (KF and GB), and Eastern Baltic Fall Spawning (GR)) which are genetically distinct (Gaggiotti et al., 2009; Limborg et al., 2012) with genetic differences corresponding to differences in salinity experienced during spawning (Teacher et al., 2013). Eggs were obtained during the spawning season by strip-spawning ripe adult herring caught via gillnets (GR, KF), by trawling (NB) or by divers collecting newly spawned and fertilized eggs from submerged macrophytes (GB). After arrival at the laboratory, the embryos were incubated at 10 °C in semi-static 90-l tanks, with 30% daily water replacement using filtered seawater (0.5 μm, Reiser Filtertechnik GmbH, Seligenstadt am Main), and light regimes (L:D) occurring at spawning (14:10 for GR, GB, KF; 12:12 for NB) at their natal salinities until hatch (see supplementary material, Tab. A1).

2.3. Experimental design and sampling

Larvae were reared in semi-static, well-aerated 90-l tanks using microalgae to improve growth, survival and prey ingestion ("green water" technique; cryptophytes *Rhodomonas baltica*). Larvae were fed *ad libitum* with known concentrations (1–2 individuals ml^{-1}) of nauplii, copepodites and adults of a calanoid copepod (*Acartia tonsa*), a prey which grows well across a range of salinities (Diekmann et al., 2012). Larvae from GB and GR were hatched and reared at S = 6 while the NB and KF larvae were hatched at their natal salinity (S = 34 and 16, respectively) and slowly adjusted within the first 10 days post–hatch to S = 6 (3.5 and 2.0 units d^{-1}, respectively). Larvae were allowed one week to acclimate prior to testing (Fig. 2A). The KF (S = 16) and NB (S = 34) larvae were also maintained at their natal salinity to compare the effect of salinity on somatic growth and biochemical condition. A similar range in prey concentrations and numbers of herring larvae was maintained in all tanks. Temperature (9.9 ± 0.4 °C, mean ± SD) and salinity (6.2 ± 0.3) were measured each day (WTW cond3110, Weilheim, Germany). Ammonia levels were tested every other day and never exceeded 0.25 mg l^{-1} (TetraNH_3/NH_4^+kit, Melle, Germany).

Acute, short-term salinity tolerance tests were conducted using individual larvae randomly transferred into a 200-ml glass tank containing water at one of 13 test salinities between 0.5 and 5.0 (10 replicates, i.e. individual fish, per salinity). The amount of transfer water had a negligible effect on the test salinity. Each larva was observed directly after transfer and then every 15 min for ~8 h. The time until the loss of equilibrium, i.e. observed inability of balance control, stop of movements and sinking to the bottom (no response even to a light stimulus) was noted. That initial time was confirmed by observing the larvae for an additional three measurement periods (total 1 h). Relative survival time was calculated by assigning the first and final observation period values of 0 and 100%, respectively. Larvae displaying normal activity at the final observation period were considered to be survivors with a 100% relative survival time. Larvae from the four groups were tested at a body size of ca. 10 mm and two groups (KF and NB) were tested again at ca. 15 mm (see supplementary material, Tab. A1). Note, no attempt was made to select larvae within a narrow size range, instead larvae were randomly selected.