Length back-calculations and growth patterns of juvenile Baltic sprat (*Sprattus sprattus L.*)

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List of Abbreviations

BH	Body Height
BI	Biological Intercept: empirical estimated length at the day of first increment formation
BI method	Biological Intercept method for length back-calculation
BIAS	Baltic International Acoustic Survey
BPH	Body Proportional Hypothesis
BR	Biting Rate
DFF	Day of First Feeding
DFIF	Day of First Increment Formation
DM	Dry Mass
ICES	International Council for the Exploration of the Sea
IW	Increment Width
YoY	Young-of-the-Year
LGR	Length Growth Rate
M method	Metamorphosis method for length back-calculation
MIP	Metamorphosis Inflection Point
MIP method	Metamorphosis Inflection Point method for length back-calculation
NLR method	Non-Linear Regression method for length back-calculation
OR	Otolith Radius
PoM	Point of Metamorphosis
SD	ICES Sub-Divisions of the Baltic Sea
SL	Standard Length
TL	Total Length
WM	Wet Mass

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Summary

Sprat (*Sprattus sprattus*) is a small pelagic fish species that is of ecological importance in the Baltic Sea, as it is a major predator on mesozooplankton and serves as forage fish for e.g. cod (Gadus morhua), harbour porpoise (*Phocoena phocoena*) and various birds. During the last decades, the sprat stock was subject to large fluctuations caused by variable recruitment strength, challenging management decisions on the Baltic ecosystem. Thus, an extensive research effort was made to find mechanistic explanations influencing the survival of the high vulnerable early life-stages, which in turn explain recruitment success. Mechanisms acting during the planktonic life-stages were in the focus of previous research, while processes influencing year-class strength in the late-larval and early juvenile stage are largely unexplored. The present thesis investigated the post-larval and juvenile pre-recruit life-stages in Baltic sprat by examining individual age and growth patterns recorded in otolith microstructures.

Length back-calculation on the basis of daily otolith micro-increments is an important tool to investigate mechanisms influencing mortality in a yearly cohort. By analysing the small part of survivors of a year class, growth characteristics can be examined, which lead to a higher survival probability. Previous length back-calculations in juvenile Baltic sprat based on the biological intercept method, assuming a linear relationship between fish length and otolith length. However, examining a comprehensive dataset including larval and juvenile life-stages in **Manuscript 1**, an allometric relation between fish length and otolith length was found in the larval stage replaced by an almost linear one in the juvenile stage. The Metamorphosis Inflection Point (MIP) method for length back-calculation was developed taking into account this non-linear ratio between fish length and otolith length on an individual basis. The change in the relationship between fish length and otolith length co-occurred with the otolith length when maximal increment widths were deposited on the otolith and with the mean fish length when the increase in body height was maximal during the development. This coincidence of three changing morphometric features (a minimum in the fish length-otolith length ratio, peak increment width on the otolith and maximal growth in body height) was defined as “point of metamorphosis” and formed the back-bone of the new back-calculation algorithm. Length growth in young sprat features two peaks, one smaller in the larval and one larger in the early juvenile stage.

During metamorphosis from larvae to juvenile sprat, dominant length growth of the larval stage was replaced with an increased growth in body height as well as reduced growth in length. After metamorphosis during the juvenile stage growth becomes almost isometric. The MIP algorithm assigned the minimum in length growth to the maximum in otolith growth at metamorphosis. Compared to the results of the linear biological intercept method, higher length growth rates were found during the larval stage. Additionally, the highest increase in length was found during the early juvenile stage, exceeding 1.0 mm•d^{-1}, in contrast to the linear method where highest growth occurred during metamorphosis. This strong potential in length growth during the early juvenile life-stage was validated by cohort tracking of wild sprat in the Western Baltic Sea (**Manuscript 3**) reaching up to 1.1 mm•d^{-1}.

Manuscript 2 combines of a laboratory experiment with field investigations. In the experimental part, length, dry and wet mass and otolith growth during the early juvenile stage was examined under *ad libitum* conditions at different constant temperatures in the laboratory. Four main aspects were investigated and quantified during the experiment: *i*) strength of length growth rates under optimal laboratory conditions, *ii*) uncoupling between otolith growth and somatic growth *iii*) the amount of food consumed under *ad libitum* conditions and *iv*) otolith growth at different temperatures under *ad libitum* conditions. An average length growth rate of about 0.7 mm•d^{-1} was observed, while maximum length growth rates of single individuals exceeded 0.8 mm•d^{-1}. Uncoupling between somatic (growth in the number of cells) and otolith growth originates most likely from the onset of lipid-storage in the early juvenile stage. Consequently, it was concluded that back-calculated length in the juvenile life-stage could be biased, even if the MIP back-calculation model is applied. Concerning food consumption (*iii*), juveniles (~50 mm standard length) were found to require ten times more food in contrast to post-metamorphic sprat at the beginning of the experiment (~30 mm standard length). This increase in food demand underlines the crucial importance of food availability in juvenile nursery areas. At a water temperature of 18°C, the food demand of a juvenile sprat corresponds to a concentration of 3.5 prey items•L^{-1} when feeding on *Acartia spp*. (14 h•d^{-1}) was assumed. Concerning the optimal otolith growth (*iv*) in relation to temperature (T) increment width was described as a quadratic function (Increment width = $-0.0344 \cdot T^2 + 1.6757 \cdot T - 12.764$, $r^2 = 0.99$) under ad libitum feeding conditions. This result was used to draw conclusions from increment widths of wild caught early juvenile sprat from the Western Baltic Sea in 2003 and 2007. As food in shallow nurseries of juvenile Baltic sprat is difficult to measure, food availability in the wild was indirectly estimated from otoliths. Assuming a major influence of the three factors size, temperature and food ingestion on somatic and otolith growth, one factor can be estimated when two are known. Hence, by calibrating the effect of temperature on otolith growth under *ad libitum* feeding at a fixed size in the laboratory, feeding conditions during the early juvenile stage can be inferred from otoliths of wild-caught sprat. Deduced from this combined analysis of a laboratory experiment and field data, sub-optimal feeding conditions during the early juvenile life-stage of Young-of-the-Year survivors in 2007 were found in

contrast to optimal feeding conditions for the majority of Young-of-the-Year survivors in 2003. Irrespective of the year, individuals that experienced peak temperatures of the season during the early juvenile stage suffered un-favourable feeding conditions. These individuals were born early in the season. Thus, results confirm previous investigations which found that summer born individuals had an advantage over spring born individuals. However, previous studies interpret this mainly as a result of the larval period favoured by high summer temperatures, while **Manuscript 2** offers an additional mechanism why early born sprat may have a disadvantage in survival, due to high temperatures in the early juvenile stage.

The difference in survival of early and late born sprat leaded to the question which specific meteorological conditions influence the seasonal location of the main spawning time and hence the survival rates and subsequent recruitment. By analysing the length growth characteristics of juvenile sprat from shallow nursery areas of the Western Baltic Sea (**Manuscript 3**), high water temperatures in spring together with low summer water temperatures were found to cause a broad window of survival including spring and summer born individuals and a low mean length growth rate. In contrast, low spring water temperatures combined with high summer water temperatures were observed in a year with a late and narrow window of survival which was accompanied by a high mean length growth rate. Additionally, low growth rates occurred in a year with low recruitment (2007), while high growth rates appeared in a year with high recruitment (2003). The influence of spring and summer water temperature on recruitment was further investigated using yearly hydro-acoustic estimates of 0-group sprat for the Western Baltic Sea and surface temperatures between 1999 and 2010. A highly significant correlation ($p < 0.01$, $r^2 = 0.66$) was found between the abundance of juvenile sprat in autumn and the ratio between minimum and maximum water temperatures of the year. It was concluded that a cold spring will delay spawning and/or egg development and hence shift the main growth phase of larvae later into the summer season, where these larvae can benefit from high temperatures, while juveniles can experience optimal conditions after the peak temperatures of the year. These findings question previous investigations suggesting an unidirectional positive effects of future warming on sprat recruitment.

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Zusammenfassung

Die Sprotte (*Sprattus sprattus*) ist ein kleiner pelagischer Schwarmfisch, der im Ökosystem der Ostsee als einer der Hauptpredatoren des Mesozooplanktons eine zentrale Rolle spielt. Gleichzeitig stellt die Sprotte eine wichtige Beuteart für Dorsch (*Gadus morhua*), Schweinswal (*Phocoena phocoena*) und verschiedene Vogelarten dar. In den letzten Jahrzehnten war der Sprottenbestand durch Veränderungen im Rekrutierungserfolg starken Fluktuationen unterworfen, welche Management Entscheidungen erschweren. Aus diesem Grund wurde bisher ein intensiver Forschungs-Aufwand betrieben diejenigen Mechanismen zu identifizieren, welche das Überleben der empfindlichen frühen Lebensstadien begünstigen und somit die Rekrutierung beeinflussen. Bisherige Studien über die Rekrutierung der Sprotte beinhalten vor allem Prozesse die das Überleben während der planktonischen Lebensweise steuern, wohingegen Prozesse welche die Jahrgangsstärke während der späten larvalen und frühen juvenilen Phase beeinflussen weitgehend unerforscht sind. Die vorliegende Arbeit untersucht die post-larvalen und frühen juvenilen Lebensstadien der Ostsee-Sprotte durch die Analyse individueller Alter- und Wachstumsmuster, welche durch die Mikrostrukturen auf den Otolithen aufgezeichnet sind.

Die Längenrückberechnung stellt eine wichtige Methode in der Untersuchung von Sterblichkeitsfaktoren einer Kohorte dar und basiert auf täglich angelegten Mikroinkrementen der Otolithen. Durch die Untersuchung des kleinen Anteils an überlebenden juvenilen Individuen eines Jahrgangs können Wachstumscharakteristiken beschrieben werden, welche zu einer erhöhten Überlebenswahrscheinlichkeit führen. Bisherige Längenrückberechnungen bei juvenilen Sprotten basierten auf der „Biological Intercept“ Methode, welche von einem linearen Verhältnis zwischen Fischlänge und Otolithenlänge ausgeht. In **Manuskript 1** wird jedoch eine allometrische Beziehung zwischen den beiden Längen in der larvalen Lebensphase der Sprotte beobachtet, welche von einem nahezu linearen Verhältnis in der juvenilen Lebensphase abgelöst wird. Um dieses nicht-lineare Verhältnis zwischen Fischlänge und Otolithenlänge auf individueller Basis zu berücksichtigen wurde die „Metamorphosis Inflektion Point“ (MIP) Methode zur Längenrückberechnung entwickelt. Die Änderung in dem Fischlängen-Otolithenlängen-Verhältnis von allometrisch zu linear tritt zeitgleich mit der Anlage der maximalen Inkrementbreiten sowie einem maximalen Wachstum in die

Körperhöhe während des Übergangs zum juvenilen Stadium auf. Das Zusammenfallen dieser drei morphometrischen Veränderungen wurde als „Point of Metamorphosis“ bezeichnet und bildet die Grundlage des neuen Rückberechnungs-Algorithmus. Das Längenwachstum von jungen Sprotten wird durch zwei Maxima charakterisiert, ein kleineres in der larvalen Lebensphase und ein größeres in der juvenilen Lebensphase. Während der Metamorphose verringert sich das zunächst ausgeprägte Längenwachstum der larvalen Phase und wird durch ein verstärktes Wachstum in die Körperhöhe unterbrochen. Nach der Metamorphose ist das Wachstum in der juvenilen Phase nahezu isometrisch. Der MIP-Algorithmus beschreibt das minimale Längenwachstum genau dort wo das maximale Otolithenwachstum während der Metamorphose auftritt. Im Vergleich zur „Biological Intercept“ Methode verzeichnet die MIP Methode höhere Wachstumsraten während der larvalen Lebensphase Der höchste Anstieg im Längenwachstum mit mehr als 1.0 mm•Tag^{-1} trat nach der MIP Methode während der frühen juvenilen Phase auf wohingegen die lineare Methode das stärkste Wachstum während der Metamorphose beschreibt. Dieses hohe Längenwachstums-Potential während des frühen juvenilen Stadiums rekonstruiert durch die MIP Methode, konnte durch Kohorten-Verfolgung in der westlichen Ostsee validiert werden (**Manuskript 3**), wobei Wachstumsraten über 1.1 mm•Tag^{-1} gemessen wurden.

In **Manuskript 2** wurden Ergebnisse aus einem Laborexperiment auf Felddaten angewendet. Im experimentellen Teil der Studie sind Längen-, Gewichts- und Otolithenwachstum unter *ad libitum* Bedingungen bei verschiedenen konstanten Wassertemperaturen untersucht worden. Dabei wurden vier Aspekte erforscht und quantifiziert: *i*) die Höhe des Längenwachstums unter optimalen Laborbedingungen, *ii*) die Entkopplung von Otolithenwachstum und somatischem Wachstum, *iii*) die Menge an Nahrung welche unter *ad libitum* Bedingungen benötig wird und *iv*) das Otolithenwachstum bei unterschiedlichen Temperaturen. Im Durchschnitt wurde eine Längenwachstumsrate von 0.7 mm•Tag^{-1} gemessen, wobei maximale Längenwachstumsraten einzelner Individuen 0.8 mm•Tag^{-1} überstiegen. Die Entkopplung des somatischen Wachstums (definiert als Zunahme der Zellanzahl) vom Wachstum des Otolithen resultiert wahrscheinlich aus dem Beginn der Fetteinlagerung während der frühen juvenilen Lebensphase. Daraus wurde gefolgert das Längenrückberechnungen in der juvenilen Phase fehlerbehaftet sein können, auch bei Anwendung der MIP Methode. Die Nahrungskonsumption betreffend (*iii*) konnte gezeigt werden, dass juvenile Sprotten (~50 mm Standardlänge) zehnmal mehr Nahrung benötigen als junge Sprotten direkt nach der Metamorphose (~30 mm Standardlänge). Der Anstieg im Nahrungsbedarf während der Entwicklung unterstreicht die Bedeutung der Nahrungsverfügbarkeit in den Aufwuchsgebieten. Bei einer Wassertemperatur von 18 °C und einer ausschließlichen (14 h•Tag^{-1}) Ernährung von Copepoden der Gattung *Acartia* spp. entspricht der Nahrungsbedarf einer juvenilen Sprotte einer Konzentration von 3.5 Copepoden•L^{-1}. Bezüglich des optimalen Otolithenwachstums (*iv*) wurde ein quadratisches Verhältnis zwischen Inkrementbreite und Wassertemperatur (T) unter *ad libitum* Bedingungen beschrieben (Inkrementbreite = -0.0344•T^2 + 1.6757•T – 12.764, r^2 = 0.99). Mit Hilfe dieses Ergebnisses konnten

Rückschlüsse auf die Nahrungsverfügbarkeit juveniler Sprotten in der westlichen Ostsee in den Jahren 2003 und 2007 gezogen werden. Da die Nahrungsverfügbarkeit in Flachwassergebieten schwer zu messen ist, wurde sie auf diese Weise indirekt bestimmt. Angenommen, das somatische und das Otolithenwachstum werden im Wesentlichen von den drei Faktoren, Größe, Temperatur und Nahrungsverfügbarkeit bestimmt, dann lässt sich ein Faktor abschätzen wenn die Größe der beiden anderen bekannt ist. So konnte durch die Kalibrierung des Temperatureffekts auf das Otolithenwachstum einer bestimmten Fischlänge unter *ad libitum* Bedingungen im Labor mittels der Otolithen auf die Nahrungsverfügbarkeit der jeweiligen Fischgröße im Feld geschlossen werden. Durch diese kombinierte Analyse aus Laborexperiment und Felddaten ließen sich die Nahrungsbedingungen in der juvenilen Phase von überlebenden Sprotten rekonstruieren, welche im Jahr 2003 für die meisten Individuen optimal waren, 2007 jedoch sub-optimal. Unabhängig vom Untersuchungsjahr zeigte sich, dass Individuen welche ihre juvenile Lebensphase im Sommer während der maximalen Jahrestemperaturen erlebten, ungünstige Nahrungsbedingungen vorfanden. Diese Individuen waren im Frühjahr geboren. Dies bestätigt Untersuchungen einer früheren Studie wonach im Sommer geborene Individuen einen Überlebensvorteil gegenüber den Sprotten haben die im Frühjahr geboren sind. Der Vorteil der später geborenen Individuen wurde bisher mit einem durch hohe Temperaturen begünstigten stärkeren Wachstum in der larvalen Phase erklärt. **Manuskript 2** liefert allerdings einen weiteren Mechanismus der erklärt warum im Frühjahr geborene Individuen einen Überlebensnachteil haben, nämlich wegen den hohen Temperaturen während der juvenilen Phase.

Der Unterschied im Überleben früh und spät geborener Sprotten wirft die Frage auf, welche meteorologischen Faktoren die Hauptlaichzeit der Sprotte steuern, und somit auch die Überlebensrate und die Rekrutierungsstärke beeinflussen. Durch die Analyse von Wachstumscharakteristiken juveniler Sprotten aus den flachen Aufwuchsgebieten der westlichen Ostsee wurde herausgefunden, dass hohe Wassertemperaturen im Frühjahr zusammen mit geringen Wassertemperaturen im Sommer zu einem breiten Überlebensfenster (Frühling bis Sommer) und zu geringen Wachstumsraten führen. Im Gegensatz dazu wurden geringe Temperaturen im Frühjahr kombiniert mit warmen Sommertemperaturen in einem Jahr gefunden in dem ein engeres Überlebensfenster und hohe Wachstumsraten auftraten. In dem Untersuchungsjahr mit geringer Rekrutierung (2007) waren auch die Wachstumsraten gering, während ein starkes Wachstum in einem Untersuchungsjahr mit hoher Jahrgangsstärke beobachtet wurde (2003). Der Einfluss der Frühjahrs- und Sommertemperaturen auf die Rekrutierung der Sprotte wurde durch das Verhältnis der Anzahl von 0-Gruppen in der westlichen Ostsee bestimmt, abgeschätzt anhand des jährlichen Hydroakustik-Surveys und Messung der Oberflächentemperaturen zwischen 1999 und 2010. Dabei wurde eine hochsignifikante Korrelation zwischen der Abundanz juveniler Sprotten im Herbst und dem Verhältnis zwischen minimaler und maximaler Wassertemperatur gefunden. Demnach führt ein kalter Frühling zu einer Verzögerung des Laichgeschehens, wodurch die Hauptwachstumsphase der Larven in die Sommermonate verschoben

wird. Dabei profitieren die Larven von hohen Temperaturen, wohingegen die juvenilen Sprotten optimale Bedingungen nach dem Temperaturmaximum des Jahres erfahren. Dieses Ergebnis stellt frühere Aussagen in Frage, welche von einem einfachgerichteten positiven Effekt einer zukünftigen Erwärmung auf die Größe des Sprottenbestandes in der Ostsee ausgehen.

3

General Introduction

3.1 Ecological importance of Baltic sprat

Sprat (*Sprattus sprattus*) is a small pelagic, herring-like swarm-fish that can reach high biomasses in all sub-areas of the Baltic Sea (ICES 2012a). Its biology and ecology has been investigated intensively during the last decades (see references in Peck et al. 2012, Voss et al. 2012) as it was identified as key species in the brackish ecosystem of the Baltic Sea. Sprat is important as prey species for top-predators like cod (*Gadus morhua*), seals and birds (Bagge et al. 1994) and is a dominant consumer of meso-zooplankton (Rudstam et al. 1992). Thus, sprat can exert a "top-down control" on the copepod stock together with herring (Arrhenius and Hansson 1993, Möllmann et al. 2000). Furthermore, it has been shown that sprat density influences the condition of herring and sprat by inter- and intraspecific competition (Cardinale and Arrhenius 2000, Möllmann et al. 2005, Casini et al. 2011).

Presently, sprat constitutes the largest part of the commercial fishery together with Baltic herring and Baltic cod (ICES 2012a). The high biomass of sprat in the Baltic Sea during the last decades developed during a regime shift which involved all trophic levels of the ecosystem during the late 1980s (Wasmund et al. 1998, Alheit et al. 2005, Möllmann et al. 2008). The upper trophic level of the Baltic ecosystem changed from a cod dominated to a clupeid dominated system (Parmanne et al. 1994), as consequence of high fishery intensity combined with recruitment failure in Baltic cod (Bagge et al. 1994, Casini et al. 2008). Formerly controlled by cod predation, the poorly harvested sprat stock increased to an overall higher biomass compared to the early 1980s. Recently, the cod stock in the Bornholm Basin of the central Baltic Sea increased and affected sprat abundance in this area, but this is assumed to have a limited influence on the whole Baltic sprat stock (ICES 2012a).

Despite its large stock biomass, sprat is subject to strong fluctuations in recruitment success (ICES 2012a), making the setting of effective management quotas difficult. The high variability in recruitment is insufficiently explained by spawning stock biomass (Köster et al. 2003) alone. Therefore, processes that influence individual survival during the early life-stages and consequently determine the strength of a new year-class are in focus of present research on Baltic sprat (Voss et al. 2012).

3.2 Recruitment theories and the critical life-stage in Baltic sprat

Beside a dependence of recruitment on spawning stock size, the strength of the next year-class in marine fish is determined by the survival rate of vulnerable early life-stages, where mortality is highest during a fish's life (Hjort 1914, Leggett and Deblois 1994, Houde 2008). During the early life-stages, small changes in survival can have a pronounced effect on year-class strength (Houde 1989). Various recruitment hypotheses were developed during the last century with mechanisms acting during early life-stages (Anderson 1988, Houde 2008). One of the first and most famous theories is Hjort`s "Critical Period" hypothesis (Hjort 1914), proposing that fate of a year class is determined shortly after the yolk-sac stage, when fish larvae must find suitable amounts and types of prey. Cushing (1974) extended Hjort's idea and formulated the "Match-Mismatch" hypothesis, where the temporal overlap between plankton production and development of larvae is of general importance, including larvae that are older than first feeding larvae. Also focusing on food availability, Lasker (1981) suggested that there are times and areas when prey aggregates and thus enhances the possibility of larval survival in Northern anchovy (*Engraulis mordax*). He further stated that these food aggregations occur in stratified water columns and calm oceans leading to the term "Stable Ocean" hypothesis. In the "Stage Duration" hypothesis postulated by Houde (1987), year-class strength is regulated by predation. Here, larval growth rate is the important factor contributing to recruitment variability, as early life-stages are more vulnerable to predation than later developmental stages.

However, as in many species, these single-factors hypotheses are not able to explain the variability in year-class strength of Baltic sprat (Voss et al. 2012). In fact, series of events that act together over the entire egg to pre-recruit juvenile period often influence the survival of offspring and subsequent year-class strength (Anderson 1988, Houde 2008). Processes influencing the survival of eggs and larvae in Baltic sprat have been identified and investigated during an extensive sampling period of the GLOBEC Germany project in the Bornholm Basin in 2002 and 2003. Here, variations in survival during the egg and larval stage were not fully able to explain recruitment strength (Voss et al. 2012). As the abundance of juvenile sprat in autumn is a good predictor for year-class strength in contrast to the abundance of larvae in spring and summer, the post-larval and early juvenile life-stage was previously described as the "critical" life-stage in sprat (Köster et al. 2003). Therefore, it was assumed that mechanisms potentially influencing the survival rate act during the post-larval and juvenile life-stage. These life-stages were not sampled during the GLOBEC Germany project where research focused on a spawning site in the Bornholm Basin. It is assumed that nursery habitats of post-larval and juvenile sprat are located in coastal regions (Lindquist 1971, Aro 1989, Ojaveer and Kalejs 2010), since young sprat is being caught in the Western Baltic Sea (Peck et al. 2004, Meskendahl et al. 2010, Brachvogel et al. 2012).

3.3 The life cycle and habitats of Baltic sprat

Sprat is a typical r-strategist (Peck et al. 2012) with a short life span (rarely older than five years, Bailey 1980), early maturation (age 1-2, Reglero et al. 2007, ICES 2012a) and a high reproductive capacity (George and Alheit 1987). In the Baltic Sea it exhibits a prolonged spawning season from February/March to August (Elwertowski 1960, Ojaveer and Kalejs 2010). As extremely euryhaline species sprat spawns from the saltier Western Belt Sea with up to 20 PSU to the North Eastern Baltic Sea with about 5 PSU (Ojaveer and Kalejs 2010). Due to their specific gravity, sprat eggs float near the surface in the Western Baltic Sea (Morawa 1954) and sink to the more saltier deep water layers in the Central and North Eastern part (Nissling et al. 2003). Thus, successful spawning in the Eastern Baltic Sea is restricted to the deep basins (Bornholm Basin, Gdansk Deep and Gotland Basin) characterised by saline bottom waters, while spawning in the western part, including the Kiel Bight, can cover the whole area (Heidrich 1925, Morawa 1954).

Following a peak spawning time in May/June (Morawa 1954, Karasiova 2002), larvae experience late spring and summer conditions coinciding with the seasonal zooplankton maximum (Möllmann et al. 2004) and the highest water temperatures of the year. In the late larval stage, small sprat start to form schools (Peck et al. 2012) and are assumed to passively drift and/or actively migrate from offshore spawning to coastal nursery areas (Desilva 1973, Rudstam et al. 1992, Baumann et al. 2006b). It is assumed that young sprat benefit from the conditions in coastal areas, where high plankton concentrations can be provided (Lindquist 1971, Aro 1989, Rudstam et al. 1992). However, mean food availability is difficult estimate using standard plankton gears in shallow waters due to the patchiness of zooplankton. In autumn young sprat leave the shallow nursery areas and start to recruit to the adult stock in the deeper offshore waters for over-wintering (ICES 2012b). After the first winter pre-mature sprat are fully recruited to fishery (ICES 2012a).

3.4 Length growth and survival

Growth rates during early life-stages of sprat can vary widely from e.g. 0.39 $mm \bullet d^{-1}$ (Dänhardt et al. 2007) to 0.69 $mm \bullet d^{-1}$ (Baumann et al. 2006a) during the larval stage. These individual differences in growth rates provide a template for selective survival and support the idea that larger and thus faster growing individuals of a cohort have a higher probability of survival compared to smaller and slow growing individuals (Sogard 1997). This “bigger is better” of “growth-mortality” (Anderson 1988) concept inherently links growth and mortality as growing faster decreases the cumulative mortality due to shorter stage durations (Houde 1987). Being larger at an earlier time in life may be useful in many respects including enhanced resistance of starvation, decreased vulnerability to predators and better tolerance of environmental extremes (Sogard 1997). The survival of faster growing individuals has been observed in various marine fish species (e.g. Meekan and Fortier 1996, Robert et al. 2007, Islam et al. 2010).

In Baltic sprat, survival during the first summer of life also depends on growth rate (Baumann et al. 2006b, Voss et al. 2012) favouring the survival of faster growing larvae. As faster growing larvae mainly stem from summer months when warm water temperatures coincide with suitable feeding conditions, it is suggested that summer born individuals have an advantage over spring-born sprat (Baumann et al. 2008). However, it was also observed that summer caught starving late-larval and early juvenile sprat had lower growth rates than autumn caught recruiting sprat in the Kiel Bight of the Western Baltic Sea (Baumann et al. 2007). However, research is needed to investigate the mechanisms leading to selective survival of faster growing individuals in nursery habitats. Baumann et al. (2007) detected starving juveniles and thus identified food supply as a detrimental factor influencing year-class strength. Extraordinary high year-class strength during the year the starving event was observed (Baumann et al. 2007) questions the validity of these observations. Hence, it is required to further investigate the growth performance of sprat and its environmental influences to explore in detail recruitment-relevant mechanisms acting in nursery areas of Baltic sprat. To investigate processes affecting mortality, analyses of surviving Young-of-the-Year (YoY) sprat is useful to examine which characteristics finally lead to a higher survival probability.

3.5 Otolith function and the storage of information

An important tool to investigate the characteristics of survivors including length growth and age is the microstructure analysis of otoliths (Stevenson and Campana 1992, Campana 2005). Otoliths are mechano-electrical sound and displacement transducers (Fay 1984, Gauldie and Radtke 1990, Morales-Nin 2000) located in the endolymphatic sac of the inner ear of teleost fish. They are acellular organs which are about three times denser than the rest of the fish`s body, which makes them move at a different amplitude and phase (Popper and Lu 2000). A sensory epithelium close to the otolith detects movements of the ear-stone and translates the signal into a nerve impulse (Lowenstein 1971). The otolith as an essential component of this highly balanced measuring system is assumed to grow in a constant proportion of the body of the fish. Due to their metabolically inert nature (Gauldie and Nelson 1990), otoliths are like black boxes recording growth. Age and growth can be deduced by analysing confined increments which are formed on a daily basis (Pannella 1971). A daily growth increment is composed of calcium-carbonate in the form of twinned aragonite (Gauldie and Nelson 1988) and a collagen-like protein (Degens et al. 1969). The deposition of material on the otolith occurs in a daily periodicity where organic and inorganic components alternate resulting in the translucent and opaque zone of an increment (Watabe et al. 1982, Edeyer et al. 2000). Hereby, the precipitation of inorganic components is regulated by the pH-value of the endolymphatic fluid which in turn is influenced by the blood plasma (Morales-Nin 2000). Thus, somatic growth is recorded on the otoliths as a consequence of nutrient transport by the blood plasma. In other words, somatic growth is expected to be proportional to otolith growth.

The assumption of the proportionality between otolith and somatic growth is used to reconstruct previous growth from otolith increment structures (Carlander 1981, Campana and Neilson 1985) by forming the basis of various back-calculation methods (Francis 1990, Vigliola and Meekan 2009). Furthermore, the proportionality between somatic and otolith growth provides the opportunity to investigate environmental factors influencing growth (Methot and Kramer 1979, Kurita et al. 2004, Comerford et al. 2013). Growth of young fish is mainly influenced by three factors: temperature, food availability and ontogeny. If the influence of two of these factors is known, the effect of the third can be estimated. Thus, otoliths offer the possibility to investigate previous food availability in the wild (Aguilera et al. 2009): By calibrating the influence of temperature on otolith growth under constant feeding conditions in a certain life-stage in the laboratory, the amount of food ingested by an individual wild fish can be inferred from increment width. Hence, on the one hand results from otolith microstructure analysis can be used to back-calculate length growth in Baltic sprat and on the other hand it is a promising tool to investigate food availability of growth in shallow nursery areas where estimates of plankton concentrations are strongly influenced by patchiness.

3.6 Length back-calculation

Based on the assumption that somatic and otolith growth are proportional, length growth can be reconstructed using various back-calculation models (Francis 1990, Vigliola and Meekan 2009). Simple length back-calculation models suppose a linear relationship between somatic and length growth (i.e. isometric growth). Length at a previous day X before the catch (L_X) can be calculated using the otolith length (O_C) and fish length (L_C) at catch and the otolith length at day X (O_X) (see also Fig.3-1):

$$L_X = \frac{L_C}{O_C} * O_X \quad (1)$$

Using this simple proportionality fish length is zero at zero otolith length. However, otolith length and fish length are not strictly proportional as the otolith is formed later during the development of the larvae. Thus, alternatively a linear relationship between fish and otolith length with an intercept (d) is used for back-calculation intercepting the fish-length axis at a value larger than zero (see also Fig.3-1):

$$L_X = d + \frac{(L_C - d)}{O_C} * O_X \quad (2)$$

Equation (2) is known as the Fraser-Lee back-calculation model (Lee 1920, Francis 1990), where d is the intercept of a fish length-otolith length regression derived from samples of a population. The Fraser-Lee method for back-calculating previous length is sensitive to age- and sample dependent variations in the intercept of the fish length-otolith length relationship that is employed (Campana 1990). As it has been demonstrated that the fish length-otolith length relationship is dependent on

growth rate (e.g. Secor and Dean 1989, Francis et al. 1993, Takasuka et al. 2008) which has been named the "growth effect" in otolith literature, biased length growth rates can arise due to the use of a regression based intercept.

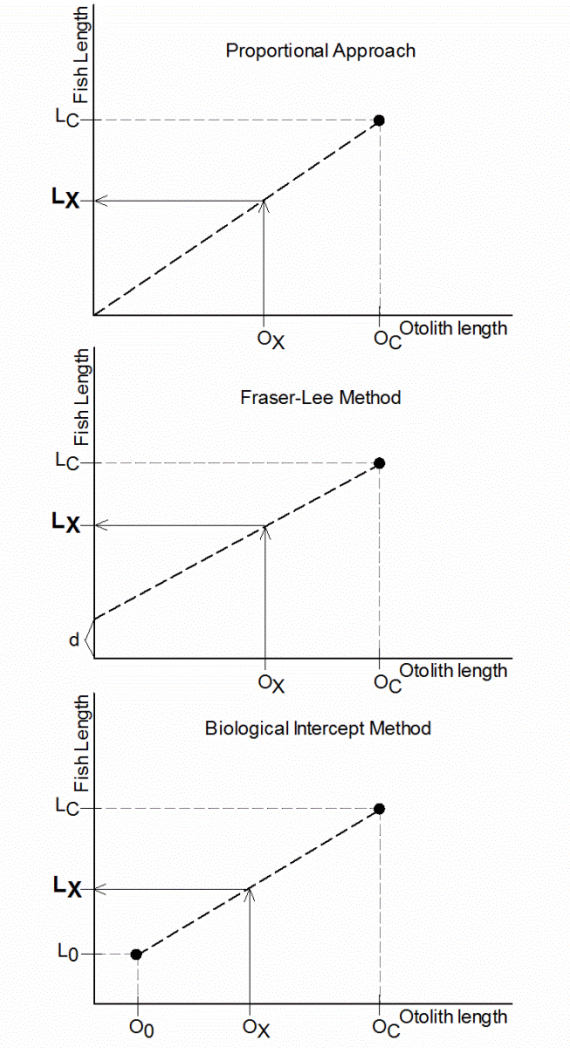

Fig.3-1. Schematic illustration of linear back-calculation methods. L_C: fish length at catch, L_X: fish length at age X, L_0: *Biological Intercept*, O_C: Otolith length at catch, O_X: Otoltih length at age X, O_0: Otolith radius at the *Biological Intercept*.

To overcome the problem of a sample dependent intercept, Campana (1990) developed the Biological Intercept model. Here, the statistically estimated intercept is replaced by an empirically determined intercept – the Biological Intercept (L_0) - the fish length when the first growth increment is laid on the otolith (O_0) (see also Fig.3-1):

$$L_X = L_C + (O_X - O_C) * \frac{(L_C - L_0)}{(O_C - O_0)} \quad (3)$$

Using this linear back-calculation method with a biological intercept of about 5 mm derived from observations of Alshuth (1988) and Shields (1989), length growth rates of juvenile Baltic sprat have previously been reconstructed (e.g. Baumann et al. 2006a, 2008, 2009). However, assuming a linear relationship between otolith length and fish length throughout the whole development until the juvenile stage is a simplification of the complex changes during the transition from the larval to the juvenile life-stage. Peck et al. (2005) observed strong ontogenetic changes in the allometric scaling of the mass-length relationship for sprat smaller than 44 mm length indicating pronounced changes in body-proportions and a protracted metamorphic period. Thus, the performance of the back-calculation model applied to reconstruct growth should be investigated in detail (Wilson et al. 2009), especially when the analysis comprises the transitions between the larval and juvenile stage. There is a need to investigate if the previously used biological intercept model for sprat displays important length growth features during the transition between the larval and the juvenile stage.

3.7 Goals of the thesis

The reconstruction of growth histories of individual sprat previous to the day of catch via otoliths is of particular importance when investigating characteristics of surviving individuals. The first goal of the thesis focuses on the development of a sprat-specific length back-calculation model using otoliths of juvenile Baltic sprat. In previous in investigations of otolith derived length growth of Baltic sprat, the biological intercept method (Campana 1990) was applied which assumes a linear relationship between length and otolith growth throughout the life-time (e.g. Baumann et al. 2006a). However, Peck et al (2005) described ontogenetic changes in the allometric scaling of the mass-length relationship for small sprat revealing pronounced changes in body-proportions. This indicates a non-linear relationship between length growth and somatic growth in early life-stages as well as the relationship between length growth and otolith growth. In fact, the relationship between fish length and otolith length for larval sprat was previously described by an asymptotic function (Lee et al. 2006) in contrast to a linear one assumed in the juvenile stage (Baumann et al. 2006a). Considering changes in the relationship between fish length and otolith length due to ontogeny, back-calculated lengths during the transition from the larval to the juvenile stage will deviate from previously assumed growth patterns derived from the biological intercept model which assumes a linear fish length-otolith length relationship. The stepwise development of a back-calculation method in **Manuscript 1** concentrates on the length reconstruction in this recruitment-relevant life-stage focusing on the allowance for individual variation.

In **Manuscript 2** the influence of the main effects on otolith and somatic growth, temperature, food availability and ontogeny are investigated in a laboratory experiment. The central aim of this study is to quantify and disentangle the influence of temperature and ontogeny on increment width to infer previous food availability of individual wild sprat from otolith growth. As food availability is difficult to measure in shallow nursery areas were standard gear cannot be operated (Barnett et al. 1984, Rey et

al. 1987), the goal was to reconstruct previous feeding histories and thus food availability from otolith microstructure analysis.

Length, otolith and somatic growth during the early juvenile stage is studied under *ad libitum* feeding conditions in the laboratory at different and constant water temperatures which occur in the nursery habitat. At constant temperature and feeding conditions changes in increment width during the experiment can be attributed to ontogeny. Additionally, the influence of temperature on otolith growth at maximal food availability can be quantified. Lastly, maximum food consumption during the early juvenile stage which is suggested to generate maximum increment width can be estimated. Finally, we compare laboratory generated increment widths with those of field caught sprat. By detracting the effect of temperature and ontogeny from increment width we want to reconstruct previous individual feeding histories from otoliths and thus indirectly quantify shallow nursery habitats of Baltic sprat.

In the last section of the thesis (**Manuscript 3**) characteristics of young sprat were studied by applying microstructure analysis of otoliths and length back-calculation in two successive seasons. Previously, selective survival of offspring spawned during summer of the protracted spawning season (spring to summer) has been observed in sprat recruits from the Western and Central Baltic Sea (Baumann et al. 2008). Hereby, summer-born individuals experience higher temperatures and better prey fields than spring born individuals. Thus, stronger growth rates of summer-born sprat lead to an advantage of survival of summer over spring-born sprat. However, these previous findings stem from seasons with high overall sprat recruitment in the Baltic Sea (ICES 2012a). This provokes the question if strong year-classes are coupled to a late window of survival and to strong growth rates of YoY-survivors in Baltic sprat. Studying temporal origins and length growth rates of post-larval, early juvenile and juvenile sprat from shallow and offshore habitats of the Western Baltic Sea, we want to investigate the temporal origin, growth rates, selective survival during summer month and influences on year-class strength in the Western Baltic Sea.

3.8 References

Aguilera, B., Catalan, I.A., Palomera, I., and Olivar, M.P. 2009. Otolith growth of European sea bass (Dicentrarchus labrax L.) larvae fed with constant or varying food levels. Sci. Mar. **73**(1): 173-182.

Alheit, J., Möllmann, C., Dutz, J., Kornilovs, G., Loewe, P., Mohrholz, V., and Wasmund, N. 2005. Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. ICES Journal of Marine Science: Journal du Conseil **62**(7): 1205-1215. 10.1016/j.icesjms.2005.04.024.

Alshuth, S. 1988. Bestimmung von Alter und Wachstumsraten bei Larvaen und juvenilen der Sprotte, *Sprattus sprattus L.* PhD, Biology, University of Bremen, Bremen.

Anderson, J.T. 1988. A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. J. Northwest. Atl. Fish. Sci. **8**: 55-66.

Aro, E. 1989. A review of fish migration patterns in the Baltic. Rapports et Proces-verbaux des Réunions. Conseil International pour l'Éxploration de la Mer **190**: 72-96.

Arrhenius, F., and Hansson, S. 1993. Food-Consumption of Larval, Young and Adult Herring and Sprat in the Baltic Sea. Mar. Ecol. Prog. Ser. **96**(2): 125-137.

Bagge, O., Thurow, F., Steffensen, E., and Bray, J. 1994. The Baltic cod. Dana **10**: 1-28.

Bailey, R.S. 1980. Problems in the management of short-lived pelagic fish as exemplified by North Sea sprat. Rapports et Proces-verbaux des Réunions. Conseil International pour l'Éxploration de la Mer **177**: 477-488.

Barnett, A.M., Jahn, A.E., Sertic, P.D., and Watson, W. 1984. Distribution of Ichthyoplankton Off San-Onofre, California, and Methods for Sampling Very Shallow Coastal Waters. Fishery Bulletin **82**(1): 97-111.

Baumann, H., Hinrichsen, H.-H., Voss, R., Stepputtis, D., Grygiel, W., Clausen, L.W., and Temming, A. 2006a. Linking growth to environmental histories in central Baltic young-of-the-year sprat, *Sprattus sprattus*: an approach based on otolith microstructure analysis and hydrodynamic modelling. Fish. Oceanogr. **15**(6): 465-476. doi: 10.1111/j.1365-2419.2005.00395.x.

Baumann, H., Hinrichsen, H.H., Möllmann, C., Köster, F.W., Malzahn, A.M., and Temming, A. 2006b. Recruitment variability in Baltic Sea sprat (*Sprattus sprattus*) is tightly coupled to temperature and transport patterns affecting the larval and early juvenile stages. Can. J. Fish. Aquat. Sci. **63**(10): 2191-2201. doi:10.1139/f06-112.

Baumann, H., Malzahn, A.M., Voss, R., and Temming, A. 2009. The German Bight (North Sea) is a nursery area for both locally and externally produced sprat juveniles. Journal of Sea Research **61**(4): 234-243.

Baumann, H., Peck, M.A., Götze, H.E., and Temming, A. 2007. Starving early juvenile sprat *Sprattus sprattus* (L.) in western Baltic coastal waters: evidence from combined field and laboratory observations in August and September 2003. J. Fish. Biol. **70**(3): 853-866. doi: 10.1111/j.1095-8649.2007.01346.x.

Baumann, H., Voss, R., Hinrichsen, H.-H., Mohrholz, V., Schmidt, J.O., and Temming, A. 2008. Investigating the selective survival of summer- over spring-born sprat, *Sprattus sprattus*, in the Baltic Sea. Fish. Res. **91**(1): 1-14. doi: 10.1016/j.fishres.2007.11.004.

Brachvogel, R., Meskendahl, L., Herrmann, J.P., and Temming, A. 2012. Functional responses of juvenile herring and sprat in relation to different prey types. Mar. Biol.: 1-14. 10.1007/s00227-012-2104-5.

Campana, S.E. 1990. How reliable are growth back-calculations based on otoliths? Can. J. Fish. Aquat. Sci. **47**(11): 2219-2227. doi:10.1139/f90-246.

Campana, S.E. 2005. Otolith science entering the 21st century. Marine and Freshwater Research **56**(5): 485-495.

Campana, S.E., and Neilson, J.D. 1985. Microstructure of Fish Otoliths. Can. J. Fish. Aquat. Sci. **42**(5): 1014-1032.

Cardinale, M., and Arrhenius, F. 2000. Decreasing weight-at-age of Atlantic herring (Clupea harengus) from the Baltic Sea between 1986 and 1996: a statistical analysis. ICES Journal of Marine Science: Journal du Conseil **57**(4): 882-893. 10.1006/jmsc.2000.0575.

Carlander, K.D. 1981. Caution on the use of the regression method of back-calculating lengths from scale measurements. Fisheries **6**(1): 1-4. 10.1577/1548-8446-6-1.

Casini, M., Kornilovs, G., Cardinale, M., Möllmann, C., Grygiel, W., Jonsson, P., Raid, T., Flinkman, J., and Feldman, V. 2011. Spatial and temporal density dependence regulates the condition of central Baltic Sea clupeids: compelling evidence using an extensive international acoustic survey. Population Ecology **53**(4): 511-523.

Casini, M., Lovgren, J., Hjelm, J., Cardinale, M., Molinero, J.C., and Kornilovs, G. 2008. Multi-level trophic cascades in a heavily exploited open marine ecosystem. Proceedings of the Royal Society B-Biological Sciences **275**(1644): 1793-1801.

Comerford, S., Brophy, D., Fox, C.J., Taylor, N., van der Veer, H.W., Nash, R.D.M., and Geffen, A.J. 2013. Temperature effect on growth and larval duration of plaice Pleuronectes platessa in three regions of the Northeast Atlantic. Mar. Ecol. Prog. Ser. **476**: 215-226.

Cushing, D.H. 1974. The natural regulation of fish populations. *In* Sea fisheries research. *Edited by* F.R. Harden-Jones. John Wiley and Sons, New York. pp. 399-412.

Dänhardt, A., Peck, M.A., Clemmesen, C., and Temming, A. 2007. Depth-dependent nutritional condition of sprat *Sprattus sprattus* larvae in the central Bornholm Basin, Baltic Sea. Mar. Ecol. Prog. Ser. **341**: 217-228.

Degens, E.T., Deuser, W.G., and Haedrich, R.L. 1969. Molecular Structure and Composition of Fish Otoliths. Mar. Biol. **2**(2): 105-&.

Desilva, S.S. 1973. Food and Feeding Habits of Herring Clupea-Harengus and Sprat C Sprattus in Inshore Waters of West Coast of Scotland. Mar. Biol. **20**(4): 282-290.

Edeyer, A., de Pontual, H., Payan, P., Troadec, H., Severe, A., and Mayer-Gostan, N. 2000. Daily variations of the saccular endolymph and plasma compositions in the turbot Psetta maxima: relationship with the diurnal rhythm in otolith formation. Marine Ecology Progress Series **192**: 287-294.

Elwertowski, J. 1960. Biologische Grundlagen der Sprottenfischerei in der östlichen und mittleren Ostsee. Fischerei-Forschung **3**(4): 1-19.

Fay, R. 1984. The goldfish ear codes the axis of acoustic particle motion in three dimensions. Science **225**(4665): 951-954. 10.1126/science.6474161.

Francis, M.P., Williams, M.W., Pryce, A.C., Pollard, S., and Scott, S.G. 1993. Uncoupling of Otolith and Somatic Growth in Pagrus-Auratus (Sparidae). Fishery Bulletin **91**(1): 159-164.

Francis, R.I.C.C. 1990. Back-Calculation of Fish Length - a Critical-Review. J. Fish. Biol. **36**(6): 883-902.

Gauldie, R.W., and Nelson, D.G.A. 1988. Aragonite twinning and neuroprotein secretion are the cause of daily growth rings in fish otoliths. Comparative Physiology Biochemistry **90**: 501-509.

Gauldie, R.W., and Nelson, D.G.A. 1990. Otolith Growth in Fishes. Comparative Biochemistry and Physiology a-Physiology **97**(2): 119-135.

Gauldie, R.W., and Radtke, R.L. 1990. Microincrementation - Facultative and Obligatory Precipitation of Otolith Crystal. Comparative Biochemistry and Physiology a-Physiology **97**(2): 137-144.

George, M.R., and Alheit, J. 1987. Ovarian maturation cycle of sprat, *Sprattus sprattus*. ICES CM **H:47**.

Heidrich. 1925. Über die Fortpflanzung von *Clupea sprattus* in der Kieler Bucht. Wissenschaftliche Meeresunteruchungen **20**(Neue Folge, Abteilung Kiel): 1-47.

Hjort, J. 1914. Fluctuations in the great fisheries of Northern Europe viewed in the light of biological research. Rapports et Proces-verbaux des Réunions. Conseil International pour l'Éxploration de la Mer **20**: 1-228.

Houde, E.D. 1987. Fish early life dynamics and recruitment variability. American Fisheries Society Symposium **2**: 17-29.

Houde, E.D. 1989. Comparative Growth, Mortality, and Energetics of Marine Fish Larvae - Temperature and Implied Latitudinal Effects. Fishery Bulletin **87**(3): 471-495.

Houde, E.D. 2008. Emerging from Hjort's Shadow. J. Northwest. Atl. Fish. Sci. **41**: 53-70. 10.2960/J.v41.m634.

ICES. 2012a. Report of the Baltic Fisheries Assessment Working Group 2012. **ICES CM 2010/ACOM:10**.

ICES. 2012b. Report of the Baltic International Fish Survey Working Group. ICES CM 2012/SSGESST:02.

Islam, M.S., Ueno, M., and Yamashita, Y. 2010. Growth-dependent survival mechanisms during the early life of a temperate seabass (Lateolabrax japonicus): field test of the 'growth-mortality' hypothesis. Fish. Oceanogr. **19**(3): 230-242.

Karasiova, E. 2002. The variability of sprat peak spawning and larvae appearance timing in the southeastern Baltic Sea during the past six decades. Bull. Sea Fish. Inst. **156**: 57-58.

Köster, F.W., Hinrichsen, H.H., Schnack, D., St John, M.A., Mackenzie, B.R., Tomkiewicz, J., Möllmann, C., Kraus, G., Plikshs, M., Makarchouk, A., and Aro, E. 2003. Recruitment of Baltic cod and sprat stocks: identification of critical life stages and incorporation of environmental variability into stock-recruitment relationships. Sci. Mar. **67**: 129-154.

Kurita, Y., Nemoto, Y., Oozeki, Y., Hayashizaki, K., and Ida, H. 2004. Variations in patterns of daily changes in otolith increment widths of 0+ Pacific saury, Cololabis saira, off Japan by hatch date in relation to the northward feeding migration during spring and summer. Fish. Oceanogr. **13**: 54-62.

Lasker, R. 1981. Factors contributing to variable recruitment of the northern anchovy (*Engraulis mordax*) in the California Current: contrasting years, 1975 through 1978. Rapports et Proces-verbaux des Réunions. Conseil International pour l'Éxploration de la Mer **178**: 375-388.

Lee, O., Danilowicz, B.S., and Dickey-Collas, M. 2006. Temporal and spatial variability in growth and condition of dab (*Limanda limanda*) and sprat (*Sprattus sprattus*) larvae in the Irish Sea. Fish. Oceanogr. **15**(6): 490-507. doi: 10.1111/j.1365-2419.2006.00406.x.

Lee, R.M. 1920. A review of the methods of age and growth determination in fishes by means of scales. Fishery Investigations, London Series 2 **4**(2): 1-32.

Leggett, W.C., and Deblois, E. 1994. Recruitment in Marine Fishes - Is It Regulated by Starvation and Predation in the Egg and Larval Stages. Netherlands Journal of Sea Research **32**(2): 119-134.

Lindquist, A. 1971. Contribution to the knowledge of Baltic sprat (*Sprattus sprattus*). ICES CM **H:19**.

Lowenstein, O. 1971. The labyrinth. Fish Physiology **5**: 207-240.

Meekan, M.G., and Fortier, L. 1996. Selection for fast growth during the larval life of Atlantic cod Gadus morhua on the Scotian Shelf. Mar. Ecol. Prog. Ser. **137**(1-3): 25-37.

Meskendahl, L., Herrmann, J.P., and Temming, A. 2010. Effects of temperature and body mass on metabolic rates of sprat, Sprattus sprattus L. Mar. Biol. **157**(9): 1917-1927.

Methot, R.D.J., and Kramer, D. 1979. Growth of northern anchovy, *Engraulis mordax*, larvae in the sea. Fishery Bulletin **77**: 413-423.

Möllmann, C., Kornilovs, G., Fetter, M., and Köster, F.W. 2004. Feeding ecology of central Baltic Sea herring and sprat. J. Fish. Biol. **65**(6): 1563-1581.

Möllmann, C., Kornilovs, G., Fetter, M., and Köster, F.W. 2005. Climate, zooplankton, and pelagic fish growth in the central Baltic Sea. ICES J. Mar. Sci. **62**(7): 1270-1280.

Möllmann, C., Kornilovs, G., and Sidrevics, L. 2000. Long-term dynamics of main mesozooplankton species in the central Baltic Sea. Journal of Plankton Research **22**(11): 2015-2038.

Möllmann, C., Müller-Karulis, B., Kornilovs, G., and St John, M.A. 2008. Effects of climate and overfishing on zooplankton dynamics and ecosystem structure: regime shifts, trophic cascade, and feedback loops in a

simple ecosystem. ICES Journal of Marine Science: Journal du Conseil **65**(3): 302-310. 10.1093/icesjms/fsm197.

Morales-Nin, B. 2000. Review of the growth regulation processes of otolith daily increment formation. Fish. Res. **46**(1-3): 53-67.

Morawa, F.W.F. 1954. Laichen, Laichbedingungen and Laichplätze des Sprottes (*Clupea sprattus L.*), dargestellt auf Grund von Untersuchungen in der Kieler Bucht. Zeitschrift für Fischerei und deren Hilfswissenschaften **4**(5): 343-373.

Nissling, A., Muller, A., and Hinrichsen, H.H. 2003. Specific gravity and vertical distribution of sprat eggs in the Baltic Sea. J. Fish. Biol. **63**(2): 280-299.

Ojaveer, E., and Kalejs, M. 2010. Ecology and long-term forecasting of sprat (Sprattus sprattus balticus) stock in the Baltic Sea: a review. Reviews in Fish Biology and Fisheries **20**(2): 203-217.

Pannella, G. 1971. Fish Otoliths - Daily Growth Layers and Periodical Patterns. Science **173**: 1124-1127.

Parmanne, R., Rechlin, O., and Sjöstrand, B. 1994. Status and future of herring and sprat stocks in the Baltic Sea. Dana **10**: 29-59.

Peck, M.A., Baumann, H., Bernreuther, M., Clemmesen, C., Herrmann, J.P., Haslob, H., Huwer, B., Kanstinger, P., Koster, F.W., Petereit, C., Temming, A., and Voss, R. 2012. Reprint of: The ecophysiology of Sprattus sprattus in the Baltic and North Seas. Progress in Oceanography **107**: 31-46.

Peck, M.A., Clemmesen, C., Herrmann, J.-P., Stäcker, S., and Temming, A. 2004. The feeding–growth relationship in post-larval Baltic sprat (*Sprattus sprattus L.*): Comparison of somatic, nucleic acid- and otolith-based growth rates. CM 2004 **L:25**.

Peck, W.A., Clemmesen, C., and Herrmann, J.P. 2005. Ontogenic changes in the allometric scaling of the mass and length relationship in *Sprattus sprattus*. J. Fish. Biol. **66**(3): 882-887.

Popper, A.N., and Lu, Z.M. 2000. Structure-function relationships in fish otolith organs. Fish. Res. **46**(1-3): 15-25.

Reglero, P., Mosegaard, H., and Hinrichsen, H.H. 2007. Date of otolith first increment formation in Baltic sprat Sprattus sprattus and its relation to onset of maturity. Mar. Ecol. Prog. Ser. **330**: 223-233.

Rey, J.R., Crossman, R.A., Kain, T.R., Vose, F.E., and Peterson, M.S. 1987. Sampling Zooplankton in Shallow Marsh and Estuarine Habitats - Gear Description and Field-Tests. Estuaries **10**(1): 61-67.

Robert, D., Castonguay, M., and Fortier, L. 2007. Early growth and recruitment in Atlantic mackerel Scomber scombrus: discriminating the effects of fast growth and selection for fast growth. Mar. Ecol. Prog. Ser. **337**: 209-219.

Rudstam, L.G., Hansson, S., Johansson, S., and Larsson, U. 1992. Dynamics of Planktivory in a Coastal Area of the Northern Baltic Sea. Marine Ecology-Progress Series **80**(2-3): 159-173.

Secor, D.H., and Dean, J.M. 1989. Somatic Growth Effects on the Otolith–Fish Size Relationship in Young Pond-reared Striped Bass, Morone saxatilis. Can. J. Fish. Aquat. Sci. **46**(1): 113-121. 10.1139/f89-015.

Shields, R.J. 1989. Studies of Growth and Nutritional Status in 0-Group sprat, Sprattus sprattus (Clupeidae), using Otolith Microstructure and Lipid Analytical Techniques. PhD thesis, School of Ocean Science, University of Wales, Bangor.

Sogard, S.M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: A review. Bull. Mar. Sci. **60**(3): 1129-1157.

Stevenson, D.K., and Campana, S.E.e. 1992. Otolith microstructure examination and analysis Canadian Special Publication of Fisheries and Aquatic Sciences **117**.

Takasuka, A., Oozeki, Y., Aoki, I., Kimura, R., Kubota, H., Sugisaki, H., and Akamine, T. 2008. Growth effect on the otolith and somatic size relationship in Japanese anchovy and sardine larvae. Fisheries Science **74**(2): 308-313.

Vigliola, L., and Meekan, M. 2009. The back-calculation of fish growth from otoliths. *In* Tropical Fish Otoliths: Information for Assessment, Managemant and Ecology. *Edited by* B.S. Green, B.D. Mapstone, G. Carlos and G.A. Begg. Springer, Heidelberg, London, New York. pp. 174-211.

Voss, R., Peck, M.A., Hinrichsen, H.-H., Clemmesen, C., Baumann, H., Stepputtis, D., Bernreuther, M., Schmidt, J.O., Temming, A., and Köster, F.W. 2012. Recruitment processes in Baltic sprat – A re-evaluation of GLOBEC Germany hypotheses. Progress in Oceanography.

Wasmund, N., Nausch, G., and Matthaus, W. 1998. Phytoplankton spring blooms in the southern Baltic Sea - spatio-temporal development and long-term trends. Journal of Plankton Research **20**(6): 1099-1117.

Watabe, N., Tanaka, K., Yamada, J., and Dean, J.M. 1982. Scanning Electron-Microscope Observations of the Organic Matrix in the Otolith of the Teleost Fish Fundulus-Heteroclitus (Linnaeus) and Tilapia-Nilotica (Linnaeus). J. Exp. Mar. Biol. Ecol. **58**(1): 127-134.

Wilson, J.A., Vigliola, L., and Meekan, M.G. 2009. The back-calculation of size and growth from otoliths: Validation and comparison of models at an individual level. J. Exp. Mar. Biol. Ecol. **368**(1): 9-21. doi: 10.1016/j.jembe.2008.09.005.

A novel length back-calculation approach accounting for ontogenetic changes in the fish length – otolith size relationship during the early life of sprat (*Sprattus sprattus L.*)

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4.1 Abstract

An individual-based length back-calculation method was developed for juvenile Baltic sprat accounting for ontogenetic changes in the relationship between fish length and otolith length. In sprat, metamorphosis from larvae to juveniles is characterized by the coincidence of low length growth, strong growth in body height and maximal otolith growth. Consequently, the method identifies a point of metamorphosis for an individual as the otolith radius at maximum increment widths. By incorporating this information in our back-calculation method, estimated length growth for the early larval stage was more than 60% higher compared to the result of the Biological Intercept model. After minimal length growth during metamorphosis, we found the highest increase in length during the early juvenile stage. We thus located the strongest growth potential in the early juvenile stage, which is supposed to be critical in determining recruitment strength in Baltic sprat.

4.2 Introduction

An important research focus in fisheries ecology is the relationship between year class strength and variable mortality rates of early life stages. Mortality during early life-stages is often regarded as size dependent and explained with the growth-mortality hypothesis (Anderson 1988), where faster growing individuals have a higher probability to survive. However, survival may either be regulated during the larval (Bailey and Houde 1989) or the juvenile life-stage (Sogard 1997, Takahashi et al. 2008). To reconstruct length and growth histories of survivors and to uncover stage-specific mechanisms influencing recruitment strength, otolith microstructure analysis has been developed as a powerful tool. Generally, the otolith microstructure analysis bases on two assumptions (Campana and Jones 1992): The daily accretion of increments and a known relationship between fish length and otolith length (hereafter: FL-OL relationship). Validation of daily increment formation is a mandatory procedure before applying otolith microstructure analysis to a species. However, when reconstructing growth rates it is likewise important to investigate the characteristics of the FL-OL relationship to ensure that the model chosen for back-calculating length is consistent with the data (Francis 1990, Francis 1995, Hare and Cowen 1995).

One of the first approaches to back-calculate fish length via hard-parts (e.g. otoliths) is the Fraser-Lee method (Lee 1920), which uses a linear regression of the FL-OL relationship. However, it has been shown that the FL-OL relationship varies with growth rate (Mosegaard et al. 1988, Secor and Dean 1992), potentially leading to bias in back-calculated lengths derived from the Fraser-Lee method. To consider this growth-effect, Campana (1990) developed the Biological Intercept method (hereafter: BI method), that uses an empirical rather than statistical (regression-based) intercept. An extension of the BI method is the Modified Fry Model (Vigliola et al. 2000) allowing for an allometric instead of a linear FL-OL relationship. However, the use of a back-calculation model assuming a steady FL-OL relationship is often limited to the larval stage as the shape of the FL-OL relationship may change between life-stages (e.g. Takahashi et al. 2008). For instance, in our case study sprat, the larval stage is described by an allometric FL-OL relationship (Lee et al. 2006), whereas a linear form is assumed for the juvenile stage (Baumann et al. 2006a). Only few approaches consider ontogenetic changes in the FL-OL relationship (Butler 1989, Laidig et al. 1991, Hobbs et al. 2007), allowing length reconstruction over different life stages. However, these approaches all use a population-based rather than an individual transition point between life-stages. As transitions between life-stages may act as critical periods with increased mortality determining the strength of a year-class, there is a need to develop back-calculation methods which are applicable beyond ontogenetic changes on an individual basis (Francis 1990, Vigliola and Meekan 2009).

As it has been proven difficult to grow sprat larvae in the laboratory (Petereit et al. 2008), longitudinal records of otolith and somatic growth (e.g. Wilson et al. 2009) are not possible in Baltic sprat. In contrast to the worthwhile experimental approach to develop a back-calculation method by monitoring individual growth, we use field data of fish and otolith length and follow a regression-based approach.

For this purpose, we combined data of various sampling years collected mainly during the German GLOBEC project, which focused on sprat as a key species in the Baltic Sea. Sprat influences plankton communities (Kornilovs et al. 2001) as well as top predators (Bagge et al. 1994) and its population dramatically increased after the regime-shift in the late 1980ies (Möllmann et al. 2009). Special attention was given to the late larval and early juvenile stage, as this stage was identified as crucial for the determination of recruitment strength (Baumann et al. 2006b). However, this length range (20 – 55 mm) cannot be captured quantitatively by commercial or scientific fishing trawls (Baumann et al. 2007). In this study we were able to close the size class gap by sampling late larval and early juvenile stages in shallow coastal waters. The shape of the relationship between standard length and otolith radius (hereafter: SL-OR relationship) of the final dataset over all life-stages irrevocably challenges the so far used length reconstruction method for Baltic sprat.

The objective of the study was to develop a regression-based non-linear back-calculation model taking into account an allometric FL-OR relationship in the larval stage and a linear one in the juvenile stage. We hypothesize that changing body-proportions during ontogeny coincide with characteristics in increment patterns on the otolith allowing us to define an individually based point of metamorphosis. We integrated this point of metamorphosis in length back-calculation algorithms and compared the outcome with a simple non-linear approach and a linear one, so far used for Baltic sprat.

4.3 Materials and Methods

4.3.1 Samples

For the investigation of the relationship between standard length (SL) and otolith radius (OR), sprat larvae (length range: ~ 4-20 mm SL) were sampled between 2002 and 2003 during the German GLOBEC project in the central Baltic Sea (Fig.4-1, Tab.4-1). Sampling gear was a Bongo-net (diameter: 0.6 m) with a mesh-size of 500µm. Larvae were sorted out of the plankton samples directly and stored frozen. In the laboratory, SLs were recorded and sagittal otoliths prepared to measure otolith radii at the longest axis from the core to the edge. In total, data of 230 larvae from seven cruises were used. Additional to the larvae analyzed in this study, data of 58 individuals from Dänhardt et al. (2007) were added to the analysis of the SL-OR relationship (Tab.4-1).

To detect morphometric changes in body-proportions during the ontogeny of Baltic sprat, an additional sub-set of larvae was sampled in April 2009 in the central Baltic Sea (Tab.4-1). Here, body heights (at half SL) and SLs were measured to the nearest hundredth millimeter. Sampling and treatment of larvae were identical as described for the larvae used for the analysis of the SL-OR relationship (see above).

Post-larval (length range: ~ 20 – 30 mm SL) and early juvenile sprat (length range: ~ 30 – 60 mm SL) were sampled along Germany's Baltic Sea coast (Fig.4-1) between July-September in 2006, 2007, and

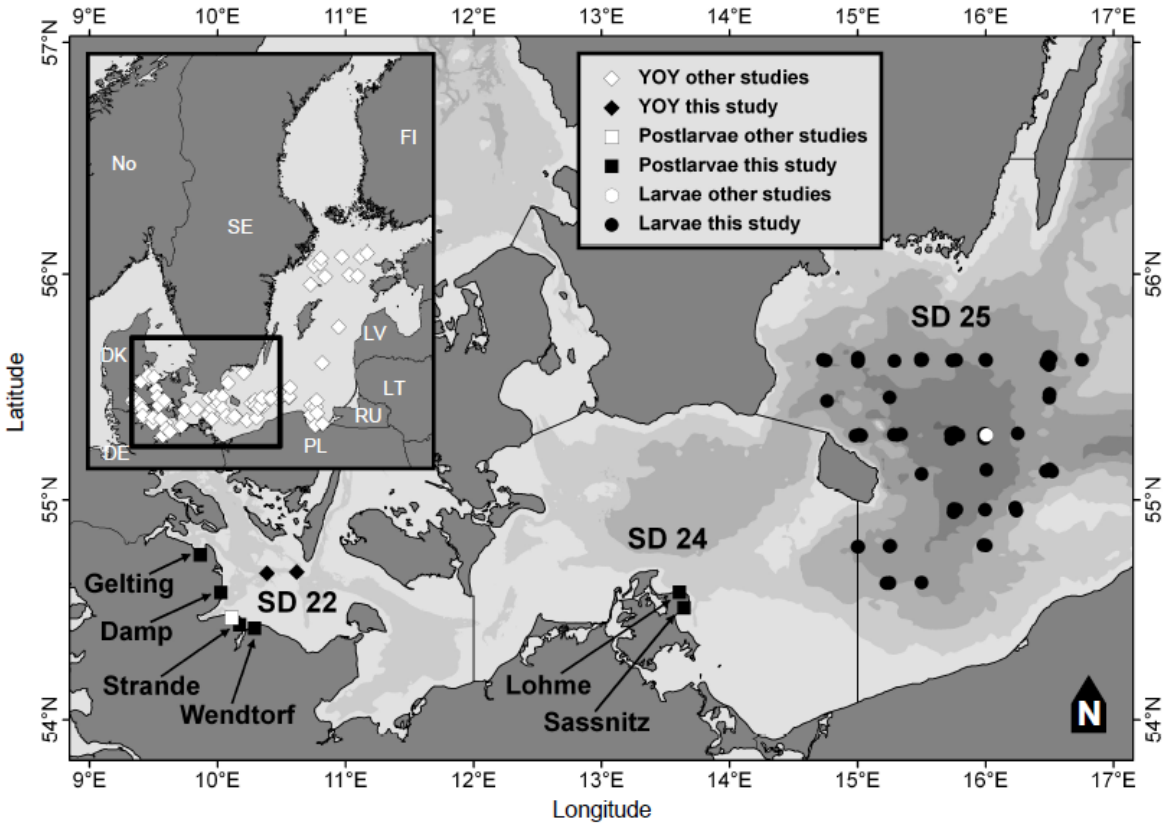

Fig.4-1. Study area with sampling sites in the Baltic Sea. Black symbols represent sample sites of this study; white symbols are sample sites of other studies (see Tab.4-1). Different shadings in the sea represent different water depths, with light grey planes corresponding to shallow areas. DE, Germany; DK, Denmark; FI, Finland; LT, Lithuania; LV, Latvia; NO, Norway; PL, Poland; RU, Russian Federation; SE, Sweden; SD, ICES subdivision.

2008 (Tab.4-1). A 2 x 3 m dip-net with a stretched mesh size of 6 mm was used. When available, approximately 100 specimens were randomly selected, directly frozen with dry ice, and further stored at –20°C. In the laboratory body heights (at half SL) and SLs were measured to the nearest hundredth millimeter. Sagittal otoliths were extracted from randomly selected sub-samples of individuals caught west (ST : Strande) and east (WE : Wendtorf) of the outer Kiel Fjord (Tab.4-1). The OR was measured along the post-rostral section of the otolith from the core to the edge. Thus, the following analysis of the SL-OR relationship based on the assumption, that the longest axis of the circular larval otolith will develop into the post-rostral section when the otolith starts to form its characteristic shape in the post-larval stage.

Young-of-the-year (YoY) recruits (length range: ~ 60 – 90 mm SL) from the Kiel Bight were sampled in October 2007 during the annual Baltic International Acoustic Survey (BIAS). Standard fishing gear of the annual BIAS has a stretched mesh size of 20 mm in the codend. Random sub-samples of YoY-sprat were obtained from 2 hauls within the Kiel Bight and stored at –20°C. In the laboratory the same examination followed as described for post-larvae and early juveniles. YoY-sprats were distinguished

from 1-year-old specimens by the modes of the length frequency distribution, with specimens smaller 90 mm SL being identified as YoY-sprat, according to Baumann et al. (2006c).

For the investigation of the SL-OR relationship SL and OR data of YoY-sprat from previous studies were used (Tab.4-1, Baumann et al. 2006c, 2008).

Tab.4-1. Source of individuals used for the examination of the SL-OR relationship, the body height-SL relationship and for otolith microstructure analysis and back-calculation. YoY: Young-of-the-Year survivors; SD: ICES-Subdivision; ST: Strande; LO: Lohme; SA: Sassnitz; DA: Damp; WE: Wendtorf; GE: Gelting Mole (see Fig.4-1).

Life stage	Type of sampling/ Gear	Source	Sampling date	Year	Location	Mean SL	Range SL	Type of analysis		
								SL-OR	BH - SL	Back-calculation
						(mm)	(mm)	n	n	n
Larvae										
	BIOMOC	Dänhardt *et al.* 2007	9-10 June	2000	SD25	13.1	9.3 - 21.1	58	-	-
	Bongo	This study	2.-30.Apr.	2002	SD25	8.3	4.6 - 11.7	29	-	-
		This study	5 -24 May	2002	SD25	11.0	10.1 - 12.2	9	-	-
		This study	11-23 June	2002	SD25	8.6	4.8 - 17.6	59	-	-
		This study	1-16 July	2002	SD25	12.4	8.2 - 26.0	36	-	-
		This study	22 Jul -7 Aug.	2002	SD25	14.6	8.6 - 23.0	41	-	-
		This study	15.May-3.Jun	2003	SD25	11.8	10.1 - 14.5	23	-	-
		This study	1-19 July	2003	SD25	10.9	6.5 - 15.8	33	-	-
		This study	8-20 Apr.	2009	SD25	8.0	4.3 - 15.0	-	192	-
Postlarvae - early juveniles										
	Dip - Net	Baumann *et al.* 2007	28 Aug.	2003	SD22/ST	35.7	28.4 - 45.1	51	-	-
		This study	1 Aug.	2006	SD22/ST	29.3	23.0 - 36.7	30	183	23
		This study	3 Aug.	2006	SD24/LO	29.7	22.4 - 48.6	-	73	-
		This study	3 Aug.	2006	SD24/SA	35.0	22.6 - 41.7	-	100	-
		This study	18 Aug.	2006	SD24/LO	43.4	36.7 - 55.5	-	20	-
		This study	22 Aug.	2006	SD22/DA	50.2	44.1 - 58.9	-	150	-
		This study	23 Aug.	2006	SD22/WE	57.9	46.6 - 65.2	29	199	26
		This study	30 Aug.	2006	SD22/WE	60.7	42.7 - 69.4	16	140	15
		This study	12 Sept.	2006	SD22/GE	43.5	33.0 - 59.9	-	150	-
		This study	19 July	2007	SD22/ST	41.1	35.8 - 52.2	36	99	26
		This study	26 July	2007	SD22/WE	51.6	43.5 - 56.6	27	43	21
		This study	14 Aug.	2007	SD22/WE	25.2	21.8 - 29.6	83	178	31
		This study	31 July	2008	SD22/WE	23.4	19.1 - 25.9	27	55	-
YoY										
	Trawl	Baumann *et al.* 2006	7 Oct. - 29 Oct.	2002	SD24-26, 28+29	74.1	53 - 91	350	-	-
		Baumann *et al.* 2008	14 Oct. - 24 Oct.	2002	SD22	73.8	59 - 86	45	-	-
		Baumann *et al.* 2008	5 Oct. - 14 Oct.	2003	SD22	69.6	52 - 82	77	-	-
		Baumann *et al.* 2008	6 Oct. - 23 Oct.	2003	SD 24+25	77.2	67 - 89	69	-	-
		This study	13 Oct.	2007	SD22	72.0	62.1 - 80.0	27	68	20
							Sum:	1155	1650	162

4.3.2 Otolith processing

Otolith microstructure analysis and subsequent back-calculation was performed for post-larvae and early juveniles sampled in summer 2006 and 2007 from the Kiel Fjord and for YoYs caught in October 2007 in the Kiel Bight (Tab.4-1).

Following the extraction, sagittal otoliths were mounted on microscopic slides with a drop of thermoplastic glue (Crystalbond® 509). All otoliths were ground from the convex side with a 3 µm lapping film (266x Imperial PSA 3M®) until the core was reached. After re-heating and turning, the other side was polished to detect the outmost increments at the edge of the post-rostral section precisely. Irrespective of left or right, the otolith with the most distinct increments was chosen for analysis.

Pictures for measurement were recorded at 400x magnification with a digital camera (Leica®DC300, 3132 x 2328 pixels) connected to an image analysis system (ImagePro Plus 6.0). Increments were counted and their width was measured along the axis from core to post-rostrum of the otolith, beginning with the first clearly visible increment outside the core. Age estimates derived from the analysis hereafter refer to days after first increment formation.

Sufficient precision in increment counts was ascertained through inter-calibration with an experienced reader, using an independent otolith subset (n = 32) of post-larval and juvenile sprat (20-60 mm SL). The linear regression was significant ($P < 0.001$) and explained 99% of the variance, while the slope of the regression (0.99) was not significantly different from 1 (95% - confidence: 0.95-1.03). The mean coefficient of variation (Campana 2001) of all individuals was 4.4%.

Regarding otoliths used for back-calculation, increments were counted three times by the same reader, while increment widths were measured on the first and second reading. During the first reading 222 otoliths were processed and the quality of each reading was judged according to a scale from 1 (best) to 4 (worst). Otolith-readings with quality 4 (n = 45) were excluded from further procedure after the first reading, such that in the second and third reading only the residual 177 otoliths were processed. Out of the first two readings where increment width was measured, the one closest to the mean of all three counts was used for further analyses, allowing a difference from the mean of maximal two increments. If the counts of the first two readings were equal, the second reading was preferred over the first one assuming a learning curve. 74% of all otoliths exhibited a difference less than 1, while 17% showed a difference between 1 and 2. 15 otoliths with differences from the mean greater than 2 were excluded from the subsequent analysis. The mean coefficient of variation (Campana 2001) for the estimation of precision for the readings of the final 162 otoliths used for further analysis was 9.0%.

4.3.3 Standard length – otolith radius relationship and non-linear regression models

Two different approaches were used to model the overall regression of SL versus OR, which represent the basis of the length back-calculation methods explained below. Both models were developed to describe the non-linear shape of the SL-OR relationship which is generated by the change in body proportions during the metamorphosis from larvae to juveniles (see results).

The first regression model describes the increase of SL with increasing OR during the larval stage by an asymptotic function followed by a linear relationship for juveniles. Both sub-models, the asymptotic section and the linear section, were connected by a logistic switch-function allowing a change between sub-models and a gradual transition. SL-OR model (1) is a 6 parameter function of the form

$$SL = \left[SL_{\infty} \times \left(1 - e^{-k\times(OR+SL_{BL})}\right)\right] \times \left[1 - \frac{1}{1+e^{-\alpha\times(OR-OR_M)}}\right] + \\ + \left[a \times OR + \left(SL_{\infty} - a \times OR_M\right)\right] \times \left[\frac{1}{1+e^{-\alpha\times(OR-OR_M)}}\right] \quad (1)$$

with the parameters SL_{∞}, k, SL_{BL} for the asymptotic section, a (slope) for the linear section and α and OR_M for the logistic connection. In the section explaining length back-calculations, special attention is paid to the parameter OR_M. OR_M describes the OR at metamorphosis when the influence of the function for the larval stage is removed by the function for the juvenile stage.

The SL- OR model (2) is structured like model (1) with the difference that the sub-models for both life-stages were changed. For the juvenile stage, SL-OR model (2) used a sigmoid function instead of a linear relationship, as length growth in relation to otolith growth seems to decrease for larger juveniles. To fit the sigmoid function for the juvenile stage smoothly to the data, an offset-parameter (SL_{LOG}) was added to the sub-model. For the larval stage, the asymptotic function of SL-OR model (1) was replaced by a power function. The technical advantage of these substitutions is that the steady increase of the power function together with the offset-parameter of the sigmoid function enables the model to match the inflection point (see results) with the parameter OR_M. To permit a smooth transition between the power and the sigmoid function while keeping the inflection point of the curve and OR_M in coincidence, α was fixed to 0.1. OR_M of the overall model was fixed to 136 µm corresponding to the inflection point estimated by SL-OR model (1) (see results) to permit comparability between the back-calculation approaches. Therefore, only seven of the nine parameters of SL-OR model (2) were estimated by the least square method. SL-OR model (2) was given as follows:

$$SL = \left[SL_{POW} + b \times OR^{c}\right] \times \left[1 - \frac{1}{1+e^{-\alpha\times(OR-OR_M)}}\right] + \\ + \left[SL_{LOG} + SL_{MAX} \times \left(\frac{1}{1+e^{-\beta\times(OR-OR_J)}}\right)\right] \times \left[\frac{1}{1+e^{-\alpha\times(OR-OR_M)}}\right] \quad (2)$$

The parameters SL_{POW}, b, c belong to the power section, SL_{LOG}, SL_{MAX}, β, OR_J to the sigmoid section and α and OR_M to the logistic connection.

To assure an equal influence of all life-stages on the regression, a subset of 40 individuals per 10 mm length class was randomly selected to estimate the parameters of SL-OR model (1) and (2). Therefore, only 360 individuals were finally applied for the estimation using SPSS 17.0. To proof if the random selection of 40 individuals per length class has an influence on the estimation, four additional datasets were created in the same way and used for the same regression. Parameters and confidence limits of

the totally five regression runs were compared for profound differences in each model. For the evaluation of the best regression model Akaike Information Criterion (AIC) was used.

4.3.4 Body height – standard length relationship

A modification of the Gompertz-Model was fitted to the relation of relative body height (as percentage of SL) and SL (n = 1650; Tab.4-1), in order to detect changes in body proportions throughout the development of young sprat:

$$BH = s + BH_{\infty} \times e^{-e^{-g(SL \times x_0)}} \quad (3)$$

BH is the relative body height, BH_{∞}, *g* und x_0 are the common parameters of the Gompertz-Model, and *s* is an added offset parameter. Parameters *s* and BH_{∞} add up to the maximum in relative body height.

4.3.5 Length back-calculation

Three different approaches for back-calculating previous length in Baltic sprat were developed (Fig. 2, Tab.4-2) and compared with each other as well as with the BI method (Campana 1990) with a biological intercept of 5 mm SL as in Baumann et al. (2006a). All length back-calculations were performed in MS Excel 2000.

The BI method is independent of the regression of SL and OR but assumes a linear relationship between SL and OR throughout the back-calculation period and considers the growth effect by generating a back-calculation line between two known fixed-points (Fig.4-2): the empirically estimated biological intercept and the point defined by fish length and otolith length at capture.

Our first approach is based on the regression of SL-OR model (1) and is called the Non-Linear Regression method (hereafter: NLR – method) (Tab.4-2). The general goal of this approach is to generate a line between two fixed-points in a non-linear way. This procedure is also known as the body-proportional hypothesis (BPH) and assumes a constant proportional deviation of an individuals' fish length from the mean fish size throughout life (Francis 1990). In other words, the individual back-calculation line of the *j*th individual ($f(OR_j)$) was developed by the multiplication of the overall regression $f(OR_{all})$ with the ratio of the *j*th individuals SL at the time of capture (SL_{cj}) and the corresponding SL of $f(OR_{all})$ at the *j*th individuals OR at time of capture ($f(OR_{all\,cj})$):

$$f(OR_j) = f(OR_{all}) * \left(\frac{SL_{cj}}{f(OR_{all\,cj})} \right) \quad (4)$$

The only difference between the NLR method and the BPH (equation (4)) is a common y-intercept for all individual back-calculation lines. This common starting point is generated by subtracting the

regression based y-intercept of SL-OR model (1) from the overall SL-OR relationship before multiplying it with the individual length ratio and adding it again afterwards. Thus, the non-linear overall regression curve of SL-OR model (1) is rotated around the y-intercept until the curve crosses the fish length and otolith length at capture (Fig.4-2). The y-intercept equals the theoretical length when the otolith radius is zero. Therefore, resulting SL at first increment formation (comparable to the biological intercept) depends on the individuals' back-calculation line and on the OR at the first increment. After generating individual back-calculation lines, the procedure of reconstructing length at earlier ages was the same for all back-calculation approaches established here: By inserting otolith radii at ages earlier than the time of capture into the individual form of the regression model, previous length of the corresponding specimen can be calculated.

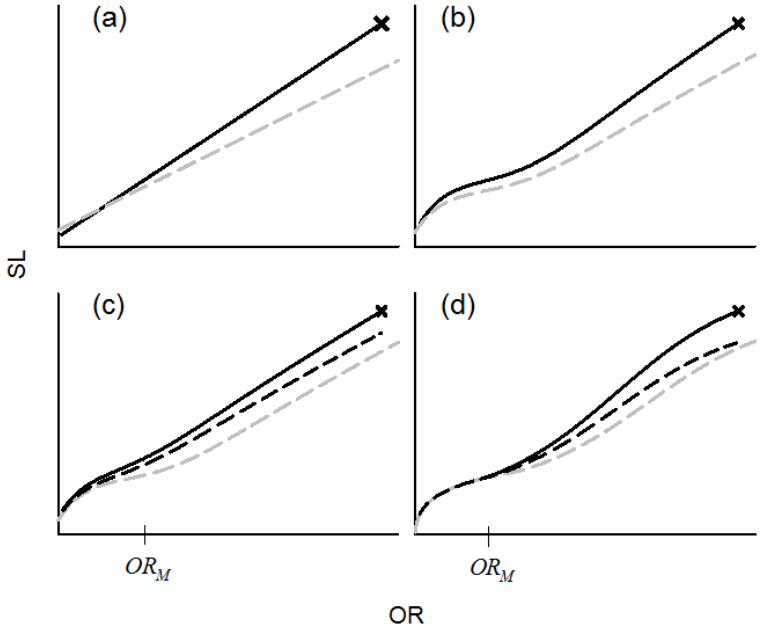

Fig.4-2. Schematic illustration of back-calculation approaches: (a) biological intercept method (Campana 1990); (b) nonlinear regression method; (c) metamorphosis method; (d) metamorphosis inflection point method. Black cross: length at catch of individual j. Grey dashed line: overall regression of the SL–OR relationship $f(OR_{all})$. Black solid line: back-calculation line $f(OR_j)$ of individual *j*. Black dashed line: initial back-calculation line $f(OR_{Mj})$ with OR-at maximum increment width as OR_M

In contrast to the former approach, the following two methods implement an additional fixed-point into the back-calculation procedure (Fig.4-2): the point of metamorphosis (see results). As opposed to the y-intercept (or biological intercept) and the length at capture, the point of metamorphosis is defined by an x-value (OR) only. Furthermore, this point is not common for all individuals from the population (as it is the case with the biological intercept) but specific for every individual, as it refers to the OR when the maximal increment widths (hereafter: OR-at-maximum increment width) are

established on the individual otolith. To determine the OR-at-maximum increment width, the following model was fitted to increment width versus age for every single individual:

$$IW = R \times e^{(a_1 \times AGE)} \times \left(1 + \frac{1}{1 + e^{-a_2 \times (AGE - AGE_M)}}\right) \quad (5)$$

The parameters R, a_1, a_2 and AGE_M are being estimated by the least square method. Originally created to describe a temperature optimum of a physiological rate (Temming 1995), the model is likewise able to reproduce the exponential increase of increment width in the larval stage combined with a maximum and followed by a decrease in the juvenile stage. The corresponding OR at the age when maximum increment width occurred was used as point of metamorphosis and applied in the parameter OR_M in the following back-calculation approaches. As we assume metamorphosis as a period in life rather than a single day, we model OR-at-maximum increment width instead of using the observed OR when the maximal increment occurred on the otolith. By doing so, we estimate a value that describes the middle of metamorphosis.

Tab.4-2. Characteristics and differences of back-calculation approaches.

Approach	Assumption for SL-OR relationship	Additional fixed point at meta-morphosis	Adjustment to individual back-calculation line	Type of larval sub-model	Type of juvenile sub-model
Biological Intercept Method	Linear (regression independent)	No	n.a.	n.a.	n.a.
Non - Linear Regression Method	Non-linear (regression dependent)	No	Rotation around intercept	Asymptotic	Linear
Metamorphosis Method	Non-linear (regression dependent)	Yes	Rotation around intercept	Asymptotic	Linear
Metamorphosis Inflection Point Method	Non-linear (regression dependent)	Yes	Rotation around OR_M	Power	Sigmoid

We called our second back-calculation approach Metamorphosis method (hereafter: M method) (Tab.4-2) as it was the first attempt to incorporate OR-at-maximum increment width on an individual basis. The M method is based on the regression of SL-OR model (1) and individual back-calculation lines were created in two steps. In step (A) OR-at-maximum increment width was derived from the individual fit of equation (5) and was then applied in SL-OR model (1) as OR_M, i.e. the otolith radius when the influence of the asymptotic section is removed by the linear section. All other parameters of SL-OR model (1) were fixed as estimated by the overall regression. The resulting curve is referred to as $f(OR_{Mj})$ (Fig.4-2). In step (B), the individual back-calculation line ($f(OR_j)$) is generated as in NLR-method, by rotating $f(OR_{Mj})$ around the intercept (Fig.4-2).

Our last and final approach based on the regression of SL-OR model (2) and was called the Metamorphosis Inflection Point method (hereafter: MIP method) (Tab.4-2). As variability in the larval phase was low compared to the juvenile stage, only the right part of the back-calculation line starting at OR_M (instead of the intercept) was rotated in the MIP method, resulting in an almost identical line for individual larval phases. The development of individual back-calculation lines in this approach followed four steps: In step (A) the OR-at-maximum increment width was used as OR_M, as in the M method. The difference between OR_M of the overall regression and the OR-at-maximum increment width was added to OR_J in step (B). Depending on the value of OR_M, the model may exhibit an abrupt change between the power-function and the sigmoid-function. To smooth the generated curve the offset-parameter SL_{LOG} of the sigmoid function was corrected for the SL of the power function at OR_M in step (C). In other words, the sigmoid-fraction for the juvenile stage was adjusted in y-direction to allow a smooth transition. Finally, the initial back-calculation line ($f(OR_{Mj})$) for individual j is rotated around OR_M to the corresponding SL-OR point at capture in step (D). In doing this, the starting point for the BPH (equation (4)) and thus the multiplication of $f(OR_{Mj})$ with the ratio of $SL_{c\ j}$ and the corresponding SL of $f(OR_{Mj})$ at the OR at the time of capture ($f(OR_{M\ cj})$ is OR_M (Fig.4-2).

To compare and demonstrate the performances of the different back-calculation approaches data from 2006 and 2007 (Tab.4-1) caught in the Kiel Bight (Fig.4-1) were used for implementation and illustration.

4.4 Results

4.4.1 Ontogenetic changes in morphometry

The raw data of the SL-OR relation exhibited two conspicuous features (Fig.4-3.a, b): A distinct pattern for early life stages and an increasing variability in SL with increasing OR. Concerning the former, SL in the early larval stage was increasing rapidly with OR, while in the late larval stage, this increase was gradually reduced resulting in a minimum of the gradient. In the subsequent juvenile phase, the slope of the raw data increased again to remain constant for most of the juvenile stage.

Both models developed here to describe the SL-OR relation (SL-OR model (1) and (2)) showed an equal performance and were able to appropriately model the course of both life stages by explaining more than 97% of the overall variability in SL. The selection of a subset of data to assure an equal influence of all life-stages on the regression has only a negligible effect on the parameter estimates (Tab.4-3). Parameters of five equally performed estimation runs, basing on five randomly selected datasets, were inside the confidence limits of each other for both SL-OR models. Regarding the Akaike Information Criterion, SL-OR model (2) performed slightly better than SL-OR model (1).

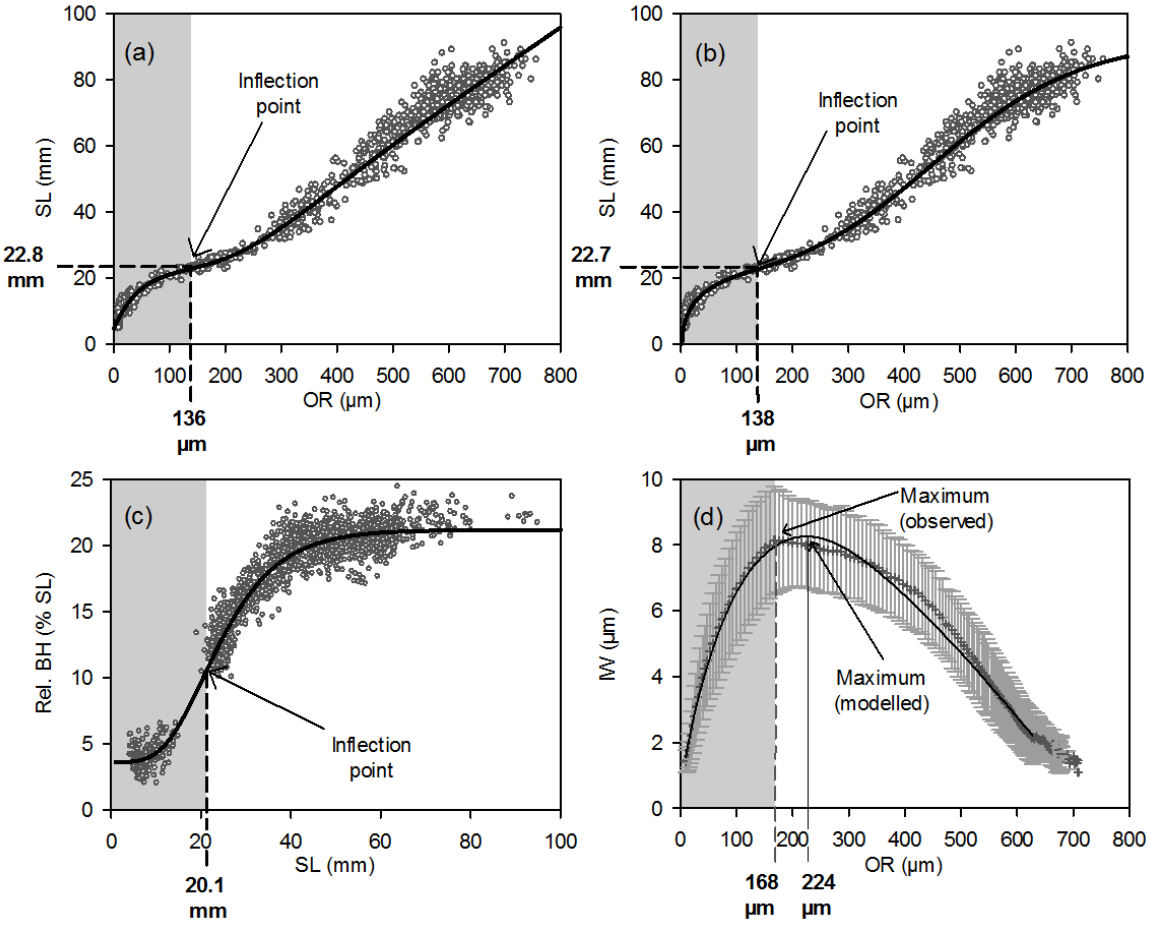

Fig.4-3. Morphometric changes between the larval and the juvenile stage. (a) SL–OR relationship with all available data described by SL–OR model 1. The larval stage (grey plane) is separated from the juvenile stage (white plane) by the inflection point of SL–OR model 1. Lengths at the inflection point are highlighted. (b) SL–OR relationship with all available data described by SL–OR model 2. The larval stage (grey plane) is separated from the juvenile stage (white plane) by the inflection point of SL–OR model 2. Lengths at inflection point are highlighted. (c) Relationship between relative body height (BH) and SL with all available data described by model 3. The larval stage (grey plane) is separated from the juvenile stage (white plane) by the inflection point of model 3. SL at inflection point is highlighted. (d) Mean observed increment width (IW, dark grey crosses) and standard deviation (grey bars) versus OR. Mean observed maximum IW separates the larval (grey plane) from the juvenile stage (white plane). OR at mean observed maximum IW and OR at mean modelled maximum IW is highlighted. Mean modelled increment width versus OR is shown by the black line.

Common for both models was the logistic switch-function with the parameter OR_M describing the OR when the influence of the function for the larval stage was replaced by the function for the juvenile stage. In SL-OR model (1), where an asymptotic function for the larval stage was combined with a linear function for the juvenile phase, OR_M was estimated at 198 µm OR. However, the inflection point of SL-OR model (1), where the gradient was lowest and thus otolith growth was strongest in relation to length growth, was located at 136 µm OR (Fig.4-3.a).

In contrast, SL-OR model (2) was composed of a power function for the larval stage and a sigmoid function for the juvenile phase (Fig.4-3.b). The combination of these sub-models and its offset-parameters enabled the overlay of the inflection point of the curve (138 µm, Fig.4-3.b) with the parameter OR_M (136 µm).

Model (3) was used to describe the relationship between relative body height and SL and explained 96% of the variability in body height. Despite the lack of data between 15 and 20 mm SL (Fig.4-3.c), relative body height showed a distinct s-shaped form with increasing SL. The inflection point of model (3), where growth in body height was strongest in relation to SL was estimated near to the edge of the data lack at 20.1 mm SL. When relative body height reached 20.2 % at about 50 mm SL, length and height approximately grew in the same relation, indicating isometric growth in body proportions at sizes bigger than 50 mm SL.

Tab.4-3. Parameter estimates, standard errors and confidence limits of the first estimation run and AICs of SL – OR model (1) and (2). Parameters of the 2. – 5. estimation run are listed.

Model (1) AIC = 415.08	No. of estimate	SL_∞	SL_{BL}	k	α	OR_M	a
Estimates	1	26.084	10.746	0.019	0.012	197.967	0.116
	2	25.126	10.851	0.020	0.012	185.771	0.116
	3	26.015	9.729	0.021	0.012	200.931	0.119
	4	25.802	12.383	0.019	0.013	194.477	0.118
	5	26.347	14.824	0.016	0.013	198.878	0.118
Standard Error	1	2.203	6.827	0.008	0.005	29.972	0.003
95% Confid. Limits	1	21.752 - 30.416	-2.680 - 24.172	0.004 - 0.035	0.003 - 0.022	139.020 - 256.914	0.111 - 0.121

Model (2) AIC = 403.74	No. of estimate	SL_{POW}	b	c	β	OR_J	SL_{MAX}
Estimates	1	-38.261	36.398	0.104	0.007	449.565	76.415
	2	-32.116	30.589	0.118	0.007	454.926	78.338
	3	-22.241	21.550	0.148	0.008	448.988	77.369
	4	-44.961	43.097	0.089	0.007	453.275	78.375
	5	-88.793	85.481	0.054	0.008	449.065	77.489
Standard Error	1	131.048	125.074	0.265	0.000	7.775	1.736
95% Confid. Limits	1	-295.996 - 219.474	-209.587 - 282.384	-0.418 - 0.627	0.007 - 0.008	434.274 - 464.857	73.001 - 79.829

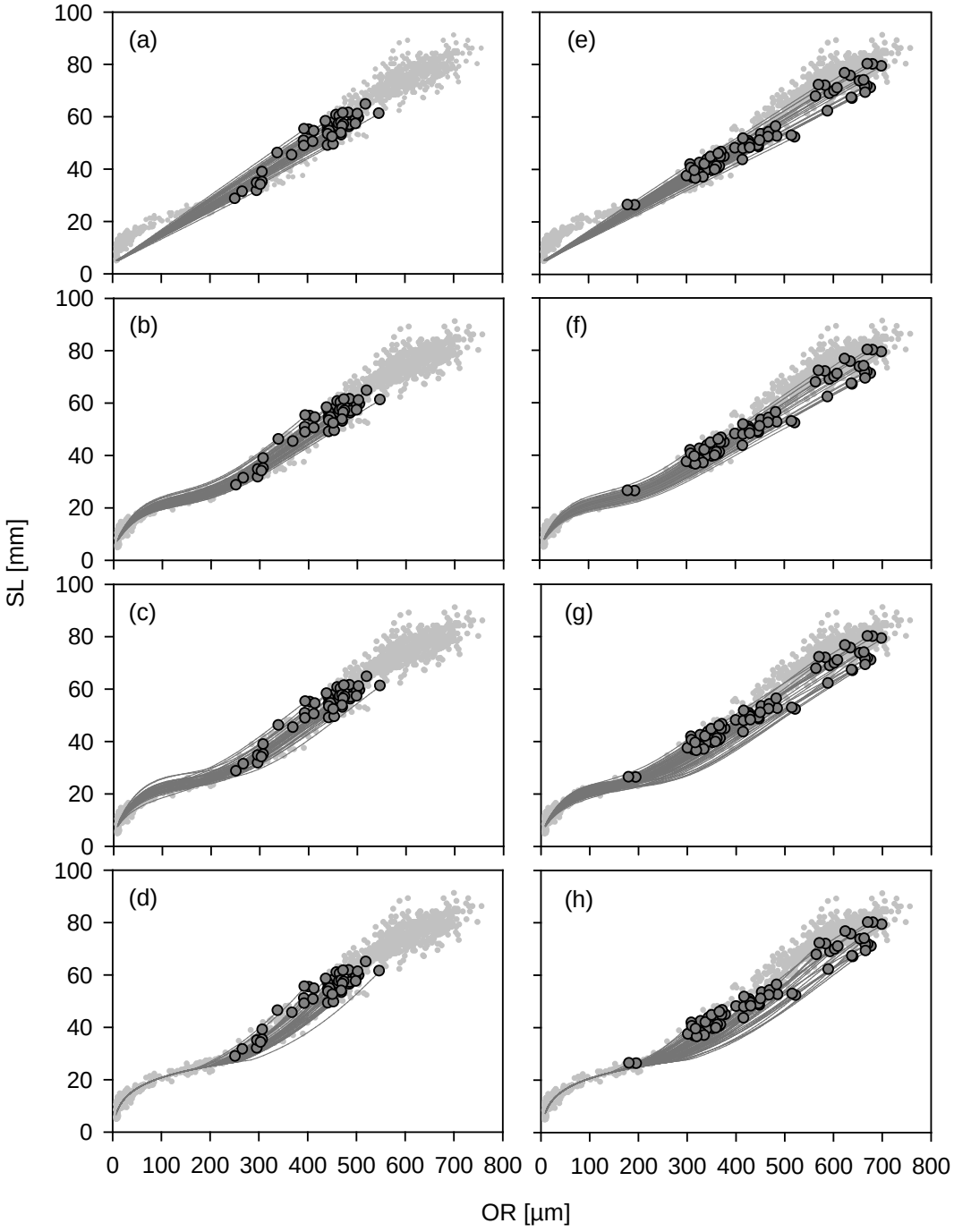

Fig.4-4. Individual back-calculation lines (dark grey) of the different back-calculation methods generated for a subsample (black-bordered grey dots) of postlarval–early juvenile sprat caught in summer 2006 (left side) and summer and autumn 2007 (right side). (a and e) BI method; (b and f) NLR method; (c and g) M method; (d and h) MIP method. Light grey dots represent all available data.

The mean OR corresponding to maximum increment width of all individuals was calculated as 168 µm (Fig.4-3.d). For the M method and the MIP method, model (5) was fitted to individual increment width-at-age trajectories to obtain the age when maximum increment width occurred. As age and OR-at-maximum increment width were highly correlated ($p < 0.05$, $r^2 = 0.82$), the corresponding otolith

radius was used as OR-at-maximum increment width, and therefore as individual OR_M for length back-calculation. Model (5) explained on average 89.99 ± 0.05 % of the variability in increment width. On average, modelled and observed OR-at-maximum increment width differed by 56 µm (Fig.4-3.d).

The length when all three ontogenetic changes in morphometry occurred (changing SL-OR relationship, strongest increase in the body height-SL relationship, and maximum increment width on the otolith) could be located between 20.1 mm (SL at maximal growth in height) and 24.2 mm SL (corresponding SL of mean OR-at-maximum increment width). In the following, this length is called "point of metamorphosis" from larvae to juveniles. Around this point, reduced growth in length was compensated by growth in body height coinciding with maximal growth rates as reflected in largest increments on the otolith. This observation was used as base for the M method and the MIP method, by inserting the individual OR-at-maximum increment width in the back-calculation algorithm. In other words, the aim was to create a back-calculation method that could model reduced length growth rates at the point of metamorphosis on an individual level.

4.4.2 Length back-calculation

In contrast to the previously used linear approach (Fig.4-4.a, e) to reconstruct length at age in juvenile Baltic sprat (e.g. Baumann et al. 2008), back-calculation lines of the three approaches developed here followed the non-linear shape of the SL-OR relationship (Fig.4-4.b-d, f-h).

Individual back-calculation lines in the NLR method were generated assuming proportionality of the individual back-calculation line to the overall regression (Fig.4-4.b, f). This approach, which is also known as the BPH (Francis 1990) implies that a fast growing individual will grow faster than the population mean throughout all development stages and vice versa for a slow growing fish. In contrast, the M and the MIP method utilise the otolith radius at maximal increment width and thus define an otolith length when the larval stage ended and the juvenile stage started. This was attained by inserting the OR-at-maximum increment width as OR_M in SL-OR model (1) and (2), respectively. As the point of metamorphosis was fixed on an individual level, poor growth in early life may be compensated by accelerated growth as juvenile. As in the NLR method, back-calculation lines in the M method were produced by rotating the curve around the intercept after inserting OR-at-maximum increment width in the regression model (Fig.4-4.c, g). In contrast, rotation of the individual back-calculation lines in the MIP method started at OR_M. This procedure generated almost one common back-calculation line in the larval stage, as the individual OR_M was the only feature influencing the course at the beginning (Fig.4-4.d, h).

As inferred by length growth rates of all back-calculation methods, specimens caught in 2006 grew considerably faster than those of 2007 (Fig.4-5.a, b). Maximum growth rate of the linear back-calculation method was 25% lower in 2007 than in 2006. All non-linear back-calculation methods generate bimodal growth rate patterns with high growth in the larval and maximum growth rates in the early juvenile phase, separated by a growth rate minimum around metamorphosis. The BI method

reproduced highest length growth rates when widest increments were deposited on the otolith. The differences in length growth rates between the MIP method and the BI method revealed, that higher length growth during the larval and the juvenile stage is estimated by the new method, whereas length growth rates at metamorphosis are reduced (Fig.4-5.c-f). Mean back-calculated length at metamorphosis (OR_M) using the MIP method was 25.2 ± 1.0 mm SL in 2006 and 24.7 ± 1.4 mm SL in 2007, respectively.

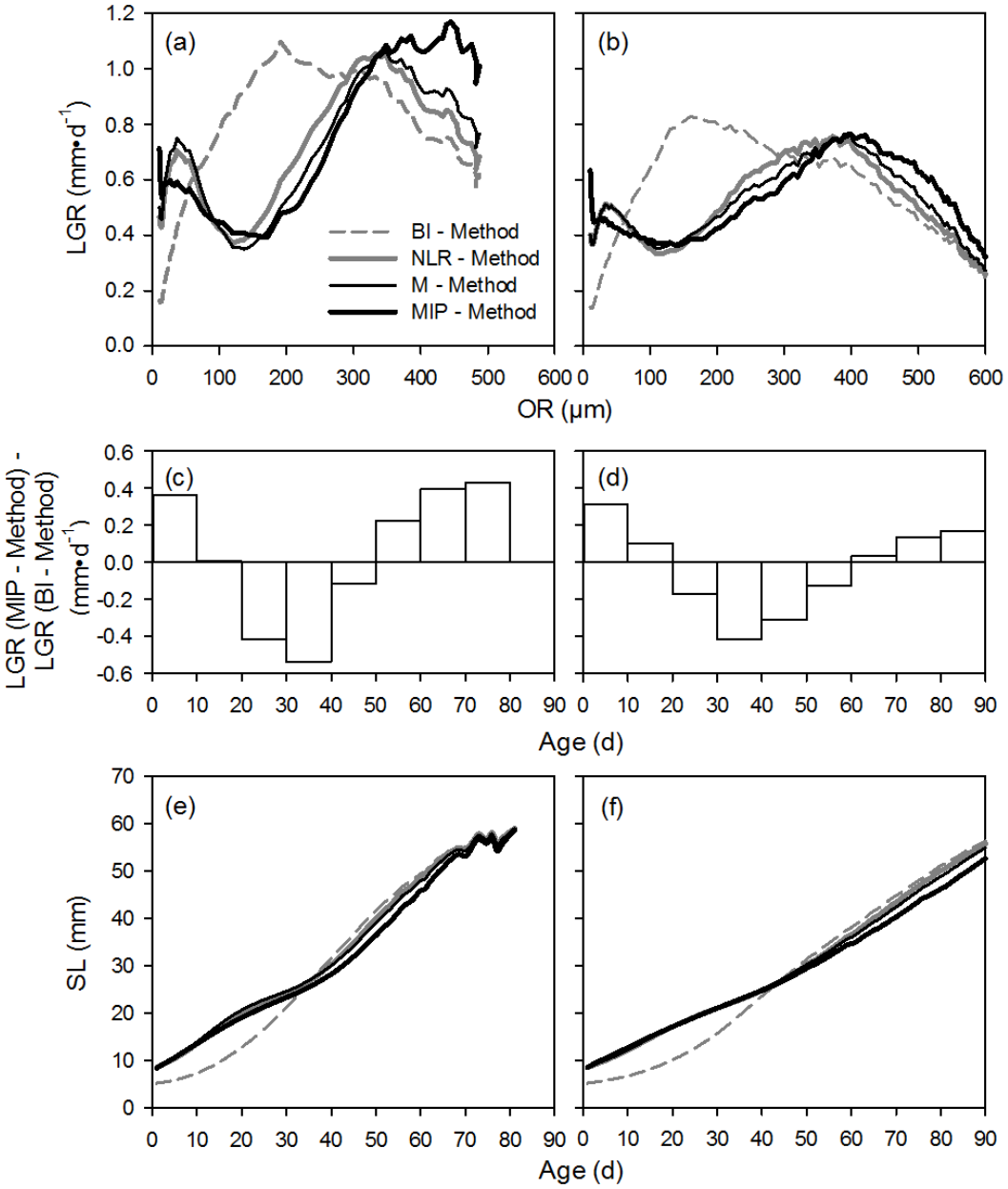

Fig.4-5. Illustration of the different back-calculation methods for the mean growth of sprat caught in 2006 (left side) and 2007 (right side). (a and b) Mean back-calculated length growth rates (LGR) versus OR; (c and d) Differences between LGR calculated by the MIP method and BI method for 10-day age intervals; (e and f) Mean SL versus age.

During the larval stage, mean length growth estimated by the MIP method was more than 0.3 mm•d^{-1} higher as estimated by the BI method (Fig.4-5.c, d), corresponding to a 61% and 65% increase in 2006 and 2007, respectively. In contrast, the linear BI method estimated 48% higher length growth rates during metamorphosis in both years. In the early juvenile stage the MIP method estimated again higher values than the BI method, according to 35% and 5% in 2006 and 2007 in an age-range of 60 – 70 days, respectively.

Non-linear back-calculation approaches differed mainly in the location of length growth minima (Fig.4-6). In the NLR method all individual length growth minima were located near the OR where the regression of SL-OR model (1) exhibited its inflection point. In the M method, the individual OR-at-maximum increment width (Fig.4-6.a, b) influenced the back-calculation line leading to a different location of growth minima for each individual (Fig.4-6.c-f). The larger the otolith was at the point of metamorphosis, the larger the discrepancy was between the NLR method and the M method. The MIP method displays peak larval growth for the youngest larval stages, while in the NLR and the M method this initial peak is weaker and a second pronounced peak appeared in the middle of the larval phase. In total, length growth rates of the MIP method during the larval stage were lower than those calculated by the NLR method and the M method, but mean length growth rates at metamorphosis were slightly higher (Fig.4-5.a, b). The strongest growth in length was estimated in the juvenile stage using the MIP – method. Finally, length growth minima of the MIP method were located nearest to the otolith radii where maximal increment widths occur on the otoliths (Fig.4-6.a-f).

4.5 Discussion

4.5.1 Point of metamorphosis

The point of metamorphosis between the larval and the juvenile stage based on three morphometric features observed in a narrow length range (20.1-24.2 mm SL): (i) a minimum SL-OR ratio, (ii) maximal growth in body height and (iii) peak increment width on the otolith. Feature (i) was derived from a dataset of field-caught individuals from various years, diverse sampling sites, different seasons and sampling methods. The detection of a consistent pattern in the SL-OR relationship of such a heterogeneous dataset supports the interpretation of a true ontogenetic change. A comprehensive dataset increases the likelihood of covering the whole range of growth rates occurring in nature. On the other hand, as the SL-OR relationship is known to vary with growth rate (e.g. Secor and Dean 1992), differences in the origin of individuals may be a source of uncertainty. The combined data from larvae and surviving juveniles are potentially influenced by non-random mortality, so that the shape of the SL-OR relationship for average larvae and for surviving juveniles may differ. However, in this case we would expect a larger variability in the SL-OR relationship of the smallest individuals which is not supported by our data.

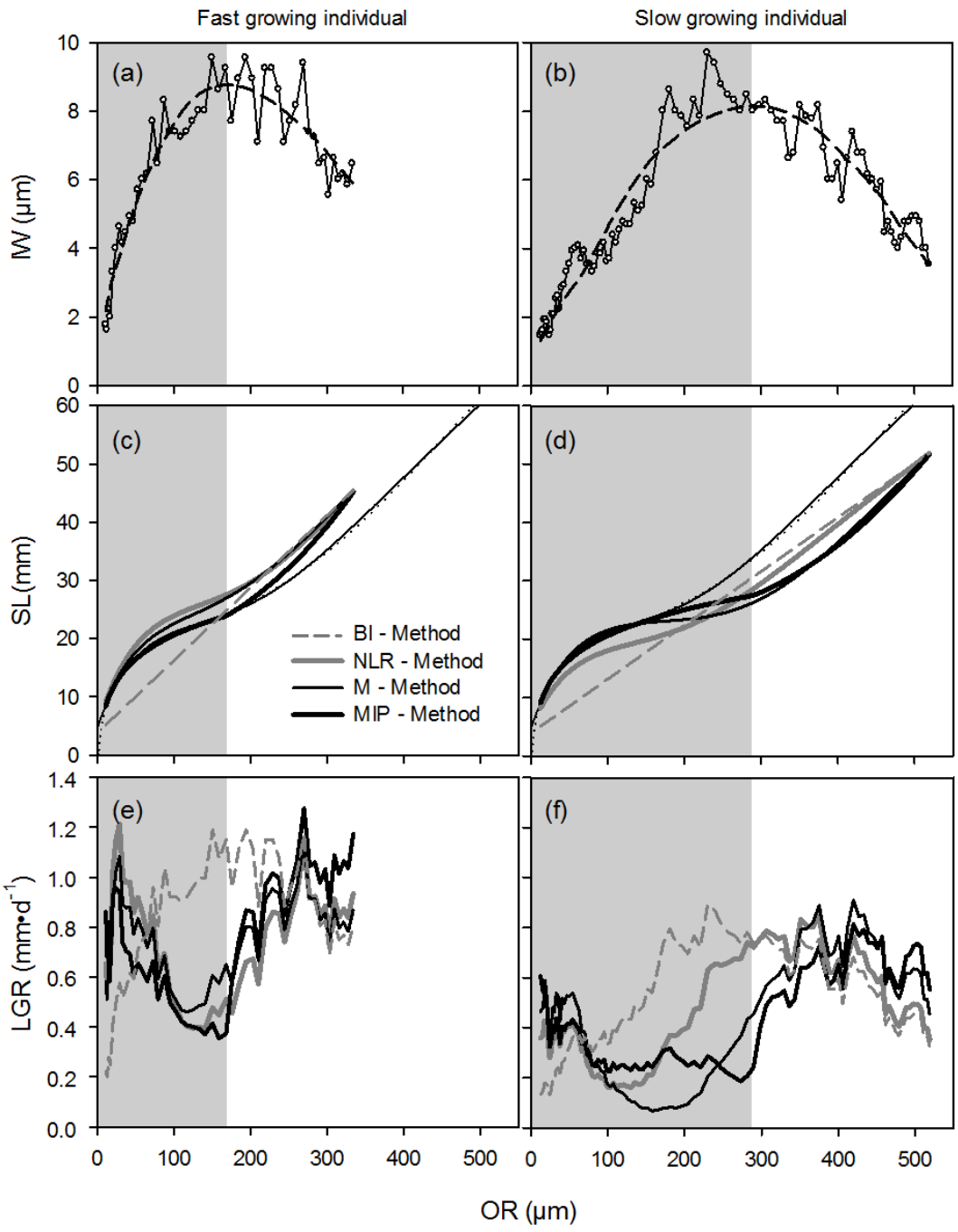

Fig. 4-6. Illustration of the different back-calculation methods for a faster growing 50-day-old sprat from 2006 (left side) and a slower growing 98-day-old sprat from 2007 (right side). (aandb) Connected dots show observed increment width (IW) versus OR. Dashed line indicates IW versus OR as described by model 5. (candd) Individual back-calculation lines of SL versus OR. The thin solid line represents SL–OR model 1; the thin dotted line indicates the SL–OR model 2. (eandf) Length growth rate (LGR) versus OR. The grey plane indicates the larval stage defined by the modelled OR-at-maximum increment width (dashed line in panels (a) and (b)).

The coincidence of reduced length growth and maximal daily accretion on the otolith can be explained by accelerated growth in body height (feature (ii)). During metamorphosis the shape of young sprat alters from an elongate, slender larval to a spindle-shaped juvenile body form. The change in body

form comes along with an exponent of about 5 in the length-weight relationship at metamorphosis (Peck et al. 2005). Corresponding to nearly isometric growth (an exponent of 3) found for sprat beyond a SL of 44 mm described by Peck et al. (2005), we observed a constant ratio of body-dimensions above a SL of 50 mm. As the otolith is assumed to record somatic growth rather than length growth, "uncoupling" in growth of fish-length and otolith-length would be a consequence for sprat smaller than 50 mm SL.

The third feature characterising the point of metamorphosis is the otolith increment pattern of sprat. The average OR-at-maximum increment width approximately coincides with the otolith radius where the SL-OR models have its inflection point. Strongest otolith growth during ontogeny at the same timing as lowest length growth can be explained by maximal growth in body height or weight (see above), respectively. Therefore, all three morphometric changes are linked to the same process.

4.5.2 Comparison of the different versions for back-calculation

Individual back-calculation lines in the NLR method were generated by two fixed points: the intercept, which is common for all individuals and the individual length at catch. A similar nonlinear approach was already used by Laidig et al. (1991), who modelled the SL-OR relationship by a segmented regression. The disadvantage of the NLR method is that length at metamorphosis is implicitly dependent on the length at catch.

The M method is the first attempt to consider the point of metamorphosis by the application of an individual-based OR-at-maximum increment width. In the M method, the inflection point of an individual back-calculation line is deduced from the increment pattern of this individual. By modelling the OR-at-maximum increment width, we also determined age at metamorphosis. However, fish length at metamorphosis is defined by the overall SL-OR model (1) and is therefore almost the same for all individuals. As length at metamorphosis is fixed, but age is individually defined, the model is able to prolong the duration of the larval stage while shortening the juvenile stage and vice versa. A prolonged larval stage is associated with slow growth rates, while high growth rates occur after metamorphosis in a short juvenile stage.

However, the M method still exhibits three disadvantages: Firstly, it is not able to implement the coincidence of maximal increment growth and minimal length growth on an individual level. Secondly, estimated length growth rates during metamorphosis of slow growing fish may be negative: If an individual has a large OR at metamorphosis, the initial SL-OR back-calculation line may produce zero growth in length during metamorphosis. In the following step of the back-calculation algorithm the initial SL-OR line is rotated around the y-intercept. If an individuals' length at catch has a lower SL-OR ratio than the corresponding length of the initial SL-OR line, the final back-calculation line will have a negative gradient. Lastly, individual back-calculation lines of the M method can deviate substantially from the raw-data observed in the larval stage, although the variability of the data in early life stages is low.

Our favoured back-calculation approach is the MIP method, which was developed to specifically address the problems of the M method. The MIP method is based on SL-OR model (2) which is able to generate individual lines, where minimal length growth rates are generated when maximum increment widths occur on the otolith. Mean back-calculated length at metamorphosis using the MIP method was slightly larger than the length range defined by a minimum SL-OR ratio, maximal growth in body height and peak increment width on the otolith. However, the otolith independent measure of metamorphosis is the inflection point of the relation between body height and SL. In contrast to the inflection point of model (3) at 20.1 mm SL, the raw data indicate strongest growth in body height at about 25 mm SL, which coincides with the mean back-calculated length at metamorphosis using the MIP method. Therefore, the MIP method can reproduce length growth rates considering the individual point of metamorphosis. Additionally, negative growth rates and the deviation of single back-calculation lines from the raw data in the larval stage are avoided by rotating the back-calculation line around the point of metamorphosis, instead of rotating it around the population intercept. The MIP method is quite flexible and able to reproduce length growth of individuals that are either fast growing as larvae and slow growing as juveniles or slow growing as larvae and fast growing as juveniles.

4.5.3 Traits of new and existing back-calculation models

Various back-calculation models have been developed concentrating on different factors influencing the relationship of somatic and otolith growth. In general, factors that control the SL-OR relationship can be grouped into two main categories: external and internal (Francis 1990, Vigliola and Meekan 2009). External factors comprise environmental conditions like temperature and food availability, whereas internal factors are related to ontogeny.

So far, particular attention was paid to the external factors (Mosegaard et al. 1988, Secor and Dean 1992, Sirois et al. 1998), generally termed as growth effect. The growth-effect describes the phenomenon that a slow growing individual has a larger otolith than a fast growing one of the same fish size. In the NLR and the M method, the growth effect is considered in a simple way by fixing the starting point of the back-calculation lines while constraining single lines through individuals' length at catch. In our approaches we used the regression based y-intercept of SL-OR model (1) as Campana (1990) pointed out, that a regression based intercept may account for the growth effect in the same way than a biological intercept, if sufficient observations near the origin exist. As a comprehensive dataset is required anyway when applying regression-based back-calculation models we did not include a biological intercept in our non-linear models. Regarding the MIP method, all individual back-calculation lines follow the overall regression of the SL-OR model (2) in the early larval stage. As a consequence, the MIP method largely neglects the growth effect during the early larval stage. Individual back-calculation lines start to deviate from each other near the point of metamorphosis. Therefore, in the juvenile stage the growth effect is considered as back-calculation lines were rotated around the individual based point of metamorphosis independent of the population-based regression.

Thereby, the point of metamorphosis itself implements the growth-effect as individuals that were slow growing during the larval stage have larger otoliths at metamorphosis than fast growing ones.

Only few studies have investigated the role of internal, ontogenetic effects acting independently of growth- and age-influences on the SL-OR relationship. A modified version of the stage-specific BI model (Campana 1990), where each life-stage has its own biological intercept was implemented by Hobbs et al. (2007) to back-calculate length across a stage-specific transition of the SL-OR relationship in delta smelt larvae (*Hypomesus transpacificus*). In doing this, the authors used two biological intercepts, one for the early and the other one for the late larvae stage. Fish length at the second biological intercept was set to a fixed, population based value. The aim of our approach was to implement the individual variation at the transition point. We observed only little variation in fish size at the point of metamorphosis in contrast to a broad range of otolith sizes. Therefore, our final approach, the MIP method, accounts for individual variation by introducing otolith size at metamorphosis in the back-calculation algorithm. Furthermore, the individual point of metamorphosis in the MIP method allows the reproduction of different growth histories per life-stage. For instance, one individual may be a slow growing larva that experienced favourable conditions as juvenile accelerating its growth rate while another individual grows fast in the larval but experiences poor conditions as juvenile decelerating its growth rate. Both individuals may have the same age, fish length, and otolith radius at the end of the juvenile stage. Using a method with a fixed transition point between both life-stages like the stage-specific BI method or the NLR method, both individual growth histories would be described with exactly the same back-calculation line.

4.5.4 Length growth during the larval and juvenile stage of Baltic sprat

Young-of-the-Year Baltic sprat caught in autumn are predominantly composed of individuals born late in the season (Baumann et al. 2008). The strength of the year-class is assumed to be determined during the late-larval and early juvenile stage (Köster et al. 2003). Interestingly, our non-linear back-calculation methods located the strongest potential for length growth likewise in the early juvenile stage.

Beside a high and non-random mortality, strong length growth potential is a required condition for the occurrence of size-selective mortality (Sogard 1997). The survival of faster growing juveniles and the subsequent disadvantage of slow growing individuals may be the consequence of two mortality sources: starvation and predation (Heath 1992). Sogard (1997) highlighted the association of size-selective mortality caused by starvation with the over-winter mortality in temperate fish species. However, Köster et al. (2003) examined the relationship between successive life-stages and found the abundance of 0-group Baltic sprat in autumn as a good predictor of the abundance of one year old recruits. This suggests that over-winter mortality cannot explain strong inter-annual recruitment variability in Baltic sprat.

Concerning predation, bigger size may benefit the survival in the presence of predators (e.g. Anderson 1988). Juvenile sprat are predominantly found in near-shore habitats (Parmanne et al. 1994, Arrhenius 1998). Studies discussing possible predators of juvenile sprat in these near-shore nursery areas are rare. Generally, one of the most important predators of adult sprat in the Baltic Sea is cod (*Gadus morhua*) (Bagge et al. 1994). Although, it is known that predation by cod can influence the size of the sprat stock (Rudstam et al. 1994), there is no evidence that small differences in prey-size have an effect on total mortality. However, during our sampling period in shallow waters of the Kiel Bight, we observed young garfish (*Belone belone*) frequently hunting on schools of early juvenile sprat. As sprat became larger (~ 50 mm SL) at the end of the season, predation could no longer be observed, whereas juvenile sprat seemed to be highly mobile. Being larger may improve swimming and escaping abilities and therefore benefit the survival. Further research on nursery areas is needed to confirm these observations and to identify predators, their size preferences and their role in influencing the year-class strength of Baltic sprat.

4.5.5 Back-calculating length beyond ontogenetic transitions

By incorporating the point of metamorphosis in a nonlinear back-calculation model, the MIP method produces mean length growth rates during the early larval stage that were more than 60% higher than estimates of the so far used BI method. This bias in growth estimates can cause profound misinterpretations of ecological processes. For instance, an underestimation of length growth during the larval stage would suggest high mortality rates induced by predators as these small larvae would remain for a prolonged period in the size spectrum of many predators (Ware 1975, Anderson 1988). In drift simulations such an underestimation of length growth rates may lead to a biased estimation of the planktonic stage duration. As the onset of active swimming starts earlier if larvae grow faster, the predicted locations of post-larvae habitats may be likewise biased (Baumann et al. 2006b).

Beside considerable differences in length growth rates during the larval stage, profound changes between the MIP and the BI method were found at metamorphosis from larvae to juveniles. Using the MIP method, low length growth is recorded during metamorphosis followed by maximal length growth rates during the juvenile stage. In contrast, the BI method generates a maximum growth rate in length during metamorphosis and a decrease afterwards. Laboratory studies on investigating growth during the first months of life which encompass the larval as well as the juvenile stage are rare. Nakamura et al. (1991) conducted a rearing experiment from hatching to the juvenile stage with Japanese Sardine (*Sardinops melanostictus*), a species similar to Baltic sprat exhibiting a transition from an elongate larval to a spindle-shaped juvenile body form. Results of this study located low growth rates in length at the transition between both life-stages, whereas highest growth rates in length occur during the juvenile stage.

In general, transitions between ontogenetic stages are often accompanied by changes in behaviour. In the case of clupeids, metamorphosis comes along with a niche shift from transparent larvae, which are

passive drifting planktonic particles to pigmented and scaled juveniles, which are active swimmers. Such a change between life-stages may cause short-time stagnation of length growth, because other adaptions to new lifestyle requirements (e.g. spindle-shape, scales) were favoured over size increase. Beside clupeids, time-varying reduced growth during ontogeny can also be observed at the settlement of reef fishes (Wilson and McCormick 1997) and metamorphosis of flatfishes (e.g. Joh et al. 2011). A reduction in length growth that is accompanied with a change in the relationship of fish and otolith length, leads to complications in back-calculations of length like in Baltic sprat. Just as metamorphosis in sprat, settlement of reef fishes and metamorphosis of flatfish are critical events influencing survival and subsequent recruitment (e.g. Fukuhara 1988, Doherty et al. 2004), which makes growth reconstruction across transition points desirable for fishery ecologists. As increment pattern and morphometrics of growth differ per species and ecological niche shift, our MIP method has to be validated and adjusted for each case and species. Beside the reconstruction of length growth in sprat, the MIP method may facilitate length back-calculation over life-stage transitions like settlement of reef fish or metamorphosis in flatfish.

Sampling post-larvae and juvenile sprat in shallow waters of the Baltic Sea enabled us to close the size class gap between the larvae and the juvenile life-stage and to develop a new non-linear back-calculation method. In contrast to the so far used BI method, the MIP method uses an individual specific point of metamorphosis and treats the allometric growth in the larval stage separately from the nearly isometric growth of the juvenile stage. Growth rates generated by the MIP method are higher during the early larval and juvenile stage than those estimated with the BI method. This result suggest, that a shift in attention towards the early juvenile phase may be needed for a better understanding of processes influencing year-class strength. The approach may be applicable to other species, where similar growth characteristics occur during early life history. However, to apply this approach, samples of all early life-stages prior to the stage of interest are needed.

4.6 References

Anderson, J.T. 1988. A review of size dependent survival during pre-recruit stages of fishes in relation to recruiment. J. Northwest. Atl. Fish. Sci. **8**: 55-66.

Arrhenius, F. 1998. Food intake and seasonal changes in energy content of young Baltic Sea sprat (*Sprattus sprattus* L.). ICES J. Mar. Sci. **55**(2): 319-324.

Bagge, O., Thurow, F., Steffensen, E., and Bray, J. 1994. The Baltic cod. Dana **10**: 1-28.

Bailey, K.M., and Houde, E.D. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. ICES J. Mar. Sci. **25**: 1-83.

Baumann, H., Gröhsler, T., Kornilovs, G., Makarchouk, A., Feldmann, V., and Temming, A. 2006c. Temperature-induced regional and temporal growth differences in Baltic young-of-the-year sprat *Sprattus sprattus*. Mar. Ecol. Prog. Ser. **317**: 225-236. doi: 10.3354/meps317225.

Baumann, H., Hinrichsen, H.-H., Voss, R., Stepputtis, D., Grygiel, W., Clausen, L.W., and Temming, A. 2006a. Linking growth to environmental histories in central Baltic young-of-the-year sprat, *Sprattus sprattus*: an approach based on otolith microstructure analysis and hydrodynamic modelling. Fish. Oceanogr. **15**(6): 465-476. doi: 10.1111/j.1365-2419.2005.00395.x.

Baumann, H., Hinrichsen, H.H., Möllmann, C., Köster, F.W., Malzahn, A.M., and Temming, A. 2006b. Recruitment variability in Baltic Sea sprat (*Sprattus sprattus*) is tightly coupled to temperature and transport patterns affecting the larval and early juvenile stages. Can. J. Fish. Aquat. Sci. **63**(10): 2191-2201. doi:10.1139/f06-112.

Baumann, H., Peck, M.A., Götze, H.E., and Temming, A. 2007. Starving early juvenile sprat *Sprattus sprattus* (L.) in western Baltic coastal waters: evidence from combined field and laboratory observations in August and September 2003. J. Fish. Biol. **70**(3): 853-866. doi: 10.1111/j.1095-8649.2007.01346.x.

Baumann, H., Voss, R., Hinrichsen, H.-H., Mohrholz, V., Schmidt, J.O., and Temming, A. 2008. Investigating the selective survival of summer- over spring-born sprat, *Sprattus sprattus*, in the Baltic Sea. Fish. Res. **91**(1): 1-14. doi: 10.1016/j.fishres.2007.11.004.

Butler, J.L. 1989. Growth during the larval and juvenile stages of the northern anchovy, *Engraulis mordax*, in the California current during 1980-84. Fish. Bull. **87**: 645-652.

Campana, S.E. 1990. How reliable are growth back-calculations based on otoliths? Can. J. Fish. Aquat. Sci. **47**(11): 2219-2227. doi:10.1139/f90-246.

Campana, S.E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish. Biol. **59**(2): 197-242. doi: 10.1111/j.1095-8649.2001.tb00127.x.

Campana, S.E., and Jones, C.M. 1992. Analysis of otolith microstructure data. *In* Otolith Microstructure Examination and Analysis. *Edited by* D.K. Stevenson and S.E. Campana. Canadian Special Publications of Fisheries and Aquatic Sciences 117. pp. 73-100.

Dänhardt, A., Peck, M.A., Clemmesen, C., and Temming, A. 2007. Depth-dependent nutritional condition of sprat *Sprattus sprattus* larvae in the central Bornholm Basin, Baltic Sea. Mar. Ecol. Prog. Ser. **341**: 217-228.

Doherty, P.J., Dufour, V., Galzin, R., Hixon, M.A., Meekan, M.G., and Planes, S. 2004. High mortality during settlement is a population bottleneck for a tropical surgeonfish. Ecology **85**(9): 2422-2428.

Francis, R.I.C.C. 1990. Back-Calculation of Fish Length - a Critical-Review. J. Fish. Biol. **36**(6): 883-902.

Francis, R.I.C.C. 1995. The analysis of otolith data - a mathematician's perspective (What, precisely, is your model?). *In* Recent Developments in Fish and Otolith Research. *Edited by* D.H. Secor, J.M. Dean and S.E. Campana. University of South Carolina Press, Columbia pp. 81-95.

Fukuhara, O. 1988. Morphological and Functional-Development of Larval and Juvenile Limanda-Yokohamae (Pisces, Pleuronectidae) Reared in the Laboratory. Mar. Biol. **99**(2): 271-281.

Hare, J.A., and Cowen, R.K. 1995. Effect of age, growth rate, and ontogeny on the otolith size – fish size relationship in bluefish, *Pomatomus saltatrix*, and the implications for back-calculation of size in fish early life history stages. Can. J. Fish. Aquat. Sci. **52**(9): 1909-1922. doi:10.1139/f95-783.

Heath, M.R. 1992. Field investigations of the early-life stages of marine fish. ICES J. Mar. Sci. **28**: 1-174.

Hobbs, J.A., Bennett, W.A., Burton, J.E., and Baskerville-Bridges, B. 2007. Modification of the biological intercept model to account for ontogenetic effects in laboratory-reared delta smelt (*Hypomesus transpacificus*). Fish. Bull. **105**: 20-38.

Joh, M., Matsuda, T., Satoh, N., Tanaka, N., and Ueda, Y. 2011. Otolith microstructure of brown sole Pseudopleuronectes herzensteini: validation of daily ring formation and the occurrence of microstructure denoting metamorphosis. Fisheries Science **77**(5): 773-783.

Kornilovs, G., Sidrevics, L., and Dippner, J.W. 2001. Fish and zooplankton interaction in the Central Baltic Sea. ICES J. Mar. Sci. **58**(3): 579-588. doi: 10.1006/jmsc.2001.1062.

Köster, F.W., Hinrichsen, H.H., Schnack, D., St John, M.A., Mackenzie, B.R., Tomkiewicz, J., Möllmann, C., Kraus, G., Plikshs, M., Makarchouk, A., and Aro, E. 2003. Recruitment of Baltic cod and sprat stocks: identification of critical life stages and incorporation of environmental variability into stock-recruitment relationships. Sci. Mar. **67**: 129-154.

Laidig, T.E., Ralston, S., and Bence, J.R. 1991. Dynamics of Growth in the Early Life History of Shortbelly Rockfish *Sebastes jordani*. Fish. Bull. **89**: 611-621.

Lee, O., Danilowicz, B.S., and Dickey-Collas, M. 2006. Temporal and spatial variability in growth and condition of dab (*Limanda limanda*) and sprat (*Sprattus sprattus*) larvae in the Irish Sea. Fish. Oceanogr. **15**(6): 490-507. doi: 10.1111/j.1365-2419.2006.00406.x.

Lee, R.M. 1920. A review of the methods of age and growth determination in fishes by means of scales. Fishery Investigations, London Series 2 **4**(2): 1-32.

Möllmann, C., Diekmann, R., Müller-Karulis, B., Kornilovs, G., Plikshs, M., and Axe, P. 2009. Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea. Glob. Change Biol. **15**(6): 1377-1393. doi: 10.1111/j.1365-2486.2008.01814.x.

Mosegaard, H., Svedang, H., and Taberman, K. 1988. Uncoupling of somatic and otolith growth-rates in arctic char (*Salvelinus alpinus*) as an effect of differences in temperature response. Can. J. Fish. Aquat. Sci. **45**(9): 1514-1524.

Nakamura, M., Takii, K., Takaoka, O., Furuta, S., and Kumai, H. 1991. Rearing of japanese sardine from hatching through juveniles. Nippon Suisan Gakkaishi **57**(2): 345-345.

Parmanne, R., Rechlin, O., and Sjöstrand, B. 1994. Status and future of herring and sprat stocks in the Baltic Sea. Dana **10**: 29-59.

Peck, W.A., Clemmesen, C., and Herrmann, J.P. 2005. Ontogenic changes in the allometric scaling of the mass and length relationship in *Sprattus sprattus*. J. Fish. Biol. **66**(3): 882-887.

Petereit, C., Haslob, H., Kraus, G., and Clemmesen, C. 2008. The influence of temperature on the development of Baltic Sea sprat (*Sprattus sprattus*) eggs and yolk sac larvae. Mar. Biol. **154**(2): 295-306. doi: 10.1007/s00227-008-0923-1.

Rudstam, L.G., Aneer, G., and Hildén, M. 1994. Top-down control in the pelagic Baltic ecosystem. Dana **10**: 105-129.

Secor, D.H., and Dean, J.M. 1992. Comparison of otolith-based back-calculation methods to determine individual growth histories of larval striped bass, *Morone saxatilis*. Can. J. Fish. Aquat. Sci. **49**(7): 1439-1454.

Sirois, P., Lecomte, F., and Dodson, J.J. 1998. An otolith-based back-calculation method to account for time-varying growth rate in rainbow smelt (*Osmerus mordax*) larvae. Can. J. Fish. Aquat. Sci. **55**(12): 2662-2671. doi:10.1139/f98-170.

Sogard, S.M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: A review. Bull. Mar. Sci. **60**(3): 1129-1157.

Takahashi, M., Nishida, H., Yatsu, A., and Watanabe, Y. 2008. Year-class strength and growth rates after metamorphosis of Japanese sardine (Sardinops melanostictus) in the western North Pacific Ocean during 1996–2003. Can. J. Fish. Aquat. Sci. **65**(7): 1425-1434. doi:10.1139/F08-063.

Temming, A. 1995. Die quantitative Bestimmung der Konsumtion von Fischen. Experimentelle, methodische und theoretische Aspekte. Habilitation treatise, Fakultät für Mathematik und Naturwissenschaften, University of Hamburg, Hamburg.

Vigliola, L., Harmelin-Vivien, M., and Meekan, M.G. 2000. Comparison of techniques of back-calculation of growth and settlement marks from the otoliths of three species of *Diplodus* from the Mediterranean Sea. Can. J. Fish. Aquat. Sci. **57**(6): 1291-1299. doi:10.1139/f00-055.

Vigliola, L., and Meekan, M. 2009. The back-calculation of fish growth from otoliths. *In* Tropical Fish Otoliths: Information for Assessment, Managemant and Ecology. *Edited by* B.S. Green, B.D. Mapstone, G. Carlos and G.A. Begg. Springer. pp. 174-211.

Ware, D.M. 1975. Relation between egg size, growth, and natural mortality of larval fish. J. Fish. Res. Board. Can. **32**(12): 2503-2512.

Wilson, D.T., and McCormick, M.I. 1997. Spatial and temporal validation of settlement-marks in the otoliths of tropical reef fishes. Mar. Ecol. Prog. Ser. **153**: 259-271. 10.3354/meps153259.

Wilson, J.A., Vigliola, L., and Meekan, M.G. 2009. The back-calculation of size and growth from otoliths: Validation and comparison of models at an individual level. J. Exp. Mar. Biol. Ecol. **368**(1): 9-21. doi: 10.1016/j.jembe.2008.09.00

Deducing *in situ* feeding conditions of early juvenile sprat (*Sprattus sprattus L.*) from otoliths

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5.1 Abstract:

We experimentally quantified the influence of temperature on otolith and length growth under *ad libitum* conditions in early juvenile Baltic sprat to evaluate previous feeding conditions in field caught recruits. In the laboratory, we investigated otolith, length and mass growth at four different temperatures (16, 18, 20, 22°C), feeding a mixture of dry pellets and living brine shrimp. We observed uncoupling between somatic and otolith growth with increasing increment width in relation to temperature in contrast to temperature independent length growth rates. Instead of a coupling between length and otolith growth we found coupling between the ratio of dry mass and wet mass and otolith length, which we attributed to the storage of energy reserves (lipids). This indicates that otoliths record metabolic processes rather than somatic growth. Using total dry mass at the beginning and the end of the experiment we estimated a 10-fold increase in food demand from post-metamorphosed larvae (30mm SL) to juveniles (50 mm SL). We compared otolith increment width (IW) in the juvenile stage in relation to ambient temperatures of recruits from 2003 and 2007 of the western Baltic Sea with the relationship between *ad libitum* increment growth and temperature observed from the experiment ($IW = -0.0344T^2 + 1.6757 \cdot T - 12.764$). By assuming that sprat grew optimally under *ad libitum* laboratory conditions, we found optimal feeding conditions for juvenile sprat born later in the season of 2003 and sub-optimal feeding conditions for juveniles in 2007.

5.2 Introduction

Growth during the first year of a fish`s life influences its survival (Sogard 1997, Hurst 2007) and subsequently the recruitment of young fish to the parental generation. Hence, growth studies of early life-stages have received much attention during the last decades. Generally, growth during early life-stages of fish is mainly determined by three factors: The two exogenously controlled factors temperature and food availability (Houde 1989, Heath 1992) and the endogenously controlled factor ontogeny. The former two that primarily define the environmental habitat of a small fish exhibit pronounced variability in their characteristics, depending on habitat and season. Temperature is the factor receiving most attention in the last years (Harley et al. 2006) as it is the most dominant climate variable influencing marine ecosystems (Drinkwater et al. 2010). In contrast to temperature, food availability is much more difficult to examine in field studies, since patchiness of zooplankton (Folt and Burns 1999) causes inhomogeneous prey fields for zooplanktivorous fish. Similarly, standard measurements of plankton density by net samples can be strongly influenced by patchiness (Omori and Hamner 1982). Therefore, it may occur that the average plankton abundance seems quite high, whereas stomach contents of zooplanktivorous fish are lower than expected or vice versa. Investigations with image systems (e.g. video plankton recorders, laser optical plankton counters) are needed to gather more precise information on patchiness structures of zooplankton in the field (e.g. Möller et al. 2012).

However, the frequency and temporal occurrence of successful feeding events can also be estimated by natural tags like otoliths (Meekan et al. 2003, Kurita et al. 2004). In young fish, the food intake is directly correlated to the increase of body-tissues and it is assumed that individual feeding success is recorded by the width of growth structures in hard parts like otoliths (Campana and Neilson 1985). The study of otoliths as indicators for fish growth, is the topic of numerous studies (e.g. Stevenson and Campana 1992, Wilson et al. 2009). Otoliths are assumed to grow in a constant relation to somatic growth, a characteristic that is called “coupling” in otolith literature, forming the basis of all growth reconstructions (Campana and Neilson 1985). Thus, growth is recorded on the otolith with increment width reflecting environmental influences. Otoliths are natural storage tags that display the realized and/or successful habitat, while being mainly influenced by temperature, food availability and ontogeny in the same way as somatic growth. To decode the natural tag, the impact of these major factors on otolith growth has to be known and the possibility of uncoupling of otolith and somatic growth has to be investigated to allow estimations of the resulting bias.

Concerning the daily formation of growth increments (Campana and Jones 1992), for Baltic sprat, the central assumption of the microstructure analysis of otoliths is valid (Alshuth 1988, Shields 1989). Regarding the influence of feeding level on otolith and somatic growth, Baumann et al. (2005) found a pronounced positive relationship in early juvenile Baltic sprat, validating the influence of food intensity on daily increment width. Thus, the central premises for the estimation of feeding conditions from otoliths have already been demonstrated for Baltic sprat. To evaluate the influence of feeding

ration on otolith increment width in a particular life-stage with the aim to reconstruct previous prey concentrations from field caught sprat, the exact impact of temperature on otolith growth has to be known. Therefore, the first aim of the study was to quantify the effect of temperature on length, somatic and otolith growth in a laboratory experiment by keeping the feeding environment maximal and constant. We hypothesized that length and mass growth are dependent on temperature in the same way as otolith growth (coupling) and that higher temperatures (between 16 and 22°C) lead to higher growth rates. Previously, it has been stated that ontogeny influenced increment width (Baumann et al. 2006) resulting in decreasing increment widths after metamorphosis (**Manuscript 1**). As the effects of temperature and ontogeny mostly coincide in the decreasing increment width of wild recruits because temperatures decline at the end of the season when fish are older, the second aim of the study was to separate the effect of temperature from the effect of ontogeny on otolith growth. The third aim was to apply the results on the analysis of field caught individuals from a previous study (Baumann et al. 2008, **Manuscript 1**) to investigate feeding conditions in the field in two years with contrasting conditions.

5.3 Materials and Methods

5.3.1 Laboratory experiment

Post-larval sprat were caught in July 2010 in a small harbour of the eastern Kiel Fjord in the Western Baltic Sea (54°25′N, 10°18′E). Fishing gear was a cubical-shaped net with the top side open and a mesh-size of 3 mm. The base area was about 6 m^2 and the height of the side walls was 2.5 m. This net-cage was used like a dip-net, in that the walls were lifted when a school of fish swam over the area. Approximately 1500 post-larval sprat were caught on 27 July 2010. The following day, fish were transported to the laboratory using an aerated transport tank. We deployed a marine temperature logger (Onset® Optic StowAway Datalogger) at the harbour site, to record water temperature in the natural juvenile habitat. Water depth was ~ 3m and the logger was fixed 1m below the water surface near the catch site. Additionally, temperature profiles from the nearby measurement station “Kiel Lighthouse” were obtained (http://www.bsh.de/de/Meeresdaten/Beobachtungen/MARNET-Messnetz). In the laboratory, fish were transferred to a 800 L flow-through tank connected to a seawater re-circulation system filled with artificial seawater. Fish were kept at a salinity of 15.0 ± 0.5 psu, similar to the natural environment (~16 psu) and a light regime of 14L:10D. Before the start of the experiment, water temperature was maintained at 16 ± 0.5°C and sprat where fed with a mixture of live brine shrimp, *Artemia salina* nauplii (Inve, SepArt®) and dry pellet food for fish (Larviva, Dana feed A/S). Small sprat feed on nauplii without acclimation, whereas they needed a few days to start feeding on dry pellet food.

The aim of the experimental set-up was to investigate growth at four different temperatures (16°C, 18°C, 20°C and 22°C), while the effect of feeding on growth was minimised by constant and *ad*

libitum food ratios. In total, 12 identical circular 150 L tanks (diameter 0.8 m water column 0.3 m) were equipped with aeration and a temperature probe (DS 1820, Hygrosens Instruments GmbH) in the middle of the tank. For each temperature, three of the tanks were installed on a 700 L source tank that was connected to the re-circulating system. In the source tanks, the water was preheated to the respective temperature (16°C, 18°C, 20°C or 22°C) and pumped to the three connected tanks. Thus, we had three replicate tanks per temperature treatment. The basis temperature of the re-circulating system of the whole aquarium was adjusted to the lowest experimental temperature treatment, so that pre-heating for the 16°C tanks was unnecessary.

We avoided otolith marking at the beginning of the experiment because in earlier trials this caused increased mortality rates (Baumann et al. 2007). Before stocking, all tanks were regulated at 16°C to avoid abrupt temperature changes at transition. On 1 August 2010, each tank was loaded with ~ 60 specimens randomly selected from the 800 L flow-through tank. Remaining specimens were sacrificed as initial sample (hereafter: starter group) to evaluate length and mass at the start of the experiment. Additionally, the otolith radius of a subset of 15 individuals was measured. Finally, regulated heaters of the source tanks were switched on. After 24h, pre-set temperatures were reached in the tanks. During the experiment, temperature deviations from the pre-set temperature were not larger than 0.2°C.

The diet during the experiment was composed of two-third pellets (Larviva, Dana feed A/S) and one-third living brine shrimp nauplii (Inve, SepArt®). The daily amount of food offered was calculated assuming maximal food consumption (C_{max}) of 15 to 25 % dry mass per individual and day for 16 to 22°C, respectively. To assure *ad libitum* feeding throughout the experimental period taking into account the growth in body mass, a gross conversion rate of 33% per fish was assumed. Until day 9 of the experiment, fish were fed six times a day (dry diet: 9am, 12am, 5pm; living *Artemia salina* nauplii: 10am, 1am, 6pm, respectively). From day 10 to day 20 of the experiment, sprat were fed eight times daily to ensure *ad libitum* food conditions (dry diet: 9am, 11:30am, 2:39pm, 5pm; living *Artemia salina* nauplii: one hour after dry diet, respectively). Feeding took place during the light period of the day.

In the following analysis, we distinguish between five phases in the life of experimental fish: (1) the field period until catch on 27 July 2010, (2) the maintenance period in the laboratory until the start of the experiment, (3) the experimental period comprising the (4) acclimation period of the experiment until the 10^{th} day and (5) the "period in interest" when sprat were fed eight times a day for 20 days. However, the period of interest does not include the last day of the experiment when individuals were killed.

At 1 September 2010, we killed all specimens with an overdose of anesthetics (MS – 222, > 0,2g•l^{-1}). For all fish SL, body height at half SL (BH) and wet mass (WM) of all individuals was measured. The resulting data set comprising all individuals of the experimental set-up is called data set (1) in the following analysis. According to the modes of length frequency distributions per temperature

treatment, 21 to 30 individuals were selected for the microstructure analysis of the otoliths. The subset of data used for otolith analysis is termed data set (2). Additionally, otoliths of the smallest fish were also analysed (n = 11) but not included in data set (2). A further subset of data set (1) is data set (3) consisting of ten individuals per tank, which were selected for the additional estimation of dry mass (DM). DM was estimated after 48 h drying at 70°C when constant mass was reached.

5.3.2 Otolith analysis

Individual sagittal otoliths were dissected and deposited on microscopic slides with a drop of thermoplastic glue (Crystalbond® 509) the convex side facing upwards. Irrespective of left and right, the otolith with the clearest microstructure was used. Otoltihs were polished wet using a grinding machine (Presi Mecapol P260) equipped with a lapping film (Silicon Carbid 1200/4000). The degree of the polished surface was controlled with a light microscope. When the polished surface intersected the core of the otolith, it was turned upside down by reheating the thermoplastic glue on the microscopic slide. Now the otolith was ground from the other side until the outermost increments were clearly visible along the post-rostral measurement axis.

Each otolith was photographed with a digital camera (Leica®DC300, 3132 x 2328 pixels) connected to an image analysis system (ImagePro® Plus 6.0) at 400 times magnification. Increments were measured along the post-rostrum axis from the core to the edge. We started with the first clearly visible increment outside the core which we defined as day of first increment formation (DFIF). Every otolith was only read once by the same experienced reader.

5.3.3 Statistics

To test differences in SL, relative BH (as percentage of SL), relative DM (as percentage of WM) and otolith growth (mean increment width) between the temperature treatments and replicate tanks we used two-factorial analysis of variances (ANOVA). We applied post-hoc Scheffè tests to detect which level of the factor differed significantly. As data are slightly skewed to the left in data set (1), we performed a Levene test (car-package in R) for the homogeneity of variances between all tanks, because homogeneity is the most important assumption when applying an ANOVA. We further fitted a generalized linear model (GLM) using a gamma distribution to account for non-normality in the distributions of the response variable. However, as gamma distributions can only account for positively (right) skewed data and not for negatively (left) skewed data, we inverted the SL data before applying the GLM.

For the statistical investigations of otolith growth and relative DM (data set (2) and (3)), we excluded the exceptional small individuals that existed in each tank (see results). We justified the exclusion of these slow growing individuals for further analysis because length distributions of wild 0 – group sprat follow an almost normal distribution in the western Baltic Sea (Baumann et al. 2008). The lack of small individuals in field data suggests that slow growing individuals like those in the laboratory do

not contribute to surviving juveniles at the end of the summer. Additionally, we suggest that the exceptional small individuals at the end of the experiment did not feed and are thus not suitable for an analysis assuming an *ad libitum* feeding ratio. To exclude slow growing individuals, we averaged the three most frequent one millimetre length classes per temperature treatment. The difference in the number of length classes between this mean and the largest length of the distribution was subtracted from the mean in order to get a lower limit of the length distribution that separates slow growing from fast growing individuals.

5.3.4 Length growth of laboratory and field sprat

We compared length and otolith growth during the early juvenile life-stage of laboratory sprat and growth rates of surviving wild juveniles analysed previously by Baumann et al. (2008) and **Manuscript 1**. Surviving juveniles were caught in autumn 2003 and 2007 by a research vessel in the Western Baltic Sea (ICES Subdivision 22). Survivors in 2003 are known to have high growth rates in contrast to individuals caught in 2007 exhibiting low growth rates. In total, 75 individuals were available for 2003 and 20 individuals for 2007.

We calculated observed growth rates from laboratory fish and back-calculated length growth rates from laboratory and field fish. The mean observed length growth rate from the laboratory was estimated as the difference in mean length at day 31 and the mean length at day 0 (starter group) of the experiment divided by the number of days. For back-calculated length growth we used the Metamorphosis Inflection Point (MIP) method (**Manuscript 1**) taking into account a changing relationship between otolith and fish length due to metamorphosis from larvae to juveniles. We applied the back-calculation also to the laboratory data to validate the performance of the model. However, the algorithm of the MIP method had to be modified for experimental fish as it failed in estimating the point of metamorphosis. The MIP-algorithm defined the individual point of metamorphosis as the otolith radius where maximal increment width occurred and estimated it using a non-linear regression with a model accounting for an optimum (**Manuscript 1**). However, the regression and estimation of the optimum failed, because the natural pattern of increment width in laboratory held fish was interrupted by catch, maintenance period, temperature change and/or experimental conditions. Instead of modelling increment width versus otolith radius with the non-linear regression used in the MIP algorithm to estimate the otolith radius at maximum increment width (OR_M, see **Manuscript 1**), we applied the otolith radius observed at the maximum increment width as point of metamorphosis.

5.3.5 The period of interest

The rate of otolith accretion in relation to temperature from the laboratory experiment was described by a simple quadratic equation using the mean increment width per investigated temperature treatment. We assumed acclimation to experimental conditions and temperature treatments to be

completed after day 10 of the experiment and thus averaged increment width over the period of interest.

We defined the post-metamorphic early juvenile life-stage in field caught sprat using age after the point of metamorphosis. As the point of metamorphosis coincides with the occurrence of maximal increment width on the otolith, the corresponding day of metamorphosis can be estimated from increment analysis. We added the mean time period in days between the day of metamorphosis and the 10^{th} day of the experiment (maintenance and acclimation period) from laboratory sprat to each individual day of metamorphosis of wild sprat to identify the comparable life phase. Hence, we calculated the period of interest in wild sprat to allow a comparison in the same life-stage as laboratory reared sprat.

5.3.6 Estimation of the feeding history of field caught sprat

We constrained the following analysis to the early juvenile stage in order to minimize any ontogenetic influence on growth during the development of Baltic sprat. Finally, we compared laboratory and field conditions in 2003 and 2007 using surface water temperatures recorded at Kiel Lighthouse to assess the likely ambient field temperatures experienced by the individuals from 2003 and 2007. We assigned an ambient temperature value to every increment during the period of interest. We avoided analysing single increment width due to high autocorrelation of consecutive increments (Campana and Jones 1992). Instead of analysing single increments, we averaged the increment width and according temperatures during the period of interest in four intervals of five days. According to the assigned mean temperature, we split the corresponding means of increment width-intervals in classes of one degree Celsius, to compare the mean increment width of laboratory and field caught sprat in respect of temperature dependence. The average DFIF, day of metamorphosis and date of the period of interest in field caught sprat was estimated using the corresponding DFIFs, days of metamorphosis and days during the period of interest of contributing increments in the according temperature. For instance, if two intervals of increments contribute to the increment width at temperature A, ten DFIFs, tens days of metamorphosis and the ten days of increment formation were used to calculate the mean DFIF, the mean day of metamorphosis and the mean day of the period of interest for temperature A.

To investigate the relationship between increment width and length growth rate during the experiment independently of back-calculation methods we included small growing individuals (n = 11) to encompass the whole range of growth rates. We applied a random intercept model with increment width as response and length growth rate as explanatory variable, where the intercept of the linear regression is allowed to change per temperature treatment but the slope stays constant.

5.3.7 Estimation of the food amount required for laboratory growth

The experimental set-up used to evaluate temperature effects on otolith and length growth was not designed to estimate the amount of food finally ingested. To ensure optimal growth we fed a mixture

of live food (brine shrimp) and pellets to cover a range as wide as possible of chemical components necessary for growth. As pellets partly dissolve in water the consumed amount is difficult to quantify. We therefore estimated the likely food intake from a simple bioenergetic budget approach.

In a first step, we calculated the daily average energy gain per fish in each temperature treatment based on the mean relative DM (percentage of WM) of the starter group and the final sample for each temperature treatment. In accordance to Pederson and Hislop (2001), the relative dry mass of a fish can be used to estimate its energy density. We used the reciprocal value of the mean relative DM as relative water content (*WC*) to calculate the energy contents (*EC*) in Joule per gram DM. The *EC* was computed for the starter group (Index: *ST*) and for each temperature treatment (Index: *T*) of the final sample at the last day of the experiment (Index: *Last*) using the linear equation (unpublished data from the authors):

$$EC = -28964 \bullet WC + 46153 \quad (1)$$

The *EC*s were used to calculate the total energy (*TE*) in Joule per individual for the starter group and each temperature treatment by the multiplication with the respective mean dry mass. Using the *TE*s we calculated the specific energy gains (*g*) per day for each temperature treatment, assuming an exponential increase in DM over the experimental period according to the equation

$$g_T = \frac{\left(\ln\left(TE_{Last_T}\right) - \ln\left(TE_{ST}\right)\right)}{t} \quad (2)$$

where *t* is the experimental period in days. Lastly, energy gains (*EG*) in Joule per day were derived by temperature treatments for the first day of the experiment (Index: *First*) using the *TE* of the starter group

$$EG_{First_T} = TE_{ST} \bullet \left(e^{g_T} - 1\right) \quad (3)$$

and for the last day of the experiment using the *TE*s from the final samples:

$$EG_{Last_T} = TE_{Last_T} \bullet \left(e^{g_T} - 1\right) \quad (4)$$

This resulted in eight values of energy gains corresponding to the energy gain for the four temperatures at the beginning (first day) and at the end (last day) of the experiment.

In a second step, we estimated the mean consumptions (*C*) in Joule per day using the bio-energetic equation with *EG* as growth term. Like for the energy gain, we calculated four consumption values corresponding to each temperature treatment at the first day of the experiment:

$$C_{First_T} = R_{std} + R_{act} + R_{SDA} + E + F + EG_{First_T} \quad (5)$$

and four consumption values corresponding to each temperature at the last day of the experiment:

$$C_{Last_T} = R_{std} + R_{act} + R_{SDA} + E + F + EG_{Last_T} \quad (6)$$

Here, R_{std} is the respiration term for the standard metabolism, R_{act} the respiration term for the active metabolism, R_{SDA} the respiration term for specific dynamic action, *E* the term for excretion and *F* the term for faeces. We assumed that R_{act}, R_{SDA}, *E* and *F* account each for 10% of the consumption. For R_{std} we used an equation established by Meskendahl et al. (2010), which expresses standard metabolism in relation to WW and temperature for sprat. As standard metabolism is expressed in mg oxygen consumed per hour, we used the oxy-caloric factor (13.72 J•mg O_2) of Elliot and Davidson (1975) for the conversion into Joule per day. We calculated values for standard metabolism for each temperature treatment using the mass at the first and at the last day of the experiment.

In a third step we converted the total energy intake into the equivalent number of *Acartia spp.* copepods. We chose *Acartia spp*. as it is an important prey item of Baltic sprat during summer (Möllmann et al. 2004). For *Acartia spp*. we used the energy contents for C5/C6 stages (17920 J•g) of *Acartia clausii* as determined by Kerambrun (1987) and a DM of *Acartia tonsa* ($9.454 \cdot 10^{-6}$ g) published by Durbin et al. (1983).

Finally, we calculated the biting rates (*BR*) as number of prey items ingested per second assuming light dependent feeding and thus 14h feeding per day according to the experimental conditions. Corresponding to the relationship between biting rate and prey concentration (*PC*) published by Brachvogel et al. (2012), we calculated the mean prey concentration required for this biting rate for the first day:

$$PC_{First_T} = \frac{\left(BR_{First_T} \cdot 25.42\right)}{\left(BR_{First_T} \cdot 1.06\right)} \quad (7)$$

and for the last day of the experiment:

$$PC_{Last_T} = \frac{\left(BR_{Last_T} \cdot 25.42\right)}{\left(BR_{Last_T} \cdot 1.06\right)} \quad (8)$$

5.4.Results

5.4.1 Mortality

During the experiment mortality was differentiated between mortality inside and mortality outside of the tank as some individuals jumped out of the tank (hereafter: accidental mortality). On average mortality increased with temperature (Tab.5-1). Lowest mortality rate over the experimental period was 3% (replicate tank number 2 and 3) at 16°C, while the highest was 18% (tank number 3) at 20°C. Three tanks had mortalities over 10% (20°C replicate tank number 3, 22°C replicate tank number 1, 22°C replicate tank number 3). Accidental mortality was lowest at 20°C (~3%) and highest at 22°C with maximal mortality of 20% in replicate tank number 2.

Tab.5-1. Numbers of individuals per tank and temperature at the beginning of the experiment, mortality and accidental mortality. Additionally, mean standard length and length growth rate (observed) basing on data set (1) are listed. Data set (1) comprises length and height data of all individuals at the end of the experiment.

Temperature			**16°C**				**18°C**	
Tank number	**1**	**2**	**3**	**mean**	**1**	**2**	**3**	**mean**
n (start)	61	62	61		60	66	59	
Absolute mortality	5	2	2	**3**	5	2	5	**4**
Absolute accidental mortality	2	8	1	**4**	7	2	10	**6**
n (dataset 1)	54	52	58	**164**	48	62	44	**154**
mean SL [mm]	49.5	50.6	49.2	**49.7**	49.1	48.8	51.0	**49.5**
GR (linear) [mm/d]	0.66	0.69	0.65	**0.67**	0.65	0.64	0.71	**0.66**

Temperature			**20°C**				**22°C**	
Tank number	**1**	**2**	**3**	**mean**	**1**	**2**	**3**	**mean**
n (start)	60	59	60		61	59	62	
Absolute mortality	5	4	11	**7**	8	3	8	**6**
Absolute accidental mortality	3	3	3	**3**	7	12	7	**9**
n (dataset 1)	52	52	46	**150**	46	44	47	**137**
mean SL [mm]	50.8	51.0	48.4	**50.1**	50.4	50.6	51.0	**50.7**
GR (linear) [mm/d]	0.70	0.71	0.62	**0.68**	0.69	0.69	0.71	**0.70**

5.4.2 Effect of temperature on growth

The starter group had a mean standard length of 29.09 ± 1.97 mm, a mean BH of 4.20 ± 0.59 mm and mean WM 147 ± 42 mg.

For data set (1) (Fig.5-1.a, b), which comprises all data, we used relative BH, SL and WM as response variables and tested for effects of temperature treatments and replicate tanks. Using the Levene test we found variance homogeneity of all tanks for SL, relative BH and WM ($p > 0.1$). For relative BH, we found normally distributed data (Shapiro-Wilk-test, $p > 0.1$), performed a two-factorial ANOVA and found an effect of temperature and no effect of replicate tank (Tab.5-2). Relative BH at the 18 and

20°C temperature treatments (Fig.5-1.b) were slightly lower than at 16 and 22°C. A post-hoc Scheffè significance test revealed that the 18 and 20 °C treatment were significantly different from the 16 °C treatment but not from the 22°C treatment. In contrast to relative BH, distributions of SL and WM were significantly different from normal distributions (Shapiro-Wilk-test, $p < 0.05$) and (negatively) skewed to the left (see Fig.5-2 for SL), with few slow growing individuals in all tanks. A two factorial ANOVA with SL as response variable indicated neither a replicate tank nor a temperature effect (Tab.5-2). To consider the effect of a non-normally distributed response variable, we additionally performed a GLM with gamma distribution on inverted SL data. However, neither the GLM nor an ANOVA on inverted data detected a temperature or replicate tank effect (Tab.5-2). For WM, we found a slight effect of temperature and no effect of replicate tank using a two-factorial ANOVA. As data of WM were also negatively skewed, we performed the same procedure as for SL and inverted the WM data. A GLM and the ANOVA on inverted WM produced the same result as on non- inverted WM data (Tab.5-2). A post-hoc Scheffè significance test revealed that the 18 and 22 °C treatments were significantly different from each other. As we found no replicate tank effect in data set (1), we pooled individuals from all replicate tanks by temperature treatment in the following analysis of data subsets.

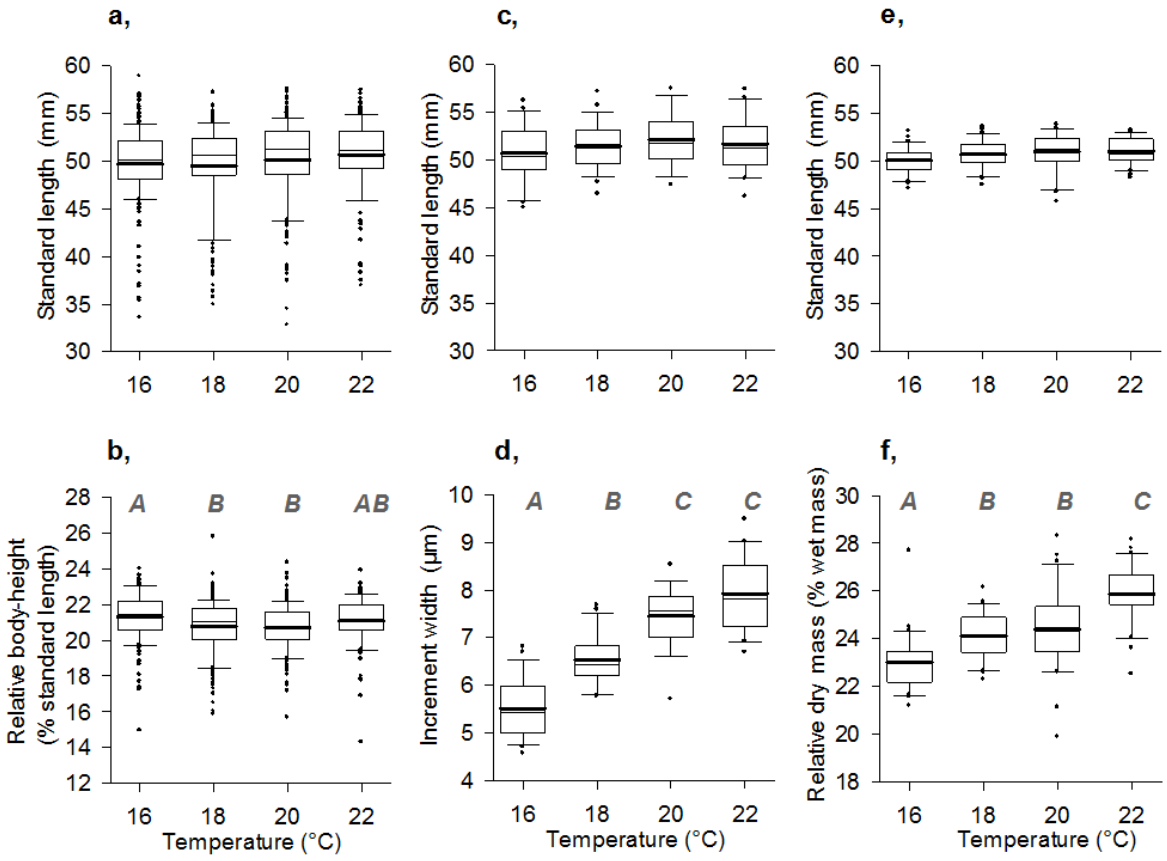

Fig.5-1. Temperature dependent box-plots for standard length, relative body height, increment width and relative Dry mass; panel a and b base on data set (1) (all fish), c and d on data set (2) (sub-sample for otolith analysis) and e and f on data set (3) (sub-sample for dry mass analysis). Grey capital letters in the lower panels show results of the Scheffè post-hoc significance test with the same letters in one panel indicating no significant differences between temperature treatments.

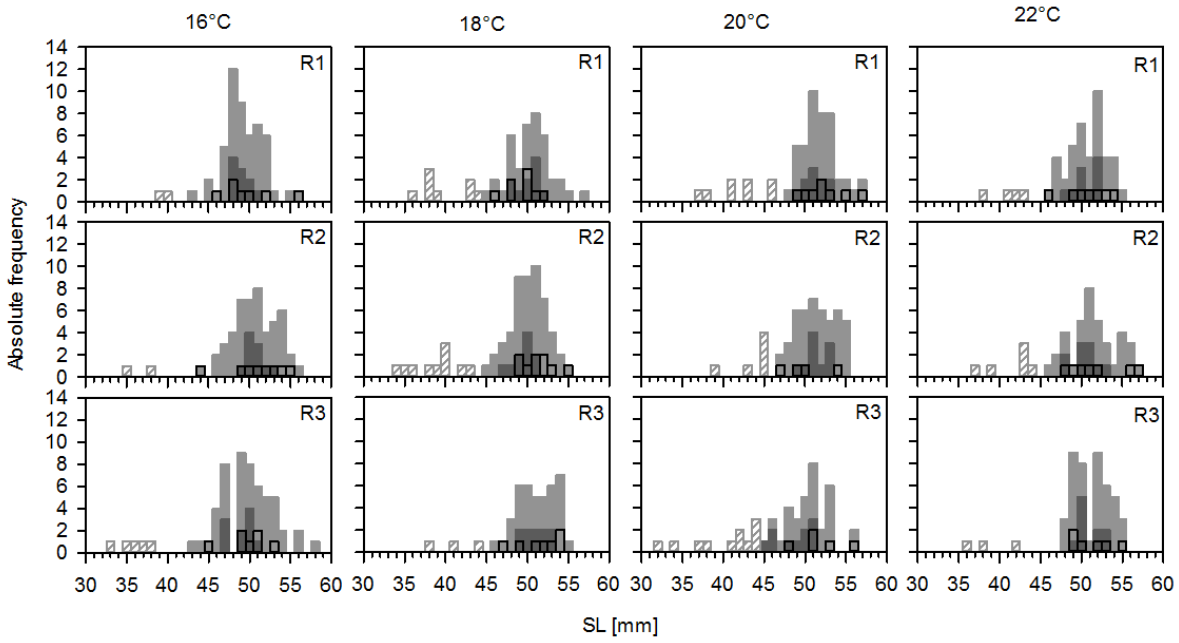

Fig.5-2. Distribution of SL per temperature (column) and replicate tank (row). R1, R2, R3: Number of replicate tank. Data set (1) comprises all individuals in the tanks and is illustrated by the filled light grey bars plus the shaded light grey bars (slow growing individuals). Data set (2) is composed of individuals used for otolith analysis and is depicted by black empty bars. Data set (3) is illustrated by the dark grey filled bars and represents individuals used for DM estimation.

Tab.5-2: Summary of statistical analysis investigating effects of replicate tanks and temperature treatments on body-morphometrics and otoliths. Data set (1) constitutes of all data, whereas data set (2) and (3) only consider fast growing individuals (see text); RV: response variable, EV: explanatory variable, T: temperature, R: replicate tank, SL: standard length, RelBH: relative body height, WM: wet mass, Invert: inverted data; Mean IW: mean increment width during the last 20 days of the experiment (Period of interest), RelDM: relative dry mass, SumSq: sum of the squares, MeanSq: mean squares and Df: degrees of freedom.

data set	RV	Method	EV	SumSq	MeanSq	F value	p value (F)		Resid.Dev	Deviance	p value (Chi)	
(1)	SL	ANOVA	T	105.300	35.113	1.939	0.122					
			R	14.700	7.372	0.407	0.666					
(1)	SL Invert	ANOVA	T	103.100	34.37	1.878	0.132					
			R	12.300	6.126	1.335	0.716					
(1)	SL Invert	GLM (gamma)	T						5.772	0.059	0.129	
			R						5.765	0.007	0.715	
(1)	Rel BH	ANOVA	T	38.100	12.699	6.756	< 0.001	***				
			R	4.530	2.263	1.204	0.301					
(1)	WM	ANOVA	T	1.027	0.342	3.322	0.029	*				
			R	0.173	0.087	0.840	0.432					
(1)	WM Invert	ANOVA	T	0.974	0.324	3.133	0.025	*				
			R	0.141	0.070	0.678	0.508					
(1)	WM Invert	GLM (gamma)	T						18.360	0.300	0.024	*
			R						18.317	0.043	0.508	
(2)	SL	ANOVA	T	20.630	68.762	0.919	0.435					
	Mean IW	ANOVA	T	71.297	237.656	56.246	< 0.001	***				
(3)	SL	ANOVA	T	17.607	58.689	2.252	0.086					
	RelDW	ANOVA	T	124.770	41.591	23.348	< 0.001	***				

For the analysis of otolith growth (data set (2)) and relative DM (data set (3)) we excluded slow growing individuals that occurred in each replicate tank (Fig.5-2). In general, fast growers comprise the bulk of all individuals (89%). After the exclusion of slow growers (n = 69), SL, increment width and relative DM data follow a normal distribution (Shapiro-Wilk-test, $p > 0.05$).

For data set (2) (Fig.5-1.c and d), we used SL and mean increment width during the period of interest as response variables and tested for effects of temperature treatment. As in data set (1), SL showed no significant difference between temperatures treatments (Tab.5-2). However, mean increment width over the period of interest differed significantly between temperature treatments (Tab.5-2). Mean increment width increased with temperature within the observed temperature range. A post-hoc Scheffè significance test revealed that the 16, 18 and 20 °C treatment were significantly different from each other, whereas there was no significant difference between 20 and 22°C, denoting a nearby maximum in otolith growth beyond 22°C.

For data set (3) (Fig.5-1.e and f), we used SL and relative DM as response variables and tested for effects of temperature. As in data set (1) and (2), there were no differences in SL between temperatures. In contrast, relative DM depends on temperature (Tab.5-2) and increases with temperature. A post-hoc Scheffè significance test revealed that the 16, 18 and 22 °C treatments were significantly different from each other, whereas there was no significant difference between 18 and 20°C.

In summary, we found no temperature effect on standard length but a distinctive temperature effect on increment width (Fig.5-3). Temperature had also a significant effect on body height. We observed a weak increase of WM with temperature but a clear increase in relative DM.

5.4.3 Increment patterns of laboratory reared and wild fish

The patterns of the mean increment widths from laboratory reared sprat of the different temperature treatments are quite similar until the start of the experiment (Fig.5-3). During the larval stage increment width increased steadily, while individuals lived in the Baltic Sea. After the transfer from the field to the laboratory, mean increment width dropped during the maintenance period by approximately 12%. After the start of the experiment, increment width at 20 and 22°C increased, while it remained almost at a constant level (~ 5 or 6 µm) at 16 and 18°C at, respectively. After reaching a maximum of ~7 and 8 µm, the mean increment width at 20 and 22°C slightly decreased during the period of interest which we ascribed to ontogeny. Thus, we found only a minor effect of ontogeny on otolith growth during the early juvenile stage.

Compared to the increment width in laboratory reared sprat, increment width of wild individuals gradually decreased after metamorphosis (Fig.5-4). In 2003, the mean point of metamorphosis occurred 31 days after the DFIF. The mean peak increment of all temperature treatments from laboratory reared sprat occurred at an age of 32 days. Thus, the periods of interest of 2003 and

laboratory fish exhibit similar age ranges. In contrast, the mean point of metamorphosis in 2007 occurred with an age of 44 days after the DFIF resulting in a period of interest with a higher age range.

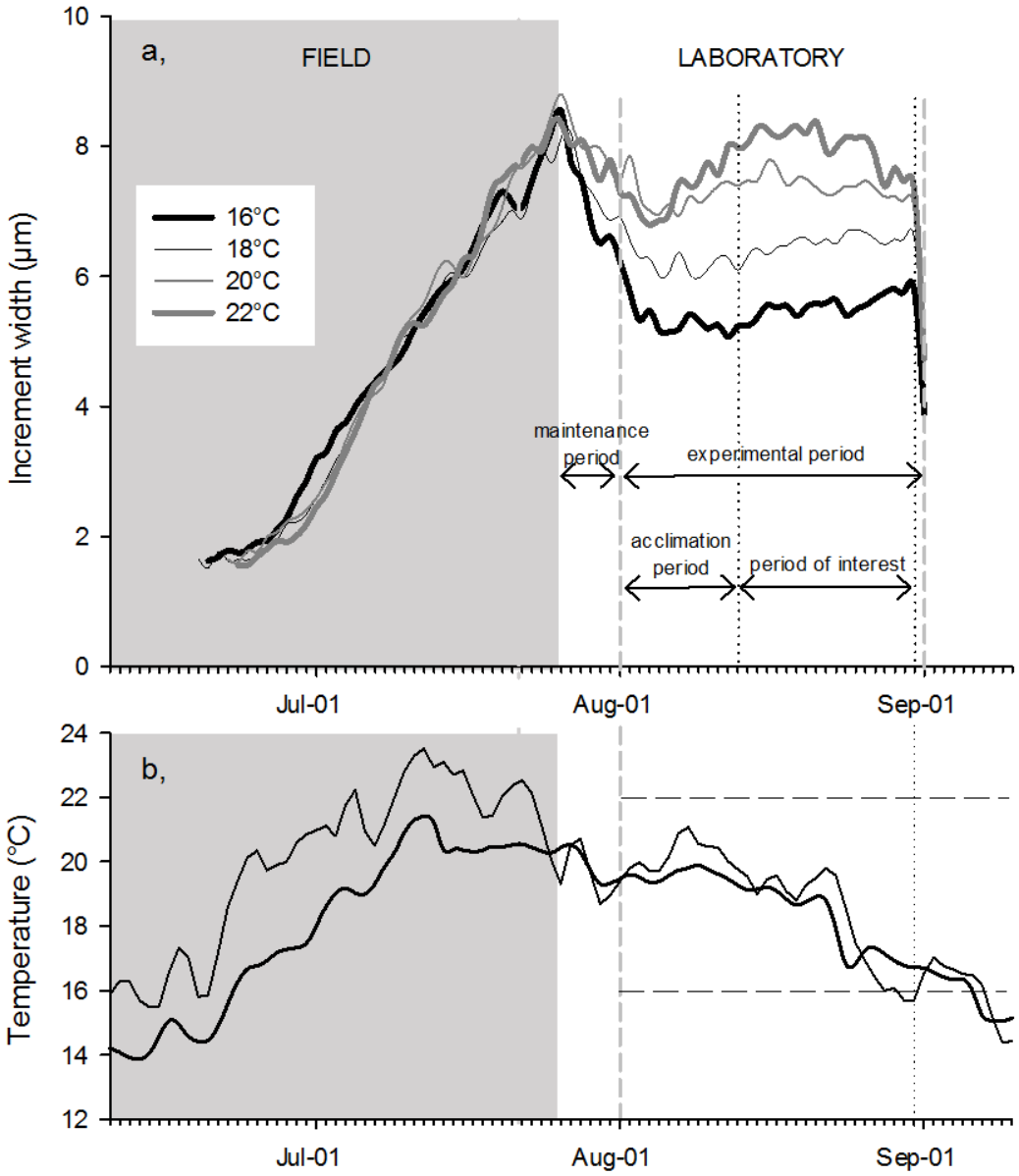

Fig.5.3. a, Mean increment width per temperature versus date. Increments are averaged per temperature treatment starting with the last day in life. Means comprise at least 5 individuals. b, Mean water temperatures logged in the field. Thin black line: Temperature logged near the catch-site, thick black line: Temperature logged in the middle of the Kiel Fjord (Kiel Lighthouse). Horizontal dashed lines: Experimentally examined temperature range. The grey plane indicates the period in the field while the white plane indicates the time in the laboratory. The grey dashed line depicts the start and the end of the experiment and the dotted line the start and the end of the period of interest.

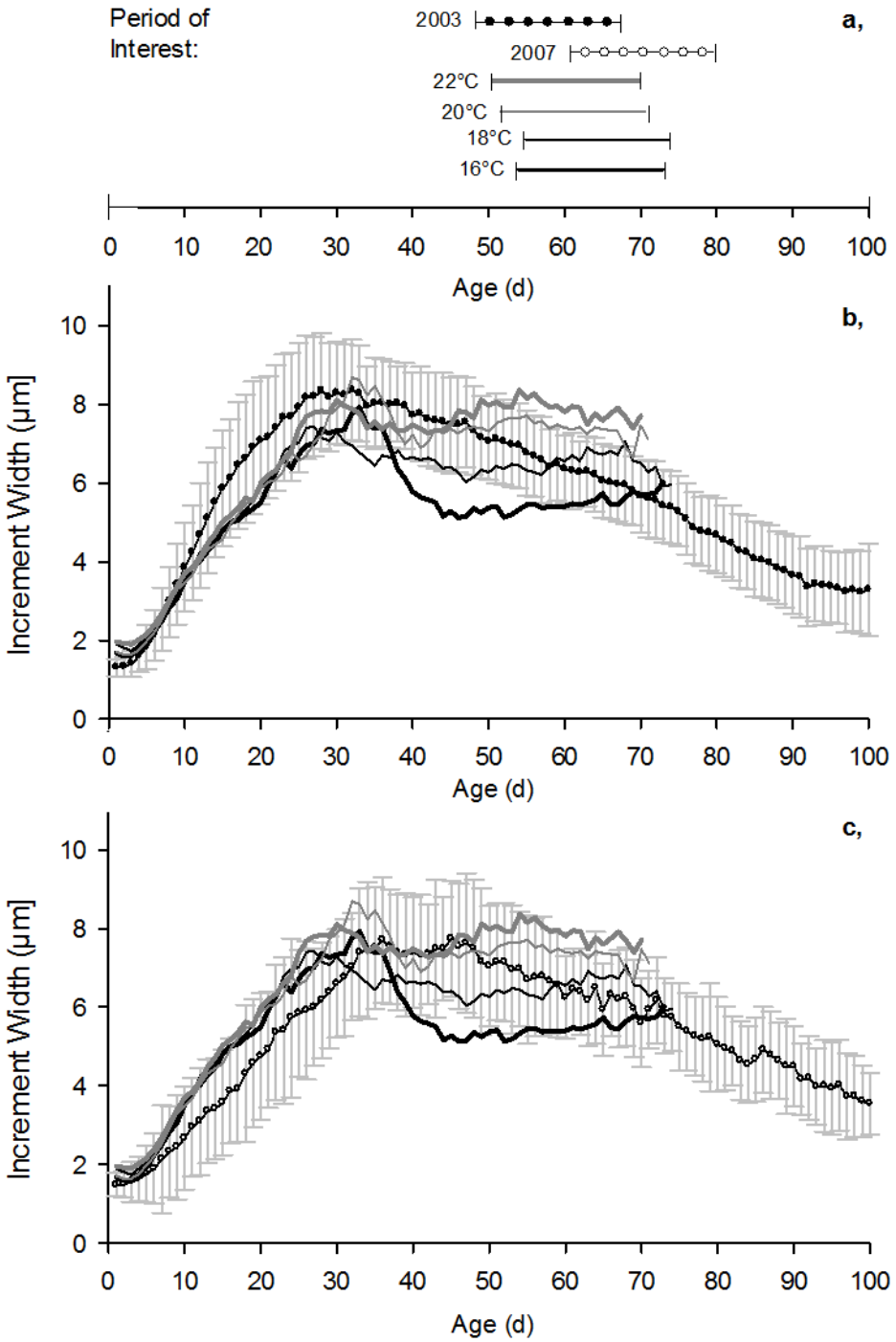

Fig.5-4. a, Age during the period of interest. b, c, Mean increment width versus age of field caught sprat from 2003 and 2007 and of sprat transferred to the laboratory in 2010 (averaged per temperature treatment) starting at the day of first increment formation. Means comprise at least 5 individuals. Black filled dots indicate mean increment width in 2003, white dots mean increment width in 2007. Error bars designate standard deviation of mean increment width from field caught sprat. Mean increment width of sprat transferred to the laboratory in 2010 is grouped by temperature treatment during the experiment: the thick grey line indicates the 22°C treatment, thin grey line the 20°C treatment, the thin black line the 18°C treatment and the thick black line 16°C treatment.

Tab.5-3. Mean SL, otolith radius and length growth rates at the start and the end of the experimental period for laboratory reared individuals and field caught survivors of the western Baltic Sea from 2003 and 2007; OR: otolith radius; OR_{PoM}: otolith radius at the point of metamorphosis; LGR: length growth rate; OBS: observed; MIP: Metamorphosis Inflection Point method.

Source	Type of LGR	SL_{Start} (mm)	OR_{Start} (µm)	OR_{PoM} (µm)	SL_{End} (mm)	OR_{End} (µm)	LGR ($mm*d^{-1}$)
Laboratory 2010*	LGR_{OBS}	29.09	227	164	51.47	418	0.72
	LGR_{MIP}	26.90	214	164	51.47	418	0.79
Field 2003	LGR_{MIP}	26.70	222	182	51.41	438	0.80
Field 2007	LGR_{MIP}	28.43	272	224	48.10	463	0.63

* dataset (I) without "slow growers" (see text)

5.4.4 Laboratory and field length growth and growth back-calculations

When comparing mean observed growth of laboratory reared fish with back-calculated growth rates, the latter caused an overestimation 0.07 $mm•d^{-1}$ using (Tab.5-3). The observed length from the starter group was slightly underestimated by 2.2 ± 1.4 mm SL (8%). On average, the MIP method underestimated the observed starter length at 22°C as well as at 16°C by 2.7 and 1.4 mm SL, respectively.

When comparing observed laboratory and back-calculated field growth in the life-stage examined during the experiment, observed laboratory length growth rates were 0.08 $mm•d^{-1}$ smaller than the corresponding growth rates of field caught sprat in 2003 and 0.09 $mm•d^{-1}$ larger than corresponding growth rates of field caught sprat in 2007 using the MIP method (Tab.5-3).

5.4.5 Comparison of otolith growth between field and laboratory

The overall laboratory-based mean increment width per temperature treatment during the period of interest was described as a non-linear function of temperature. The resulting quadratic equation ($IW = -0.0344•T^2 + 1.6757•T – 12.764$; $r^2 = 0.99$) was used to compare laboratory-based increment widths with field increment widths at corresponding field water temperatures.

Daily increment widths of five consecutive days during the period of interest of field caught sprat were averaged and were allocated according to their mean ambient temperature to temperature classes of one degree Celsius (Fig.5-5.a and d). In each temperature class, a different number of five-day increment width intervals contributed to the mean (Fig.5-5.b and e), whereby most increments were deposited at 17°C in 2003 and 18°C in 2007, respectively. No increments were formed at 15°C in 2003 and at 20, 21 and 22°C in 2007 and only one group of measurements was formed at 16 and 22°C in 2003. Increment widths of field caught individuals were on average equal to or smaller than the mean increment widths of laboratory reared sprat, except of the 16°C-interval in 2003. At 20, 21 and

22°C mean increment widths of field caught sprat in 2003 were considerably smaller than increment width

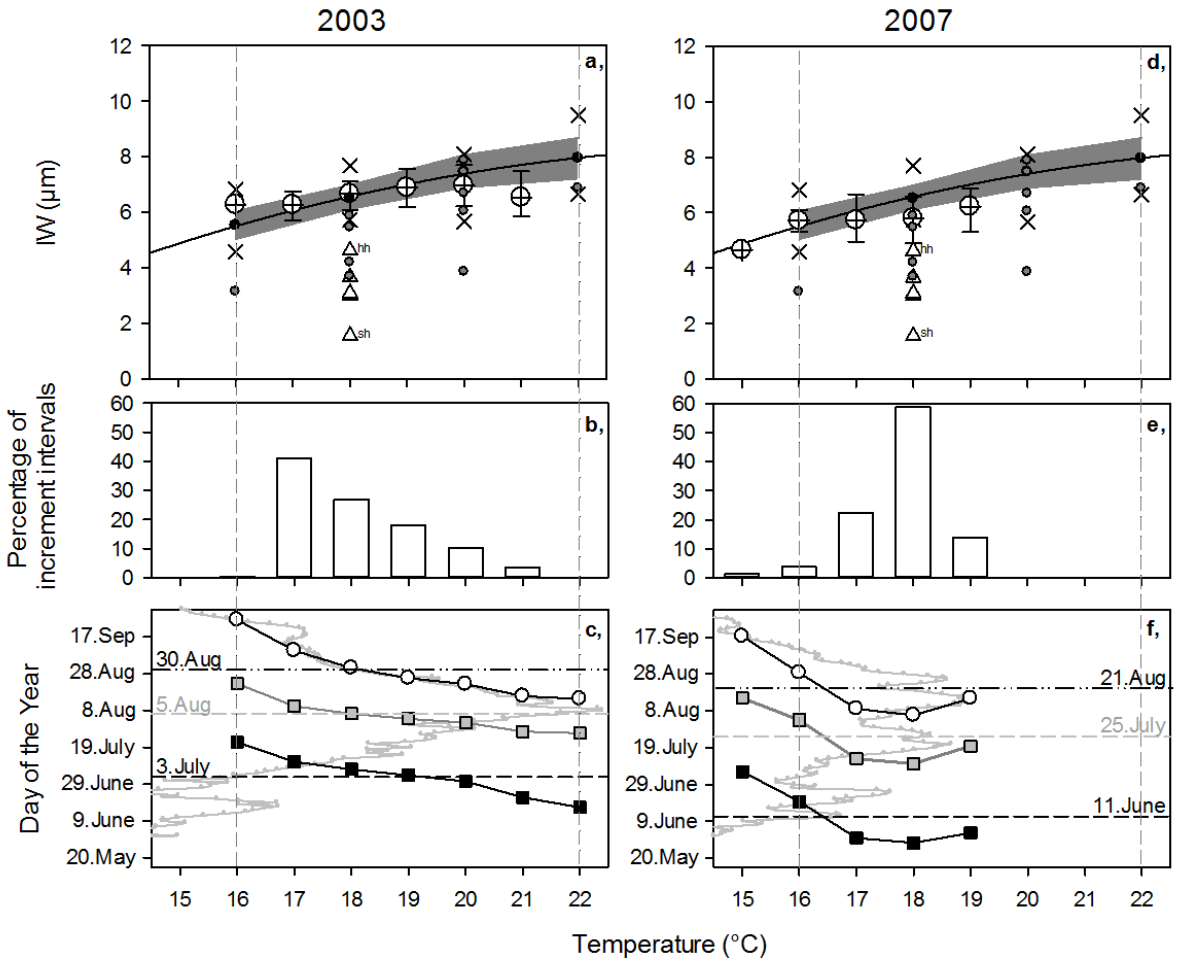

Fig.5-5. Left panels: 2003, right panels: 2007. a and d: Mean increment width versus temperature for laboratory reared fish (black dots) and field caught individuals (white crossed dots). Error bars of field caught individuals (white crossed dots) represent 25th and 75th percentile of data. Black line: quadratic regression for laboratory based means; dark grey area: range between the 25th and 75th percentile of laboratory based data extrapolated between observations (at 16, 18, 20 and 22°C). Grey dots: Slow growing individuals (see text); black thin crosses: Minimum and maximum of increment width per temperature treatment; white triangles: data of Baumann et al. 2005 (hh: High food – high food treatment; sh: starving – high food treatment). b and e: Percentage of increment intervals by temperature contributing to the mean plotted in a and d (white crossed dotes). c and f: Mean day of first increment formation (black squares), mean day of metamorphosis (grey squares) and mean day of the early juvenile stage of individuals plotted in a and d (white crossed dotes). Light grey line with dots: Water temperature at the surface at Kiel Lighthouse. Thin dashed-dotted black line (horizontal): mean day of the early juvenile stage used for temperature intervals (panel a and d); thick black dashed line (horizontal): mean DFIF of all individuals used in the analysis, grey dashed line (horizontal): mean DoM of all individuals used in the analysis. Thin grey dashed lines (vertical): Temperatures that were investigated experimentally.

of laboratory reared sprat. Similarly, field and laboratory increment width diverge at 17, 18 and 19°C in 2007. In 2007, only increments deposited at 16°C exhibit the same width as in laboratory reared sprat.

In 2003, most individuals underwent their period of interest at 17°C after the temperature peak of the season at the beginning of September. On average, individuals that contributed to the temperature interval of 17°C experienced their DFIFs at the beginning of July and underwent their metamorphosis during August (Fig.5-5.c and f). In contrast, most individuals in 2007 experienced a temperature of 18°C during the period of interest at the middle of August during the peak water temperature of the season. Here, individuals contributing to the temperature interval of 18°C experienced their DFIFs at the beginning of June and underwent their metamorphosis in the middle of July.

To estimate the magnitude and impact of the deviance between mean laboratory and field increment width we established a temperature dependent relationship from laboratory data between the mean increment width during the period of interest of the experiment and the observed growth rate using a random intercept model (Fig.5-6) with the following equation for the population model:

$$IW_T = 4.159 + 3.576 \bullet LGR_T + \varepsilon_T \qquad \varepsilon_T \sim N\left(0, \sigma^2\right) \qquad (9)$$

Hereby, the variable length growth rate (*LGR*) was highly significant ($p < 0.001$), the residual variance was 0.348 and the variance for the random intercept was 0.909 µm. To estimate relationships between increment width and length growth rate of temperatures that were not examined experimentally, we established a quadratic equation between the intercept of each experimental temperature treatment and temperature which explained 99% of variability (Y-Intercept = $-0.0279 \bullet T^2 + 1.4223 \bullet T - 12.648$). Thus, we found that slight differences of 0.35, 0.78 and 0.79 µm in increment width between field and laboratory fish at 17, 18 and 19°C in 2007 correspond to pronounced changes in length growth rate with 0.10, 0.22 and 0.22 $mm \bullet d^{-1}$ lower values in the field compared to the laboratory. In contrast, differences in length growth rates between the field fish in 2003 and laboratory fish were small with 0.05 and 0.03 $mm \bullet d^{-1}$ higher growth rates in the field compared to the laboratory at 17 and 18°C and a 0.03 $mm \bullet d^{-1}$ lower growth rate in the field at 19°C.

5.4.6 Estimated biting rate and ad libitum prey concentrations

The estimation of consumed prey items per day based on the DM-increase resulted in a mean biting rate of 0.01 and 0.1 Ind•sec^{-1} at the beginning and the end of the experiment when feeding on *Acartia spp*. is assumed (Tab.5-4). This increase in biting rate corresponds to an increase in consumed prey items of about 500 per day for a sprat of 30 mm SL to about 6500 per day for sprat with 50 mm SL when averaging all temperature treatments. An increase in temperature from 16 to 22°C resulted in an increase of about 2000 prey items per day for a sprat of 50 mm SL. Following the equation of Brachvogel et al. (2012), the prey concentrations needed to maintain these biting rates were 0.23 and 0.25 Ind•L^{-1} at the beginning of the experiment and 3.01 and 4.25 Ind•L^{-1} at the end of the experiment at 16 and 22°C, respectively.

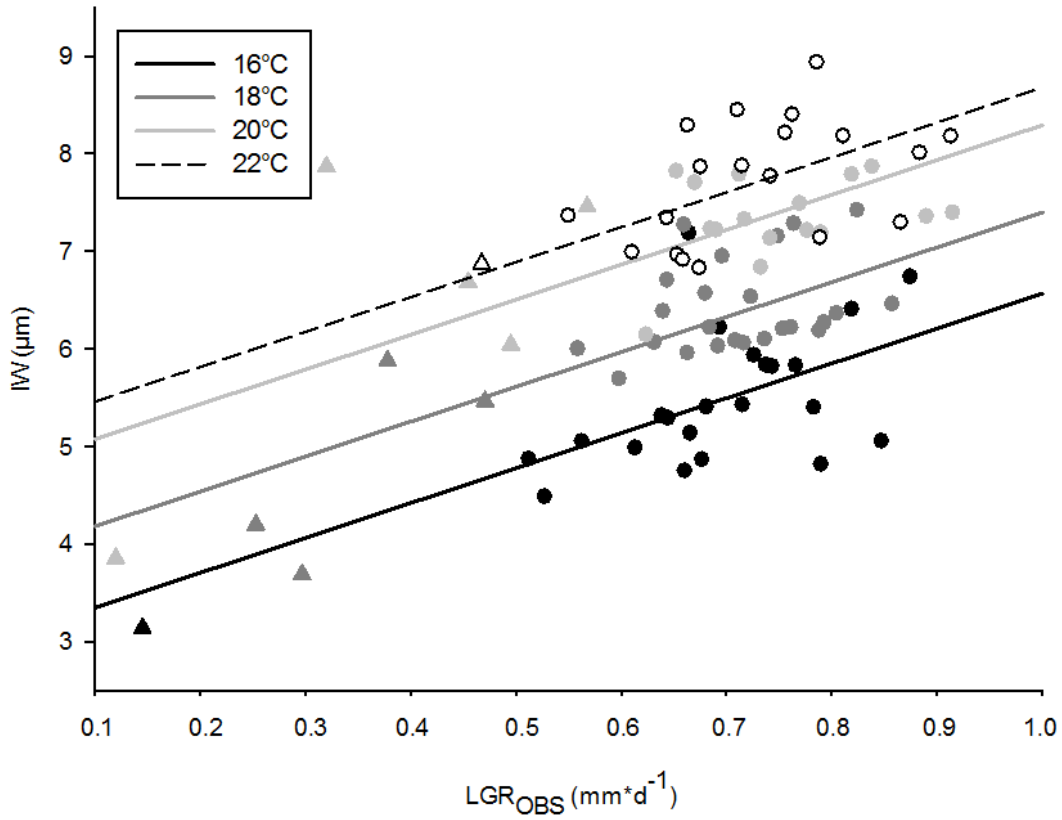

Fig.5-6. Relationship between increment width and observed length growth rate during the experimental period. Continuous lines represent the random intercept model for 16, 18, 20 and 22°C. Circles represent single individuals of data set (2), while triangles indicate small growing fish of data set (1). Black symbols: 16°C; dark grey symbols: 18°C; grey symbols: 19°C; white symbols: 22°C.

Tab.5-4: Estimated number of prey items (*Acartia spp.*) ingested per day (with 14h feeding) and corresponding mean prey concentrations required for the observed growth at the first day and the last day of the experiment. BR: Biting rate.

	Temperature (°C)	Prey items per day	Prey items per second (BR)	Prey concentration (Ind/l)
Day 1	16	500	0.01	0.23
	18	520	0.01	0.24
	20	529	0.01	0.24
	22	547	0.01	0.25
Day 31	16	5660	0.11	3.01
	18	6442	0.13	3.49
	20	6846	0.14	3.74
	22	7654	0.15	4.25

5.5. Discussion

5.5.1 Uncoupling

We recorded no significant difference due to temperature in length growth in contrast to a considerable temperature-dependent difference in otolith growth. Such an uncoupling was firstly described by Mosegaard et al. (1988), where the authors conducted an experiment with Arctic char (*Salvelinus alpinus*). They found that the response of somatic growth rates (measured as mass) to temperatures between 8.0 and 18.8 °C was an optimum curve. In contrast, otolith growth rate (measured as rostral axis length) increased steadily with increasing temperature. In Arctic char, otolith growth increased with somatic growth below 13.9°C indicating coupling conditions, while uncoupling occurred in higher temperatures. Mosegaard et al. (1988) investigated a wider range of the thermal habitat of Arctic char compared to the narrow range of ambient temperature reflecting the likely range of conditions in the natural juvenile habitat which we investigated for Baltic sprat. Our results do not indicate that we exceeded the temperature optimum of length or somatic growth. Thus, uncoupling during our experiment had a different reason and started before the temperature optimum of growth where Mosegaard et al. (1988) observed coupling between length and otolith growth.

While temperature dependent otolith growth was not reflected in length growth we observed distinct differences in relative DM between temperature treatments coinciding with temperature dependent differences in otolith growth. However, an increase in relative dry mass does not necessarily reflect an increase in somatic growth. Strictly speaking, somatic growth is the increase in the number of cells and an increase in relative DM (relation between dry mass and wet mass) indicates rather an increase in energy density of the fish body (Pedersen and Hislop 2001) and thus an increase in the mass of cells. We suggest that this increase in relative DM was caused by an increase in energy reserves in

form of lipids, which are stored in the cells and reduce their water content. Following this assumption we agree with previous studies (Mosegaard et al. 1988, Wright 1991, Folkvord et al. 2004) concluding that the otolith recorded a metabolic process.

As we analysed dry mass in addition to wet mass, we were able to describe this metabolic process as the storage of energy reserves in the fish body. Confirming the assumption that uncoupling is induced by energy storage which starts in the early juvenile stage in sprat, studies on the larval stage (before the onset of lipid storages) in other clupeids reported coupling between somatic and otolith growth with increasing temperature below the temperature optimum of growth (e.g. Folkvord et al. 2004, Aldanondo et al. 2008). Thus, we assume that somatic growth is coupled to otolith growth in early life-stages where storing energy is of minor importance, while uncoupling between otolith and somatic below the temperature optimum of growth occurred in the juvenile life-stages when the storage of energy reserves becomes more important (Sogard 1997). Thus, we conclude that the metabolic process of energy storage is recorded in addition to somatic growth in the early juvenile stage of sprat and can finally lead to uncoupling between fish and otolith length.

5.5.2 The storage of energy reserves in the juvenile stage

The storage of energy reserves during the early juvenile stage in the laboratory can be explained in two different ways: On the one hand (explanation A), somatic growth might have been maximal and laboratory conditions were comparable to optimal conditions in the field. As food in the laboratory was available in excess, fat reserves were built up additionally. This implies that young sprat can eat more than necessary for maximal somatic growth. On the other hand (explanation B), somatic growth might have been limited even under *ad libitum* feeding because the food given in the laboratory might have lacked certain essential components. Hence, laboratory conditions were not necessarily identical with optimal conditions in the field. Sprat have stored lipids partly instead of growing in body-size.

Supporting explanation A, a comparison of length growth shows similar growth rates of laboratory and field caught sprat. In 2003, a year with considerably high growth rates of autumn caught survivors (Baumann et al. 2008), length growth rates during the juvenile stage were only marginally higher (0.08 $mm \bullet d^{-1}$) compared to the laboratory when using the MIP method for back-calculation. Therefore, we assume that conditions in the laboratory and in the field of 2003 were approximately equivalent supporting maximal length growth during the early juvenile stage. These conclusions also imply that maximal length growth was realized in the field, at least in 2003. A further indication for the occurrence of maximal growth rates under natural conditions in the Baltic Sea in 2003 is that growth rates of survivors in 2003 are among the highest growth rates observed in the field (Huwer 2004, Lee et al. 2006, Voss et al. 2012).

In order to avoid a low food quality (explanation B) we fed pellets during the experiment, which are assumed to be optimized food. In a previous study on growth of juvenile Baltic sprat, Baumann et al. (2005) fed exclusively living *Artemia salina* nauplii. Mean increment width of post-metamorphic sprat

in the *ad libitum* food treatment at 18°C in the study of Baumann et al. (2005) was about 30% lower compared to the mean increment at 18°C of the present study. Thus, we assume that *Artemia salina* nauplii as food lacks in essential nutrients needed for growth of juvenile sprat. As increment widths during our experiments was similar to that of field caught individuals, we conclude that the mixture of pellets with the major component fish meal and *Artemia salina* nauplii offered a comparable quality as food in the field. Thus, we exclude explanation B and assume that maximal length growth rates occurred in the laboratory.

The storage of lipids during the experiment suggests a change in the energy allocation during the early juvenile stage from growth in length to storage of energy reserves. It has been described for various fish species that lipid levels remain low throughout larval and early juvenile stages, before abruptly increasing in the juvenile stage (e.g. Deegan 1986, Post and Parkinson 2001, Wuenschel et al. 2006). In sprat we observed this increase as an increase in relative DM during the juvenile stage between 29 and 52 mm SL. The transitions in energy allocation from length growth to length growth and energy storage might indicate the end of a life-stage where size-selective forces such as predation play an important role (Sogard 1997). When building up energy reserves, young sprat start to prepare for over-wintering in order to prevent suffering starvation and temperature-stress (Sogard 1997, Hurst 2007).

5.5.3 Back-calculated and observed length

The MIP-method overestimated the length growth rate of laboratory reared sprat, because the algorithm was designed for field caught sprat. In field caught sprat increment width after metamorphosis gradually decreases (**Manuscript 1**). However, the increment patterns of experimental fish were influenced by stress due to catch and transport and by artificial temperature changes, leading to a disruption in the natural increment width pattern. Because of this disruption, the MIP-algorithm was not able to detect the actual point of metamorphosis when maximal growth in body height coincides with maximal increment growth on the otolith. Beside the length and otolith radius at catch, length growth rates reconstructed by the MIP-method depend on the otolith radius at metamorphosis. Thus, a mis-estimation of the point of metamorphosis can lead to biases in back-calculated length using the MIP-method. As the MIP – method was designed on the basis of field data, we recommend to use it for field caught sprat and not for individuals with artificially manipulated increment width patterns.

5.5.4 The influence of uncoupling on the estimation of feeding conditions

Otolith increment widths have previously been used to estimate the feeding conditions of early life-stages in the field (e.g. Suthers and Sundby 1996, Meekan et al. 2003, Kurita et al. 2004). However, when reconstructing food availability from otoliths, a bias might emerge by the uncoupling of otolith and somatic growth. During the experiment we observed uncoupling of length and otolith growth due to temperature as discussed above. We concluded that the otolith recorded the storage of energy in

addition to somatic growth as displayed by the increase in relative DM. As the storage of energy depends on feeding rate like somatic growth, the observed uncoupling has only little influence on the reconstruction of previous feeding conditions from otoliths.

However, uncoupling between otolith and somatic growth is also known to appear temporally when environmental conditions change (Neilson and Geen 1985, Molony and Choat 1990, Tonkin et al. 2008). Thereby, the response of otolith growth to changes in somatic growth is delayed. Baumann et al. (2005) observed temporal uncoupling in juvenile Baltic sprat by changing the feeding conditions in the laboratory. They found that the otolith needed about 9 days after a change in the feeding regime to correctly display somatic growth again. This temporal delay in recording somatic growth can bias the analysis of otolith growth as a proxy for the feeding environment, while the bias increases with the duration of the delay of otolith response (Tonkin et al. 2008, Aguilera et al. 2009). We believe that the delay of the otolith response in early juvenile sprat is smaller than 9 days. We assume that the temporal delay of the otolith response is fortified in this study, as Baumann et al. (2005) fed sub-optimal food (*Artemia salina* nauplii) over the whole experimental period.

Lastly, we assume that a single increment width is not the result of the food ration of a single day, but rather inflects integrated conditions over a few days. Thus, we conclude that the influence of the ration dependent uncoupling on our analysis is limited as we expect a smaller time lag than proposed 9 days by Baumann et al. (2005). However, we emphasize the need to repeat this experiment with appropriate food.

5.5.5 Feeding conditions derived from otolith increments

As observed, length growth rates from the laboratory are at the same level as growth rates from field samples of 2003, a year with optimal growth conditions (Baumann et al. 2008), we concluded that increments in the laboratory were developed under optimal feeding conditions. Together with the relation of increment width and temperature we were thus able to infer feeding conditions from field otoliths: Increments that are smaller than the laboratory reference at a given temperature indicate sub-optimal feeding conditions. By definition, increments that are larger than the increments from the laboratory should not exist, because they would question if laboratory growth was actually optimal. We observed only very few increment widths at 16°C in 2003 which were considerably higher than the mean increment width from the laboratory reference. In this case, the mean increment width was in fact higher than the 75% percentile of laboratory increments but still in the range of laboratory generated increment widths. Individuals of the experimental group as well as sprat caught in the field might be influenced by the selection of particular genotypes causing the observed deviation.

While most individuals in 2003 exhibited optimal feeding conditions, a small part of individuals had smaller increments indicating sub-optimal feeding conditions at temperatures higher than 20°C. These individuals that suffered sub-optimal feeding conditions in the early juvenile stage were born earlier in the season than the majority of the survivors in 2003. The advantage of summer- over spring-born

individuals due to better feeding conditions and temperature fields has already been reported by Baumann et al. (2008). However, Baumann et al. (2008) stated in their study that recruits mainly originate from summer month because these individuals experience high temperatures and good feeding conditions during the larval stage. In the present study, we concentrated our analysis on the juvenile stage and likewise concluded that individuals benefit if they were born later in the season. However, we found that individuals born early in the season pass the juvenile stage during the highest water temperatures of the year. Hereby, temperatures above 20°C in the juvenile stage might reduce growth rates and potential survival, at least under sub-optimal feeding conditions. In contrast, individuals that where born later in the season, experience the juvenile stage after the peak temperature of the year and thus do not depend on the high food concentrations needed to support optimal growth. In 2007, a similar pattern can be observed as in 2003 with individuals born earlier in the season experiencing sub-optimal feeding conditions in the juvenile stage in contrast to optimal feeding conditions for later born individuals. Sub-optimal feeding conditions in 2007 were found at temperatures below 20°C, reflecting an overall poorer feeding condition in contrast to 2003.

According to the growth-mortality hypothesis (Anderson 1988), which suggests that faster growing individuals have a higher chance to survive, sprat recruitment in the western Baltic Sea should have been higher in 2003 than in 2007. Actually, recruitment was quite different in both years with a more than 3-fold higher recruitment in 2003 in contrast to 2007 (ICES 2012). As stated previously (**Manuscript 1**), 2007 was a season with colder temperature conditions, where we found additionally sub-optimal feeding conditions for early juvenile sprat. During the experiment performed in this study, an average length growth rate of 0.72 $mm \bullet d^{-1}$ have been observed under *ad libitum* feeding conditions when slow growing individuals were excluded. This growth rate was higher than length growth rates in 2007 and slightly lower than those in 2003. However, slow growing individuals with small increment widths during the juvenile stage like those from the laboratory of this study do not appear in autumn caught surviving sprat, even in a year with low growth rates and sub-optimal feeding conditions like in 2007. Early juvenile sprat reared at the high food treatment in the study of Baumann et al. (2005) exhibited similar increment widths than slow growing individuals from the present study, indicating that these experiments could not simulate natural feeding conditions. We conclude that early juvenile sprat with low increment width like slow growing individuals of this study and individuals reared by Baumann et al. (2005) do not survive until autumn irrespective of seasonally varying conditions.

5.5.6 Ad libitum prey concentration

Previous studies identified the post-larval and early juvenile stage as crucial for the determination of recruitment strength in Baltic sprat (Köster et al. 2003, Baumann et al. 2007). Voss et al. (2012) pointed out that food availability may influence survival by intra- and/or inter-specific competition. We evaluated that a sprat of 50 mm SL requires a 10 fold higher amount of food compared to a sprat

of 30 mm SL to grow optimal. These vast differences in food demand in relation to body length highlight the crucial importance of food availability in juvenile nursery areas. According to our results, sprat of 50 mm SL at 18 °C need a constant plankton concentration of 3.5 *Acartia spp*. copepods per liter to support maximal growth. To our knowledge there is no study on zooplankton concentrations in the shallow and coastal areas of the Western Baltic Sea where young sprat have been sampled repeatedly (Baumann et al. 2005, Meskendahl et al. 2010, **Manuscript 1**). However, Javidpour et al. (2009) described the annual cycle of mesozooplankton in the central Kiel Fjord of 2007. They recorded concentrations below 1 copepodit and adult copepod per liter during August and September, which would imply food shortage for a young sprat of 50 mm SL irrespective of ambient temperature. This food shortage supported sub-optimal feeding conditions in the early juvenile stage which we reconstructed from otolith growth for the late summer in 2007. Thus, the results of this study highlight the need for combined small-scale studies of juvenile otoliths, feeding conditions and plankton density in juvenile nursery areas, taking patchiness into account.

5.6 Literature

Aguilera, B., Catalan, I.A., Palomera, I., and Olivar, M.P. 2009. Otolith growth of European sea bass (Dicentrarchus labrax L.) larvae fed with constant or varying food levels. Sci. Mar. **73**(1): 173-182.

Aldanondo, N., Cotano, U., Etxebeste, E., Irigoien, X., Alvarez, P., de Murguia, A.M., and Herrero, D.L. 2008. Validation of daily increments deposition in the otoliths of European anchovy larvae (Engraulis encrasicolus L.) reared under different temperature conditions. Fish. Res. **93**(3): 257-264.

Alshuth, S. 1988. Daily Growth Increments on Otoliths of Laboratory-Reared Sprat, Sprattus-Sprattus L, Larvae. Meeresforschung-Reports on Marine Research **32**(1): 23-29.

Anderson, J.T. 1988. A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. J. Northwest. Atl. Fish. Sci. **8**: 55-66.

Baumann, H., Hinrichsen, H.-H., Voss, R., Stepputtis, D., Grygiel, W., Clausen, L.W., and Temming, A. 2006. Linking growth to environmental histories in central Baltic young-of-the-year sprat, *Sprattus sprattus*: an approach based on otolith microstructure analysis and hydrodynamic modelling. Fish. Oceanogr. **15**(6): 465-476. doi: 10.1111/j.1365-2419.2005.00395.x.

Baumann, H., Peck, M.A., Götze, H.E., and Temming, A. 2007. Starving early juvenile sprat *Sprattus sprattus* (L.) in western Baltic coastal waters: evidence from combined field and laboratory observations in August and September 2003. J. Fish. Biol. **70**(3): 853-866. doi: 10.1111/j.1095-8649.2007.01346.x.

Baumann, H., Peck, M.A., and Herrmann, J.P. 2005. Short-term decoupling of otolith and somatic growth induced by food level changes in postlarval Baltic sprat, Sprattus sprattus. Marine and Freshwater Research **56**(5): 539-547.

Baumann, H., Voss, R., Hinrichsen, H.-H., Mohrholz, V., Schmidt, J.O., and Temming, A. 2008. Investigating the selective survival of summer- over spring-born sprat, *Sprattus sprattus*, in the Baltic Sea. Fish. Res. **91**(1): 1-14. doi: 10.1016/j.fishres.2007.11.004.

Brachvogel, R., Meskendahl, L., Herrmann, J.P., and Temming, A. 2012. Functional responses of juvenile herring and sprat in relation to different prey types. Mar. Biol.: 1-14. 10.1007/s00227-012-2104-5.

Campana, S.E., and Jones, C.M. 1992. Analysis of otolith microstructure data. *In* Otolith Microstructure Examination and Analysis. *Edited by* D.K. Stevenson and S.E. Campana. Canadian Special Publications of Fisheries and Aquatic Sciences 117. pp. 73-100.

Campana, S.E., and Neilson, J.D. 1985. Microstructure of Fish Otoliths. Can. J. Fish. Aquat. Sci. **42**(5): 1014-1032.

Deegan, L.A. 1986. Changes in Body-Composition and Morphology of Young-of-the-Year Gulf Menhaden, Brevoortia-Patronus Goode, in Fourleague-Bay, Louisiana. J. Fish. Biol. **29**(4): 403-415.

Drinkwater, K.F., Beaugrand, G., Kaeriyama, M., Kim, S., Ottersen, G., Perry, R.I., Portner, H.O., Polovina, J.J., and Takasuka, A. 2010. On the processes linking climate to ecosystem changes. Journal of Marine Systems **79**(3-4): 374-388.

Durbin, E.G., Durbin, A.G., Smayda, T.J., and Verity, P.G. 1983. Food Limitation of Production by Adult Acartia-Tonsa in Narragansett Bay, Rhode-Island. Limnology and Oceanography **28**(6): 1199-1213.

Elliott, J.M., and Davison, W. 1975. Energy Equivalents of Oxygen-Consumption in Animal Energetics. Oecologia **19**(3): 195-201.

Folkvord, A., Johannessen, A., and Moksness, E. 2004. Temperature-dependent otolith growth in Norwegian spring-spawning herring (Clupea harengus L.) larvae. Sarsia **89**(5): 297-310.

Folt, C.L., and Burns, C.W. 1999. Biological drivers of zooplankton patchiness. Trends in Ecology & Evolution **14**(8): 300-305.

Harley, C.D.G., Hughes, A.R., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S., Rodriguez, L.F., Tomanek, L., and Williams, S.L. 2006. The impacts of climate change in coastal marine systems. Ecology Letters **9**(2): 228-241.

Heath, M.R. 1992. Field investigations of the early-life stages of marine fish. ICES J. Mar. Sci. **28**: 1-174.

Houde, E.D. 1989. Comparative Growth, Mortality, and Energetics of Marine Fish Larvae - Temperature and Implied Latitudinal Effects. Fishery Bulletin **87**(3): 471-495.

Hurst, T.P. 2007. Causes and consequences of winter mortality in fishes. J. Fish. Biol. **71**(2): 315-345.

Huwer, B. 2004. Larval growth of *Sardina pilchardus* and *Sprattus sprattus* in relation to frontal systems in the German Bight. Diploma thesis, Leibniz-Institut für Meereswissenschaften, Christian Albrechts Universität, Kiel.

ICES. 2012. Report of the Baltic Fisheries Assessment Working Group 2012. **ICES CM 2010/ACOM:10**.

Javidpour, J., Molinero, J.C., Peschutter, J., and Sommer, U. 2009. Seasonal changes and population dynamics of the ctenophore Mnemiopsis leidyi after its first year of invasion in the Kiel Fjord, Western Baltic Sea. Biological Invasions **11**(4): 873-882.

Kerambrun, P. 1987. Elementary Chemical-Composition (C,H,N) and Energy Equivalent of Acartia-Clausi (Crustacea, Copepoda), an Important Species in the Bioenergetics of the Coastal Ecosystems of the Northwest Mediterranean. Mar. Biol. **95**(1): 115-121.

Köster, F.W., Hinrichsen, H.H., Schnack, D., St John, M.A., Mackenzie, B.R., Tomkiewicz, J., Möllmann, C., Kraus, G., Plikshs, M., Makarchouk, A., and Aro, E. 2003. Recruitment of Baltic cod and sprat stocks: identification of critical life stages and incorporation of environmental variability into stock-recruitment relationships. Sci. Mar. **67**: 129-154.

Kurita, Y., Nemoto, Y., Oozeki, Y., Hayashizaki, K., and Ida, H. 2004. Variations in patterns of daily changes in otolith increment widths of 0+ Pacific saury, Cololabis saira, off Japan by hatch date in relation to the northward feeding migration during spring and summer. Fish. Oceanogr. **13**: 54-62.

Lee, O., Danilowicz, B.S., and Dickey-Collas, M. 2006. Temporal and spatial variability in growth and condition of dab (*Limanda limanda*) and sprat (*Sprattus sprattus*) larvae in the Irish Sea. Fish. Oceanogr. **15**(6): 490-507. doi: 10.1111/j.1365-2419.2006.00406.x.

Meekan, M.G., Carleton, J.H., McKinnon, A.D., Flynn, K., and Furnas, M. 2003. What determines the growth of tropical reef fish larvae in the plankton: Food or temperature? Mar. Ecol. Prog. Ser. **256**: 193-204.

Meskendahl, L., Herrmann, J.P., and Temming, A. 2010. Effects of temperature and body mass on metabolic rates of sprat, Sprattus sprattus L. Mar. Biol. **157**(9): 1917-1927.

Möller, K., St John, M., Temming, A., Floeter, J., Sell, A., Herrmann, J., and Möllmann, C. 2012. Marine snow, zooplankton and thin layers: indications of a trophic link from small-scale sampling with the Video Plankton Recorder. Mar. Ecol. Prog. Ser. **468**: 57-69. 10.3354/meps09984.

Möllmann, C., Kornilovs, G., Fetter, M., and Köster, F.W. 2004. Feeding ecology of central Baltic Sea herring and sprat. J. Fish. Biol. **65**(6): 1563-1581. 10.1111/j.0022-1112.2004.00566.x.

Molony, B.W., and Choat, J.H. 1990. Otolith Increment Widths and Somatic Growth-Rate - the Presence of a Time-Lag. J. Fish. Biol. **37**(4): 541-551.

Mosegaard, H., Svedang, H., and Taberman, K. 1988. Uncoupling of somatic and otolith growth-rates in arctic char (*Salvelinus alpinus*) as an effect of differences in temperature response. Can. J. Fish. Aquat. Sci. **45**(9): 1514-1524.

Neilson, J.D., and Geen, G.H. 1985. Effects of Feeding Regimes and Diel Temperature Cycles on Otolith Increment Formation in Juvenile Chinook Salmon, Oncorhynchus-Tshawytscha. Fishery Bulletin **83**(1): 91-101.

Omori, M., and Hamner, W.M. 1982. Patchy Distribution of Zooplankton - Behavior, Population Assessment and Sampling Problems. Mar. Biol. **72**(2): 193-200.

Pedersen, J., and Hislop, J.R.G. 2001. Seasonal variations in the energy density of fishes in the North Sea. J. Fish. Biol. **59**(2): 380-389. 10.1111/j.1095-8649.2001.tb00137.x.

Post, J.R., and Parkinson, E.A. 2001. Energy allocation strategy in young fish: Allometry and survival. Ecology **82**(4): 1040-1051.

Shields, R.J. 1989. Studies of Growth and Nutritional Status in 0-Group sprat, Sprattus sprattus (Clupeidae), using Otolith Microstructure and Lipid Analytical Techniques. PhD thesis, School of Ocean Science, University of Wales, Bangor.

Sogard, S.M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: A review. Bull. Mar. Sci. **60**(3): 1129-1157.

Stevenson, D.K., and Campana, S.E.e. 1992. Otolith microstructure examination and analysis Canadian Special Publication of Fisheries and Aquatic Sciences **117**.

Suthers, I.M., and Sundby, S. 1996. Role of the midnight sun: comparative growth of pelagic juvenile cod (Gadus morhua) from the Arcto-Norwegian and a Nova Scotian stock. ICES Journal of Marine Science: Journal du Conseil **53**(5): 827-836. 10.1006/jmsc.1996.0104.

Tonkin, Z., King, A.J., and Ramsey, D.S.L. 2008. Otolith increment width responses of juvenile Australian smelt Retropinna semoni to sudden changes in food levels: the importance of feeding history. J. Fish. Biol. **73**(4): 853-860.

Voss, R., Peck, M.A., Hinrichsen, H.-H., Clemmesen, C., Baumann, H., Stepputtis, D., Bernreuther, M., Schmidt, J.O., Temming, A., and Köster, F.W. 2012. Recruitment processes in Baltic sprat – A re-evaluation of GLOBEC Germany hypotheses. Progress in Oceanography.

Wilson, J.A., Vigliola, L., and Meekan, M.G. 2009. The back-calculation of size and growth from otoliths: Validation and comparison of models at an individual level. J. Exp. Mar. Biol. Ecol. **368**(1): 9-21. doi: 10.1016/j.jembe.2008.09.005.

Wright, P.J. 1991. The Influence of Metabolic-Rate on Otolith Increment Width in Atlantic Salmon Parr, Salmo-Salar L. J. Fish. Biol. **38**(6): 929-933. DOI 10.1111/j.1095-8649.1991.tb03632.x.

Wuenschel, M.J., Jugovich, A.R., and Hare, J.A. 2006. Estimating the energy density of fish: The importance of ontogeny. Transactions of the American Fisheries Society **135**(2): 379-385.

Temperature effects on growth of spring and summer cohorts and implications for survival in young sprat (*Sprattus sprattus L.*) of the western Baltic Sea

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6.1 Abstract

The post-larval and early juvenile life-stage in Baltic sprat is of increasing interest as recruitment relevant processes are assumed to act on post-metamorphic fish. We examined the length growth and the temporal origin of young sprat from the Western Baltic Sea in two seasons with contrasting water temperature profiles using microstructure analysis of otoliths. We found *in situ* length growth rates by tracking age-based cohorts which exceeded 1.0 $mm \bullet d^{-1}$ in the post-metamorphic life-stage. We compared the performance of two different back-calculation methods and found smaller deviations from observed *in situ* length when using a regression-based non-linear model considering individual metamorphosis compared to deviations when applying the linear biological intercept model. Higher mean length growth rates in 2006, a year with cold winter and warm summer water temperatures coincide with a late window of survival and a strong year-class. In contrast, low length growth rates occurred in 2007 with high winter and low summer water temperatures leading to a broad window of survival including spring born individuals and a weak year-class strength. The pattern of year-class strength being related to the combination of a cold winter and a warm summer was confirmed by a high correlation of 0-group sprat abundance in autumn from the Baltic International Acoustic Survey and the ratios of minimal and maximal surface water temperatures of the year. This correlation explains more than 60% of variability when including 11 years of observation. We assume that delayed spawning after cold winters shifts more of the offspring to suitable summer conditions which are optimal in years when high water temperatures occur and thus ensure an increase in year-class strength.

6.2 Introduction

An extended spawning season to ensure the survival of at least some offspring in hydro-graphic variable systems is a widely distributed adaptation in marine fish species. Despite of a broad spawning season, successful reproduction is often constrained to a limited temporal period, when environmental conditions ensure optimal development and growth of early life-stages (e.g. Anderson 1988). Sprat (*Sprattus sprattus L.*) as a key species in the upper trophic level of the Baltic ecosystem exhibiting a prey as well as a predator role (Bagge et al. 1994) is a multiple batch spawner with a spawning period from February to August (Ojaveer and Kalejs 2010). Using age-estimates from otoliths, Baumann et al (2008) observed that the temporal window of survival of young-of-the-year (YoY)-sprat caught in autumn was located during the last month of the spawning seasons in 2002 and 2003. The same study stated that young sprat born in summer had an advantage to survive over spring born individuals in the Baltic Sea. Otolith-based reconstructed growth rates from this study showed that YoY-sprat born later in the season benefited from better food conditions and higher temperatures in the larval and early juvenile stages. As a consequence, the bulk of the offspring in the central Baltic Sea died in 2002 and 2003, because peak egg production occurred earlier in the spawning season not coinciding with the window of survival of autumn caught juveniles (Baumann et al. 2008). Despite of the high mortality in eggs and larvae (Voss et al. 2012a), the seasons of 2002 and 2003 resulted in strength above average year-class (ICES 2012a). Thus, results of the study of Baumann et al. (2008) provoke the question if strong year-classes are coupled to a late window of survival and to strong growth rates of YoY-survivors in Baltic sprat. There is no comparable study investigating the growth rates and the window of survival in a season with a weak year-class. To disentangle mechanisms influencing recruitment strength, data on the characteristics of YoY-sprat in years with low recruitment are needed.

The goal of this study was to investigate additional growth seasons of YoY-sprat to examine the relation between growth, window of survival and year-class strength in a year with a level below the average recruitment. For the examination of growth we used the analysis of otolith microstructures and sampled young juveniles in two consecutive years in the coastal area of the Western Baltic Sea. In contrast to the previous studies on characteristics of Baltic sprat survivors, we investigated two seasons with contrasting year-class strength. We hypothesize that (a) the windows of survival will differ in years with different recruitment (b) that mean growth rates will differ in years with different recruitment and (c) that these differences are mainly driven by water temperature.

6.3 Materials and Methods

6.3.1 Sprat sampling and otolith processing

Sampling of early juvenile sprat took place during summer of 2006 and 2007 in two harbours sites west and east of the Kiel Fjord (Fig.6-1). To catch small sprat in the harbours, we used a 2•3 m dip-net with a stretched mesh-size of 6 mm. Sampling effort was equal in both years with a one to two times

per week search for small clupeids at the catch-sites from the middle of July to the end of August. Sampling was successful at 1, 23 and 30 August of 2006 and at 17 and 26 July as well as at the 14 August of 2007. In 2007, YoY-sprat from the Kiel Bight (Fig.6-1) were sampled in October during the Baltic International Acoustic Survey (BIAS). Here, the trawl was equipped with a stretched mesh-size of 20 mm in the cod-end. All samples were stored at –20°C until standard length (SL) and otoliths were measured and processed in the laboratory.

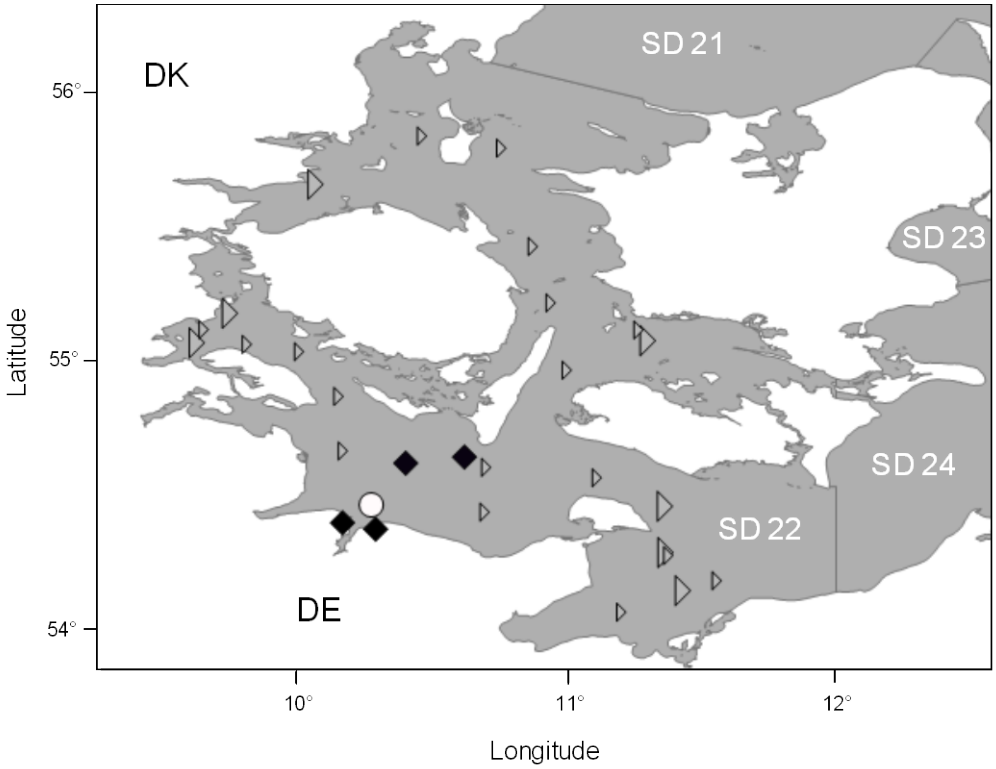

Fig.6-1: Study area in the western Baltic Sea. Black diamonds: sampling sites of this study. Coastal sites have been sampled in 2006 and 2007, while offshore sites have only be sampled in 2007. White dot: measurement station Kiel Lighthouse. Grey triangles: sampling sites of the study of Baumann et al. 2008 in 2002 (large symbols) and 2003 (small symbols). SD: ICES subdivision; DK: Denmark; DE: Germany.

After unfreezing, SL was measured in all individuals while only a subset of individuals was randomly chosen for microstructure analysis of otoliths. Irrespective of left and right, the otolith with the clearest view was chosen for further analysis. Fixed by thermoplastic glue on a microscopic slide, each otolith was polished from both sides using a 3 µm lapping film until the axis between the core and the post-rostral section was clearly visible. Digital images were taken at 400 times magnification with different planes of focus to enhance the identification of increments and age reading afterwards.

Reading was performed three times by the same experienced reader with increment widths being measured in the first and second reading. During the first reading, otoliths were judged according to a scale from 1 (best) to 4 (worst). Otoliths with scale 4 were excluded from further processing. Finally, we chose the age reading with the increment measurement which was closest to the mean age of all

three measurements allowing a difference from the mean of maximal two increments. In total, we used 162 individuals for the following analysis. For further details on sampling and otolith processing of the dataset see **Manuscript 1**.

6.3.2 Temporal origin and growth rates

We defined the first clearly visible increment around the core of the otoliths as "day of first increment formation" (DFIF) following (Reglero et al. 2007). According to their DFIFs and the year of catch, we merged individuals into DFIF cohorts of their temporal origin. Using these weekly DFIF cohorts, we calculated observed length growth rates between sampling dates when mean length was increasing. We compared these observed *in situ* length growth rates with back-calculated length growth rates from increment measurements.

For the reconstruction of length growth via otolith analysis we used two different methods: the BI method (Campana 1990) and the MIP method (**Manuscript 1**). The BI method assumes a linear relationship between fish length and otolith length throughout the period of length back-calculation, while being independent on the population investigated by applying an empirical evaluated intercept. In contrast, the MIP method based on a non-linear regression model which takes a change in the relationship between fish length and otolith length into account, when individuals undergo metamorphosis between larvae and juveniles.

6.3.3 Inter-annual differences of DFIF-distributions

We compared the DFIF distributions of individuals caught in 2006 and 2007 with the temporal origin of YoY-sprat analysed by Baumann et al. (2008) sampled in SD 22 during October 2002 and 2003 (Fig.6-1). To examine the influence of temperature on the DFIF distributions we used surface water temperatures logged at Kiel Lighthouse located outside the Kiel Fjord (Fig.6-1) and surface temperature model outputs for 2002 and 2003 from Baumann et al (2008).

We investigated the influence of surface water temperatures on the abundance of YoY-sprat and one year old sprat (1-group) in SD 22 between 1999 to 2011 and 2000 to 2011, respectively. Minimal and maximal temperatures of the years were taken from the surface temperature profiles at Kiel Lighthouse with the exception of two years. In 2002 and 2011, the measurement system failed in the summer and autumn months. Here, we applied the maximal temperature measured at "Kiel Institute" in the inner Fjord (http://www.geomar.de/service/wetter). We used the number of 0-group and 1-group sprat of the following year estimated during the hydro-acoustic survey in autumn (BIAS) which is published by subdivision and age in the WGBIFS – Reports (ICES 2000 to ICES 2012b) as a proxy for year-class strength.

6.4 Results

6.4.1 Length distribution and temporal origin

In 2006, we found progressing modes in the length distributions of sequential sampling dates with a mean of 29.3 mm SL on 1 August, 57.1 mm SL on 23 August and 60.4 mm SL on 30 August (Fig.6-2). According to the otolith based age readings, individuals from the three catch dates in 2006 exhibit similar temporal origins with a mean DFIF at the 24, the 21 and the 23 June of individuals caught on the 1, the 23 and the 30 August, respectively. It has to be mentioned that some length classes of the overall distributions of SL were not represented in the sub-samples used for otolith microstructure analysis. In 2006, four weekly DFIF cohorts can be used to investigate growth between sampling dates.

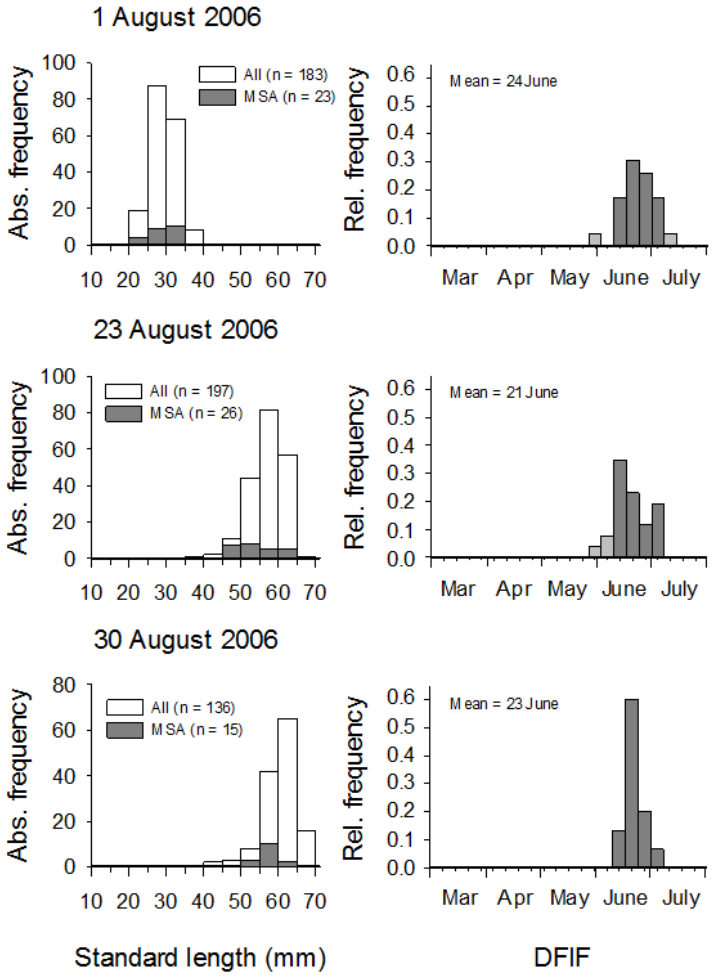

Fig.6-2. Distribution of standard lengths and DFIFs of the three sampling dates in 2006. Left panels: absolute frequency of length distributions in 5 mm classes. Grey bars indicate individuals taken for microstructure analysis of the otoliths and are plotted in the right panels. Right panels: relative frequency of DFIFs with individuals pooled into DFIF cohorts corresponding to calendar weeks. Dark grey bars: DFIF cohorts that were used to track *in situ* length growth in the field. Light grey bars: other DFIF cohorts.

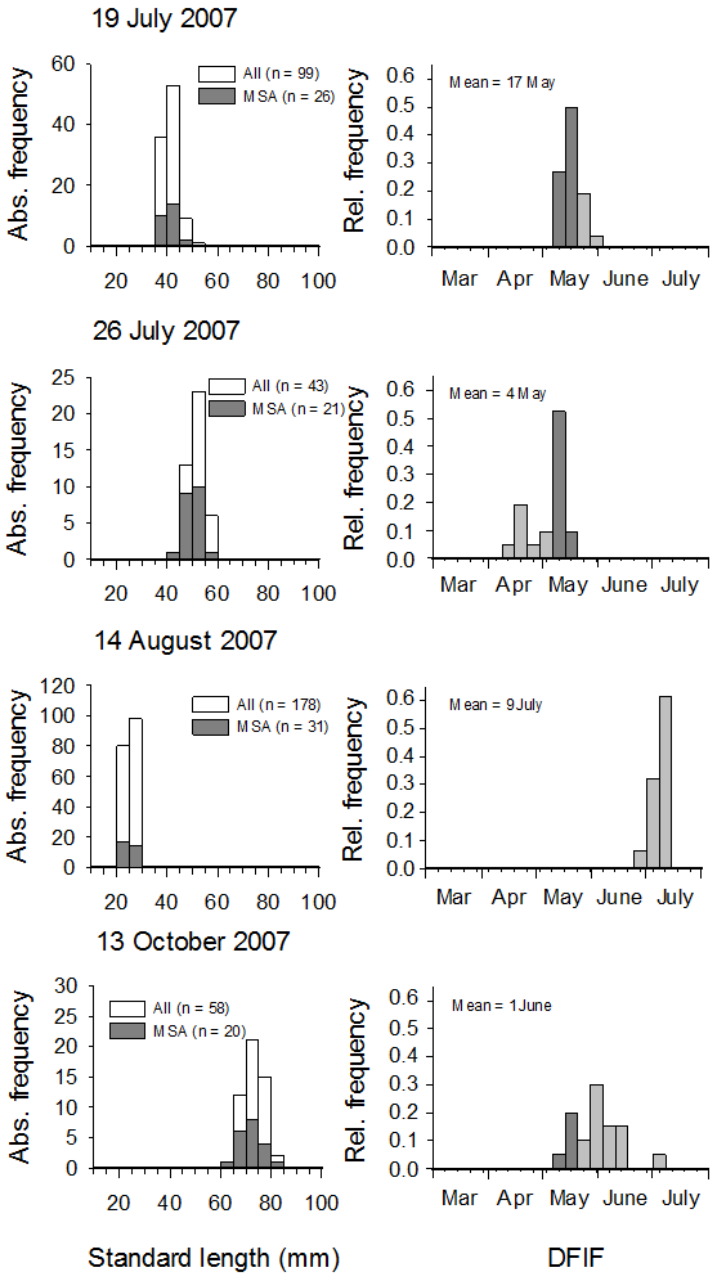

Fig.6-3. Distribution of standard lengths and DFIFs of the four sampling dates in 2007. Left panels: absolute frequency of length distributions in 5 mm classes. Grey bars indicate individuals taken for microstructure analysis of the otoliths and are plotted in the right panels. Right panels: relative frequency of DFIFs with individuals pooled into DFIF cohorts corresponding to calendar weeks. Dark grey bars: DFIF cohorts that were used to track *in situ* length growth in the field. Light grey bars: other DFIF cohorts.

In the summer samples of 2007 we found an increasing mean length between the first two sampling dates from 41.1 mm SL on the 19 July to 51.6 mm SL on the 26 July (Fig.6-3). However, individuals from the third sampling date on the 4th August 2007 were on average 25.2 mm SL and thus considerably smaller than individuals from the first and second sampling dates. We found overlapping

DFIF distributions of the first and second sampling date only for two DFIF cohorts from the middle of May. Corresponding to the small mean length, individuals caught on 14 August were born later compared to those of the first and second sampling date. The DFIF distribution of YoY-sprat sampled in October comprised the two DFIF cohorts from the middle of May, which also occurred at the first and second sampling date in summer. However, the bulk of the DFIF distribution from YoY-sprat occurred at the end of May and at the beginning of June.6.4.2 Observed and reconstructed length growth

Growth in 2006

Using individuals from different sampling dates belonging to the same weekly DFIF cohorts, we examined observed (*in situ*) length growth rates during the juvenile life-stage.

In 2006, back-calculated length of the first DFIF cohort (2006/1, see Tab.6-1) do not match with the observed lengths at the first sampling date of the year, irrespective of the back-calculation model used (Fig.6-4). Hereby, average observed length growth rate during the first growth period (time between the first and the second sampling date) of the 2006/1 DFIF cohort was 1.16 $mm \bullet d^{-1}$, while the BI- and the MIP-method underestimated length growth by 30 and 22%, respectively. Back-calculated length were considerably larger than the directly observed lengths at the first sampling date with 21 and 13% overestimation using the BI- and the MIP-method, respectively. During the second growth period (time between the second and the third sampling date) of the 2006/1 DFIF cohort the BI- and the MIP-method overestimated the observed length growth rate by 0.11 and 0.18 $mm \bullet d^{-1}$ (Tab.6-1).

In the three following DFIF cohorts of 2006, back-calculated lengths correspond well with the observed lengths (Fig.6-4). Deviations of back-calculated and directly observed length during the first growth period was smaller when using the MIP-method with maximal 5% overestimation in contrast to the BI-method with maximal 9% overestimation (Tab.6-1). Observed length growth rates from the earliest (2006/1) to the latest DFIF cohort (2006/4) showed a decreasing trend from 1.16 $mm \bullet d^{-1}$ to 0.94 $mm \bullet d^{-1}$. With the exception of the first DFIF cohort (2006/1), length growth rates from the MIP-method exhibit the same trend as observed length growth rates. In contrast, the BI – method showed an increasing trend of growth rates with the highest growth rate in the latest DFIF cohort (2006/4).

In general, mean observed length growth rates during the first growth period in 2006 were higher than back-calculated values, regardless of the method used (Tab.6-1). During the second growth period of 2006, we found both back-calculation models to slightly overestimate observed length growth rates, while deviations of directly observed and back-calculated length were negligible (maximal 4%).

Growth in 2007

Length growth rates of the 2007/1 DFIF cohort (Tab.6-1) had similar characteristics than the 2006 DFIF cohorts during the first growth period: Observed length growth rates were highest, followed by back-calculated growth rates estimated with the MIP – method. Smallest length growth rates were

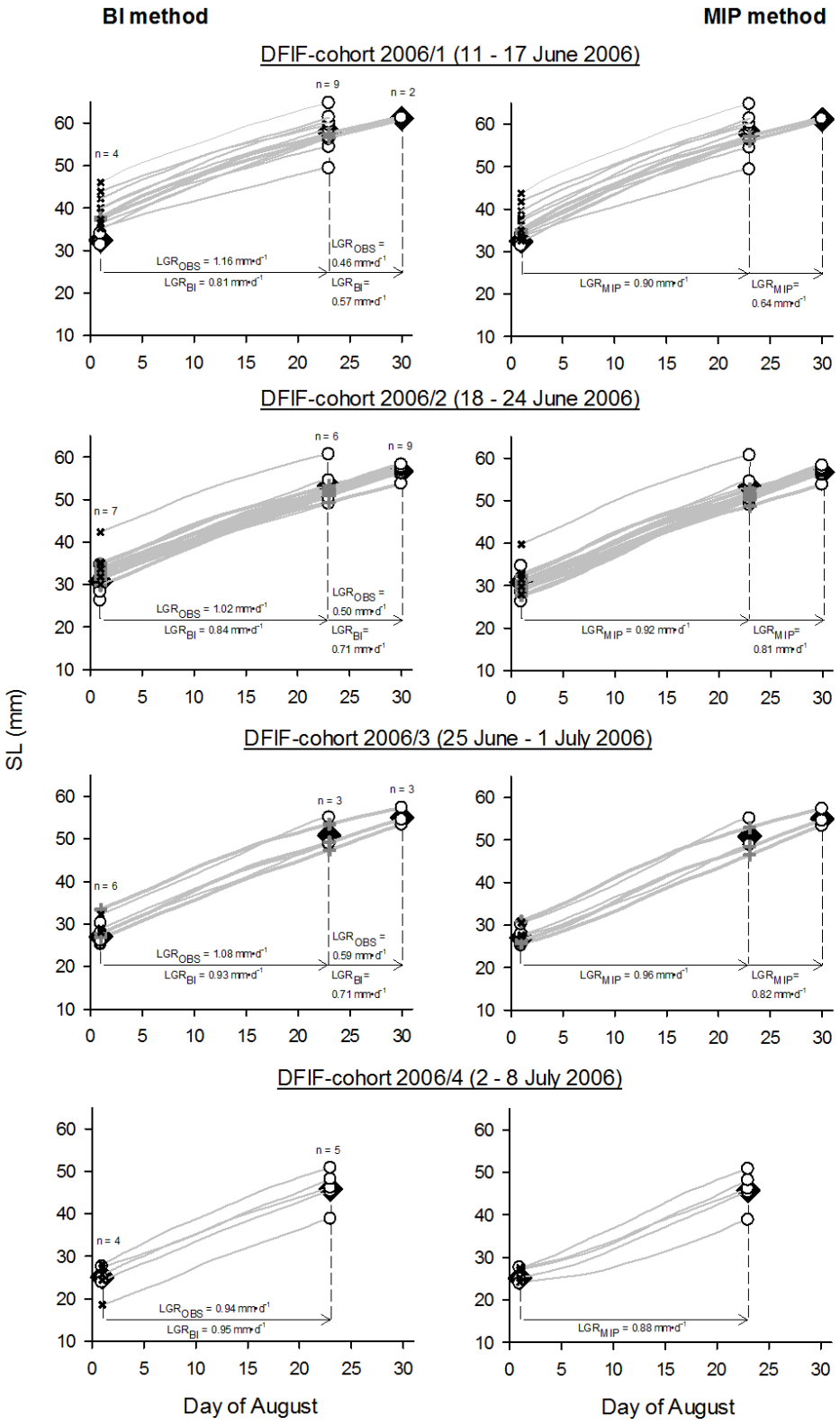

Fig.6-4. Caption on next side

Fig.6-4 (page 84). Observed and back-calculated length growth of selected DFIF cohorts in 2006 (see dark grey bars in the DFIF distribution of Fig.6-2). Black rhomb: mean length of the considered DFIF cohort per sampling date; white circles: observed length of single individuals; grey crosses: back-calculated length from fishes of the last sampling date with thick grey lines representing the corresponding back-calculation lines; black crosses: back-calculated length from fishes of the median sampling date with thin grey lines representing corresponding back-calculation lines. Left panels show back-calculated length using the BI method, right panels show back-calculated length using the MIP method. LGR: mean length growth rate; OBS: observed length; numbers (n) and LGR_{OBS} are identical in the associated left and right panels.

Tab.6-1. Observed and back-calculated length growth rates (LGR) and the percentage deviation of back-calculated length from observed length for the BI and MIP method. SL of DFIF cohorts are illustrated in Fig.6-4 (2006) and in Fig.6-5 (2007).

2006

First growth period (Mean SL - range: 29 - 54 mm)
1 - 23 August

			BI method		MIP method	
Name of weekly DFIF cohort	Calendar week of DFIF	Observed LGR (mm* d^{-1})	LGR (mm* d^{-1})	% deviation of SL from observed SL	LGR (mm* d^{-1})	% deviation of SL from observed SL
2006/1	11. - 17. June	1.16	0.81	21	0.90	13
2006/2	18. - 24. June	1.02	0.84	8	0.92	0
2006/3	25. June - 1. July	1.08	0.93	9	0.96	4
2006/4	2. - 8.July	0.94	0.95	1	0.88	5

Second growth period (Mean SL - range: 54 - 57 mm)
23 - 30 August

			BI method		MIP method	
Name of weekly DFIF cohort	Calendar week of DFIF	Observed LGR (mm* d^{-1})	LGR (mm* d^{-1})	% deviation of SL from observed SL	LGR (mm* d^{-1})	% deviation of SL from observed SL
2006/1	11. - 17. June	0.46	0.57	1	0.64	2
2006/2	18. - 24. June	0.50	0.71	3	0.81	4
2006/3	25. June - 1. July	0.59	0.71	2	0.82	3
2006/4	2. - 8.July	-	-	-	-	-

2007

First growth period (Mean SL - range: 41 - 51 mm)
19 - 26 July

			BI method		MIP method	
Name of weekly DFIF cohort	Calendar week of DFIF	Observed LGR (mm* d^{-1})	LGR (mm* d^{-1})	% deviation of SL from observed SL	LGR (mm* d^{-1})	% deviation of SL from observed SL
2007/1	7. - 13.May	0.84	0.61	4	0.71	2
2007/2	14. - 20.May	1.17	0.28	3	0.21	8

Second growth period (Mean SL - range: 51 - 72 mm)
26 July - 13 October

			BI method		MIP method	
Name of weekly DFIF cohort	Calendar week of DFIF	Observed LGR (mm* d^{-1})	LGR (mm* d^{-1})	% deviation of SL from observed SL	LGR (mm* d^{-1})	% deviation of SL from observed SL
2007/1	7. - 13.May	-	-	-	-	-
2007/2	14. - 20.May	0.51	0.67	16	0.72	21

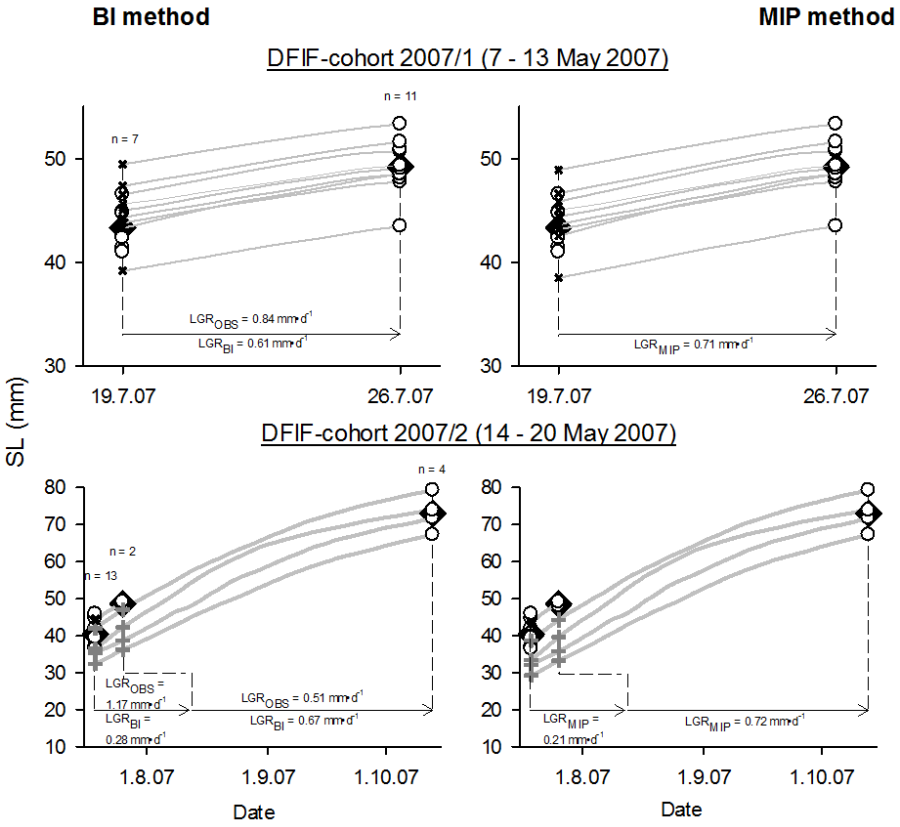

Fig.6-5. Observed and back-calculated length growth of selected DFIF cohorts in 2007 (see dark grey bars in the DFIF distribution of Fig.6-3). Black rhomb: Mean length of the considered DFIF cohort per sampling date; white circles: observed length of single individuals; grey crosses: back-calculated length from fishes of the last sampling date with thick grey lines representing the corresponding back-calculation lines; black crosses: back-calculated length from fishes of the median sampling date with thin grey lines representing corresponding back-calculation lines. Left panels show back-calculated length using the BI method, right panels show back-calculated length using the MIP method. LGR: mean length growth rate; OBS: observed length; numbers (n) and LGR_{OBS} are identical in the associated left and right panels.

estimated using the BI – method. The largest deviation of observed versus back-calculated length growth rates was found for the first growth period of the 2007/2 DFIF cohort with an underestimation of 76 and 82% using the BI- and MIP-method, respectively. Thus, the mean observed length growth rate, was about 5 times higher than back-calculated values, irrespective of the method (Tab.6-1). Consequently, we found a high deviation of observed and back-calculated length for the second growth period of the 2007/2 DFIF cohort with 16 and 21% lower reconstructed length when using the BI- and the MIP-method respectively.

Comparison between growth in 2006 and 2007

We focussed the year-to-year comparison of growth rates on a sub-sample of data to exclude any possible effects of selective mortality. Selective mortality is indicated during the first growth period of

the 2006/1 DFIF cohort and during the first and second growth period of the 2007/2 DFIF cohort when back-calculated and directly observed length and growth rate considerably deviate from each other. Comparing average back-calculated length growth rates of YoY-sprat caught in autumn 2007 with length growth rates from the last two sampling dates of 2006, individuals from 2006 grew better than those of 2007 (Tab.6-2). Using the MIP algorithm we estimated an average age of metamorphosis indicating the end of the larval stage at an age of 37 days in 2006 and 43 days in 2007. Hereafter, higher length growth rates in 2006 occurred during the larval as well as the juvenile life-stage.

Tab.6-2: Back-calculated length growth rates of individuals caught at the end of August in 2006 and October 2007. The larval stage ends with the day of metamorphosis which is defined by the occurrence of maximal increment width on the otolith.

Larval stage	LGR ($mm*d^{-1}$)		*Juvenile stage*	LGR ($mm*d^{-1}$)	
	2006	2007		2006	2007
BI method	0.65	0.52	**BI method**	0.90	0.49
MIP method	0.52	0.39	**MIP method**	0.93	0.51

6.4.3 Inter-annual comparison of DFIF distributions

Young sprat of 2006 and 2007 differed considerably in two features: the average length growth rates and the DFIF distributions. Individuals of 2006 grew considerably faster than those of 2007 during the larval as well as the juvenile stage. While sprat in 2006 originated mainly from June, individuals of 2007 had a broad distribution of DFIFs ranging from April to July.

By comparing individuals of 2006 and 2007 with autumn-caught young sprat of 2002 and 2003 from the study of Baumann et al. (2008), we found a similar narrow DFIF distribution as in 2006 in the year 2003 (Fig.6-6). Taking the 0-group abundance in autumn estimated from the survey data (BIAS), year-class strength revealed high values in 2006 as well as in 2003. In contrast, 2007 exhibited a broad DFIF distribution earlier in the season coinciding with low 0-group abundance in autumn. 2002 exhibited a relatively broad DFIF distribution with a mean DFIF of about one month later compared to 2007 and an intermediate abundance of 0-group sprat between the values for 2006 and 2007 (Fig.6-6).

2006 and 2007 vary considerably in their water temperature profiles (Fig.6-6). Surface water temperatures at Kiel Lighthouse during 2007 exceeded 5 °C already by mid of March, while maximal summer temperatures in August barely exceeded 18°C. In contrast, the temperature profile in 2006 (as well as in 2003) showed relatively cold water temperatures in spring with values above 5°C occurring mid of April and maximal summer temperatures above 20°C.

When jointly analysing the data of these four years we identified a coincidence of a cold spring coupled to a hot summer with a narrow DFIF distribution in summer, which occurs together with a high abundance of 0-group sprat in autumn. Vice versa, high temperatures in spring combined with low summer temperatures coincides with a broad DFIF-distribution including spring month and a weak year-class strength.

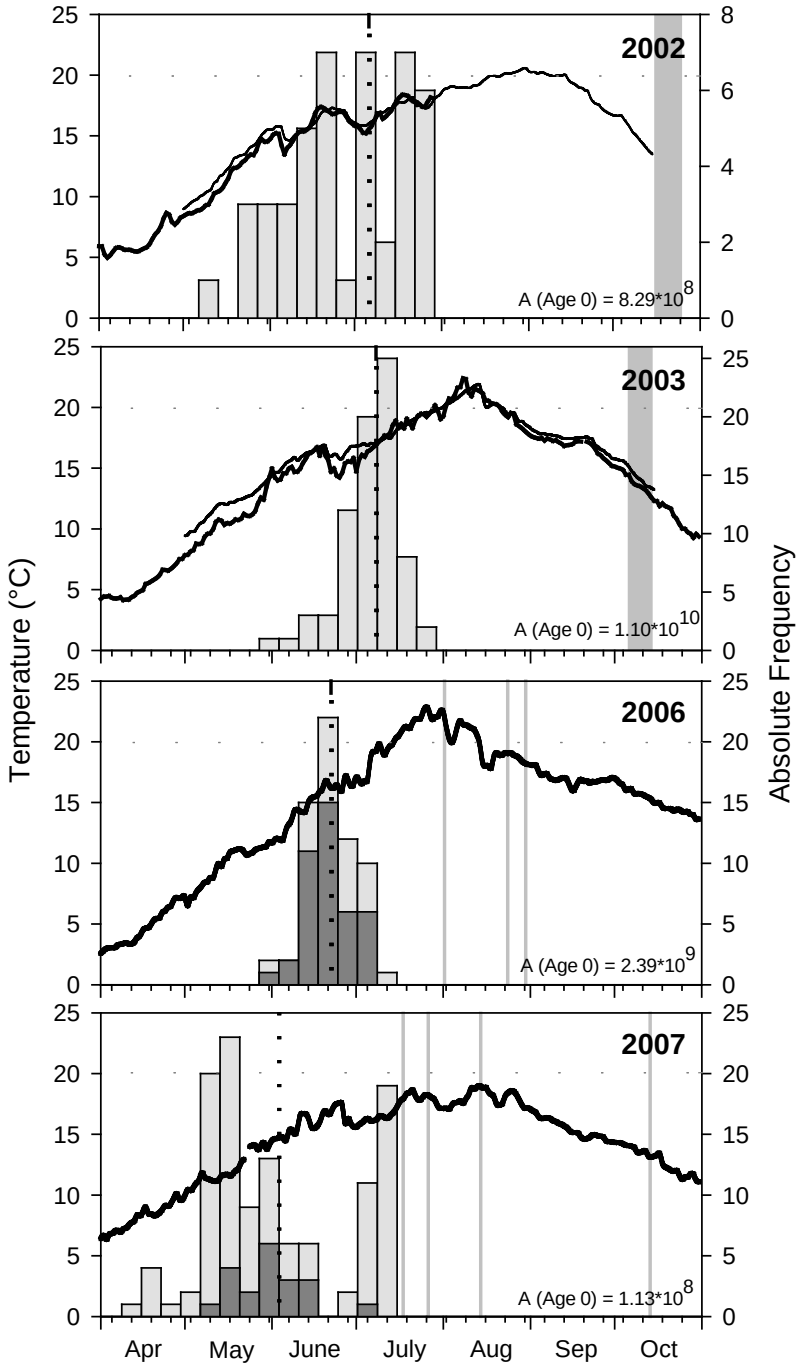

Fig.6-6. DFIF distributions of young sprat and surface water temperature profiles from ICES subdivision 22 during four years. Light grey bars: absolute frequency of DFIF distribution; dark grey bars: absolute frequency of DFIF of the last two sampling dates in 2006 and autumn caught individuals in 2007 (individuals used for length growth comparison in Tab.6-2); vertical grey planes and lines: period or day of catch; vertical dashed black lines: mean of the DFIF distribution; thick black curve: surface temperature at Kiel Lighthouse; thin black curve: modelled surface temperature (see Baumann et al. 2008); horizontal dashed line indicates values of 20°C. A(Age 0): Abundance of 0-group sprat estimated from survey data (BIAS) for ICES subdivision 22.

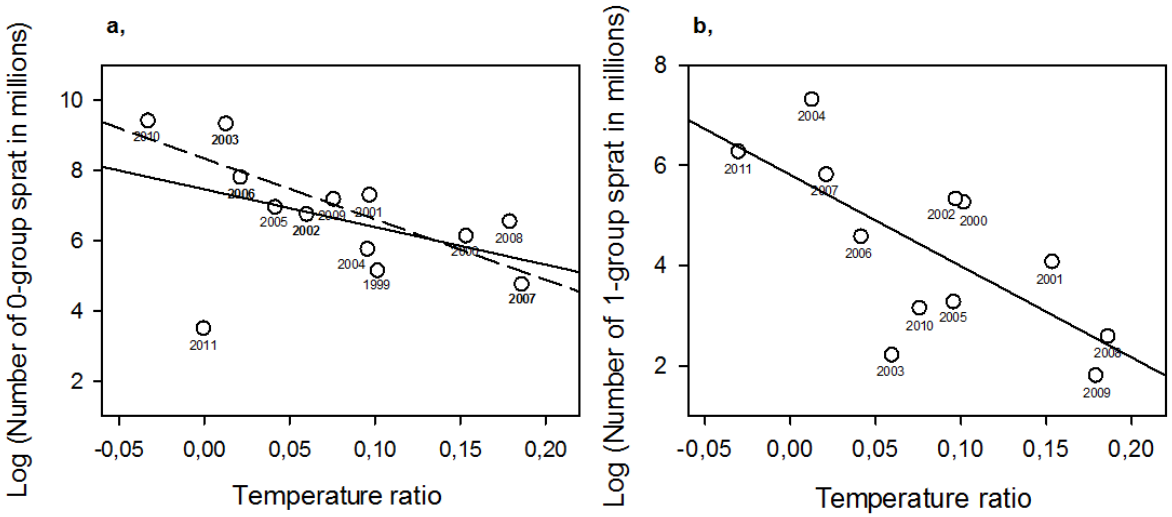

Fig.6-7: Abundance of 0-group (a) and 1-group sprat (b) in autumn estimated by the hydro-acoustic survey (BIAS) for ICES subdivision 22 in relation to the ratio of minimum and maximum temperature of the year. Solid line panel (a): The solid line indicate a model for all years ($\log(y) = -10.729 \cdot x + 7.457$, $r^2 = 0.19$) , the dashed line a model excluding 2011 ($\log(y) = -17.292 \cdot x + 8.3368$, $r^2 = 0.66$) and numbers indicate the year of the 0-group cohort , panel b: The line indicate a model for all years ($\log(y) = -18.220 \cdot x + 5.809$, $r^2 = 0.51$) and numbers indicate the year of the 1-group cohort.

6.4.4 Influence of seasonal temperature patterns on the abundance of recruits

We examined the relationship between minimal temperature in spring and maximal temperature in summer and the abundance of 0-group and 1-group sprat of the following year in the period between 1999 to 2011 and 2000 to 2011, respectively. Sprat in the Baltic Sea is managed as one stock (ICES 2012*a*) and thus recruitment indices were calculated for sprat in the whole Baltic area. As sprat in the western Baltic Sea only represents a small part of the Baltic sprat stock, we disclaimed using estimates for the whole Baltic Sea. Instead, we constrained our analysis on SD 22 (Fig.6-1) using estimates of the hydro-acoustic survey (BIAS).

By correlating the log-transformed abundance of 0-group sprat from SD 22 with minimal surface water temperatures in spring we found a weak negative and insignificant linear relationship ($r^2 = 0.19$; $p = 0.13$). The correlation of the log-transformed abundance with the maximal surface water temperatures in summer revealed a positive and significant linear relationship ($r^2 = 0.41$; $p < 0.05$). The year 2011 exhibited a strong influence on the explained variability. When excluding the year 2011, both regressions are significant ($p < 0.05$) and the explained variability for the correlation with the minimal and maximal temperatures changes to 68 and 40%, respectively. A linear regression of the log-transformed number of 0-group sprat and the ratio between minimal and maximal temperature explained 19% of the variability ($p = 0.13$). By excluding the year 2011 the model gains significance ($p < 0.01$) and explains 66% of the variability in abundance (Fig.6-7.a). Using the log-transformed abundance of 1-group sprat of the following year as response variable, minimal and maximal temperatures explained 50% ($p < 0.05$) and 40% ($p < 0.05$) of the variability. The linear relationship

between the log-transformed number of 1-group sprat and the ratio between minimal and maximal temperature was also significant ($r^2 = 0.51$; $p < 0.01$; Fig.6-7.b).

6.5 Discussion

6.5.1. Length growth during the juvenile stage

Length growth rates from cohort tracking

By sampling the same DFIF cohorts of young fishes several times we were able to reconstruct *in situ* length growth rates from wild sprat without back-calculating previous length from otoliths. This way to calculate length growth rates is not independent of age-reading, however, it is independent of increment measurements and back-calculation methods. Additionally, we were able to generate seasonally resolved growth rates for each weekly DFIF cohort in contrast to one average growth rate between two sampling dates.

To our knowledge, length growth rates of 0.9 – 1.1 mm•d^{-1} are among the highest reported for the early juvenile stage in sprat. A previous laboratory (**Manuscript 2**) found a mean growth rate of about 0.7 mm•d^{-1} between 29 and 50 mm SL in the early juvenile stage, when feeding young sprat *ad libitum* with a mixture of pellets and brine shrimp (*Artemia salina*). Also studying growth in the laboratory Shields (1989) found even lower growth rates of 0.5 mm•d^{-1} between 41 and 46 mm SL in North Sea sprat. A field study examining back-calculated length from survivors of the central Baltic Sea with the BI method found a maximal growth rate of sprat at the transition between larvae and juveniles of 0.97 mm•d^{-1} and decreasing values of about 0.8 mm•d^{-1} in the early juvenile stage (Baumann et al. 2006b). However, length growth rates reconstructed with the linear BI method are biased because maximal increment widths at the transition between the larval and the juvenile stages do not indicate maximal length growth, but mostly growth in body height (**Manuscript 1**), which is discussed in more detail in the following section. Length growth rates of other clupeids in the juvenile stage varied strongly with 0.6 mm•d^{-1} found for laboratory reared Baltic herring (*Clupea harengus*, Arrhenius & Hansson 1996) and 1.7 mm•d^{-1} reported in laboratory reared Japanese sardine (*Sardinops melanostictus*, Nakamura et al. 1991). However, irrespective of the growth rates, those studies found the highest growth rates during development occur in the juvenile stage after metamorphosis, where we observed the highest length growth rates previously reported for Baltic sprat.

Back-calculated length growth rates

In **Manuscript 1** a comprehensive dataset of fish length and corresponding otolith radii was analysed and a species-specific non-linear back-calculation model for juvenile sprat was designed. This model, the MIP method, located the highest length growth potential in Baltic sprat after the metamorphosis in the early juvenile stage. According to this analysis, length growth rates at the transition between the larval and the juvenile stage were minimal while broad increments represent maximal growth in body height. So far there is no independent evidence from field observations that highest length growth rates

occur actually during the early juvenile stage after metamorphosis. The present study is the first to report *in situ* growth rates confirming the previous results of the MIP method (**Manuscript 1**) with length growth rates after metamorphosis reaching more than 1.0 mm•d^{-1}. Length growth rates that were back-calculated with the MIP method were almost as high as *in situ* length growth rates when excluding the 2006/1 and 2007/2 DFIF-cohort, which are discussed below. In contrast, the linear BI method revealed 14% lower length growth rates during the early juvenile stage than *in situ* length growth rates.

Seasonal pattern of length growth rates in 2006

To further investigate the performance of the BI and MIP method we examined seasonally varying length growth. This was only possible for 2006 as we sampled only two DFIF cohorts repeatedly in 2007. In 2006, a decreasing trend of *in situ* juvenile length growth rates occurred from the earliest to the latest cohorts. This finding for the juvenile stage is in contrast to previous observations for the larval stage. In the larval stage, an increasing trend in length growth rates with proceeding season has been found, caused by an increase in water temperatures (Baumann et al. 2006a). The inversed seasonal trend of the larval and juvenile stage found in this study can be explained with the seasonal water temperature profile: All DFIF cohorts were born before the seasonal maximum in a period of steadily increasing temperatures. This implies that larvae of later cohorts experience higher temperatures than larvae of earlier cohorts. Assuming a positive relation between growth and temperature, later born individuals exhibit higher larval growth rates than earlier born individuals. With an average duration of the larval stage of about 30 days, late cohorts experience their juvenile stage when water temperatures are already decreasing after the summer maximum. In contrast, individuals that were born early in the season undergo their early juvenile stage during maximum water temperatures. Consequently, length growth rates during the early juvenile stage decrease from the earliest to the latest DFIF cohort.

This decreasing trend of *in situ* length growth rates from the earliest to the latest DFIF cohort is reproduced by the MIP method with the exception of the 2006/1 DFIF cohort. The BI method however, revealed an inverse trend of an increase in length growth rate during the early juvenile stage with proceeding season. The reproduction of the decreasing trend of *in situ* length growth rates from the earliest to the latest DFIF cohort supports the use of the MIP method instead of the BI method for length growth reconstructions in Baltic sprat.

Selective survival

In situ length at the first sampling date and back-calculated length using otoliths from individuals of following sampling dates deviated strongly in the 2006/1 and the 2007/2 DFIF cohort. We suggest that these differences were the result of selective mortality and/or a low sample size, rather than the consequence of a bias due to back-calculation. As only few individuals contribute to the analysis at

some sampling dates of these cohorts, we were not able to exclude the latter possibility. If selective mortality is the reason for the deviation between observed and back-calculated lengths, selectivity for fast growing individuals occurred in the 2006/1 DFIF cohort and selectivity for slow growing individuals in the 2007/2 DFIF cohort. Selective survival of fast growing individuals has often been observed (e.g. Meekan and Fortier 1996, Shoji and Tanaka 2006, Robert et al. 2007) and was previously described in young Baltic sprat (Baumann et al. 2007). The selective survival of slower growing individuals is, however by far more rarely documented (Litvak and Leggett 1992). However, as we found only two DFIF cohorts with a low sample size supposing selective mortality, a detailed analysis of the underlining mechanism is constricted.

6.5.2. Inter-annual comparison of the DFIF distributions

Selective survival between summer and autumn

When analysing the temporal origins of individuals from this study and from Baumann et al. (2008), we compare summer caught sprat from 2006 with autumn caught sprat from 2002, 2003 and 2007. As autumn survivors were not sampled in 2006, we assume that summer caught individuals of 2006 exhibited the same DFIF distribution that hypothetical autumn caught individuals of 2006 would have had. As we found an indication for selective survival of faster growing individuals between the first and the second sampling of 2006, we excluded the first sampling date from the comparison of DFIF distributions. Further, we assume that the critical life-stages, when the strength of the year-class can be determined are already completed when examining individuals sampled at the end of August. Previous studies described the late-larval and early juvenile stage critical for recruitment (Köster et al. 2003, Voss et al. 2012a). Individuals of 2006 that were used for the inter-annual comparison (first sampling date excluded) had a mean length of 57 mm SL and 60 mm SL (second and third sampling date). and are hence larger than a late-larval and early juvenile sprat described by Köster et al. (2003). Therefore, we conclude that a comparison between autumn caught sprat from 2002, 2003 and 2007 with summer caught sprat from 2006 is not biased by selective survival of juvenile sprat between summer and autumn.

Window of survival and growth

In the following, we discuss the characteristics of the DFIF distributions and growth rates of surviving young sprat from the western Baltic Sea from the four seasons 2002 and 2003 from Baumann et al. (2008) and 2006 and 2007 from this study.

The growth seasons of 2006 and 2007 exhibit pronounced differences in their temperature profiles and individuals caught in both years differ considerably in their growth rates with overall higher growth rates in 2006 than in 2007. In 2007, spring temperatures exceeded 5°C in the middle of March which enhanced the survival of spring spawned eggs and larvae (Nissling 2004, Petereit et al. 2008). Later born con-species, however, did not experience summer temperatures above 20°C. The low

temperatures in the summer of 2007 finally lead to overall low length growth rates in later born individuals. In contrast, conditions in 2006 with low spring and high summer temperatures favoured the survival of summer over spring born individuals (Baumann et al. 2008). Water temperatures of 5°C were exceeded one month later compared to 2007 impeding the development of early born individuals. Furthermore, summer born sprat experienced higher summer temperatures which accelerated length and mass growth of young sprat favouring the survival and leading to a higher year-class strength compared to 2007.

Individuals from the strong year-class of 2003 which were examined by Baumann et al. (2008) had their DFIF peak in summer at high temperatures similar to our findings for 2006. In contrast, high spring and low summer temperatures in 2002 were similar to 2007, leading to the survival of some spring born individuals and a moderate year-class. Starting from these observations, we finally discuss if the temperature in spring combined with the temperature in summer defines the strength of a year-class in western Baltic sprat by determining the timing of the window of survival and mean growth rates.

6.5.3.From DFIF distributions to temperature abundance correlations

The year 2011

A strong correlation between the abundance of young sprat and the ratio of minimal temperature in winter and maximal temperature in summer was only evident when the year 2011 was excluded from the analysis. Therefore, we are discussing in this section possible reasons for the exceptional situation in 2011 before we are trying to draw more general conclusions in the following section.

2011 was characterized by a low abundance of 0-group sprat in spite of hydrographical conditions correlating generally with high year-class strength. Potentially, there are three factors that influence the abundance of 0-group sprat in SD 22 in 2011: (1) spawning stock biomass (SSB), (2) drift of eggs and larvae and (3) migration of young sprat in and out of the area. We found only a week correlation between SSB and 0-group sprat in SD 22 when analysing the estimates of the hydro-acoustic survey (Tab.6-3). The abundance of adult sprat during the spawning season in spring and summer may differ from the abundance of adult sprat in autumn due to spawning and feeding migrations out of the area. However, even a correlation between SSB of the whole Western Baltic area (SD 21-24) and 0-group sprat from SD22 assuming that adult sprat are distributed throughout this area during autumn does not improve the relation of SSB and 0-group abundance.

Concerning factor (2), Hinrichen et al. (2005) performed a drift study to investigate the passive transport of sprat eggs and larvae in the Southern Baltic Sea. They found a mainly eastwards drift due to prevailing westerly winds. An eastwards drift of larvae into SD 24 will reduce the abundance of young sprat in SD 22. However, the abundance of 0-group sprat in SD 24 was likewise low in 2011 (Fig.6-8), a fact that does not indicate a drift of offspring to SD 24 which explains the low abundance of 0-group sprat in autumn in SD 22.

Tab.6-3. Correlations of abundance estimates from the international hydro-acoustic survey in the Baltic Sea in the period from 1999 to 2011. RV: Response variable, EV: Explanatory variable; SSB: Spawning Stock Biomass (individuals equal or older Age 2), SD: ICES subdivision.

RV	EV	gradient	intercept	r^2	p-value
0-group (SD 22)	1-group (SD 22)	8.30	594.34	0.68	<0.001
0-group (SD 22)	SSB (SD 22)	-2.33	2967.65	0.02	>0.5
0-group (SD 22)	SSB (SD 21 - 24)	-0.82	4010.70	0.04	>0.5

Migration of young sprat (factor (3)) might be important in explaining the low abundance of 0-group sprat in 2011. Sprat during the early juvenile stage often occur in shallow regions of the western Baltic Sea (e.g. Baumann et al. 2005, Baumann et al. 2007, Meskendahl et al. 2010). At the end of summer, young sprat start to move offshore joining the adult stock (ICES 2012b). In autumn 2011, extraordinary high water temperature values have been reported at Kiel Lighthouse (http://www.geomar.de/service/wetter) of about 17°C at the beginning of October. These high temperatures might have influenced the timing of migration as has been reported for other temperate fish species (Olla et al. 1980, Jonsson and Ruud-Hansen 1985). The offshore migration of young sprat in 2011 might have thus been delayed leading to unusually low abundances of 0-group sprat during the BIAS, which is regularly performed in October.

Temperature-recruitment relations of Baltic sprat

Excluding the year 2011, we found a strong correlation between the abundance of 0-group sprat and the ratio of minimal temperature in spring and maximal temperature in summer. Additionally, we found a significant correlation between this temperature ratio and the abundance of one year old sprat in the following year. After cold winters, spawning is known to be delayed (Grimm and Herra 1984, Karasiova 2002). A delayed spawning activity implicates that a larger part of the total offspring develops and grows later in the season. We suggest, that in years when a warm summer follows a cold winter, development and growth rates of eggs, larvae and juveniles are increased resulting in a strong year-class. On the other hand, a warm winter combined with a cold summer leads to early spawning and a broad temporal origin of survivors with juveniles from spring month, a low population growth rate and low recruitment strength.

A positive effect of high summer temperatures on recruitment by favouring the growth of post-larval sprat has previously been observed (Baumann et al. 2006c). However, previous studies on temperature-recruitment correlations in Baltic sprat found a positive influence of high spring temperature on year-class strength (MacKenzie and Koster 2004, Baumann et al. 2006c, Ojaveer and Kalejs 2010).

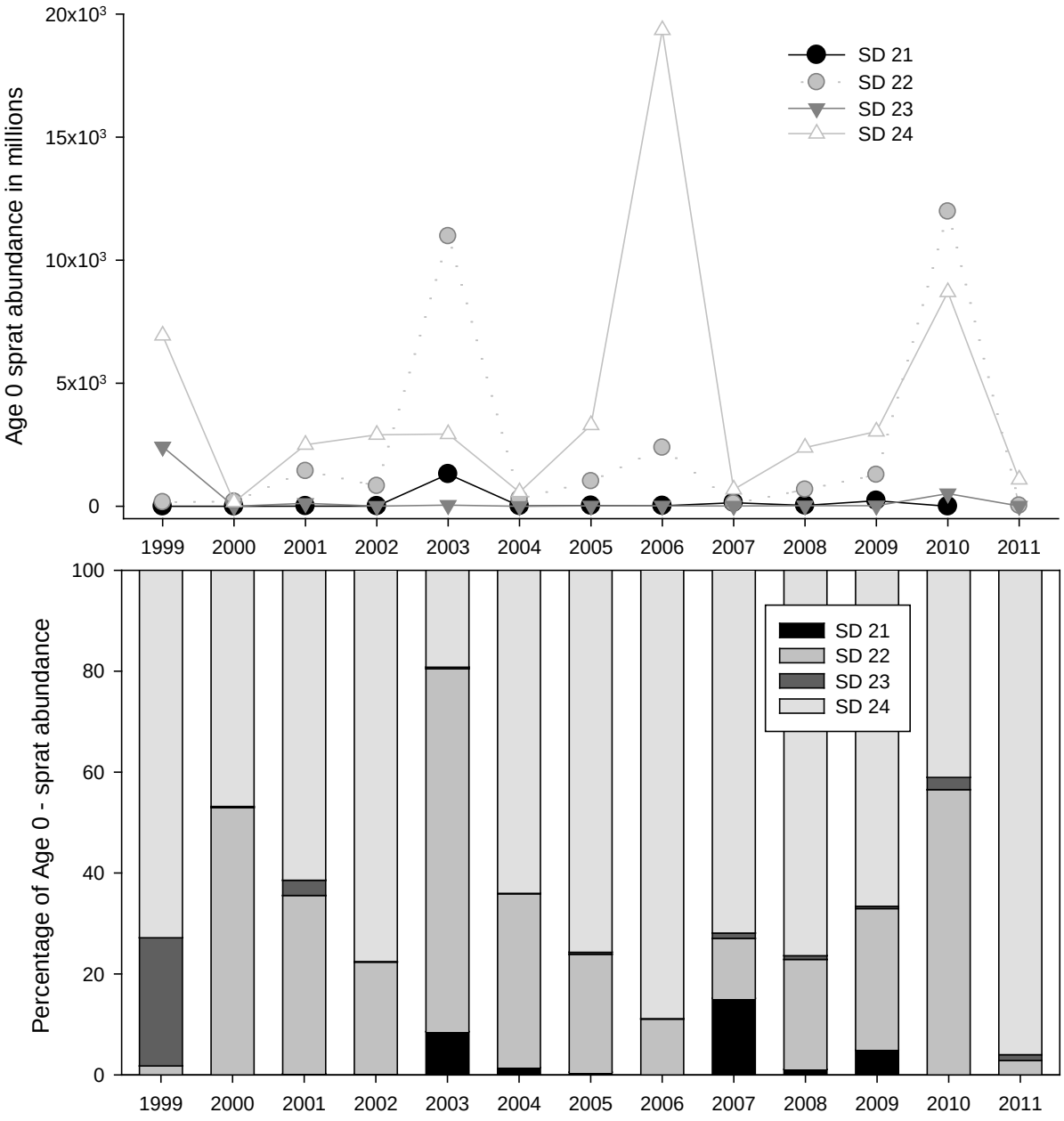

Fig.6-8. Estimates of the abundance of 0-group sprat from the International hydro-acoustic survey (BIAS). Upper panel: Abundances in ICES subdivisions 21 - 24; lower panel: Percentage of 0-group sprat in ICES subdivisions 21 – 24.

There are two major reasons for the contradicting results of previous studies with our study concerning spring temperatures: (1) differences in the way, how water temperatures were integrated into the analysis and (2) differences in study areas. Concerning reason (1) year-class strength in this study was correlated with the ratio of minimum and maximum water temperatures of each season, while earlier authors used absolute values of mean late spring water temperatures (Köster et al. 2003, MacKenzie and Koster 2004, Baumann et al. 2006c). Regarding reason (2), we performed this study in the shallow Western Baltic Sea with focus on SD22 that rarely has a water depth of more than 20 m and is characterised by a well mixed water column in winter and early spring. In contrast, other studies

(MacKenzie and Koster 2004, Baumann et al. 2006c, Ojaveer and Kalejs 2010) concentrate their analysis of the major spawning ground in the deep basins of the Baltic Sea. Here, the water column is characterised by permanent stratification and different layers. Adult sprat overwinter and mature in the deeper water layer (Stepputtis 2006). In contrast, eggs and larvae may float or migrate to upper water layers (Nissling et al. 2003, Voss et al. 2003). Thus, processes affecting recruitment in the main spawning ground may be more complex than in the shallow Western Baltic Sea as life-stages are vertically separated.

However, conclusions that a cold spring temperature has a positive effect on recruitment can indirectly be drawn from observations in the Bornholm Basin made during the Globec Germany programm (Voss et al. 2012a). Here, a considerably mis-match between reproductive effort and the onset of favourable conditions for survivors was observed (Baumann et al. 2008). Summer born individuals constituted the major part of the year-classes in 2002 and 2003, although peak-spawning occurred in spring (Voss et al. 2006, 2012a). The early peak spawning of sprat which releases the offspring in unfavourable conditions was explained by high water temperatures in winter below the permanent halocline, where adult maturing sprat stay. While warm water temperatures of the bottom water stimulate spawning in adult sprats, conditions for larvae (Voss et al. 2007) were unsuitable for early born offspring. Thus, a similar mechanism which we concluded in the Western Baltic Sea has been previously proposed for the Bornholm Basin.

We observed that cold spring temperatures in combination with warm summer temperatures in the Western Baltic Sea support sprat recruitment. Hence, recruitment in sprat would not benefit from warm winters contrary to previous findings that a potential future warming of the Baltic Sea (IPCC 2007) would unilaterally support the population growth of Baltic sprat (Haslob et al. 2012, Voss et al. 2012b).

6.6 Literature

Anderson, J.T. 1988. A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. J. Northwest. Atl. Fish. Sci. **8**: 55-66.

Arrhenius, F., and Hansson, S. 1996. Growth and seasonal changes in energy content of young Baltic Sea herring (Clupea harengus L). ICES J. Mar. Sci. **53**(5): 792-801.

Bagge, O., Thurow, F., Steffensen, E., and Bray, J. 1994. The Baltic cod. Dana **10**: 1-28.

Baumann, H., Gröhsler, T., Kornilovs, G., Makarchouk, A., Feldmann, V., and Temming, A. 2006a. Temperature-induced regional and temporal growth differences in Baltic young-of-the-year sprat *Sprattus sprattus*. Mar. Ecol. Prog. Ser. **317**: 225-236. doi: 10.3354/meps317225.

Baumann, H., Hinrichsen, H.-H., Voss, R., Stepputtis, D., Grygiel, W., Clausen, L.W., and Temming, A. 2006b. Linking growth to environmental histories in central Baltic young-of-the-year sprat, *Sprattus sprattus*: an approach based on otolith microstructure analysis and hydrodynamic modelling. Fish. Oceanogr. **15**(6): 465-476. doi: 10.1111/j.1365-2419.2005.00395.x.

Baumann, H., Hinrichsen, H.H., Möllmann, C., Köster, F.W., Malzahn, A.M., and Temming, A. 2006c. Recruitment variability in Baltic Sea sprat (*Sprattus sprattus*) is tightly coupled to temperature and transport patterns affecting the larval and early juvenile stages. Can. J. Fish. Aquat. Sci. **63**(10): 2191-2201. doi:10.1139/f06-112.

Baumann, H., Peck, M.A., Götze, H.E., and Temming, A. 2007. Starving early juvenile sprat *Sprattus sprattus* (L.) in western Baltic coastal waters: evidence from combined field and laboratory observations in August and September 2003. J. Fish. Biol. **70**(3): 853-866. doi: 10.1111/j.1095-8649.2007.01346.x.

Baumann, H., Peck, M.A., and Herrmann, J.P. 2005. Short-term decoupling of otolith and somatic growth induced by food level changes in postlarval Baltic sprat, Sprattus sprattus. Marine and Freshwater Research **56**(5): 539-547.

Baumann, H., Voss, R., Hinrichsen, H.-H., Mohrholz, V., Schmidt, J.O., and Temming, A. 2008. Investigating the selective survival of summer- over spring-born sprat, *Sprattus sprattus*, in the Baltic Sea. Fish. Res. **91**(1): 1-14. doi: 10.1016/j.fishres.2007.11.004.

Campana, S.E. 1990. How reliable are growth back-calculations based on otoliths? Can. J. Fish. Aquat. Sci. **47**(11): 2219-2227. doi:10.1139/f90-246.

Grimm, S.K., and Herra, T. 1984. Spawning cycles of southern Baltic fishes based on survey of eggs and larvae. ICES CM **J:30**.

Haslob, H., Hauss, H., Petereit, C., Clemmesen, C., Kraus, G., and Peck, M.A. 2012. Temperature effects on vital rates of different life stages and implications for population growth of Baltic sprat. Mar. Biol. **159**(11): 2621-2632.

Hinrichsen, H.H., Kraus, G., Voss, R., Stepputtis, D., and Baumann, H. 2005. The general distribution pattern and mixing probability of Baltic sprat juvenile populations. Journal of Marine Systems **58**(1-2): 52-66.

ICES. 2000. Report of the Baltic International Fish Survey Working Group. **ICES CM 2000/H:2**(Ref.D).

ICES. 2001. Report of the Baltic International Fish Survey Working Group. **ICES CM 2001/H:02**(Ref.D).

ICES. 2002. Report of the Baltic International Fish Survey Working Group **ICES CM 2002/G:05**(Ref. H).

ICES. 2003. Report of the Baltic International Fish Survey Working Group. **ICES CM 2003/G:05** (Ref.D, H).

ICES. 2004. Report of the Baltic International Fish Survey Working Group (WGBIFS). **ICES CM 2004/G:08**(Ref. D, H).

ICES. 2005. Report of the Baltic International Fish Survey Working Group (WGBIFS). **ICES CM 2005/G:08** (Ref. D, H).

ICES. 2006. Report of the Baltic International Fish Survey Working Group (WGBIFS). **ICES CM 2006/LRC:07**(Ref. ACFM, BCC, RMC).

ICES. 2007. Report of the Baltic International Fish Survey Working Group (WGBIFS). **ICES CM 2007/LRC:06**(REF. ACFM).

ICES. 2008. Report of the Baltic International Fish Survey Working Group (WGBIFS). **ICES CM 2008/LRC:08** (Ref. ACOM).

ICES. 2009. Report of the Baltic International Fish Survey Working Group (WGBIFS). **ICES CM 2009/LRC:05** (REF. TGISUR, ACOM).

ICES. 2010. Report of the Baltic International Fish Survey Working Group (WGBIFS) **ICES CM 2010/SSGESST:07**(Ref. SCICOM, WGISUR, ACOM).

ICES. 2011. Report of the Baltic International Fish Survey Working Group (WGBIFS). **ICES CM 2011/SSGESST:05**(Ref. SCICOM, WGISUR, ACOM).

ICES. 2012a. Report of the Baltic Fisheries Assessment Working Group 2012. **ICES CM 2010/ACOM:10**.

ICES. 2012b. Report of the Baltic International Fish Survey Working Group. ICES CM 2012/SSGESST:02.

IPCC. 2007. Climate Change 2007: The Physical Science Basis, IPCC, Geneva.

Jonsson, B., and Ruud-Hansen, J. 1985. Water Temperature as the Primary Influence on Timing of Seaward Migrations of Atlantic Salmon (Salmo salar) Smolts. Can. J. Fish. Aquat. Sci. **42**(3): 593-595. 10.1139/f85-076.

Karasiova. 2002. The variability of peak spawning and larvae appearence timing in the southeastern Baltic Sea during the past six decades. Bulletin of the Sea Fisheries Institute **156**(2): 57-67.

Köster, F.W., Hinrichsen, H.H., Schnack, D., St John, M.A., Mackenzie, B.R., Tomkiewicz, J., Möllmann, C., Kraus, G., Plikshs, M., Makarchouk, A., and Aro, E. 2003. Recruitment of Baltic cod and sprat stocks: identification of critical life stages and incorporation of environmental variability into stock-recruitment relationships. Sci. Mar. **67**: 129-154.

Litvak, M.K., and Leggett, W.C. 1992. Age and Size-Selective Predation on Larval Fishes - the Bigger-Is-Better Hypothesis Revisited. Mar. Ecol. Prog. Ser. **81**(1): 13-24.

MacKenzie, B.R., and Koster, F.W. 2004. Fish production and climate: Sprat in the Baltic Sea. Ecology **85**(3): 784-794.

Meekan, M.G., and Fortier, L. 1996. Selection for fast growth during the larval life of Atlantic cod Gadus morhua on the Scotian Shelf. Mar. Ecol. Prog. Ser. **137**(1-3): 25-37.

Meskendahl, L., Herrmann, J.P., and Temming, A. 2010. Effects of temperature and body mass on metabolic rates of sprat, Sprattus sprattus L. Mar. Biol. **157**(9): 1917-1927.

Nakamura, M., Takii, K., Takaoka, O., Furuta, S., and Kumai, H. 1991. Rearing of japanese sardine from hatching through juveniles. Nippon Suisan Gakkaishi **57**(2): 345-345.

Nissling, A. 2004. Effects of temperature on egg and larval survival of cod (Gadus morhua) and sprat (Sprattus sprattus) in the Baltic Sea - implications for stock development. Hydrobiologia **514**(1-3): 115-123.

Nissling, A., Muller, A., and Hinrichsen, H.H. 2003. Specific gravity and vertical distribution of sprat eggs in the Baltic Sea. J. Fish. Biol. **63**(2): 280-299.

Ojaveer, E., and Kalejs, M. 2010. Ecology and long-term forecasting of sprat (Sprattus sprattus balticus) stock in the Baltic Sea: a review. Reviews in Fish Biology and Fisheries **20**(2): 203-217.

Olla, B.L., Studholme, A.L., Bejda, A.J., and Samet, C. 1980. Role of Temperature in Triggering Migratory Behavior of the Adult Tautog Tautoga-Onitis under Laboratory Conditions. Mar. Biol. **59**(1): 23-30.

Petereit, C., Haslob, H., Kraus, G., and Clemmesen, C. 2008. The influence of temperature on the development of Baltic Sea sprat (*Sprattus sprattus*) eggs and yolk sac larvae. Mar. Biol. **154**(2): 295-306. doi: 10.1007/s00227-008-0923-1.

Reglero, P., Mosegaard, H., and Hinrichsen, H.H. 2007. Date of otolith first increment formation in Baltic sprat Sprattus sprattus and its relation to onset of maturity. Mar. Ecol. Prog. Ser. **330**: 223-233.

Robert, D., Castonguay, M., and Fortier, L. 2007. Early growth and recruitment in Atlantic mackerel Scomber scombrus: discriminating the effects of fast growth and selection for fast growth. Mar. Ecol. Prog. Ser. **337**: 209-219.

Shields, R.J. 1989. Studies of Growth and Nutritional Status in 0-Group sprat, Sprattus sprattus (Clupeidae), using Otolith Microstructure and Lipid Analytical Techniques. PhD thesis, School of Ocean Science, University of Wales, Bangor.

Shoji, J., and Tanaka, M. 2006. Growth-selective survival in piscivorous larvae of Japanese Spanish mackerel Scomberomorus niphonius: early selection and significance of ichthyoplankton prey supply. Mar. Ecol. Prog. Ser. **321**: 245-254.

Stepputtis, D. 2006. Distribution patterns of Baltic sprat (*Sprattus sprattus* L.) - causes and consequences, Mathematisch-Naturwissenschaftliche Fakultät Christian-Albrecht-Universität Kiel.

Voss, R., Clemmesen, C., Baumann, H., and Hinrichsen, H.H. 2006. Baltic sprat larvae: coupling food availability, larval condition and survival. Mar. Ecol. Prog. Ser. **308**: 243-254. doi: 10.3354/meps308243.

Voss, R., Koster, F.W., and Dickmann, M. 2003. Comparing the feeding habits of co-occurring sprat (Sprattus sprattus) and cod (Gadus morhua) larvae in the Bornholm Basin, Baltic Sea. Fish. Res. **63**(1): 97-111.

Voss, R., Peck, M.A., Hinrichsen, H.-H., Clemmesen, C., Baumann, H., Stepputtis, D., Bernreuther, M., Schmidt, J.O., Temming, A., and Köster, F.W. 2012a. Recruitment processes in Baltic sprat – A re-evaluation of GLOBEC Germany hypotheses. Progress in Oceanography.

Voss, R., Petereit, C., Schmidt, J.O., Lehmann, A., Makarchouk, A., and Hinrichsen, H.H. 2012b. The spatial dimension of climate-driven temperature change in the Baltic Sea and its implication for cod and sprat early life stage survival. Journal of Marine Systems **100**: 1-8.

Voss, R., Schmidt, J.O., and Schnack, D. 2007. Vertical distribution of Baltic sprat larvae: changes in patterns of diel migration? ICES J. Mar. Sci. **64**(5): 956-962.

7

General Discussion

The present thesis investigated the growth of young Baltic sprat in the post-larval and juvenile stages. Fundamentals of length reconstruction from otolith microstructure analysis were re-examined by developing a new length back-calculation model for sprat (**Manuscript 1**). This back-calculation model was designed to enable length reconstructions beyond ontogenetic transitions like metamorphosis and results in more realistic growth patterns compared to a previously used model in Baltic sprat. In a laboratory experiment the role of temperature on length and otolith growth was investigated under *ad libitum* feeding conditions to disentangle the influence of temperature and ontogeny on otolith and somatic growth in early juveniles (**Manuscript 2**). On the one hand, the laboratory study detected uncoupling between otolith and somatic growth due to temperature and on the other hand the laboratory calibration of otoliths growth was used for the reconstruction of previous prey availability in field caught early juvenile sprat. Investigating two year-classes of young sprat from successive years with contrasting temperature profiles (**Manuscript 3**), the relationship between the temporal origin, growth rates, temperature and year-class strength in the Western Baltic Sea was discussed and analysed by temperature-recruitment relationships.

7.1 A non-linear individual length back-calculation method

Length back-calculation from otoliths of juvenile fish is a commonly used method to investigate characteristics of survivors (Sogard 1997, Takasuka et al. 2003) and to detect size-selective mortality (Campana and Jones 1992, Shoji and Tanaka 2006). In earlier studies, length of Baltic sprat juveniles was back-calculated from otoliths (Baumann et al. 2006a, 2008, 2009) using the biological intercept method (Campana 1990), which assumes a linear (isometric) relationship between otolith length and fish length. However in sprat, allometric changes in the length-mass relationship during the ontogeny were observed by Peck et al. (2005), obviously arising from morphometric changes during metamorphosis from the larval to the juvenile stage. In sprat metamorphosis is characterized by the transition from the elongated, slender larvae to the spindle shaped juvenile fish (Iles and Johnson 1962, Alshuth 1988). During this developmental event, dominant length growth of the larval stage is replaced with an increased growth in body height as well as reduced growth in length. After

metamorphosis during the juvenile stage growth becomes mostly isometric. In **Manuscript 1** it was found that also the relationship between fish length and otolith lengths becomes strongly non-linear due to these transformations.

Such changes in fish length-otolith length relations during ontogeny were previously observed and non-linear back-calculation approaches considering morphometric changes have been presented (e.g. Butler 1989, Laidig et al. 1991, Hobbs et al. 2007). However, these approaches back-calculate length beyond ontogenetic transitions using for all individual fish one and the same population-based value of fish and otolith length for metamorphosis. The aim of our approach was to implement the individual variation at this transition point between the larval and the juvenile stage. Here, individual metamorphosis was defined as the time in life when maximal increment widths were deposited on the otolith (**Manuscript 1**). During this "point of metamorphosis", length growth is reduced according to the change in the otolith growth-length growth relationship. In the algorithm of the Metamorphosis Inflection Point (MIP) back-calculation model this "point of metamorphosis" was used to separate the larval stage (life-time before metamorphosis) with its allometric otolith length-fish length relationship from the juvenile life-stage (life-time after metamorphosis), characterised by an almost isometric otolith length-fish length relationship. Through this step, the model can be used to reproduce different growth histories by life-stage.

Apart from sprat, similar changing relationships between otolith length and fish length were found in other clupeiformes (Takahashi et al. 2008, Aldanondo et al. 2011) and also in reef fishes at settlement (Wilson and McCormick 1997) and in flatfish (Joh et al. 2011). Settlement of reef fishes and metamorphosis of sprat or flatfish are also discussed as critical events that can influence survival and subsequent recruitment (Fukuhara 1988, Köster et al. 2003, Doherty et al. 2004). Thus, the newly developed MIP alogrithm for the reconstruction of individual growth from otoliths of surviving juvenile fish is a useful tool to examine successful traits related to survival and recruitment.

7.2 Length growth in sprat revealed by the new back-calculation method

The MIP method (**Manuscript 1**) locates individual metamorphosis at the time of maximal increment widths on the otolith. At this "point of metamorphosis" (**Manuscript 1**) back-calculated length growth was reduced as a result of the change in the otolith length-fish length relationship. As a consequence, two length growth peaks were generated in the back calculation, one in the larval and one in the juvenile stage of Baltic sprat both being separated by a minimum of length growth during metamorphosis. Maximum length growth rates during ontogeny have been found after metamorphosis in the early juvenile stage, however also the larval length growth rates were higher when compared to those derived from the biological intercept method (e.g. Baumann et al. 2006a). This result was supported by findings of Peck et al. (Peck et al. 2012) who found that back-calculated length from otoliths of juvenile survivors using the biological intercept method underestimated lengths of most field sampled sprat larvae. The under-estimation arising from the linearity assumption of the biological

intercept model for the larval growth may lead to misinterpretations of ecological processes. For instance, the underestimation of length growth results in a corresponding overestimation of larval stage duration. As fish are particularly vulnerable to predation during the larval stage (Houde 1987, Anderson 1988) and as predation is the dominant cause of natural mortality (Gislason et al. 2010), mortality estimates will directly be affected by erroneous length-back-calculations. Also simulated dispersal and drift patterns during the planktonic phase would be biased by incorrectly estimated larval stage durations.

During metamorphosis reduced length growth at the end of the larval stage was found (**Manuscript 1**) instead of the maximum length growth rates revealed by the linear model (e.g. Baumann et al. 2006a). Back-calculated length growth rates using the MIP method during metamorphosis were only half as high as those calculated from the linear biological intercept model (Campana 1990). A decrease in length growth rate at the end of the larval stage corresponding to metamorphosis has previously been observed in other clupeiformes such as Japanese sardine (*Sardinops melanostictus*, Watanabe & Saito 1998), European anchovy (*Engraulis encrasicolus*, Aldanondo et al 2011) and Baltic Sea herring (*Clupea harengus membras*, Arrhenius & Hansson 1996). This implies that the MIP method should also be applied in these species to investigate the potential differences from previous results based on the Biological Intercept method.

Using the non-linear MIP back-calculation method, strongest growth in length was found during the early juvenile stage, when length growth rates from the linear Biological Intercept method decrease (**Manuscript 1**). During that period back-calculated length growth rates can exceed 1.0 mm•d^{-1} (**Manuscript 1**). Such maxima in length growth were reported for other clupeiformes fish during the early juvenile stage. For example, Nakamura et al. (1991) reared Japanese sardine from eggs to juveniles under *ad libitum* feeding conditions in the laboratory and measured the steepest length increase after metamorphosis with a growth rate of 1.7 mm•d^{-1}. Analysing growth trajectories of Young-of-the-Year juvenile European anchovy (*Engraulis encrasicolus*) from the Bay of Biscay, Aldanondo et al (2011) recorded up to 1.8 mm•d^{-1} length growth rates exceeding those from the larval stage. Arrhenius and Hansson (1996) and Johnston et al (1998) reported higher length growth rates in herring (*Clupea harengus*) in the juvenile stage compared to the larval stage with a peak-growth rate of 0.6 mm•d^{-1} found for juvenile Northern Baltic herring (Arrhenius & Hansson 1996). Thus, the occurrence of highest growth rates during the post-metamorphic stage, even if highly variable and species-dependent, seem to be common in clupeiformes fishes.

Two approaches can be used to test if the relatively high back-calculated growth rates of juvenile sprat (1.0 mm•d^{-1} in comparison to 0.6 mm•d^{-1} in herring) are realistic: laboratory experiments or cohort tracking in the field. Both approaches have been applied. In **Manuscript 2** the maximum growth rates under *ad libitum* feeding conditions were 0.8 mm•d^{-1}, which is already higher that the values reported for herring. However, laboratory growth does often not reflect *in situ* growth under optimal conditions (Mackenzie et al. 1990). By sampling three times the same weekly cohorts within one month

(**Manuscript 3**), it was possible to monitor *in situ* field growth during the early juvenile life-stage of Western Baltic sprat. Growth rates exceeding 1.0 mm•d^{-1} were found, which have been the highest growth rates reported for young sprat. As back-calculated length growth rates were similar to *in situ* ones, it was concluded that the MIP method is capable of reproducing natural length growth patterns in the early juvenile stage of Baltic sprat.

7.3 Uncoupling in the juvenile stage

In **Manuscript 1** a back-calculation method taking into account the non-linearity between length and somatic growth during the ontogeny of Baltic sprat was developed. In applying this non-linear relationship for length back-calculation it is however assumed, that increment width and length growth are strongly correlated, however the strength of this correlation changes through metamorphosis. This change in the relationship between increment widths and length growth during metamorphosis is not to be confused with the term "uncoupling" from otolith literature (Templeman and Squires 1956). Under uncoupling conditions the relationship between otolith growth and length growth is disrupted and thus, the central assumption for growth back-calculations is violated (Campana and Neilson 1985).

In the experimental part of this thesis (**Manuscript 2**), the relationship between length, dry and wet mass and otolith growth was investigated across a temperature range occurring naturally in juvenile nursery areas (16 to 22°C) and uncoupling was detected. Despite a lack of any temperature dependent difference in length growth, a considerable difference in otolith growth was found. Uncoupling between otolith and length growth rates has previously been reported and it is a common phenomenon in fish (Templeman and Squires 1956, Secor and Dean 1989, Takasuka et al. 2008). Temperature-induced uncoupling (otolith growth increases further at higher temperatures, while somatic growth decreases) above the temperature optimum for somatic growth has been reported by Mosegaard et al. (1988) for the first time. However, uncoupling found in **Manuscript 2** had a different reason because it was detected below the temperature optimum for somatic growth at 22°C (Baumann et al. 2008). Differential otolith growth in response to different temperature treatments was reflected only in different water contents of the fish bodies (**Manuscript 2**). In this case the increase in relative dry mass with temperature indicates an increase in energy density of the fish body (Pedersen and Hislop 2001), hence increased storage of lipids.

The deposition of lipids in young fishes after metamorphosis is common in clupeids (Blaxter and Hunter 1982). Shields (1989) found that juvenile North Sea sprat larger than 40 mm standard length deposited neutral lipids as energy reserves. In sprat, energy reserves are built up for the following winter period (Peck et al. 2012). In the experiment (**Manuscript 2**) more lipids have been stored at higher temperatures under *ad libitum* feeding conditions, indicating that at higher temperatures the food intake was actually further increased. This finding can be interpreted in two ways, either a physiological shift in energy allocation was triggered to prepare the sufficiently large fish for the

overwintering period, or a lack of an essential diet component limited further protein synthesis. The specific combination of temperature and feeding conditions during the early juvenile stage can therefore influence the amount of energy reserves stored by young sprat and subsequently effect the survival during the first winter (Hurst 2007).

The coincidence of otolith growth and lipid increase with temperature is an indication that the otolith growth actually reflects not only somatic growth (protein synthesis and cell number growth) but also the metabolic rate (Mosegaard et al. 1988, Wright 1991, Wright et al. 2001). However, in the larval and metamorphic stage and at the beginning of the early juvenile stage, when the bulk of energy is invested only in the increase of new body tissue, otolith and somatic growth are strictly proportional. When juveniles start to store lipids, uncoupling between somatic and otolith growth can occur. It can be speculated that the storage of energy may influence the results of length back-calculation by inducing uncoupling between somatic and otolith growth. However the experiment resulted in only minor deviations between observed and back-calculated lengths (**Manuscript 2**). This result may be different, if back-calculations were made for ages well above the metamorphosis. In conclusion back-calculated length in the juvenile life-stage could be biased, even if the MIP back-calculation model (**Manuscript 1**) is applied.

7.4 Deducing food availability from otolith growth

Food availability for planktivorous fishes is difficult to measure due to the patchy distribution of zooplankton in nature (Folt and Burns 1999). This is especially a problem in shallow habitats such as nurseries of juvenile Baltic sprat where standard gear cannot be operated (Barnett et al. 1984, Rey et al. 1987). In theory, natural tags logging somatic growth like otoliths contain information on individual ingestion rates and thus, indirectly information on food availability. Somatic growth is primarily influenced by size, temperature and food ingestion (Houde 1989, Heath 1992). Hence, by calibrating the effect of temperature on growth under *ad libitum* feeding at a fixed size, feeding conditions during the early juvenile stage from otoliths of wild-caught sprat can be inferred (**Manuscript 2**).

Otolith increment widths have previously been used to estimate the feeding conditions of early life-stages of fish in the field (Suthers and Sundby 1996, Meekan et al. 2003, Kurita et al. 2004). The assumption that the accretion rate on the otolith is proportional to the ingestion rate has specifically been validated for sprat (**Manuscript 2**) even under uncoupling conditions. In the laboratory experiment the increment width correlated closest with the energy gain of sprat, hence with food intake.

When reconstructing food availability from otoliths, however, two factors have to be considered: (i) temporal uncoupling between somatic growth and the response of otolith growth under changing feeding conditions (e.g. Molony and Choat 1990) and (ii) the assumption that growth under *ad libitum* feeding during the laboratory calibration represents the upper limit of food intake also under natural

conditions. Various studies have investigated the time-lag in different species reporting from an almost immediate response of otolith growth to changes in somatic growth (Tonkin et al. 2008, Aguilera et al. 2009) to a three weeks delay (Neilson and Geen 1985). Baumann et al. (2005) observed a temporal uncoupling of somatic and ototlith growth of nine days for the same life-stage of sprat as investigated in **Manuscript 2**. However, these individuals were fed sub-optimal food producing about 30% narrower increments compared to sprat otoliths examined for this thesis. Sprat with narrow increments such as those in the experiment of Baumann et al. (2005) did not appear in survivors caught in autumn, even in a year with low growth rates and sub-optimal feeding conditions such as in 2007 (**Manuscript 1**, **2** and **3**). Thus, results of a nine day delay may not be representative for field situations as analysed in **Manuscript 2**. The nine day period furthermore refers the period needed to establish a new equilibrium between otolith growth and fish growth. Therefore it may overestimate the time lag between the shift in the environment and the reaction on the otolith, if this is rather defined as the point where 50% of the response has developed. In conclusion a major bias in the interpretation of the ambient feeding situation due to this effect is not expected, also because the transitions in temperature and prey production are relatively smooth in the field situation.

However, *in situ* length growth rates of juveniles from the Western Baltic Sea (**Manuscript 3**) were up to 20% higher in specific years (2006), than those used to calibrate otolith growth in **Manuscript 2**. This discrepancy can be explained in three ways: 1) feeding conditions did not reach the true optimum, 2) growth was lower in laboratory due to a potential extra cost term such as stress related activity or 3) growth measurements in the field were biased. Without additional experiments or samplings no decision is possible about the most likely explanation. However, the laboratory based growth rates were comparable to maximum growth rates in two other years 2002 and 2003, both characterized by good growth conditions and high recruitment success and significantly higher than the maximum growth rates of 2007, a year with poor recruitment. Furthermore, even if the calibration experiment did not produce the absolute maximum growth rates, the results can still be used to characterize different seasons and years with regard to their relative food supply.

Reconstructing the feeding history of marine fish by means of analyzing otolith increment widths is promising to investigate prey availability in habitats where unbiased sampling of plankton by standard gear is difficult. Thus, it is suggested to further investigate both, temporal uncoupling and the calibration of optimal otolith growth to deduce previous food availability from increment widths of field-caught sprat. Specifically, calibration exercises under more natural conditions are required to re-evaluate the response of the otolith growth to somatic growth under changing feeding conditions and to generate the optimal growth rates in the natural ambient temperature range. As it is uncertain if optimal length growth rates can be generated in the laboratory, experiments should be performed on-site in shallow regions of the Western Baltic Sea. For instance, young sprat can be held in net cages in the nursery area. Optimal food availability can be generated by a pump replacing seawater in the net

cage and by extra feeding of ambient zooplankton. Logging temperature, otolith growth under natural conditions can be calibrated and additionally validated by daily stomach samples.

7.5 Growth and feeding in the early juvenile stage of Baltic sprat

Voss et al. (2012a) summarized that year-class strength in Baltic sprat is determined in more than one life-stage including the late-larval and early juvenile stage. Concerning the late-larval stage, Baumann et al. (2006b) suggested that high summer temperatures favour the growth of larval sprat and thus recruitment. This finding was confirmed for larval sprat of the Western Baltic Sea (**Manuscript 3**) where the abundance of 0-group sprat estimated by the yearly acoustic survey in autumn (BIAS) was positively correlated to warm summer temperatures. In contrast, growth of the subsequent early juvenile stage did not steadily increase with higher water temperatures, as deduced from a combined analysis of a laboratory experiment and field data (**Manuscript 2**).

This differential response of larval and early juvenile sprat to high temperature has strong implications for the optimal seasonal window of growth and survival. Larvae should be spawned such, that their growth occurs at peak seasonal temperatures, while early juveniles should have their growth phase later in the season with decreasing temperatures. The impact of temperature on growth during the early juvenile stage is influenced by ontogenetic and seasonal effects. Concerning the former, the optimal temperature for growth in fish generally decreasing with increasing body size (Morita et al. 2010). The early juvenile stage might thus have a lower temperature optimum than the larval stage. Hence, during peak temperature of the year larval growth might be favoured, while juvenile growth is lower than maximal as the optimum temperature is already exceeded. Additionally, a juvenile sprat of 50 mm length requires already ten times more food compared to a 30 mm post-metamorphic sprat feeding *ad libitum* (**Manuscript 2**). This increase in food demand in the juvenile stage supports previous findings that total population food consumptions by young sprat is highest in August and September (Arrhenius and Hansson 1993, Arrhenius 1998), when most sprat become juveniles.

This elevated food demand due to an increase in body-size is modulated by the effect of temperature on metabolism and the resulting additional energy demand. In situations where large size and high temperatures coincide, the total food requirements for optimal growth might not be met by a sufficient food production in the field. This situation will most likely be encountered by early spawned sprat with metamorphosis occurring before peak season temperatures. Thus, food availability in the field for these early born individuals might be too low to support maximal growth. In contrast, later born cohorts experience the larval stage during the temperature peak and grow optimally. Additionally, later born cohorts experience the post-metamorphic life-stage when temperatures already decrease after the temperature peak of the year. Thus, they have a lower metabolism related food demand due to lower ambient temperatures (**Manuscript 2**) and a higher probability to maintain maximum growth.

Sprat that experience high temperatures during the juvenile stage and hence grow sub-optimally are born early in the season. This result confirms observations of Baumann et al. (2008) that individuals

born later in the season have a survival advantage over early born sprat. However, Baumann et al. (2008) interpret this mainly as a result of the larval period, while the results of **Manuscript 2** offer an additional mechanism why early born sprat may have a disadvantage in survival, which is related with the early juvenile stage.

7.6 Recruitment success and temperature

The results of the previous section about the differential survival of early and late born sprat leads to the question if specific meteorological and hydrographic conditions can be identified, which influence the seasonal location of the main spawning time and hence also the survival rates and subsequent recruitment. Generally warm years and warm summers are expected to benefit sprat recruitment (e.g. MacKenzie and Koster 2004), the mechanism being optimal growth of the larvae under such conditions. Furthermore years with a cold spring will delay spawning and/or egg development and hence shift the main growth phase of larvae later into the summer season, where these larvae can benefit from high temperatures.

Spawning in the Eastern Baltic Sea was found to be delayed due to cold minimum water temperatures (Grimm and Herra 1984, Karasiova 2002) and as consequence of this delay, most of the reproductive effort is invested later in the season. Successful recruits in years with high recruitment originate from these late periods (Baumann et al. 2008). In years with a cold spring, the overall egg-survival until the larval stage is generally higher, as a smaller share of the total offspring suffers from unsuitable spring conditions (**Manuscript 3**). Thus a combination of a cold spring and a warm summer maximise the possibility for young sprat to grow fast both as larvae and as juveniles and survive until autumn, generating a strong year-class (**Manuscript 3**).

Previously, sprat has been described as a boreal-mediterranean warm-water fish species (Ojaveer and Kalejs 2010), with limits of its northern distribution in the Baltic Sea (Muus and Nielson 1999). Thus, it appears puzzling that a cold winter benefits the development of the next year-class in Baltic sprat. Previous studies investigated the relationship between temperature and recruitment strength in sprat, concentrating either on the whole Baltic Sea (MacKenzie and Koster 2004) or on main spawning areas in the deep basins of the Central (e.g. Köster et al. 2003, Baumann et al. 2006b), Eastern (Karasiova and Zezera 2000) and Northern part (Ojaveer and Kalejs 2010). Here, these authors observed or supposed a positive relationship between temperature in winter and spring and year-class strength of the subsequent cohort. It was stated that a warm winter enhances the development of gonads (Grauman and Yula 1989, Parmanne et al. 1994) and/or increases the habitat volume of sprat in the eastern and northern areas of the Baltic Sea (Ojaveer and Kalejs 2010).

On the one hand, the different results of this thesis (**Manuscript 3**) and previous studies can be caused by the way, how water temperatures were integrated into the analysis. In this study year-class strength was correlated with the ratio of minimum and maximum water temperatures of each season, while earlier authors used absolute values of mean late spring water temperatures (e.g. Köster et al. 2003,

MacKenzie and Koster 2004, Baumann et al. 2006b). On the other hand, the different results can be related to the different regional conditions with regard to stock structure and hydrography. The western Baltic spawning ground and the deep main spawning grounds in the central, eastern and northern parts of the Baltic Sea differ fundamentally in their bathymetry and hydrography (Ojaveer and Kalejs 2008). In the deep basins, pre-spawning adult sprat occur in deeper waters layers (Stepputtis 2006) which differ from upper water layers in temperature and salinity. However, after hatching larvae migrate to the surface water layers (Voss et al. 2007) and experience different conditions than the spawning adults. Thus, mechanisms regulating spawning, development, growth and survival in the eastern spawning grounds are more complex compared to the shallow Western Baltic Sea.

Nevertheless, the positive recruitment effect of cold winters in combination with warm summers is indirectly confirmed by suggestions of Baumann et al. (2008), who noted that most of the reproductive effort in the Bornholm Basin is wasted in early spawning e.g. in the years 2002 and 2003, because survivors almost exclusively originated from the end of the spawning season. Hence, year-class strength was not positively affected by warm spring temperatures in bottom waters, where adult sprat overwinter and mature earlier in warm winters. As both years investigated in the GLOBEC Germany project (2002 and 2003) resulted in a generally high recruitment even though spawning started early in the season, Baumann et al. (2008) assume that the loss of reproductive energy is compensated by favourable summer conditions and a high survival rate of summer born individuals. Thus, a similar mechanism which was observed in this study in the Western Baltic Sea (**Manuscript 3**) has been previously proposed for the Bornholm Basin. The new result of a positive recruitment effect of a combination of cold winters and warm summers questions some earlier conclusions about the unidirectional positive effects of future warming on sprat recruitment (e.g. MacKenzie and Koster 2004, Haslob et al. 2012, Voss et al. 2012b). The level of future recruitment will most likely depend more on the specific patterns of seasonal temperature differences and higher summer and autumn temperatures may even be detrimental if the seasonal timing of sprat spawning leads to a peak of metamorphosing larvae well before the seasonal temperature maximum.

7.7 References

Aguilera, B., Catalan, I.A., Palomera, I., and Olivar, M.P. 2009. Otolith growth of European sea bass (Dicentrarchus labrax L.) larvae fed with constant or varying food levels. Sci. Mar. **73**(1): 173-182.

Aldanondo, N., Cotano, U., and Etxebeste, E. 2011. Growth of young-of-the-year European anchovy (Engraulis encrasicolus, L.) in the Bay of Biscay. Sci. Mar. **75**(2): 227-235.

Alshuth, S. 1988. Bestimmung von Alter und Wachstumsraten bei Larvaen und juvenilen der Sprotte, *Sprattus sprattus L.* PhD, Biology, University of Bremen, Bremen.

Anderson, J.T. 1988. A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. J. Northwest. Atl. Fish. Sci. **8**: 55-66.

Arrhenius, F. 1998. Food intake and seasonal changes in energy content of young Baltic Sea sprat (*Sprattus sprattus* L.). ICES J. Mar. Sci. **55**(2): 319-324.

Arrhenius, F., and Hansson, S. 1993. Food-Consumption of Larval, Young and Adult Herring and Sprat in the Baltic Sea. Mar. Ecol. Prog. Ser. **96**(2): 125-137.

Arrhenius, F., and Hansson, S. 1996. Growth and seasonal changes in energy content of young Baltic Sea herring (Clupea harengus L). ICES J. Mar. Sci. **53**(5): 792-801.

Barnett, A.M., Jahn, A.E., Sertic, P.D., and Watson, W. 1984. Distribution of Ichthyoplankton Off San-Onofre, California, and Methods for Sampling Very Shallow Coastal Waters. Fishery Bulletin **82**(1): 97-111.

Baumann, H., Hinrichsen, H.-H., Voss, R., Stepputtis, D., Grygiel, W., Clausen, L.W., and Temming, A. 2006a. Linking growth to environmental histories in central Baltic young-of-the-year sprat, *Sprattus sprattus*: an approach based on otolith microstructure analysis and hydrodynamic modelling. Fish. Oceanogr. **15**(6): 465-476. doi: 10.1111/j.1365-2419.2005.00395.x.

Baumann, H., Hinrichsen, H.H., Möllmann, C., Köster, F.W., Malzahn, A.M., and Temming, A. 2006b. Recruitment variability in Baltic Sea sprat (*Sprattus sprattus*) is tightly coupled to temperature and transport patterns affecting the larval and early juvenile stages. Can. J. Fish. Aquat. Sci. **63**(10): 2191-2201. doi:10.1139/f06-112.

Baumann, H., Malzahn, A.M., Voss, R., and Temming, A. 2009. The German Bight (North Sea) is a nursery area for both locally and externally produced sprat juveniles. Journal of Sea Research **61**(4): 234-243.

Baumann, H., Peck, M.A., and Herrmann, J.P. 2005. Short-term decoupling of otolith and somatic growth induced by food level changes in postlarval Baltic sprat, Sprattus sprattus. Marine and Freshwater Research **56**(5): 539-547.

Baumann, H., Voss, R., Hinrichsen, H.-H., Mohrholz, V., Schmidt, J.O., and Temming, A. 2008. Investigating the selective survival of summer- over spring-born sprat, *Sprattus sprattus*, in the Baltic Sea. Fish. Res. **91**(1): 1-14. doi: 10.1016/j.fishres.2007.11.004.

Blaxter, J.H.S., and Hunter, J.R. 1982. The Biology of the Clupeoid Fishes. ICES J. Mar. Sci. **20**: 3-223.

Butler, J.L. 1989. Growth during the larval and juvenile stages of the northern anchovy, *Engraulis mordax*, in the California current during 1980-84. Fish. Bull. **87**: 645-652.

Campana, S.E. 1990. How reliable are growth back-calculations based on otoliths? Can. J. Fish. Aquat. Sci. **47**(11): 2219-2227. doi:10.1139/f90-246.

Campana, S.E., and Jones, C.M. 1992. Analysis of otolith microstructure data. *In* Otolith Microstructure Examination and Analysis. *Edited by* D.K. Stevenson and S.E. Campana. Canadian Special Publications of Fisheries and Aquatic Sciences 117. pp. 73-100.

Campana, S.E., and Neilson, J.D. 1985. Microstructure of Fish Otoliths. Can. J. Fish. Aquat. Sci. **42**(5): 1014-1032.

Doherty, P.J., Dufour, V., Galzin, R., Hixon, M.A., Meekan, M.G., and Planes, S. 2004. High mortality during settlement is a population bottleneck for a tropical surgeonfish. Ecology **85**(9): 2422-2428.

Folt, C.L., and Burns, C.W. 1999. Biological drivers of zooplankton patchiness. Trends in Ecology & Evolution **14**(8): 300-305.

Fukuhara, O. 1988. Morphological and Functional-Development of Larval and Juvenile Limanda-Yokohamae (Pisces, Pleuronectidae) Reared in the Laboratory. Mar. Biol. **99**(2): 271-281.

Gislason, H., Daan, N., Rice, J.C., and Pope, J.G. 2010. Size, growth, temperature and the natural mortality of marine fish. Fish and Fisheries **11**(2): 149-158.

Grauman, G., and Yula, E. 1989. The importance of abiotic and biotic factors in the early ontogenesis of cod and sprat. Rapports et Proces-verbaux des Réunions. Conseil International pour l'Éxploration de la Mer **190**(207-210).

Grimm, S.K., and Herra, T. 1984. Spawning cycles of southern Baltic fishes based on survey of eggs and larvae. ICES CM **J:30**.

Haslob, H., Hauss, H., Petereit, C., Clemmesen, C., Kraus, G., and Peck, M.A. 2012. Temperature effects on vital rates of different life stages and implications for population growth of Baltic sprat. Mar. Biol. **159**(11): 2621-2632.

Heath, M.R. 1992. Field investigations of the early-life stages of marine fish. ICES J. Mar. Sci. **28**: 1-174.

Hobbs, J.A., Bennett, W.A., Burton, J.E., and Baskerville-Bridges, B. 2007. Modification of the biological intercept model to account for ontogenetic effects in laboratory-reared delta smelt (*Hypomesus transpacificus*). Fish. Bull. **105**: 20-38.

Houde, E.D. 1987. Fish early life dynamics and recruitment variability. American Fisheries Society Symposium **2**: 17-29.

Houde, E.D. 1989. Comparative Growth, Mortality, and Energetics of Marine Fish Larvae - Temperature and Implied Latitudinal Effects. Fishery Bulletin **87**(3): 471-495.

Hurst, T.P. 2007. Causes and consequences of winter mortality in fishes. J. Fish. Biol. **71**(2): 315-345.

Iles, T.D., and Johnson, P.O. 1962. The Correlation Table Analysis of a Sprat Year-Class to Separate two Groups Differing in Growth Characteristics. Journal du Conseil pour L'Exploration de la Mer **27**(3): 287-303.

Joh, M., Matsuda, T., Satoh, N., Tanaka, N., and Ueda, Y. 2011. Otolith microstructure of brown sole Pseudopleuronectes herzensteini: validation of daily ring formation and the occurrence of microstructure denoting metamorphosis. Fisheries Science **77**(5): 773-783. DOI 10.1007/s12562-011-0382-3.

Johnston, I.A., Cole, N.J., Abercromby, M., and Vieira, V.L.A. 1998. Embryonic temperature modulates muscle growth characteristics in larval and juvenile herring. Journal of Experimental Biology **201**(5): 623-646.

Karasiova. 2002. The variability of peak spawning and larvae appearence timing in the southeastern Baltic Sea during the past six decades. Bulletin of the Sea Fisheries Institute **156**(2): 57-67.

Karasiova, E.M., and Zezera, A.S. 2000. On influence of long-term variability of temperature regime in the Gdansk deep of the Baltic sea on the sprat reproduction and the offspring survival. ICES CM **L:06**.

Köster, F.W., Hinrichsen, H.H., Schnack, D., St John, M.A., Mackenzie, B.R., Tomkiewicz, J., Möllmann, C., Kraus, G., Plikshs, M., Makarchouk, A., and Aro, E. 2003. Recruitment of Baltic cod and sprat stocks: identification of critical life stages and incorporation of environmental variability into stock-recruitment relationships. Sci. Mar. **67**: 129-154.

Kurita, Y., Nemoto, Y., Oozeki, Y., Hayashizaki, K., and Ida, H. 2004. Variations in patterns of daily changes in otolith increment widths of 0+ Pacific saury, Cololabis saira, off Japan by hatch date in relation to the northward feeding migration during spring and summer. Fish. Oceanogr. **13**: 54-62.

Laidig, T.E., Ralston, S., and Bence, J.R. 1991. Dynamics of Growth in the Early Life History of Shortbelly Rockfish *Sebastes jordani*. Fish. Bull. **89**: 611-621.

MacKenzie, B.R., and Koster, F.W. 2004. Fish production and climate: Sprat in the Baltic Sea. Ecology **85**(3): 784-794.

Mackenzie, B.R., Leggett, W.C., and Peters, R.H. 1990. Estimating Larval Fish Ingestion Rates - Can Laboratory Derived Values Be Reliably Extrapolated to the Wild. Mar. Ecol. Prog. Ser. **67**(3): 209-225.

Meekan, M.G., Carleton, J.H., McKinnon, A.D., Flynn, K., and Furnas, M. 2003. What determines the growth of tropical reef fish larvae in the plankton: Food or temperature? Mar. Ecol. Prog. Ser. **256**: 193-204.

Molony, B.W., and Choat, J.H. 1990. Otolith Increment Widths and Somatic Growth-Rate - the Presence of a Time-Lag. J. Fish. Biol. **37**(4): 541-551.

Morita, K., Fukuwaka, M., Tanimata, N., and Yamamura, O. 2010. Size-dependent thermal preferences in a pelagic fish. Oikos **119**(8): 1265-1272.

Mosegaard, H., Svedang, H., and Taberman, K. 1988. Uncoupling of somatic and otolith growth-rates in arctic char (*Salvelinus alpinus*) as an effect of differences in temperature response. Can. J. Fish. Aquat. Sci. **45**(9): 1514-1524.

Muus, B.J., and Nielson, J. 1999. Die Meeresfische Europas in Nordsee, Ostsee und Atlantik. Franckh-Kosmos Verlags-GmbH & Co., Stuttgart, Germany.

Nakamura, M., Takii, K., Takaoka, O., Furuta, S., and Kumai, H. 1991. Rearing of japanese sardine from hatching through juveniles. Nippon Suisan Gakkaishi **57**(2): 345-345.

Neilson, J.D., and Geen, G.H. 1985. Effects of Feeding Regimes and Diel Temperature Cycles on Otolith Increment Formation in Juvenile Chinook Salmon, Oncorhynchus-Tshawytscha. Fishery Bulletin **83**(1): 91-101.

Ojaveer, E., and Kalejs, M. 2008. On ecosystem-based regions in the Baltic Sea. Journal of Marine Systems **74**(1-2): 672-685.

Ojaveer, E., and Kalejs, M. 2010. Ecology and long-term forecasting of sprat (Sprattus sprattus balticus) stock in the Baltic Sea: a review. Reviews in Fish Biology and Fisheries **20**(2): 203-217.

Parmanne, R., Rechlin, O., and Sjöstrand, B. 1994. Status and future of herring and sprat stocks in the Baltic Sea. Dana **10**: 29-59.

Peck, M.A., Baumann, H., Bernreuther, M., Clemmesen, C., Herrmann, J.P., Haslob, H., Huwer, B., Kanstinger, P., Koster, F.W., Petereit, C., Temming, A., and Voss, R. 2012. Reprint of: The ecophysiology of Sprattus sprattus in the Baltic and North Seas. Progress in Oceanography **107**: 31-46.

Peck, W.A., Clemmesen, C., and Herrmann, J.P. 2005. Ontogenic changes in the allometric scaling of the mass and length relationship in *Sprattus sprattus*. J. Fish. Biol. **66**(3): 882-887.

Pedersen, J., and Hislop, J.R.G. 2001. Seasonal variations in the energy density of fishes in the North Sea. J. Fish. Biol. **59**(2): 380-389. 10.1111/j.1095-8649.2001.tb00137.x.

Rey, J.R., Crossman, R.A., Kain, T.R., Vose, F.E., and Peterson, M.S. 1987. Sampling Zooplankton in Shallow Marsh and Estuarine Habitats - Gear Description and Field-Tests. Estuaries **10**(1): 61-67.

Secor, D.H., and Dean, J.M. 1989. Somatic Growth Effects on the Otolith–Fish Size Relationship in Young Pond-reared Striped Bass, Morone saxatilis. Can. J. Fish. Aquat. Sci. **46**(1): 113-121. 10.1139/f89-015.

Shields, R.J. 1989. Studies of Growth and Nutritional Status in 0-Group sprat, Sprattus sprattus (Clupeidae), using Otolith Microstructure and Lipid Analytical Techniques. PhD thesis, School of Ocean Science, University of Wales, Bangor.

Shoji, J., and Tanaka, M. 2006. Growth-selective survival in piscivorous larvae of Japanese Spanish mackerel Scomberomorus niphonius: early selection and significance of ichthyoplankton prey supply. Mar. Ecol. Prog. Ser. **321**: 245-254.

Sogard, S.M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: A review. Bull. Mar. Sci. **60**(3): 1129-1157.

Stepputtis, D. 2006. Distribution patterns of Baltic sprat (*Sprattus sprattus* L.) - causes and consequences, Mathematisch-Naturwissenschaftliche Fakultät Christian-Albrecht-Universität Kiel.

Suthers, I.M., and Sundby, S. 1996. Role of the midnight sun: comparative growth of pelagic juvenile cod (Gadus morhua) from the Arcto-Norwegian and a Nova Scotian stock. ICES Journal of Marine Science: Journal du Conseil **53**(5): 827-836. 10.1006/jmsc.1996.0104.

Takahashi, M., Nishida, H., Yatsu, A., and Watanabe, Y. 2008. Year-class strength and growth rates after metamorphosis of Japanese sardine (Sardinops melanostictus) in the western North Pacific Ocean during 1996–2003. Can. J. Fish. Aquat. Sci. **65**(7): 1425-1434. doi:10.1139/F08-063.

Takasuka, A., Aoki, I., and Mitani, I. 2003. Evidence of growth-selective predation on larval Japanese anchovy Engraulis japonicus in Sagami Bay. Mar. Ecol. Prog. Ser. **252**: 223-238.

Takasuka, A., Oozeki, Y., Aoki, I., Kimura, R., Kubota, H., Sugisaki, H., and Akamine, T. 2008. Growth effect on the otolith and somatic size relationship in Japanese anchovy and sardine larvae. Fisheries Science **74**(2): 308-313.

Templeman, W., and Squires, H.J. 1956. Relationship of Otolith Lengths and Weights in the Haddock Melanogrammus-Aeglefinus (L) to the Rate of Growth of the Fish. J. Fish. Res. Board. Can. **13**(4): 467-487.

Tonkin, Z., King, A.J., and Ramsey, D.S.L. 2008. Otolith increment width responses of juvenile Australian smelt Retropinna semoni to sudden changes in food levels: the importance of feeding history. J. Fish. Biol. **73**(4): 853-860.

Voss, R., Peck, M.A., Hinrichsen, H.-H., Clemmesen, C., Baumann, H., Stepputtis, D., Bernreuther, M., Schmidt, J.O., Temming, A., and Köster, F.W. 2012a. Recruitment processes in Baltic sprat – A re-evaluation of GLOBEC Germany hypotheses. Progress in Oceanography.

Voss, R., Petereit, C., Schmidt, J.O., Lehmann, A., Makarchouk, A., and Hinrichsen, H.H. 2012b. The spatial dimension of climate-driven temperature change in the Baltic Sea and its implication for cod and sprat early life stage survival. Journal of Marine Systems **100**: 1-8.

Voss, R., Schmidt, J.O., and Schnack, D. 2007. Vertical distribution of Baltic sprat larvae: changes in patterns of diel migration? ICES J. Mar. Sci. **64**(5): 956-962.

Watanabe, Y., and Saito, H. 1998. Feeding and growth of early juvenile Japanese sardines in the Pacific waters off central Japan. J. Fish. Biol. **52**(3): 519-533.

Wilson, D.T., and McCormick, M.I. 1997. Spatial and temporal validation of settlement-marks in the otoliths of tropical reef fishes. Mar. Ecol. Prog. Ser. **153**: 259-271. 10.3354/meps153259.

Wright, P.J. 1991. The Influence of Metabolic-Rate on Otolith Increment Width in Atlantic Salmon Parr, Salmo-Salar L. J. Fish. Biol. **38**(6): 929-933. DOI 10.1111/j.1095-8649.1991.tb03632.x.

Wright, P.J., Fallon-Cousins, P., and Armstrong, J.D. 2001. The relationship between otolith accretion and resting metabolic rate in juvenile Atlantic salmon during a change in temperature. J. Fish. Biol. **59**(3): 657-666.

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

Manuscript 1: **A novel length back-calculation approach accounting for ontogenetic changes in the fish length – otolith size relationship during the early life of sprat (*Sprattus sprattus* L.).**
Claudia C. Günther, Axel Temming, Hannes Baumann, Bastian Huwer, Christian Möllmann, Catriona Clemmesen, Jens-Peter Herrmann

CCG did all analysis and text writing under close cooperation with AT and JPH, who critically reviewed the manuscript. HB, BH and CM provided valuable comments. CC provided data of sprat larvae.
The manuscript is published in the peer reviewed Canadian Journal of Fisheries and Aquatic Science (2012): 69: 1214-1229

Manuscript 2: **Deducing *in situ* feeding conditions of early juvenile sprat (*Sprattus sprattus*) from otoliths**
Claudia C. Günther, Jens-Peter Herrmann, Axel Temming

CCG did all analysis, graphical presentations and text writing under close cooperation with AT, who critically reviewed the manuscript. The experiment was conducted by CCG under supervision of JHP., who was involved in the development of the experimental design.
The manuscript will be submitted to a peer reviewed journal.

Manuscript 2: Temperature effects on growth of spring and summer cohorts and implications for survival in young sprat (*Sprattus sprattus L.*) of the western Baltic Sea
Claudia C. Günther, Jens-Peter Herrmann, Axel Temming

Field-sampling was conducted by CCG under the supervision of JPH. CCG did all analysis, graphical presentations and text writing under close cooperation with AT, who critically reviewed the manuscript. JPH provided valuable comments on the manuscript.
The manuscript will be submitted to a peer reviewed journal.

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Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift „Length back-calculation and growth patterns of juvenile Baltic sprat (*Sprattus sprattus L.*)“ selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Hamburg, August 2013

Claudia Günther