Bottom-up effects on growth and survival of larval Atlantic herring (*Clupea harengus*) from the North- and Baltic Seas

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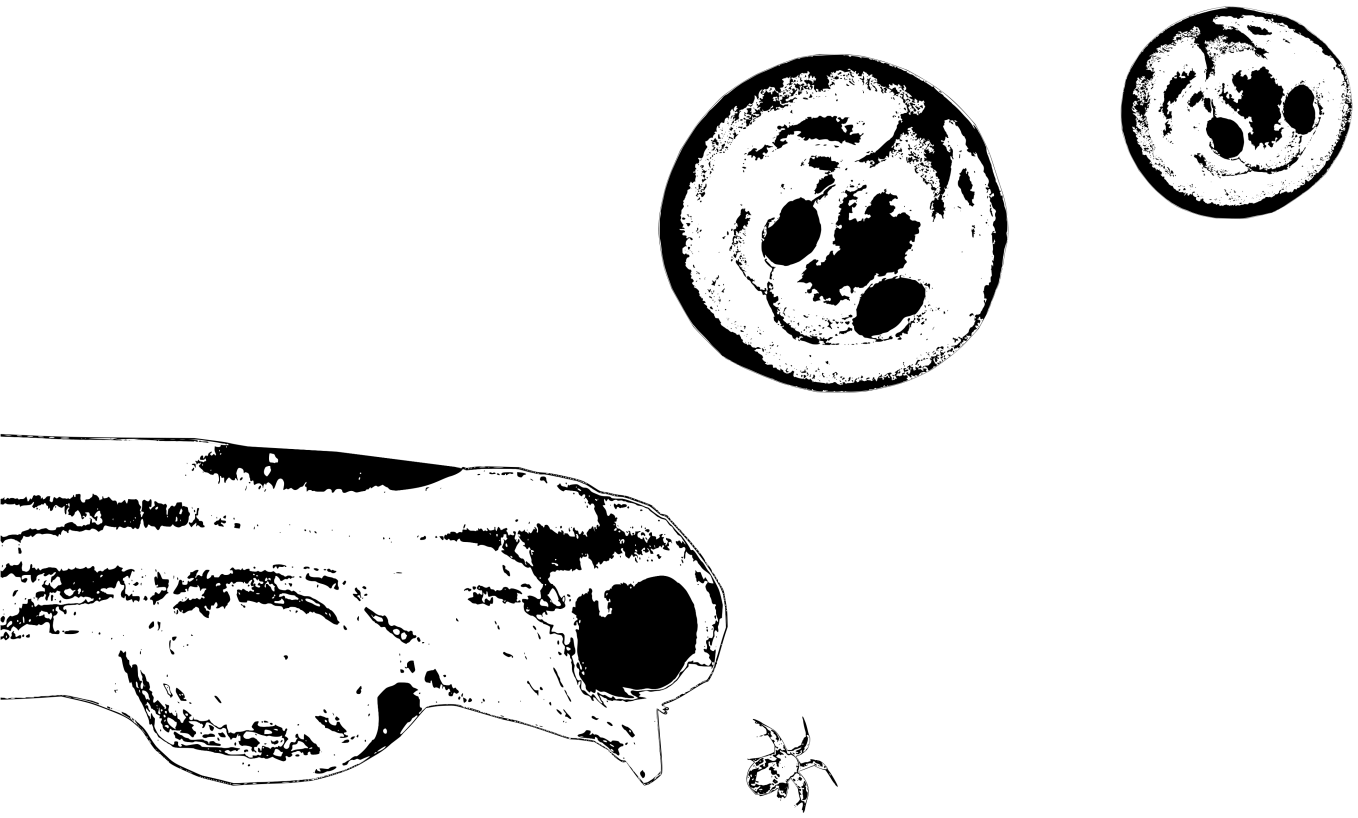

"What is a scientist after all? It is a curious man looking through a keyhole, the keyhole of nature, trying to know what's going on."

— Jacques Yves Cousteau, 1971

Abstract

The stability of marine fish populations is, next to natural or fishing mortality, based on the annual recruitment of the young-of-the-year. The variability in the number of these recruited fish is determined by effects of several abiotic and biotic factors on the vulnerable early life stages (eggs and larvae). Predation, the main driver of mortality, acts contrarily to the energy flow from “top-down", whereas factors such as temperature, salinity or prey availability primarily operate from “bottom-up". In this thesis, a closer look was taken on the effects of these bottom-up factors on Atlantic herring (*Clupea harengus*, L.) larvae from the North and Baltic Seas by measuring their influence on vital rates such as growth, survival, metabolism, nutritional condition as well as feeding and swimming activity under different conditions.

In experiments simulating match or mismatch situations with spring phyto- and protozooplankton blooms, spring-spawned Atlantic herring yolk sac larvae from the Baltic Sea were observed to directly benefit from a spatio-temporal match with microalgae and dinoflagellates. In particular, it could be observed that herring larvae initiated their digestive system more rapidly (precocious production of trypsin) and possessed an earlier and enlarged “window of opportunity" for foraging on larger prey, both supporting the change from endogenous to exogenous feeding. However, survival spans could not be prolonged by microalgae and dinoflagellates after yolk resources had been depleted. Yet, trials with additional, larger prey (copepods), continuously supplied during rearing, suggested an indirect, trophodynamic benefit.

In further trials with older spring- (Baltic Sea) and winter-spawned (North Sea) herring larvae, previously reared beyond the first-feeding stage, the physiological and behavioral effects of prey scarceness were investigated during a mismatch with copepod prey. Larvae that were confronted with prey-poor environments reduced their swimming and feeding activity dramatically within 2-4 days, concomitant with decrements in nutritional and somatic condition. After a couple of days without prey, larvae were observed to have their standard metabolic rate down-regulated up to a third. Using the obtained swimming activity data in an individual-based model simulating the winter condition (7 °C), the survival of e.g. 25-mm larvae was observed to be reduced from 8 to 6 days, assuming no metabolic down-regulation. In the laboratory experiments, exacerbated reductions in

performance parameters were found in prey-poor treatments under warmer spring conditions (10 °C), resulting in a more pronounced selection against smaller larvae.

Temperature can influence larval fish condition and performance by affecting both physiological (biochemical reactions) and physical (e.g. water viscosity) levels. When larval herring were reared under *ad libitum* conditions at three different temperatures (7, 11, and 15 °C), their growth rates and morphology were strongly depending on the rearing temperature with highest growth and fastest development found at the highest temperature. Critical swimming speed (U_{crit}) was tested throughout ontogeny and observed to increase exponentially after yolk-sac absorption. Herring larvae entered the transition to less viscous, and hence advantageous environments (Reynolds numbers ≥ 300), at smaller body sizes when kept at warmer temperatures (14 mm at 15 °C and 17 mm at 7 °C).

In light of predicted climate-driven changes, higher projected water temperatures will play an important role for the growth and survival of marine fish species' offspring. A less well investigated factor with regard to climate change is salinity (S) that is projected to decrease up to two units in the Baltic Sea due to increases in precipitation and river-runoff. Coastal regions, likely affected at most, pose valuable spawning and nursery areas for Atlantic herring, hence low critical salinity thresholds needed for survival of larvae were identified in short-term trials using three herring populations from the Baltic Sea and one from the North Sea ($S = 1.9 - 2.7$). No significant differences in these thresholds were found between the tested populations, however, the relative survival time of the Baltic Sea populations at low salinities was size-dependent. Based on model projections of future salinity in the Baltic Sea (modelled until the end of the 21$^{\mathrm{st}}$ century) and the experimentally determined physiological thresholds, most north and northeastern regions were identified to become presumably unsuitable for larval Atlantic herring survival.

The results of this thesis help clarify the effects of different bottom-up factors (temperature, salinity and prey match-mismatch) on specific vital rates of Atlantic herring larvae. Moreover, the present findings from controlled laboratory experiments with larvae of different age, size, origin and nutritional condition can assist in parametrizing individual-based models more realistically - promoting their use as tools for fisheries management. The thorough investigation of physiological responses to altered environmental conditions in the laboratory can help as well defining threshold values needed for survival of larval

fish and assess how these current thresholds might be affected by projected climate-driven changes.

Zusammenfassung

Die Bestandsentwicklung mariner Fischpopulationen basiert, zusätzlich zu der natürlichen oder der Fischereisterblichkeit, auf der jährlichen Rekrutierung. Die Variabilität der Anzahl von Rekruten ist durch verschiedene abiotische und biotische Faktoren bestimmt, die auf die empfindlichen frühen Lebensstadien (Eier und Larven) wirken. Prädation, der Hauptgrund von Sterblichkeit, wirkt dem Energiefluss von Nahrungsnetzen entgegen und steuert Nahrungsnetze von oben nach unten („top-down“). Faktoren wie Temperatur, Salzgehalt oder Beuteverfügbarkeit haben ihre Wirkrichtung hingegen von unten nach oben („bottom-up“) und liegen vor, wenn positive Korrelationen zwischen Biomassen benachbarter trophischer Ebenen existieren. In dieser Arbeit wurden die Auswirkungen der genannten „bottom-up“ Faktoren auf die Larven des Atlantischen Herings (*Clupea harengus*, L.) ermittelt, indem Vitalraten wie Wachstum, Überleben, Metabolismus, Ernährungszustand sowie Fress- und Schwimmaktivität unter verschiedenen Beutedichten, Temperaturen und Salzgehalten erfasst wurden.

In Laborexperimenten wurde das Zusammen- („match“) oder Nichtzusammentreffen („mismatch“) von im Frühjahr geschlüpften Dottersacklarven des Atlantischen Herings aus der Ostsee mit Phyto- und Protozooplanktonblüten während des Frühjahrs simuliert. Hierbei wurde festgestellt, dass die Larven von einem Zusammentreffen mit Mikroalgen und Dinoflagellaten direkt profitieren konnten. Insbesondere wurde beobachtet, dass Heringslarven durch die Präsenz von Mikroalgen und Dinoflagellaten ihr Verdauungssystem schneller initialisierten (frühzeitigere Produktion von Trypsin) und sie früher und länger die Gelegenheit hatten größeres Plankton zu fressen, beides während der Umstellung von der endo-zur exogenen Ernährung hilfreich. Allerdings konnte nach dem Aufbrauchen der Dottersackreserven die Überlebenszeit der Larven allein durch Mikroalgen und Dinoflagellaten nicht verlängert werden. Es deutete sich aber an, dass bei zusätzlicher Versorgung mit größerer Beute (Copepoden) in den Versuchsbecken für die Heringslarven ein indirekter, trophodynamischer Vorteil existierte.

In weiteren Versuchen wurden die physiologischen und verhaltensbezogenen Auswirkungen von Beutemangel während einer „mismatch“ Situation mit Copepoden an älteren Heringslarven getestet. Hierfür wurden zum einen im Frühjahr geschlüpfte Larven aus der Ostsee und zum anderen im Winter geschlüpfte Larven aus der Nordsee getestet, die

den Umstieg auf die exogene Nahrungsaufnahme erfolgreich absolviert hatten. Die Larven, die beutearmen Umgebungen ausgesetzt waren, reduzierten innerhalb von 2 bis 4 Tagen dramatisch ihre Schwimm- und Fressaktivität, einhergehend mit Abstufungen ihres Ernährungs- und Gesamtzustands. Nach einigen Tagen ohne Beute konnte beobachtet werden, dass die Grundstoffwechselrate der Larven aus der Ostsee um bis zu ein Drittel herunterreguliert war. Die in den Laborexperimenten erfassten Daten zur Schwimmaktivität wurden zusätzlich in ein auf Individuen basierendes Modell („individual-based model“, IBM) übertragen, um in Simulationen das Überleben von virtuellen, 25 mm langen Heringslarven unter Winterbedingungen (7 °C) zu untersuchen. In den Simulationen wurde eine Reduktion der Überlebenszeit von 8 auf 6 Tage beobachtet, wenn die Larven bei geringer Beuteverfügbarkeit keine Verringerung ihrer Aktivität vornahmen. In den Laborexperimenten verstärkten sich die negativen Auswirkungen des Beutemangels auf die Leistungsparameter unter wärmeren Frühjahrsbedingungen (10 °C), was in einem stärkeren Selektionsdruck gegen kleinere Larven resultierte.

Die Temperatur kann den Zustand und die Leistung von Fischlarven sowohl auf physiologischer (biochemische Reaktionen) als auch physikalischer Ebene (z.B. Viskosität des Wassers) beeinflussen. So waren die Wachstumsraten und die Morphologie von Heringslarven, die unter *ad libitum* Bedingungen bei drei verschiedenen Temperaturen gehalten wurden (7, 11 und 15 °C), stark temperaturabhängig. Die kritische Schwimmgeschwindigkeit (U_{crit}) wurde über den Verlauf der Ontogenie untersucht, wobei eine exponentielle Zunahme beobachtet werden konnte nachdem der Dottersack vollständig resorbiert worden war. Der Übergang zu weniger viskosen, und damit vorteilhafteren Umgebungen (Reynoldszahlen ≥ 300), wurde bei höheren Temperaturen bereits bei geringeren Körpergrößen erreicht (14 mm bei 15 °C und 17 mm bei 7 °C).

Angesichts der prognostizierten Änderungen durch den Klimawandel spielen höhere Wassertemperaturen eine wichtige Rolle für das Wachstum und Überleben des Nachwuchses mariner Fischarten. Ein in Bezug auf den Klimawandel weniger gut untersuchter Faktor ist der Salzgehalt (S), der sich Prognosen nach in der Ostsee durch erhöhten Niederschlag und Frischwassereintrag durch Flüsse bis zu zwei Einheiten reduzieren könnte. Die dadurch am stärksten beeinflussten Küstenregionen stellen für den Hering wichtige Laich- und Aufwuchsgebiete dar, weshalb in Kurzzeitexperimenten mit drei Populationen aus der Ostsee und einer aus der Nordsee Schwellenwerte für das Überleben bei niedrigen

Salzgehalten identifiziert wurden ($S = 1,9 - 2,7$). An Hand der Schwellenwerte konnten keine signifikanten Unterschiede zwischen den getesteten Populationen gefunden werden, allerdings war die relative Überlebenszeit der Ostseepopulationen bei niedrigen Salzgehalten größenabhängig. Basierend auf Modellprognosen für den zukünftigen Salzgehalt der Ostsee (bis zum Ende des 21. Jahrhunderts modelliert) und den experimentell bestimmten physiologischen Schwellenwerten, wurden die nördlichen und nordöstlichen Bereiche der Ostsee als Gebiete identifiziert, die sich in Zukunft für das Überleben der Heringslarven als unbrauchbar herausstellen könnten.

Die Ergebnisse dieser Arbeit verdeutlichen den Einfluss verschiedener „bottom-up“ Faktoren (Temperatur, Salzgehalt, „match-mismatch“ mit Beute) auf spezifische Vitalraten der Larven des Atlantischen Herings. Außerdem können die hier gefundenen Resultate aus kontrollierten Laborexperimenten mit Larven verschiedenen Alters, Größe, Ursprung und Ernährungszustand dazu dienen, vorhandene Modelle (IBMs) zu parametrisieren und realistischer zu gestalten, um sie als Werkzeuge für das Fischereimanagment voranzubringen. Die eingehende, experimentelle Untersuchung physiologischer Reaktionen auf veränderte Umgebungsbedingungen kann dazu beitragen, Grenzwerte für das Überleben von Fischlarven zu definieren und helfen zu beurteilen, wie die gegenwärtigen Grenzen zukünftig durch den Klimawandel beeinflusst werden könnten.

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Chapter 1

General Introduction

Marine resources, in particular fish stocks, are limited and require sustainable managment. However, the average world per capita apparent fish consumption has nearly doubled since the 1960s (9.9 to 19.2 kg in 2012; FAO 2014). In order to meet this increased demand, an alarming practice has been established in the past decades that is best described as “fishing down the food web" (Pauly et al., 1998). In other words, fish stocks have been rigorously depleted by size and market value of their individuals, resulting in 90 % of the world's fish stocks now being either fully or overfished (FAO, 2014). The very likely consequence is that after a century of biomass decline in the oceans, forage fish species, including smaller prey fishes such as sardines, anchovies, menhadens or herrings, will become more dominant (Christensen et al., 2014). With a reduced “top-down" control by predatory fishes and barring anthropogenic fishing mortality, the early life stages and year class strengths of these forage fish species will be increasingly controlled by factors that act “bottom-up".

1.1 Importance of marine fish early life stages to recruitment

A major, ongoing task in fisheries science is to provide accurate predictions of the year class success of fish stocks responding to various pressures by displaying spatial and temporal dynamics. Understanding recruitment processes may help provide sound advice needed to better manage fish stocks, a key issue concerning the increasing human demand for fish and fish-related products. Generally, thoughtful fisheries management relies on profound knowledge of the fundamental factors driving fish stock dynamics and their inter-annual variability in order to obtain a maximum sustainable yield (MSY). Since the beginning of the 20th century, several theories have been established to explain this variability and most

of them identified recruitment, i.e. the number of maturing fish that enter the spawning stock, as decisive for the variation of population dynamics. This passage presents a (mostly) chronological overview of the hypotheses that were developed to explain recruitment variability.

The first fisheries scientist who assumed that year class success was determined in the early life stages of marine fish was Hjort (1914), who addressed fluctuations in fish stock abundances to recruitment variability. Hjort's "Critical Period Hypothesis" stated that year class success is determined shortly after yolk absorption when larvae switch from endogenous feeding to planktonic prey suggesting starvation-induced mortality during first-feeding to be a bottleneck for recruitment. Hjort extended his first hypothesis by including hydrodynamic advection in his "Aberrant Drift" hypothesis (1926). Therein he stressed that an unfavourable drift of eggs and larvae away from nursery grounds can as well have a major influence on larval survival. In the years after and especially from the 1960s onwards a bulk of laboratory studies investigated the starvation resistance of first-feeding stages of fish larvae to assess effects of prey composition, quantity and quality on larval fish survival (Leggett and Deblois, 1994). Both of Hjort's tropho- and hydrodynamic hypotheses were fundamental for the development of more recent theories attempting to explain recruitment variability (Houde, 2008).

An important extension of Hjort's hypotheses was made by Cushing (1975; 1990) who united both assumptions into the "Match/Mismatch Hypothesis". Cushing suggested that a match in timing of fish spawning and larval production with spring phyto- and zooplankton blooms is crucial for larval survival and that starvation can lead throughout the whole larval period to high mortality and not only during first-feeding. Furthermore, he added the critical depth concept (depth at which total photosynthesis is balanced by total plant respiration), which highlighted the importance of water-column mixing for the intensity of bloom dynamics (Cowan and Shaw, 2002). Similarly, different extensions or modifications were made to Hjort's second hydrodynamic hypothesis: the first was Lasker's (1978) "Stable Ocean Hypothesis" which says that the occurrence and frequency of calm periods with low wind speeds ("Lasker events") leads to a vertical stratification of the water column, and therefore aggregates fish larvae and planktonic prey in favourable water layers which increases larval survival. Contrariwise, Rothschild and Osborn (1988) formulated in their "Plankton Contact Hypothesis" that microturbulence can increase

the encounter rate between larvae and relatively rare prey. Another modified concept is called “Larval Retention/Membership-Vagrancy Hypothesis" wherein Iles and Sinclair (1982) hypothesized that physical retention of early-life stages has a major influence on recruitment. With adults spawning at the same place and time throughout the years some of the passively moved eggs and larvae will drift in favourable areas where parts of the offspring are retained due to physical processes (“members") and some will be lost to areas of lesser quality (“vagrants") (Cowan and Shaw, 2002). In 1989, Cury and Roy came up with a model called “Optimum Environmental Window", meaning that in upwelling areas, were deeper water masses are transported to the surface, annual recruitment is dome-shaped and increasing until wind speeds become too strong. All of the aforementioned hypotheses are based at least on one of Hjort’s initial ideas of how recruitment is influenced by mortality of early life stages with starvation as the driving factor.

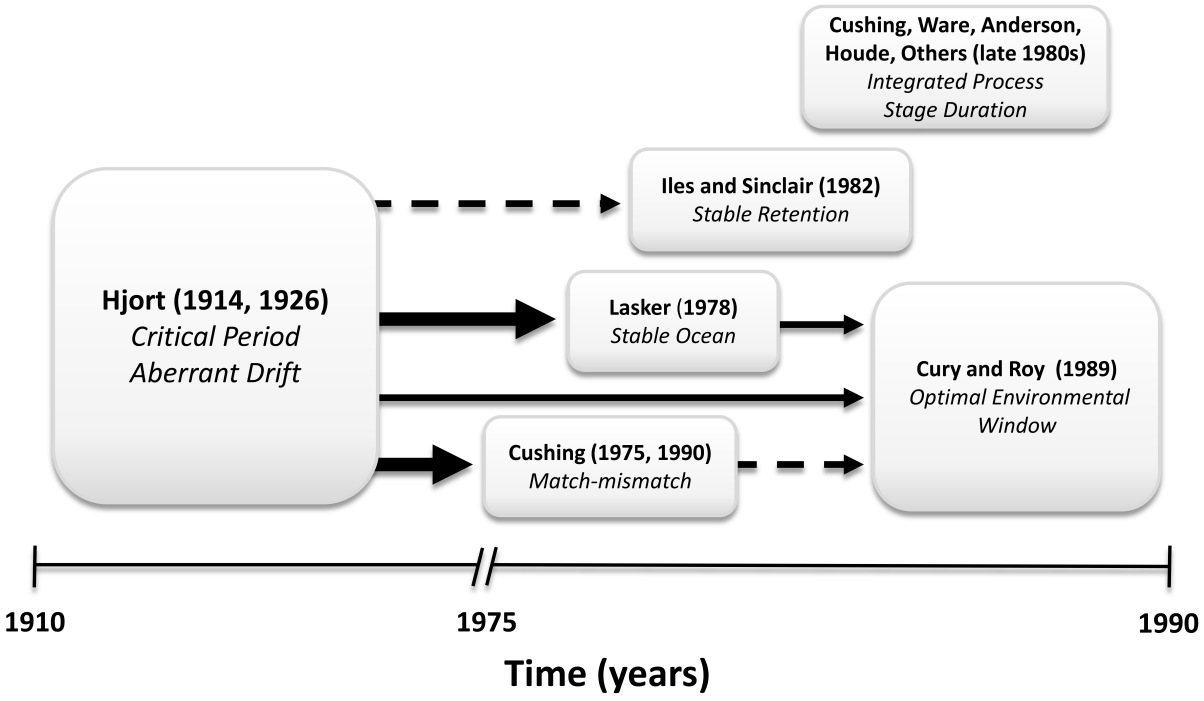

Figure 1.1: Schematic and chronological overview of major recruitment hypotheses derived from Hjort’s initial hypotheses (modified from Houde 2008). Solid arrows indicate direct and broken arrows indirect influence; the arrow thickness represents the strength of the relationship.

Although the potential importance of predation as a recruitment regulator has already been mentioned by Cushing in 1975, a paradigm shift was not observed before the end of the 1980s when prey level based concepts were assigned a less important meaning. Houde

(1987), Anderson (1988) and also Bailey and Houde (1989) suggested predation to be the major factor controlling recruitment (Cowan and Shaw, 2002). Houde's (1987) "Stage Duration Hypothesis" for example holds that larvae experience lower cumulative mortality rates by predation when they reach metamorphosis due to beneficial feeding conditions and rapid growth at an early age. This includes the "bigger is better" concept meaning that larger larvae, with larger sizes at hatch or faster growth rates, have a higher chance of survival (Houde, 1987; Anderson, 1988; Pepin, 1991). It is noteworthy that size-selective mortality plays an important role in this process (e.g. Takasuka et al., 2003). Summarizing all foresaid concepts (see Fig. 1.1), Houde (2008) stated that recruitment depends on the effects of hydrographic features and predation as the critical agent of mortality, with the latter being strongly affected by temperature, nutritional condition and growth rates of larvae that are themselves determined by prey availability and other environmental factors.

1.2 Atlantic herring in the North and Baltic Seas: ecological and economic aspects

At the global level, Atlantic herring (*Clupea harengus*) is the fourth most caught marine fish species and forms one of the most thriving and economically important fisheries in the northern hemisphere with worldwide catches of Atlantic herring adding up to 1.8 million tons in 2012 (FAO, 2014). Due to this economic importance, its wide distribution and not least its intermediate trophic position between zooplankton and larger predators, stock dynamics as well as basic ecophysiological processes of early life stages have become focus of fisheries research in the last decades. Atlantic herring can be found at both sides of the North Atlantic, as well as the adjacent shelf seas (e.g. North and Baltic Sea) where it shows a unique plasticity concerning spawning time and place with populations spawning in autumn, winter or spring (Geffen, 2009; Melvin et al., 2009). The North Sea contains, next to relatively small spring-spawning components close to Norway, large autumn- and winter-spawning herring populations (see Fig. 1.2). The total catch of the North Sea autumn spawners (NSAS) was 435 kt in 2012, whereas the North Sea spring spawners off the Norwegian coast contributed only circa 10 kt in 2012 (ICES, 2013b). Catch records began already in the 1940s and due to its long history of exploitation, its fishery-induced collapse in the 1970s and its recovery until the mid 1990s, the NSAS is often considered as a model fish stock (Payne et al., 2009). The NSAS consists of the spawning components

Shetland/Orkney, Buchan, Banks and Downs, who start spawning in September in the North until January in the South along the east coast of Great Britain (Schmidt et al., 2009). Year-class strength is determined during overwintering (Nash and Dickey-Collas, 2005) but despite a large spawning stock biomass (SSB), the NSAS experienced a recent recruitment failure in the early 2000s (Payne et al., 2009). Recent studies ascribed the unprecedented low recruitment to unfavourable hydrodynamic advection, an increase in temperature and a regime shift in phyto- and zooplankton compositions during the overwinter period (Payne et al., 2009; Dickey-Collas et al., 2009; Fässler et al., 2011; Alvarez-Fernandez et al., 2012; Corten, 2013). Reduced growth rates were observed in larvae that had hatched after the regime shift around 2000, indicating changes in the quantity and/or quality of available food (Payne et al., 2013). By combining long term field data and biophysical model simulations, Hufnagl et al. 2016 substantiated the critical impact of temperature and prey-fields during overwintering on growth and survival of young herring larvae.

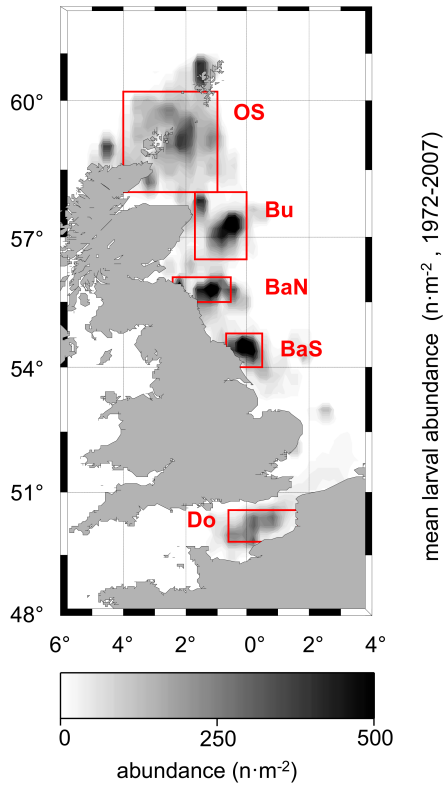

Figure 1.2: Abundances of North Sea autumn spawned Atlantic herring larvae (*Clupea harengus* L.) based on data from the International Herring Larvae Survey (larvae <10 mm) from 1977 to 2006. According to the larval abundances found, the respective spawning grounds are indicated by red boxes (OS = Orkney/Shetland; BU = Buchan; BaN = Banks north; BaS = Banks south; Do = Downs). The figure was kindly provided by Hufnagl et al. (2016) and slightly modified afterwards.

The distribution range of Atlantic herring extends from the North Sea through the

connecting straits Skagerak and Kattegat into the Baltic Sea, a semi-enclosed and brackish environment. Most marine fish species, such as Atlantic herring, have large spawning populations with low genetic drift, live in highly connected marine environments and produce widely dispersed early life stages (Ward et al., 1994; Jørgensen et al., 2005). Despite that, it was proven that a sub-species of Atlantic herring has formed in the Baltic Sea with distinctive genetic characteristics compared to North Sea stocks (Lamichhaney et al., 2012; Limborg et al., 2012). Genetic differentiation was even possible between Baltic Sea populations and was correlated to different environmental drivers such as salinity that decreases in the Baltic Sea with a strong gradient from almost fully marine conditions in the South to nearly freshwater in the North (Teacher et al., 2013; Corander et al., 2013). Although some of the mainly spring-spawning Baltic herring populations show positive trends in their SSB development, e.g. Gulf of Riga (Raid et al., 2010), SSB has generally decreased since the early 1970s mostly due to fishing mortality (ICES, 2013a). Current stock dynamics, at least in the central Baltic, were also found to be significantly influenced by inter-specific and density-dependent competition with sprat (Möllmann et al., 2004; Casini et al., 2006, 2010). The specific sub-stocks are managed separately due to area-specific differences in SSB and recruitment dynamics and total landings of Atlantic and Baltic herring caught in the transition area Skagerak, Kattegat and SW Baltic added up to 49 kt in 2012 (ICES subdivisions 22-24, IIIa) (ICES, 2013b). Catches of Baltic herring in the main basins amounted to 232 kt in 2012 (ICES subdivisions 25-32) (ICES, 2013a). Similarly to the NSAS, most of the Baltic herring populations, such as the Western Baltic Spring Spawners (WBSS), have produced several poor year-classes in the last decades and some authors have highlighted the influence of food web structure, temperature and climate-driven changes in atmospheric circulation patterns as drivers of the current situation (Cardinale et al., 2009; ICES, 2013b; Gröger et al., 2014; Polte et al., 2014).

1.3 Effects of climate-driven changes for herring stocks

Global climate has changed due to anthropogenic influence and from the 1980s onwards, temperature in the northern hemisphere has been observed to be warmer than at any comparable time during the last 2000 years (Philippart et al., 2011; IPCC, 2014). Climate indices of large-scale atmospheric circulation patterns such as the Atlantic Multidecadal Oscillation (AMO), the North Atlantic Oscillation (NAO), the Arctic Oscillation (AO)

or the Baltic Sea Index (BSI), help to identify and quantify climate-driven effects that can, next to fishing, ultimately lead to changes in biodiversity on all trophic levels (Alheit et al., 2005; Beaugrand et al., 2008; Rijnsdorp et al., 2009). These ecological “regime shifts" are defined as changes in complete ecosystems that can be classified into three types: smooth, abrupt or discontinuous (Collie et al., 2004). A recent definition describes them as “dramatic, abrupt changes in the [marine] community structure, encompassing multiple variables, and including key structural species" (Conversi et al., 2015). According to analyses from Beaugrand et al. (2015), pelagic ecosystem dynamics in the Northern Hemisphere have been strongly affected by physical/bottom-up factors such as temperature and arctic atmospheric circulation patterns since the end of the 1980s. In the North Sea, a strong connection between temperature and trophodynamic structure was shown for the last 50 years by Kirby et al. (2009) with a regime shift between 1982 and 1988, most likely due to increased sea surface temperatures and changes in wind intensity (Reid et al., 2001; Beaugrand, 2004; Weijerman et al., 2005). Analyses of changes in climate and recruitment time series show at least in parts the connection between temperature changes and reproduction success for North Sea herring (Gröger et al., 2010).

In the Baltic Sea, a transition in species composition has been observed especially in the period $1988 - 1993$ which was presumably induced by abiotic drivers and later stabilized by anthropogenic influences such as fisheries (Möllmann et al., 2009). Strongest changes were observed at zooplankton and fish trophic levels with recruitment of Baltic herring stocks being mostly influenced by temperature and to a minor degree by prey abundances and spawning stock biomass (Möllmann et al., 2008; Cardinale et al., 2009). Furthermore, annual dynamics of herring recruitment could reliably be coupled to regional climate indices such as the BSI (Gröger et al., 2014). Future climate projections for the Baltic Sea indicate, next to an overall warming trend, a considerable freshening due to increased precipitation and river run-off from the large drainage area (Meier et al., 2006; Hänninen et al., 2000). As a consequence, distribution ranges of marine fish species will shorten whereas boundaries of freshwater species will most likely expand (Mackenzie et al., 2007). Furthermore, herring populations in the northern regions of the Baltic Sea will be influenced by less sea ice and less days of frost during winter around the Baltic Sea which is supported by a number of studies (Omstedt et al., 2004; Jevrejeva et al., 2004; Jaagus, 2006; Jylhä et al., 2008). Bartolino and colleagues (2014) combined the projected climate-driven increases in temperature and decreases in salinity between $2010 - 2050$

with variables such as recruitment, predation, competition and fishing pressure for Central Baltic herring and concluded that fishery exploitation has nevertheless a strong influence on future population dynamics and acts synergistically with climate forcing. Nevertheless, a quantification of the projected habitat shrinkage and a physiological examination of the consequences for early life stages of Atlantic herring during different salinity scenarios in the Baltic Sea is needed to obtain a comprehensive picture of how climate-driven effects might alter future species distribution.

1.4 Bottom-up factors and their effects on the early life stages of marine fish

Bottom-up factors act in the direction of the energy flow, namely from the base of autotrophic producers up to the large number of heterotrophic consumers at higher levels. In the following, the effects of three bottom-up acting factors are described on both the population and the individual organism level, namely prey availability ("match-mismatch"), temperature and salinity. Generally, the impact of environmental factors at the individual level, i.e. on physiology and metabolism, can be classified, following a scheme developed by Fry (1971; 1971), into five categories: lethal, controlling, limiting, masking and directive. Lethal factors can be of any identity that restricts the range in which an individual can exist with the effect of destroying the integration of the organism outside the boundaries. Controlling factors, such as temperature, govern the metabolic rate by setting its pace whereas limiting factors, for instance the supply of oxygen, set the boundaries of the metabolic rate. A masking factor, e.g. given salinity, is an identity that prevents a second one in the organism from operating to the extent that it normally would.

Most temperate marine fish species spawn during spring with increasing water temperature and correlated to the phenology of phyto- and zooplankton blooms. Spatio-temporal mismatches of larval fish with plankton blooms, induced by annual variability in temperature or ocean currents, have been identified already a century ago to critically influence larval fish survival, recruitment and population dynamics (see chapter 1.1) (Hjort, 1914; Cushing, 1990; Platt et al., 2003; Edwards and Richardson, 2004). Matching the planktonic blooms during spring helps ensuring rapid growth that is a premise for better predator avoidance and key to successful survival. When fish larvae, that generally have poor energy reserves, miss their prey they grow slower and stay longer in the dangerous

larval stage (Houde, 1987). After an extended period of starvation (mismatch) larvae soon reach a “point of no return" (PNR), at which irreparable tissue damage has been inflicted on the organism leading inevitably to death even if prey becomes available again (Blaxter and Hempel, 1963). Depending on water temperature and individual condition this PNR can vary intra- and inter-specifically and lies around 100 °d (degree in °C x days) for first-feeding Atlantic herring larvae (Blaxter and Hempel, 1963). Numerous studies, mainly from the field of aquaculture, have reported a beneficial influence of phytoplankton on larval fish during the switch from endogenous (yolk-sac) to exogenous feeding, especially with regard to digestive enzymes and gut microbial flora, prey visibility or stimulation of appetite (Reitan et al., 1997). Traditionally, fish larvae were assumed to feed mainly on various copepod species and stages but is has been acknowledged by several authors that microzooplankton, such as protists, plays a critical role for first-feeding stages too (Lasker et al., 1970; Fukami et al., 1999; Montagnes et al., 2010). The interrelation between microzooplankton, other plankton organisms and their influence on fish larvae has been beautifully depictured by Conover (1982; see Fig. 1.3). Protozoans have been previously suggested to be part of the first food of larval herring (Spittler et al., 1990) and albeit their tiny size spectra they were considered as essential (Arndt, 1991; Friedenberg et al., 2012). Matching phyto-, micro- and mesozooplankton blooms during spring will likely increase survival chances of marine fish’s offspring and result in good year-class success, however it is not clear which specific organismal and physiological effects occur in larval Atlantic herring during a match with phyto-and microzooplankton blooms.

Although spring-spawning offers considerable advantages for the progeny, some sub-stocks of temperate marine fish species reproduce in autumn and winter months – the latter with its cold and prey-poor environments commonly associated as critical season for early stages of fish. In the North Sea, Sandeel (*Ammodytes tobianus*), European plaice (*Pleuronectes platessa*), Saithe (*Pollachius virens*), Cod (*Gadus morhua*) and Atlantic herring (*Clupea harengus*) have been observed to spawn during late autumn and winter (Daan et al., 1990 and references therein). The main hypotheses explaining the life history strategy of autumn and winter spawning generally assume lower feeding requirements as well as lower probabilities of predation during winter (Taylor and Collie, 2003a,b). Pepin (1991) also stated that predation is less important during winter since predators have reduced activity and feeding rates, whereas Hurst (2007) noted that reduced swimming activity could also lead to increased predation especially when predators are less affected

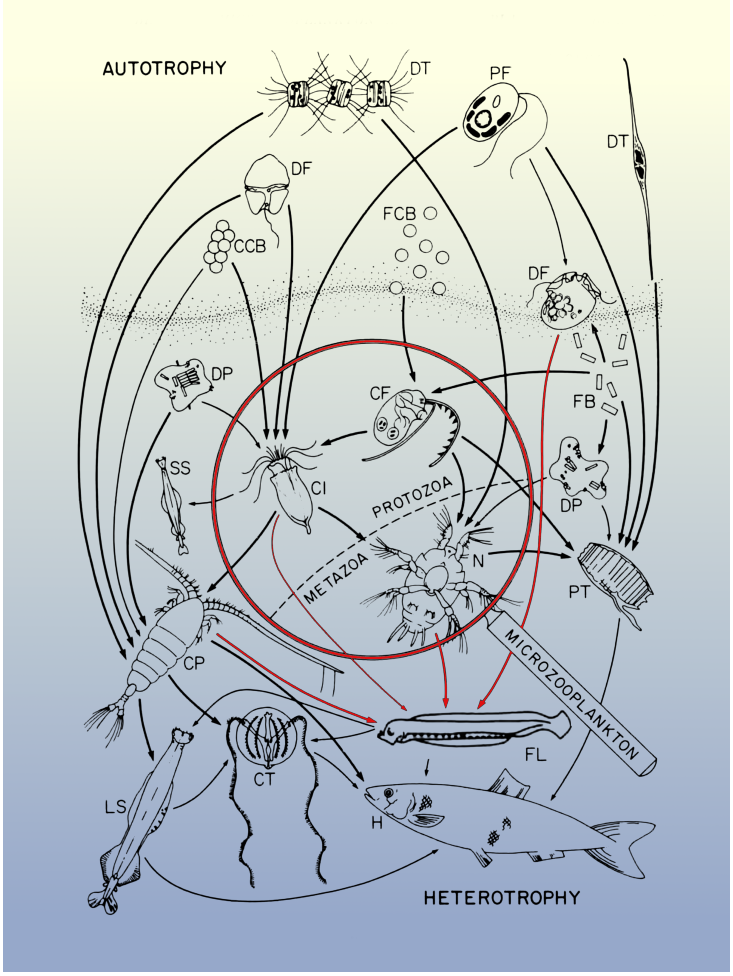

Figure 1.3: Trophic relations between planktonic organisms with a focus on microzooplankton (red circle). Heavier arrows represent pathways of greater importance. Highlighted in red are relationships affecting fish larvae. CI, ciliate; CF, colorless flagellate; PF, pigmented flagellate, N, nauplius; DT, diatom; DF, dinoflagellate; DP, detritus particle; FCB, Free-living cyanobacteria; CCB, clumped cynobacteria; FB, free-living bacteria, PT, peralgic tunicate; SS, small chaetognath; LS, large chaetognath; CP, copepod; CT, ctenophore; LF, larval fish, H, grazing fish (taken from Conover (1982) and slightly modified).

by temperature. Next to predation, thermal stress can strongly affect overwinter survival, either directly or in combination with other factors. Although metabolism decreases with temperature, metabolic expenditures can exceed energy intake, resulting in a negative scope for growth (Hurst, 2007). Several studies on post-larval stages have shown that under winter conditions small fish deplete their energy reserves faster than larger fish due to their allometry-bound higher metabolic rates and comparatively lower energy reserves (Thompson et al., 1991; Schultz and Conover, 1999; Hurst, 2007). This size-selective mortality during winter can regulate annual cohort strength (Henderson et al., 1988; Post and Evans, 1989; Conover, 1992; Schultz et al., 1998), which shows that larger energy reserves presumably increase starvation resistance and favour the survival of bigger individuals (Sogard, 1997; Cargnelli and Gross, 1997). Enhanced survival of smaller individuals was only found in few cases, where acute thermal stress superimposed starvation effects with higher survival of smaller fish being presumably caused by high protein turnover rates that might had a beneficial influence on resistance to extremely low temperatures (Lank-

ford and Targett, 2001). In contrast to overwintering post-metamorphic stages, autumn- or winter-spawned larvae of temperate fish cannot rely on internal energy resources after the absorption of their yolk-sac. Prey-deprivation in combination with cold temperatures was demonstrated by Laurel et al. (2011) to result in lower growth potential and survival of Pacific cod larvae (*Gadus macrocephalus*). Atlantic herring larvae were observed to withstand periods of prey shortage with minimal growth (Johannessen et al., 2000), but generally survival rates of larval Atlantic herring during winter are very sensible to changes in bottom-up factors, with many processes acting on the overwintering larvae as well as their adaptational response to prey scarceness still poorly studied (Hufnagl et al., 2016).

Besides shaping individual activity patterns, gene expression levels, enzyme kinetics, growth and metabolic rates, temperature strongly affects larval fish ontogeny. At warmer temperatures, larvae reach morphometric and behavioural milestones earlier than conspecifics of same age in colder water and will benefit in terms of e.g. muscle development and hence swimming performance (Leis, 2007; Fisher and Leis, 2010). The swimming muscles of teleost fish are formed by large numbers of almost identical elements - the myotomes (Sänger and Stoiber, 2001). About 90 % of the swimming muscles are fast contracting, white (glycolytic) muscles that are used for escape responses or rapid movements during foraging. Red (oxidative) muscle fibers are used for cruise swimming and a pink, intermediate tissue layer connects the other two (Goldspink et al., 2001). Temperature has a remarkable effect on the rate and type of muscle that is produced within the myotomes, and some fish are even capable of altering the composition of the myosin proteins, the most abundant muscle protein, with changes in temperature to obtain myosin chains with more power at colder temperature (Goldspink et al., 2001). During ontogeny, the swimming muscles of Atlantic herring were observed to benefit from warmer temperatures with regard to the expression of myofibrillar protein and the development of muscle innervation (Johnston et al., 1997, 1998).

Young fish larvae are not able to withstand ocean currents and are therefore considered as “passive particles", until their caudal fin is far enough developed to produce sufficient thrust to impact on their dispersal. Then, in terms of relative locomotor speed (body lengths per second), fish larvae can even outperform older stages, consistent with the general negative relationship between relative locomotor speed and body size (Bellwood and

Fisher, 2001). To measure swimming performance, standardized protocols are regularly used to determine critical swimming speeds (U_{crit}) via stepwise increases of swimming speeds over fixed time intervalls (e.g. Silva et al., 2014, 2015). In view of foraging activity or escape abilities, swimming performance represents a decisive entity for growth and survival. However, information about ontogeny of swimming performance in larval fish exists more often for warm-water (Fisher et al., 2005; Faria et al., 2009; Silva et al., 2014) compared to temperate species (Peck et al., 2006; Guan et al., 2008; Silva et al., 2015). At colder temperatures, water viscosity is higher, usually described by low Reynolds numbers. Besides that, the body length of a fish larva determines how viscous the surrounding medium is (the smaller, the more viscous). Moreover, temperature does not only affect the physical characteristics of water but also controls physiological characteristics of fish (*sensu* Fry, 1971) and differentiating between both is necessary for precise measurements of e.g. Q_{10} values (a measure of the effect of temperature on biological systems) (Fuiman and Batty, 1997).

Another major physical water property affecting fish and their offspring is salinity (S). In fully saline ($S \sim 35$) environments, fish are hypotonic, i.e. they face a continuous loss of water to the environment which they compensate by drinking a lot and excreting highly concentrated amounts of urine, whereas in freshwater fish drink less and excrete highly diluted urine (Evans, 2008). Not surprisingly, experimental quantifications of osmoregulatory costs differ widely and are estimated to lie between $10 - 50\,\%$ of the total energy budget (Boeuf and Payan, 2001). At isotonic salinity ($S = 9 - 12$; Brett and Groves, 1979; Zydlewski and Wilkie, 2013), the cost of osmoregulation is assumed to be lowest and, albeit not systematically the case, faster growth has been observed in a lot of studies (see references in Boeuf and Payan, 2001). Apart from the amounts of energy needed for osmoregulation, a strong interaction exists between salinity and growth since some hormones regulate both osmoregulatory and growth processes (see Boeuf and Payan, 2001.

Brackish waterbodies, such as the Baltic Sea, pose challenges for marine fish and can even lead to intra-specific differences in salinity adaptation and hence affect biodiversity (Ojaveer et al., 2010). The strong gradient in Baltic Sea salinity (see Fig 6.1), has supported the intra-specific formation of sub-populations of Atlantic herring (Jørgensen et al., 2005; Teacher et al., 2013). Marine fish larvae hatch without gills and, although possessing chloride cells all over their integument (Shelbourne, 1957b; Bodenstein, 2012),

they are less well prepared for e.g. living at lower salinities compared to juvenile or adult stages that posess for instance gills, the main osmoregulatory organs (see App. C). In the light of projected climate-driven changes in rainfall patterns leading to increases in river-runoff and presumably a decrease of Baltic Sea salinity of up to two units within the next century, future habitat ranges of marine fish species might shift (Meier et al., 2006, 2011). However, the specific effects of this freshening on the growth and survival of early life stages of marine fish, especially in the coastal regions used as nursery areas, are unclear.

1.5 Measuring vital rates in fish larvae

It is widely acknowledged that for early life stages of marine fish predation is generally the “agent of mortality" (Houde, 2008), albeit investigating the direct effect of predation is still highly challenging for both experimental and field studies. Even though predation might be the ultimate cause of mortality, starvation increases the larvae's susceptibility to predation or unfavourable drift (Catalán, 2003). Fish larvae have poor energy resources and during starvation they use liver glycogen, free amino acids and fatty acids for short-term energy supply, then, if present, lipids and finally structural proteins as last reserves (Ferron and Leggett, 1994 and references therein). Signs of starvation are sinking activity, lowered respiration rates, decrease of storage metabolites (and even muscle tissue) as well as a diminished production of metabolic and digestive enzymes (Ferron and Leggett, 1994). Over the past decades, several morphological, histological, and biochemical indices have been established in order to detect poor feeding conditions in larval fish and to help assess larval recruitment. Changes in body morphology and in tissue structure have already been used around the 1960s to assess the nutritional condition of fish larvae (Shelbourne, 1957a).

With improvements in technology and increasing knowledge about processes at the cellular level, biochemical indices have become more important. They include measurements of proteins, lipids and essential fatty acids, metabolic (e.g. citrate synthase and lactate dehydrogenase) or digestive (e.g. trypsin-like peptidases) enzymes as well as the ratio of RNA to DNA (Ferron and Leggett, 1994; Catalán, 2003; Rønnestad et al., 2013). Especially the standardized RNA:DNA ratio (sRD) has evolved from the 1980s onwards as a rapid, widely applicable and standardized method (Buckley, 1980; Buckley et al., 1984;

Caldarone et al., 2001, 2006). The ratio of all RNA to DNA is a proxy for the protein biosynthesis activity with the underlying assumption that DNA levels per cell remain constant, whereas the amount of RNA varies depending on the amount of protein synthesis (Meyer et al., 2012). The biggest advantage of biochemical indices is, next to their accuracy, objectivity and fast processing of large sample numbers that they quickly respond to changes in nutritional condition. Depending on temperature, changes in *sRD* or trypsin activity for instance can already be detected after 1-3 days of starvation (Clemmesen, 1994; Buckley et al., 1999; Ueberschär, 1999). Additively to the above listed indices, activity measurements have often been performed in order to describe changes or compensatory behaviour in feeding and swimming activity during exposure to variable prey densities or prolonged periods of starvation (Kiørboe et al., 1985; Kiørboe and Munk, 1986; Gallego, 1994; MacKenzie and Kiørboe, 1995; Skajaa et al., 2004; Faria et al., 2011). In order to calibrate and fine-tune condition indices, a large number of laboratory experiments with stable environmental conditions have been conducted from the 1960s on until to date to reliably estimate the individual condition of in situ sampled marine fish larvae (see App. A, Tab.A1).

Next to condition indices or digestive enzyme activities, vital rates can be assessed by respiration measurements as a direct measure of metabolic activity. According to several authors (e.g. Fry, 1947; Cech Jr. and Brauner, 2011), energetic losses due to respiration can be subdivided into four metabolic categories: i) R_{S} = standard metabolism, defined as an approximation of the minimum metabolic rate required for maintenance functions to sustain life (e.g. chemical gradients, blood circulation, ventilation). Generally, it has been established to use a lower quantile of long term measurements of unfed, resting/anesthetized individuals for its determination (Meskendahl, 2013). ii) R_{R} = routine metabolism, which includes costs for spontaneous movements. iii) R_{A} = active metabolism, the maximum aerobic metabolic rate during swimming at the greatest sustainable velocity. As a rule of thumb, active metabolism was usually estimated to be one to three times the standard metabolic rate, however more recent publications highlighted that swimming mode and species-specific life style induce a certain amount of variability in costs for active metabolism which impedes a generalization (see references in Meskendahl, 2013). iv) R_{SDA} = feeding metabolism, i.e. the energy used to digest food, also called the “specific dynamic action" or “heat increment" which Brett and Groves (1979) defined as the energy required for the “biochemical transformation of ingested food into a

metobolizable, excretable form". Finally, the metabolic rate of fish subdued to exhaustive swimming exercise for a limited period of time is named “maximum metabolic rate". The difference between maximum and minimum metabolic rates demonstrates the “aerobic scope" and is species-specific and temperature-dependent (Pörtner and Peck, 2010).

Body weight has a strong influence on metabolism and the relative magnitude of the differences between body mass and metabolism usually increases as body mass increases. This (mostly allometric) relationship between metabolic rate and body weight is hence described by a power function, aM^b, where M is body mass, a is the elevation, and b is the slope. According to Peck et al. (2012), the scaling exponent in this power function lies, with regard to marine fish larvae, between 0.5 and 1.0 but based on a multi-taxa comparison of larval fish respiration rates, this can sometimes even be exceeded ($b > 1$). However, there is some debate about the general applicability of different scaling exponents as well as the allometric power function in general, especially when results are extrapolated for larger fish (see references in Payne et al., 2015). With the help of conversion factors it is possible to directly calculate the costs of growth (16-20 μmol O_2 mg DW^{-1}) from the amount of consumed oxygen and appraise growth dynamics, prey requirements as well as the influence of the aforementioned environmental factors on the metabolic rate (Peck et al., 2012 and references therein).

1.6 Merging laboratory work and modelling efforts

Laboratory as well as field studies on marine fish larvae have proven that strong inter-individual differences for instance in growth, swimming, feeding and metabolic performances exist. For understanding ecosystem dynamics it is therefore necessary to take the lowest level of their building blocks into account: the individual organisms. Since the 1980s, first links between individual traits and system dynamics have been developed that considered inter-individual differences as well as individual adaptation capacities. In so called individual-based models (IBMs) particular traits of fish larvae were connected with key environmental factors, such as light or temperature, with fish larvae being treated as autonomous entities (Grimm and Railsback, 2005). Additively, the implementation of physical models helped project the drift of larvae to nursery areas or their retention within over time, which gave IBMs a better spatio-temporal resolution and elevated bio-

physical IBMs to today's presumably strongest tools for estimating mortality rates of marine fish early life stages (Hinrichsen et al., 2011). Nowadays, even prey-field models can be coupled to larval fish IBMs (Daewel et al., 2008) and the number of publications using biophysical IBMs has, not surprisingly, strongly increased in the last decade (Miller, 2007). Since biophysical IBMs use individual traits of larvae such as growth, swimming or foraging behaviour, assimilation efficiency and other metabolic characteristics, they strongly rely on studies that help parameterizing these intrinsic factors. Reviewing 50 IBM studies, Peck and Hufnagl (2012) stated that only one quarter of them included sensitivity analyses that explore potential sources of uncertainty and pointed moreover out that generally further biological research is needed to provide more confidence in model results. They especially highlighted larval swimming behaviour, foraging parameters and criteria correlated to growth physiology to be important for a better projection of larval fish mortality. According to Hauss and Peck (2009), currently used IBMs calculate growth rates of Atlantic herring at each time step based on balanced energy budgets as:

$$G = C\beta(1 - SDA) - R \tag{1.1}$$

where growth (G) is a function of consumed prey (C), assimilation efficiency of food (β), expenditures for digestion and protein synthesis (specific dynamic action, SDA) as well as total respiration (R), which can be subdivided into active and standard respiration. For obtaining reliable growth rates, each of these parameters should be based on results from laboratory experiments on individual larvae - which is, with regard to e.g. respiration data (Hufnagl and Peck, 2011), until today not the case which leaves improvement potential for the future. Therefore, integrative approaches combining physical/oceanographic information, prey field dynamics and information on larval physiology, swimming performance and behaviour are crucial for increasing the predictive power and the credibility of model results.

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Chapter 2

Goals and outline of the thesis

The present thesis aims at experimentally identifying prerequisites and features of Atlantic herring (*Clupea harengus*) larvae, relevant to cope with the effects of specific biotic (prey) and abiotic (temperature, salinity) environmental factors that influence larval survival. In order to attain a holistic picture of these "bottom-up" effects, a wide spectrum of cellular (e.g. digestive enzyme activity, standardized ratio of RNA to DNA) to organismal level parameters (such as swimming and foraging behaviour) was investigated. The observed results shall help improve the ecophysiological knowledge about Atlantic herring larvae, especially needed for the assessment of recruitment dynamics of North and Baltic Sea populations (e.g. by parameterizing the above mentioned IBMs). Generally, a large part of the thesis deals with the match-mismatch concept, which describes in marine environments the timing between seasonally variable micro- and mesozooplanktic prey and more stable larval fish occurrences. It was examined both, during a simulated spring bloom phenology with yolk-sac and later exogenously-feeding stages (Baltic Sea), as well as in an overwintering scenario (North Sea). Furthermore, potential climate-driven effects such as increases in temperature on the ontogenetic development of swimming performance as well as the low salinity tolerance of herring larvae of different North and Baltic Sea populations were evaluated in laboratory experiments. Four general research questions form the basis of this thesis:

1. What are the specific benefits of microplankton (microalgae and protists) for yolk-sac and first-feeding stages of Atlantic herring larvae?

2. How do exogenously feeding Atlantic herring larvae respond to unfavourable feeding conditions, i.e. during mismatches with copepod prey, and how does temperature affect their resilience?

3. To what degree affects temperature the ontogenetic development of critical swimming speeds of herring larvae?

4. Are there any inter-populational differences in low salinity adaptation in Baltic herring and which populations could be affected by the projected climate-driven freshening of the Baltic Sea?

In **chapter 3**, benefits of microplankton on yolk-sac and first-feeding stages of Atlantic herring were evaluated in an integral approach by simulating a match-mismatch situation of larval fish with autotrophic and related zooplankton blooms during spring. Hence, WBSS herring larvae were subjected to treatments mimicking naturally occurring plankton concentrations with sea water or microalgae + dinoflagellates, but without copepod prey. Measurements included biochemical analyses of digestive enzyme (trypsin) activities, biochemical condition (sRD), growth as well as swimming and foraging activity (naïve larvae were presented nauplii on a daily basis). This chapter highlights the importance of protozooplankton for early life stages of marine fish larvae and emphasizes the necessity to include regular microplankton sampling in field monitoring.

Starvation imposes not only deleterious effects during the first-feeding period of marine fish larvae but can moreover adversely alter condition throughout the complete larval phase. Therefore, the main focus in **chapter 4** was shifted to more developed Atlantic herring larvae that had successfully established exogenous feeding. Larval herring from the Baltic (WBSS) and North Sea (NSAS) were thus reared past the first-feeding stage and subsequently subjected to prey-poor environments, simulating mismatch situations during spring blooms and overwintering. Growth, metabolic rate (standard respiration), morphometric and biochemical condition factors (sRD) as well as foraging and swimming activity were measured daily to determine the resilience to prey shortage and to quantify the magnitude of degradation. The obtained results were afterwards implemented into a physiological IBM to assess effects of reduced swimming activity after prolonged periods of starvation - a parameter that was previously not well defined in the model. In this chapter, a detailed analysis of starvation-induced effects on larval Atlantic herring is presented with a depiction of energy saving mechanisms at physiological, metabolic and behavioural levels.

The survival of fish larvae is strongly coupled to their locomotory abilities: larvae that can actively impact on their dispersal have higher chances of finding prey patches and staying within them. Moreover, high maximum or critical swimming speeds help during predator escape response. In **chapter 5**, the ontogenetic development of critical swimming speeds (U_{crit}) of Baltic Sea (WBSS) herring larvae is described at three different temperatures (7,11 and 15 °C). Besides U_{crit}, growth rate, developmental stage (defined by various morphological characteristics such as the notochord flexion) and biochemical condition (sRD) were determined up to 63 days post hatch. This chapter highlights the strong effects of temperature on the developmental process of swimming capacity in Atlantic herring larvae and integrates the findings into data found in the literature to obtain a comprehensive picture from the larval to the juvenile stage.

Atlantic herring is a euryhaline species with a broad spectrum of inhabited salinities; nevertheless its larvae are limited in their low salinity tolerance due to non-developed osmoregulatory organs such as gills. In **chapter 6** the questions are addressed if there are size-related and inter-populational differences in low salinity tolerance of externally feeding larvae from different regions of the North (Banks) and Baltic Sea (Greifswalder Bodden, Gulf of Riga, WBSS). Batches of larvae were incubated at their natural salinities and subsequently acclimated to the lowest salinity (S) experienced in the selected populations (Gulf of Riga, $S = 6$). Biochemical condition and survival thresholds were investigated, the latter via acute short-term stress tests with salinities ranging from 0.5 to 5. The results are interpreted with regard to the projected climate-induced freshening of the Baltic Sea that will likely lead to a reduction in distribution areas for populations inhabiting the northern parts of the Baltic Sea.

Chapter 3

Direct effects of microalgae and protists on herring (*Clupea harengus*) yolk sac larvae

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3.1 Abstract

This study investigated effects of microalgae (*Rhodomonas baltica*) and heterotrophic protists (*Oxyrrhis marina*) on the daily growth, activity, condition and feeding success of Atlantic herring (*Clupea harengus*) larvae from hatch, through the end of the endogenous (yolk sac) period. Yolk sac larvae were reared in the presence and absence of microplankton and, each day, groups of larvae were provided access to copepods. Larvae reared with microalgae and protists exhibited precocious (2 days earlier) and $\geq 60\,\%$ increased feeding incidence on copepods compared to larvae reared in only seawater (SW). In the absence and presence of microalgae and protists, life span and growth trajectories of yolk sac larvae were similar and digestive enzyme activity (trypsin) and nutritional condition (RNA-DNA ratio) markedly declined in all larvae directly after yolk sac depletion. Thus, microplankton promoted early feeding but was not sufficient to alter life span and growth during the yolk sac phase. Given the importance of early feeding, field programs should place greater emphasis on the protozooplankton-ichthyoplankton link to better understand match-mismatch dynamics and bottom-up drivers of year class success in marine fish.

3.2 Introduction

For nearly a century, fisheries scientists have been trying to gain a firm understanding of the processes affecting larval fish growth and survival, particularly during first feeding - a period that can act as a bottleneck for larval survival (Hjort, 1914; Houde, 2008). Besides abiotic factors (e.g. temperature, hydrography), the spatio-temporal overlap with predators and prey is assumed to be the strongest selection pressure affecting the survival of the offspring of marine fish species (Bailey and Houde, 1989; Leggett and Deblois, 1994). According to Houde's "Stage Duration" hypothesis (1987), early and intense feeding is favorable since fast-growing individuals pass more rapidly through early stages most vulnerable to predation mortality and, in some years, fast growing larvae have a greater chance of survival than slower growers (Peck et al., 2012b). The potential for fast growth of marine fish larvae depends on a match in time and space between autotrophs and related blooms of zooplankton (Cushing, 1990; Platt et al., 2003; Edwards and Richardson, 2004). Marine fish larvae have poor energy reserves and a mismatch with their prey (traditionally considered to be various copepod species / stages) will soon cause them to pass

the “point of no return" (Blaxter and Hempel, 1963), when poorly fed larvae are too weak to survive even if suitable prey becomes available.

In marine fish larviculture, microalgae and/or protists (“green water") are thought to increase the visual contrast of prey (Naas et al., 1992) helping young larvae forage more effectively, supply nutrients (Moffat, 1981; van der Meeren, 1991), help establish gut microbial flora by affecting bacterial populations in rearing water (Skjermo and Vadstein, 1993; Salvesen et al., 1999), and stimulate the appetite and production of digestive enzymes (Cahu et al., 1998; Lazo et al., 2000; Overton et al., 2010). Furthermore, microalgae and protists may form a considerable portion of the gut contents of young larvae in nature (Lasker et al., 1970; Fukami et al., 1999). However, few laboratory studies have examined this protozooplankton-ichthyoplankton link in detail and none, to the best knowledge, have examining the potential direct effects of microplankton at both the biochemical and organismal levels (Peck et al., 2012b).

In this study we tested whether the passive ingestion of microalgae (*Rhodomonas baltica*) and heterotrophic protists (*Oxyrrhis marina*) by yolk sac larvae of southwest Baltic herring (*Clupea harengus*) would improve the success of early foraging of larvae on their preferred prey (nauplii of copepods; Hufnagl and Peck, 2011). Furthermore, we tested whether phytoplankton and protists benefitted larvae by extending the time between yolk-sac depletion and the “point of no return" , defined here as the time when larvae are too weak to feeding on copepods. In the southwest Baltic, the year class success of herring appears established during the larval ($< 20\,\mathrm{mm}$) phase (Oeberst et al., 2009) and successful first feeding by yolk sac larvae is one potential bottleneck to survival. The present study constitutes the first integrative (organismal- and biochemical-level) approach to explore the direct effects of microalgae and protists on the growth, development and aspects of nutritional fitness of marine fish yolk sac larvae.

3.3 Material and Methods

3.3.1 Ethical statement

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 which is part 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 offered for sale by a commercial fisherman.

3.3.2 Artificial spawning and egg incubation

Adult herring from the southwest Baltic Sea were caught using gillnets on 10$^{\text{th}}$ April 2012 in Kiel Bight by a commercial fisherman (Northern Germany; 54.36 °N, 10.16 °E) and transferred on ice to the University of Hamburg. Two hours later, the eggs from 17 females were fertilized using the milt from 12 males at 9.3 °C and a salinity of 15.0. The large number of parents was used to avoid the influence of maternal effects on offspring characteristics. The mean ($\pm$ SD) standard length (SL) and wet weight of females were 23.0 ($\pm$ 1.5) cm and 141.6 ($\pm$ 25.1) g, and males were 23.3 ($\pm$ 1.2) cm and 163.0 ($\pm$ 32.2) g. Developing eggs were transferred to 90-l tanks within a temperature-controlled room and incubated at 9.9 $\pm$ 0.2 °C and a salinity of 16.0 $\pm$ 0.4 (mean $\pm$ SD). All tanks (used here and in experiments) were semi-static with 50 % water replacements d^{-1} of filtered sea water (0.5 μm, Reiser Filtertechnik GmbH, Seligenstadt am Main), had gentle aeration and a light regime of 14:10 (L:D) was used. The embryos synchronously hatched at 13 days post-fertilization.

3.3.3 Experimental design and sampling

Within ca. 10 h of hatch, yolk sac larvae were randomly attributed to one of two treatments and carefully transferred to experimental dark-green 50-l tanks with 3 replicate tanks per treatment (1200 larvae per tank). The two treatments consisted either of only seawater (SW) or SW with a combination of the cryptophycean algae *Rhodomonas baltica* (RB, 10,000 cells ml^{-1} = 540 $\mu g\,C\,l^{-1}$) and the heterotrophic dinoflagellate *Oxyrrhis marina* (OX, 1,000 cells ml^{-1} = 196 $\mu g\,C\,l^{-1}$), abbreviated with RB + OX. Carbon content was based upon literature values (Dutz, 1998; Pelegri et al., 1999; Møller and Nielsen, 2001). The RB concentration was close to in situ estimates of total phytoplankton carbon biomass from April through May in the southwest Baltic Sea (750 to 1500 $\mu g\,C\,l^{-1}$; Wasmund and Nausch, 2012). *Oxyrrhis marina* normally inhabits shallow water tide pools (Watts et al., 2010) but was used here since it is a valuable ecological model organism that is easy to cultivate at large quantities needed for these experiments (Montagnes et al., 2010a). In all tanks, abiotic and biotic parameters were measured at least once a day including temperature (9.64 $\pm$ 0.17 °C; TLog64-USB, 10-min intervals, Hy-

grosens, Donaueschingen, Germany), salinity (16.4 ± 0.3; WTW cond3110 probe, Weilheim, Germany), and dissolved oxygen (9.4 ± 0.1 mg ml^{-1}; WTW Oxi 340i probe, Weilheim, Germany) (mean ± SD). Ammonium concentrations were always < 0.1 mg l^{-1} (Tetra NH_3/NH_4^+ kit, Melle, Germany). Concentrations of RB and OX in each tank were measured every morning using a coulter counter (Beckman Multisizer 3 Coulter Counter, Krefeld, Germany) and adjusted by adding RB and OX as needed. Larval morphometrics, nutritional condition (RNA-DNA ratios), swimming and feeding activity, as well as digestive enzyme (trypsin) concentrations were measured each day throughout the 14-day experiment.

3.3.4 Feeding and swimming activity

Each day, a total of 20 larvae was removed from each tank and carefully transferred to a 5-l opaque tank filled with 4 l of water (salinity 16.2 ± 0.7 and 9.8 ± 0.5 °C; mean ± SD). Larvae were acclimatized for 15 min then 2-d old, well-nourished nauplii of the calanoid copepod *Acartia tonsa* were added at a concentration of 2 ind ml^{-1}. This prey was chosen, since copepods in the *Acartia* genus are one of the dominant prey items for larval herring in the Baltic Sea (Hesse, 2010). Aeration was supplied to tanks which gently mixed the water. This did not appear to interfere with the ability of larvae to successfully forage for prey. Aeration was stopped during observations of swimming activity. A larva was randomly chosen and its activity was visually recorded for 2 min. This was repeated 6 times for each tank. Feeding activity was calculated as the sum of the number of aiming postures (typical s-shape) and feeding strikes performed by a larva. Pause duration was calculated as the total observation time minus the time spent moving divided by the number of stops. All measurements were done between 11.30 am and 4.00 pm with alternating observations between treatments. Larvae were allowed to forage for 4 h, after which the water level was reduced and larvae were anaesthetized with clove oil (50 ppm, 3 min) to prevent them from regurgitating or egesting prey items, and then immediately transferred to 4% buffered formalin for gut content analysis. Copepods were dissected from larval guts under a binocular microscope (Leica MZ 16, Wetzlar, Germany, 100x magnification) and counted. The *SL* of the preserved larvae was corrected for shrinkage as determined from pre- and post-preservation measurements of 20 larvae ($R^2 = 0.896$, $p < 0.001$):

$$SL(corrected) = 0.826 \cdot SL(preserved) + 0.844 \tag{3.1}$$

3.3.5 Digestive capacity

Trypsin was our primary measure of digestive capacity. It is the most abundant proteolytic enzyme in marine fish larvae (Ueberschär, 1993) which is present directly after hatching and has been used to monitoring short-term variability in feeding (Ueberschär and Clemmesen, 1992). Each day, a total of 20 larvae was collected at the same time (∼11:00 am) and immediately frozen at −80 °C. Larvae were collected from random areas of each tank using a large bore pipette. To measure trypsin activity, individual larvae were slowly thawed on ice, dipped in de-ionized distilled water and their *SL* measured. Next, the tissue was homogenized with a micro pestle in Tris-buffer (0.1 M) with $CaCl_2$*H_2O (0.02 M) (Sigma-Aldrich, Hamburg, Germany). Trypsin activity was measured spectrofluorometrically (Safas Monaco, Xenius, Monaco) in 96-well microplates (Nunc plates, VWR, Darmstadt, Germany) with Nα-benzoyl-L-arginin-4-methylcoumarinyl-7-amid as the substrate and 7-amino-4-methylcoumarin (both Bachem AG, Bubendorf, Swiss) as the fluorophore following a modified protocol from Ueberschär (1999).

3.3.6 Larval growth and condition

Twenty larvae were sampled each day from each tank to track changes in length, weight, and biochemical condition. After removing larvae from the tank, they were photographed (WILD M8 stereomicroscope, Olympus SZH and a Leica DC 300 camera, using Motic Images 2.0 software), dipped in de-ionized distilled water, and individually frozen at − 80 °C. Measurements of *SL* and yolk sac area were made using image analysis software (Image J, version 1.43u, freeware, Wayne Rasband, NIH, USA). All frozen larvae were freeze-dried (Christ Alpha 1-4 LSC, 0.200 mbar; > 16 h) and weighed (Sartorius Genius SE2 microbalance, DW ± 0.1 μg).

In order to have a sufficient amount of tissue to measure nucleic acids, 2 or 3 freeze-dried larvae were combined and the tissue was homogenized with 1 % sarcosil Tris-EDTA buffer (Sigma-Aldrich, Hamburg, Germany) and glass beads (0.2 − 2.1 mm) in a Retsch shaking mill (both Retsch, Haan, Germany). Following a modified protocol from Caldarone (2001), amounts of RNA and DNA were determined spectrofluorometrically (using the aforementioned equipment) with ethidium bromide as a fluorescence-dye and restriction enzymes to eliminate the nucleic acids (as in Peck et al., 2012a). The ratio of RNA to DNA was standardized (*sRD*) using methods outlined by Caldarone (2006) using a factor

of 2.4.

3.3.7 Statistical analysis

Data were tested for normality using Shapiro-Wilk tests ($P = 0.05$; feeding incidence data were previously arcsin transformed). Depending on the outcome, repeated measures ANOVA (RM-ANOVA) or the non-parametric alternative, the Friedman repeated measures ANOVA on ranks (Friedman-test), was performed to check for differences between replicates. For all investigated parameters, no significant differences ($P > 0.05$) were found among the 3 replicated tanks in both treatments and hence no replicates were excluded. The daily means ($n = 3$) throughout the 14 days experimental period (total $n = 42$) were again tested for normality (Shapiro-Wilk test, $P = 0.05$) and checked for significant differences between the SW and RB+OX treatments (RM-ANOVA and Friedman-test, $P = 0.05$, $df = 1$). Tukey's HSD tests were used as post-hoc tests, to control the level of the type 1 error probability. The time when 50 % of the larvae had no yolk sac was calculated for all tanks with logistic regressions. All tests and regressions were executed in Sigma Plot (Systat, San Jose, CA).

3.4 Results

3.4.1 Swimming and feeding activity

Organismal level

Larval swimming activity was relatively constant until 10 dph and then progressively declined in older larvae (longer pause durations, Fig. 3.1a). No significant differences in swimming activity were observed between larvae in the presence or absence of RB + OX (Friedman-test, $P = 0.76$). When larvae were presented with copepods, the maximum number of feeding events occurred at 7 to 9 dph (Fig. 3.1b) and was significantly higher in the RB + OX compared to the SW treatment (Friedman-test, $P = 0.01$). Copepods were found in larval gut contents of naïve larvae at 8 and 9 dph in the SW treatment and from 6 to 11 dph in the RB + OX treatment (Fig. 3.1c). No significant differences in the incidence of feeding were found between the two treatments (Friedman-test, $P = 0.10$) and the percentage of larvae that contained nauplii was generally low ($< 15\%$ of sampled larvae).

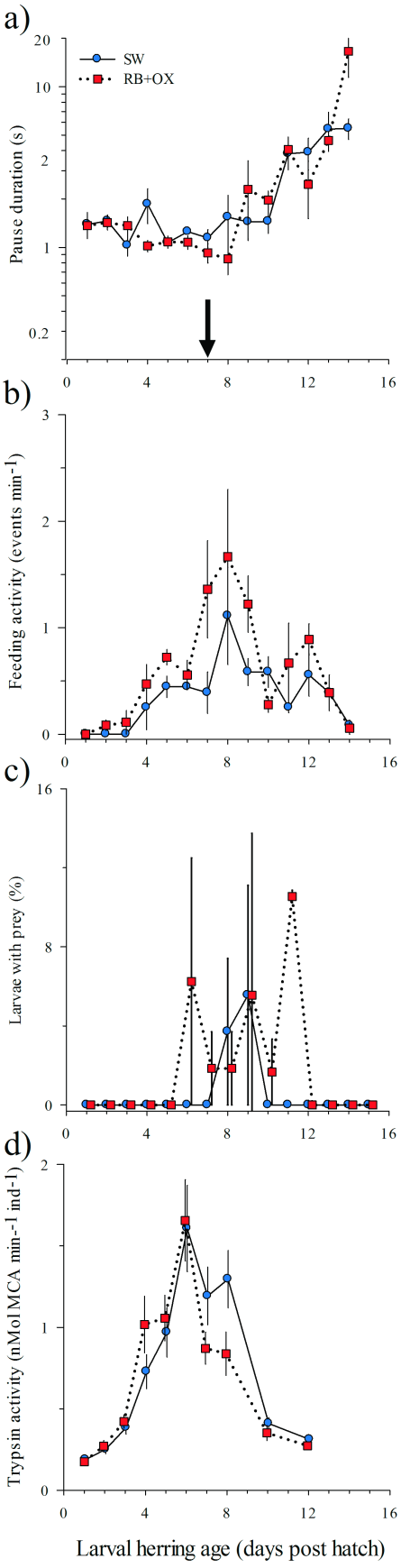

Figure 3.1: Mean ($\pm$S.E., $n = 3$ tanks) swimming activity (a), feeding activity (b), number of prey within the gut (c) and trypsin activity (d) versus age (days posthatch, dph) for yolk sac larval herring (*Clupea harengus*) reared in the absence and presence of *Rhodomonas baltica* (RB) + *Oxyrrhis marina* (OX). The black arrow indicates the age of complete yolk absorption. Significant differences between treatments were observed in feeding activity (panel b, $P = 0.01$, one-way repeated measures ANOVA on ranks).

Biochemical level

Trypsin activity ranged from 0.2 to 1.7 nmol hydrolyzed substrate MCA $\text{min}^{-1}\,\text{ind}^{-1}$ and the highest values were observed at 6 dph for larvae in both treatments (Fig. 3.1d). Although trypsin activity increased at an earlier age (4 and 5 dph) and more rapidly declined (after 7 dph) in larvae in the RB + OX treatment, no significant differences were found compared to the SW control (RM-ANOVA, $P = 0.39$).

3.4.2 Growth

Organismal level

The logistic regressions predicted that 50 % of the larvae had depleted their yolk by a mean ($\pm$ S.E.) of 4.0 ($\pm$ 0.2) and 3.8 ($\pm$ 0.1) dph in the SW and RB + OX treatments, respectively. Yolk sacs were absent in all larvae $\geq$ 7 dph.

The larvae increased their length-at-age in both treatments until complete yolk-depletion at 6 dph (Fig. 3.2a) and larval growth rates were essentially zero at $\geq$ 7 dph. Larvae in the RB+OX treatment were slightly smaller than those in the SW treatment and selection against larger individuals was greater in the RB + OX treatment (noted by the larger decrease in mean length of larvae sampled from tanks toward the end of the experiment). Weight decreased with increasing age (Fig. 3.2b) and the decrease appeared to be most rapid from 0 to 4 dph and from 8 dph until the "point of no return" at 10 dph. Between 10 and 14 dph, larvae appeared to reach a lower weight threshold. At 14 dph, the dry weight (mean $\pm$ S.E.) for larvae in SW (51.5 $\pm$ 1.6 μg) and RB + OX (45.1 $\pm$ 1.7 μg) treatments was half the initial weight-at-hatch (99.6 $\pm$ 2.4 μg).

Biochemical level

Initial *sRD* values ($0 - 4$ dph) of yolk-sac larvae were between 3 and 5 and then steadily decreased (Fig. 3.2c). No significant differences in the mean ($\pm$ S.E.) *sRD* were observed between treatments (RM-ANOVA, $P = 1.00$), and at 14 dph larvae in the SW (1.32 $\pm$ 0.09) and RB+OX (1.24 $\pm$ 0.07) treatments had similar *sRD*.

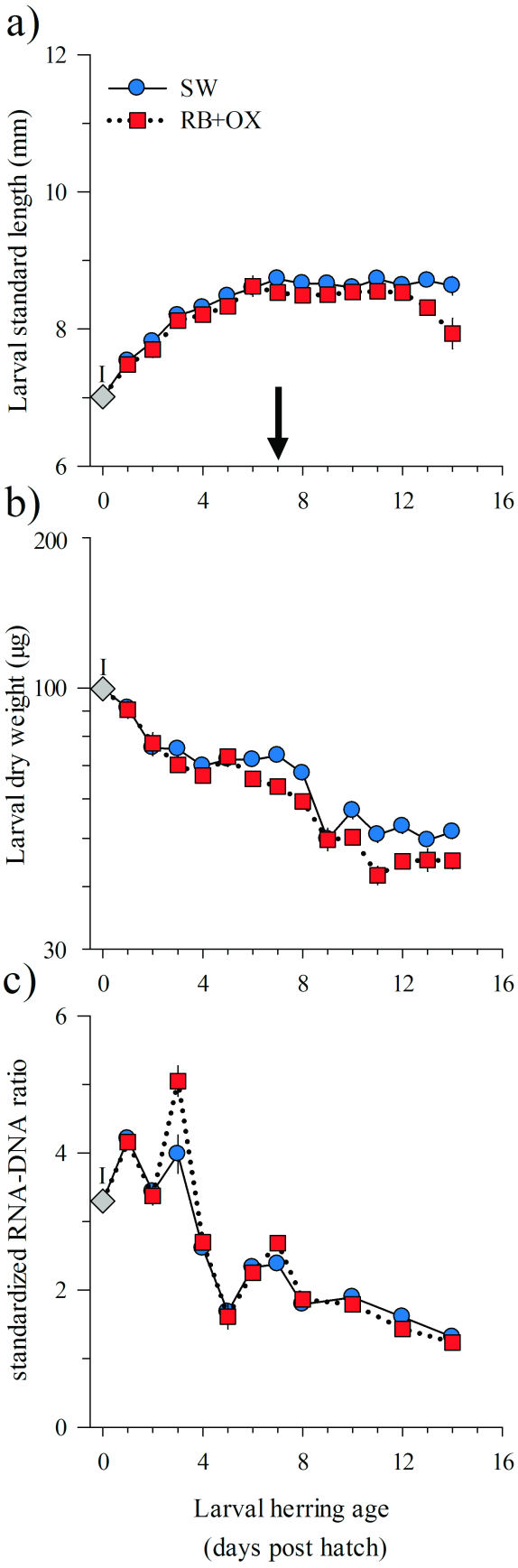

Figure 3.2: Mean (±S.E., $n = 3$ tanks) standard length (a), dry weight (b) and standardized RNA-DNA ratio (c) versus age (days post hatch, dph) in yolk sac larval herring (*Clupea harengus*) reared in the absence or presence of microalgae (RB) and protists (OX). Significant differences between treatments were observed in standard length (panel a, $P \leq 0.001$, one-way repeated measures ANOVA on ranks) and dry weight (panel b, $P \leq 0.001$, one-way repeated measures ANOVA). The black arrow indicates the age of complete yolk absorption. The letter "I" represents the initial (common) measurement at 0 dph.

3.5 Discussion

During the first days after hatch, marine fish larvae rely on their yolk reserves, a phase which can last < 1 day in warm-water species to > 30 days in colder-water species (Peck et al., 2012b). Regardless of treatment, 50 % of the herring larvae had depleted their yolk sac by an age of 4 dph, and no yolk remained after 7 dph. Larvae reared in the presence of microalgae and protists depleted their yolk sac marginally faster than those in the SW treatment. We speculate that this small difference was due to increased swimming activity in the presence of microalgae and protists leading to slightly higher energy (yolk) demands. In this species, the decline in the size of the yolk sac is needed before prey items such as copepod nauplii can pass through the esophagus (Busch, 1996) which explains the strong coupling between the decline in yolk reserves and the timing of the increase in feeding on copepods and trypsin activity. Yolk sac larvae are often capable of digesting prey using pancreatic enzymes such as trypsin prior to or at the time of first-feeding (Yúfera and Darias, 2007; Rønnestad et al., 2013). In our study, trypsin activity increased at 4 dph, coincident with the onset of feeding strikes on copepods. During this endogenous feeding phase, no clear distinction in growth or survival of larvae grown in the presence or absence of algae and/or protists was observed and larval biochemical condition (*sRD*) was most variable, likely due to the maternal transfer of RNA and differences in yolk mass (Meyer et al., 2012).

At the time of first-feeding, herring larvae initially exhibit a low percentage of attacks leading to capture (40 %, Kiørboe et al., 1985) but quickly learn how to catch copepod nauplii and other zooplankton. Phytoplankton and protists can form an adequate prey for young, small larvae of some marine fish species while in other species larger zooplankton such as copepods are required for growth and survival (Peck et al., 2012b; Llopiz, 2013). Some protists can be more energetically costly for marine fish larvae to hunt and consume compared to larger metazoans (Hunt von Herbing et al., 2001) but this drawback appears to be outweighed by the positive effect of microalgae and protists on priming the digestive system which leads to precocious and intensified feeding on larger prey (Overton et al., 2010). In their study on Atlantic cod, Overton and colleagues (2010) observed that the "window of opportunity" for feeding (when > 50 % feeding was observed among naïve larvae) was longest and initiated 2 days earlier in larvae reared in the presence of microalgae and dinoflagellates compared to larvae in SW controls. We found similar results for larval

herring, although these results should be interpreted cautiously since the total feeding incidences we observed for herring was relatively low compared to that reported by Overton et al. (2010) for Atlantic cod. When naïve herring larvae were confronted with copepods for the first time, those reared in the presence of microalgae and dinoflagellates fed more intensely and exhibited both precocious and prolonged feeding leading to a 6-day window of opportunity (6 to 11 dph) compared to only ~ 2 days (8 to 9 dph) of observed feeding by larvae in the SW treatment. Our results agree with recent reviews on the diets of marine fish larvae feeding which suggest that clupeids such as herrings, anchovies and sardines are amongst the taxa having the lowest (40 %) median feeding incidence (Peck et al., 2012b; Llopiz, 2013).

For first-feeding fish larvae, trypsin is the most important proteolytic enzyme (Rønnestad et al., 2013). Fish larvae deprived of larger prey tend to accumulate trypsin during the yolk-sac phase and reduce trypsin shortly after the depletion of yolk reserves (Pedersen et al., 1987; Hjelmeland et al., 1988). We observed a similar trend with a peak in trypsin activity at 6 dph, coinciding with the complete depletion of yolk reserves, followed by a subsequent decline in trypsin activity. The decline was more rapid in larvae exposed to microalgae and protists (RB + OX) compared to larvae reared in SW.

At some point, fish larvae must start exogenous feeding or they will suffer starvation-induced physiological decrements leading to a “point of no return" when yolks sac larvae are too weak to feed and will not survive even when prey becomes available. The ratio of nucleic acids (RNA:DNA) has been widely used as a biochemical indicator of nutritional condition (protein synthesis rate) in marine fish larvae and can rapidly decline (within 1 to 2 days) after the onset of poor feeding conditions (Buckley, 1980; Meyer et al., 2012). Well-nourished Atlantic herring larvae are known to have *sRD* between 2 and 4 (Meyer et al., 2012). Since herring larvae were not exposed to larger prey, except during the feeding trials, decrements in *sRD* and trypsin activity occurred at 60 to 80 °d (10 °C x 6 to 8 dph). This agrees with timing of the most rapid decline in nucleic acid ratios (60 °d) observed by Peck et al. (2012a) for yolk sac herring reared at 8 temperatures between 5 and 19 °C. Larval herring can survive about 140 °days ($127-153$ and $110-140$ °days) (Blaxter and Hempel, 1963; Peck et al., 2012a) on endogenous (yolk) reserves. The decrements in physiological indicators starting at 60 °d and the maximum life span of 140 °d observed in this study indicate that algae and protists add little or no direct nutritional benefit to

young larvae of this marine fish species.

3.6 Conclusions

The role of microplankton organisms have largely been overlooked in studies examining early feeding in marine fish larvae (the “protozooplankton-ichthyoplankton link"; Montagnes et al., 2010b; Peck et al., 2013) despite laboratory studies demonstrating that larvae pursue, attack and consume microplankton (Lasker et al., 1970; Hunt von Herbing and Gallager, 2000; Figueiredo et al., 2007), and field studies reporting that protists can form a large portion of the gut contents of marine fish larvae (Hunt von Herbing and Gallager, 2000; Pepin and Dower, 2007). In this study, the duration of the “window of opportunity" for first-feeding was $\sim$3-fold greater in herring larvae reared in the presence compared to the absence of phytoplankton and an heterotrophic protist. When naïve larvae were exposed to copepod nauplii, larvae reared with algae and protists attacked prey more frequently than those reared in only seawater. The presence of microalgae and dinoflagellates did not change the trajectory of growth or life span but the precocious feeding may have important implications when larger micro- and meso-zooplankton are available. Precocious feeding is likely important to growth and survival of marine fish larvae and there are potential nutritional benefits/decrements for larvae foraging on larger prey (copepods) which have consumed different types of algae and protists. Therefore, we recommend that future studies examining the role of algae and protists on yolk sac larvae larvae include additional treatments with larger prey (copepods) and that measurements be extended into the exogenously feeding period. Furthermore, to adequately assess match-mismatch dynamics of larvae in the field, measurements of microalgae and protists should be integrated within routine monitoring programs as well as both indirect markers such as stable isotopes (Pepin and Dower, 2007) and direct markers such as proteomics or genetic analyses of gut contents (Riemann et al., 2010).

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Chapter 4

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

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4.1 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 behaviour 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 behaviour 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 to 34 %). An individual-based model depicting the time course of these behavioural and physiological responses suggested that 25-mm larvae experiencing a mismatch would survive $25 - 33\,\%$ ($10,7\,^{\circ}\mathrm{C}$) longer than 12-mm larvae. Warmer temperatures exacerbate starvation-induced decrements in performance. Without behavioural and metabolic adjustments, survival of 25-mm larvae would be reduced from 8 to 6 days at $7\,^{\circ}\mathrm{C}$. Our findings highlight how adaptive behavioural 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.

4.2 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 meso-zooplankton). 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., 2012b) 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; Hufnagl et al., 2016). 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 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 to 6 °C in the spring and spawning females continue to arrive for several weeks to a month when waters can reach 12 to 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 to 11 °C in the autumn and larger, pre-metamorphic larvae experience the coldest temperatures of the year (5 to 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., 2009; Nash and Dickey-Collas, 2005; Hufnagl et al., 2016). 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., 2016). A number of shortcomings and improvements to larval fish IBMs were suggested by Hufnagl and Peck (2011) 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 modelling experiments to better understand the

behavioural and physiological responses of larvae of NSAS and WBSS herring to different feeding conditions. Growth, condition (somatic, biochemical), behaviour (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 behaviour 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.

4.3 Material and Methods

4.3.1 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).

4.3.2 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 net catches 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 Tab. 1 for incubation/rearing conditions).

4.3.3 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 Tab. 1). The larvae within the match (fed) treatment were supplied *ad libitum* concentrations of *A. tonsa* nauplii, copepodites and adults (Fig. 4.1) 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.

Table 4.1: Fertilisation, incubation, rearing and experimental conditions for both Atlantic herring populations used for match-mismatch experiments with copepod prey.

Population	Adults used (f/m)	Fert. success (%)	Light regime (L:D)	Egg incubation				Larval rearing				Match-Mismatch experiment				
				Tank size* (l)	Hatch (dph)	T (°C)	S	Tank size* (l)	Age (dpf)	T (°C)	S	Tank size* (l)	Treatments (replicated tanks; fish per tank)	Age (dph)	T (°C)	S
NSAS	24/12	75	10 : 14	90	14	8.9± 1.4	31.7± 0.4	90	0 − 18	7.4± 0.5	30.6± 0.2	50	2(3; 2000)	18−32	7.3± 0.5	31.3± 0.1
WBSS	24/12	65	14 : 10	90	13	9.9± 0.2	16.0± 0.4	90	0 − 31	10.1± 0.3	16.1± 0.6	50	2(3; 2000)	18−32	10.2± 0.3	15.7± 0.3

*50 % water replacement d^{-1}, ammonium always $< 0.1 mg\,l^{-1}$; dpf = days post fertilization; dph = days post hatch

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 behaviour after recovering from anesthesia. Measurements were made between 10:00 and 17:00 h at a temperature of 10.1 ± 0.1 °C and a salinity of 16.0 ± 0.2.

Young herring larvae are pause-travel predators which have short bouts of swimming activity followed by a pause to search for prey (Rosenthal and Hempel, 1970). To measure swimming and feeding activity, 20 larvae were gently removed from each tank and transferred to a 1-l beaker for 3 h (to empty larval guts) and then transferred to a 15-l acrylic cylinder surrounded by black plastic to reduce stress and increase the visual contrast of prey. These experimental tanks were within 1 °C of the rearing conditions and had the same salinity. After a 15-min period of acclimation to the new environment, *A.tonsa* nauplii (9 d old) and copepodites were added (total prey concentration 1.5 ind ml^{-1}) and foraging and swimming activity of a randomly chosen larva was visually measured during a 2-min period. This process was repeated 10 times for each cylinder. The number of feeding strikes and aiming postures, the time spent motionless (Pause Duration, *PD*, *s*) and the frequency of stops (Pause Frequency, *PF*, *nr* s^{-1}) were measured. Feeding activity was calculated as the sum of the number of aiming postures (the typical s-shape) not resulting in an attack plus the number of feeding strikes (where larvae pushed forward to attack a prey item). Pause duration was calculated as the difference between total observation time and time spent moving divided by the number of stops. Activity was measured between 11:00 and 17:00.

After measuring respiration, foraging and swimming activity each larva was digitally photographed for measurements of standard length ($L \pm 0.01$ mm) (WILD M8 stereomicroscope with Motic Images 2.0 software; or Olympus SZH and a Leica DC 300 camera, Image J, version 1.43u, freeware, Wayne Rasband, NIH, USA). The larva was then dipped in distilled water and rapidly shock frozen at −80 °C. Subsequently, each larva was freeze-dried (Freeze-dryer Christ Alpha 1-4 LSC, 0.200 mbar; > 16 h) and its dry weight (DW ± 0.1 μg) determined (Sartorius Genius SE2 microbalance). Fulton's somatic condition factor (S_{CF}) was calculated as:

$$S_{CF} = \varphi \cdot \frac{DW}{L^b} \tag{4.1}$$

where DW = mg, L = mm, b = the slope of the linear regression of log DW versus log L of all larvae used in experiments, and φ = a scaling factor (10^4).

The biochemical condition of freeze-dried larvae was measured based on standardized nucleic acid ratios (*sRD*) (Caldarone et al., 2001; Meyer et al., 2012). Since DNA levels per cell remain constant and the amount of RNA varies depending on the amount of protein synthesis, the ratio of RNA to DNA allows one to ascertain nutritional status. Values of *sRD* in larval fish are known to change within 1 and 3 days of starvation (Buckley et al., 1999). Spectrofluorometric measurements of *sRD* were made following a 96-well microplate protocol modified from Caldarone et al. (2001, 2006), using ethidium bromide as a fluorescence-dye and restriction enzymes to eliminate the nucleic acids (see Peck et al., 2012a).

4.3.4 Statistical analysis of laboratory data

For each parameter investigated, the measurements of the replicate tanks ($n = 3$) were tested for normality over the complete experimental duration (12 d NSAS/ 10 d WBSS; Shapiro-Wilk), homogeneity of variance (F-test), and subsequently checked for differences between them with One-Way Repeated Measures Analysis of Variance (One-Way RM ANOVA) or, if needed, by the non-parametric alternative based on ranks (Friedman-test). The significance level was 0.05 and to identify tanks that were significantly different Tukey's HSD tests were used. Generally, the replicate tanks did not differ within treatments except in measurements of *sRD* (2x NSAS, 1x WBSS) and feeding activity (1x NSAS). The respective replicates were pooled for all statistical analyses of differences between the match and mismatch treatments. Data analysis and statistical tests were performed in R (R, 2011) and Sigma Plot (Systat Software, San Jose, CA).

4.3.5 Individual-based modelling

A physiological IBM depicting the foraging and growth of larval herring was modified based on the match-mismatch laboratory experiments measuring growth, activity, metabolism and survival. The general assumptions and extensive validation of the IBM were presented by Hufnagl and Peck (2011) and Hufnagl et al. (2016). In brief, the model is based on a balanced energy budget where energy available for growth G in each time step (1 h) is determined by the energy consumed (C), which is related to foraging success, and different loss terms. The latter are assimilation efficiency (β), additional metabolic

costs associated with routine activity R as well as the digestion of a meal (specific dynamic action , SDA):

$$G[\mu g\ dw \cdot h^{-1}] = -R + \beta \cdot (1 - SDA) \cdot (C) \tag{4.2}$$

In the model, the standard respiration rate (R_{S}, $\mu \mathrm{l\,O_2\,larva^{-1}\ h^{-1}}$) was based on measurements made on herring larvae (M. Peck unpublished data) and depended on DW (μg) and T (°C) according to:

$$R_{\mathrm{S}} = 1.3921 \cdot \left(\frac{DW}{1000}\right) \tag{4.3}$$

The R_{S} was assumed to represent inactive (non-foraging) larvae. During daytime, R_{S} was increased by an activity multiplier (k), the value of which depended on gut fullness (GC) and prey concentration (pc):

$$k = 1.22 \cdot pc^{-0.1922} \cdot \left[-2 \cdot \left(\frac{GC}{GC_{max}}\right)^2 + 2 \cdot \frac{GC}{GC_{max}} + 1\right] \tag{4.4}$$

To better examine the tradeoffs between swimming/foraging activity, metabolic losses, and rates of growth, the parameterization of k was re-formulated based on the proportion of time spent swimming by larvae in match and mismatch treatments (e.g. $1 - PF \cdot PD$):

$$k = (k_{n,d}) \cdot (1 - PD \cdot PF)^6 + k_s \tag{4.5}$$

where k_s ($0.5 \cdot R_{\mathrm{S}}$) represents the minimum respiration rate of anaesthetized larvae after a long period of food deprivation; k_n (0.75), and k_d (2.5) are activity multipliers for night (routine) and day (active) respiration, respectively. In this scheme, $k_d \cdot R_{\mathrm{S}}$ represents the highest metabolic rate of an active larvae during daytime and $k_n \cdot R_{\mathrm{S}}$ represents the respiration rate of an inactive larvae at night. The value $k_s \cdot R_{\mathrm{S}}$ represents the lowest respiration rate (e.g., displayed by a starved, anesthetized larvae), while $(k_s + k_d) \cdot R_{\mathrm{S}}$ is the highest average daily respiration rate of an actively foraging larvae. Four model scenarios were conducted based on the two experiments (WBSS and NSAS) and two treatments (match, mismatch). The L, DW, respiration, PD and foraging rate were tracked for all simulated larvae. Foraging rate was calculated based on the angle of visual acuity which is related to the optimum prey size and larval length, swimming speed of larvae, and the concentration and size of prey (see Hufnagl and Peck, 2011).

The IBM was initialized using a total of 2500 larvae with L and DW drawn from normal distributions having the same mean $\pm$ SD as that measured at the start of the laboratory experiments and a condition index CI_{start} was assumed to be 1.0 ± 0.1 (mean $\pm$ SD). The CI was calculated as:

$$CI = \frac{DW}{DW_{\text{ref}}}, \text{with } DW_{\text{ref}} \text{ as } DW_{\text{ref}} = 0.018521 \cdot L^{3.6028 \cdot e^{0.006267 \cdot T}} \tag{4.6}$$

Prey concentration, temperature and the light regime matched those used in the laboratory experiments. For simulations, the size of copepod nauplii was assumed to be $180 \pm 30\,\mu$m ($210 \pm 30\,\mu$m) and adults were $500 \pm 100\,\mu$m ($600 \pm 100\,\mu$m) in the NSAS (WBSS) scenarios. The minimum threshold for survival of a larva was set to $CI = 0.5$. At the end of each day, mean values for length, dry weight, volume searched, and pause duration were calculated for the last 24 h.

4.4 Results

4.4.1 NSAS laboratory experiment (7 °C)

Prey concentrations in tanks in the mismatch treatment continuously declined with time and nauplii and copepods were absent on day 3 or 4. A few larger (adult) copepods were found in tanks on subsequent days (see Fig. 4.1). Atlantic herring larvae had growth rates of 0.08 ± 0.01 and 0.03 ± 0.01 mm d^{-1} in the match and mismatch treatments, respectively.

Cumulative length-frequency distributions (CLFDs) calculated on different sampling days were largely parallel for larvae in the match (Fig. 4.2a) and mismatch (Fig. 4.2b) treatments suggesting similar changes in size of relatively small and large larvae with time. In the mismatch treatments, the size of NSAS larvae (Fig. 4.2b) at the 80$^{\text{th}}$ percentile was relatively large compared to the initial size. The percentage increase in the size of larvae in the match treatments at the 20$^{\text{th}}$ and 80$^{\text{th}}$ percentiles was 8 and 10 %, and in the mismatch treatments was 5 and 7 %, respectively. Despite low growth rates, significant differences in length-at-age existed between larvae in the match and mismatch treatments ($P = 0.007$, One-Way RM-ANOVA, Fig. 4.3a). The linear regression of the log-transformed length-weight relationship from all larvae used in the experiments resulted in:

$$log(DW) = 3.6909\,(\pm 0.041)\,log(L) - 1.6919\,(\pm 0.046); \\ P < 0.0001, R^2 = 0.847, n = 1478 \tag{4.7}$$

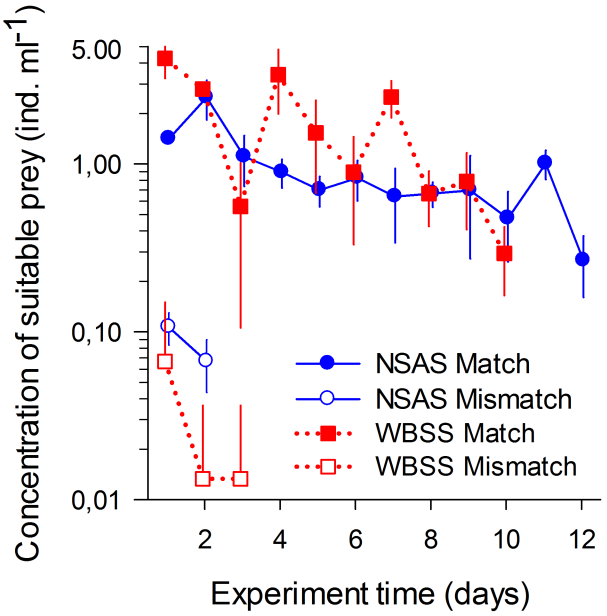

Figure 4.1: Mean ($\pm$ SD, $n = 3$) prey concentration (all calanoid copepod *A. tonsa* stages) in match and mismatch treatments for both WBSS and NSAS experiments. Few adult copepods ($2 - 5$ ind l^{-1}) survived in the mismatch treatments until the end of the experiments.

The somatic condition factor (S_{CF}) of larvae in the mismatch treatment ranged from 0.15 to 0.21 and was significantly lower than that (0.17 to 0.22) for conspecifics in the well fed (match) treatment (One-Way RM ANOVA, $P < 0.001$, Fig. 4.3c). Food deprivation of larvae in the mismatch treatment led to significantly lower sRD, starting on day 5 onward ($P < 0.001$, One-Way RM-ANOVA, Fig. 4.3e). After 10 days, larvae in the match and mismatch treatments had a mean ($\pm$ SE) sRD of 2.63 ± 0.19 and 1.98 ± 0.12, respectively.

Larvae experiencing a mismatch with prey rapidly reduced their swimming and feeding activity, compared to conspecifics held with prey. The swimming activity of larvae in the match treatment was fairly stable with time ($PD = 0.5$ to 1.1 s) whereas the swimming activity of larvae in the mismatch treatment was significantly different ($P < 0.001$, Friedman test) and characterized by fewer and longer pauses with time (Fig. 4.3b). On the final day, larvae from the match and mismatch treatments had a pause duration of 0.7 s and 26.9 s, respectively. The feeding activity of larvae in the mismatch treatment continually declined with time and was significantly different compared to larvae in the match treatment ($P < 0.001$, One-Way RM ANOVA, Fig. 4.3d). NSAS herring larvae from the food-deprived treatment reduced their initial feeding activity from 2.2 to 0.1 events min^{-1} over time, whereas larvae from prey-enriched tanks had a feeding activity between 1.5 and 3.5 events min^{-1} throughout the whole experiment.

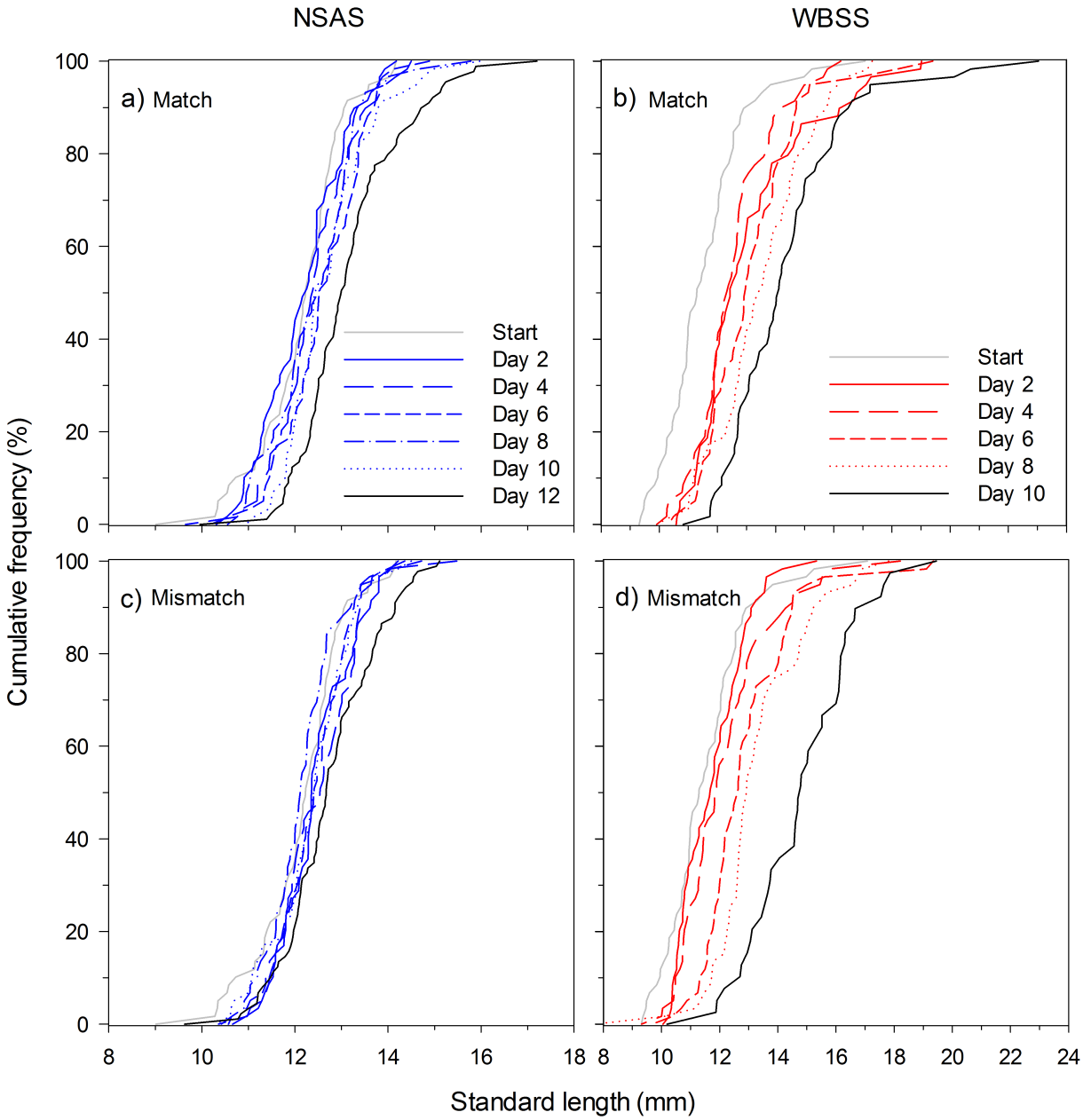

Figure 4.2: Cumulative size (length, mm) frequency distributions at the start (day 0) and every subsequent two days for NSAS (left) and WBSS (right panels) herring larvae exposed to a prey match (upper) or mismatch (lower) situation in the laboratory. Each cumulative size frequency distribution was based on 60 to 90 (NSAS) or 40 to 60 (WBSS) larvae.

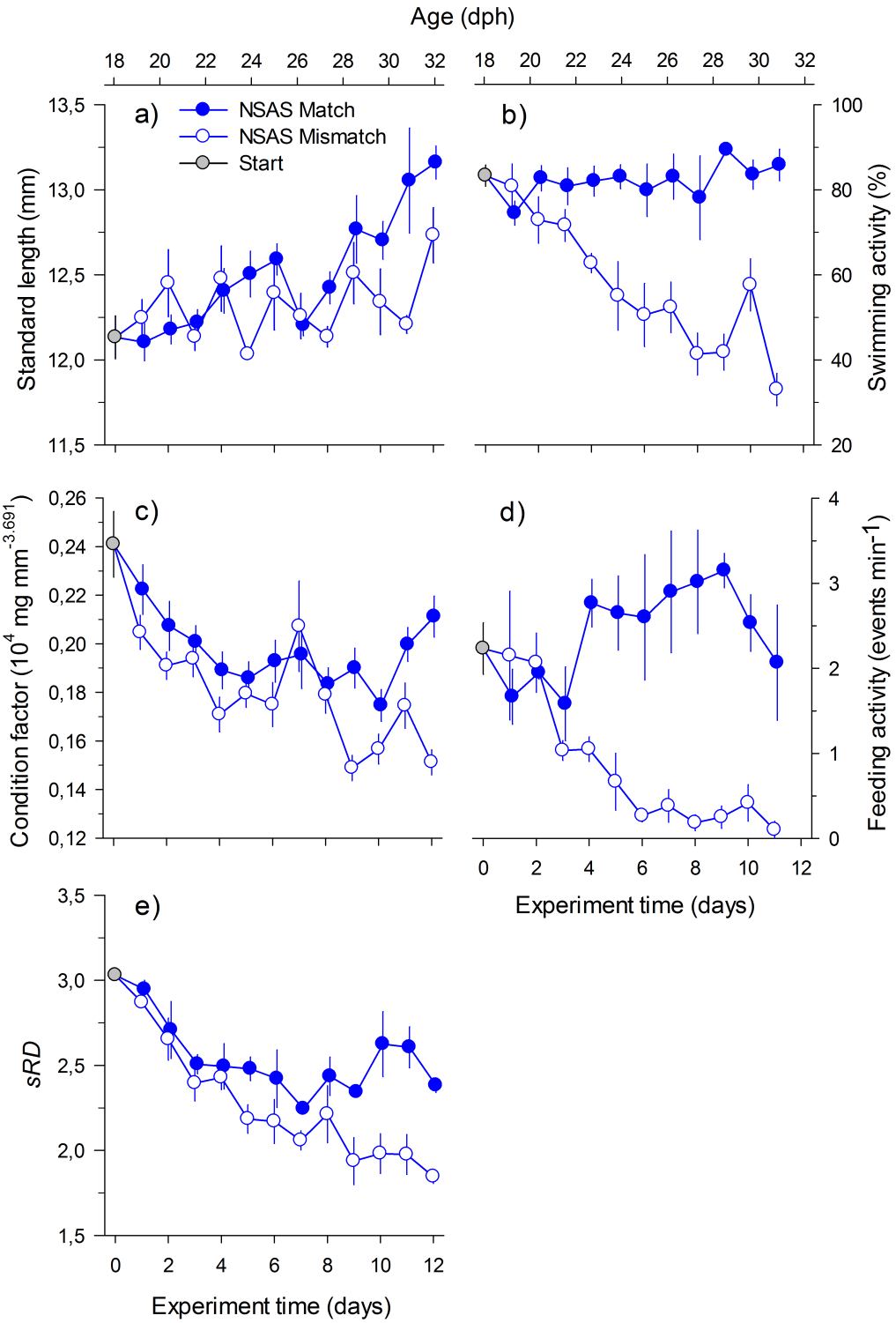

Figure 4.3: Mean (± SE) standard length (a), condition factor (b) standardized RNA-DNA ratio (c), swimming activity (d) and foraging rate (e) versus time for laboratory reared North Sea autumn spawning (NSAS) herring (*Clupea harengus*) at 7 °C. Match treatments, slightly shifted for visual clarity, have filled and mismatch treatments open symbols (each symbol: $n = 3$).

4.4.2 WBSS laboratory experiment (10 °C)

Larvae in the mismatch treatment had available prey for 1 to 3 days depending on the tank (see Fig. 4.1). A few, relatively large copepodites and adult copepods were found on subsequent sampling days. The mean (± SE) growth rate of mismatch larvae was 0.26 ± 0.01 mm d^{-1} across the experiment, a value influenced by the loss of some of the smallest larvae as noted in the shift in CLFDs after day 3 or 4 (Fig. 4.2, right panels). More specifically, in the mismatch treatments, the final size of WBSS larvae at the 20$^{\text{th}}$ and 80$^{\text{th}}$ percentiles was relatively large compared to the initial size (see Fig. 4.2d). Larvae in the match treatment had a mean (± SE) growth rate of 0.24 ± 0.01 mm d^{-1} and parallel CLFDs over time indicated similar rates of growth for all sizes of larvae. The percentage change in size of the larvae in the match treatments was at the 20$^{\text{th}}$ and 80$^{\text{th}}$ percentiles 22 and 26 %, and in the mismatch treatments 26 and 30 %, respectively. The length-at-age of larvae in the match and mismatch treatments differed significantly, with larvae from the match treatment being larger most of the days, however not on the last two days, where the selective loss of smaller larvae in the mismatch treatment had reached its maximum ($P = 0.018$, One-Way RM-ANOVA, Fig. 4.4a).

The S_{CF} was significantly higher in larvae in the match (0.20 to 0.23) compared to the mismatch (0.14 to 0.18) treatment from day 2 onwards ($P < 0.001$, One-Way RM ANOVA, Fig. 4.4c). The *sRD* continuously decreased in larvae in the mismatch treatment and, after 10 days, mean (± SE) values were 1.99 ± 0.03 which was significantly less than that (3.06 ± 0.35) in the match treatment ($P < 0.001$, One-Way RM ANOVA, Fig. 4.4e).

Larvae in the mismatch treatment decreased their swimming activity with time (particularly after day 6) whereas activity of larvae in the match treatment was relatively constant ($PD = 0.4$ to 0.7 s) (Fig. 4.4b). On the final day of the experiment, larvae in the match treatment were significantly more active ($PD = 0.4$ s) than those in the mismatch treatment ($PD = 7.6$ s) ($P < 0.001$, One-Way RM-ANOVA, Fig. 4.4b). Similarly, larval feeding activity in the mismatch treatment continuously declined from 3.5 to 0.6 events min^{-1} over time with significant differences to larval feeding activity in the match treatment ($P < 0.001$, One-Way RM-ANOVA, Fig. 4.4d). The feeding activity of fed larvae constantly ranged between 2.0 and 4.5 events min^{-1}.

The standard metabolic rate (R_S) of larvae was between 1.3 to 2.4 and 1.1 to 2.2

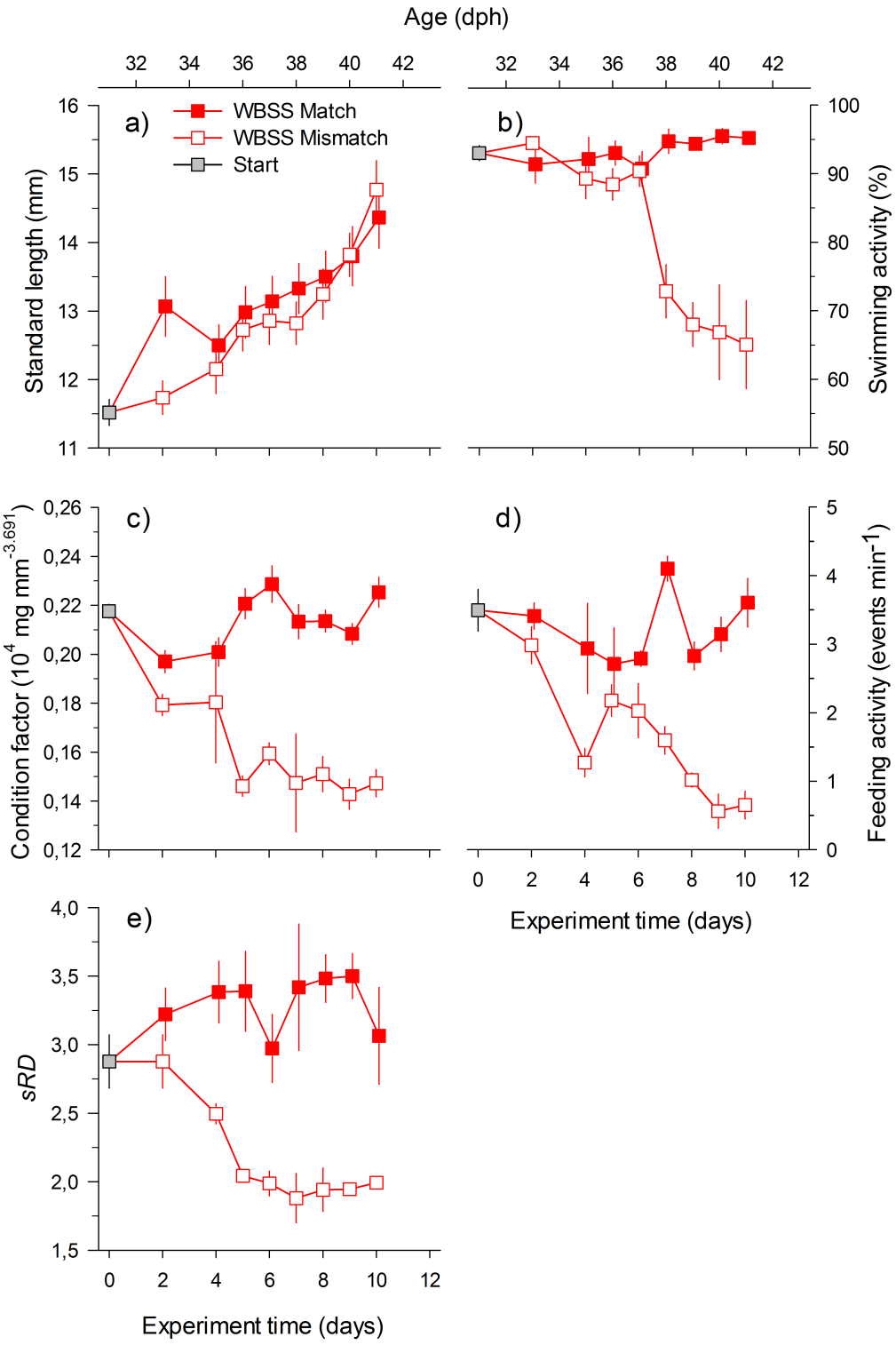

Figure 4.4: Progression of mean (±SE) standard length (a), condition factor (b) standardized RNA-DNA ratio (c), swimming activity (d) and foraging rate (e) over time for laboratory reared Western Baltic spring spawning (WBSS) herring (*Clupea harengus*) at 7 °C. Unfilled symbols = "mismatch" treatment, filled symbols = "match" treatment (slightly shifted along x-axis for visual clarity), in each case, $n = 3$ tanks

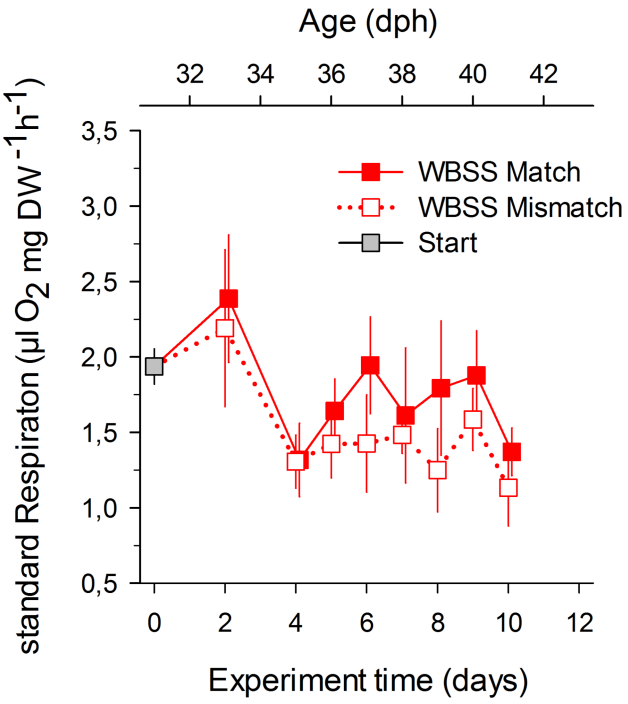

Figure 4.5: Mean (± SE) standard respiration (R_S) versus experiment time for WBSS herring larvae at 10 °C. For calculating the weight specific R_S larval weights ranged between 100 – 550 μg. Mean (± SD) number of samples averaged per symbol is 4.1± 1.1 in "match" and 4.6± 0.7 in "mismatch" treatments. See Fig. 4.4 for symbol description.

μl O_2 mg DW^{-1} h^{-1} in the match and mismatch treatments, respectively (Fig. 4.5) and R_S of larvae in the match treatment was significantly higher (P = 0.004, One-Way RM ANOVA, Fig. 4.5). The R_S of larvae from prey-poor tanks was lower compared to well-fed larvae and treatments differed between 8-25 % (days 6 – 10).

4.4.3 Individual-based modeling

Changes in pause duration (PD) of larvae in the mismatch treatment in both the NSAS and WBSS experiments were best described as an exponential increase with "physiological time" (t_{mismatch}, expressed in degree days T (°C) · experiment running time (d))):

$$PD = 0.5613 \cdot e^{0.0352 \cdot t_{\text{mismatch}}} \tag{4.8}$$

Pause frequency (PF) was more-or-less constant but declined after PD increased beyond a high threshold:

$$PF = \min\left(0.16\, s^{-1}, \frac{1}{PD}\right) \tag{4.9}$$

These experimental results, when used as input to Eq. 4.5, suggested values of $k_s = 0.5$, $k_n = 0.75$ and $k_d = 2.5$. Observed and modelled survival and growth agreed best (Fig. 6a-d) when a strong (power 6) reduction of metabolic rate in relation to swimming activity

was employed. Moreover, modelled nighttime and observed/measured R_S also agreed well (Fig. 6i+j). In both match scenarios, L and DW increased over time but at a higher rate for the WBSS scenario. In the WBSS mismatch scenario, L and DW also increased mainly due to the selective removal of smaller larvae due to starvation (see individual trajectories Fig. 6a).

The model predicted that a 25-mm larva experiencing a mismatch would survive 25 to 33 % longer than a 12-mm larva. In the model, larvae with a high CI channeled all available energy into length growth. Thus, most simulated larvae, particularly larger individuals, decreased their DW during the first two days of the simulation. Respiration rate decreased in all scenarios but for different reasons. In the match scenario larvae grew larger and, due to allometric reasons, had a lower weight-specific metabolic rate. In the mismatch scenario, metabolic losses decreased due to the increase in PD with increasing t_{mismatch}. Due to an increase in starvation time the foraging rate declined with time in the mismatch scenarios (where prey was lacking) but increased with time in the match scenarios due to increases in larval length (Fig. 6q-t). As previously mentioned, pause duration (PD) was parameterized based upon the results obtained from these experiments. In the mismatch treatments, PD increased exponentially with time in close agreement with the observed changes. At relatively cold (7 °C) water temperatures, the model predicted that 25-mm larvae would survive only 6 instead of 8 days without reducing their swimming activity and metabolic rates as observed during the laboratory experiments.

4.5 Discussion

A spatial and temporal match with suitable prey is a prerequisite for survival of marine fish early life stages. Different populations of herring have developed different life history strategies (e.g., spring versus autumn/winter spawning) which, over an evolutionary time scale, have been successful. In temperate areas, the winter period is characterized by relatively low zooplankton abundance (Hurst, 2007; ICES, 2013b) and the coldest temperatures. Temperature has a strong effect on growth and mortality rates of larvae (Pepin, 1991), consequently, NSAS herring larvae grow slowly and undergo a prolonged larval stage. Although cold temperatures also reduce predator activity, slow-growing fish have a higher probability of death due to predators and potentially due to starvation since small body size is related to higher metabolic rates per unit dry weight (Anderson,

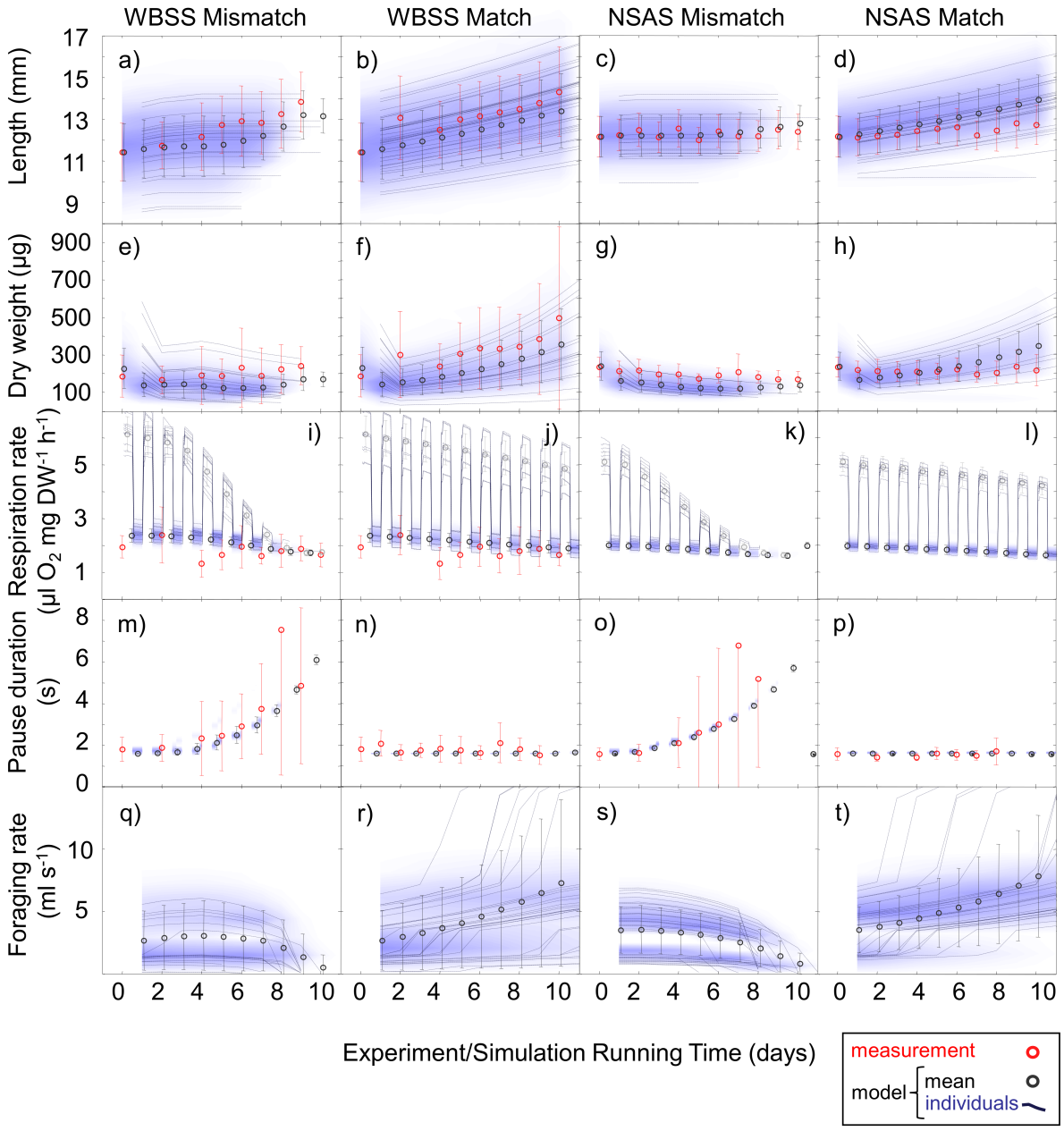

Figure 4.6: Mean (± SD) observed (red) and modelled (black) standard lengths (panels a-d), dry weights (e-h), standard respiration rates (i-l), pause durations (m-p) and foraging rates (q-t), separated by four scenarios for NSAS/WBSS experiments and "match/mismatch" treatments. Moreover, trajectories of individual larvae (blue) are plotted based on the experimentally gained data from the NSAS and WBSS laboratory trials. Note that panels k+l and q-t present the individual-based model results only. Model parameters were chosen close to experimental conditions (please be referred to the methods section for a detailed description).

1988; Sogard, 1997). Especially for young fish experiencing their first winter, obtaining a large enough body size with sufficient energy reserves is a prerequisite for survival in many fishes (Henderson et al., 1988; Schultz and Conover, 1999; Hurst, 2007).

The larvae initially loaded into the laboratory experiments (and initially simulated with the IBM) had a range in sizes-at-age and these differences had important consequences for the ability to withstand/survive a mismatch situation. Cold temperatures reduce metabolic losses which could explain the stronger, size-selective mortality observed in the mismatch treatment in the warmer (10 °C) WBSS experiment compared to the colder (7 °C) NSAS experiment. However, direct comparison of the trends in changes in CSFDs between these experiments is difficult since larvae were larger in the spring (WBSS) experiment and larger larvae are less susceptible to changes in environmental factors (Pepin, 1991). Some changes in the CSFDs between the start and the end of the experiments in the mismatch treatments may have been due to the presence of low amounts of relatively large copepod prey which could have been eaten by relatively large but not small larvae. In a previous study, Johannessen et al. (2000) reported that autumn-spawned larvae could withstand periods of prey shortage at low temperatures and survive while displaying minimal growth rates. Those results were confirmed by the present study, where larvae survived more than one week without food. In both experiments, larvae displayed clear adaptations to reductions in available prey and we discuss the tradeoffs associated with this flexible foraging and activity strategy.

4.5.1 Somatic and biochemical indicators of prey match-mismatch

Atlantic herring larvae reared under laboratory conditions or caught in the field have been reported to have growth rates between $0.13 - 0.44\ \mathrm{mm\,day^{-1}}$, depending on temperature, spawning season, day length, and the abundance and quality (size/species) of prey (Oeberst et al., 2009). Although Johannessen et al. (2000) and also Folkvord et al. indicated that herring larvae can survive at zero growth in the laboratory, such low (or zero) growth rates could not be inferred from changes in the length distributions of field-caught WBSS larvae (Oeberst et al., 2009) suggesting that either prey was always available in surplus or that slow growers were culled from the population. Although NSAS and WBSS larvae experience contrasting conditions, the ability of larvae to survive periods of low prey availability would be highly advantageous for both stocks. For example, larvae hatching prior to the spring bloom of zooplankton in the WBSS herring might be able to wait for

bloom conditions to become established as stressed by Polte et al. (2014). In agreement with previous studies (e.g. Anderson, 1988), the mismatch of WBSS herring larvae with copepod prey was associated with some degree of size-selective mortality of relatively small larvae (as suggested by changes in initial and final CSFDs). On the other hand, NSAS larvae grow into the season of lowest primary and secondary production and would need to decrease costs to successfully overwinter when prey resources are not abundant.

A mismatch with prey during the winter (NSAS) and spring (WBSS) experiments led to significant decrements in fitness and nutritional condition of larvae compared to well-fed conspecifics. Both somatic and biochemical indices have been well documented techniques to identify individuals in poor condition, although the trajectory of change (nutritional history) is not known when measurements are made on field-caught larvae (Ferron and Leggett, 1994). Generally, somatic condition factor (S_{CF}) of herring larvae decrease during starvation but direct comparison of our results with others is difficult. Unfortunately, S_{CF} has previously been calculated based on the assumption of isometric growth ($b = 3$) (e.g. Blaxter 1971; Suneetha et al. 1999) which is a false assumption for fish larvae (see Peck et al. 2005). The weight versus length relationship of herring larvae from both populations was described by a b-value of 3.69. The extended periods of prey-deprivation in the mismatch treatment resulted in an accelerated and more pronounced decrease in somatic condition at 10 °C (WBSS) compared to 7 °C (NSAS). In the WBSS, differences in condition were apparent already after 5 days of prey mismatch compared to 9 days in NSAS. We speculate that initial decline in the S_{CF} of well fed (match) NSAS larvae was likely due to prey size (the larvae could consume larger prey when offered later in the experiment). Prey size was not a factor in the WBSS match treatment and S_{CF} remained high throughout that experiment.

Previous work on herring larvae reported minimum values of biochemical condition (RNA-DNA ratios) ranging from 1.0 to 2.5 (Suneetha et al., 1999; Skajaa et al., 2004). Most previous studies employed different methodologies and a method of standardization procedure was published by Caldarone et al. (2006). Using that standardized approach Illing et al. (see chapter 3) reported a minimum threshold sRD of 1.3 for first-feeding larvae. Not all individuals in the population (even when reared in the same tank) are in the same condition and mean values can, therefore, be misleading, particularly when attempting to ascertain rates of change during starvation. Meyer et al. (2012) developed

an approach using percentiles and re-analyzed the *sRD* data stemming from starvation trials previously conducted at different temperatures using the larvae and young juveniles of eight fish species. Using the *sRD* data from Folkvord et al. (2009) collected on herring larvae unfed at initial ages of 14, 28 and 42 dph at 6 °C ($227 - 906\,\mu g\,DW$) and 10 °C ($207 - 1739\,\mu g\,DW$), Meyer et al. (2012) calculated a lower threshold *sRD* of $1.5 - 2.3$ and $1.0 - 2.3$ respectively. Based on that re-analysis, the time to death was between $45 - 67$ and $66 - 90$ degree-days (°C days) at 6 °C and 10 °C, respectively. These results compare well to the present study, where starved NSAS (initial age 18 dph, $167 - 298\,\mu g\,DW$) and WBSS (initial age 31 dph, $168 - 499\,\mu g\,DW$) herring larvae have lower threshold values of *sRD* of 1.6 at 7 °C and 1.4 at 10 °C and a time to death of 38 and 54 °d, respectively.

4.5.2 Behavioural responses and prey match-mismatch

After exogenous feeding has become well established, herring larvae are known to be cruise predators that search for prey while they swim (Rosenthal and Hempel, 1970), and similarly to findings of Munk and Kiørboe (1985), larvae in prey-poor environments changed their swimming behaviour from normal, slow meandering to more infrequent use of abrupt swimming to save energy (and simultaneously avoid sinking). Colder temperatures have a strong influence on water viscosity as well as the physiology of poikilotherms. Increased water viscosity can sometimes exceed the benefits from decreased metabolic costs at colder temperatures (Wieser and Kaufmann, 1998; Hunt von Herbing, 2002). Moreover, small Atlantic herring larvae (10 mm *L*) have been shown to be more affected in their swimming ability by colder water than larger ones (18 mm *L*) (Fuiman and Batty, 1997). Swimming performance can also decrease with cooling due to decrements in the efficiency of muscles (Hunt von Herbing, 2002). In larval herring, muscle-contraction was observed to be reduced by one third between 5 and 15 °C (Batty and Blaxter, 1992).

The observed values of pause duration for well-nourished NSAS larvae at 7 °C ($0.5 - 1.1$ s, $12 - 13$ mm *L*) and WBSS larvae at 10 °C ($0.4 - 0.7$ s, $12 - 14$ mm *L*) are similar to values reported by MacKenzie and Kiørboe (1995) for well-fed WBSS herring larvae at 7 °C ($1.8 - 2.4$ s, 9 mm *L*) and Hauss (2008) (1.2 to 2.0 and 0.8 to 1.0 s for 10 and 15 mm *L*, respectively). Similar to previous observations conducted at 8 to 12 °C using larvae of similar age, individuals experiencing a match with prey were actively swimming between 80 and 100 % of the time (Blaxter and Staines, 1971). At low prey concentrations, larval activity increases likely due to increasing search effort (Munk and Kiørboe, 1985). Prey-

deprived herring larvae significantly decreased their swimming and feeding activity likely due to the effects of starvation (see references in Gallego, 1994). In the present study, higher PD and reduced feeding activity were presumably an energy saving mechanism or a sign for approaching the "point of no return" (PNR), which describes the threshold associated with the irreversible loss of the ability to forage and survive even if prey becomes available (Blaxter and Hempel, 1963). Studies on other temperate fish species suggested that decreases in swimming activity as well as cold temperatures were both beneficial for energy conservation and, hence, survival during prey shortages (Johnston and Mathias, 1996; Sogard and Olla, 1996). The IBM was able to depict these behavioural responses and simulations suggested that immediate decreases in activity were required to balance metabolic costs as observed in the loss of dry weight of food deprived larvae.

The IBM suggested a clear survival advantage of reducing swimming and metabolic rates when prey resources were scarce; herring larvae with these adaptations could survive about 30 % longer than larvae that maintained high rates of swimming. Standard respiration (R_S) is defined as the energy cost for self-maintenance, and depends on body mass, phylogeny and temperature as well as other environmental factors (Burton et al., 2011; Peck and Moyano, In Press). Individuals with low metabolic costs may better survive periods of prey mismatch (Burton et al., 2011) and evidence suggests that fish have the capacity to adapt their metabolic expenditure to the level of available prey. For example juvenile catfish *Siluris meridionales*, starved for 15 days, significantly down-regulated their R_S compared to individuals that were starved for $2-5$ days (Fu et al., 2005). In another example, O'Connor (2000) reported that juvenile Atlantic salmon (*Salmo salar*) down-regulated their R_S during food deprivation and up-regulated it when prey became available again. That study also noted distinct inter-individual differences in the ability to down- and up-regulate R_S. Kiørboe et al. (1987) found that oxygen uptake of anaesthetized herring larvae was increased with increasing feeding history, i.e. lower respiration rates were observed in prey-poor environments. On the other hand, Houlihan et al. (1995) reported no connection between prey intake and rates of oxygen consumption of larval herring. Our results from WBSS herring larvae suggest a down-regulation of the R_S when larvae were exposed to a mismatch with prey for several days which agrees well with the decreases in swimming activity in those larvae. It is important that models depicting short-term growth dynamics in dynamic prey environments incorporate such flexibility in the behavioral and metabolic responses of individuals to recent feeding.

The re-formulated IBM suggested that a rapid and strong response in behaviour to a mismatch situation markedly increased survival. If no behavioural adaptation was included survival times were reduced by about a third. The conditions simulated in the laboratory and in the model were an extreme situation and, although mismatch situations undoubtedly occur in nature, it is unknown whether larvae typically endure one week or longer with no (zero) prey. However, larvae clearly have a tradeoff between active searching with increasing energy demands and increased probability of encountering prey versus little activity with low energy losses and decreased probability of prey encounter. During winter (e.g. for NSAS) where turbulence and mixing and thus “passive" encounter with prey is generally high, a low energy/ambush feeding strategy might be just as successful as an energy-demanding search strategy. In spring (e.g. WBSS), increases in stratification and a reduction of turbulent mixing might favor a more energy-demanding active foraging strategy. Analyzing these differences between populations and seasons is only possible if these basic behavioral mechanisms are understood and included in simulations. The approach of a direct coupling of experimental results and modelling forms a valuable first step (Peck and Hufnagl, 2012).

In conclusion, Atlantic herring larvae from populations in the North and Baltic Sea display adaptive changes in swimming activity and metabolism concomitant with changes in somatic and biochemical condition. Mismatch situations with prey lead caused larvae to decrease swimming activity within one to two days and to decrease standard metabolic rate several days later. Larval IBMs directly linking feeding history, behavior and metabolic costs appear most suitable for examining tradeoffs in behavior in different prey environments. Future laboratory experiments should examine how physical factors (temperature and turbulence) interact with biological factors (prey abundance and quality) to better simulate the consequences of match-mismatch dynamics to the survival and growth of marine fish larvae.

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Chapter 5

Thermal impacts on the ontogeny of critical swimming speed in Atlantic herring larvae

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5.1 Abstract

Increases in swimming ability have a profound influence on larval fish growth and survival by rising feeding behavior, predator avoidance and transport success. Understanding how development and environmental factors combine to influence swimming performance is particularly important during the transition from the viscous to inertial environment. Here we studied for the first time the development of critical swimming speed (U_{crit}) of Atlantic herring (*Clupea harengus*) throughout larval ontogeny at three different rearing temperatures (7, 11, 15 °C). Temperature had a significant effect on growth rates (from 0.21 at 7 °C to 0.34 mm $\cdot$ d^{-1} at 15 °C), and on larval morphology (higher dry weight and body height and, faster development at warmer temperatures). These morphometric differences influenced swimming performance, which increased exponentially after yolk-sac absorption, faster at warmer temperatures. Larvae entered the transition to an inertial environment (Reynolds numbers $\geq$ 300) at sizes between 14 (15 °C) and 17 mm (7 °C). Inter-individual differences in U_{crit} were not related to size-at-age or nutritional condition measured as *RNA/DNA* or *DNA/DW*. Compiling the data from this and previously published studies on Atlantic herring, four phases in U_{crit} are identified: 1) yolk-sac (<0.6 cm $\cdot$ s^{-1}), 2) preflexion ($1-4$ cm $\cdot$ s^{-1}, thermal effects not constant), 3) postflexion (up to $6-8$ cm $\cdot$ s^{-1}, $Q_{10} \sim 1.8-2.0$), 4) juvenile-adult period ($20-170$ cm $\cdot$ s^{-1}, thermal effects not constant). These results on swimming ontogeny are very useful not only for parameterizing individual-based models linking biophysical transport and larval herring growth and survival, but also provide a strong basis for latitudinal comparisons of the swimming capacity of marine fish.

5.2 Introduction

Understanding how swimming ability changes with ontogeny can yield considerable insight on how various processes may interact to affect the survival of marine fish early life stages. Increases in swimming capacity confer distinct survival advantages to larvae in terms of better foraging capacity (e.g larger water volumes searched, faster attacks, Munk and Kiørboe 1985) and increased ability to avoid predators (faster escape responses, Yin and Blaxter 1987). A critical developmental stanza is the period of time when larvae become strong enough swimmers and they are no longer “passive" with respect to their dispersal and transport. Currently the majority view is that fish larvae, at least at some advanced

developmental stage, can modify their dispersal trajectories through behavior (Leis, 2015). For example, coral reef larvae display directional swimming and can maintain extraordinary sustained speeds of up to $30 - 50$ body lengths (bl) s^{-1}, more than double those of great swimmers such as adult tunas or swordfish (Bellwood and Fisher, 2001; Nilsson et al., 2007). However, the larvae of cold-temperate species are relatively poor swimmers (maximum sustained speeds up to $4 - 5$ bl s^{-1}) and pre-metamorphic (small) larvae are, in most cases, unable to swim against prevailing water currents (generally $10 - 15$ cm s^{-1}, Fisher et al. 2005; Leis 2010; Peck et al. 2012). These differences in swimming endurance and speeds are not merely due to differences in water temperature but also (and mainly) due to differences in development, morphology and life history strategies: e.g. coral-reef fish larvae often perform directional swimming in response to environmental cues (e.g. odor, sound) to recruit back to reefs (Atema et al., 2015), whereas cold-temperate species may use other swimming behaviors such as selective tidal transport to be effectively transported into estuaries forming juvenile nursery areas (Boehlert and Mundy, 1988).

Temperature is arguably the most important environmental factor setting the pace of various physiological processes such as the rate of metabolism which alter swimming capacity (Fry, 1947; Beamish, 1978). Temperature not only influences swimming directly, via physical changes in the water properties (i.e. viscosity; cold waters are more viscous) but also indirectly via physiological and developmental changes (e.g. changes in muscle contraction and fin development, Johnston et al. 2001). Changes in viscosity are especially meaningful for larvae from cold-temperate and polar waters living at low Reynolds numbers (Re). Relatively few studies have been conducted on the swimming of larvae of cold-temperate and polar species. However, these larvae offer a great opportunity to evaluate the ontogeny of swimming capacity as larvae transition from a viscous to an inertial environment. This transition begins at intermediate Re of $\sim$ 300 and be completed when $Re > 1000$ (Leis, 2006, 2010). For small larvae of cold-temperate species ($Re < 450$), changes in water viscosity as opposed to physiological responses are thought to have a stronger effect on routine swimming speed (Fuiman and Batty, 1997; Hunt von Herbing, 2002). Previous studies on larval fish exploring thermal effects on swimming behavior (e.g. muscle contraction, tail beat frequency) did not accounted for thermal history. However, early thermal history (before first-feeding) has a significant impact on larval development, which can lead to phenotypes with different escape responses (Johnston et al., 2001). The controlling impact of temperature can then uncouple growth and

development, which has been fairly well studied in fish, where increased temperatures generally lead to faster growth and development and a shorter time to reach metamorphosis (Chambers and Legget, 1987; Johnston et al., 2001). Several of the variable structures in those morphological phenotypes relevant to fish locomotion, include, among others, development and innervation of dorsal and anal fins, notochord flexion and changes in the recruitment of red and white muscle fibers. These phenotypic effects may be persistent up to adulthood in some species (Scott, 2012).

Measuring the critical swimming speed (U_{crit}) is the most common approach to estimating swimming performance in fish (Brett, 1964; Fisher et al., 2005; Plaut, 2001). This method is easy to use, repeatable and allows one to quantify how “athletic" individual fish are within a group. Also, U_{crit} has been proposed as better estimator of the maximum speeds that a larva can achieve to alter their position in the water column, and escape from predators, than burst swimming (U_{max}), which is an anaerobic, very fast (seconds) response (Fisher and Leis, 2010). Relatively few measurements have been made of the U_{crit} for larvae of cold-temperate and polar species, probably due to the poor swimming abilities of larvae from higher as opposed to lower latitudes. Therefore, other methods such as measuring and comparing U_{max} during escape responses (Batty et al., 1993; Johnston et al., 2001) or routine swimming speeds (Fuiman and Batty, 1997; Peck et al., 2006; Maneja et al., 2015) at different body sizes are more common for these cold-water species. Unfortunately, data derived from different measurement techniques are challenging to compare either within species or across taxa and/or latitudes. The effect of environmental (mainly temperature), morphological (size, shape) and physiological factors (growth) on U_{crit} has been thoroughly explored for the larvae of coral-reef fishes (Green and Fisher, 2004; Fisher et al., 2005; Leis, 2010). However, the effect of changes in nutritional condition on swimming ability has been rarely examined on larvae from any latitude (but see Faria et al. 2011b; Silva et al. 2014, 2015). Understanding whether and how swimming capacity changes between poorly and well-nourished individuals may be important to understanding how bottom-up (starvation) and top-down (predation) processes interact to influence survival and recruitment strength.

In this study, we explored the ontogeny of swimming capacity of Atlantic herring (*Clupea harengus*) larvae reared at three different temperatures. Despite being a particularly well studied fish species (Geffen, 2009), this is the first study to measure changes in swim-

ming capacity (U_{crit}) throughout the larval period in Atlantic herring. Previous work on herring larvae has focused on relative changes in routine swimming (Munk and Kiørboe, 1985; Maneja et al., 2015) or escape responses (Yin and Blaxter, 1987; Batty et al., 1993) among treatments (e.g. changes in prey concentration, pCO_2, viscosity) containing similar-sized larvae. Estimating the increase in swimming capacity through the larval stage is vital for quantifying the size at which larvae could actively avoid dispersal (Re $300 - 1000$). Such information not only provides a stronger basis for latitudinal comparisons of the swimming capacity of marine fish, but also is important for parameterizing individual-based models examining biophysical transport and the foraging and growth of Atlantic herring larvae (Hufnagl and Peck, 2011; Hufnagl et al., 2016).

5.3 Material and Methods

5.3.1 Ethics

Animal handling and experiments were done 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. Adult herring were bought to a commercial fisherman, therefore no special permission was required.

5.3.2 Strip-spawning and larval rearing

Western Baltic spring-spawning (WBSS) adult herring were obtained from a local fisherman in the Kiel Fjord (54.36°N, 10.13°E) on April 22$^{\mathrm{nd}}$ 2013, and transported on ice to the Elbe Aquarium (University of Hamburg). Once in the laboratory, eggs were extruded onto plastic plates and fertilized with activated milt for 10 min at 8.5 °C and a salinity (S) of 18.5. In order to avoid differences in the offspring stemming from maternal/parental effects, 16 females and 16 males were used. Mean ($\pm$ SD) standard length (SL) of females and males was 26.1 (1.5) and 26.1 (1.6) cm, respectively, and the corresponding wet weight (WW) was 148.1 (21.4) and 149.8 (25.6) g, respectively. After incubation, the egg plates were transferred to 90-L tanks where embryos were incubated at 10.2 (0.3) °C at a $S = 16.9$ (0.1), and a light regime of 14 L:10 D. Filtered (0.5 μm, Reiser Filtertechnik GmbH, Seligenstadt am Main) water was renewed at 50 % d^{-1}. After 24h, fertilization success was ca. 55 %. Hatching occurred at night 12 days after fertilization (daf) and

was synchronized using a 48 h period of constant light during the prior two days ($10-11$ daf).

After hatching, ca. 2500 larvae were transferred into each of six, dark green, 90-L rearing tanks (50 % water renewal $\cdot\,\mathrm{d}^{-1}$). Larvae were adjusted $0.5\,^{\circ}\mathrm{C}\cdot\mathrm{d}^{-1}$ to one of three temperatures (7, 11 or 15 °C), with 2 replicate tanks at each temperature. These new temperatures were reached by 12 days post-hatch (dph). The mean ($\pm$ SD) temperature of tank 7A, 7B, 11A, 11B, 15A and 15B was 7.8 (0.3), 7.2 (0.4), 11.0 (0.6), 11.0 (0.4), 15.0 (0.3) and 15.0 (0.3) °C, respectively. In all tanks, the salinity was $\sim$16.5 with minimal fluctuation (range 1.0). During four days ($43-47$ dph), a technical problem occurred and the larvae at 7 and 11 °C, experienced slightly warmer water temperatures fluctuating daily between 9.5 and 12.0 °C, and 11.2 and 13.9 °C, respectively. Larvae were reared in the presence of algae (*Rhodomonas baltica*, 10,000 cells mL^{-1}) and dinoflagellates (*Oxyrrhis marina*, 1000 cells mL^{-1}), which promote early feeding and faster growth (Illing et al., 2015). After 2 dph, natural prey (nauplii from a calanoid copepod *Acartia tonsa*) was introduced in the tanks. Later copepod stages (copepodites and adults) were added when larvae were 9 and 12 dph, respectively, and supplemented with small amounts of brine shrimp nauplii (*Artemia salina*) from 16 dph.

5.3.3 Swimming and morphometric measurements

Every $5-7$ days, larvae were sampled from each tank to assess growth, changes in morphology and critical swimming speed. On each sampling day, $5-10$ larvae were randomly removed from a tank, and the U_{crit} of each larva was estimated. The swimming chamber was designed following Stobutzki and Bellwood (1994, 1997). See Faria et al. (2009) for further details. Water temperature and salinity was measured prior to each test and the conditions were similar to those in the rearing tanks ($\pm\,0.3$ °C, $\pm\,0.3$ salinity). Larvae were acclimatized for 5 min at the slowest water current speed ($0.6\,\mathrm{cm\,s}^{-1}$). Those that showed signs of stress after this period were removed and replaced. After this acclimation time, the water speed was incrementally increased in $\sim 1\,\mathrm{cm\,s}^{-1}$ steps from (0.6 to $9.5\,\mathrm{cm\,s}^{-1}$) every 2 min until the larva was unable to swim for 2 min at a given speed. The U_{crit} was determined following Brett (1964)

$$U_{\mathrm{crit}} = U + (t \cdot t_i^{-1} \cdot U_i) \tag{5.1}$$

where U is the penultimate speed a fish was able to maintain; U_i is the velocity increment ($1 - 1.2\,\mathrm{cm\,s^{-1}}$, depending on the level); t is the time spent swimming at the final velocity increment; and t_i is the time interval for each velocity increment (2 min).

After the swimming test, larvae were anesthetized (metomidate, Aquacalm, Syndel laboratories, Canada), digitally photographed under a stereomicroscope (Leica MZ 16, Wetzlar, Germany), shock frozen, and stored at -80 °C. Morphometric features were measured using ImageJ (Rasband, 2014) including standard length (SL), body height at the head (BH), height of the caudal peduncle (Hcp), and flexion angle ($Fang$). Considering these morphometric measurements, the stage of each larva was categorized according to Doyle (1977): 1) yolk sac larvae, 2) yolk sac absent, dorsal fin differentiating from primordial fin, 3) flexion begins (notochord turns dorsally at its posterior tip), 4) postflexion larvae, pelvic fins are visible. For further details on the sub-stages, see Doyle (1977). Finally, larvae were freeze-dried (Christ Alpha $1-4$ LSC, 0.200 mbar; >16 h) and weighed (Sartorius Genius SE2 microbalance, $DW \pm 0.1\mu$g).

The Reynolds number, Re, was calculated for each larva according to Webb and Weihs (1986):

$$Re = U_{\mathrm{crit}} \cdot SL \cdot \nu^{-1} \tag{5.2}$$

where U_{crit} and SL were specific for each larva and ν is the kinematic viscosity of seawater at a salinity of 16.5 ($1.45 \cdot 10^{-2}$, $1.30 \cdot 10^{-2}$ and $1.17 \cdot 10^{-2}$ $\mathrm{cm^2\,s^{-1}}$ at 7, 11 and 15 °C, respectively).

5.3.4 Biochemical analysis (*RNA/DNA*)

The concentrations of nucleic acids were measured on randomly selected individuals used in U_{crit} trials to explore the potential effect of nutritional condition on swimming performance. A standard protocol was used (Caldarone et al., 2001), with slight modifications (Meyer et al., 2012). Briefly, tissue was homogenized with with 1 % sarcosil Tris-EDTA buffer (Sigma-Aldrich, Hamburg, Germany) and glass beads ($0.2 - 2.1$ mm) in a Retsch shaking mill (both Retsch, Haan, Germany). For larvae >2 mg DW, a pre-cooled metal bead was used to homogenize the larvae. Concentrations of RNA and DNA were determined spectrofluorometrically with ethidium bromide as a fluorescence dye and restriction

enzymes to eliminate the nucleic acids. The RNA-DNA ratio was standardized (sRD) using a factor of 2.4 (Caldarone et al., 2006). The critical sRD (sRD_{crit}) was estimated for each temperature (T, °C) following Buckley et al. (2008). A second estimated condition index was DNA/DW (Bergeron and Person-Le Ruyet, 1997).

5.3.5 Statistical Analysis

Growth rates of larvae in SL and DW were calculated for each tank when larvae were >12 dph, the age at which the yolk sac was absorbed and the test temperature (7, 11, or 15 °C) was reached in all tanks. Variables were log-transformed if needed (e.g. DW). An analysis of covariance (ANCOVA) was run to test for differences in all the morphometric variables between tanks within each temperature treatments. In the cases where significant differences were noted, growth was estimated as a simple linear regression for each tank. If no significant differences were found, data were pooled for regressions.

For statistical modeling of U_{crit}, we used a nonlinear least squares method to fit Gompertz functions of the form:

$$U_{\text{crit}} = U_{\text{inf}} \cdot e^{\frac{-a}{b} \cdot e^{(-b \cdot SL)}} \tag{5.3}$$

to the data. In this parameterization, a and b determine a sigmoid shape between zero and the asymptotic critical swimming speed U_{inf}. The value of U_{inf} was fixed at 170 cm s^{-1} for the sake of consistency with juvenile U_{crit} data (Blaxter and Dickson, 1959). Note that modeled larval U_{crit} was so insensitive to U_{inf} that halving or doubling U_{inf} had almost no effect on the fitted curves. Permutation tests were used to estimate the statistical significance of SL, temperature, and tank on U_{crit}. First, the significance of SL was determined by comparing the explained variance among Gompertz models fit to the observed data and to 10,000 data sets with randomly shuffled SL. Second, the observed increase in explained variance for separate 7 and 11 °C models (as compared to a single model) was compared to 10,000 data sets with shuffled temperatures. This was repeated for the two other pairings of temperature treatments (11 and 15 °C, 7 and 15 °C). Equivalent permutation tests for significant increases in explained variance were performed for tank effects within each temperature treatment.

Finally, we binned data for each temperature treatment by *SL* (rounded to the nearest mm), excluded bins with n < 3 individuals, and fit Gompertz models (as above) to median U_{crit} values. In the case of significant tank effects, medians for both tanks were determined separately and then averaged. This method was designed to reduce the adverse effects of outliers, uneven sample sizes among *SL* bins, variability in stage-at-length, and random tank effects on the resulting model. All statistical analysis and graphs were done using R (version 3.1.1)

5.4 Results

The mean (±SD) *SL* of newly-hatched herring larvae was 7.2 (0.4) mm. The yolk sac was depleted in all larvae by 10 dph. After the yolk sac was absorbed and after the different rearing/treatment temperatures were reached (dph ≥ 12), growth rates were calculated for all tanks (Tab. 5.1). A significant difference in growth rate of the larvae within two tanks at the same temperature was only observed at 7 °C (ANCOVA, p<0.001). Larvae in 7B were initially (at 15 dph) smaller in *SL* (10 %) and *DW* (40 %) than those in 7A (8.9 vs 9.7 mm and 83.1 vs 118.2 μg, respectively in 7B and 7A), but grew faster and were the same size as the larvae in 7A by the end of the experiment. For all further morphometric analysis, no significant tank effect was observed (ANCOVA, p<0.001), therefore data were pooled.

Table 5.1: Regressions for morphometric measurements for Atlantic herring larvae reared at three different temperatures (7, 11 and 15 °C). Abbreviations: *SL*, standard length (mm); *DW*, dry weight (*mu*g); *BH*, body height at the head (mm). All regressions significant at p < 0.001, and data in parentheses indicate SE.

T (°C)	Tank	Age (dph)	Regression	n	R^2
7	7A	15 − 63	$SL = 6.335\,(\pm 0.658) + 0.215\,(\pm 0.215) * \mathrm{Age})$	66	0.759
	7A	15 − 63	$DW = 46.033\,(\pm 8.309) * e^{(0.060\,(\pm 0.004) * \mathrm{Age})}$	66	0.768
	7B	15 − 63	$SL = 5.144\,(\pm 0.494) + 0.224\,(\pm 0.011) * \mathrm{Age}$	66	0.856
	7B	15 − 63	$DW = 28.603\,(\pm 4.038) * e^{0.065\,(\pm 0.003) * \mathrm{Age}}$	68	0.895
	7A+7B	15 − 63	$DW = 0.013\,(\pm 0.002) * SL^{3.965\,(\pm 0.050)}$	133	0.979
	7A+7B	15 − 63	$BH = -0.220\,(\pm 0.035) + 0.075\,(\pm 0.002) * SL$	58	0.955
11	11A+11B	15 − 53	$SL = 6.619\,(\pm 0.573) + 0.249\,(\pm 0.015) * \mathrm{Age}$	116	0.710
	11A+11B	15 − 53	$DW = 40.885\,(\pm 5.898) * e^{0.078\,(\pm 0.004) * \mathrm{Age}}$	120	0.783
	11A+11B	15 − 53	$DW = 0.008\,(\pm 0.002) * SL^{4.221\,(\pm 0.085)}$	116	0.955
	11A+11B	15 − 53	$BH = -0.314\,(\pm 0.105) + 0.089\,(\pm 0.006) * SL$	45	0.818
15	15A+15B	16 − 38	$SL = 4.296\,(\pm 0.572) + 0.341\,(\pm 0.019) * \mathrm{Age}$	85	0.782

Table 5.1 – continued from previous page

T (°C)	Tank	Age (dph)	Regression	n	R^2
	15A+15B	$16-38$	$DW = 19.075\,(\pm 3.711) * e^{0.114\,(\pm 0.007)*\mathrm{Age}}$	86	0.776
	15A+15B	$16-38$	$DW = 0.005\,(\pm 0.001) * SL^{4.440\,(0.077)}$	84	0.976
	15A+15B	$16-38$	$BH = -0.291\,(\pm 0.055) + 0.091\,(\pm 0.004) * SL$	37	0.942

Growth rate in *SL* and *DW* increased with increasing rearing temperature. The *DW*-specific growth rate was 6 % and 11 % at 7 and 15 °C, respectively. Larvae at warmer temperatures not only grew faster but they were also heavier at a given *SL* than larvae reared at colder temperatures (Fig. 5.2a, Tab. 5.1). Larval *BH* also increased with increasing temperature (Fig. 5.2b). For example, an 18-mm larvae at 15 °C weighed 65 % more and had a 30 % greater *BH* than an 18-mm larva reared at 7 °C. The *Hcp* increase non-linearly with increasing *SL* (Fig. 5.2c) and was not significantly different at 7, 11 and 15 °C. Larvae not only grew faster and had a greater weight-at-length at the warmer temperatures, but they also started (Stage 2c) and completed (Stage 3c) notochord flexion earlier (Fig. 5.3). The mean *SL* at 50 % notochord flexion was 19.3, 17.3 and 16.1 mm at 7, 11 and 15 °C (Fig. 5.2d).

Table 5.2: Fitted Gompertz models for critical swimming speed (U_{crit}) at size (standard length, *SL*) for Atlantic herring larvae reared at three different temperatures (7, 11 and 15 °C). Models fitted to both raw data and median values for each temperature are shown, see text for further details. All model estimates are significant (permutation test, $p<0.05$).

Formula: $U_{\mathrm{crit}} = U_{\mathrm{inf}} \cdot e^{\frac{-a}{b} \cdot e^{(-b \cdot SL)}}$						
Models fit to	n	U_{inf}	a	b	R^2	Type of data
All data	416	170	0.290	0.0379	**66 %**	raw data
7 °C	181	170	0.274	0.0354	73 %	raw data
11 °C	132	170	0.329	0.0414	73 %	raw data
15 °C	103	170	0.474	0.0524	69 %	raw data
7 °C,11 °C,15 °C					**73 %**	raw data
Tank 7A	74	170	0.257	0.0334	76 %	raw data
Tank 7B	77	170	0.321	0.0398	77 %	raw data
7A, 7B, 11 °C,15 °C					**74 %**	raw data
7 °C	181	170	0.280	0.0357	93 %	medians
11 °C	132	170	0.456	0.0494	95 %	medians
15 °C	103	170	0.497	0.0533	95 %	medians

Most (57 to 67 % depending on the temperature) preflexion larvae were not able to

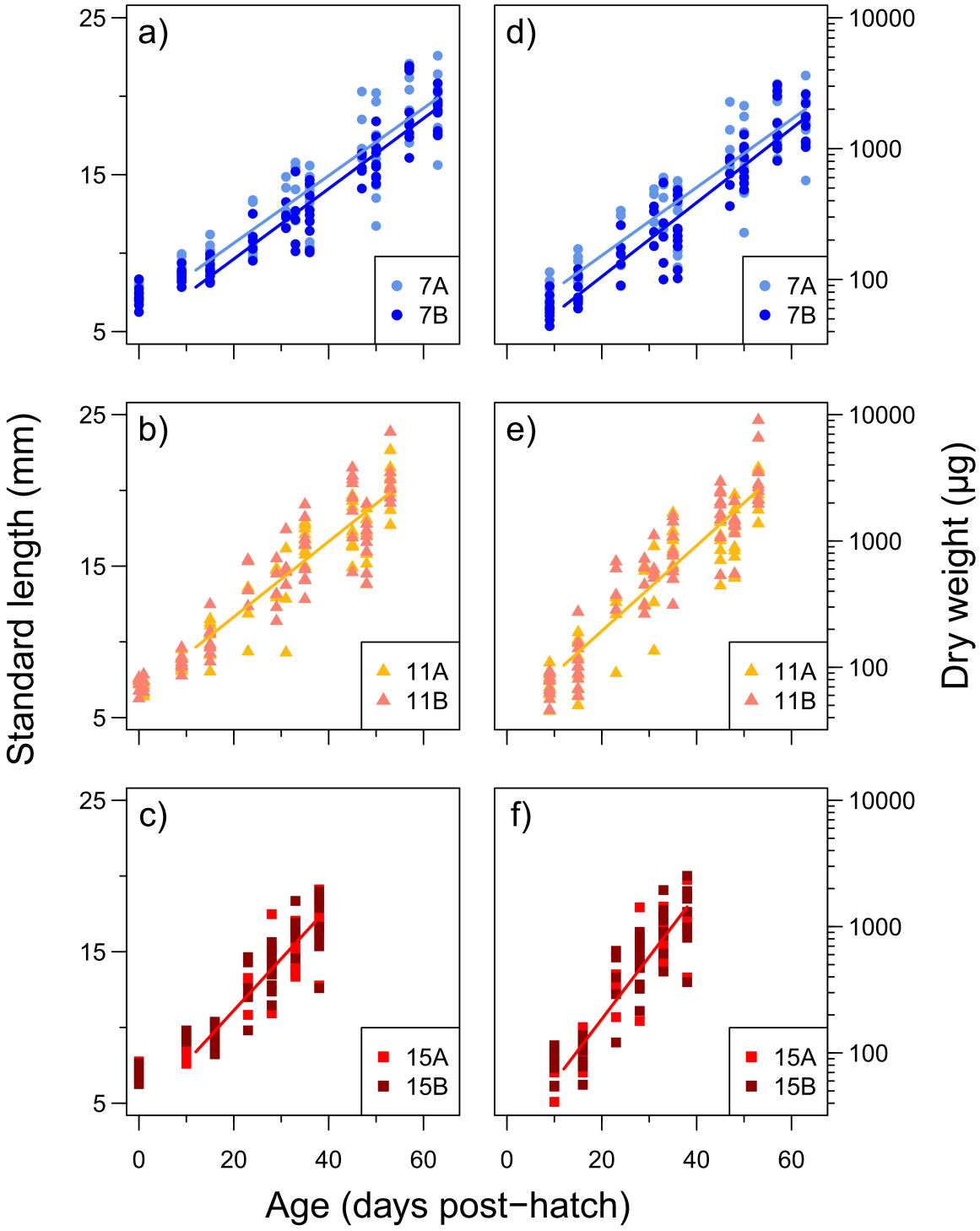

Figure 5.1: Growth trajectories in standard length (a-c) and dry weight (d-f) of Atlantic herring larvae reared at 7 °C, 11 °C and 15 °C. Symbols are shape-coded by temperature (7, 11, 15 °C) and color-coded by rearing tank (A, B).

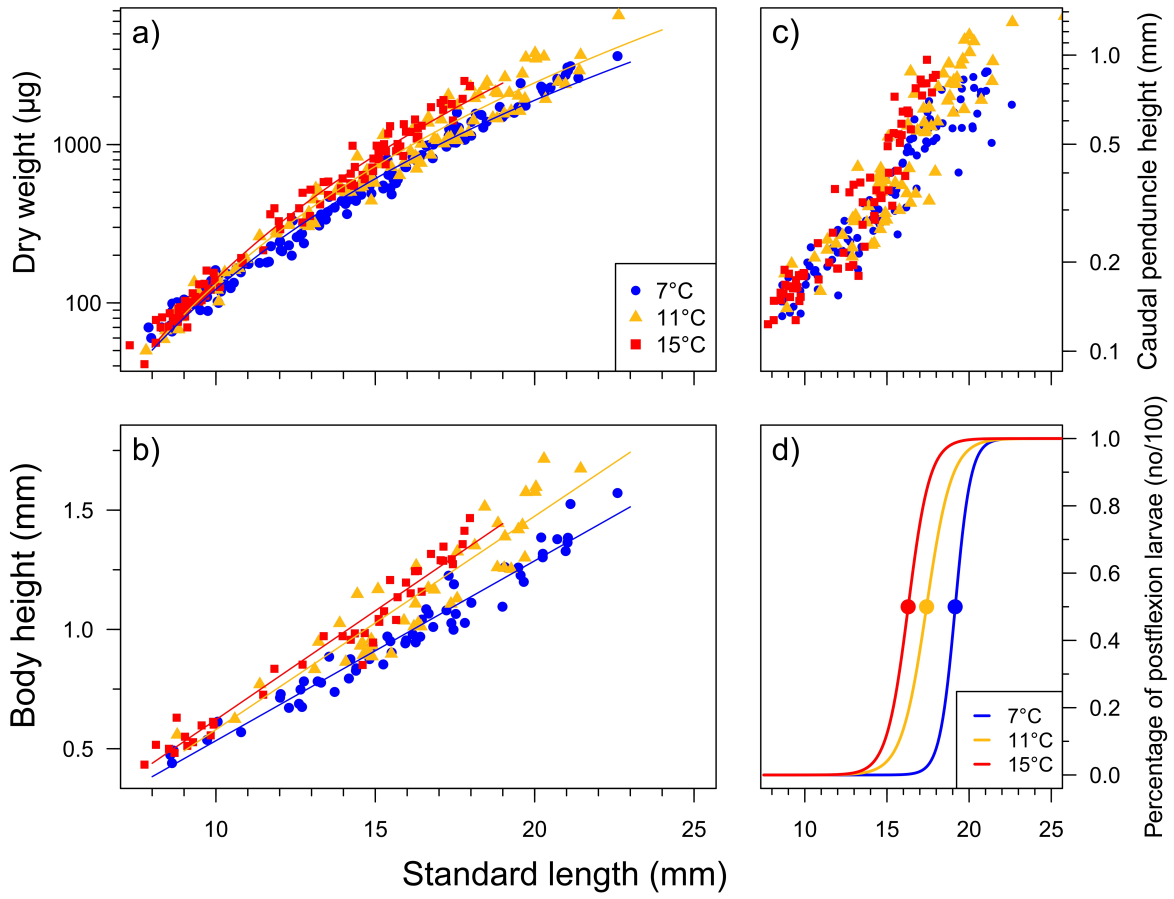

Figure 5.2: Larval morphometrics of Atlantic herring reared at three different temperatures (7, 11, 15 °C): relationship between a) dry weight, DW (μg) and standard length, SL (mm); b) body height at head, BH (mm) and SL (mm); c) body height at caudal peduncle, Hcp (mm) and SL (mm). d) Logistic regression showing the percentage of larval which have finished notochord flexion for a given SL (mm). Symbols are color-coded by temperature. Equations for the linear regressions are displayed in Tab. 5.1.

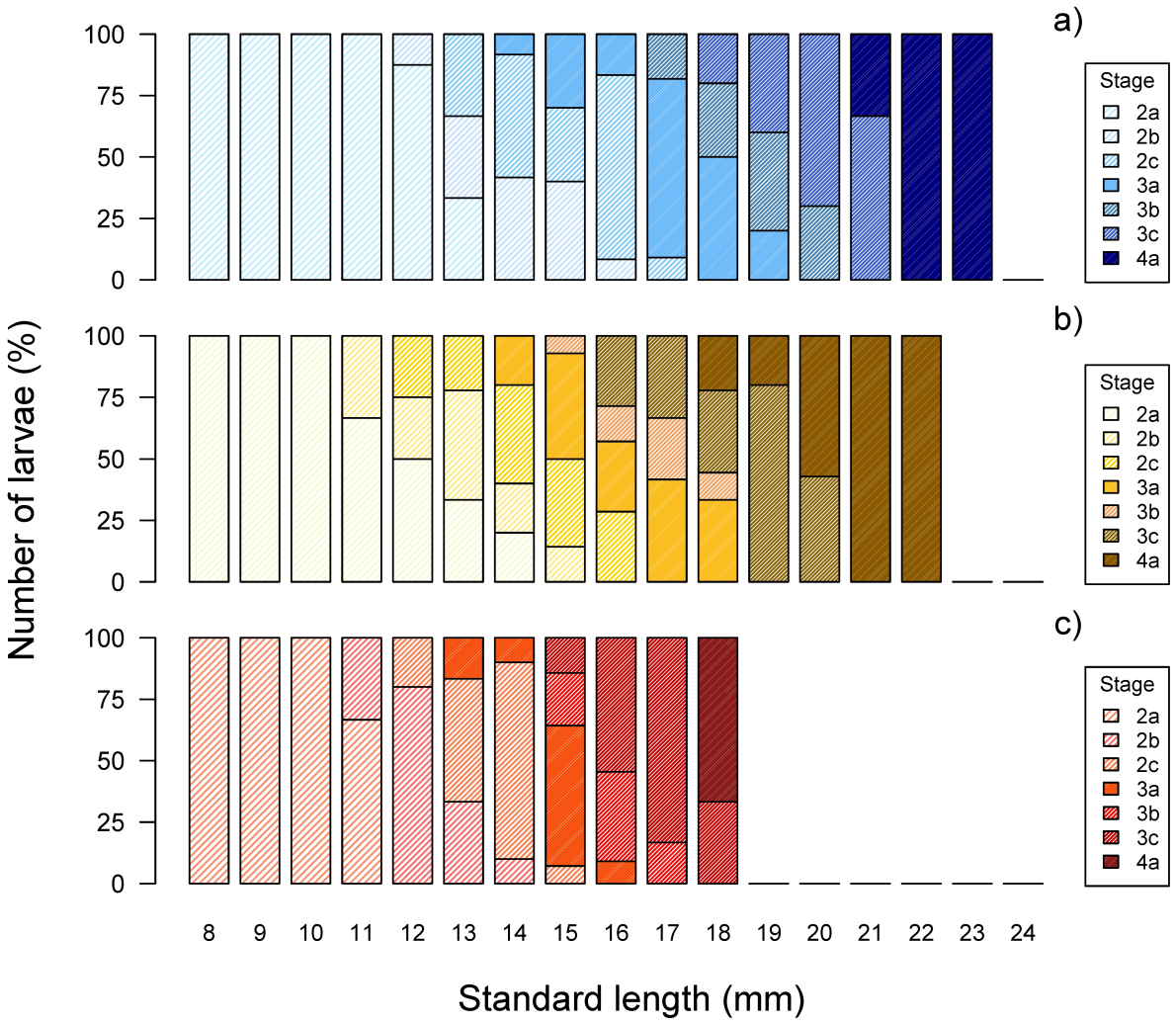

Figure 5.3: Distribution of larval stages of Atlantic herring with size for larvae reared at a) 7 °C, b) 11 °C, c) 15 °C. Staging done according to Doyle (1977), see text for further details.

swim at the minimum water current speed (0.6 cm s^{-1}) during the acclimation period. In the other preflexion larvae, swimming speeds were relatively low and, in most cases, >3 cm s^{-1} (2 bl s^{-1}) (Fig. 5.4). However, with the onset of notochord flexion ($13-14$ mm *SL*), swimming capacity increased exponentially faster at warmer temperatures. The fastest U_{crit} (9.2 cm s^{-1}, up to 5 bl s^{-1}) was calculated for a 20-mm larva reared at 11 °C.

In the fitted Gompertz model for all U_{crit} data pooled, the effect of *SL* was statistically significant (permutation test, $p<0.05$) and explained $R^2 = 66\,\%$ of variance in U_{crit} (Tab. 5.2). Fitting different models for 7, 11, and 15 °C (tanks pooled) revealed signifi-

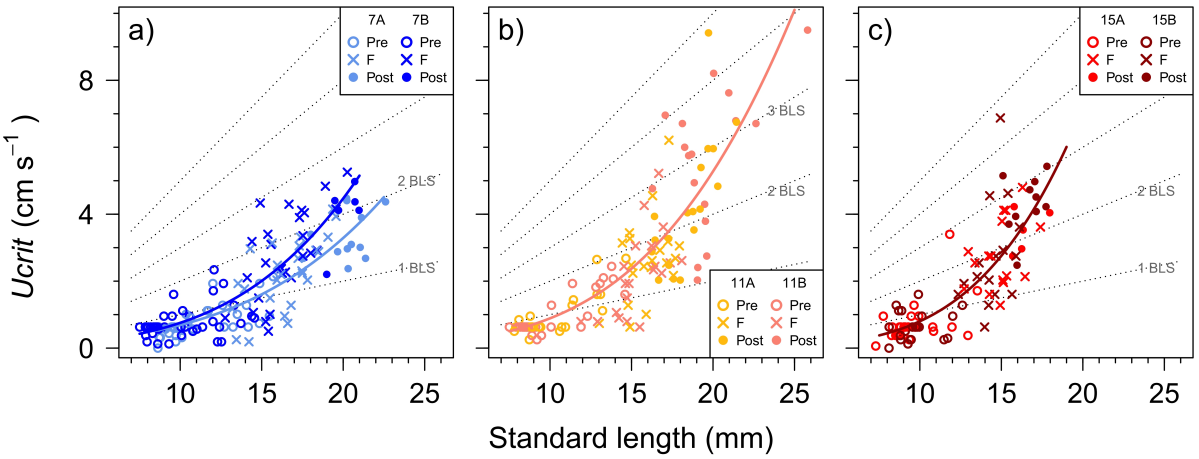

Figure 5.4: Ontogeny of critical swimming speed (U_{crit}, $cm\,s^{-1}$) in larvae of Atlantic herring (*Clupea harengus*) reared at 7 (blue), 11 (orange) and, 15 °C (red). Symbols are coded by flexion stage into preflexion (open circles), flexion (cross) and postflexion (filled circles). Dotted lines represent isolines for swimming speeds in body lengths per second (BLS).

cant temperature effects (three permutation tests, all $p<0.05$), and improved the overall fit to $R^2 = 73\,\%$ explained variance. Fitting different models for replicates A and B of each temperature showed a significant tank effect (permutation test, $p<0.05$) only in the 7 °C treatment. Using separate models for tanks 7A and 7B improved the overall fit to $R^2 = 74\,\%$ (Fig. 5.4).

The temperature-specific models fit to *SL*-bin median U_{crit} values (Fig. 5.5) are more statistically robust than the models fit to raw data and explain 93 % to 95 % of variance in median U_{crit} (Tab. 5.2).

Values of *sRD* ranged from 1.84 to 7.29, 1.54 to 8.79, and 1.84 to 6.70 for individual larvae reared at 7, 11 and 15 °C. In order to test whether the high inter-individual variability observed in U_{crit} was related to nutritional condition, the residuals from the U_{crit}-*SL* regression were compared to the *sRD*. No significant trends were observed. Values of *DNA/DW* were also highly variable (0.007 to 0.37, 0.007 to 0.037 and 0.005 to 0.18 at 7, 11, 15 °C respectively) but there was also no significant trend between *DNA/DW* and the residuals from the U_{crit}-*SL* model. Only a few larvae (>25 mm *SL*) in the present study displayed *Re* >1000, a regime in which larvae experience an inertial environment during routine or maximum sustained swimming.

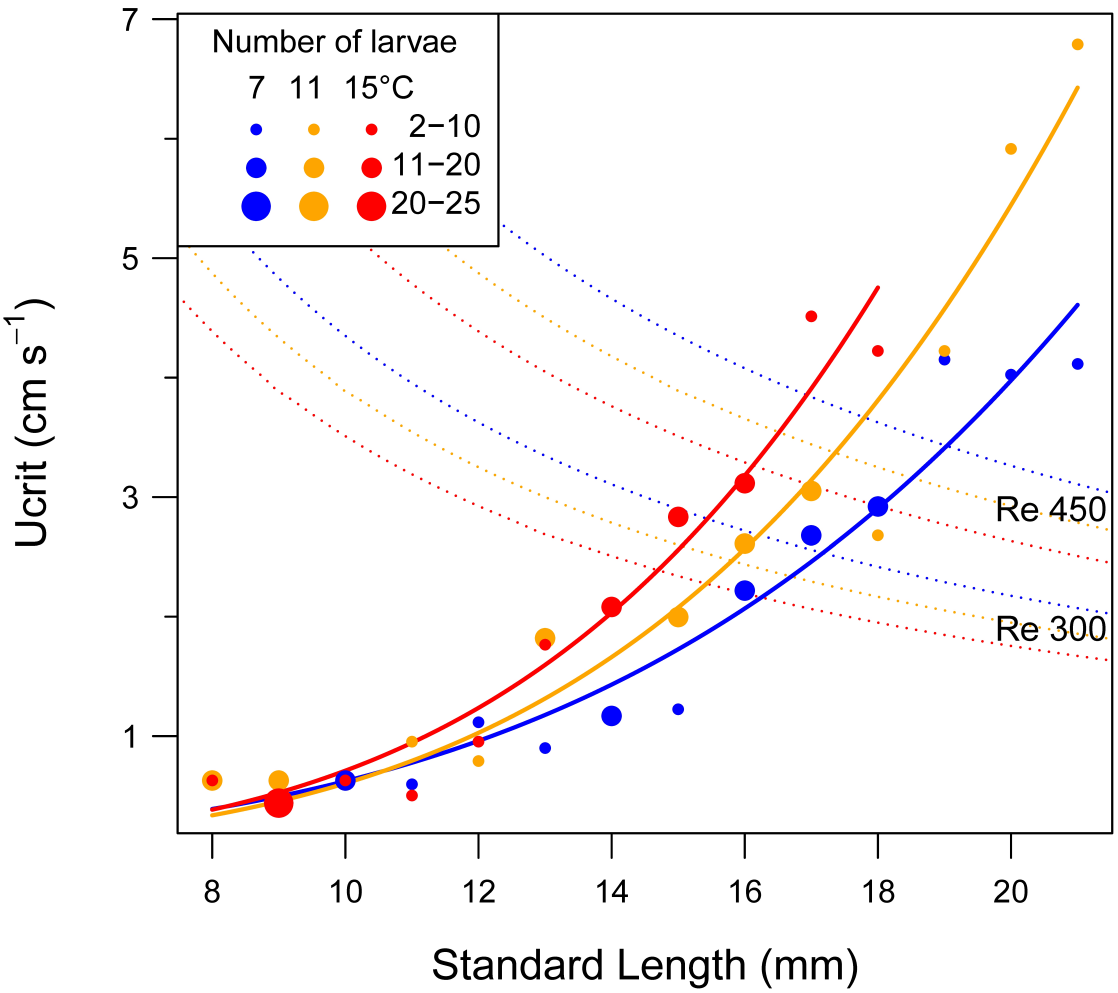

Figure 5.5: Ontogeny of critical swimming speed (U_{crit}, $cm\,s^{-1}$) in larvae of Atlantic herring (*Clupea harengus*) reared at 7 (blue), 11 (orange) and, 15 °C (red). Symbols represent median values for 1 mm-size bins, size-coded by number of larvae included in the median calculations. Solid lines represent the Gompertz function used to model the data at each temperature (Tab. 5.2). Dotted lines represent isolines for a Reynolds number of 300 and 450 at each temperature (color code same as for symbols).

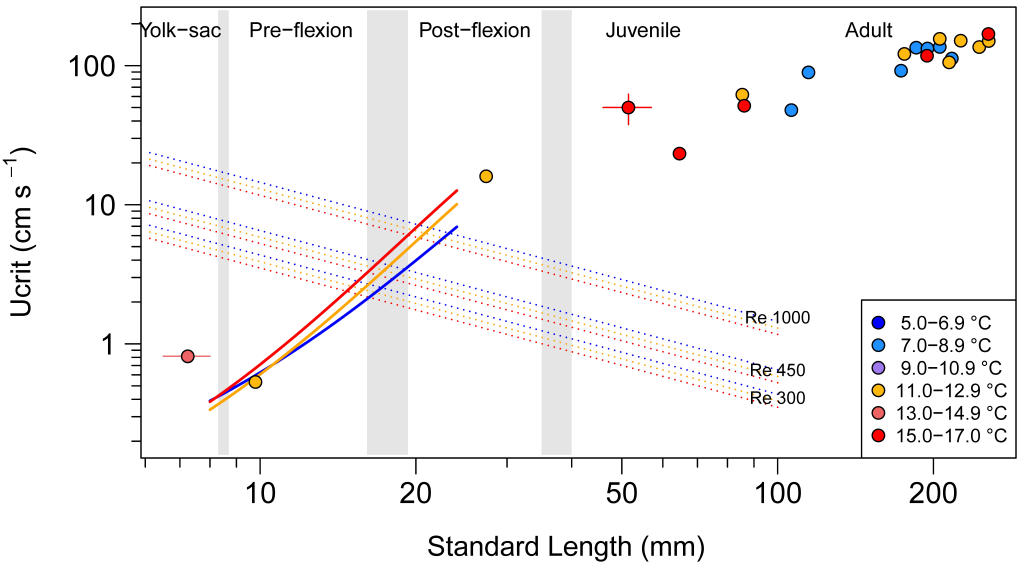

Figure 5.6: Review of the ontogeny of critical swimming speed (U_{crit}) in Atlantic herring (*Clupea harengus*), from larvae to adults. Model fits from the present study are included as a solid line, all the other available datasets are included as mean (± range). Points and model fits are color-coded by temperature. Source of the studies: Bishai (1961), Blaxter and Dickson (1959) and Johnston et al. (2001).

Published U_{crit} estimates for Atlantic herring, together with those measured here, were compiled for a wide range in body sizes including small, newly hatched larvae through metamorphosed juveniles (Fig. 5.6). During the yolk-sac phase, U_{crit} was <0.6 cm s^{-1} and thus difficult to estimate. As larvae develop through the preflexion stage there was an exponential increase in U_{crit} and the rate of increase was faster at warmer temperatures. After notochord flexion (16 − 19 mm *SL*), thermal differences in U_{crit} exist which are described by a Q_{10} of 1.8 to 2.0. In the juvenile stage (>50 mm), the rate of increase in U_{crit} with increasing body length is slower and no differences with water temperature were reported. Herring at body sizes just prior to or during metamorphosis (30 − 50 mm), the size at which the trends in U_{crit} change, have not been examined.

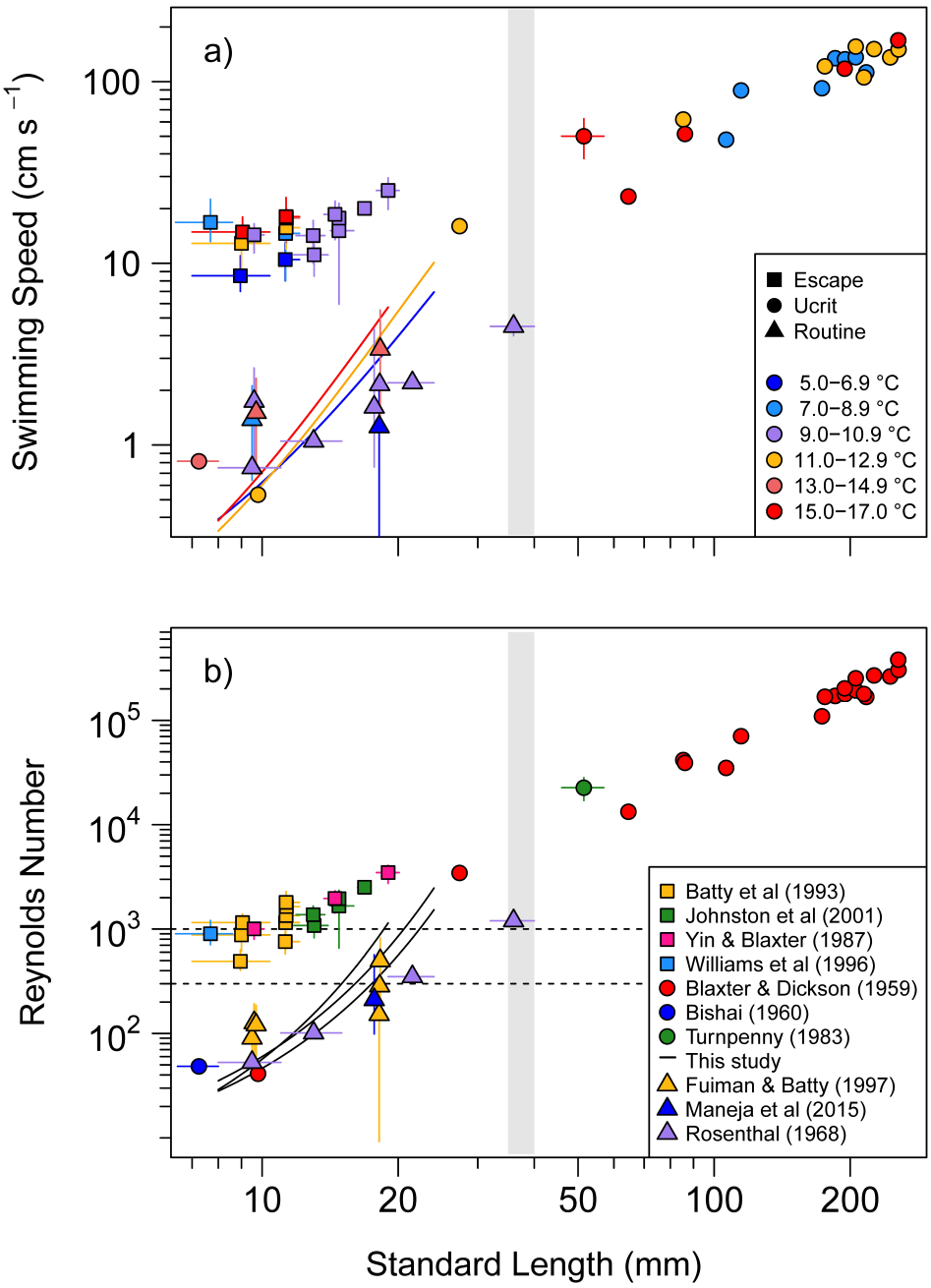

Figure 5.7: Compilation of published literature on the ontogeny of swimming performance of Atlantic herring. a) Swimming speed (mean ± range) at size for escape (squares), U_{crit} (circles) and routine (triangles) swimming studies, color coded by testing temperature. b) Estimations from Reynolds number (mean ± range) from the same studies as a), symbols are color-coded by study; dashed lines indicate the transition from a viscous to an inertial environment ($Re = 300-1000$). Gray box in both panels represent size at metamorphosis ($35-40$ mm). The model fit from the present study are included in both panels as solid lines.

Table 5.3: Compilation of swimming studies for Clupeiform larvae and juveniles.

Species	Swimming type	T (°C)	*SL* (mm)	Swimming speed		*n*	Study
				cm s	bl s		
Atlantic herring (*Clupea harengus*)	Routine	10	8.0 – 40.0	1.0 – 5.0	0.7 – 1.3	250	Rosenthal (1968)
	Routine	10	17.7	0.7 – 4.3	0.4 – 2.5	>1000	Maneja et al. (2015)
	Routine	7 – 14	9.6	0.0 – 5.5	0.0 – 3.0	60	Fuiman and Batty (1997)
			18.2				
	Routine	8 – 14	11.0	0.5 – 2.0	0.4 – 1.8	np	Batty (1984)
			22.0	0.5 – 6.0	0.2 – 2.8	np	
	Routine	10	17.7 – 44.8	0.2 – 1.3	3.4 – 10.8	np	Munk (1992)
	U_{crit}	7, 11, 15	8.0 – 22.0	0.0 – 9.2	0.0 – 4.8	386	This study
	U_{crit}	13.1 – 14.8	6.5 – 8.0	0.6 – 1.0	0.8 – 1.4	35	Bishai (1961)
	U_{crit}	5 – 18	9.8 – 255.9	0.5 – 169.1	0.5 – 7.8	20	Blaxter and Dickson (1959)
	U_{crit}	16	46.0 – 57.0	37.7 – 62.4	7.3 – 12.1	28	Turnpenny (1983)
	U_{crit}	1.4 – 11.2	60.0 – 220.0	30.5 – 131.1	1.5 – 9.6	1551	Boyar (1961)
	U_{max}	5.0 – 11.0	5.4 – 8.6	13.2 – 22.5	16.0 – 29.8	19	Williams et al. (1996)
	Escape	10 – 12			5.8 – 11.6	np	Blaxter and Batty (1985)
	U_{max}	5 – 17	7.0 – 12.1	7.0 – 23.0	7.0 – 20.3	np	Batty et al. (1993) (only spring-spawned)
	U_{max}	9 – 10	9.1 – 20.1	11.4 – 29.5	10.4 – 16.2	32	Yin and Blaxter (1987)
	U_{max}	8 – 11	11.7 – 17.4	8.5 – 20.8	6.5 – 12.3	40	Johnston et al. (2001)
Pacific herring (*Clupea pallasi*)	Routine	9 – 10	8.4 – 10.8	0.4 – 2.3	0.4 – 2.5	32	Von Westernhagen and Rosenthal (1979)
	U_{crit}	10	91.0 – 105.0*		5.2 – 5.4	35	Kennedy and Farrell (2006)
Northern anchovy (*Engraulis mordax*)	Routine	17 – 18	0.4 – 25.2	0.2 – 2.8	0.3 – 1.6	25	Hunter (1972)
	U_{max}	17	2.0 – 14.0*	4.0 – 32.0	16.0 – 37.0	85	Webb and Corolla (1981)

Table 5.3 – continued from previous page

Species	Swimming type	T (°C)	SL (mm)	Swimming speed		n	Study
				cm s	bl s		
Sprat (*Sprattus sprattus*)	U_{crit}	16	37.0 – 42.0	28.2 – 62.4	7.1 – 15.8	13	Turnpenny (1983)
Sardine (*Sprattus sprattus*)	U_{crit}	15	7.0 – 23.0	1.6 – 9.5	7.1 – 15.8	13	Silva et al. (2014)
Round herring (*Jenkinsia* ssp)	U_{crit}	28 – 30	25.0 – 50.4	23.4 – 41.2	6.2 – 10.9	7	Fisher et al. (2005)
Round herring (*Spratelloides* ssp)	U_{crit}	28 – 30	14.8 – 46.8	4.7 – 28.9	1.5 – 9.4	16	Fisher et al. (2005)

*standard length estimated from dry weight following Quast (1986)

5.5 Discussion

5.5.1 Thermal impacts on growth and development

Thermal effects on survival, development rate/stage duration, and growth rate have been well studied in the early life stages of commercially important fish species (Houde, 1989; Blaxter, 1991; Pepin, 1991). It is generally accepted that, under stable conditions, faster growth rates would lead to a lower probability of predation mortality because larvae would spend less time in stages particularly vulnerable to predators (Anderson, 1988; Pepin, 1991). The larvae of Atlantic herring exhibit a wide range in thermal tolerance and can survive, at least for short periods of time, temperatures from -1.7 to 24 °C (Blaxter, 1960). The growth rates of larvae in this study ranged from 0.21 at 7 °C to 0.34 mm d^{-1} at 15 °C. The only study, to our knowledge, to have reared herring larvae from WBSS population at warmer temperatures, reported growth rates in the range of $0.13 - 0.32$ mm d^{-1} at 17 °C (Borchardt, 2010), suggesting that the temperature leading to maximum growth in the laboratory is between 15 and 17 °C, at least for this population. Repeated sampling and length-frequency analysis of field-caught larvae suggested that growth rates increased with increasing temperature to 17.5 °C (Oeberst et al., 2009), although one needs to take into account the potential for size-selective mortality to bias field growth rates. Nonetheless, WBSS herring larvae encounter relatively warm waters and, considering the predicted 2 °C future warming in surface seawater by the end of the century for the southern Baltic Sea (HELCOM, 2013), it is important to thoroughly understand how temperatures beyond 15 °C may affect the developmental physiology and vital rates of these larvae. These ecophysiological data can help parameterize models used to explore and predict climate change impacts on the growth and survival of larval stages (and thus recruitment to the fishery) (Fouzai et al., 2015).

In the present study, higher temperatures not only resulted in faster growth but also accelerated development so that larvae at colder temperatures were less developed at a given body length. Generally, larval fish reach an ontogenetic state at a species-specific body size (Fuiman and Higgs, 1997) and length-at-stage can be influenced by temperature. For example, flatfish larvae reared at colder temperatures had a larger body size at metamorphosis than conspecifics reared at warmer temperatures (e.g. Chambers and Legget, 1987; Minami and Tanaka, 1992). The same pattern was observed here in Atlantic herring larvae where larvae reared at 15 °C were larger (in terms of DW, BH) and

finished notochord flexion at a shorter length (15 mm *SL*) compared to larvae at 7 °C which completed notochord flexion at 19 mm *SL*.

The phenomenon of accelerated development at warmer temperatures has been previously reported for Atlantic herring in laboratory and field studies focused on differences in muscle composition, time of notochord flexion and fin ossification and innervation (Johnston et al., 1998, 2001; Temple et al., 2000). The development of these structures which occurs at larval sizes between 12 and 24 mm *SL* seems to be programmed (and influenced by temperature experienced) during the embryonic period and prior to first-feeding. Interestingly, differences in thermal history experienced after this period do not lead to developmental differences (Johnston et al., 2001). Moreover, late larvae (ca. 24 mm *SL*) reared at different temperatures display few if any morphological differences. Thus, there is a window of time during which being exposed to warm temperatures can accelerate development (if prey resources are sufficient) leading to a variety of benefits such as increases in the resistance to starvation, swimming and foraging capacity, and escape response (Fuiman and Higgs, 1997). However, warmer temperatures also place larger metabolic costs on individuals which need to be paid by increases in the rate of food consumption. For example, a mean 18 mm herring larvae would weight 1233 μg reared at 7 °C, and 50 % more (1872 μg) reared at 15 °C, leading to three times larger standard metabolic rates (64 vs 192 nmol O_2 ind^{-1} h^{-1}; Moyano, unpub). A complex balance between near-optimal temperatures for growth and a match with the prey seem to be driving larval herring survival in the Baltic Sea, where early spring cohorts tend to collapse year after year in favor of the late spring-spawned cohorts (Polte et al., 2014).

5.5.2 Ontogeny of swimming in Atlantic herring

Critical swimming speed of Atlantic herring increases exponentially during larval ontogeny and this increase is temperature-dependent. Preflexion larvae had very poor swimming abilities at 7, 11 and 15 °C. As soon as notochord flexion was completed, however, larval swimming performance was significantly improved (up to 8 $cm\,s^{-1}$ or $3-5$ $bl\,s^{-1}$), especially at the warmer temperatures. Our U_{crit} estimates are in accordance with the results reported in three previous studies conducted on herring including one study on 6.5− to 8−mm *SL* larvae, and two other studies performed on larger juveniles (Tab. 5.3). A fourth study attempted to describe the changes in U_{crit} from larvae to juveniles, but

the dataset was relatively small which limited the conclusions that could be drawn (Blaxter and Dickson, 1959). Compiling the data from this and all the previously published studies, four phases of swimming can be described: 1) the yolk-sac period, in which U_{crit} is <0.6 cm s^{-1} and difficult to measure, probably the reason of the slightly higher values in Bishai (1961); 2) preflexion period, during which the larvae still swim in a viscous environment, and the temperature impact on U_{crit} is not constant; 3) post-flexion phase, directly after notochord flexion, U_{crit} increases up to $6 - 8$ cm s^{-1}, and thermal effects seems to stabilize into a Q_{10} of 2.0; and 4) juvenile-adult phase when the rate of increase in U_{crit} with increasing body size is more modest as appears unaffected by temperature (Blaxter and Dickson, 1959). Unfortunately, there is a lack of data for Atlantic herring between 20 and 50 mm *SL* which makes it challenging (and likely unwise) to create a general model of how U_{crit} changes from the larval through the juvenile stage. Future studies should examine U_{crit} throughout the larval-juvenile metamorphic period ($20 - 50$ mm *SL*) to help understand how achieving important morphological landmarks (e.g. fast and slow muscle fibres and functional gills at 29 mm, changes in swimming style; Batty, 1984; Vieira and Johnston, 1992) is related to changes in swimming speed.

A compilation of all published studies on routine, U_{crit} and escape (U_{max}) swimming speeds in Atlantic herring (Fig. 5.7) suggests the body sizes at which important transitions in swimming performance occur. Inter-individual variability at any given size was substantial for any swimming type, especially for the early stages ($\leq$ 10 mm). In <10 mm *SL* larvae between 7 and 15 °C, routine and U_{crit} speeds were very similar evidencing the poor swimming capacity of these young larvae (where estimating U_{crit} is often impossible since larvae do not hold station against even the slowest water currents). By 18 to 19 mm *SL*, the swimming capacity of larvae has greatly increased and U_{crit} speeds found here are higher than those reported for routine movements. The differences in routine speeds across studies (e.g. Rosenthal, 1968; Fuiman and Higgs, 1997; Maneja et al., 2015) were probably due to methodological differences such as the size of the chambers (e.g. 0.4-, 1.7- or 8-L) and the method of visualizing the larvae (e.g. 2d- vs 3d- silhouette video photography). The speed of the escape response of herring larvae is an order of magnitude higher than the routine swimming speeds but far less variable among studies (likely due to a common methodology).

Inter-specific comparisons of the swimming capacity of marine fish larvae are chal-

lenging because of a lack of a common denominator. For example, at the same body size, maximal sustained swimming speed of herring larvae in this study is slightly lower than that reported for European sardine (*Sardina pilchardus*) at the same temperature (Tab. 5.3). However, this is not unexpected since the larvae of sardine have a more advanced stage-at-size compared to herring. In sardine, notochord flexion occurs at 12 mm and a caudal fin is developed at 16 mm *SL* (Silva et al., 2014). Given vast differences in the developmental characteristics of marine fish larvae, it is not surprising that comparisons are more similar within families than within habitats. For example, when compared to U_{crit} measurements made on coral reef species (28 to 30 °C, Tab. 5.3), our estimates for herring larvae agree more closely with those of other Clupeidae but are much lower compared to Carangids or Holocentrids (mean of 71 and 75 $\mathrm{cm\,s^{-1}}$ for 29 and 36 mm fish) (Fisher et al., 2005). Species of demersal reef fishes in the tropics have likely faced stronger selective pressure against larvae with poor swimming performance: tropical larvae often display directional swimming and homing behavior to reefs (Gerlach et al., 2007; Atema et al., 2015) which is likely linked to increased survival and fitness (Fisher et al., 2005). On the other hand, selection may have acted to enhance starvation resistance in temperate/sub-polar species such as herring confer the larvae some competitive advance, e.g. higher feeding success, lower predation mortality (Anderson, 1988).

5.5.3 Thermal impacts on swimming performance

Although the direct effect of temperature on swimming performance of fish has long been acknowledged (Beamish, 1978), temperature plays both a direct (physiological) and an indirect (physical) role on the swimming performance of young, small larvae (Fuiman and Higgs, 1997; Wieser and Kaufmann, 1998; Hunt von Herbing, 2002). The physical changes in water viscosity at different temperatures are likely more important than temperature-dependent changes in physiology for larvae swimming at low Re (<300). In small larvae, although tail-beat frequency increases with increasing temperature, they do not possess the adequate musculature and, at cold temperatures, must decrease tail amplitude and stride length, uncoupling tail-beat frequency from swimming speed (Fuiman and Higgs, 1997). Above a Re of 300, there is a transition to the inertial environment, where viscous forces still operate. The upper limit of this transition area has been generally set in 1000 for fish larvae (Leis, 2010). However, Fuiman and Batty (1997) observed that routine swimming speed of large herring larvae ($Re > 450$) was not affected by changes in

viscosity, which may suggest that the upper limit (Re) for this transition to the inertial environment occurs at lower Re for herring larvae.

It is difficult to make an accurate estimate of the body size at which larvae enter the inertial environment, where swimming is much more energy efficient and behavior may ultimately dictate transport dynamics of pelagic larvae. In larvae <15 mm SL, escape responses occurring over very brief time periods (milliseconds) have $Re > 700$ while both routine and U_{crit} swimming speeds occur at Re between 30 and 200, independent of temperature. Larvae >18 mm SL have U_{crit} speeds associated with $Re > 450$, suggesting that these larvae perform sustained swimming within the inertial environment. Unfortunately, the length of this period of time is not known, since endurance tests have never been performed on larvae of cold-temperate species. At cold temperatures ($< 10\,^{\circ}\mathrm{C}$), when swimming at routine speeds, a much larger body size would be needed to cross the threshold ($Re \sim 450$) between transitional and inertial regimes. Despite the lack of data on this size range, one could speculate that this transition to the inertial environment occurs at body sizes between 20 and 30 mm SL, which correspond to larval-juvenile metamorphosis as was observed in the larvae of Atlantic cod (*Gadus morhua*) by Peck et al. (2006).

Estimating the physiological effect of temperature on swimming speed in small larvae using an index such as Q_{10} may be problematic (Fuiman and Higgs, 1997; Hunt von Herbing, 2002). The Q_{10} assumes an exponential increase with warming temperatures which does not occur in small larvae whose movements are constrained by the viscosity of water. In the present study, mean U_{crit} for a 10 mm herring larvae did not increase with increasing temperature (in fact, it was higher for 11 °C than for 7 °C or 15 °C). For larger larvae, $15 - 18$ mm, in which viscosity effects would be insignificant ($Re > 450$), a Q_{10} of $1.8 - 2.0$ was consistently estimated for that size range (between 7 and 15 °C). This Q_{10} is lower than that estimated for routine swimming speed in 18-mm SL herring ($Q_{10} = 2.2$) reported by Fuiman and Higgs (1997) and cod larvae ($Q_{10} = 2.5$ for $4 - 60$ mm SL, Peck et al., 2006). Unfortunately, few measurements of U_{crit} were made at 15 °C using relatively large individuals so that definitive statements regarding how the impacts of temperature on swimming may change with ontogenetic stage or body size. For juvenile herring ($Re > 10000$), Blaxter and Dickson (1959) reported that temperature had no effect on U_{crit}. These discrepancies suggest that the Q_{10} varies with swimming type

as suggested by Peck et al. (2006). Few studies have estimated the impact of temperature on the cost of transport for larvae (Wieser and Kaufmann, 1998) and no studies have been performed on marine fish species due to the technical challenge of measuring active metabolism in these small organisms (Peck and Moyano, In Press). Wieser and Kaufmann (1998) suggested that metabolic requirements would be higher at cold temperatures due to the inefficiency of the muscle fibers. Therefore, there is a clear need of obtaining metabolic measurements under different temperature and activity levels in order to further understand the potentially complex relationship between metabolic demands, muscle dynamics, swimming speed, viscosity, and temperature.

5.5.4 Larval condition and swimming performance

Inter-individual variability is substantial in fish swimming studies, both on larvae (Fisher et al., 2005; Peck et al., 2006; Faria et al., 2009) and adults (Kolok, 1999). Size and/or morphology are generally the best predictors of U_{crit}. In adults, thermal history during the early stages, feeding history, dietary fatty acids and growth rates have been reported to influence U_{crit} (Billerbeck et al., 2001; Scott, 2012; Benítez-Santana et al., 2014). For larval stages, studies evaluating these parameters are much scarcer and results not always consistent.

Poor nutritional condition is associated with slow growth which increases an individual's vulnerability to predators (by increasing stage duration) (Hoey and McCormick, 2004). At low levels of nutritional condition, one may also expect swimming endurance to be compromised which has implications for transport and feeding success. The strength of the relationship between condition and U_{crit} appears to depend on the time scale of the measurements. For instance, differences in short-term (3- to 4-day) condition indices such as *sRD* or Fulton condition factor (Clemmesen, 1994; Peck et al., 2015) appear unrelated to differences in U_{crit} (Faria et al., 2011b; Silva et al., 2014, 2015, this study). In the present study all larvae were in good condition, well above critical limit sRD_{crit} (1.72 for 7 °C, 1.24 for 11 °C and 0.96 for 15 °C) for each temperature. Under starvation, previous works on burst swimming (U_{max}) in herring suggested that swimming performance only decreases after larvae have reached the point of no return, PNR (Yin and Blaxter, 1987). Similar results were reported for Senegalese sole (*Solea senegalensis*) and gilt-head seabream (*Sparus aurata*), in which short starvation times (ca. 3 days) did not

have any effect on U_{crit} (Faria et al., 2011a,b). Therefore nutritional condition for herring, and other species with high resistance to starvation, does not seem to influence U_{crit} and U_{max} performance unless larvae are beyond the PNR. These results for U_{crit} and U_{max} contrasts to those for routine swimming, which is extremely affected by both prey type and abundance, due to changes in foraging behavior (Munk and Kiørboe, 1985; Chick and Van den Avyle, 2000). The different swimming levels (U_{max}, U_{crit}, routine swimming) are thus affected by prey type and abundance in different ways.

On the other hand, when longer-term condition (derived from otolith measurements) was examined, coral reef larvae in better condition, grew faster and had a higher U_{crit} (Grorud-Colvert and Sponaugle, 2006). In another study, European sardine growing at different rates in the laboratory had no differences in U_{crit} (Silva et al., 2014). Moreover, Billerbeck et al. (2001) reported that faster-growth in Atlantic silversides (*Menidia menidia*) was related to lower U_{crit} speeds. In the present study, faster-growing larvae at 7 °C (Tank 7B vs 7A) tended to have lower U_{crit} suggesting an energy deficit and preferential allocation of available energy into growth in a predator-free environment. Unfortunately the experimental design and the absence of replicates precludes any strong conclusion about any potential cause-and-effect response between growth and U_{crit}. A comparative approach including the effects of both recent and long-term growth and condition on larvae growing at different rates would be extremely relevant to further understand any potential ecological consequences on larval fitness and survival.

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Chapter 6

Projected habitat loss for Atlantic herring in the Baltic Sea

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6.1 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 ($S = 1.9$ to 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.

6.2 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 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 At-

lantic 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. 6.1). 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 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 nursery areas for marine fishes.

6.3 Material and Methods

6.3.1 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.

6.3.2 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 $\pm$ 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. 6.1). 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 $10\,^{\circ}C$ 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

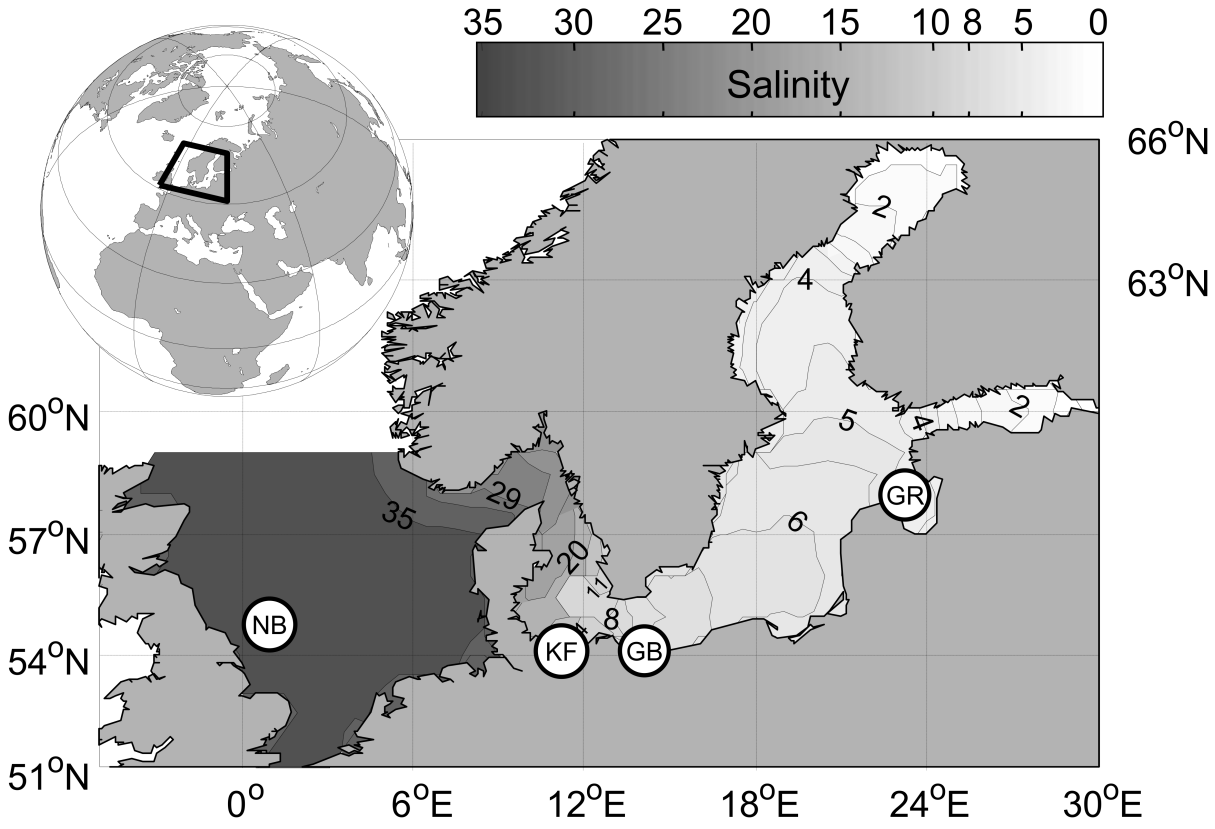

Figure 6.1: Mean annual salinity (1980 − 2004) of the North and Baltic Sea (grid resolution $S = 0.1$, ICES WGOOFE data, see Janssen et al. 1999). Symbols denote the location of spawning areas of Atlantic herring examined in the present study given: Gulf of Riga (GR); Greifswalder Bodden (GB); Kiel Fjord (KF); and North Sea Banks (NB). Isohaline lines differ by 0.5 ($S = 1$ to 8) and 3 units ($S = 8$ to 35), respectively.

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. C1).

6.3.3 Experimental Design and Sampling

Larvae were reared in semi-static, well-aerated 90−l tanks using using microalgae to improve growth, survival and prey ingestion("green water" technique, cryptophytes *Rhodomonas baltica*). Larvae were fed *ad libitum* with known concentrations (1 to 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. 6.2a). 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 ($9.9 \pm 0.4\,°C$, mean $\pm$ 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).

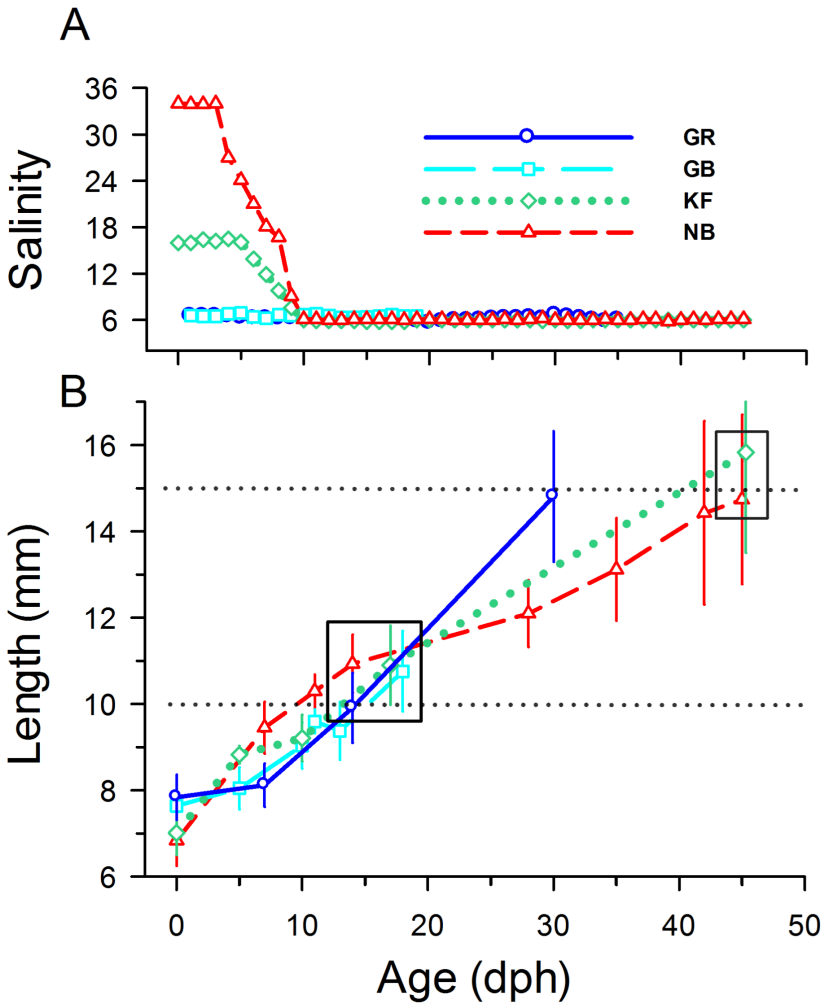

Figure 6.2: Salinity experienced during laboratory rearing (a) and standard length (means±SD) of larvae versus age (days post hatch, dph) (b). Boxes indicate when acute salinity stress tests were performed with Atlantic herring larvae.

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 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. C1). No attempt of grading the larvae into a narrow size range was made but instead larvae were selected randomly.

6.3.4 Biochemical Measurements

Measurements of biochemical condition were made on all larvae used in tests as well as individuals randomly selected from rearing tanks during and after the acclimation period. Each larva was digitally photographed for length measurement (WILD M8 stereomicroscope with Motic Images 2.0 software; Olympus SZH and a Leica DC 300 camera; Image J software) and rapidly shock frozen at −80 °C. Larvae were freeze-dried (Christ Alpha $1-4$ LSC, 0.200 mbar; $>$ 16 h), their dry weight was measured (Sartorius Genius SE2 microbalance ± 0.1 μg) and they were homogenized with 1 % sarcosil Tris-EDTA buffer and glass beads ($0.2-2.1$ mm) in a Retsch shaking mill. Following a modified protocol from Caldarone et al. (2001), concentrations of RNA and DNA were determined spectrofluorometrically with ethidiumbromide as a fluorescence-dye and restriction enzymes to eliminate the nucleic acids (as in Peck et al. 2012). Larvae $>$ 10 mm standard length (L) were measured individually, whereas 2 or 3 smaller larvae were pooled for a measurement. Standardized RNA-DNA ratios were then calculated based on the slopes of calibration lines (Caldarone et al., 2006).

6.3.5 Statistical Analysis

The salinity at which 50 % survival occurred (LC_{50}) was calculated from a four parameter logistic curve:

$$\text{Survival} = ST_{\min} + \frac{ST_{\max} - ST_{\min}}{1 + (\frac{S}{LC_{50}})^{-a}} \tag{6.1}$$

where $ST_{\min}$ and $ST_{\max}$ are minimum and maximum survival (%), S is salinity and a is a fitted constant describing the steepness of the curve. The LC_{50} values were compared across the Baltic and North Sea origins (10-mm larvae only) and across the two larval sizes (10 mm, $n = 4$ per S and 15 mm, $n = 2$ per S) using a permutation test (1000 iterations). For larvae tested at salinities close to the LC_{50} value in each trial ($S = 1.5-3.0$), nonlinear regressions were applied to describe the effect of larval standard length (L; 1-mm size bins) on survival time (h):

$$\text{Survival time} = b + c \cdot (1 - e^{(-d \cdot L)}) \tag{6.2}$$

where b, c and d were constants and L is standard length in mm. Differences among populations in the *sRD* of 10-mm larvae were tested using a one-way ANOVA and a pairwise multiple comparison post-hoc test (Holm-Sidak). For 15-mm larvae, population comparisons (only KF and NB) were made with a Mann-Whitney rank sum test. For all analyses a significance level of p = 0.05 was used. All statistical analyses were conducted using R (R Development Core Team, 2011) and Sigma Plot (Systat Software, San Jose, CA).

6.3.6 Baltic Sea Salinity Projections

Annual ensemble means and ranges of projected sea surface salinity (*SSS*) were calculated for the time periods 1969 to 1998 and 2070 to 2099 based on RCO−SCOBI (Rossby Centre Ocean model and Swedish Coastal and Ocean Biogeochemical model) simulations, driven by four regionalized Global Climate Models (Meier et al., 2011, 2012). The four projections were A1B (RCAO-HadCM3-A1B-REF), A1B-1 (RCAO-ECHAM5-A1B-1-REF), A1B-3 (RCAO-ECHAM5-A1B-3-REF) and A2-1 (RCAO-ECHAM5-A2-1-REF). Previous runs with similar settings resulted in modeled average salinities that have been validated against observed *SSS* from Janssen et al.'s 1999 combined field observations (see Meier et al., 2006). Although some small differences were observed between field and model salinities ($S < 1$), these variations were stable and the authors were confident about the reliability of their model results. Similarly, salinity data compiled by Janssen et al. (1999) were used in this study to calculate present day suitable habitat regions for survival of herring (using our salinity trial results). Present day and projected future *SSS* (for all four scenarios) were averaged to $0.75\,^{\circ} \cdot 0.75\,^{\circ}$ subareas. Based on these average hindcast and forecast *SSS* values we determined habitat suitability following Eq. 6.1 and using the parameter sets determined for the four populations. Only experiments including

small larvae were considered. As herring in the Baltic Sea spawn in shallow coastal area we further extracted from the $0.75\,^{\circ} \cdot 0.75\,^{\circ}$ gridded data the reconstructed and projected salinity and the respective suitability value for all coastal areas (defined as having at least one land neighbor rectangle). For each scenario and each population the mean salinity and habitat suitability was once determined based on all Baltic Sea estimates (hindcast and projection) and once as mean of all coastal rectangles.

6.4 Results

6.4.1 Larval Herring Condition

During and after acclimation to $S = 6$, mortality was low and did not differ from that observed in tanks maintained at the natal S. After acclimation, larvae from all four populations were in good nutritional condition ($sRD > 2.5$; Tab. C1) but the mean sRD for small (10-mm) larvae was significantly lower in NB compared to KF and GB (one-way ANOVA, df = 2, F = 4.386, p = 0.017, no data from GR). Between the mean sRD of larger (15-mm) larvae from KF and NB, no significant differences were observed (Mann-Whitney rank sum test, $p = 0.641$, see Tab. C1).

6.4.2 Salinity Tolerance

Based on the loss of equilibrium of larvae, LC_{50} values from 1.9 to 2.7 and from 2.0 to 2.1 were calculated for small (10-mm) and large (15-mm) larvae, respectively (Fig. 6.3, see Tab. 6.1 for parameters of nonlinear regressions). There was no significant difference in the LC_{50} values of the different Baltic Sea populations ($p > 0.46$, permutation test, $n = 1000$), nor between those (all populations pooled) and the North Sea population ($p > 0.85$, permutation test, $n = 1000$). In the KF and NB populations, larger (15-mm) larvae were slightly, although not significantly, more tolerant to low salinity (lower LC_{50} values, $p > 0.25$, permutation test, $n = 1000$) than 10-mm larvae (Fig. 6.3). Focusing on the narrow range in salinities bracketing the LC_{50} values ($S = 1.5$ to 3.0), survival time increased with increasing body size (Fig. 6.4). The positive correlation between survival time and standard length was strongest for GB larvae, followed by KF larvae, with no clear trend in NB (Fig. 6.4C; GR not determined).

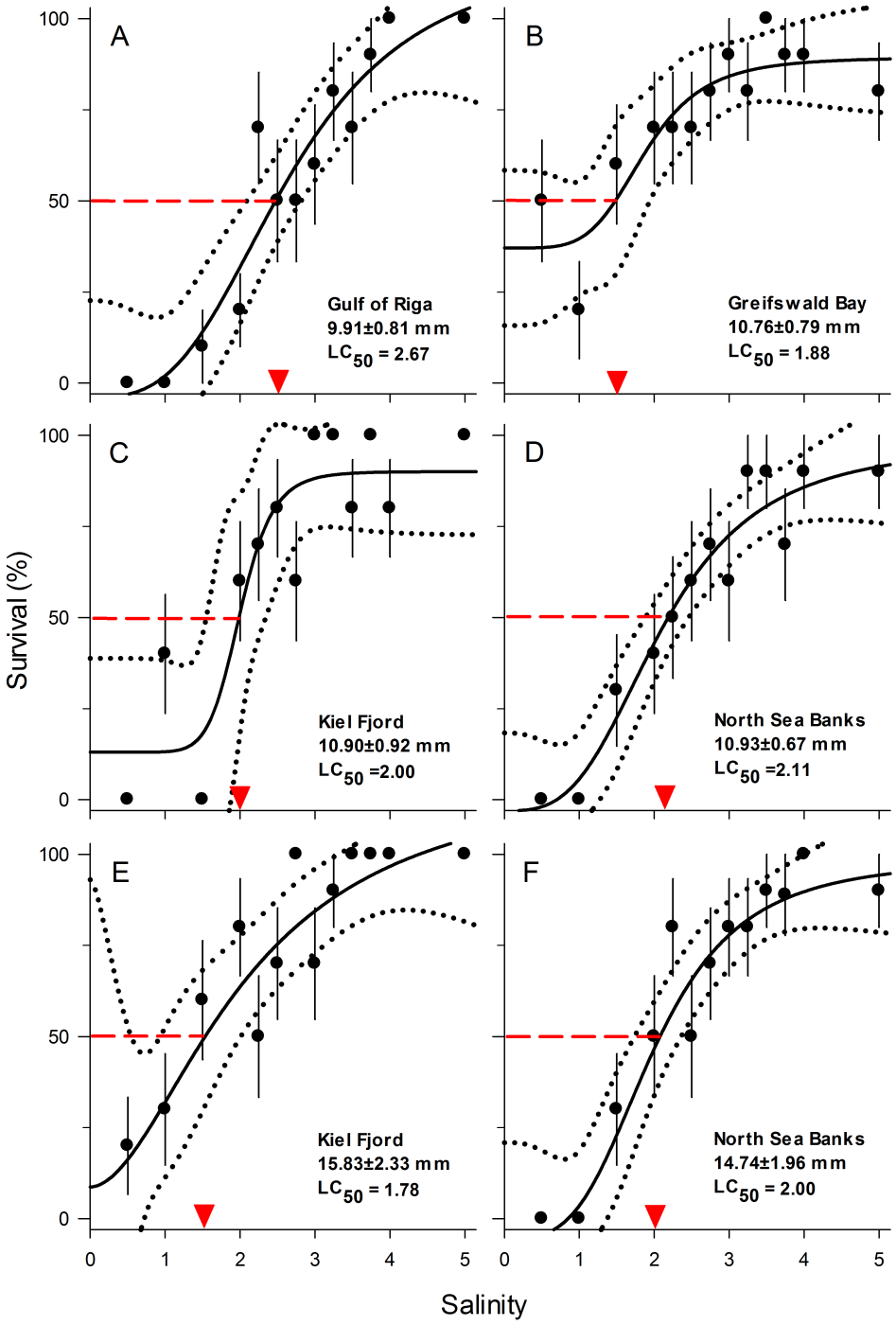

Figure 6.3: Survival of herring larvae over varying salinity levels for all acute short term salinity tolerance tests of 10 and 15 mm L larvae (mean±SD) with L, LC_{50} values (red triangle) and 95 % confidence bands given. Different panels show a) GR ($R^2 = 0.91$), b) GB ($R^2 = 0.80$), c) KF 10 mm ($R^2 = 0.82$), d) NB 10 mm ($R^2 = 0.94$), e) KF 15 mm ($R^2 = 0.84$) and f) 15 mm ($R^2 = 0.93$) trials. Medium dashed line (red) indicates 50 % survival. All logistic regressions were significant with $p < 0.001$, and GB and KF 10 mm with $p = 0.002$ and 0.001, respectively.

Table 6.1: Parameters of the nonlinear regressions between survival and salinity for all short-term trials with Atlantic herring larvae. Nonlinear regressions were based on Eq. 6.1 and parameter estimates are based on the overall best-fit solutions shown in Fig. 6.3 (see Fig. 6.3 caption for R^2 values). The parameters are abbreviated as follows: $ST_{\min}$ = minimum survival (%), $ST_{\max}$ = maximum survival (%), LC_{50} = salinity at which 50 % survival occurred, a = a fitted constant describing the steepness of the curve (also called hillslope). Please see Fig. 6.1 for a description of the population legend.

Population (body length)	Parameter	Coefficient	Std. error	t-value	p-value
KF (10 mm)	$ST_{\min}$	13.03	11.39	1.14	0.28
	$ST_{\max}$	90.09	7.70	11.70	< 0.0001
	LC_{50}	2.00	0.19	10.56	< 0.0001
	a	9.15	7.50	1.22	0.25
GR (10 mm)	$ST_{\min}$	-3.81	11.70	-0.33	0.75
	$ST_{\min}$	118.24	33.16	3.57	0.01
	$ST_{\min}$	2.67	0.52	5.18	0.00
	a	3.05	1.52	2.00	0.08
GB (10 mm)	$ST_{\min}$	37.08	9.42	3.94	0.00
	$ST_{\max}$	89.41	7.76	11.52	< 0.0001
	LC_{50}	1.88	0.30	6.19	0.00
	a	4.70	3.31	1.42	0.19
NB (10 mm)	$ST_{\min}$	-3.05	9.47	-0.32	0.75
	$ST_{\max}$	97.78	14.08	6.94	< 0.0001
	LC_{50}	2.11	0.24	8.79	< 0.0001
	a	3.14	1.21	2.59	0.03
KF (15 mm)	$ST_{\min}$	8.69	37.30	0.23	0.82
	$ST_{\max}$	122.86	54.58	2.25	0.05
	LC_{50}	2.08	0.84	2.48	0.04
	a	1.86	1.97	0.94	0.37
NB (15 mm)	$ST_{\min}$	-5.26	11.55	-0.46	0.66
	$ST_{\max}$	98.63	12.22	8.07	< 0.0001
	LC_{50}	2.00	0.22	9.07	< 0.0001
	a	3.43	1.38	2.48	0.04

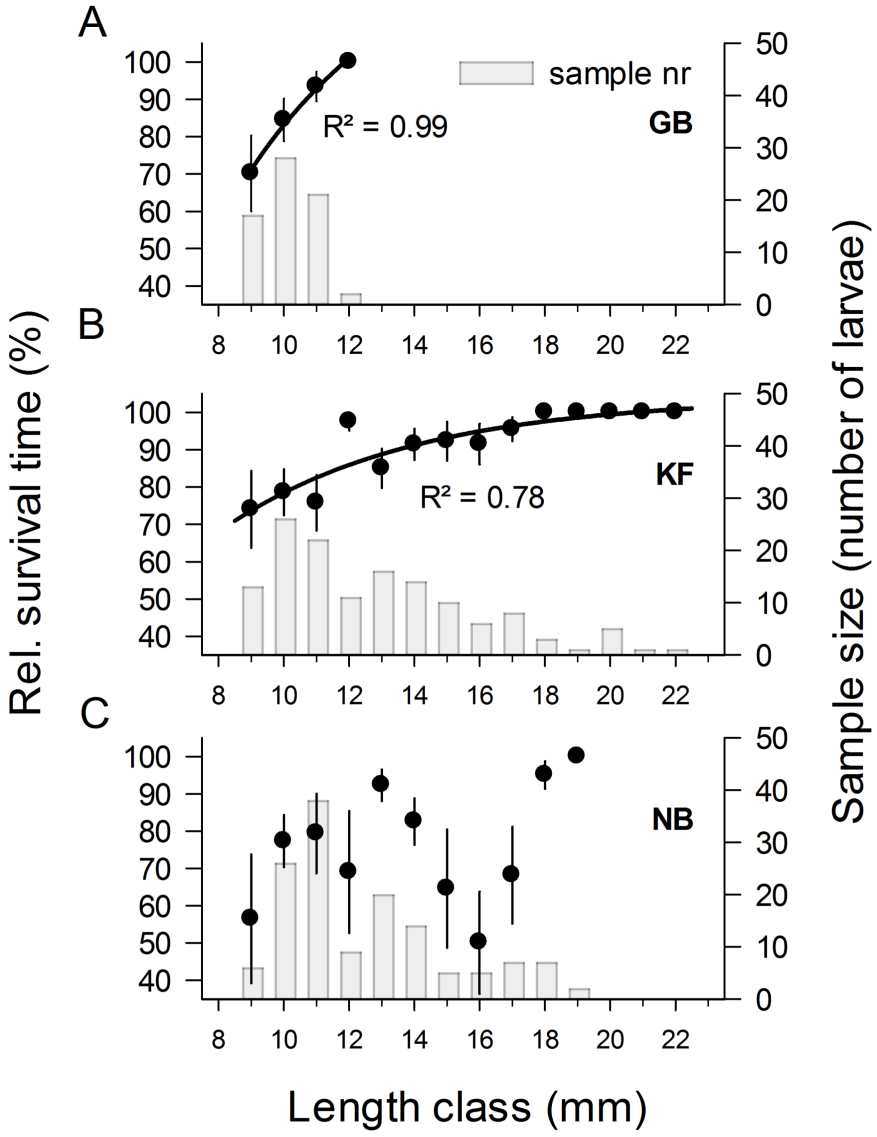

Figure 6.4: Effect of standard length on relative survival time (mean±SE) for Atlantic herring larvae of a) GB, b) KF and c) NB populations tested between $S = 1.5 - 3.0$ (around LC_{50}). A size bin range of 1 mm was used and 10 and 15 mm runs merged (b+c); bar plots represent sample size per bin. Nonlinear regressions were significant in a) GB ($p = 0.0154$) and b) KF ($p < 0.0001$) but not in c) NB ($p = 0.3240$).

6.4.3 Baltic Sea Salinity Projections and Suitabilities

Based on the reconstructed hindcast the average salinity in the Baltic Sea including all $0.75° \cdot 0.75°$ rectangles (coastal rectangles) was 6.17 (5.56) (Tab. 6.2). Depending on the future scenario, mean salinity decreased to values of $S = 4.32$, 4.36, 4.39 and 4.68 in A1B, A2-1, A1B1-1 and A1B1-3, respectively. In coastal areas projected average salinities were between 3.87 and 4.21. Applying Eq. 6.1, the parameter sets determined for smaller larvae (Tab. 6.1) and the salinity values obtained from the four forecast scenarios yielded in total 16 combinations (Fig. 6.5A). Considering coastal areas, lowest average suitabilities (56−58) were obtained for the combinations KF, GB, GR and A2-1 and A1B-3, the highest average suitability was 72 for NB in A1B whereas in the hindcast coastal suitability was

77 (NB) to 83 (GR) (see Tab. 6.2). Within the reconstructed hindcast, salinity was lowest in the Gulf of Bothnia and in the Gulf of Finland with values below 5. Within the central Baltic Sea salinity values between 4 and 7 and in the Kattegat above 10 were reported. Within all future scenarios salinity decreased in the whole Baltic Sea and was below 4 for the whole northern and eastern Baltic Sea (Fig. 6.5C) and between 4 and 6 in the central Baltic Sea. Following the low salinity, the suitability of the Bothnian Bay and the Gulf of Finland also decreased in the future scenarios to values below 40 in contrast to values of above 90 at least in the Southern Bothnian Bay.

Table 6.2: Current and projected habitat suitability of Atlantic herring larvae in the Baltic Sea. The mean salinity and suitability is based on a hindcast (Janssen et al., 1999), projections for sea surface salinity (Meier et al., 2011) and the parameters derived from nonlinear regressions describing the experimentally determined survival of 10-mm herring larvae from four different populations at low salinities (see Eq. 6.1, Tab. 6.1, Fig. 6.3). Data were gridded as $0.75° \cdot 0.75°$ rectangles and coastal areas defined by having at least one land rectangle as neighbor. Please see Fig. 6.1 for the population legend and be referred to Meier et al. (2011) for a description of the different climate scenarios.

Population	Scenario	mean salinity all areas	mean salinity coast	mean suitability all areas	mean suitability coast
GB	Hindcast	6.17	5.56	84	82
KF	Hindcast			82	78
NB	Hindcast			82	77
GR	Hindcast			90	83
GB	A1B	4.32	3.87	76	71
KF	A1B			76	71
NB	A1B			77	72
GR	A1B			76	71
GB	A1B-1	4.39	3.96	71	63
KF	A1B-1			71	63
NB	A1B-1			73	66
GR	A1B-1			71	63
GB	A1B-3	4.68	4.21	66	57
KF	A1B-3			64	56
NB	A1B-3			68	60
GR	A1B-3			64	56
GB	A2-1	4.36	3.91	66	57
KF	A2-1			66	58
NB	A2-1			71	62
GR	A2-1			66	58

6.5 Discussion

Understanding and comparing physiological thresholds for survival can provide a more thorough, mechanistic understanding of how climate-driven changes in key environmental factors will potentially impact on the productivity and distribution of species in the future. In addition, physiological measurements can help reveal the adaptive capacity of individuals and populations to persist within altered habitats (Hollowed et al., 2013). Within species, tolerance to factors such as water temperature, pH and salinity is stage-specific and larvae have a narrower range in tolerance than adults (see references in Llopiz et al. 2014) Although considerable work has focused on the effects of temperature (Pörtner and Peck, 2010) and OA (Kroeker et al., 2013), the main factors projected to change in a future ocean, changes in salinity may also cause considerable changes in the abundance and composition of species in brackish water environments (Mackenzie et al., 2007).

6.5.1 Salinity Tolerance and Survival

The relatively high biochemical-based condition (e.g. $sRD > 2.5$, see Meyer et al. 2012) of the larvae from populations stemming from both intermediate ($S = 16$) as well as fully marine ($S = 34$) conditions suggests that herring larvae are fully capable of acclimating to low ($S = 6$) salinity. Larvae also displayed growth rates at $S = 6$ (see Tab. C1) which were similar to those obtained at their natal salinity in the laboratory as well as measured in field-caught larvae (von Dorrien et al., 2013), although faster mean growth rates (to $0.52\,\mathrm{mm\,d^{-1}}$) have been calculated for herring larvae collected from more northern areas of the Baltic Sea (Hakala et al., 2003). However, the lack of any significant difference in the low salinity tolerance (LC_{50} values) of larvae from brackish ($S = 6$) versus marine ($S = 35$) populations, suggests that capacity of herring to adapt to salinities lower than those associated with current habitats is limited. The larvae from each population had a similar, physiological threshold despite large differences in natal salinities.

Salinity is a key factor affecting the distribution of fish in the Baltic Sea and the low salinity thresholds for early life stages (eggs, larvae, juveniles) of the five, main resident marine fishes (Atlantic herring, Atlantic cod, European sprat, European flounder (*Platichthys flesus*), and plaice (*Pleuronectes platessa*)) have been previously examined (Holliday and Blaxter 1960; Holliday and Pattie Jones 1965; 1967; Yin and Blaxter 1987; Nissling and Westin 1997; Nissling et al. 2002; Petereit et al. 2009) (see interspecific-

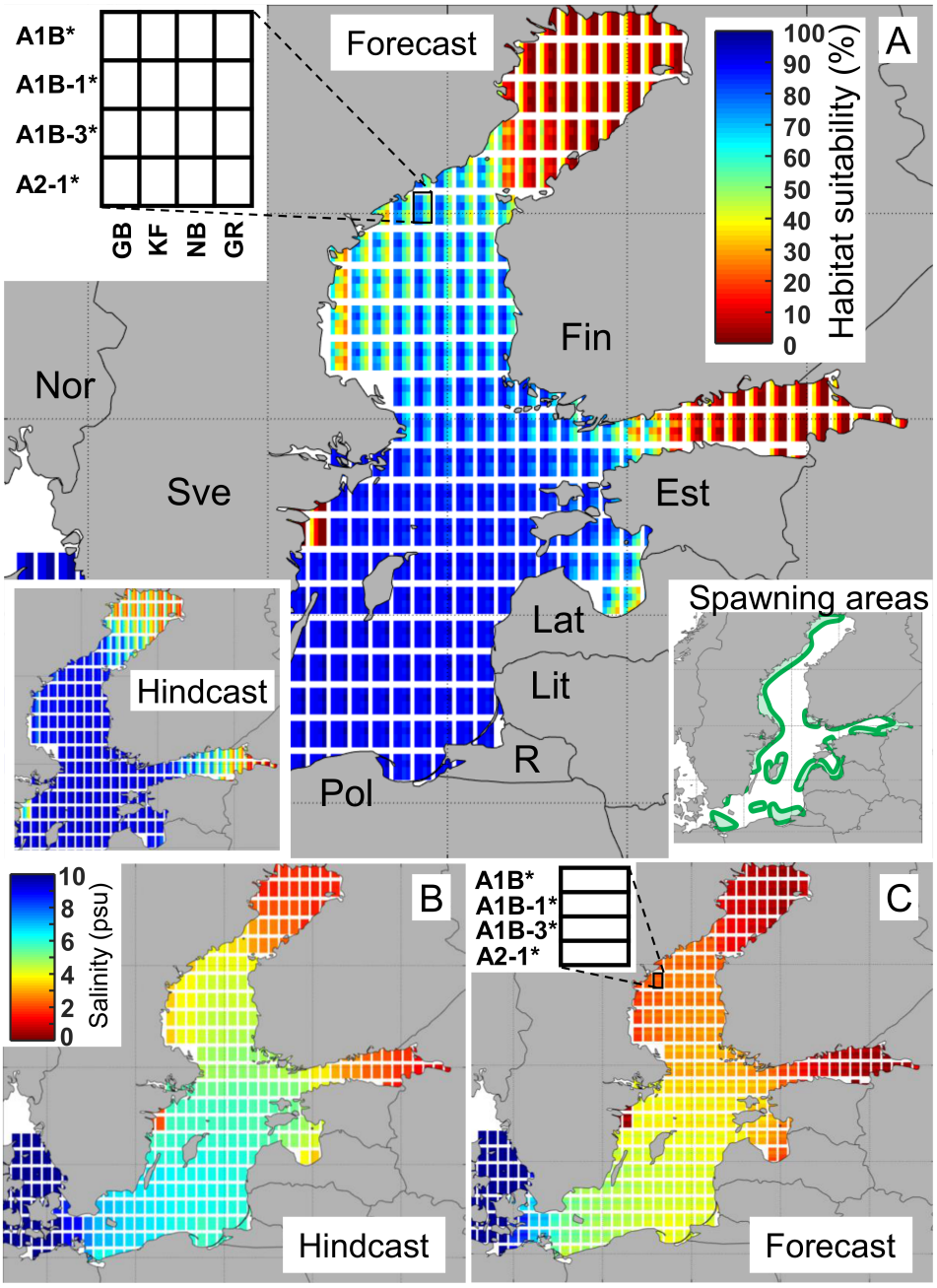

Figure 6.5: Baltic Sea regions suitable for survival of Atlantic herring larvae at present (panel A, Hindcast) and at the end of the 21st century (panel A, Forecast). The projections are based on projected sea surface salinity changes (panel C, Forecast) and nonlinear model estimates (see Eq. 1) of 50 % survival of 10-mm larvae in the laboratory (Tab. 6.1). The sea surface salinity (*SSS*) between 1969 – 1998 (panel B, Hindcast) and 2070 – 2099 (panel C, Forecast) has been calculated and projected by Meier et al. (2011, 2012) in RCO-SCOBI simulations and was driven by four regionalized Global Climate Models (see text for further details). Spawning habitats (A, Spawning areas) have been included using GIS maps derived from available literature (see text for further details). Note, that the color code describes habitat suitability in panel A while it refers to salinity in panel B.

comparison in Fig. C1, Tab. C2). Salinity thresholds for fertilization of eggs and normal embryonic development appear to be lowest in Atlantic herring ($S = 3-5$) and European flounder ($S = 5-7$) and higher in plaice ($S = 9-15$) and Atlantic cod ($S = 11-15$) (Petereit et al., 2009; Nissling and Westin, 1997; Nissling et al., 2002). However, to the best knowledge, no previous study has examined how body size or population influence low salinity tolerance of feeding stages of Atlantic herring larvae. Our short-term tolerance tests suggested that 10- to 15-mm herring larvae could not tolerate salinities < 2. Previous studies on herring larvae noted an absence of a heartbeat at $S = 1.4$ (Holliday and Blaxter, 1960) or $S = 1.0$ to 1.5 (Yin and Blaxter, 1987) which agree with our results (based on the loss of equilibrium of larvae). The 24-h survival of young (yolk sac) and older (exogenously feeding) larvae of plaice suggested a tolerance of $S = 5$ and 1, respectively (Holliday and Pattie Jones, 1967) whereas yolk sac larvae of Atlantic cod and European flounder could tolerate $S = 2$ to 3 and 0 to 1, respectively (Yin and Blaxter, 1987).

These salinity tolerance results collected on embryos and larvae stem from studies that employed either short-term (measuring heartbeat and/or equilibrium), or longer-term (survival end point) tests. Short-term tolerance tests are relatively simple, rapid and can provide useful, physiological-based information on climate sensitivity of species and life stages. Standard protocols and endpoints are needed to make robust comparisons of climate sensitivity within (as well as among) taxa (compare Fig. C1). Moreover, long-term experiments are needed to explore the potential for adaptation and the potential life history trade-offs associated with survival and growth at sub-optimal environmemtal conditions (Llopiz et al., 2014). Donelson et al. (2012), for example, have highlighted that transgenerational acclimation can be a strong mechanism to cope with rapid climate change and single generation studies might underestimate the adaptive capacity of fish species.

Some populations of Atlantic herring reside year-round in the Baltic Sea and, given the body size at which gills develop, individuals ≥ 20 mm in length are expected to have relatively strong osmoregulatory capacity (de Silva, 1974). Prior to gill formation, small/young larvae rely on their integument for ionic homoeostasis (Glover et al., 2013), with chloride (mitochondrial rich) cells distributed across the yolk sac and body (Shelbourne, 1957; Kaneko et al., 2002). Since chloride cells do not increase in number but

merely change distribution during ontogeny (Wales and Tytler, 1996), the tendency for increased salinity tolerance in 15- compared to 10-mm larvae in this study was most likely related to increased energy available for osmoregulation in larger compared to smaller larvae. In other marine fishes residing in estuarine waters, salinity tolerance also tends to increase with increasing age/development. Examples of this include Pacific herring (*Clupea pallasi*), European plaice, gilt-head bream (*Sparus aurata*), European sea bass (*Dicentrarchus labrax*), starry flounder (*Platichthys stellatus*) and striped mullet (*Mugil cephalus*)(Holliday 1969; Varsamos et al. 2005 and references therein; Bodinier et al. 2010; Fig. C1, Tab. C2). However, changes in salinity tolerance during ontogeny depend on the life history strategy of the fish species. For example, anadromous species tend to become less tolerant to low salinity as they develop (see DiMaggio et al., 2015). However, changes in salinity tolerance during ontogeny depend on the life history strategy of the fish species. For example, anadromous species tend to become less tolerant to low salinity as they develop (see DiMaggio et al., 2015).

6.5.2 Salinity and Growth Optima of Marine Fishes

It is important to note that, within tolerable limits, increased or decreased salinity can influence aquatic organisms via a variety of more subtle direct and indirect pathways. Indirect effects include adjustments to metabolic costs associated with osmoregulation (e.g. masking factors; Fry 1971; Yamashita et al. 2001) which, in fish, can be 10 to 50 % of the energy assimilated from food (Boeuf and Payan, 2001; Kidder et al., 2006). Direct effects include altering protein digestibility, food conversion efficiency, hormone production or feeding behavior (Boeuf and Payan, 2001). Depending on the geomorphology of different habitats and estuarine conditions, future freshening could have positive effects on marine fishes. For example, most marine fish are hypotonic in full strength seawater and are isotonic and often display maximum growth rates at lower (brackish) salinity (e.g. $S \sim$12, Boeuf and Payan 2001; Zydlewski and Wilkie 2013). For marine fish in the Baltic Sea such as European flounder, Atlantic cod and turbot (*Scophthalmus maximus*) as well as Atlantic herring, juveniles often display the highest growth rates at $S = 12$ to 19 (Gutt, 1985; Boeuf and Payan, 2001; Imsland et al., 2002; Rajasilta et al., 2011). However, some not all marine fish using estuaries as nursery grounds are expected to benefit from climate-driven freshening of those habitats (e.g. Deacon and Hecht 1999; O'Neill et al. 2011). Responses to changes in salinity within tolerable limits may be positive or negative and appear to be species specific.

6.5.3 Future Climate-Driven Challenges for Marine Fishes in the Baltic Sea

The salinity of the Baltic Sea is determined by the balance between river runoff, evaporation and highly stochastic, wind-driven inflow events of North Sea water into the deep basins during winter and spring and albeit several large inflow events have occurred during summer (starting in 1996), no general trend has been observed so far (BACC, 2015). In the future, diminished inflow events and increased precipitation in the whole Baltic area will increase (Meier et al., 2006; BACC, 2015). In the future, diminished inflow events and increased precipitation across the Baltic region will increase (Meier et al., 2006; BACC, 2015). The severity of freshening of the Baltic Sea is projected to be 4 to 13 % with the magnitude of decline in salinity depending on assumptions of the magnitude of the increase in river runoff (from 15 to 22 % increase) (Meier et al., 2012). Salinity changes with depth will depend on the topography of individual basins, with shallower and currently weakly stratified basins, such as the Gulf of Finland and the Bothnian Bay, likely to experience greater freshening in surface and bottom layers resulting in a reduction in vertical stability. On average, a 1.5 to 2.0 $\mathrm{g\,kg^{-1}}$ decrease in salinity is projected at the end of the 21$^{\mathrm{st}}$ century with strong implications for the productivity and biodiversity of the Baltic Sea (BACC, 2008; Meier et al., 2012). Based on these projected changes in salinity (and barring any potential future physiological adaptation), the physiological thresholds determined in our larval experiments suggest that large regions of the Baltic Sea, including areas now used for spawning, would be unsuitable for herring larvae by 2100 (compare Fig. 6.5). For example, a complete loss of spawning areas in most northern ($> 59\,^{\circ}\mathrm{N}$) areas such as Bothnian Bay and the Gulf of Finland (Oulasvirta et al., 1985) is expected. These losses of herring spawning habitat in a less saline Baltic Sea agree well with the expected shift in species composition towards a dominance of freshwater species (Mackenzie et al., 2007). Optimal salinities for growth of many freshwater species such as perch (*Perca fluviatilis*) and pike-perch (*Sander lucioperca*) are reported to range from $S = 0$ to 5 (Overton et al., 2008; Ložys, 2004). Other species, such as whitefish (*Coregonus sp.*) are able to tolerate low salinity and are expected to expand their spawning habitat in the future (Albert et al., 2004). The extent of changes in marine fishes inhabiting brackish waters will depend on the location of spawning and nursery areas in relation to projected changes in salinity gradients as well as the ability to compete with freshwater fishes for resources.

Projected climate-driven changes in the salinity of brackish environments are far less

examined compared to warming and acidification, but salinization or freshening may be just as an important driver of habitat loss/expansion either alone or in combination with changes in other factors (Najjar et al., 2010). The present study utilized a fairly simple "challenge test" to examine how climate-driven freshening of the Baltic Sea can reduce suitable spawning habitat for a marine fish species. Larvae from Baltic populations had the same low salinity tolerance as larvae from marine populations suggesting a "hard limit" on habitat suitability and limited adaptive capacity to future freshening in the Baltic Sea. This study highlights the importance of the physiological tolerance of fish early life stages as a potential bottleneck constraining population persistence of fishes in a future climate (Llopiz et al., 2014). We recommend including multiple, interacting factors (T, O_2, pH, S) and comparing short-term (acute) effects with the results of longer-term (chronic) experiments testing growth and acclimation potential (Pörtner et al., 2005; DePasquale et al., 2015).

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Chapter 7

General Discussion

In the marine ecosystems of the northern hemisphere Atlantic herring (*Clupea harengus* L.) represents a valuable forage fish species with its intermediate trophic position ensuring the energy flow between plankton and larger, piscivorous predators. Since fluctuations in abundances and recruitment of forage fish populations are often induced by climate variability (physical forcing) and sometimes directly provoke negative ecological corollaries, a proper management of these species is needed to maintain marine ecosystem functioning (Peck et al., 2014). To support a sustainable use, this thesis aimed at deepening the current understanding of behavioral and physiological responses of individual Atlantic herring larvae in the North and Baltic Seas to challenges caused by so called “bottom-up" factors. In particular, variation in temperature and changes in salinity as well as match-mismatch situations with plankton blooms and prey and their effects on larval growth, condition, swimming performance and ultimately survival were experimentally investigated and partly implemented into model simulations.

7.1 Implications for Atlantic herring larvae matching spring blooms

With regard to global climate change, projected warming will have a strong effect on marine ecosystems, covering dimensions on the scale of individual metabolic rates to plankton bloom dynamics. Temperature plays a dominant role for the timing and magnitude of seasonal plankton blooms (Edwards and Richardson, 2004) and, according to Richardson (2008), there is a “growing appreciation that the composition, abundance, and trophic efficiency of plankton communities are tightly linked to water temperature". A good example of the climate-driven effects on plankton blooms is the observed earlier onset of bloom

dynamics, that is not of based on annual variability but part of a distinct trend (Hays et al., 2005; Kahru et al., 2011). Experiments, testing the effect of future temperature scenarios, have revealed a decreasing trend of phytoplankton biomass with temperature (Sommer and Lengfellner, 2008). When examined in warmed mesocosms, the succession of planktonic components of Baltic Sea spring blooms was more rapid (Aberle et al., 2012, 2015) potentially narrowing the time window for herring larvae to feed and grow in the presence of not only copepods, but also algae and protists.

The phytoplankton blooms in the Baltic Sea are largely composed of diatoms and dinoflagellates, albeit climate-driven changes appear to have altered this composition, especially in the central regions, from diatom- to dinoflagellate-dominated blooms (Wasmund and Uhlig, 2003; Klais et al., 2011; Wasmund et al., 2011). During spring, these two phytoplankton groups compete for nutrients and with warmer winters, dinoflagellates are favoured (Klais et al., 2013; Wasmund et al., 2013). Due to well mixed water bodies the spring blooms in shallow coastal areas, where Western Baltic Spring Spawning (WBSS) herring reproduce (Kiel and Mecklenburg Bight), are still dominated by diatom blooms that start during February-March (Wasmund et al., 2013). However, in the central Baltic Sea areas the spring bloom starts later (April-May) and diatom blooms are often succeeded by dinoflagellates, or blooms are initially dominated by them (Wasmund et al., 2013).

In order to gain a deeper insight into the benefits for young WBSS Atlantic herring larvae matching the start of the above described phenology of spring phyto- and protozooplankton production, the direct effects of microalgae and dinoflagellates on individual larvae have been experimentally investigated in this thesis (see chapter 3). An increased “window of opportunity" was observed for yolk sac herring larvae when reared together with the cryptophyte *Rhodomonas baltica* (RB) and the dinoflagellate *Oxyrrhis marina* (OX) - meaning larvae reared with both phyto- and protozooplankton had a longer time frame compared to larvae reared in sea water, during which they were priming their digestive apparatus (precocious production of trypsin). Accompanied with this earlier production of digestive enzymes (trypsin), larvae reared in the presence of microalgae and protists showed precocious and more intense feeding when offered adequate prey (copepod nauplii). However, the passive and exclusive ingestion of microalgae and protists could not compensate for the larvae’s energetic requirements and hence did not prolong

life-span after the first-feeding period. Previously, studies on first-feeding Northern Anchovy (*Engraulis mordax*) larvae have shown that rearing based solely on the unormared dinoflagellate *Gymnodinium splendens* (2-4 times larger than *O. marina*) was sufficient to maintain survival levels comparable to wild plankton diets, although growth became asymptotic after a while due to the low energetic content of the prey (Lasker et al., 1970; Hunter, 1977). The quantity and quality of prey are both key factors establishing realized growth rates of consumers and in terms of food quality, essential fatty acids (EFA) are known to be important for the growth of early life stages of herring (Paulsen et al., 2013). In fact, microalgae conservatively transfer EFA compositions to consumers and protists can even exert trophic upgrading to improve algal EFA for tertiary consumers (Klein Breteler et al., 1999; Malzahn et al., 2007). Hence, the benefits of microalgae and protists must become most clear in fish larvae that have successfully overcome the critical phase of first-feeding.

To pursue this assumption in more detail, an additional experiment with unreplicated tanks (not previously mentioned) had been conducted with larval herring from the same WBSS batch as used in chapter 3. Simultaneously to the previously described experiments in chapter 3, larvae were reared in single 90-l tanks (using identical environmental conditions and methods), however, with continuous access to *ad libitum* rations of *A. tonsa* stages. Similarly, the treatments contained a) sea water, b) RB and c) RB+OX, but swimming and feeding activity was measured directly in the 90-l tanks. Although all *Acartia* stages were well-fed prior to feeding them to the larvae, markedly different growth trajectories could be observed after 16 days, with growth rates of 0.12, 0.16 and $0.25\,\mathrm{mm\,d^{-1}}$ in the SW, RB and RB+OX tanks, respectively (see App. B, Fig. B.1). Furthermore, larvae had a 1.6-times greater dry mass, 1.3-times higher nutritional condition (standardized RNA-DNA ratio), 60 % higher swimming and 2.5-times higher feeding activity and demonstrated an increased tryptic activity in RB+OX compared to tanks without microalgae and heterotrophic protists (see App. B, Fig. B.1+B.2). An increase in trypsin activity in larvae reared in microalgae has been previously reported (Cahu et al. 1998; Lazo et al. 2000; note, prey items contribute very little (1-2 %) to the measured amounts of tryptic enzymes (Rønnestad et al. 2013; Ueberschär, GMA Büsum, pers. comm)). These provisional data suggest indirect benefits of trophic upgrading that may affect even growth and condition of tertiary consumers (Malzahn et al., 2007).

Body size is an important factor affecting foraging ability, the resistance to starvation, and risk of predation, hence Miller et al. (1988) and other authors have postulated that "bigger is better". A recent study from Garrido et al. (2015) has, for example, highlighted, using otolith-diameter-at-hatch from both laboratory and field sampling, that larger-sized larvae at hatch have higher overall survival chances. This assertion is supported for in situ measurements of the larvae of the WBSS population where mortality rates are higher for smaller members of larval cohorts in some nursery grounds (Hesse, C., GEOMAR Kiel, pers. comm.). The abundance of larvae > 20 mm standard length (L) is strongly correlated with year class indicating that the critical mortality processes are acting on smaller larvae (Oeberst et al., 2009). Given the trends observed (see previous paragraph), larvae with continual access to copepods would be expected to reach 20 mm L in 52 days in the presence of RB+OX compared to 108 days in the absence of phytoplankton and protists. Thus it seems that growing rapidly through this critical period requires that larval cohorts not only match the timing of copepod production (Cushing, 1990) but also the timing of abundant phytoplankton and protists. However, in the case of WBSS herring, mechanisms defining larval mortality are more complex. In the Greifswalder Bay for example, Polte et al. (2014) have found the cohorts occuring later during the spawning season to be decisive for the surviving year class, i.e. larvae that are produced very early in the year have reduced chances of survival. The complex interactions of factors, such as temperature, prey availability or the presence of predators (see Kotterba et al., 2014) still make it difficult to disentangle the multiple causes of the currently low recruitment of WBSS herring.

7.2 Effects of temperature and prey abundance on larval Atlantic herring performance and survival

Apart from controlling the above described temporal match-mismatch dynamics of spring plankton blooms with larval fish occurrences, temperature can also affect autumn-spawned offspring during winter months when larvae are naturally confronted with prey-poor environments. A study from Laurel et al. (2011), using Pacific cod larvae, observed a cooler temperature bridging gaps in prey availability (for short-term periods), similar to the findings presented in chapter 4. Here, a cooler temperature (7 °C vs 10 °C) likely reduced metabolic expenditures and minimized size-selective mortality (although a comparison between the differently aged/sized larvae from the two populations is rather difficult).

With regard to the observed and projected climate-driven increases in temperature (e.g. $\sim 1\,^{\circ}\mathrm{C}$ between 1977 and 2001 in the North Sea), habitat usage of marine fish in temperate regions was observed to underlie changes in latitude and depth (Perry, 2005). Besides that, elevated temperatures will likely increase metabolic rates and therefore metabolic expenditures which will entail an accompanied increase of foraging due to the higher energetic requirements. Given the lower productivity during winter, this might have serious implications for autumn- and winter-spawned fish larvae such as North Sea herring (see Fig. 1.2). In the case of autumn-spawned North Sea herring larvae, a recent study from Alvarez-Fernandez et al. (2015) has, however, highlighted that zooplankton abundance seems to have a stronger effect on larval herring survival than temperature.

Regardless of the season, a mismatch with prey can rapidly cause a life-threatening situation for larvae that generally possess little reserves and starvation might affect older larvae even stronger than smaller ones due to their exclusively exogenous feeding (Suneetha et al., 1999; Malzahn et al., 2007). In chapter 4, behavioral (reduction in swimming activity after $2-4$ days) and metabolic adjustments (down-regulation of standard metabolic rates by $8-13\,\%$) were observed for exogenously feeding larvae that were confronted with a complete mismatch situation with prey over a sustained period of time. When the experimental results were applied in a physiological individual-based model (IBM), larvae that did not adjust their metabolic rate had their life span reduced by about one third. These inter-individual differences in resilience to starvation have been previously observed in laboratory studies and often been linked to physiological or nutritional variability (e.g. Navarro and Sargent 1992; compare Tab. A.1). Biochemical condition indices, such as the standardized ratio of all RNA to DNA (*sRD*), are indicative for the nutritional status and commonly used to identify its decrements in starving larvae (Buckley et al., 1984; Clemmesen, 1994; Caldarone et al., 2001, 2006; Catalán, 2003). Meyer et al. (2012) have recently published an approach that uses percentiles instead of average *sRD*, in order to take the large variability between individuals into account and better "[...] estimate the time required to reach threshold *sRD* levels [...]", the so called "time-to-death". Moreover, the authors highlighted temperature to be decisive for differences in the "time-to-death", an observation that was confirmed in chapter 4 by applying the same percentile approach to the *sRD* results.

Temperature shapes the individual metabolic rates of aquatic poikilotherms (Fry, 1947,

1971) and in combination with body mass, temperature can as well predict developmental time in a wide range of species (Gillooly et al., 2001, 2002). Studies focusing on early life stages of temperate marine fishes, such as Haddock and Atlantic herring, have shown a strong effect of temperature on ontogeny (Martell et al., 2005; Peck et al., 2012). In chapter 5 it is highlighted how temperature can control growth rates (0.21 at 7 °C to 0.34 mm d^{-1} at 15 °C) and affect larval morphology, inducing higher dry weight and body height at warmer conditions. With regard to larval fish development, Johnston et al. (1998, 2001) have observed temperature to control the relative timing of muscle development, i.e. the degree of expression of the myogenic programme over the larval period, and similarly, the larval herring reared at 15 °C showed the fastest development (see chapter 5).

Temperature-induced modifications of muscle developmental rates can have severe implications for swimming performance of individual organisms when compared to similarly-aged conspecifics. The presented critical swimming speed (U_{crit}) results for Atlantic herring larvae support the findings of elevated developmental rate and swimming performance at warmer temperatures by Green and Fisher (2004). In their literature review dealing with swimming speeds in larval fishes, Fisher and Leis (2010) noted that the common measure of swimming performance, critical swimming speed, is difficult to use for estimating overall dispersal patterns, since it describes a speed that is not sustainable for fish larvae over a long time period. However, due to a positive correlation with more sustained swimming speeds (over 24 h) one could get an idea of *in situ* swimming speeds that are otherwise difficult to determine. Likewise, the authors mention a number of different coral reef fish species which show maximum sustainable swimming speeds at 50 % of the respective U_{crit}. With regard to modelling dispersal, they recommend therefore using a value of $50 - 60$ % of U_{crit} to estimate the "[...] maximum potential impact of larval behavior [...]". When comparing routine swimming speeds of similar sized herring larvae ($18 - 22$ mm, slightly different temperatures) to the U_{crit} of herring larvae from the experiments in chapter 5, the derived percentages are very similar to the above mentioned values (the routine swimming speeds given in the literature represent $47 - 65$ % of the observed U_{crit}; see chapter 5, Tab. 5.2; Fuiman and Batty 1997; Batty 1984). Fisher and Leis (2010) have as well speculated, given temperature has a substantial effect on swimming performance, that there are likely "[...] differences in the fundamental mechanistic processes behind larval growth and survival at different latitudes", emphasizing the need to conduct experiments on fish larvae from colder regions. Furthermore, they noted

“[...] important implications for the parameterization of foraging based individual models [...]", which underlines the necessity of including chapter 5's results of temperature-driven ontogenetic differences in swimming speeds into currently existing larval herring IBMs.

In individual-based models, swimming speeds of herring larvae have been previously derived from studies that were all conducted at around 10 °C (see Hufnagl and Peck, 2011). Hence, for a more realistic modelling of larval dispersal and survival, the next crucial step would be to include the larval herring swimming performance at different temperatures into physiological IBMs coupled to hydrodynamic drift models to optimally depicture the interplay between swimming speed, metabolic demands, and viscosity (at low temperatures water becomes more viscous, indicated by low Reynolds numbers (Fuiman and Batty, 1997)). These efforts would result in a more precise estimate of the time when the virtual and initially “passive" particles become “active" ones that can impact both on their dispersal and autonomously determine their encounter rates with prey (by increasing the volume of water searched).

One might argue that focusing merely on starvation effects, ignoring predation as the most dominant driver of larval fish mortality (Fuiman and Magurran, 1994; Houde, 2008), could be a one-sided, biased or insufficient contemplation of the processes governing larval Atlantic herring survival and potential recruitment in the North and Baltic Seas. Predation can affect all larval stages with some predators preferring larger, more conspicuous larvae (see Pepin et al. 1992; Litvak and Legget 1992). However, well-designed studies such as the one on Japanese anchovy from Takasuka et al. (2003) propose that smaller, slow-growing fish larvae, likely in a bad nutritional state due to previous and prolonged mismatches with prey, are statistically more often victims of predation. Experimental studies (see Skajaa et al. 2004 and references within) have highlighted how the responsiveness to stimulation (e.g. by a predator) can be affected by previous periods of starvation. Here, the authors highlight furthermore that differences in escape capabilities may be driven by the strong correlation between size and ontogeny and mention pronounced inter-individual differences. Laboratory experiments using physiological performance measures can therefore help quantifying the effect of potential predation. For example, Fuiman (1989) and Blaxter and Fuiman (1990) observed the susceptibility to a predator to decline faster in herring larvae that are larger in size. Apart from the functional development of auditory bullae, as speculated by the authors, this can be likely

attributed to higher swimming speeds of larvae that developed faster (further ways of larval fish predator defenses are reviewed by Fuiman and Magurran 1994). Based on the above mentioned studies, predation and starvation effects on survival rates of fish larvae might be strongly overlapping, implying that mortality caused by starvation effects might already explain a lot of potential mortality induced by predation.

7.3 How salinity affects Atlantic herring in the Baltic Sea

The brackish Baltic Sea is strongly structured by a horizontal salinity gradient (see Fig. 6.1), which is, compared to temperature, a less well investigated “bottom-up" acting environmental factor. Although sheltered coastal habitats provide the best nursery areas for marine fish larvae such as Atlantic herring in the Baltic Sea (Höök et al., 2008; Paulsen et al., 2013), river-runoff can pose a challenge for marine fish species' offspring in these coastal areas. Due to increased energetic expenditures for osmoregulation above or beneath an iso-osmotic salinity (salinity of 12, Zydlewski and Wilkie 2013), the freshening can compromise an individual's energetic scope, which can affect swimming performance and hence have implications for foraging and predator escape responses (see McKenzie and Claireaux 2010). At hatch, Atlantic herring larvae possess an advantageous volume to surface ratio and are already equipped with specialized chloride cells all over the integument for regulating the osmolality of their body fluids (Bodenstein, 2012). However, important morphological alterations needed for a more efficient osmoregulation, such as gill formation and a fully functional stomach, are initially missing making the larvae more susceptible to changes in salinity compared to further developed conspecifics. In chapter 6, resilience (relative survival time) to an acute, short-term confrontation with low salinity was higher for larger-sized and likely better developed Atlantic herring larvae from the Baltic Sea compared to their smaller and younger conspecifics (10 versus 15 mm standard length). Furthermore, chapter 6's results have also shown a similar, physiological threshold in low salinity tolerance across different populations of both, North Sea and Baltic herring larvae (LC_{50} values $= 1.9 - 2.7$). A size-dependency of osmoregulatory ability was observed by Varsamos et al. (2005) in European seabass as well, and the authors suggest an early development of osmoregulating organs to result in an advantageous flexibility. Additionally, Wang et al. (2013) observed increasing osmoregulatory capacity throughout ontogeny in the marine Japanese devil stinger (*Inimicus japonicus*), with the larval stages being most suceptible to low salinity ($S = 5$).

The interaction of low salinity tolerance with prey availability and temperature is generally scarcely investigated in marine fish larvae. In a study testing the low salinity tolerance of North Sea herring, cod and flounder larvae, Yin and Blaxter (1987) could not observe prey-scarceness to impair the low salinity tolerance until the larvae became moribund. Although temperature (T) - salinity (S) interactions have long been in the focus of marine scientists (see e.g. Kinne, 1964), there are, to the best of knowledge, surprisingly no studies testing the effect of temperature on low salinity tolerance in marine fish larvae. However, there are a few studies investigating the effect of temperature on the osmoregulatory capacity of salmonid smolts. Handeland et al. (1998), for instance, reared Atlantic salmon smolts at different $T-S$ combinations ($T = 4, 8\,^{\circ}\mathrm{C}$ and $S = 28, 34$), and observed temperature to significantly influence the hypo-osmoregulatory ability with a longer acclimation time at low temperatures. Similarly, Claireaux and Audet (2000) observed brook charr (*Salvelinus fontinalis*) smolts to show increased hypo-osmoregulatory capacities under natural spring compared to winter temperature conditions, where acute transfer to sea water resulted in sharp increases in plasma osmolality and chloride levels, a decrease in white muscle water content and high mortality.

Especially in the northern parts of the Baltic catchment region river-runoff to the Baltic Sea is strongest after ice melt and winter precipitation (April to June) which strongly overlaps with the Atlantic herring spawning season in spring (Hänninen and Vuorinen, 2011). Additionally to the current, annual fluctuations in Baltic Sea river-runoff (BSRR), climate-driven changes in direct and indirect atmospheric patterns have projected increases in BSRR (next to various simultaneous changes in other environmental factors) (Meier et al., 2006; BACC, 2015; Hänninen et al., 2015). This freshening is gauged to be $1.5 - 2.0\,\mathrm{g\,kg^{-1}}$ until the end of the 21^{st} century (Meier et al., 2012; Gräwe et al., 2013) and will likely pose a threat to marine fish offspring living in the northernmost Baltic Sea regions where the salinity is lowest. According to the observed physiological threshold (similar across the investigated populations) and based on locally-scaled climate projections, there is a high chance of potential habitat loss for Atlantic herring in the future. Similarly, other marine organisms and whole ecosystems might be affected by these changes, even reaching into the eastern North Sea (Vuorinen et al., 2015). Here, the increased river-runoff from the Baltic Sea might affect the zooplankton abundances and subsequently the metamorphosed $0-$group of Atlantic herring that comes for feeding into

the Skagerrak and eastern North Sea (Hänninen et al., 2015). Although the underlying mechanisms could not be unraveled, Hänninen et al. (2015) found an interesting correlation between the Baltic Sea outflow and Atlantic herring 0+ year class strength between 1970 and 2010, with the latter explaining a third of the variation in herring recruitment. Climate projections up to the year 2100 depend of course on a series of unsettled assumptions. One of that implies that the adaptive capacity of marine fishes is not capable to alleviate the additional pressure from a changing abiotic environment. However, a couple of genetic studies have found significant differences between populations of Baltic cod and herring (in the wide, connected marine environments genetic differences are rather seldomly observed at the population level) (Jørgensen et al., 2005; Lamichhaney et al., 2012; Berg et al., 2015). These genetic differences could mainly be traced back to differences in genes correlated with osmoregulation. It remains to be clarified, how and if marine fish populations will be able to adapt to the rapidly changing abiotic environment in the Baltic Sea within just a few decades, which is in terms of evolution only a tiny fraction of a second. A key to resolving that question could lie in multigeneration studies that, in the case of temperature-related adaptation, have proven to be useful to assess the adaptive potential of fish species (Donelson et al., 2012).

7.4 Outlook

In the “orbit of sustainability discourses" (Davinson, 2001) fisheries management and marine conservation do not necessarily have to be colliding elements. According to Hare (2014), a “multi-hypothesis, integrative, and interdisciplinary" approach should be pursued, following Hjort's original approach formulated a hundred years ago, to optimize scientific research and subsequently policy advice. To pursue that, Hare (2014) suggests a better integration and combination of multiple factors by comparing and linking existing hypotheses. Looking at marine pelagic ecosystem dynamics in a wider context, other authors have as well proposed that it might be more useful to overcome the long-lasting discussion about bottom-up or top-down control by identifying mechanisms and taking into consideration the synergistic power of multiple stressors (Conversi et al., 2015). However, on lower trophic levels bottom-up effects seem to play a larger role, especially in temperate regions of the Northern Hemisphere, and Beaugrand et al. (2015) for example identified temperature and arctic atmospheric circulation patterns as responsible for regime shifts in the late 1980s (see Möllmann et al. 2015). In the Baltic Sea, Pershing

et al. (2015) have found evidence for a more pronounced bottom-up forcing through local processes such as heating, river run off as well as through salinity and the NAO. Furthermore, the authors propose that top-down forcing decreases with the openness of the system (as described in Möllmann et al. 2015).

With regard to the experiments conducted in this study, future research should tie in with the presented findings and, chronologically ordered, next steps should include a closer examination of the indirect, trophodynamic effects of matching phyto-, proto-, and mesozooplankton blooms for marine fish larvae since the observed results were suggesting a possible benefit. An inclusion of more detailed experiments combining different temperature regimes, feeding levels, swimming performance and (routine) metabolic rate measurements of Atlantic herring larvae could result in a (even) better parameterization of currently used IBMs. Additionally, with regard to the last chapter, long-term effects of low salinity exposure could help unravel the exact costs of osmoregulation and their ecological implications (including e.g. swimming performance measurements). Additionally, a combined approach of different temperature and salinity regimes could help simulate a more precise situation of the projected abiotic environment in the Baltic Sea. This would assist in deciphering the benefits of faster development for osmoregulation in Atlantic herring larvae (for example by examining chloride cells and blood osmolality more precisely), and could help assess wether increases in temperature can improve low salinity tolerance. For comparison reasons, similar experiments could also be conducted with freshwater fish larvae that would likely benefit from a less saline Baltic Sea.

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Individual scientific contributions to the multiple-author manuscripts and outline of publications

This thesis contains chapters written as manuscripts that are either already published or in the process of it. My personal contribution to each of the multi-authorship manuscripts is described below:

Chapter 3

Direct effects of microalgae and protists on herring (*Clupea harengus*) yolk sac larvae - *published in PLOS ONE*

The experimental design was developed by Björn Illing (BI) and Dr. Marta Moyano (MM) under the supervision of Prof. Myron A. Peck (MAP). All experiments were conducted by BI, MM and Jan Niemax (JN). BI analysed the samples, performed statistical analyses and created the figures. The manuscript was written by BI, MM and MAP.

Chapter 4

Behavioural and physiological responses to prey match-mismatch in larval herring - *accepted by Estuarine, Coastal and Shelf Science*

The concept of this study was designed by BI, MM and MAP. The experiments were performed by BI, MM, JN, Julia Berg and Nina Schickenberg. Laboratory and statistical analyses were done by BI, and Prof. Marc Hufnagl (MH) implemented the experimental results into the individual-based model. Except Fig. 4.6, showing the model results (MH), all figures were created by BI. The manuscript was written by BI and MAP, and in parts by MM (respiration) and MH (model).

Chapter 5

Thermal impacts on the ontogeny of critical swimming speed in Atlantic herring larvae - *submitted to Comparative Biochemistry and Physiology Part A*

This study was conceptualized by MM and MAP. The experimental work was conducted by Philip Peschutter, with help from BI and MM. Analyses, creation of figures and writing of the manuscript was primarily done by MM, with support from MP and BI.

Chapter 6

Projected habitat loss for marine fish in the world's largest brackish sea - *accepted by Marine Environmental Research*

The study design was developed by BI and MM, and BI performed the experiments with help from Lars Christiansen, Franziska Bils, JN, and Maren Westermann. Biochemical analyses were made by Johanna Thoms. Statistical analyses were executed by BI with advice from MM and Klaus B. Huebert. Figures were produced by BI, except Figures 6.1 and 6.5, showing current and future salinity of the Baltic Sea (MH). The manuscript was written by BI and MAP.

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Declaration on oath

I hereby declare, on oath, that I have written the present dissertation by my own and have not used other than the acknowledged resources and aids

Hamburg, 12/18/2015 Björn Illing

Appendix A

Table A.1: Starvation experiments with marine fish larvae

Nr	Author(s)	Year	Species	Methods
1	Blaxter and Hempel	1963	Atlantic Herring (*Clupea harengus*)	M/B
2	Wyatt	1972	European Plaice (*Pleuronectes platessa*)	M/B
3	Ehrlich	1974	European Plaice (*Pleuronectes platessa*)	BC
4	Umeda and Ochiai	1975	Yellowtail (*Seriola quinqueradiata*)	H
5	Ehrlich et al.	1976	Atlantic Herring (*Clupea harengus*)	M/H
6	O'Connell	1976	Northern Anchovy (*Engraulis mordax*)	H
7	Laurence	1978	Atlantic Cod (*Gadus morhua*), Haddock (*Melanogrammus aeglefinus*)	M/R
8	Theilacker	1978	Jack Mackerel (*Trachurus symmetricus*)	M/H
9	Buckley	1979	Atlantic Cod (*Gadus morhua*)	BC
10	Buckley	1980	Winter Flounder (*Pseudopleuronectes americanus*)	BC
11	Eldridge et al.	1981	Striped Bass (*Morone saxatilis*)	M/H
12	Rogers and Westin	1981	Striped Bass (*Morone saxatilis*)	M
13	McGurk	1984	Pacific Herring (*Clupea pallasi*)	M
14	Buckley et al.	1984	Sand Lance (*Ammodytes americanus*)	BC
15	Martin et al.	1984	Striped Bass (*Morone saxatilis*)	M/BC
16	Powell and Chester	1985	Spot (*Leiostomus xanthurus*)	M
17	Wright and Martin	1985	Striped Bass (*Morone saxatilis*)	M/BC
18	Neilson et al.	1986	Atlantic Cod (*Gadus morhua*)	M
19	Yin and Blaxter	1986	Atlantic Cod (*Gadus morhua*), European Flounder (*Platichthys flesus*)	M
20	Clemmesen	1987	Atlantic Herring (*Clupea harengus*), Turbot (*Scopthalmus maximus*)	BC

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Nr	Author(s)	Year	Species	Methods
21	Cousin et al.	1987	Turbot (*Scopthalmus maximus*)	BC
22	Kiørboe et al.	1987	Atlantic Herring (*Clupea harengus*)	R
23	Yin and Blaxter	1987	Atlantic Herring (*Clupea harengus*), Atlantic Cod (*Gadus morhua*) European Flounder(*Platichthys flesus*)	M
24	Pedersen et al.	1987	Atlantic Herring (*Clupea harengus*)	BC
25	Gadomski and Petersen	1988	California Halibut (*Paralichthys californicus*), Diamond Turbot (*Hypsopsetta guttulata*)	M
26	Fraser et al.	1988	Atlantic Cod (*Gadus morhua*)	BC
27	Raae et al.	1988	Atlantic Cod (*Gadus morhua*)	
28	Clemmesen	1989	Atlantic Herring (*Clupea harengus*)	BC
29	Oozeki et al.	1989	Stone Flounder (*Kareius bicoloratus*)	H
30	Theilacker and Watanabe	1989	Northern Anchovy (*Engraulis mordax*)	H
31	Kjørsvik et al.	1991	Atlantic Cod (*Gadus morhua*)	M/H
32	Richard et al.	1991	Dover Sole (*Solea solea*)	BC
33	Clarke et al.	1992	Red Drum (*Sciaenops ocellatus*), Lane Snapper (*Lutjanus synagris*)	BC
34	Ueberschär and Clemmesen	1992	Atlantic Herring (*Clupea harengus*)	BC
35	Yúfera et al.	1993	Gilthead Seabream (*Sparus aurata*)	M/H
36	Bergeron and Boulhic	1994	Dover Sole (*Solea solea*)	BC
37	Malloy and Targett	1994	Summer Flounder (*Paralichthys dentatus*)	BC
38	Canino	1994	Walleye Pollock (*Theragra chalcogramma*)	BC
39	Mathers et al.	1994	Atlantic Herring (*Clupea harengus*)	BC
40	Clemmesen	1994	Atlantic Herring (*Clupea harengus*)	BC
41	McNamara and Buckley	1994	Atlantic Cod (*Gadus morhua*)	BC
42	Bisbal and Bengston	1995	Summer Flounder (*Paralichthys dentatus*)	M/H/BC
43	Houlihan et al.	1995	Atlantic Herring (*Clupea harengus*)	BC/R
44	Gotceitas et al.	1996	Atlantic Cod (*Gadus morhua*)	M
45	Suthers et al.	1996	Australian Bass (*Macquaria novemaculeata*)	M/BC
46	Clemmesen and Doan	1996	Atlantic Cod (*Gadus morhua*)	M/BC
47	Rooker and Holt	1996	Red Drum (*Sciaenops ocellatus*)	BC
48	Bergeron and Person-Le Ruyet	1997	Sea Bass (*Dicentrarchus labrax*)	BC
49	Rooker et al.	1997	Red Drum (*Sciaenops ocellatus*)	M/BC
50	McNamara et al.	1999	Atlantic Cod (*Gadus morhua*)	BC
51	Suneetha et al.	1999	Atlantic Herring (*Clupea harengus*)	BC
52	Puvanendran and Brown	1999	Atlantic Cod (*Gadus morhua*)	M/B
53	Gwak et al.	1999	Japanese Flounder (*Paralichthys olivaceus*)	BC
54	Ferron	2000	Capelin (*Mallotus villosus*)	BC

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Table A.1 – continued from previous page

Nr	Author(s)	Year	Species	Methods
55	Kimura	2000	Japanese Sardine (*Sardinops melanostictus*)	BC
56	Gwak and Tanaka	2002	Japanese Flounder (*Paralichthys olivaceus*)	BC
57	Catalán and Olivar	2002	European Seabass (*Dicentrarchus labrax*)	H
58	Kono et al.	2003	Japanese Anchovy (*Engraulis japonicus*)	M/BC
59	Caldarone et al.	2003	Atlantic Cod (*Gadus morhua*)	BC
60	Gisbert et al.	2004	California Halibut (*Paralichthys californicus*)	M/H
61	Skajaa et al.	2004	Atlantic Herring (*Clupea harengus*)	M/BC/B
62	Dou et al.	2005	Japanese Flounder (*Paralichthys olivaceus*)	M/B
63	Caldarone	2005	Haddock (*Melanogrammus aeglefinus*)	BC
64	Catalán et al.	2007	European Seabass (*Dicentrarchus labrax*)	BC
65	Tanaka et al.	2008	Bluefin Tuna (*Thunnus orientalis*)	BC
66	Folkvord et al.	2009	Atlantic Herring (*Clupea harengus*)	M/BC
67	Faria et al.	2011	Senegalese Sole (*Solea senegalensis*)	BC/B
68	Laurel et al.	2011	Pacific Cod (*Gadus macrocephalus*)	M
69	Piccinetti et al.	2014	Dover Sole (*Solea solea*)	M/H/BC

B=Behaviour, BC=Biochemistry, H=Histology, M=Morphometrics, R=Respirometry

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Appendix B

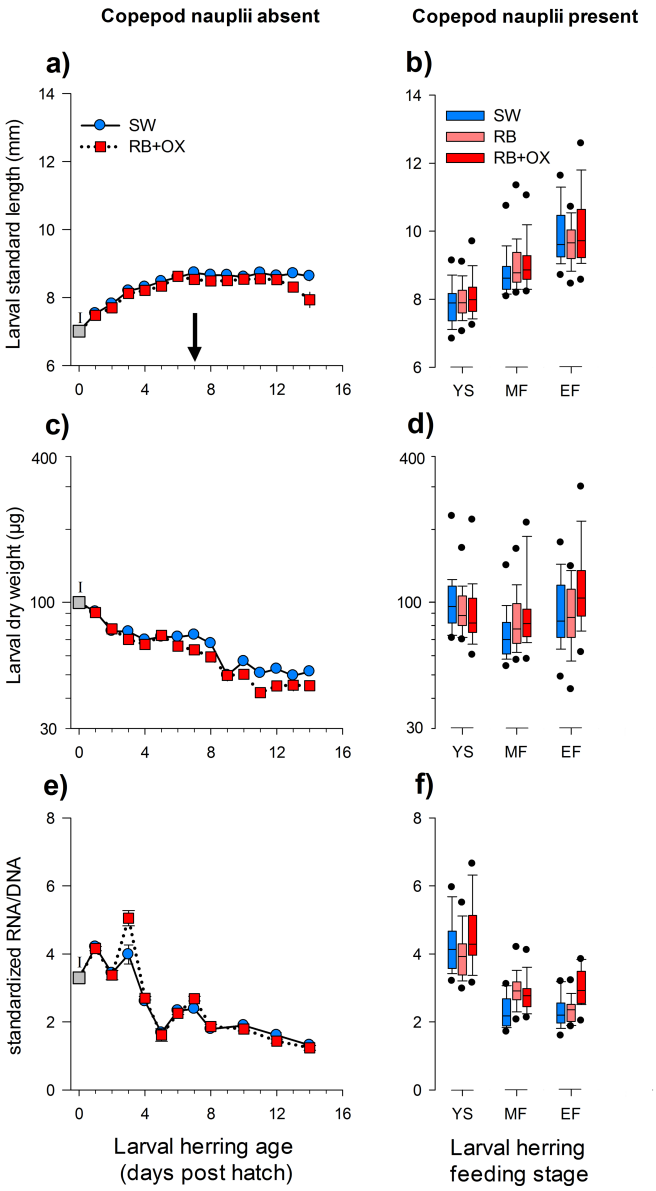

Figure B.1: Larval herring mean (± S.E., $n = 3$) standard length (a), dry weight (c) and standardized RNA:DNA ratio (e) versus age (days post hatch, dph) (left panels, same as Fig. 3.2). Larvae were kept without copepod prey in SW or RB+OX treatments, each with three replicates (see Fig. D.1 caption for treatment description). Significant differences between treatments have been observed in standard length (panel a, $P \leq 0.001$, one-way repeated measures ANOVA on ranks) and dry weight (panel c, $P \leq 0.001$, one-way repeated measures ANOVA). The black arrow indicates the moment of complete yolk absorption at 7 dph, the letter "I" represents the initial measurement at 0 dph. Furthermore, single tanks were fed with copepod prey and the same parameters noted (means± S.E. given) for different feeding stages (right panels; b,d,f, see Fig. D.1 caption for legend description). The numbers (mean± S.D.) of larvae averaged per symbol are in b) 60± 1, 53± 12 and 40± 1; d) 60± 1, 60± 1 and 40± 1; f) 18± 4, 16± 6 and 21± 2 (YS, MF and EF).

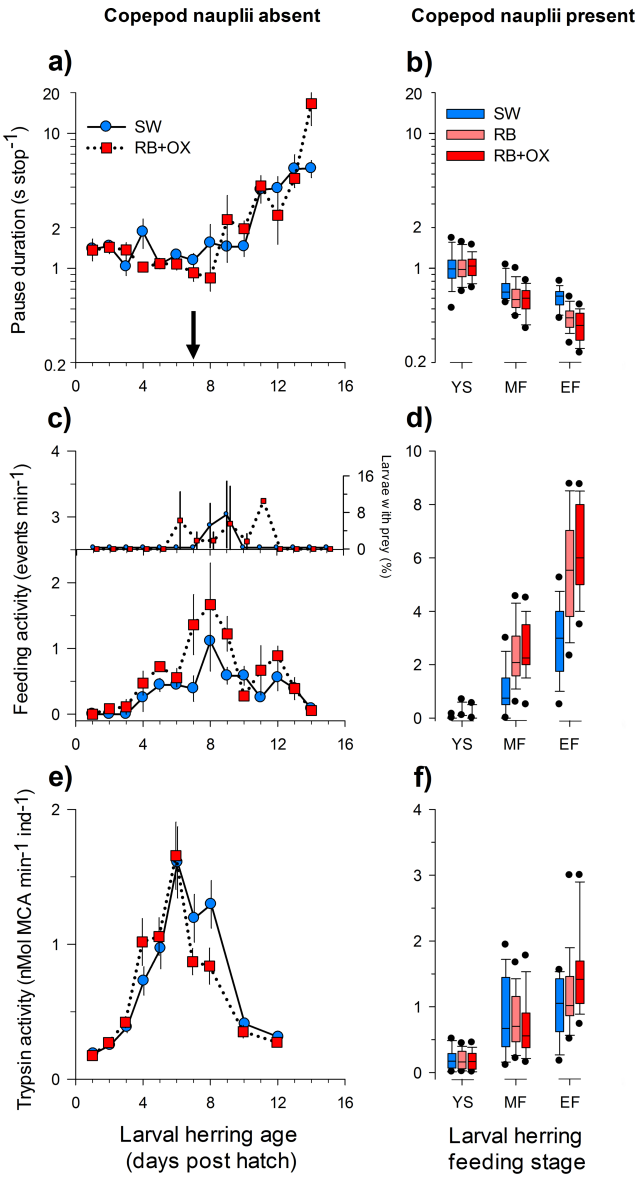

Figure B.2: Progression of mean (± S.E., $n = 3$) swimming (a), feeding (c), and trypsin (e) activity of larval herring (*Clupea harengus*) versus age (days post hatch, dph) (left panels, same as Fig. 3.1). The two treatment groups were sea water (SW), and *Rhodomonas baltica* (RB) + *Oxyrrhis marina* (OX), triplicated and kept without copepod prey. Feeding incidence of larvae, confronted with copepod nauplii, is inserted in panel c. The black arrow indicates the moment of complete yolk absorption at 7 dph. Significant differences between treatments have only been observed in feeding activity (panel c, P= 0.01, one-way repeated measures ANOVA on ranks). Additionally, single tanks with SW, RB, and RB+OX were held with copepod prey (panels b,d,f) with the same parameters measured (means± S.E. given) for three different feeding stages (YS=yolk-sac, $1-3$ dph; MF= mixed feeding, $6-8$ dph; EF= exogenous feeding, $12-14$ dph). Note, in panel b, symbols are larger than the error bars. The numbers (mean± S.D.) of larvae averaged per symbol are in b+d) 28, 30 and 20 (YS, MF and EF) and f) 42± 6, 44± 13 and 19± 1 (YS, MF and EF).

Appendix C

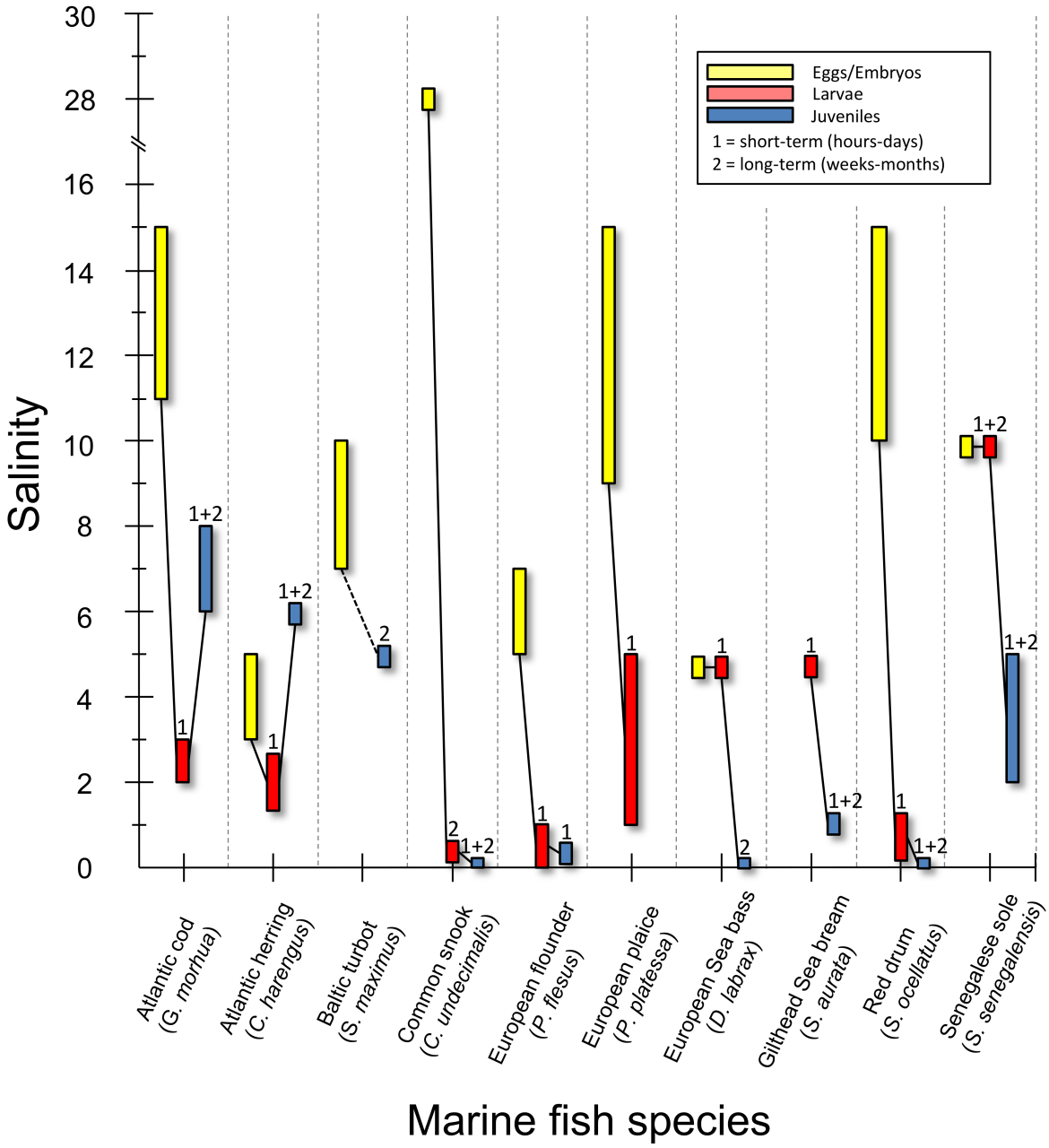

Figure C.1: Low salinity tolerances of different ontogenetic life stages of euryhaline, marine fish species of (relatively) temperate waters based on experimental literature references (see appendix C, Tab. C2).

Table C.1: Information about incubation and rearing temperature and salinity after arrival in the laboratory, size-at-hatch, incubation period (days post fertilization, dpf), growth rates after an age of 10 dph, as well as standard length (L), age (days post hatch, dph) and biochemical condition (sRD) during salinity challenge trials (means $\pm$ SD) conducted on herring larvae from four natal salinities. Sample number averaged for size-at-hatch was 20, for L during trials was 130 and for sRD was 55 in GR (15 mm), 5 in GB (10 mm), 26 and 62 in KF (10 and 15 mm) and 23 and 62 in NB (10 and 15 mm).

Region/Population (spawning area)	Season/Year	Temp.(°C)	Initial S	Test S	Size-at-hatch (mm)	Test 1 L (mm)/ sRD	Test 2 L (mm)/ sRD	Growth (mm d^{-1})/R^2
Eastern Baltic/ Gulf of Riga (GR)	Autumn/2010	9.8±0.1	6.1±0.2	6.1±0.2	7.84 ±0.52	9.91 ±0.81/ –	14.81 ±1.57/ 3.38±0.93*	0.29/R^2=0.79
South-West Baltic/ WBSS (GB)	Spring/2011	9.4±0.5	6.6±0.2	6.6±0.2	8.04±0.15**	10.76±0.79/ 2.55±0.64	–/–	0.20/R^2=0.37
South-West Baltic/ WBSS (KF)	Spring/2012	10.2±0.5	16.1±0.3	6.0±0.1	7.01±0.51	10.90±0.92/ 3.08±1.11	15.83±2.33/ 2.53±0.76	0.18/R^2=0.70
Western North Sea/ Banks (NB)	Autumn/2012	10.2±0.3	34.1±0.5	6.0±0.1	6.84±0.60	10.93±0.67/ 2.23±0.93	14.74±1.96/ 2.63±0.93	0.12/R^2=0.62

* too few larvae for salinity stress test; ** at 5 dph

Table C.2: Low salinity tolerances of commercially important euryhaline, marine fish species from (relatively) temperate waters determined by various exposure durations

Species	Life Stage	Method	Salinity	Reference(s)
Atlantic Cod	Eggs	f/i	11.0-15.0	Westin and Nissling, 1991; Nissling and Westin, 1997
(*G. morhua*)	Larvae	s	2.0-3.0	Yin and Blaxter, 1987
	Juveniles	s/l	6.0-8.0	Magill and Sayer 2004; Árnason et al. 2013
Atlantic Herring	Eggs	f/i	3.0-4.8	Ojaveer 1981; Wawrzyniak 1987
(*C. harengus*)	Larvae	s	1.0-2.7	Holliday and Blaxter, 1960; Yin and Blaxter, 1987
	Juveniles	s/l	6.0	Holliday and Blaxter 1961
Baltic Turbot	Eggs	f/i	7.0-10.0	Kuhlmann and Quantz, 1980; Nissling et al., 2006
(*S. maximus*)	Larvae	–	–	–
	Juveniles	l	5.0	Gaumet et al., 1995
Common Snook	Eggs	i	28.0	see Peters et al., 1998
(*C. undecimalis*)	Larvae	l	0.6	see Peters et al., 1998
	Juveniles	s/l	0	see Peters et al., 1998
European Flounder	Eggs	f/i	9.0-15.0	von Westernhagen, 1970; Nissling et al., 2002
(*P. platessa*)	Larvae	s	1.0-5.0	Holliday and Pattie Jones, 1967
	Juveniles	–	–	–
European Sea Bass	Eggs	i	5.0	Varsamos et al., 2001
(*D. labrax*)	Larvae	s	5.0	Varsamos et al., 2001
	Juveniles	l	0	Jensen et al., 1998; Nebel et al., 2005
Gilthead Sea Bream	Eggs	–	–	–
(*S. aurata*)	Larvae	s	0.5-1.3	Crocker et al., 1981
	Juveniles	s/l	1.0	Klaren et al., 2007; Bodinier et al., 2010
Red Drum	Eggs	i	10.0-15.0	Holt et al., 1981
(*S. ocellatus*)	Larvae	s	0.5-1.3	Crocker et al., 1981
	Juveniles	s/l	0	Crocker et al., 1981
Senegalese Sole	Eggs	i	10.0	Salas Leitón et al., 2012
(*S. senegalensis*)	Larvae	s/l	10.0	Salas Leitón et al., 2012
	Juveniles	s/l	2.0-5.0	Arjona et al., 2007

f=fertilised; i=incubated, s=short-term (hours-days); l=long-term (weeks-months)

C.1 References

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