Investigations on the feeding behaviour of juvenile sprat (*Sprattus sprattus* L.) and herring (*Clupea harengus* L.)

Dissertation

zur Erlangung des Doktorgrades an der Fakultät für Mathematik,

Informatik und Naturwissenschaften

Fachbereich Biologie

Institut für Hydrobiologie und Fischereiwissenschaften

der Universität Hamburg

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Hamburg 2018

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Tag der Disputation: 23. Februar 2018

Table of Contents

1 Summary

The general aim of this thesis was to investigate the feeding rate of sprat (*Sprattus sprattus*) and (partly) herring (*Clupea harengus*) in relation to different abiotic and biotic factors and during the daily vertical migration (DVM). These findings improve the understanding on trophodynamic interactions and are relevant for the ongoing development of bioenergetics budget models and the quantification of daily ration (DR).

In the first part of this thesis the particulate-feeding behavior of sprat (~ 6 cm) and herring (~ 8 cm) was analyzed in detail and the type of functional response (*per capita* feeding rate as a function of prey concentration) was determined experimentally (**manuscript 1**). For this purpose, we developed an experimental design to measure the feeding rates under controlled laboratory conditions using techniques that caused only minimal stress for fish. To detect the type of functional response, we determined the feeding rates especially at low prey concentrations (1-160 L^{-1}). Feeding experiments were carried out separately at 16 °C with two different types of prey. Non-evasive *Artemia salina* nauplii were used to determine the physiologically maximum possible feeding rate, comparable to feeding on cladocerans and other non-escaping copepod species such as *Temora longicornis* and *Pseudocalanus acuspes*. In contrast, experiments with the copepod *Acartia tonsa* allowed the determination of feeding on prey with high escape abilities (e.g. *Eurytemora affinis*). Sprat were strictly sticking to the particulate-feeding mode, whereas herring occasionally started to filter–feed from a prey concentration of 50 L^{-1}. At lower prey concentrations both clupeids fed more or less in a horizontal plane. At prey concentrations ≥ 15 L^{-1} they swam in a vertical ziz-zag pattern, with repeated bites while swimming upwards, followed by a 180° turn near the surface and a downwards swimming movement. Sprat and herring showed a **type II functional response** (asymptotically increasing feeding rates with increasing prey densities). Feeding rates were significantly lower when fish preyed on *A. tonsa* than on *Artemia*.

During feeding on *A. tonsa*, both clupeids showed an S-shaped deformation of their body before biting, which was related to the high escape ability of *A. tonsa*.

The sprat stock is subject to strong fluctuations, which is largely determined by the recruitment success of the early life-stages. Thus, in recent years, extensive research efforts have been made to identify the mechanisms that influence the survival of the early life stages. Investigations of the otolith microstructure of sprat recruits revealed that season cohorts born later in the year appear to have improved survival probabilities. Contrary to early born cohorts, later born cohorts experienced higher summer temperatures during larval stages, whereas juveniles grew at lower temperature in late summer and autumn. However, no mechanistic explanation for the importance of timing and thus temperatures on seasonal cohorts has been found so far. Therefore, in the second part of the work we parameterized the functional response of juvenile sprat as a function of temperature and fish size (**manuscript 2**). These findings can be used to develop a bioenergetics budget model to find out whether larger sprat at higher temperatures have a greater risk of starving than smaller sprat.

Feeding experiments at five different temperatures of 5 to 20 °C with 8 cm large sprat were conducted to determine the temperature effect on the functional response. Additional experiments with 3 cm sized sprat were performed at 16 °C to examine the size effect on the functional response of sprat on the basis of three different size classes (3, 6 and 8 cm). Maximum biting rates (*BRmax*) of sprat increased with fish size and temperature in a nonlinear function and reached asymptotically a maximum value of about 2.0 s^{-1}. The parameter *k*, which describes the prey concentration at *BRmax*/2, showed no effect with increasing temperature, but decreased in a power function with increasing body size. A comparison of the stomach contents of experimental fish with the contents calculated from the observed biting rates from video analysis revealed, on the one hand, that the estimated feeding rates in the present work reflect the physiological maximum feeding behavior of sprat and, on the other hand, that sprat cannot perform this behavior continuously, especially at lower prey concentrations. Overall, our results indicated an asymptotic increase in energy intake in contrast to the well-established exponential increase in metabolism with raising temperature. Energy cost by metabolism also increased disproportionately (exponent = 1.073) in contrast to an asymptotic increase in energy intake with

increasing fish size. This causes a hump-shaped energetic efficiency (*per capita* daily energy intake relative to energy cost) of sprat in relation to temperature. Likewise, the energetic efficiency decreased with increasing body size. As a consequence, the food demand of sprat for optimal growth increases with increasing temperature. Particularly larger sprat need higher prey concentrations at higher temperatures during summer than smaller sprat for growth. Thus being born later in the season has the advantage that the juvenile phase where sprat are larger is shifted to late summer and autumn with on average colder temperatures. During this time with colder temperatures the energetic efficiency is higher than in summer and the risk of starvation due to unfavorable food conditions is reduced.

A comparison of the functional response of similar sized sprat and herring (8 cm) revealed that at lower prey concentrations up to 50 L^{-1} sprat exhibit significantly higher feeding rates than herring. This implies that the feeding efficiency is greater in sprat than in herring and that is why at lower prey densities sprat is the stronger food competitors than herring.

The diurnal feeding periodicity of sprat is related to their DVM. Nonetheless, sprat feeding behavior and daily ration (DR) estimation are usually based on daytime stomach contents from deeper layers. We provided a new approach for DR estimation, taking into consideration the vertical feeding dynamics of sprat. For this purpose, we analyzed sprat DVM by hydroacoustics and collected stomach contents at different feeding depths from shortly before sunrise to about two hours after the sunset at three different stations in the Central Baltic Sea (**manuscript 3**). Feeding rates of sprat at different feeding phases during the DVM were quantified by modifying the established gastric evacuation model for DR estimation. The course of sprat stomach content during the feeding period was simulated by numerical integration. In the simulation, feeding rates as well as the time limits of the feeding phases were iteratively changed simultaneously in such a way that predicted contents match the observed contents from field. On average, 71 % of the daily ration was consumed by sprat in the upper water layers and feeding rates were 3.16 times higher than in deeper layers. Sprat fed on average 51% of their feeding time within upper and warmer waters. Daily rations calculated by our new approach were on average 1.40 times higher than the rations from the established approach. The underestimation by the established approach was mainly caused by ignoring the effect of higher temperatures from upper layers on

the gastric evacuation rate. A simple correction formula of the established approach was developed to reduce the discrepancy between the two approaches to 4%. Our findings emphasize the importance of adapting the sampling design on the vertical feeding dynamics to avoid a biased picture of predator prey interactions and an underestimation of DR estimation. Furthermore, our results have major implications on the interpretation of prey selectivity, since sprat seem to primarily consume prey that shows a high spatial overlap to the sprat’s location during active feeding phases in the upper water layers.

2 Zusammenfassung

Das Hauptziel dieser Arbeit war es die Fressraten von Sprotten und teilweise Heringen in Abhängigkeit von verschiedenen abiotischen und biotischen Faktoren und während der tagesperiodischen Vertikalwanderung zu untersuchen. Diese Ergebnisse verbessern das Verständnis von Räuber-Beute-Interaktionen und sind für die Weiterentwicklung von bioenergetischen Wachstumsmodellen und die Quantifizierung der Konsumption von Relevanz.

Im ersten Abschnitt der Arbeit wurde zum Einen das partikuläre Fressverhalten im Detail analysiert und zum Anderen der Typ der *functional response* von Sprotten (~ 6 cm) und Heringen (~ 8 cm) experimentell bestimmt (**Manuskript 1**). Hierfür wurde ein Versuchsdesign entwickelt, welches die Beobachtung des Fressverhaltens mittels einer Unterwasserkamera, sowie die gleichzeitige Quantifizierung der Beutekonzentration im Versuchsbecken ohne die sensiblen Fische dabei zu beeinträchtigen, ermöglichte. Um die unterschiedlichen Typen der *functional response* unterscheiden zu können, war es besonders wichtig die Fressraten bei geringen Beutekonzentrationen (1-160 L^{-1}) zu ermitteln. Die Fressversuche wurden bei 16 °C getrennt mit zwei unterschiedlichen Beutearten durchgeführt, welche sich in ihrem Fluchtverhalten unterscheiden. Nicht flüchtende *Artemia salina* Nauplien wurden verwendet um die maximale physiologische Fressrate zu ermitteln, vergleichbar zum Fressen von Cladoceren und anderen nicht fliehenden Copepodearten wie *Temora longicornis* und *Pseudocalanus acuspes*. Im Gegensatz dazu dienten Experimente mit der Copepodenart *Acartia tonsa* dazu, das Fressen von stark fliehender Beute widerzuspiegeln (z.B. auch *Eurytemora affinis*). Die Sprotten zeigten ausschließlich das partikuläre Fressverhalten, bei welchem die Beute selektiv gezielt geschnappt wurde. Dagegen begannen die Heringe ab einer Beutekonzentration von über 50 L^{-1} gelegentlich zu filtrieren. Bei geringen Beutekonzentrationen fraßen beide Fischarten mehr oder weniger in einer horizontalen Ebene. Ab einer Konzentration von 15 L^{-1} wurde eine vertikale Ziz-Zag Schwimmbewegung beim Fressen beobachtet, bei der beim Schwimmen nach oben mehrfach nach Beute geschnappt wurde, gefolgt von einer 180° Wendung nahe der Oberfläche und dem

Schwimmen zurück nach unten. Sprotten und Heringe zeigten eine ***type II functional response***. Hierbei steigt die Fressrate bei geringer Beutekonzentration linear an und nähert sich bei hohen Dichten asymptotisch dem Maximalwert an. Die Fressrate war bei *A. tonsa* signifikant geringer als bei Artemien. Beim Fressen von *A. tonsa* zeigten beide Fischarten eine S-förmige Körperbiegung unmittelbar vor dem Schnappen, welches durch die hohe Fluchtfähigkeit von *A. tonsa* verursacht wurde.

Der Sprottenbestand ist starken Fluktuationen unterworfen, welche besonders durch den Rekrutierungserfolg der jungen Stadien bestimmt wird. Deshalb wurde in den letzten Jahren versucht die Mechanismen zu identifizieren, welche das Überleben dieser empfindlichen Stadien beeinflussen. So wurde festgestellt, dass besonders solche Kohorten eine hohe Überlebenswahrscheinlichkeit aufweisen, die später in der Saison geboren werden und deshalb als Larven im Sommer hohe Temperaturen und während der juvenilen Phase die späteren kühleren Temperauren des Spätsommers/Herbstes erleben. Jedoch ist das mechanistische Verständnis für diese Beobachtungen noch unvollständig. Deshalb wurde im zweiten Abschnitt der Arbeit die *functional response* von juvenilen Sprotten in Abhängigkeit von Temperatur und Körpergröße parametrisiert (**Manuskript 2**). Die Ergebnisse können dazu genutzt werden um ein bioenergetisches Model zu entwickeln, um herauszufinden, ob größere Sprotten bei höheren Temperaruten ein höheres Risiko aufweisen zu verhungern als kleinere Sprotten.

Zur Bestimmung des Temperatureffektes wurden umfangreiche Fressversuche bei fünf unterschiedlichen Temperaturen von 5 bis 20 °C mit 8 cm großen Sprotten durchgeführt. Zusätzliche Durchläufe der Fressexperimente mit 3 cm großen Sprotten bei 16 °C dienten dazu den Größeneffekt mit drei unterschiedlichen Längenklassen (3, 6 und 8 cm) zu erfassen. Die maximale Schnapprate (*BRmax*) von Sprotten stieg S-förmig mit zunehmender Temperatur und Körpergröße an und erreichte einen Maximalwert von etwa 2.0 s^{-1}. Der Parameter *k*, welcher die Beutekonzentration bei *BRmax*/2 beschreibt, zeigte keinen Effekt mit zunehmender Temperatur, nahm jedoch in einer Potenzfunktion mit zunehmender Körperlänge ab. Ein Vergleich der Mageninhalte von Versuchsfischen mit den aus den beobachteten Schnappraten berechneten Werten ergab zum Einen, dass die ermittelte *functional response* in der vorliegenden Arbeit das physiologische maximale Fressverhalten widerspiegelt und zum Anderen, dass Sprotten dieses

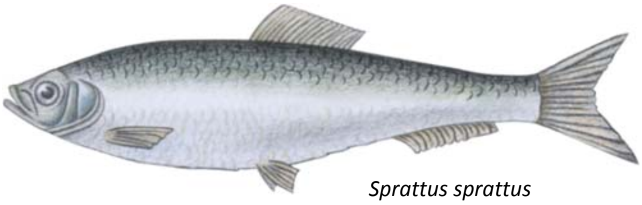
Verhalten besonders bei geringeren Beutedichten nicht kontinuierlich durchführen können. Die asymptotische Zunahme der Fressrate im Gegensatz zu einer exponentiellen Zunahme der Stoffwechselrate mit der Temperatur, erzeugte einen buckelförmigen Verlauf der energetischen Effizienz (pro-Kopf Energiezufuhr relativ zum Energieverbrauch) mit zunehmender Temperatur. In ähnlicher Weise nahm die energetische Effizienz mit zunehmender Körpergröße ab, da die metabolischen Kosten mit zunehmender Körpergröße überproportional (Exponent = 1.073) anstiegen im Gegensatz zu einer asymptotischen Zunahme der Energiezufuhr durch das Fressen. Dies impliziert, dass der Nahrungsbedarf für ein optimales Wachstum mit steigender Temperatur zunimmt und dass besonders größere Sprotten im Sommer höhere Beutekonzentrationen benötigen um dieses zu erreichen als kleinere Sprotten. Das spätere Laichen in der Saison hat also den Vorteil, dass die juvenilen größeren Sprotten kühlere Temperaturen des Spätsommers/Herbstes ausgesetzt sind, in der die energetische Effizienz höher ist als im Sommer und sie somit das Risiko des Hungertods aufgrund unzureichender Nahrungskonzentration reduzieren können.

Ein Vergleich der *functional response* gleichgroßer Sprotten und Heringe (8 cm) ergab, dass bei geringen Konzentrationen bis zu 50 L^{-1} Sprotten deutlich höhere Fressraten erreichten als Heringe. Dies bedeutet, dass Sprotten eine höhere Effizienz bei der Nahrungsaufnahme aufweisen als Heringe und diese somit bei geringen Dichten einen deutlichen Konkurrenzvorteil haben.

Die Fressaktivität von Sprotten steht im engen Zusammenhang mit der tagesperiodischen Vertikalwanderung. Konventionell wurde die Tagesration von Sprotten mit Hilfe des mittleren Mageninhaltes aus Beprobungen während des Tages im Tiefenwasser bestimmt. In dieser Arbeit wurde ein neuer Ansatz entwickelt, welcher die vertikale Fressdynamik von Sprotten mitberücksichtigt. Zu diesem Zweck wurden Daten über Mageninhalte und die vertikale Verteilung von Sprotten an drei unterschiedlichen ~12-Stunden Dauerstationen in der zentralen Ostsee erhoben (**Manuskript 3**). Die Bestimmung der unterschiedlichen Fressraten in den fünf definierten Phasen während der Wanderung erfolgte durch eine Modifizierung des Magenleerungsmodels. Dabei wurde die Veränderung des Mageninhaltes über die Zeit mittels numerischer Integration berechnet. In der Simulation wurden die Fressraten und die Zeitgrenzen

der unterschiedlichen Phasen gleichzeitig iterativ so verändert, dass die vorhergesagten Mageninhalte mit den mittleren beobachteten Mageninhalten aus dem Feld übereinstimmten. Im Durchschnitt wurden 71 % der Tagesration von Sprotten in den oberen Wasserschichten konsumiert und die Fressrate war im Mittel 3.16-mal höher als im Tiefenwasser. Insgesamt wurde im Durchschnitt 51 % der Gesamtfresszeit in den oberen Schichten verbracht. Die hier ermittelten Tagesrationen waren im Mittel 1.40-mal höher als die Rationen, welche mittels des konventionellen Ansatzes berechnet wurden. Zudem wurde ein einfaches korrigiertes Tageskonsumptionsmodell entwickelt um die Diskrepanz zwischen beiden Ansätzen auf 4% zu reduzieren. Die Ergebnisse dieser Studie machen deutlich, wie wichtig es ist die Beprobungsstrategie an die vertikalen Fressdynamiken anzupassen, um ein verzerrtes Bild von Räuber-Beute-Interaktionen und einer Unterschätzung der Konsumption zu vermeiden. Zudem müssen diese Fressdynamiken in der Interpretation von Beuteselektivität mitberücksichtigt werden, da Sprotten scheinbar hauptsächlich Beute fressen, die während ihrer aktiven Fressphase in den oberen Wasserschichten eine große räumliche Überlappung mit ihnen aufweisen.

3 General Introduction



Sprattus sprattus

3.1 The economic and ecological importance of sprat and herring

Small pelagic clupeid fish are termed “wasp-waist” species as they dominate mid trophic levels and comprise relatively few species but attain large abundances that can vary drastically in size (Shannon et al. 2009). They have been found to exert top-down control on their prey species (e.g. copepods and cladocerans) and bottom-up control on their predators (e.g. cod (*Gadus morhua*), salmon (*Salmo salar*)) and, in this way, appear to induce unsuspected ecosystem dynamics (Shannon et al. 2009). Sprat (*Sprattus sprattus* L.) and herring (*Clupea harengus* L.) are the most important fish in the food web of the Baltic Sea and presently constitute the largest share in the fish catches together with the Baltic cod (*Gadus morhua*) (Ojaveer et al. 2010). The total landings in 2016 of sprat and herring in the Baltic Sea were 246 kt and 192 kt, respectively (ICES 2017). Arrhenius and Hansson (1993) estimated that sprat and herring consumed between 60 and 80% of the annual zooplankton production in the Baltic Sea. Thus, the understanding of the trophic dynamic and energy flow in the Baltic Sea could be improved by learning more about the feeding behavior of sprat and herring. The importance of sprat in the Baltic Sea ecosystem significantly increased during the last decades as the biomass of sprat had more than tripled since the 1980s (ICES 2017). The increase was caused by a shift from a cod dominated to a clupeid (or sprat) dominated system as a consequence of change in hydrography and human exploitation (Casini et al. 2008; Möllmann et al. 2009). Due to the resulting higher intra- and interspecific competition for food resources and a change in the prey taxonomic composition, the weight-at-age (WAA) and body condition of sprat and herring declined in the last decades (Cardinale and Arrhenius 2000; Cardinale et al. 2002; Casini et al. 2011). Recently, the eastern Baltic cod population has started to recover (ICES-subdivision 25), partly due to effective management measures (Eero et al. 2012). The increase of cod stock in this area resulted in a locally high predation mortality for forage fish, but had very limited effects on the whole Baltic sprat stock which is currently more abundant in areas outside of the cod's range (Eero et al. 2012).

Like other small pelagic fish such as anchovies (*Engraulis* spp.) and sardine (*Sardinops* spp.), sprat population is characterized by strong fluctuations, making the management difficult. The assessment and management of small pelagic fish stocks is particularly difficult and uncertain because their short life expectancy, shoaling behavior, rapid response to climate and environmental signals and large and variable natural mortality make them less tractable through traditional population dynamic models and assumption (Barange et al. 2009). The high variability of sprat is mainly caused by changes in recruitment success. These recruitment fluctuations are not directly coupled to the spawning stock biomass of sprat (Köster et al. 2003), but appear to be driven by a suite of interacting environmental drivers (Voss et al. 2012). Different studies on fish identified that processes acting during the early life history contribute most to the recruitment variability (see Voss et al. 2012). Consequently, intensive research was conducted to identify factors affecting the survival of the highly vulnerable early life stages of sprat in 2002 and 2003 (Köster et al. 2003; Voss et al. 2012). Predation mortality on different stages of sprat seems to be not the major factor explaining differences in recruitment success (Voss et al. 2012). In contrast, food limitation during the early larval and juvenile phases appears to be important factor regulating the recruitment (Voss et al. 2012). Physical parameters such as salinity and temperature appear to be important physical factors influencing the survival of sprat (Voss et al. 2012). Salinity of water experienced during egg fertilization affect the egg development and buoyancy and hence the vertical habitat and potential survival of eggs and larvae. Ambient temperature strongly influence the growth rate of different stages of sprat. Overall, Voss et al. (2012) assume that bottom-up control of sprat recruitment (by e.g. temperature and prey abundance) to be more important than top-down control (predation mortality). The two factors temperature and food availability seems to be indelibly linked, and both factors simultaneously influence the growth rate and survival of early life stages of sprat. Günther et al. (2015) conducted growth experiments with post-larval sprat at different temperatures and ad libitum feeding conditions to generate a reference set of otoliths representing optimally growing sprat. These otolith increment pattern were then compared with those of young sprat sampled in two field studies with contrasting year-class strengths 2003 and 2007. Recruitment in 2003 was about 3-fold higher than in 2007. The majority of survivors in 2003 were born later in the year (July), whereas individuals from 2007 were born almost two months earlier (May). On average, increments of sprat from 2007 were narrower than laboratory references, indicating sub-optimal feeding conditions. In contrast, the bulk of surviving individuals in 2003 exhibited large increments, suggesting optimal feeding conditions. Unlike early born cohorts, later born cohorts experienced highest summer temperatures during larval stages, whereas juveniles grew at lower temperatures in late summer and autumn. However, no mechanistic explanation for the importance of timing and hence of temperature on seasonal cohorts has been found so far. Therefore, one main goal of this study is to improve the mechanistic understanding of how prey concentration, prey type, fish size and temperature affect the feeding rate of sprat, leading to realistic predictions of growth rates and survival of juvenile sprat.

3.2 Feeding ecology of sprat and herring

Planktivorous fish such as herring (Gibson and Ezzi 1985), *Engraulis mordax* (Leong & O’Connell 1969), *Sardinops sagax* (Van der Lingen 1994), *Scomber japonicus* (O’Connell & Zweifel 1972) and *Alosa pseudoharengus* (Janssen 1976) are able to switch between two feeding strategies. They can either selectively catch prey items (particulate-feeding) or filter food particles out of the water non-selectively (filter-feeding). Particulate-feeding is typically applied for relatively large prey items and / or at lower prey concentrations, whereas filter-feeding occurs in the presence of smaller food particles and at high prey concentrations or at low light intensities (Batty et al. 1990; Gibson and Ezzi 1992). However, due to the increased swimming speed the energy costs for filter-feeding are 1.4 to 4.6 times higher than for particulate-feeding (Gibson & Ezzi 1992). In contrast to herring, sprat are assumed to be an obligate particulate-feeder (Bernreuther 2007), but it has not been investigated systematically before. Both clupeids are dependent on sufficient light intensity when selectively catching a prey by biting. Batty et al.

(1990) found that herring fed by biting at light intensities above a threshold of 0.001 lux and were size-selective, taking the larger organism first.

The niche overlap in the diet of herring and sprat is high (65-80%) (Möllmann et al. 2004; Bernreuther 2007), especially among 0-groups (De Silva 1973; Maes & Ollevier 2002). Sprat and smaller herring (< 13-15 cm) are exclusively zooplanktivorous, while larger herring (> 15-20 cm) also consume larger prey species such as mysidaceas, amphipods, polychaetes, chaetognathates, decapods and fish eggs and larvae (Savage 1937; Last 1987; Casini et al. 2004). However, the dominant prey group for both clupeids are calanoid copepods, such as *Temora longicornis* and *Pseudocalanus acuspes* (Maes and Ollevier 2002; Möllmann et al. 2004; Bernreuther et al. 2013). In contrast, in coastal nursery areas 0-group herring and sprat mainly feed on the copepods *Eurytemora affinis* and *Acartia* spp. (Arrhenius 1996; Maes et al. 2005; Paulsen et al. 2016). In summer, cladocerans (e.g. *Bosmina maritima* and *Evadne nordmanni*) are also preferred in offshore as well as inshore areas (Arrhenius 1996; Bernreuther et al. 2013). However, a certain niche differentiation can be found in terms of their feeding behavior. Larger herring (> 8 cm) can filter-feed at high prey densities and in the dark (Gibson & Ezzi 1985; Batty et al. 1986; Batty et al. 1990). This allows herring to prolong the feeding period compared to sprat (Batty et al. 1986; Batty et al. 1990). The filtration is unselective, so that even smaller prey particles are eaten. Bernreuther (2007) estimated the weighted mean copepodite stage in the diet of herring and sprat from the Baltic Sea and found that the average prey concentration in the field was too low to trigger filtration in herring. However, in patches with high densities, filtration could lead to higher consumption rates of herring compared to sprat. The better utilization of high prey densities and the uptake of larger prey with increasing size could explain the difference in the maximum lengths of sprat (L_∞ = 16cm) and herring (L_∞ = 40cm). However, among the 0-group the diet of sprat and smaller herring is based on the same food resource, which is captured by simple biting. This implies that if there is insufficient food availability, the competition between these two species can be strong. A comparison of the feeding rates between sprat and herring of the same size might give some indication of why sprat has become a dominant species in the Baltic Sea, in contrast to herring.

3.3 Diel vertical migration

Diel vertical migration (DVM) is a behavioral pattern widely observed in pelagic phytoplankton, invertebrates and fish both in marine and freshwater systems (reviewed by Mehner 2012). The main proximate trigger for DVM is the change of light intensity during the day, with declining illumination at dusk causing the ascent and the increase at dawn triggering the descent (Mehner 2012). Light intensity is one of the main reasons that influence the detection rate and resulting feeding rate of a visual predator (Eggers 1978). Additional proximate cause is ambient temperature (Mehner 2012). Ultimate causes of DVM are maximization of growth (i.e. net energy assimilation) and predator avoidance (Mehner 2012). The first category includes (i) maximizing food intake, either by feeding where prey concentrations are highest (Bevelhimer and Adams 1993) and light conditions are sufficient (Cardinale et al. 2003) or by distributing at temperatures for digestion stimulation (Wurtsbaugh and Neverman 1988), and (ii) maximizing assimilation efficiency by minimizing energetic costs. Overall, DVM behavior can be very variable and seems to be a trade-off between different ultimate causes like gaining energy for growth and predator avoidance (Staby et al. 2013; Solberg and Kaartvedt 2017).

Sprat and herring perform extensive DVM (Orlowski 2001; Cardinale et al. 2003; Nilsson et al. 2003). In the deep basin of the Baltic Sea, sprat and herring show the “normal” variant of DVM, which consists of occurrence in deep waters during the day, an ascent towards surface at dusk, residence in the upper layers by night and return to the deep at dawn (Cardinale et al. 2003; Nilsson et al. 2003). Analysis of field stomach contents revealed that sprat and herring mainly feed during the day when light intensity is sufficient (Köster 1994; Cardinale et al. 2003; Peltonen et al. 2004; Bernreuther et al. 2013). However, field observations on the swimming speed and moving pattern of clupeids indicated that they start to feed already about one hour before the sunrise (Didrikas and Hansson 2009; Solberg and Kaartvedt 2017). Cardinale et al. (2003) suggested that the catchability of prey is highest at the dawn and dusk when zooplankton is distributed near the surface where light intensity is high. The DVM of sprat were expected to be controlled during the day mainly by feeding whilst the occurrence during the night in warmer upper water layers may indicate the optimization of bioenergetics (Cardinale et al. 2003; Peltonen et al. 2004). Although it is speculated that feeding during dawn and dusk in the upper water layers plays a role in the daily consumption of sprat (Cardinale et al. 2003), the intake at that time on the total daily ration (DR) has not yet been quantified. Instead, the sampling of stomach contents of sprat in the field has so far mainly focused on the time during the day in the intermediate and bottom waters (Köster 1994; Köster and Schnack 1994). Furthermore, the feeding activity of sprat was mainly restricted to the period between sunrise and sunset (Köster 1994; Köster and Schnack 1994; Arrhenius 1998). However, should it become clear that the feeding intensity of sprat is different during different phases of the DVM, previous interpretation of prey composition in the diet and hence the assumption about prey selectivity may be incorrect.

3.4 Predation act

A predation-act is a succession of different discrete events: prey search, prey encounter, prey pursuit, prey capture and prey consumption (Holling 1966). For planktivorous fish, pursuit, capture and consumption all require only a second or two (Gerking 1994). All three actions are called together "*handling time*". As a result, encounter (search time) is of much more importance for planktivorous fish than handling time. The encounter rate is mainly influenced by the prey concentration and the visual predator's *reactive distance*: the maximum distance from which a prey item is recognized by a predator (Gerking 1994). The reactive distance is depending on the optical characteristics of the environment: mainly on the contrast in the water (determined by ambient light in the water), the inherent prey conspicuousness (as a function of size, shape, pigmentation, behavior) and the visual acuity of the predator (Lazzaro 1987). Prey size is an obvious factor affecting reactive distance as larger prey will be seen at a greater distance. This fact was demonstrated in several studies, for example with sunfish and salmonids feeding on different sized Daphnia (Gerking 1994). The behavior of prey also affects the reactive distance: experiments with pumpkinseed showed that jumping copepods attracted the attention of the predator more than the characteristic gliding motion of daphnia or cladocerans (Confer and

Blades 1975). However, the escape skills of prey influence the feeding rate of a predator, because for example jumping copepods are more difficult to capture than gliding cladocerans. In addition, the feeding rate is also influenced by the predator's experience and feeling of hunger (Lazzaro 1987).

3.5 Functional response

Functional response models describe the relationship between the *per-capita* feeding rate and prey concentration (Solomon 1949; Holling 1959). The responses are affected by the predator's success rate, handling time, and digestion time (Jeschke et al. 2002, 2004). Holling (1959) assumes that feeding rates increase with increasing prey concentrations. At low concentrations, the feeding rate is limited by the search time, while at higher prey concentrations, the search time decreases and the feeding rate depends increasingly on the handling time and the degree of the predator's saturation. Holling (1959) has categorized functional responses into three main types (Fig. 3.1). The type I functional response takes a linear form, yielding a constant predation risk for the prey. This type is typical for filter-feeding organisms either having a negligibly small handling time or being able to search and capture prey while handling other food (Jeschke et al. 2004). The type II functional response has been most frequently observed (Hassell at al. 1976; Begon et al. 1996) and is characterized by a hyperbolic curve. This type is typical for planktivorous fish that particulate-feed and forage in environments where prey are patchy (Smith 1998). At low prey concentrations predation rate first increases almost linearly until it gradually slows down to reach an upper limit. The type II functional response can potentially destabilize prey populations because predation risk increases with decreasing prey population density (Sarnelle and Wilson 2008). In contrast, the type III functional responses are sigmoidal with a decreasing predation risk at low prey densities (Sarnelle and Wilson 2008). Thus, the type III has the potential to stabilize fluctuations of prey and predator populations, and to reduce prey extinction risk (Holling 1959, Sarnelle and Wilson 2008). The type III can arises when multiple prey types are available and switching behavior occurs (Smith 1998) or when the predator increases their feeding efficiency (e.g. search activity) with increasing prey density.

The type II functional response is often described by the Holling's disk equation:

$$BR = \frac{a * c}{1 + a * h * c}$$

Where, *BR* is the predation rate (s^{-1}), *a* is the success rate (dimension in SI units: m_2s^{-1} or m_3s^{-1}), *h* is predator handling time per prey item (s) and c is prey concentration (m_2^{-1} or L^{-1}). The disc equation is mathematically equivalent to the Michaelis-Menten model of enzyme kinetics:

$$BR = \frac{BR_{max} * c}{(k + c)}$$

Where, *BRmax* is the maximum predation rate (s^{-1}), *c* is prey concentration (L^{-1}) and *k* (L^{-1}) is the prey concentration at *BRmax*/2. The disc equation by Holling (1959) was originally developed as a mechanistic model for artificial predator-prey systems (Jeschke at al. 2002), especially for terrestrial systems with predators that spend a lot of time to handle a prey (e.g. lions). For planktivorous fish, where the parameter *h* (handling time) is very low, the use of the Michaelis-Menten formula makes more sense as the parameters *BRmax* and *k* are better interpretable.

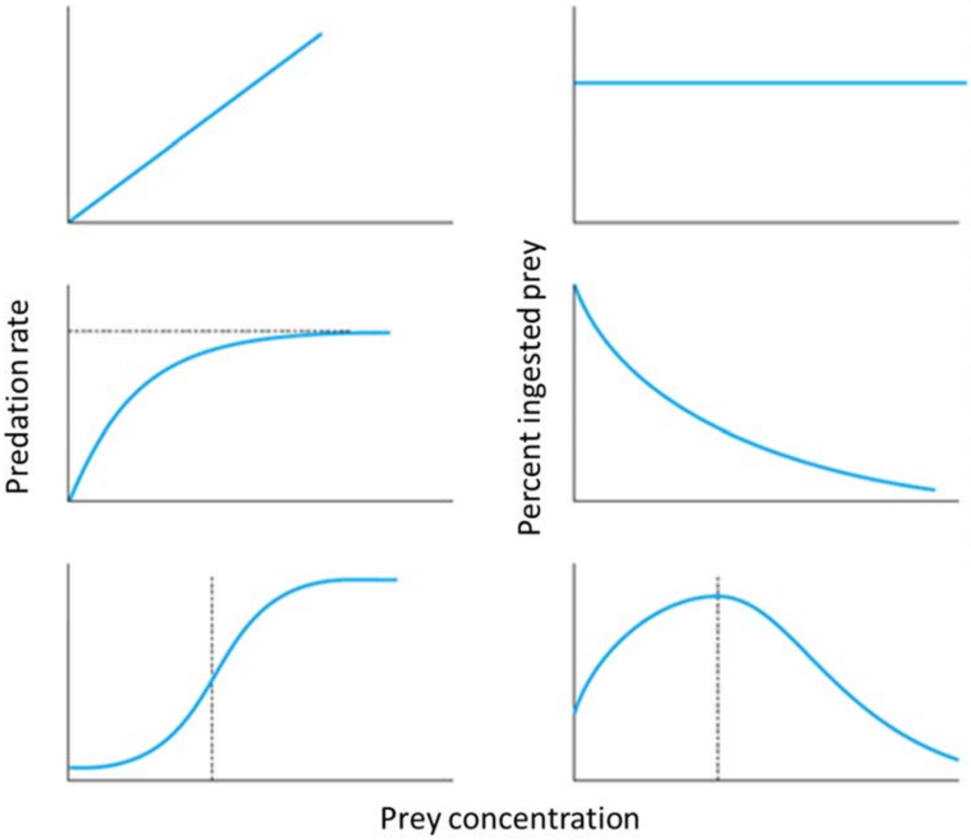


Figure 3.1: Schematic representation of different types of functional responses after Holling (1959) (top = type I, middle = type II, bottom = type III). *The left column displays the per capita predation rate (s^{-1}) as a function of prey density (L^{-1}). The right column displays the predations risk (feeding rate divided by prey density) in relation to prey concentration (L^{-1}). The type I is typical for filter-feeder, where the number of prey caught is proportional to prey concentration. The type II is most typical. The prey mortality declines with prey concentration, resulting in high maximum mortality of prey by a predator at low prey density. The type III is typical for a predator which increases their feeding efficiency (e.g. search activity) with increasing prey density. Thus the predator can regulate prey density because it is the only type for which prey mortality can increase with increasing prey density.*

3.5.1 Previous Research

A functional response type II was observed for the planktivorous fish species kokanee salmon (*Onchorhynchus nerka*) (Koski & Johnson 2002), percids (*Perca fluviatilis* and *Gymnocephalus cernuus*) (Bergman 1987), alewife (*Alosa pseudoharengus*), bloater (*Coregonus hoyi*) (Miller et al. 1992), brown trout (*Salmo trutta*) (Gustafsson et al. 2010). In contrast, a functional response type III was identified for five species of cyprinids (*Chalcalburnus chalcoides*, *Vimba vimba*, *Abramis brama*, *Rutilus rutilus*, and *Scardinius erythrophthalmus*) (Winkler and Orellana 1992; Gliwics et al. 2013). Although no alternative prey types were present in the experimental tank, the response curves were sigmoid in most cases. The authors suggest that the increase in feeding rate is related to an increase in the foraging efficiency of fish. In contrast to Gustafsson et al. (2013), Watz et al. (2014) estimated a type III instead of a type II functional response for brown trout and *Thymallus thymallus* as well.

With regard to marine species, only herring has been investigated so far (Gibson & Ezzi 1985, 1990, 1992; Bernreuther 2007). As Gibson and Ezzi (1992) conducted no experiments with herring at very low concentrations the actual from of the functional response is not known but it has been assumed to be a type II response. Bernreuther (2007) also found a functional response type II for herring. In contrast, there is no information on the relationship between the feeding rate and prey concentration of sprat. There are also no studies on the functional response of other clupeid species such as anchovies and sardines. Feeding experiments on herring and some other fish species were not optimal, making the detection of the actual form of the functional response and the application of the results to field situations difficult (see below).

Prey type and concentration

The abundance of prey (e.g. copepods) for planktivorous fish can be highly variable in space and time, with values well below 10 L^{-1} (Colebrook 1979; Broekhuizen and McKenzie 1995) to more than 100 L^{-1} in areas of higher aggregation (Soetaert and Van Rijswijk 1993; Folt and Burns 1999). Thus, it is important to determine feeding rates over a wide range of prey concentrations. Studies on kokanee salmon were performed only at low prey concentrations up to 50 L^{-1} (Koski & Johnson 2002). Feeding experiments with herring were mainly performed by Gibson and Ezzi (1985, 1990, 1992) only at very high prey concentrations from 50 to 1000 L^{-1}. In contrast, Bernreuther (2007) conducted feeding experiments with herring also at lower prey concentrations from 10 to 160 L^{-1}. However, Bernreuther (2007) used frozen copepods as prey. Studies on the functional response of brown trout were also conducted only with dead prey (Gustafsson et al. 2010). Such dead prey, however, may cause a different triggering effect on feeding than living prey. In addition, dead prey cannot swim and therefore sinks to the bottom of the experimental tank after some time, making the estimation of the actual prey concentration difficult.

Fish size

Studies on the functional response of herring were conducted with larger fish of about 16 cm (Gibson & Ezzi 1985, 1990, 1992) or between 10 and 13 cm (Bernreuther (2007). At these size ranges, herring already filter-feed at higher prey concentrations (Gibson & Ezzi 1985, 1990, 1992; Bernreuther 2007). This can lead to a biased result of the functional response. To improve the mechanistic understanding of feeding success and survival of seasonal cohorts it is necessary to study the interaction of prey concentration and fish size. In the Northern Baltic larval and juvenile sprat are responsible for up to 50% of the predation on zooplankton (Arrhenius and Hansson 1993). Thus, information on the functional response of juvenile sprat is of particular interest to understand their top-down control on the zooplankton community.

Temperature

The investigation of the temperature effect is highly relevant for Baltic sprat and herring, as water temperatures changes both seasonally and during the DVM within the water column (Cardinale et al. 2003; Nilsson et al. 2003). Nevertheless, the effect of ambient temperature on the functional response has not been investigated in clupeids. However, many studies on freshwater species demonstrated that feeding rates are strongly dependent on temperature (Persson 1986; Englund et al. 2011; Lefébure et al. 2014). For salmonids functional responses were only estimated at two different temperatures 5 and 11 °C (Watz et al. 2014). However, the actual temperature dependence on BR_{max} and k cannot be determined with just two data points. Persson (1986) investigated the functional responses of roach and perch at the temperatures 12, 15, 18 and 21 °C. *BRmax* increased in both species with increasing temperatures. In contrast, k decreased with raising temperatures. Due to the scattering of the data, however, the exact form of the increase or decrease of the parameters could not be determined. In addition, for the applicability to clupeids, it is necessary to study particularly the effects of lower temperatures $<$ 12 °C on feeding which they are exposed to during the DVM.

Trial time

Feeding experiments were often only conducted for a short time. Koski and Johnson (2002) observed the feeding of kokanee salmon for a time interval of only 10 minutes. To avoid satiation Bergman (1987) even terminated the trail when only 5-10 prey were captured by percid predators. The functional response of *Coregonus lavaretus* was only based on records of 1 minutes (Winkler and Moreno 1984). However, field observations showed that herring can feed continuously within a patch with high prey concentrations for at least 25 minutes (Kills 1992, Bernreuther 2007). To obtain realistic feeding rates, feeding experiments with clupeids should be conducted over a longer period.

3.5.2 Scope of application

The consumption of a predator is usually estimated by bioenergetics models using empirical growth data. However, the balance equation can be rearranged to determine growth using consumption estimates (Haskell et al. 2017). Consumption can then be either estimated by sampling stomach contents and associated evacuation rates or by a functional response model and prey density data from field. Hence, functional response models provide a link between growth and field food availability. If we combine the functional response model with the predator population density, we can calculate the total number of prey eaten in a given time. If we add further information, like an energy conversion factor, we can then also predict individual growth of predators (Jeschke et al. 2002). For freshwater and marine ecosystems, functional responses have mainly been implemented in single-species process models investigating bioenergetics and prey encounter (Stockwell and Johnson 1997, 1999; Moss and Beauchamp 2007; Varpe and Fiksen 2010; Haskell et al. 2017). However, functional response models are also increasingly of interest in complex ecosystem models like NEMURO (Megrey et al. 2007).

Recently, invasion ecology has discovered the advantages of using comparative functional response models (Dick et al. 2014 and 2017). Invasion ecology requires predictive methodologies that can forecast the ecological impacts of invasive species. Dick et al. (2014) argue that many ecologically damaging invaders are characterised by their more efficient use of resources. Consequently, a comparison of the functional response between invasive and trophically analogous native species may allow prediction of invader ecological impact. An example is provided by Dubs and Corkum (1996) showing that the functional response of nonindigenous round goby (*Neogobious melanastomus*) was higher than that of the native mottled sculpin (*Cottus bairdi*) in the Great Lakes of the US. Generally, this approach can also be used to compare the competitiveness between non-invasive species, such as herring and sprat. There are some studies showing the functional response between competing species in crustaceans (Bollache et al. 2008, Haddaway et al. 2012, Dick et al. 2013), birds (Monserrat et al. 2005) and insects (Griswold and Lounibos 2005). So far, very few studies have been conducted comparing the functional response between competing fish species. The functional response of guppies (*Poecilia reticulate*) was lower in the presence of a competitor species like the Hart's killifish (*Rivulus hartii*) (de Villemereuil and López-Sepulcre 2011). Watz et al. (2014) showed that the functional response of European grayling (*Thymallus thymallus*) was higher than of brown trout. They suggest that this result may explain the dominance of grayling in the stream habitats in Northern Europe. The comparison of the functional responses of sprat and herring could provide an indication of why sprat in the Baltic Sea has become a dominant species compared to herring.

In summary, three major advantages can be expected from the application of functional response models: (i) functional response models provide parameters (feeding rate, maximum feeding rate, and handling time) that describe the mechanisms driving their shape and magnitude (Dick et al. 2013); (ii) the form of the functional response model can inform whether the predator will likely regulate, stabilise or de-stabilise the prey population, and (iii) relevant environmental conditions, such as temperature, light levels, habitat structure and prey types, can be incorporated into experiments to estimate differences in the type and/or magnitude of the functional response models (Dick et al. 2014).

3.6 Daily ration estimation

Estimations on daily ration (DR) are needed to investigate the relation between ration and growth, to analyses the profitability of different habitats, to detect food limitations during the season, and to assess trophic relationships (Héroux & Magnan 1996). There are three established methods to estimate DR. The first method is the measurement of food consumption of fish in the laboratory (Richter et al. 2002). In this approach, the relation between ration and growth is often measured, which is then applied to field growth data to estimate the food ration in field (Durbin & Durbin 1983). The second method uses bioenergetics models to determine the total energy demands of the fish. This usually includes the estimation of growth rate from field and the experimentally determination of the energy utilized by metabolism and lost through faeces and excretion (Kitchell et al. 1977; Schaefer et al. 1999). The third method estimates the DR from mean stomach contents from field and a known gastric evacuation rate (Elliot and Persson 1978). The gastric evacuation model approach has yielded significantly lower DR for clupeids than the alternative bioenergetics modelling (Möllmann & Köster 1999; Maes et al. 2005; Bernreuther 2007). The discrepancy could be caused by different approaches between both models: bioenergetics models reflect the energy intake over a longer period while the gastric evacuation method produces a point estimate at the time of sampling (Maes et al., 2005; Bernreuther, 2007). However, lower results by the gastric evacuation model may also be caused by ignoring the vertical feeding dynamics of clupeids. As DVM often associated with the diurnal feeding periodicity of fish (Batty et al. 1990; Cardinale et al. 2003) it particularly important to adapt the sampling design to the specific DVM pattern to avoid a biased picture of prey consumption (Pedersen, 2000). Andersen et al. (2017), for example, investigated the diel interaction pattern between cod and sprat in the Central Baltic Sea. They analyzed the diel vertical distribution by hydroacoustics data and identified the stomach contents of cod and sprat from different depths using pelagic and bottom trawls. With a quantitative analysis of the degree of digestion of the prey items they were able to show that the predation of sprat by cod primarily took place at dusk and dawn during the ascent and descent of sprat associated with school dissolution and formation. At Devil’s Hole in the North Sea, whiting (*Merlangius merlangus*) caught with a pelagic trawl were actively feeding on sprat and sandeel (Ammodytes spp.), while whiting sampled during the day with a bottom trawl were feeding on Norway pout (*Trisopterus esmarkii*). Depending on the feeding depths, the prey composition and energy density of prey differed and hence also affected the estimated daily ration (DR) of whiting (Pedersen, 2000).

Furthermore, the gastric evacuation of sprat increases strongly with increasing temperatures (Bernreuther et al., 2009). This temperature effect, however, was ignored based on the assumption that feeding during the day takes place mainly in the deeper water layers, consisting of colder temperatures (Möllmann and Köster, 1999; Köster and Möllmann, 2000). However, due to the stratification during spring and summer in the deep basins of the Baltic Sea, this temperature is much lower than the temperatures in the upper water layers (Voss et al. 2012). If the feeding time and intensity within the upper warmer water layers play a decisive role on the consumption of sprat, as presumed by Cardinale et al. (2003), the exclusive use of temperatures from the cooler bottom layers could lead to a significant underestimation of the total DR. This could have extensive consequences on predictions on the potential scope for growth of sprat and on top-down effects on prey communities.

3.7 Aim of this work

The ***first objective*** was to examine the particulate-feeding mode in detail and to determine the type of the functional response of sprat and herring. The main focus of the present work was the parameterization of the functional response of sprat to different prey types, temperature and fish sizes. As sprat live in habitats with strong seasonal and diel fluctuations in water temperature, the accurate parameterization of the temperatures experienced during feeding is essential to develop a reliable consumption model for sprat. The findings were also used to compare the functional response of juvenile sprat and herring which form mixed schools in nature and show high niche overlap in diet. For these purposes, we developed an experimental design which enabled the measurement of feeding rates under controlled laboratory conditions using an underwater camera system and sample techniques that caused only minimal stress for the fish. In the **first manuscript**, we estimated the feeding rates of sprat (~ 6 cm) and herring (~ 8cm) at different concentrations from 1 to 160 L^{-1} with two different single prey types at temperature of 16 °C. Non-evasive *Artemia salina* nauplii, which are comparable to cladocerans in terms of their vulnerability to predation, were used to estimate the physiologically maximum feeding rates of both clupeids. In contrast, late copepodite stages of *Acartia tonsa* were used as prey with high escape capabilities. In the **second manuscript**, we extended the functional response model of sprat by the variables temperature and fish size. Therefore, we performed numerous feeding experiments with ~8 cm sized sprat preying on *A. salina* nauplii at five different temperatures from 5 to 20°C. In addition, feeding experiments with small sprat (~ 3cm) were carried out to identify the size effect on functional response. In total, the size effect was parametrized at 16 °C with three different length classes (3, 6 and 8 cm) of sprat. In order to validate the biting rates from video observations, we also analyzed stomach contents of experimental fish with the size 8 cm. Furthermore, we compared biting rates from video observations with those calculated by the decreasing prey concentrations in the experimental tank. Finally, to improve the mechanistic understanding of the survival of different seasonal cohorts of sprat, we constructed a simple energy budget model in order to determine the energetic efficiency of sprat in relation to different temperatures.

The ***second objective*** was to quantify the feeding rates of sprat at different feeding phases (FP) during the DVM (**third manuscript**). For this purpose, we collected stomach contents of sprat and zooplankton data at three ~12 h stations in the Bornholm, Arkona and southern Gotland Basin in August 2015 in the Baltic Sea. Vertical distributions of sprat were analyzed visually by hydroacoustic data. To validate the feeding depths, we also qualified the diet of sprat and determine the vertical distribution of prey in the field. The DR of sprat is usually estimated using an average stomach content weight from day time and a model of gastric evacuation. In the present study, feeding rates of sprat at different FPs were quantified by modifying the established approach. The course of sprat stomach content during the feeding period was simulated by numerical integration, whereby feeding rates and the time limits of different FPs were simultaneously changed iteratively by the SOLVER-Function (Excel) in such a way that predicted contents match the observed contents from field.

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4 Manuscript 1: Functional response of juvenile herring and sprat in relation to different prey types

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For citations use the original manuscript. Published online: 3 November 2012,

DOI 10.1007/s00227-012-2104-5

4.1 Abstract

The relationship between particulate-feeding rates and prey concentrations (functional response) of juvenile herring and sprat (5-9 cm total length) was investigated in controlled feeding experiments monitored by an underwater camera system. A special tank system was developed allowing the regulation and quantification of low prey concentrations (1-160 L^{-1}). Non-evasive *Artemia* nauplii were used as prey to estimate the maximum biting rate of both predators. In contrast, *A. tonsa* with a high escape ability was used as a realistic prey type. Herring and sprat showed a type II functional response for both prey types. Nonlinear mixed effects model revealed no significant difference between the functional responses of both predators, except that herring showed significantly higher biting rates than sprat at *A. tonsa* concentrations below ~40 L^{-1}. For both predators feeding rates were significantly higher with *Artemia* nauplii than with *A. tonsa*. Video analysis indicated that sprat, unlike herring, is an obligate particulate-feeder.

4.2 Introduction

Planktivorous fish play a key role in the pelagic ecosystem as they have a marked impact upon their prey communities and are an important source of food for piscivorous predators (Rudstam et al. 1994). The intermediate trophic level - often occupied by one or few small pelagic schooling species – can exert a major control on whole ecosystems, namely in upwelling regions (Cury et al. 2000) and in the Baltic Sea with sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) as dominant small pelagic fish (Möllmann et al. 2004). Information on the relationship between sprat and herring *per capita* feeding rates and prey concentrations (functional response; Holling 1959, 1966) is therefore of particular interest to understand their top-down control of the zooplankton community.

Functional response curves are essential components of predator-prey models (Jeschke et al. 2002) and can potentially determine the stability of predator-prey dynamics (Sarnelle and Wilson 2008). There are three main functional response models (Holling 1959, 1966) which differ in the way feeding rates depend on prey concentrations. The type I functional response takes a linear form, yielding a constant predation risk for the prey. This type is typical for filter feeding organisms either having a negligibly small handling time or being able to search and capture prey while handling other food (Jeschke et al. 2004). Clupeoid fish like herring (Gibson and Ezzi 1985), alewife *Alosa pseudoharengus* (Janssen 1976), Cape anchovy *Engraulis encrasicolus* (James and Findlay 1989), California anchovy *Engraulis mordax* (Leong and O'Connell 1969) and sardine *Sardinops sagax* (van der Lingen 1994) exhibit both filter- and particulate-feeding modes. They generally filter-feed at high concentrations of small particles and particulate-feed at low concentrations or on larger prey (Gibson and Ezzi 1985; Lazzaro 1987). Thus, at low prey concentrations particulate-feeding herring and sprat are assumed to show a type II or type III functional response as prey handling time is higher than during filter-feeding. In a type II response, the number of prey killed per time increases with increasing prey density but the rate of increase is progressively reduced until an asymptote is reached at high densities (Juliano 2001). This type of functional response can potentially destabilize prey populations because predation risk increases with deceasing prey population density (Sarnelle and Wilson 2008). In contrast, the type III response is characterized by a sigmoid shape leading to a decreasing predation risk at low prey densities (Sarnelle and Wilson 2008). The difference between both types lies in the behaviour of predators at low prey densities: the type III model assumes that predators are inefficient at finding prey if prey concentration is low or that there is a threshold level below which predators do not respond (Shin et al. 2010). The type II functional response has been implemented likewise in process models investigating single species bioenergetics and prey encounter (Stockwell and Johnson 1997, 1999; Varpe and Fiksen 2010) and in marine ecosystem models like NEMURO (Megrey et al. 2007) and ATLANTIS (Fulton et al. 2004) to model fish and plankton population interactions. However, only few data exist to validate this assumption (type II) and to set the actual model parameters. Previous research on the feeding behaviour of herring was mainly focused on factors triggering particulate- and filter-feeding, like prey size, food density and light level (Gibson and Ezzi 1985, 1990, 1992; Batty et al. 1990). For this purpose, Gibson and Ezzi (1985) examined the feeding behaviour in herring mainly at high prey concentrations of up to 1000 L^{-1}. However, the abundance of the primary prey source of sprat and herring, calanoid copepods, can be highly variable in space and time, with values below 10 L^{-1} (Colebrook 1979; Broekhuizen and McKenzie 1995) to more than 100 L^{-1} in areas of higher aggregation (Soetaert and Van Rijswijk 1993; Folt and Burns 1999). Since low prey concentrations were not tested before, the actual form of functional response remained unknown. Our study intends to fill this gap*,* with an investigation of feeding rates of juvenile sprat and herring at lower prey concentrations (1 to 160 L^{-1}) where the difference between type II and III functional responses should be detectable.

Juvenile herring and sprat form mixed species schools in the coastal waters of the Baltic and North Seas and are therefore strongly associated with each other (De Silva 1973; Arrhenius and Hansson 1993; Maes and Ollevier 2002). Both fish species mainly feed on calanoid copepods, whereas larger herring (> 15-20 cm) also consume larger prey like mysids, amphipods, polychaetes, decapods and fish eggs (Last 1987; Casini at al. 2004). Therefore, food competition, particularly among the 0-group, could be a relevant factor if food resources are limited. We hypothesize that juvenile herring reach higher feeding rates than sprat at the same prey concentrations, based on findings from field stomach data analysed by Maes and Ollevier (2002).

Feeding experiments were conducted with two different prey types differing in their escape ability. Non-evasive *Artemia salina* nauplii as prey allowed the estimation of the potential maximum biting rate of sprat and herring. Results with *Artemia* nauplii are assumed to reflect the functional response of sprat and herring feeding on non-evasive prey items such as cladocerans (Viitasalo et al. 2001), which represent a large part of the diet of both predators (De Silva 1973; Arrhenius 1996). In contrast adult *Acartia tonsa* have a well-developed escape response (Singarajah 1969; Trager et al. 1994; Kiørboe 2010) and were therefore used to represent the typical copepod diet of sprat and herring (Maes et al. 2005). We hypothesize that the feeding rates of herring and sprat are higher with *Artemia* nauplii than with *A. tonsa* due to the shorter handling time needed for a non-evasive prey.

The major objectives of this study were therefore (1) to identify and parameterize the functional response models of sprat and herring and (2) to compare the functional responses of juvenile sprat and herring to identify possible competitive advantages, and (3) to test the effect of escape behaviour of different prey types on the handling time of both predators.

4.3 Material and Methods

4.3.1 Capture and maintenance of experimental fish

Young-of-the-year (YOY) herring were caught in June 2009 with a hand-operated dip-net (area: 4 m^2; mesh size 6 mm) in the Harbour of List, Sylt (North Sea, 55°1′11N; 8°36′8 E). YOY sprat were captured in July 2009 and 2010 in the Harbour of Wendtorf (Baltic Sea, 54° 41′ N; 10° 3′E). Fish were transported in a 700 L box with aerated seawater to the aquarium facilities of the Institute of Hydrobiology and Fisheries Sciences at the University of Hamburg. Prior to experiments fish were maintained in large groups of 100-500 individuals in circular tanks (1000 L) supplied with continuous flow of mechanically and biologically filtered, artificial seawater (Aqua medic) from the recirculation system. Sprat and herring were kept at an ambient temperature of 16.0 ± 0.1°C (mean ± SD) and at salinities of 16 and 32 PSU, respectively. Fish were maintained under a 13 L:11 D light regime and were fed an artificial pellet diet (*Marico advance 0.5-0.8 mm*, Coppens International bv) and live *Artemia salina* nauplii (*SEPArt-Cysts*, INVE Aquaculture) twice a day. Both herring and sprat were acclimated to laboratory conditions for 2 months prior to the onset of the experiments.

4.3.2 Prey types

Non-evasive *Artemia salina* nauplii (771 ± 90 µm total length, N = 316; 0.00171 ± 0.00038 mg dry weight; N = 151) were used in experiments as a slow moving prey species with low escape responses in order to determine the maximum feeding rate of the fish. Contrary, late copepodites (C5) and adults of *Acartia tonsa* (690 ± 75 µm prosoma length, N = 180; 0.00207 ± 0.00091 mg dry weight, N = 50) were used as natural prey organism with a well-developed escape response (Singarajah 1969; Buskey 1994; Kiørboe 2010). Copepods were cultured within 240 L tanks at a salinity of 18 PSU and at temperatures between 20-22°C following the procedures described in Holste and Peck (2006). To ensure a better comparability of feeding rates obtained for different prey types, we used similar sized *Artemia* nauplii and *A. tonsa*. Average body lengths (µm) of the prey items from each experiment were measured using ImagePro Plus® on digital images captured with a camera (Leica-300®) mounted on a binocular microscope (Leica®) at a magnification of 50. As *Artemia* nauplii are generally reddish in colour, we fed *A. tonsa* with *Rhodomonas sp.* shortly before each experiment to assure a similar coloration of both prey types. *A. tonsa* swim in a sink-and-hop pattern, whereas *Artemia* have a smoother swimming behaviour. By comparing prey of similar size and pigmentation, it is assumed that prey with active and irregular swimming behaviour is more attractive for predators than prey with reduced motion (Buskey et al. 1993). However, we assumed this aspect can be neglected if light intensity in the water clearly exceeds the threshold for particulate-feeding (0.01 lx for herring; Batty et al. 1990) and if the offered prey is relatively large.

4.3.3 Experimental setup

Overall we used 60 sprat (63.0 ± 5.3 mm total length TL) and 50 herring (81.7 ± 7.1 mm TL) in 49 experiments (Table 4.1). The experiments were conducted using groups of fishes since it is not possible to maintain species like herring and sprat individually. Two to five experiments with different initial target prey concentrations from approx. 10 to 160 L^{-1} were performed per experimental series (Table 4.1). During an experiment the initial target prey concentration was maintained constant for 60 min by adding food continuously. This period with constant prey concentrations ensured that prey items were distributed homogeneously within the experimental tank, and that fish acclimatized to the food supply. Furthermore, the data from this period were used to test for any trends due to saturation or feeding stimulation. After this period food addition was stopped and prey concentration decreased exponentially due to feeding activity of fish and the water overflow (Fig. 4.1). A series of experiments were carried out with the same fish group of 10 individuals within one week feeding on either *A. tonsa* or *Artemia* nauplii (herring = 5 fish groups; sprat = 6 fish groups; Table 4.1). At the start of each series, fish were carefully transferred into the experimental tank and therein acclimated for 2 days. During this period no food was supplied. Unfortunately, experiments with *A. tonsa* were performed less frequently than with *Artemia* nauplii due to limits in the production of live copepods given the longer generation time compared to *Artemia* (Table 4.1).

Table 4.1: Summary of feeding experiments with herring and sprat. Within each experimental series 2-5 experiments with different initial prey concentrations of lived Artemia nauplii or A. tonsa were generated randomly. *Nomenclature of experimental series based on: fish species (H = herring; S = sprat) and the different fish groups (numeration), which each consisted of 10 fish. During an experiment, only data from the 50-60 min interval onwards was used for the statistical analysis, therefore, prey concentration at this interval was considered as starting point.*

Herring			**Sprat**		
exp. series	number of exps.	prey concentration [L^{-1}] at 50-60 min interval per exp.	exp. series	number of exps.	prey concentration [L^{-1}] at 50-60 min interval per exp.
***Artemia* nauplii as prey**					
H1	5	16; 16; 10; 40; 67	S1	3	156; 59; 26
H2	5	19; 16; 21; 55; 79	S2	5	14; 8; 70; 66; 32
H3	5	32; 41; 16; 8; 56	S3	5	42; 68; 6; 17; 144
H4	2	55; 43	S4	2	50; 78
			S5	2	73; 27
			S6	2	30; 78
***A. tonsa* as prey**					
H4	3	18, 8; 15	S4	2	44; 104
H5	4	41; 31; 16; 26	S5	2	26; 73
			S6	2	26; 97

The experimental tank (401 L; Fig. 4.1) was placed in a separate room of the laboratory to prevent external disturbance of fish during experimentation. The equipment used for food supply and the determination of prey concentrations was visually separated from the tank by a wall. Additionally, the inside of the tank was covered with black foil to minimize the stress of fish. The experimental tank was divided into a prey-mixing chamber (162 L) and a fish chamber (239 L) separated by a PVC-panel with two circular holes (Fig. 4.1) allowing water exchange between the two chambers. A gentle circular water drift of double filtered (20 and 1 µm pore diameter) artificial seawater from the recirculation system was powered by the aeration (Fig. 4.1). That water flow promoted a homogeneous distribution of prey items within both chambers. Through the upper hole prey was transported into the fish chamber and through the lower hole uneaten organisms streamed back into the mixing chamber (Fig. 4.1). To create lighting conditions of 1.3-1.0 lx, allowing particulate-feeding (Batty et al. 1990), a 40-watt bulb was placed above the tank.

Feeding behaviour of fish during experiments was recorded using an infrared camera (TV 7143 *ABUS*; Resolution: 420-600 TV-Line) mounted underwater near the bottom of the tank in the PVC-panel (Fig. 4.1). A light-reflecting box with infrared-LEDs allowed the observation of fish as dark objects against an illuminated background (Fig. 4.1). Each chamber of the experimental tank contained a tube (I + II; Fig. 4.1) for food addition to achieve a specific initial target prey concentration in the whole tank (Fig. 4.1). This concentration was maintained constant for 60 min by continuously supplying (peristaltic pump; 36 mL min^{-1}; Gilson Minipuls II) a prey suspension of a known concentration into the mixing chamber (Fig. 4.1). The necessary concentration of the prey suspension was calculated from the theoretical losses of food due to fish's feeding and the water overflow. The assessment of prey loss due to fish's feeding was initially based on biting rates observed from preliminary experiments. The additional observations from each experiment were then used to constantly update the estimation of prey loss. Experiments lasted until no feeding fish were observed on the screen. The total duration of an experiment was 90-150 min. To determine the actual prey concentrations in the tank during the entire experiment, all prey items lost through the overflow (3.83 L min^{-1}) were collected every 10 min (time intervals = 0-10, 10-20, 20-30…) by a 100-µm mesh-bottomed cup (Fig. 4.1). Collected prey items of all time intervals were counted under a binocular for all concentrations < 25 L^{-1}, and for every second time interval at concentration higher than 25 L^{-1}. If prey was not counted manually, their numbers were estimated by dry weight using weights from counted probes as a reference.

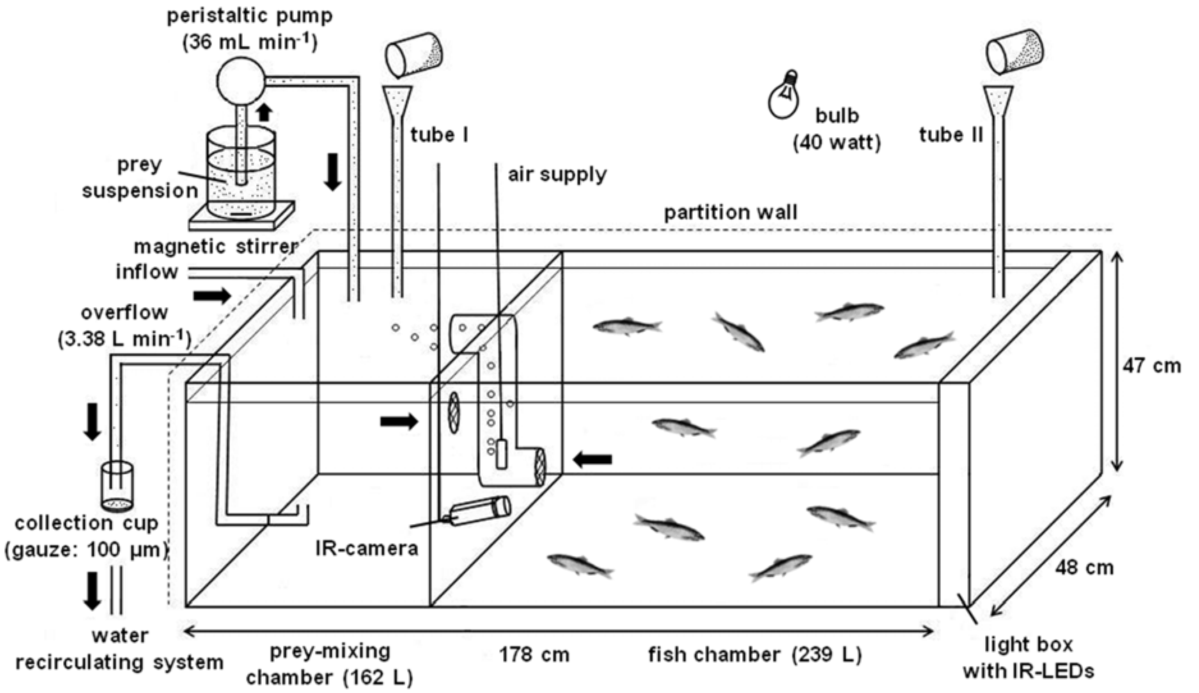

Figure 4.1: Diagram of experimental arrangement. All needed apparatus were visually separated from the tank by a partition wall (dotted line)

4.3.4 Data analyses

All statistical analyses were performed using the R statistical program version 2.13.1 (R Development Core Team 2011).

The prey concentration (C_t) for a 10 min time interval was calculated from $C_t = N_t / FR$, where N_t is the total number of prey items (N) in the collection-cup divided by the length of the time interval, and FR is the overflow rate (3.83 L min^{-1}). The recorded videos (25 frames s^{-1}) were played with half-speed to determine the average biting rate for each 10 min time interval of an experiment. In each 10 min time interval 15-20 individual fish were tracked. Fish were selected randomly by pointing with eyes closed on the computer screen and taking the nearest fish that was well in focus. Each individual fish was tracked for 10-60 s and its biting rate (biting acts s^{-1}) was determined visually. It was considered that only one prey item was consumed per biting act.

Trends in biting rates over the first 60 min of constant prey concentrations could indicate saturation effects, physical fatigue or a stimulation of feeding activity. Thus, we compared the biting rates of the 10-20 and 50-60 min time intervals for the highest initial target prey concentration of each exp. series (Table 4.1) by a student's paired *t*-test.

We also determined the duration between two biting acts on a frame-by-frame basis as total feeding time t_t. Total feeding time is composed of different activities: search (t_s), detection (t_d), approach (t_a) and prey handling (t_h). Handling time for *Artemia nauplii* and *A. tonsa* was defined as the time for prey biting: t_h is the time between opening and closing of the fish mouth. For *A. tonsa* handling time additionally included the time for *S*-shaped curvation of the body before biting. Unfortunately, it was not possible to quantify t_s, t_d and t_a separately due to the insufficient resolution of the infrared camera and the fast succession of these events. However, under the assumption that t_h was constant per prey type, we derived the relationship between the sum of t_s, t_d and t_a and prey concentration. For better comparability of total feeding times for both prey types we only used data of sprat exp. series S4, S5 and S6, as they experienced similar prey concentrations of *Artemia* nauplii and *A. tonsa* (Table 4.1). Prey specific comparisons of total feeding times on an exp. series basis were done by a student's paired *t*-test.

4.3.4.1 Model fitting

We analysed the feeding responses of sprat and herring in relation to different prey types (*Artemia nauplii* and *A. tonsa)* and concentrations using nonlinear mixed effects models. The analysis was performed with the nlme-package (version 3.1-101) in R (Pinheiro et al. 2011) and followed the descriptions in Pinheiro and Bates (2000) and Zuur et al. (2009). Nonlinear mixed effects models were chosen as they can accommodate unbalanced data (prey concentrations) as well as repeated measurements on the same exp. series (Table 4.1). In addition, the models allow for the inclusion of random factors, which account for the between-series variability and heterogeneous variance (Lindstrom and Bates 1990; Pinheiro and Bates 2000; Aggrey 2009). To avoid pseudo-replication only measurements from the 50-60 min intervals onwards were used. Since none of the data series displayed any sigmoid pattern a Michaelis-Menten-model, which is mathematically equivalent to Holling's disc equation model (1959), was used to represent the expected biting rate (*BR*) as a function of prey concentration (*c*):

$$BR_{ij} = BR\max_i \times c_{ij} / (k_i + c_{ij}) + \varepsilon_{ij},\ \varepsilon_{ij} \sim N(0, \sigma^2)$$ ***Equation 4.1***

where BR_{ij} (s^{-1}) is the *j*th observation of biting rate on the *i*th experimental series ($i = 1, \ldots, M$ $j = 1, \ldots, m_i$); M is the total number of series, and m_i is the total number of observations on the *i*th series ; c_{ij} is the corresponding prey concentration (L^{-1}); $BRmax_i$ is the maximum biting rate (s^{-1}), and k_i is a constant, which indicates the prey concentration at $BRmax_i/2$; ε_{ij} is a normally distributed noise term and σ^2 is the variance for the residuals. The series-specific parameters $BRmax_i$ and k_i are modelled as the sum of two components:

$$\begin{bmatrix} BR\max_i \\ k_i \end{bmatrix} = \begin{bmatrix} \beta_1 \\ \beta_2 \end{bmatrix} + \begin{bmatrix} b_{1i} \\ b_{2i} \end{bmatrix} = \beta + b_i,\ b_i \sim N(0, {\sigma_b}^2)$$ ***Equation 4.2***

where *β* is a vector of fixed effects parameters common to all exp. series; b_i is a random effects vector associated with series *i*, which represents the deviation of the expt. series parameters from the population average, and σ^2_b is the variance of the random effects (Lindstrom and Bates 1990; Pinheiro and Bates 2000). It is further assumed that observations made on different series are independent and the within-series errors ε_{ij} are independent of the random effects.

We introduced the covariates prey type and fish species in the model to explain the $BRmax_i$ and k_i series-to-series variation (Pinheiro and Bates 2000). Thus the formulations for $BRmax_i$ and k_i were expanded:

$$BR\max_i = \beta_1 + \gamma_{01}x_{1i} + \gamma_{02}x_{2i} + \gamma_{03}x_{1i}x_{2i} + b_{1i},$$

$$k_i = \beta_2 + \gamma_{11}x_{1i} + \gamma_{12}x_{2i} + \gamma_{13}x_{1i}x_{2i} + b_{2i},$$

Equation 4.3

$$x_{1i} = \begin{cases} -1, fish_i = herring, \\ \;\; 1, fish_i = sprat, \end{cases} \quad x_{2i} = \begin{cases} -1, prey_i = Artemia, \\ \;\; 1, prey_i = A.tonsa, \end{cases}$$

where x_{1i} and x_{2i} are binary indicator variables for fish species and prey type; β_1 and β_2 are, respectively, the average maximum biting rate *BRmax*$_i$ (*Intercept*) and constant k_i (*Intercept*); γ_{01} and γ_{11} represent the fish species main effect on *BRmax*$_i$ (*BRmax fish*) and k_i (*k fish*); γ_{02} and γ_{12} are, respectively, the prey type main effect on *BRmax*$_i$ (*BRmax prey*) and k_i (*k prey*); γ_{03} and γ_{13} represent the fish species-prey type interaction effect on *BRmax*$_i$ (*BRmax fish:prey*) and k_i (*k fish:prey*). Moreover, β_1, β_2 and γ_{01}, γ_{11}, respectively, represent the *BRmax*$_i$ and k_i for herring and sprat feeding on *Artemia* nauplii; γ_{02}, γ_{12} and γ_{03}, γ_{13}, respectively, represent the *BRmax*$_i$ and k_i for herring and sprat with *A. tonsa*.

The next step was to optimize the random part of the model. The very high correlation between *BRmax*$_i$ and k_i suggested that the random effects model was over-parameterized (Pinheiro & Bates 2000). Thus we decided that only *BRmax*$_i$ needed random effects as there appeared to be more variability in the *BRmax*$_i$ estimates than for k_i estimates. In addition, initial data analyses showed that residual spread varied per fish species and prey type, and decreased with increasing prey concentrations. To take into account the heterogeneity of variance we compared different variance functions and chose the appropriate structure by Akaike information criteria (AIC) (Zuur et al. 2009). The variance structure was finally modelled with the *varPower* variance function (Pinheiro and Bates 2000), which includes the influences of prey type, fish species and prey concentration on residual spread. To test if the random term is really needed we also compared the AIC of the mixed effects model with an extended nonlinear regression model without random effects (gnls generalized nonlinear least-squares; nlme-package in R).

4.4 Results

4.4.1 Experimental procedure

In all experiments the number of fish feeding was very high (rarely, 1-2 fish did not feed in an experiment). To test if saturation effects occurred during the experimental phases with constant food concentrations, we compared the biting rates of the 10-20 and 50-60 min intervals for the highest initial prey concentration of each exp. series (Table 4.1). Paired *t*-tests revealed no significant increases or decreases of feeding rates between these intervals for all series (Table 4.2). The strong dependence of biting rates on prey concentrations can be seen in Fig. 4.2. Prey concentrations remained stable at the first 60 min of experiment, followed by an exponential decrease of prey concentrations and biting rates after the stop of the food supply. The loss of prey items during an experiment was caused mainly by feeding activity of fishes (84 ± 8 %; N = 512 time intervals) and only to a small extent by the overflow (16 ± 8 %; N = 512 time intervals).

Table 4.2: Results of paired t-tests to compare the biting rates of the 10-20 and 50-60 min time intervals for the highest initial prey concentration of each exp. series; n.s. non significant with P > 0.05

exp. series	***t* value**	**df**	***P***	**exp. series**	***t* value**	**df**	***P***
***Artemia* nauplii as prey**				***A. tonsa* as prey**			
H1	0.0764	11	*n.s.*	H4	-1.1905	15	*n.s.*
H2	1.0472	11	*n.s.*	H5	-0.6411	14	*n.s.*
H3	0.7419	11	*n.s.*	S4	1.5894	12	*n.s.*
H4	-1.8064	16	*n.s.*	S5	0.9564	13	*n.s.*
S1	1.573	16	*n.s.*	S6	0.3637	13	*n.s.*
S2	0.9716	16	*n.s.*				
S3	-1.0158	12	*n.s.*				
S4	1.5475	13	*n.s.*				
S5	0.0371	13	*n.s.*				
S6	-1.7261	10	*n.s.*				

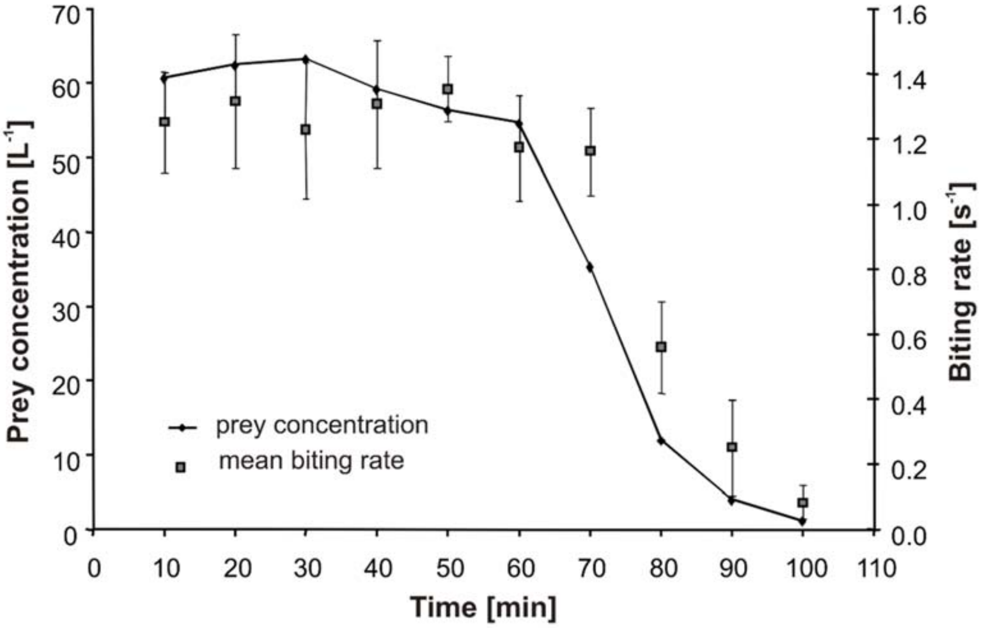

Figure 4.2: Example of change in prey concentrations (L^{-1}) and mean biting rates (s^{-1}) (± SD) over experimental time for herring feeding on Artemia nauplii (Table 4.1, H2, prey concentration at 50-60 min interval = 55 L^{-1}). *Prey items were constantly added during the first 60 min in order to maintain a stable concentration. After this period food addition was stopped and prey concentration decreased exponentially due to feeding activity of fish and the water overflow.*

4.4.2 Feeding behaviour

In the absence of food, herring and sprat swam around continuously in loose schools. The introduction of prey items initiated a feeding response, characterized by an increase of swimming speeds and the onset of particulate-feeding, depending on prey concentration. During feeding, fish did not school but aligned themselves to prey items with frequent turns and changes of direction. The act of biting, the main feeding mode of herring and sprat, was characterized by a rapid opening and closing of the mouth (Fig. 4.3 a,b). Handling time for a simple biting act lasted 0.12-0.16 s. Sprat showed only particulate-feeding, whereas herring sometimes switched to filtering or gulping when food concentrations were > 50 L^{-1}. Gulping is an intermediate feeding type between biting and filtering (Gibson and Ezzi, 1990) and lasted 0.20-0.24 s. During each filtering event of herring the mouth was opened wide and the operculum flared. A filtering event lasted on average 0.68 s (Fig. 4.3 c). When herring and sprat were feeding on *Artemia* nauplii both fed only by simple biting whereas fish feeding on *A. tonsa* mostly took up a characteristic *S*-shaped curvation of the body prior to the attack (Fig. 4.4). Handling time for a biting act with *S*-shaped curvation lasted on average 0.48 ± 0.19 s, N = 27. It appeared that the body of fish was contracted and released like a spring in order to attack a prey item with higher acceleration. The amplitude of the contraction reached a maximum just before the onset of the strike. Overall, sprat and herring attacked their prey predominantly from below (Fig. 4.3, 4.4).

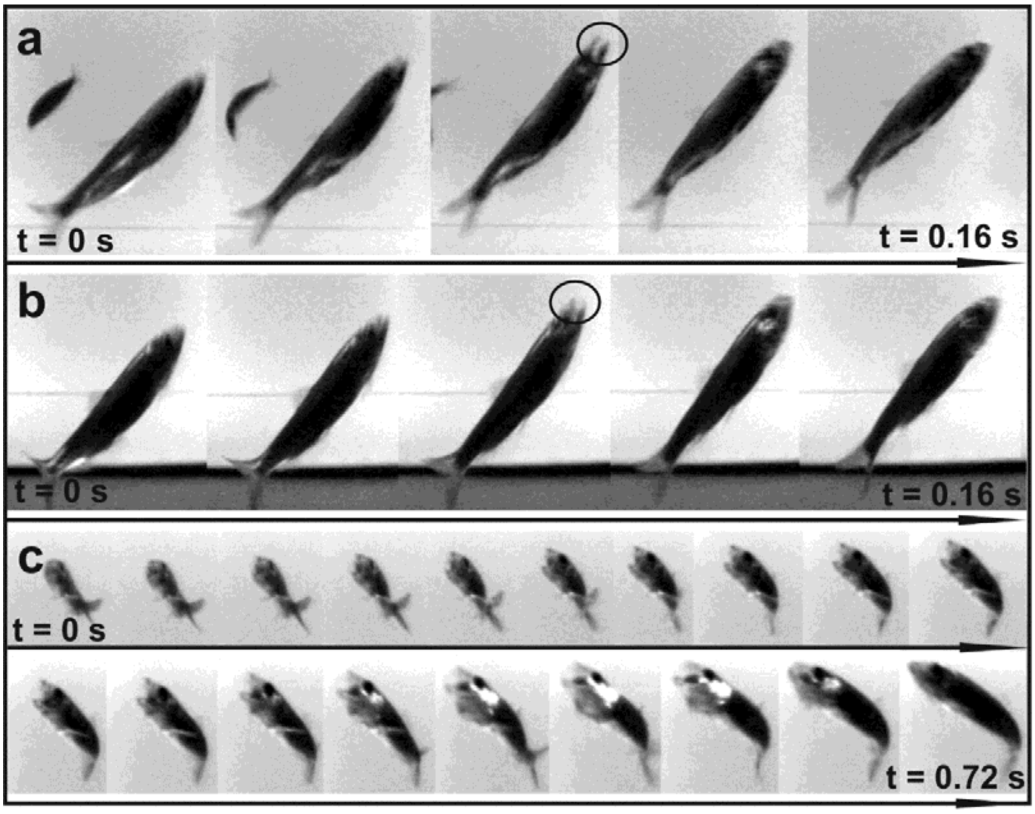

Figure 4.3: Frame-by-frame illustration of typical movements of sprat (a) and herring (b) during particulate- or filter-feeding (c) on Artemia nauplii. *Circles indicate the moment of mouth opening.*

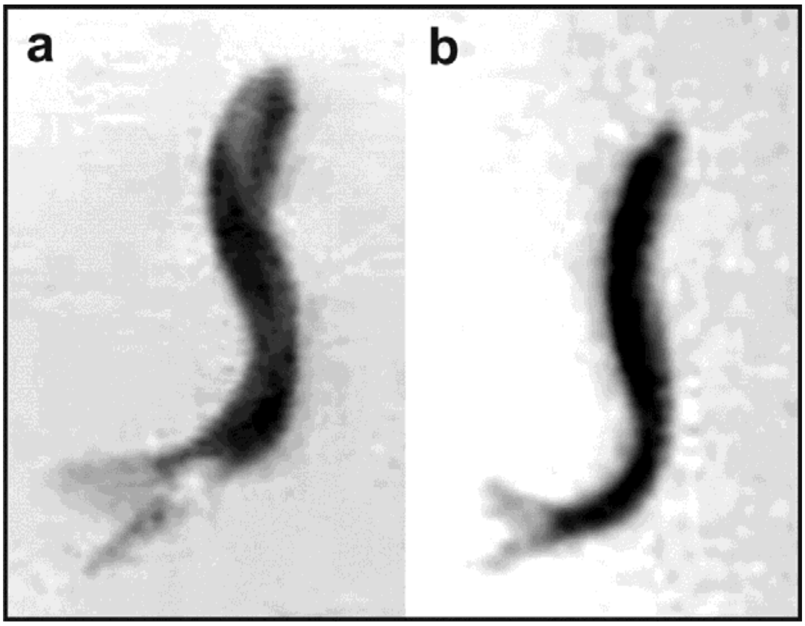

Figure 4.4: Particulate-feeding with S-shape curvation of the body of herring (a) and sprat (b) feeding on A. tonsa

At prey concentrations of > 15 L^{-1} both fish species swam in a vertical zigzag pattern, with repeated bites while swimming upwards at an angle of about 35-45° (Fig. 4.5). Near the surface fish performed a 180° turn followed by a downward swimming movement. After another turn the next feeding sequence started immediately (Fig. 4.5). In the majority of cases fish did not utilize the full height of the tank (47 cm). Mostly they stopped feeding at 5-10 cm before the surface. Between two and twelve attacks were performed in succession before fish swam downwards. The upward and downward swimming sequences lasted about 2.0-2.5 s and 0.5-0.7 s, respectively. At lower concentrations (< 15 L^{-1}) fish changed their swimming behaviour and did not show a vertical movement pattern like described above. Instead fish increasingly searched more or less at the same water depth.

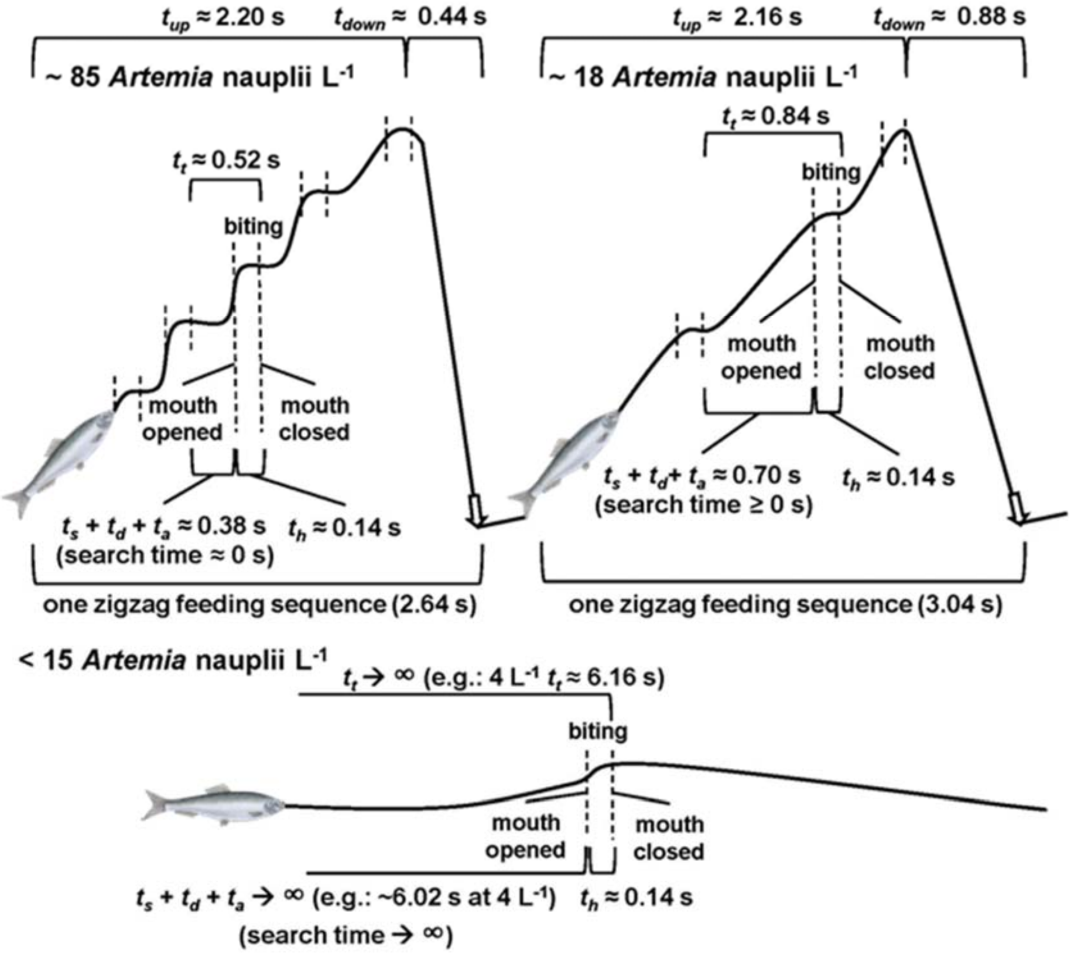

Figure 4.5: Exemplary illustration of the feeding behavior of sprat (S5, total length = 59.0 ± 4.0 mm) feeding on different Artemia nauplii concentrations. *t_{up} = time for upward swimming; t_{down} = time for downward swimming; t_t = total feeding time; t_s = search time; t_d = detection time; t_a = approach time; t_h = handling time*

4.4.2.1 Feeding time for A. tonsa and Artemia nauplii

Frame-by-frame analysis of the feeding behaviour allowed the estimation of total feeding times (s) at different concentrations for both prey types (Fig. 4.6). Total feeding time decreased strongly with increasing prey concentration *c* and asymptotically approached a minimum value ($t_{t\ Artemia\ nauplii} = 6.14c^{-0.62}$; $t_{t\ A.\ tonsa} = 6.66c^{-0.49}$; Fig. 4.6). The comparison of total feeding times at high prey concentrations (> 20 L^{-1}) for sprat exp. series 4, 5 and 6 (Table 4.1) revealed that sprat showed significantly longer total feeding times with *A. tonsa* (t_{t_min} = 1.08 ± 0.29 s, N = 22) than with *Artemia* nauplii (t_{t_min} = 0.65 ± 0.11 s, N = 17) (paired *t*-test: t_{S4} = -7.906, $P < 0.01$; t_{S5}= -51.669, $P < 0.001$; t_{S6} = -6.450, $P < 0.01$).

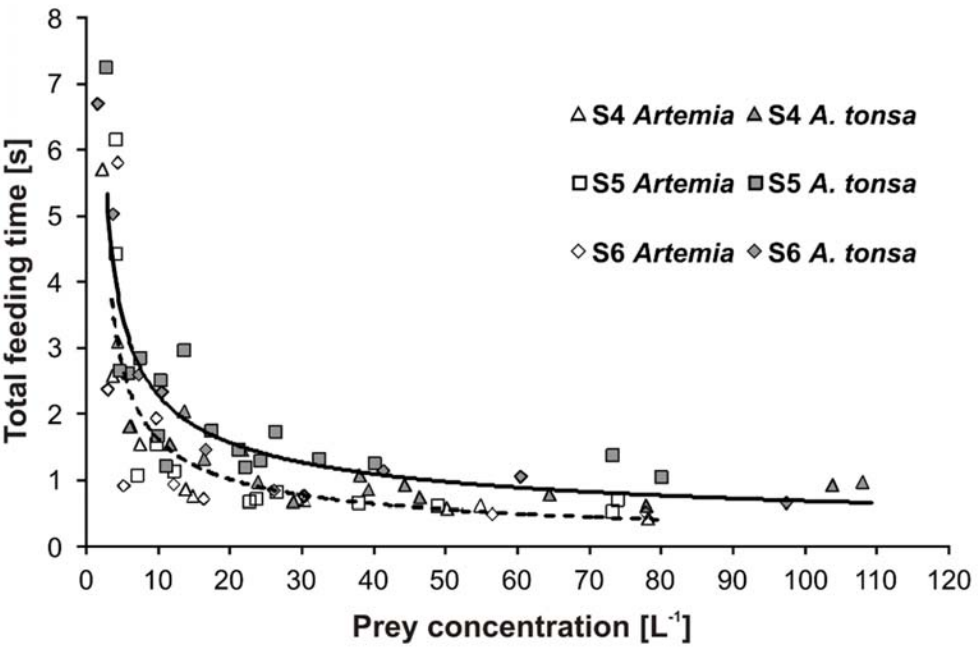

Figure 4.6: Total feeding times t_t (s) (duration between two biting acts) at different prey concentrations c (L^{-1}). *Only data from experiments with sprat exp. series S4, S5 and S6 preying on A. tonsa (filled symbols and solid line; t_t = 6.66c-0.49; r^2 = 0.77) or Artemia nauplii (unfilled symbols and dotted line; t_t = 6.14c-0.62; r^2 = 0.76) were used (Table 4.1).*

4.4.3 Functional response

Biting rates of sprat and herring as a function of *A. tonsa* or *Artemia* nauplii concentrations followed in all series a functional response type II (Fig. 4.7, 4.8). The mixed effects model described the data considerably better than the extended nonlinear regression model without a random component to account for exp. series (Table 4.1) effects (ΔAIC = 28.55). The *t*-statistics indicated a strong prey-type effect, but no significant fish species effect, with the exception of a significant fish species:prey type interaction on the parameter *k* ($P = 0.04$) (Table 4.3). This implies that at low prey concentrations (< 40 L^{-1}) the biting rates of herring ($k_{herring:A.\ tonsa}$ = 12.01) with *A. tonsa* were higher than those of sprat ($k_{sprat:\ A.tonsa}$ = 25.42) (Table 4.3). However, the estimated maximum biting rates of herring ($BRmax_{herring:A.\ tonsa}$ = 0.95 s^{-1}) and sprat ($BRmax_{sprat:A.\ tonsa}$ = 1.06 s^{-1}) feeding on *A. tonsa* were similar (Table 4.3). Both predators showed significantly higher biting rates with *Artemia* nauplii than with *A. tonsa* ($P \leq 0.0001$; Table 4.3). The estimated maximum biting rates ($BRmax_{herring:Artemia\ nauplii} = 2.17\ s^{-1}$; $BRmax_{sprat:Artemia\ nauplii} = 2.04\ s^{-1}$) and the parameter k ($k_{herring:Artemia\ nauplii} = 36.36$; $k_{sprat:Artemia\ nauplii} = 28.42$) with *Artemia* nauplii were not significantly different between herring and sprat. The goodness of the fit of the mixed effects model can be visualized by displaying the fitted and observed values in the same plot (Fig. 4.8). Both the population prediction (obtained by setting the random effects to zero) and the within-series predictions (using the estimated random effects) are illustrated (Fig. 4.8). Additionally, the coefficient of determination (r^2) from linear regressions of observed versus predicted biting rates were estimated for both fish species and prey types. Values of r^2 for herring and sprat feeding on *A. tonsa* were 0.83 ($F = 203.8$; $P < 0.001$) and 0.85 ($F = 273.4$; $P < 0.001$), and on *Artemia* nauplii 0.94 ($F = 1161$; $P < 0.001$) and 0.95 ($F = 2200$; $P < 0.001$), respectively. The residuals from the mixed effects model fulfilled the assumptions of normality and homogeneity of variance. The *varPower* (Pinheiro and Bates 2000) variance function adequately represented the within-series heteroscedasticity.

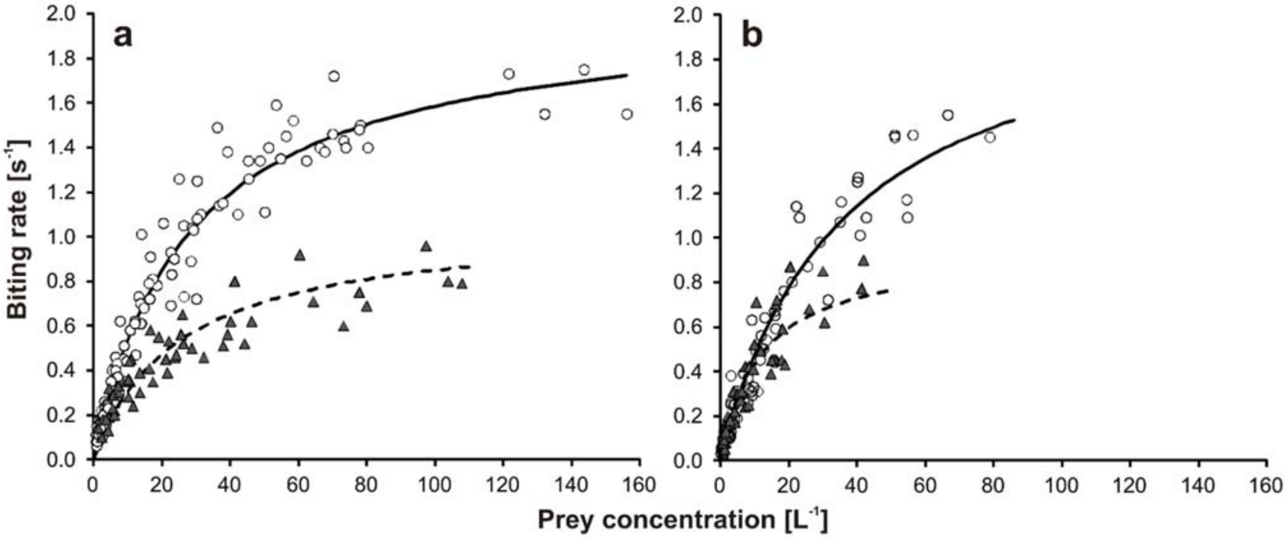

Figure 4.7: Biting rates (BR, s^{-1}) of sprat (a) and herring (b) feeding on Artemia nauplii (circles) or A. tonsa (triangles) at different concentrations (c, L^{-1}). *Plotted lines represent functional response type II fitted by the nonlinear mixed effects model ($BR = BRmax * c / (k + c)$; $BRmax_{spra:Artemia\ nauplii} = 2.04\ s^{-1}$, $k_{sprat:Artemia\ nauplii} = 28.42$; $BRmax_{sprat:A.\ tonsa} = 1.06\ s^{-1}$, $k_{sprat:A.\ tonsa} = 25.42$; BRmaxherring:Artemia nauplii = 2.17 s^{-1}, $k_{herring:Artemia\ nauplii} = 36.36$; $BRmax_{herring:A.\ tonsa} = 0.95\ s^{-1}$, $k_{herring:A.\ tonsa} = 12.01$)*

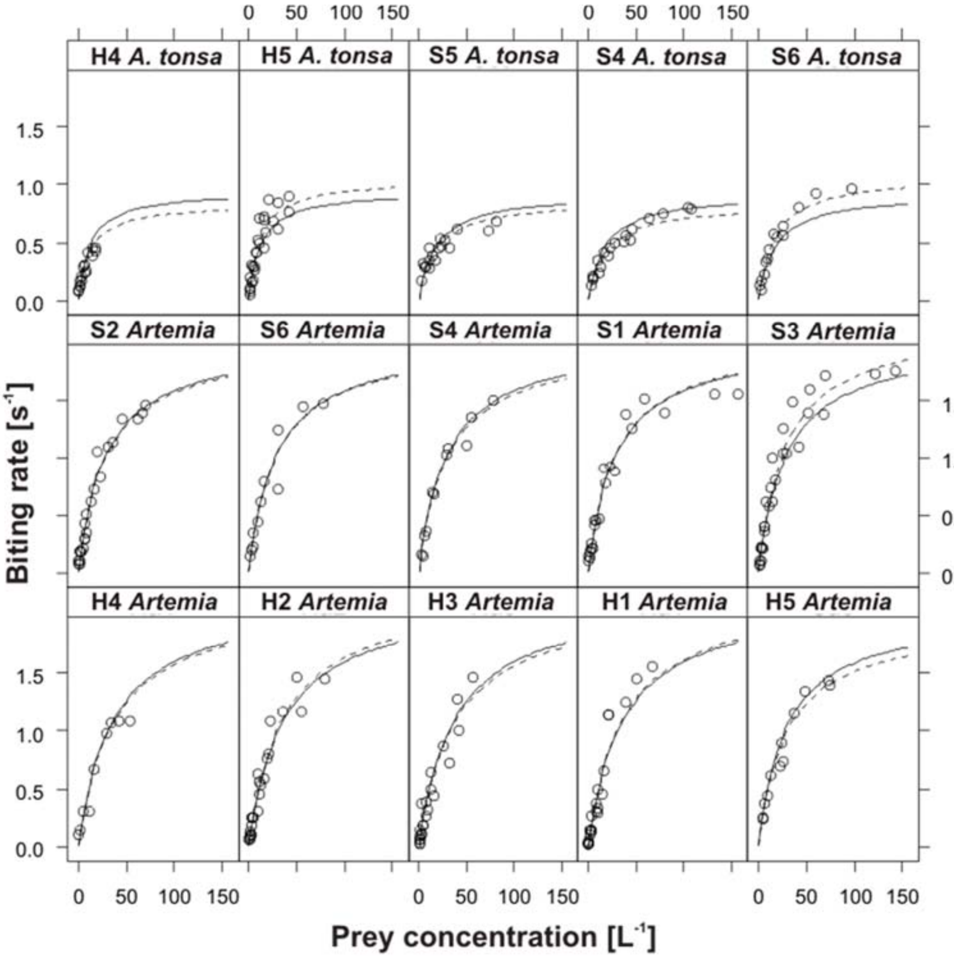

Figure 4.8: Experimental series-specific (dotted line) and population average (solid line) predicted biting rates (s^{-1}) obtained from the nonlinear mixed effects model (Table 4.3) and the corresponding observed values (circles). *The plots were created automatically by the R program using the results from the mixed effects model. The scaling per each subplot could not be changed manually. All curves are based on the obtained maximum concentration (x-axis). For herring this results in the curve extrapolating beyond the range where we have data. Nomenclature of experimental series based on: fish species (H = herring; S = sprat) and the different fish groups (numeration)*

Table 4.3: Functional response parameters and standard error estimates from the nonlinear mixed effect model. *The model was fitted by restricted maximum likelihood (REML). BRmax = maximum biting rate; k = Michaelis constant; σ2 = residual BR variance; σb2 = the series variance in BRmax within the population; AIC = Akaike information criterion; BIC = Bayesian information criterion; LogLik = log-likelihood. Parameters indicate, on the one hand, the main effect of fish species, prey type and fish:prey interaction on BRmax and k, and, on the other hand, the estimated BRmax and k values for sprat or herring feeding on Artemia nauplli or A. tonsa (listed in equation 4.3)*

	Mixed Model		
Parameter	Estimate ± SE	*t* value	*P*
BRmax (Intercept) herring : *Artemia*	2.173 ± 0.226	9.620	< 0.0001
BRmax prey herring : *A. tonsa*	0.945 ± 0.256	4.829	< 0.0001
BRmax fish sprat : *Artemia*	2.035 ± 0.243	9.051	0.5699
BRmax fish:prey sprat : *A. tonsa*	1.064 ± 0.280	5.257	0.6692
k (Intercept) herring : *Artemia*	36.359 ± 5.585	6.511	< 0.0001
k prey herring : *A. tonsa*	12.005 ± 6.011	2.459	0.0001
k fish sprat : *Artemia*	28.421 ± 5.928	5.171	0.1817
k fish:prey sprat : *A. tonsa*	25.416 ± 6.572	4.500	0.0423
σ^2	0.00156826		
σ_b^2	0.01047601		
logLik	305.293		
AIC	-582.585		
BIC	-532.207		

4.5 Discussion

4.5.1 Experimental procedure

The experimental design enabled the measurement of feeding rates under controlled laboratory conditions using techniques that caused only minimal stress for fish. This is confirmed by the high proportion of feeding fish during the experiments and the high biting rates at high prey concentrations. To actually observe a fish capturing a copepod, one would need a time resolution of two milliseconds and a spatial resolution of 15 µm in order to see the fish's mouth and the copepod's reaction (Strickler et al. 2005). Hence, the underwater images taken in the present study did not directly allow the detection of the feeding success of fish. For the analysis of the functional response type, we had to assume that each counted biting event was successful. This is most likely true when fish were feeding on *Artemia*, but less certain for experiments with *A. tonsa*, which have a relatively high escape responsibility (Singarajah 1969; Buskey 1994; Kiørboe 2010). However, we occasionally observed that fish were starting one feeding attack, but stopped abruptly and began searching for new prey items again. This behaviour most likely reflects an unsuccessful feeding event, where the copepod escaped from the visual field of the fish. We therefore assumed that a fish has successfully ingested one prey item when a biting attack was completed and the opening and closing of the fish's mouth was detectable.

At prey concentrations > 15 L^{-1} sprat and herring showed a vertical zig-zag swimming behaviour (Fig. 4.5). The extent of this upwards movement might have been limited by the height of the experimental tank (47 cm). However, fish in our experiments mostly did not utilize the full height of the aquarium. Additionally, *in situ* observations demonstrated that juvenile herring only attacked four to six times in succession while swimming upwards (Kils 1992). This is in line with our results with two to twelve attacks in succession. Thus, the observed feeding behaviour of sprat and herring at the present study is assumed to reflect a normal feeding behaviour.

4.6 Feeding behaviour

Clupeid fish like herring (Gibson and Ezzi 1985) and anchovy (Leong and O'Connell 1969; James and Findlay 1989) exhibit both filter- and particulate-feeding modes. In the present study herring started to filter-feed at prey concentrations of about > 50 L^{-1}, which is similar to the observations by Gibson and Ezzi (1985) for juvenile herring. In contrast, our results indicated that sprat, unlike other clupeids, is an obligate particulate-feeding species as previously suggested by Bernreuther (2007). Sprat exclusively sticked to particulate-feeding, even at prey concentrations of about 160 L^{-1}. Crowder (1985) suggested that the use of different feeding modes may be dependent on the relation of prey size to predator size. Durbin (1979) argued that fish particulate-feed when the prey size predator size ratio is in the range between 1:20 and 1:200, whereas filter-feeding occurs when prey size predator size ratio is in the range from 1:150 to 1:20000. He showed that even the juveniles of obligate filter-feeding Atlantic menhaden (*Brevoortia tyrannus*) are actually particulate-feeders. Filter-feeding is considered to be energetically more expensive than particulate-feeding (Gibson and Ezzi 1992) and thus seems to be beneficial only above a certain predator to prey size ratio and at higher prey concentrations. In the present study juvenile herring (7-9 cm TL) only rarely filter-fed at higher prey concentrations (> 50 L^{-1}), corresponding to an average prey size predator size ratio of 1:100 (prey item ~ 0.08 cm). *In situ* observations by Kils (1992) confirmed likewise that juvenile herring (38 mm mean length) attacked each copepod individually even at high prey concentrations of up to 850 L^{-1}. Clearly distinctive filter-feeding behaviour has only been observed for larger herring (13-20 cm TL; Gibson and Ezzi 1985, 1990, 1992). Contrary to herring, sprat stay relatively small (L-infinity = 14.9 cm TL; Alshuth 1989), which probably explains why sprat is an obligate particulate-feeder.

4.6.1 Functional response

The feeding rates of juvenile sprat and herring clearly followed a type II functional response (Holling 1959, 1966) (Fig. 4.7). Gibson and Ezzi (1992) and Bernreuther et al. (2008) supposed a type II response for herring, but due to the small amount of data at low prey concentrations these results remained uncertain. With our modified experimental design we were able to adjust and monitor feeding rates at very low prey concentrations, where the difference between a type II and a type III functional response would become evident. A type II response implies a high extinction risk for the prey as predation risk per prey capita increases with decreasing prey concentrations. Furthermore, clupeids are able to store large amounts of food items in their gastric cecum, which enables the sustained exploitation of high prey concentrations (Bernreuther et al. 2008). Hence, it appears possible that schools of sprat and herring are able to deplete local zooplankton patches within relatively short times given the combination of high maximum biting rates (~ 1 copepod s^{-1}), the high storage capacity and the type II functional response. Thus, we assume that sprat and herring are able to exert strong local top-down effects on prey populations. Hawkins et al. (2012) investigated the grazing of sprat schools on zooplankton within an enclosed Lough (Lough Hyne, Ireland). Acoustic surveys indicated that these schools rapidly depleted their surroundings of zooplankton and extensive volumes of water around them were largely devoid of zooplankton. The authors assume that this grazing effect on zooplankton also affected the primary producers with wider ranging implications for the ecosystem (Hawkins et al. 2012). Similar cascading effects have been discussed on a larger scale for the Baltic ecosystem as a consequence of the strong increase of the sprat populations in the 1990s (Rudstam et al. 1994; Köster et al. 2003; Casini et al. 2008)

A comparison of feeding rates from our study with results of previous investigations on clupeids is difficult due to differences in experimental techniques. Gibson and Ezzi (1992) investigated the feeding behaviour of herring (13-20 cm total length) at much higher prey concentrations of up to ~1000 L^{-1} observing maximum biting rates of about 1.5 s^{-1} and 1.0 s^{-1} in experiments with *Artemia* nauplii and the copepod *Calanus finmarchicus,* respectively. Bernreuther et al. (2008) used frozen copepods in experiments with herring (9-13 cm total length) and determined a maximum biting rate of 0.8 s^{-1} at prey concentrations of up to 600 L^{-1}. This rate is surprisingly low due to the non-existent escape response of the frozen food. A possible explanation is a higher proportion of filtering events with increasing prey concentration implying that the visually registered biting events were in fact rather gulping or short filtering events. Another explanation might be that feeding is stimulated more by living food (Buskey et al. 1993).

4.6.1.1 Differences in feeding rates between sprat and herring

The results have only confirmed our initial hypothesis partially: at low prey concentrations of copepods (approx. < 40 L^{-1}) herring could reach higher biting rates than sprat (Fig. 4.7). Unfortunately, we could not obtain a sufficient amount of data from herring preying on *A. tonsa* at higher concentrations due to the limit of the rearing facilities and the longer generation time of *A. tonsa* compared to *Artemia* nauplii. Thus, it remains uncertain whether herring also could reach higher maximum biting rate than sprat when feeding on *A. tonsa*. In contrast to experiments with copepods, the functional responses of both predators were very similar with *Artemia* nauplii.

It should be noted that herring in our experiments were slightly larger (~ 2 cm) in size than sprat. Actually, this size difference reflects the typical size structure of mixed schools of juvenile sprat and herring in the sea, where herring are on average 1-2 cm lager in size than sprat (Maes and Ollevier 2002). This size difference could have resulted in higher absolute swimming speeds of herring, allowing an increase of attack frequencies for active prey at low concentrations. Additionally, there is a growth-related change in the retina of planktivorous fish, which influences the ability to locate small particles or objects at larger distances (Blaxter and Jones 1967; Hairstone et al. 1982). Maes and Ollevier (2002) analysed the feeding dynamics of mixed schools of sprat and herring from the intake screens of the nuclear power plant Doel (Schelde estuary; Belgium). They found that the feeding rate of herring was significantly higher than that of sprat (principal prey group: calanoid copepods). Furthermore, the feeding intensity of sprat decreased significantly if herring became more dominant in the mixed-species schools (Maes and Ollevier 2002).

Our functional response type II model indicates that limited food environments may favor herring over sprat. Furthermore, herring have two additional competitive advantages over sprat: with increasing body size herring start to exploit larger prey items and filter-feed. Batty et al. (1986) even demonstrated that herring can filter-feed in the dark, resulting in longer daily feeding times compared to sprat.

Concluding, our results suggest that juvenile herring have a competitive advantage over sprat in mixed schools when prey concentrations are low and can therefore potentially reach higher growth rates than sprat.

4.6.1.2 Prey type effects

The feeding efficiency of sprat and herring was significantly higher ($P \leq 0.0001$) with *Artemia* nauplii than with *A. tonsa* (Table 4.3, Fig. 4.7). The lower feeding rates of both predators with *A. tonsa* are assumed to be mainly caused by copepod's well developed escape response compared to *Artemia* (Singarajah 1969; Trager et al. 1994; Kiørboe 2010). This assumption is supported by the fact that fish mostly showed an *S*-shaped curvation of the body before biting on *A. tonsa* (Fig. 4.4), while this behaviour was not observed when feeding on *Artemia* (Fig. 4.3 a,b). The feeding attack with *S*-shaped curvation was also described for herring (Rosenthal 1969) and anchovy (Hunter 1972) larvae. A simple straight biting attack of sprat and herring on *Artemia* nauplii took 0.12-0.16 s (Fig. 4.3 a,b), which is in agreement with the result of Gibson and Ezzi (1985) for herring (mean total length 15.7 cm) feeding on *Artemia*. In contrast, one attack on *A. tonsa* with curvation of the body lasted 0.24-1.08 s (Fig. 4.4). The high variability in time for feeding events with *S*-shape curvation presumably resulted from the variable spatial positions of fish in relation to the targeted prey item.

The total feeding time (duration between two biting acts) of particulate feeding planktivores includes different activities, such as search (t_s), detection (t_d), approach (t_a) and prey handling (t_h) (Fig. 4.5). Searching is defined as a non-directional swimming behaviour. Detection is indirectly deduced at the transition between search and approach, while approach is a directed movement towards the prey. The term "prey handling" originated from models of predators in terrestrial systems, which spend a lot of time on capturing, processing, and digesting of prey (Holling 1959, 1966). For planktivorous fish handling time is more difficult to measure since the different behavioural components are short and less conspicuous and digestion time plays no significant role. We defined handling time for *Artemia* nauplii as the time between opening and closing of the fish mouth. For *A. tonsa* handling time additionally included the time for *S*-shaped curvation of the body before biting.

Frame-by-frame analysis of sprat's feeding behaviour revealed that total feeding time decreased with increasing prey concentrations and asymptotically reached a minimum value ($t_{t\_min\ A.\ tonsa} \sim 1.08$ s; $t_{t\_min\ Artemia\ \mathrm{nauplii}} \sim 0.65$ s) (Fig. 4.5, 4.6). The curves were similar for both prey types, but the curve for *A. tonsa* was shifted to higher values at all concentrations. Paired *t*-test revealed that total feeding times at high prey concentrations (approx. > 20 L^{-1}) were significantly higher for *A. tonsa* than for *Artemia* nauplii ($P < 0.01$). Under the assumption of constant handling time per prey type, the proportion of search and approach time in total feeding time decreased with increasing prey concentrations. Hence, the relative contribution of handling time increases and ultimately limits the number of prey which can be consumed in a given time (Fig. 4.6). Subtracting the observed average handling time ($t_{h\ A.\ tonsa} = 0.48$ s; $t_{h\ Artemia\ \mathrm{nauplii}} = 0.14$ s) from the average total feeding time at high prey concentrations (> 20 L^{-1}) reveal similar values for the sum of search, detection and approach times for both prey types ($t_s + t_d + t_{a\ A.\ tonsa} = 0.60$ s; $t_s + t_d + t_{a\ Artemia\ \mathrm{nauplii}} = 0.51$ s).

Hence, the observed differences between the total feeding time curves and functional response curves of both prey types were mainly caused by the different prey handling times for *A. tonsa* and *Artemia* nauplii. The estimated higher biting rates for *Artemia* nauplii are assumed to reflect the maximum possible feeding rates of non-evasive prey such as cladocerans, whereas the results of experiments with *A. tonsa* are supposed to reflect their functional response in copepod dominated environments.

The confirmation of the functional response type II for two important planktivorous species and the parameterization for two relevant prey types (evasive and non-evasive) will improve model results of end-to-end ecosystem models, like NEMURO (Megrey et al. 2007) or ATLANTIS (Fulton et al. 2004). Additionally, our results can be regarded as a first step in developing a mechanistic understanding of the interaction of plankton populations and competing planktivorous fish species.

4.7 References

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5 Manuscript 2: Temperature and size-dependent maximum functional response of *Sprattus sprattus* L.

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5.1 Abstract

Functional response models (*per capita* feeding rate as a function of prey concentration) are often an essential component in ecosystem models or in process models investigating single-species growth rates. In the present study we provide a size- and temperature-dependent functional response model for juvenile and adult sprat (*Sprattus sprattus*). Functional response parameters were estimated from video observations of feeding sprat for three different size classes (3.6, 6.3 and 8.7 cm total length TL) and five temperatures from 5 to 20°C. Non-evasive *Artemia salina* nauplii were used as prey (concentration 1 to 330 L^{-1}) to estimate the physiologically possible maximum feeding rate of sprat. Sprat showed a functional response type II. Feeding rates clearly increased with increasing body sizes and temperatures. Body size effect on feeding rate was more pronounced for smaller sprat < 6 cm TL than for larger sprat. Comparison of observed biting rates from video analysis and rates calculated by the decreasing

prey concentrations in the experimental tank revealed that sprat, in particular at lower prey concentrations, did not perform their maximum feeding response continuously. This finding was also made by the contrast of predicted stomach content weight using our model with observed weight of sprat from field. A simple bioenergetics budget model of juvenile sprat (4 to 8 cm TL) feeding at mean prey concentration of 10 L^{-1} revealed a hump-shaped energetic efficiency (*per capita* energy intake by our functional response model relative to metabolism) in relation to temperature. Our study advances the mechanistic understanding of how prey concentration, temperature and body size effect interact determining feeding and growth rates of early post larval juveniles.

5.2 Introduction

The functional response describes the relationship between the *per capita* feeding rate and prey density (Solomon 1949). There are three main functional response types (Holling, 1959). The Type I functional response takes a linear form and is typical for filter-feeding organism either having a negligibly small handling time (time to kill and ingest a prey) or being able to search and capture prey while handling other food (Jeschke et al. 2004). In a Type II response, feeding rate increases with increasing prey density, but the rate increase is progressively reduced until an asymptote is reached at high concentrations (Juliano 2001). This type can potentially destabilized prey population because prey mortality increases with decreasing prey population density (Sarnelle and Wilson 2008). In contrast, the type III response is characterized by a sigmoid shape leading to decreasing prey mortality also at low prey densities (Sarnelle and Wilson 2008). Functional response models are often an essential component in larger ecosystem models that predict how fish and plankton population interact as a function of multiple variables (e.g. predator and prey body size) (Fennel 2010; Hunsicker et al. 2011) or in process models investigating single-species growth rates (Günther et al. 2015). As the feeding rate of fish strongly depends on temperature (Persson 1986; Lefébure et al. 2014, Englund et al. 2011) and the body-size relationship between predator and their prey (Moss and Beauchamp 2007; Mittelbach 1981; Persson et al. 1998) functional response models need to be parameterized for different fish sizes and temperatures to improve the prediction of feeding rate in relation to spatial-temporal variability in biological and physical conditions.

In the present study, the effects of temperature and fish size on the functional response are investigated for the ecologically and economically important planktivorous sprat (*Sprattus sprattus*). Sprat play a key role in the pelagic ecosystem of the Baltic Sea as they have a marked impact upon their prey communities (copepods and cladocerans) and are likewise an important source of food for piscivorous predators (e.g. Baltic cod (*Gadus morhua*)) (Möllmann et al. 2004; Ojaveer and Kalejs 2010). A previous study showed that juvenile sprat exhibit a functional response Type II (Brachvogel et al. 2013). However, the study was mainly focused on the comparison of two relevant prey types (evasive or non-evasive). Feeding rate of sprat was by the factor 0.53 lower when preying on *Acartia tonsa* with well-developed escape abilities than on non-evasive *Artemia salina* nauplii (Brachvogel et al. 2013). All experiments in the previous study were conducted at only one temperature (16 °C) and one sprat size (6.3 cm total length TL). Thus, the present study extents the existing functional response model for juvenile sprat by the variables temperature and body size. The effect of temperature on the feeding rate of sprat is particularly important as water temperatures not only change seasonally, but also during diel vertical migration (DVM) within the water column (Cardinale et al. 2003, Nilsson et al. 2003). Sprat moves to the surface at night and to the bottom at day (Cardinale et al. 2003). During the extensive feeding period of sprat in summer in the Bornholm Basin, temperatures could range from 7 °C in the deeper layers to 16 °C near the surface (Voss et al. 2012). If feeding rates of sprat are strongly depend on temperature, feeding in deeper layers during the day could be extremely unfavourable. Furthermore, Günther et al. (2015) highlighted that temperature influenced the survival of sprat cohorts, but the mechanism is still not fully understood. Due to the extended spawning season of sprat from March to August (Grimm and Herra, 1984; Elwertowski 1960), early juvenile sprat from different season cohorts are exposed to highest temperatures at different sizes and ages (depending on their spawning date) (Günther et al. 2015). Investigations of the otolith microstructure of sprat recruits revealed that season cohorts born later in the year appear to have improved survival probabilities. Thus, information on the temperature- and size-dependent functional response of sprat linked with seasonal temperatures and prey densities as well as temperature dependent metabolism could improve the mechanistic understanding of the differential survival of early and late season cohorts of sprat recruits.

The objective of the study was therefore to provide a temperature- and size-dependent functional response model for sprat. Body size- and temperature-related parameters of feeding rates were estimated experimentally at five temperatures from 5 to 20 °C with three different sizes classes (3.7, 6.3 and 8.7 cm total length TL). *Artemia salina* nauplii were used as prey at concentrations between 1 and 330 L^{-1}. Non-evasive *A. salina* is ideal to estimate the physiologically possible maximum feeding rate of sprat. In addition, they are comparable with the main prey species of sprat like cladocenrans, *Temora longicornis* and *Pseudocalanus acuspes* in terms of their vulnerable to fish predation (Viitasalo et al. 2001, Bernreuther et al. 2013). To validate the observed biting rates from video analysis we also quantified the stomach contents of experimental fish. In addition, we compared the observed biting rates with biting rates calculated by the decreasing prey concentrations in the experimental tank. To verify our results we also contrast the predicted stomach content weight using our functional response model with the observed weights from field. Furthermore, to provide a potential mechanistic explanation for the importance of timing for sprat cohorts, we estimated the energetic efficiency of juvenile sprat (4 to 8 cm TL) in relation to different temperatures. The energetic efficiency of an organism is the ratio between the energy intake by feeding (our functional response model) and loss through metabolism (Rall et al. 2010, Vucic-Pestic et al. 2011, Sentis et al. 2012).

5.3 Material and Methods

5.3.1 Capture and maintenance of experimental fish

Young-of-the-year sprat were caught in September 2013 and 2014 in the harbour of Wendtorf (Baltic Sea, 54°41’N; 8°36’8E) with a hand-operated dip-net (area: 4m^2; mesh size 6mm) and then transported in a 700-1000L box with aerated sea water to the aquarium facilities of the Institute of Hydrobiology and Fishery Science at the University of Hamburg. Prior to experiments, sprat were maintained in groups of 1000-2000 individuals in circular tanks (1,000L). Tanks were supplied with continuous flow of mechanically and biologically filtered, artificial sea water (Aqua medic) from the recirculation system. Before the experiments, sprat were slowly acclimated to laboratory conditions (Temperature = 12.0 ± 0.1 °C; Salinity = 16 PSU). Fish were maintained under a 13 L:11 D light regime and were fed an artificial pellet diet (Marico advance 0.5-0.8 mm, Coppens International bv) and live *Artemia salina* nauplii (SEPArt-Cysts, INVE Aquaculture).

5.3.2 Prey type

Artemia salina nauplii (771 ± 90 µm TL, N = 316; 1.6 ± 0.4 µg dry weight (dw), N = 245) with low or absent escape responses were used to determine the maximum feeding rate of sprat at different water temperatures and fish sizes. A detailed description of the rearing conditions for *A. salina* can be found in Brachvogel et al. 2013.

5.3.3 Experimental tank

The experimental tank was separated into two parts, the fish chamber (square-shaped, 486 L) where the sprat were kept and the collecting chamber (324 L) where all prey items lost through the water over-flow (2.8 Lmin^{-1}) were collected (see Brachvogel et al. 2013). Feeding behaviour of sprat during experiments was recorded by an underwater camera (GoPro Hero3). The fish and collecting chambers were connected by a gentle circular water flow. Water loss through the over-flow was compensated in the collecting chamber by the addition of filtered (20 µm pore diameter) water from the recirculation system. An aerated *S*-shaped PVC-tube in the fish chamber caused a gentle vertical circular water flow within the fish chamber and promoted a homogeneous distribution of prey items. The target water temperature was enabled by a cooling system (heat exchanger) and heating element in the collecting chamber. Prey items lost via the over-flow were collected every 10 min (time intervals = 0–10, 10–20, 20–30, etc.) in a 100-µm mesh-bottomed cup. To determine the actual prey concentration in the fish chamber prey items from each time interval (á 10 min) were counted under a binocular microscope.

5.3.4 Experimental set-up

A set of experimental tanks of different volumes (239 and 486 L) was constructed to perform simultaneous experiments with different sizes of sprat. Prior to the experiment fish were not fed for 24 hours. At the start of an experiment, a certain amount of prey was added to the experimental tank (fish chamber) to achieve an initial target prey concentration of 100-330 L^{-1}. After adding the food, sprat distributed evenly within the experimental tank. Prey concentration decreased exponentially due to feeding activity and the water overflow. Experiments lasted until no feeding fish were observed (between 1.5-5.5 hours). After each experiment sprat were removed and killed rapidly by an overdose of anaesthetic (MS222) in order to obtain biometric data and stomach contents.

Prey concentration (C_t) for a 10-min time interval was calculated from $C_t = N_t/FR$, where N_t is the total number of prey items (N) in the collection-cup divided by the length of the time interval, and FR is the overflow rate (2.8-3.8 $Lmin^{-1}$). The recorded videos were played with half-speed to determine the average biting rate for each 10-min time interval of an experiment. In each 10-min time interval 10–20 individual fish of a total 10-30 sprat were tracked. Fish were selected randomly. Each individual fish was tracked for 10–60 s, and its biting rate (biting acts s^{-1}) was determined visually. The main criterion in selection of fish was that during tracking several (>2) vertical zigzag patterns were observed. Biting while swimming upwards followed by a downward swimming movement. All tracking events within a 10-min time interval, which fulfil this criterion, were included in the evaluation. It was assumed that only one prey item was consumed per biting act.

We also determined the time for prey handling (t_h) which was defined as the time for prey biting: the time between opening and clothing the fish mouth (Brachvogel et al. 2013) for different fish size and temperature.

5.3.4.1 Temperature effect

The temperature effects on the functional response was investigated with sprat (87.2 ± 6.6 mm TL) at five temperatures: 5, 8, 12, 16 and 20 °C (± 0.2°C). Three to five experiments were performed with different fish groups of 20-30 individuals per temperature. Sprat were acclimatized slowly from 12°C to the target temperature in the experimental tank within one to four weeks (maximum change of water temperature per day = 0.6 °C).

5.3.4.2 Fish size effect

The fish size effect on the functional response was investigated with three different sprat size classes (87.2 ± 6.6, 63.0 ± 5.3 and 37.1 ± 3.2 mm TL) at 16 °C. Data for the mid-sized fish (6.3 cm TL) are from Brachvogel et al. (2013). The experimental set-up was similar for all size classes besides tank dimensions: the experimental tank was smaller for the 3.7 and 6.3 cm TL sized sprat (fish chamber = 239 L and collecting chamber = 162 L) and thus experiments were performed only with 10-20 individuals. The use of a larger experimental tank (fish chamber = 486 L and collecting chamber = 324 L) for the largest size class (8.7 cm TL) allowed normal feeding behaviour of sprat; the group size varied between 20 and 30 individuals.

5.3.5 Validation of the observed biting rates

To validate the biting rates we compared the observed stomach content dry weights of larger sprat (8.7 cm TL) from all experiments with weights predicted by the biting rates from video observations. Stomach contents of sprat were vacuum filtered through pre-weighed filter pads

(1.2 µm pore size) and dried in a drying oven (90 °C) for 48 hours. After drying, the filter pad plus stomach content weight was determined on a precision scale (0.0001 mg). For comparison the expected stomach content weight of a fish for each experiment was calculated based on the observed biting rates, the mean prey weight and the known gastric evacuation rate: starting with an empty stomach, we calculated the change in stomach content weight (formula 5.1) in 1-minute steps (*dt* = 0.017 h) and added it to the present stomach content weight. This stomach content weight was taken in the next step as new starting point. This procedure was repeated until the end of an experiment (1.2-5.5 hours).

$$\frac{dS}{dt} = F - R * {S_t}^B \qquad \textbf{\textit{Equation 5.1}}$$

Where *F* = food intake rate (*F*; g_{DW} h^{-1}), *R* = gastric evacuation rate (*R*; $g_{DW}1^{-B}$ h^{-1}), S_t = stomach content at time t (g_{DW}) and *B* = exponent describing the strength of the stomach content effect on evacuation rate. Parameters for the gastric evacuation rate of sprat were taken from Bernreuther et al. (2009). Food intake rates (g_{DW} h^{-1}) were calculated using the mean biting rates *BR* (s^{-1}) from video observations and the mean dry weight of prey (*P*) (*A. salina* nauplii = 1.6 μg_{DW}):

$$F = BR * 60 * 60 * 0.017 * P \qquad \textbf{\textit{Equation 5.2}}$$

The biting rate was changed in 10-min interval related to the observation period during the experiments. The gastric evacuation constant (*R*; $g_{DW}1^{-B}$ h^{-1}) can be expanded with additional variables and parameters:

$$\frac{dS}{dt} = F - R''_{dw} * e^{A*T} * M^C * {S_t}^B \qquad \textbf{\textit{Equation 5.3}}$$

Where R''_{DW} = evacuation constant (0.0177), *A* = temperature coefficient (0.0775), *T* = temperature (°C), *M* = fish weight (g_{DW}), C = body mass exponent (0.503) and B = 0.668.

An alternative method to verify our results was to calculate biting rates on the basis of decreasing prey concentrations in the tanks over the experimental period. As we add food only at the beginning of an experiment prey concentration decreased exponentially due to the feeding activity of sprat and the over-flow. Our experimental setup allows the estimation of the actual prey concentration in the tank and the prey loss by the over-flow every 10 minute intervals. Thus, we could determine which biting rates were required by all sprat in the tank to explain the observed reduction of prey concentrations during each 10 minute interval. The deviation factor was estimated by dividing the biting rate from video observations by the biting rate calculated from the reduction in prey concentrations. In addition, we predicted stomach content weights of sprat using the method already described above (formula 5.1-3), but using biting rates calculated from the decreasing prey concentrations in the tank.

To assess the variation of stomach content dry weights of feeding sprat we also estimated the relative standard deviation (RSD_i, %) for each experiment (i) with larger sprat (8.7 cm TL) by the following equation:

$$RSD_i = \left(\frac{SD_i}{\chi_i}\right) * 100 \qquad \textbf{Equation 5.4}$$

Where SD_i is the standard deviation and x_i the mean of stomach content weight of sprat within an experiment (i). A mean *RSD* for each temperature were then calculated from the measured RSD_i. In addition, we estimated the RSD_i of biting rates for each 10 minute interval (i). As the RSD_i's of biting rates were different between lower and higher prey concentrations we calculated two mean *RSD*'s of biting rates from results below or above 50 L^{-1}.

5.3.6 Model fitting

Nonlinear models (nls; R Core Team 2014; Version 3.1.1) were applied to describe the functional response of sprat in relation to both temperature (5 to 20°C) and fish size (3.7, 6.3 and 8.7 cm TL). Models were compared via AIC following an I-T Approach (Burnham & Anderson 2004; Mazerolle 2006). To quantify the evidence for each model *i* in the set, we calculate the (relative) likelihood $l_i = \exp(-0.5*\Delta_i)$, where Δ_i is the difference between the AIC of the best fitting model and that of model *i* (Burnham et al. 2011). In the last step, the relative likelihood were normalized (divided by the sum of the likelihoods of all models) to obtain Akaike weights w_i (Burnham & Anderson 2002). The Akaike weights can be interpreted as the probability that model *i* is the best model, given the data and the set of models (Burnham & Anderson 2002).

A Michaelis-Menten-model, which is mathematically equivalent to Holling´s disc equation model (1959), was used to represent the expected biting rate (BR; s^{-1}) as a function of prey concentration (conc; L^{-1}):

$$BR = \frac{BR_{max*}conc}{(k+conc)} \qquad \textbf{\textit{Equation 5.5}}$$

Where *BRmax* is the maximum biting rate (s^{-1}) and *k* (L^{-1}) is a constant, which indicates the prey concentration at *BRmax*/2. In a first step, we applied equation (5.5) to all data measured at 16 °C separated according to fish size (8.7, 6.3 and 3.6 cm TL) and secondly to all data measured for 8.7 cm TL fish separated according to temperature (5, 8, 12, 16 and 20 °C). This allowed visualising trends of *BRmax* and *k* with either fish size or temperature (Fig. 5.1 and 5.2). We developed four functional response models: model 1 and 2 for sprat < 9 cm TL and model 3 and 4 for larger sprat (Tab. 5.2). The models also differ in the relationship between the parameter *k* and temperature and/or fish size (see below).

BRmax increased with fish size and temperature in a nonlinear function (Fig. 5.1A and 5.2A). The parameter *k* did not show any clear trend with temperature across all experiments (Fig. 5.1B). Thus, we used for model 1 and 3 a mean *k* value of 11.16 based on the *k* values from equation 5.5 for each temperature. However, two of the 5 °C experiments showed higher *k* values compared to the other experiments. It must be mentioned here that only about a quarter of sprat were feeding within each 5 °C experiments. Without these two experiments *k* increased linearly with temperature (model 2 and 4) (Fig. 5.1B).

The parameter *k* decreased linearly with fish size from 3.7 to 8.7 cm TL (model 1 and 2, Fig. 2B) at 16°C. However, the application of this model for larger fish (> 9 cm) resulted in negative biting rates. Thus, for sprat > 9 cm TL we used a power function to describe the relationship between *k* and fish size (model 3 and 4; Fig. 5.5), so that one final model is available for field applications to larger sprat. The parameterization of the power function was only possible with additional information from field data on stomach contents and plankton densities as described in the lower section.

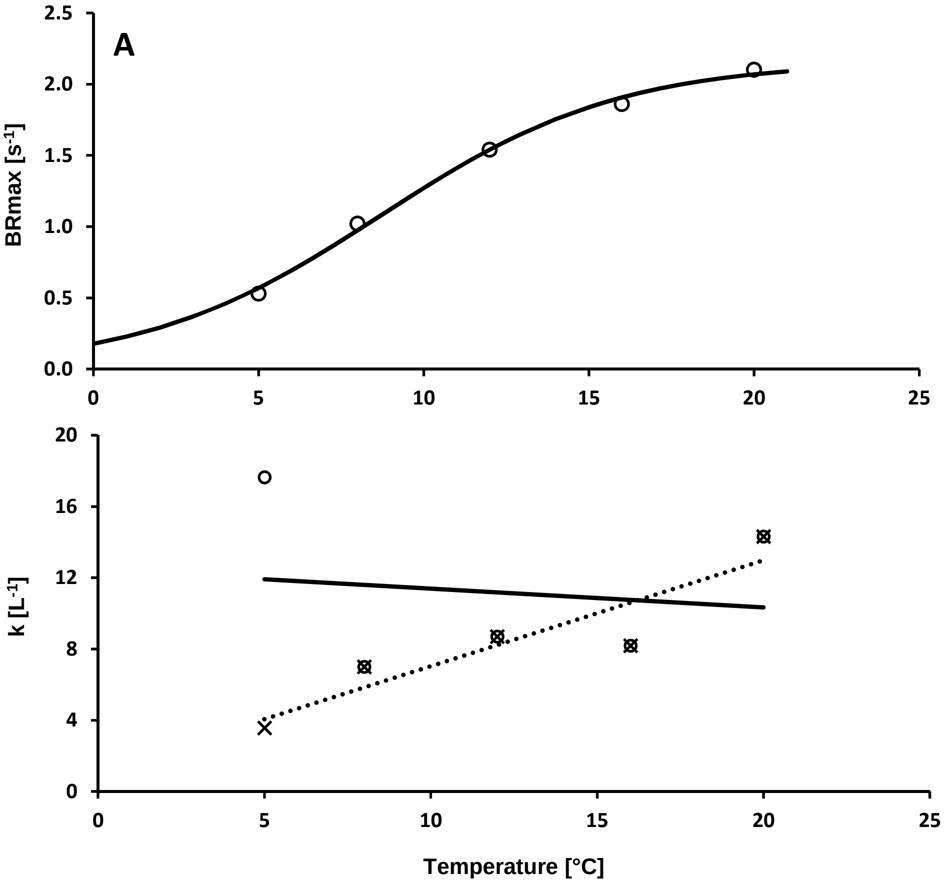

Figure 5.1: Change of the parameters BRmax and k from equation 5.5 with water temperature [°C] of 8.7 cm TL sized sprat. *A: circles and solid line described BRmax as a function of temperatures based on video observations =* $2.16/(1+11.17*exp^{(-0.28*Temp)})$ *B: circles and solid line described the parameter k as a function of temperatures (k = -0.11*Temp+12.45) based on video observation data where all 5 °C experiments were included; crosses and pointed line (k = 0.59*Temp+1.09) described the parameter k as a function of temperatures based on video observation data where 2 of the 5 °C experiments were excluded.*

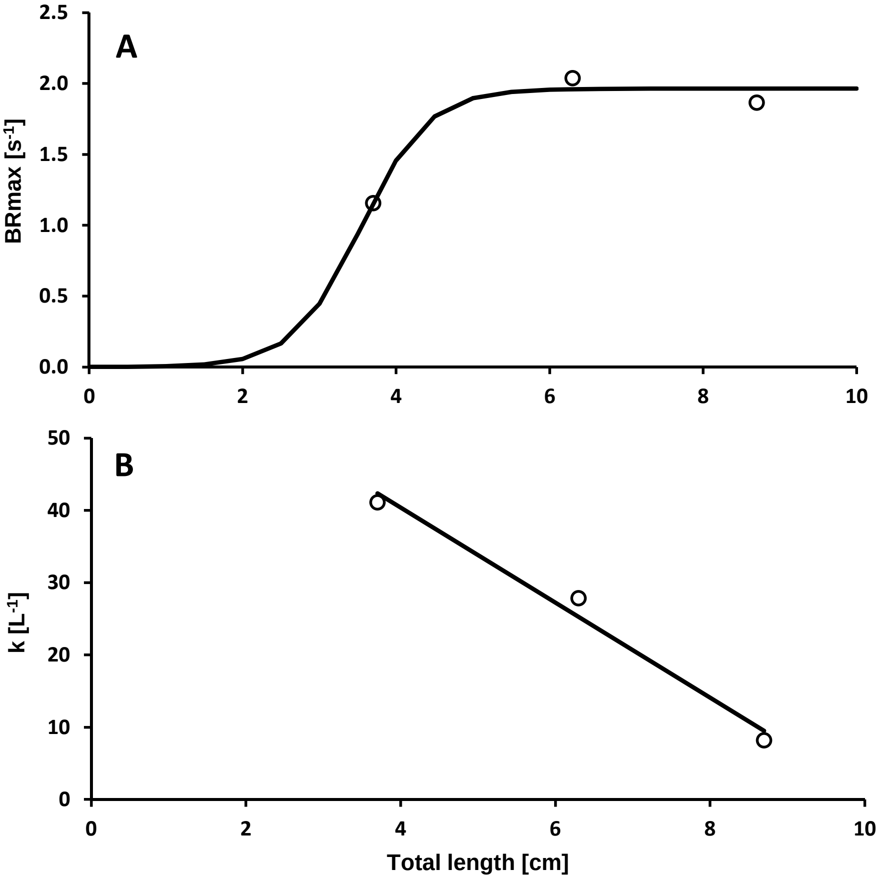

Figure 5.2: Change of the parameters BRmax and k from equation 5.5 with fish size [cm TL] at 16°C. *A: circles and solid line described BRmax as a function of length based on video observations = 1.96/(1+3258*exp*$^{(-2.27*Length)}$ *B: circles and solid line described the parameter k as a function of length based on data from video observations (k = -6.41*Length+65.15)*

5.3.6.1 Determination of parameter k for sprat larger 9 cm TL

The size range of our experiments ended at 9 cm. However the size effect of the parameter *BRmax* revealed a clear asymptote allowing the extrapolation to larger sizes with sufficient confidence. In contrast, the situation for the parameter *k* was completely different. The estimates for *k* declined more or less linearly with length of the fish pointing at a theoretically impossible intercept with the X-axis at about 10 cm. Hence extrapolation was not an option here. Instead we decided to utilize field data on stomach contents of different sprat size classes in combination of simultaneously measured prey concentrations ($conc_{field}$) from Multi-net samples to estimate *k* values for different size classes. These calculations revealed the actual biting rates (BR_{field}) assuming that BR_{max} was at the asymptotic maximum value for all sizes above 6 cm:

$$k = conc_{field}*(BRmax-BR_{field})/BR_{field} \qquad \textbf{\textit{Equation 5.6}}$$

The calculation of the BR_{field} from stomach content data required the consumption model described above (formula 5.1-3). Equation (5.3) was applied in a numerical integration to estimate the stomach content after a predefined feeding period starting with an empty stomach content at time 0. In this numerical integration the feeding rate (F) (formula 5.1 and 5.3) was varied in an iteration process until the predicted weight of stomach content at the end of the feeding period matched the observed weight from the field data. The feeding time of sprat was assumed to start at sunrise (Cardinale et al. 2003) and to end at the time of catch. Subsequently F was converted into the equivalent biting rate (BR_{field}) using formula 5.2. We applied a mean prey weight (P) of 32 μg_{WW} based on the prey composition of sprat (Bernreuther et al. 2013) and wet weight data of prey were taken from Hernroth 1985. The evacuation constant R''_{DW} = 0.0177 (formula 5.3) was estimated by Bernreuther et al. (2009) based on dry weights. However, stomach content data from field expressed in wet weight. Therefore, we used a mean dry weight factor for stomach content to get an evacuation constant for wet weight data (R''_{ww} = 0.0119).

5.3.6.1.1 Sampling in the field

For our purposes sprat stomachs (7–14 cm TL, n = 648) and Multi-Net samples (20 hauls) were collected at three permanent stations in the western of Baltic Sea in June 2001, March and July 2012. The time lag between fishery and plankton haul were between 1.5 to 24 hours and the trawl sites at each haul were located less than 1 miles apart. Ambient temperatures at which sprat occurred during day time was about 6°C in June 2001, 9°C in July 2012 and 5°C in March 2012. Vertically stratified zooplankton samples were taken with a 300 µm mesh Multi-Net. Zooplankton samples were identified by specie and stage and counted either manually under a binocular microscope on subsamples of not less than 500 individuals per sample or automatically by a Zooscan (model ZSCA02). Prey concentrations ($conc_{field}$) for k estimation within the equation 5.6 were defined as the sum of all copepods from copepodite stage CIV to adult and all cladocerans (De Silva 1973, Möllmann et al. 2004, Bernreuther et al. 2013) in water layers where sprat were present (own hydroacoustic data and literature (Stepputtis 2006)).

5.3.7 Field application of our functional response model

In order to verify our functional response model 3 we compared predicted stomach content weights of the length classes from 11 to 13 cm with observed weights from field using the procedure already described above (formula 5.1-3). For this purpose we collected stomach content weights (n = 269) and prey concentrations from Multi-Net samples at three stations in the central Baltic Sea in August 2015. The processing of samples was the same as described above.

5.3.8 Energetic efficiency of sprat

To assess the energetic efficiency of juvenile sprat (4, 6 and 8 cm TL) at different temperatures we compared the *per capita* daily energy intake at a given prey concentration based on our functional response model 1 with the energy loss by metabolism. The prey concentration was selected in such way, that our predicted daily food intakes rates were similar to intakes of sprat from other studies. The feeding period of sprat was defined as 14 day light hours. Stage- and season specific prey wet weights for daily food intake estimations of sprat (%BW) were obtained from Hernroth (1985). We applied a mean prey weight of 14µg$_{WW}$. In coastal areas, daily food intakes of juvenile sprat range between 10 and 15% body weight (Arrhenius 1998, Maes et al. 2005). This corresponded in our model to a mean prey concentration of 10 L^{-1}, which is typical for shallow nursery areas (Ojaveer et al. 1998, Gorokhova et al. 2004, Paulsen et al. 2016).

5.3.8.1 Metabolic cost

Total daily energy loss was quantified using the metabolic rate model (*MR*) of sprat by Meskendahl (2013). Temperature- and weight dependent *MR* (oxygen uptake; mgO$_2$fish^{-1}h^{-1}) (formula 5.7) was measured during spontaneous activity in sprat together with mean swimming speeds (*U,* body length BL s^{-1}) and the number of sharp turns (>90°) (*M,* fish^{-1}s^{-1}). Swimming speed and sharp turns are described by Meskendahl (2013) as a function of prey concentration. As the *MR* model was inapplicable for smaller sprat we added a weight-specific correction term (b_1, b_2) to adjust the model (formula 5.7), assuming a similar weight exponent (1.073) for *U* and *M* as for routine metabolic rate (Meskendahl et al. 2010). Metabolic rates for different temperatures und sprat wet weights (g, WW) were estimated by the following equations:

$$MR\ (\mathrm{mgO_2 fish^{-1} h^{-1}}) = a * \mathrm{WW}^{1.073} \mathrm{e}^{(0.078*T)} + b_1 * (U - 0.28)^{\mathrm{v}} * \mathrm{e}^{(0.078*T)} * WW^{1.073} + b_2 * (M - 0.22) * WW^{1.073}$$

Equation 5.7

with the constants a = 0.0279, b_1 = 0.169, b_2 = 0.083 and swimming speed exponent v = 1.287. The mean swimming speed of 0.28 BL s^{-1} and turns >90° of 0.22 $fish^{-1}s^{-1}$ are used as constants to represent the minimum activity (Meskendahl 2013). Thus, for the period when sprat are not feeding during the day (here 10 hours), we applied 0.28 for U and 0.22 for M. Wet weight values for different length classes were obtained from a length-weight relationship WW (g) = $0.019*L^{2.59}$ (own data from 47 surveys from 2002-2014, n = 5361). Mean swimming speed (U; BL s^{-1}) and turns >90° (M; $fish^{-1}s^{-1}$) as a function of prey concentration (*conc*, here 10 L^{-1}) were calculated as follows:

$$U\ or\ M = \emptyset_1 + (\emptyset_2 - \emptyset_1) * e^{(-e^{\emptyset_3} * conc)}$$

U: $\emptyset_1$= 0.917, $\emptyset_2$ = 0.614 and $\emptyset_3$ = -2.15
M: $\emptyset_1$= 0.36, $\emptyset_2$ = 0.22 and $\emptyset_3$ = -3.13

Equation 5.8

As MR was expressed in $mgO_2 fish^{-1}h^{-1}$ we used the oxy-caloric factor (13.72 J mgO_2^{-1}) from Elliott & Davison (1975) for the conversion into Joules per hour. To determine the total daily energy loss, we also take into account the loss by faeces *F*, excretion *E* and specific dynamic action *SDA*. *F*, *E* and *SDA* were assumed to account each for 10% of the total daily energy intake by feeding (Andersen & Riis-Vestergaard 2003, Temming & Herrmann 2009).

5.3.8.2 Energy intake

The daily energy intake was estimated by our functional response model 1 for smaller sprat (4, 6 and 8 cm TL). As the results from the functional response models are expressed in particles per time unit, we needed energy contents of different prey species for the conversion into Joules per day. Total content of carbohydrates, protein and lipid define the energy content of an organism (Acheampong 2011). Species-specific proportions of those three components in relation to prey dry weight (% DW) and dry weight-length relationship were obtained from different studies (Tab. 5.1). Based on the prey composition of 0-group sprat in summer at coastal areas (Arrhenius 1996, Gorokhova et al. 2004; Maes et al. 2005) we estimated a mean energy content of 0.039 J prey item^{-1} (resulting to an energy conversion factor of 16.99 J mg_{DW}^{-1}). Viitasalo et al. 2001 found that the escape ability (siphon capture success) between prey species is different. In addition, previous study showed that the biting rates of sprat preying on *A. tonsa* were reduced by a factor of 0.53 compared to non-evasive *Artemia* nauplii (Brachvogel et al. 2013). According to the prey composition of juvenile sprat in coastal areas investigated by Arrhenius (1996) and the reduction factors for different prey species estimated by Viitasalo et al. (2001) and Brachvogel et al. (2013), we reduced the predicted biting rates using our functional response model 1 by a mean factor of 0.61.

Table 5.1: Summary of species-specific weight-length relationships and the proportions of lipid, protein and carbohydrate content of different prey species of sprat. *The data was used to calculate the energy content (J ind^{-1}) of a medium prey item for the estimation of sprat total energy intake during the feeding period.*

	Acartia spp.	***Temora longicornis***	***Pseudocalanus acuspes***	***Eurytemora affinis***	***Bosmina***
prosoma length (PL) or body lenght (BL)	Holliland et al. 2012	Dutz et al. 2010	Renz et al. 2007	Holliland et al. 2012	0.45 mm Arrhenius 1996
dry weight (DW; µg) to PL or BL	CI-CVI logDW = 3.252logPL - 8.785 Hay et al. 1988	CI-CVI logDW = 2.815logPL - 7.181 Hay et al. 1988	CI-CVI logDW = 3.346logPL - 8.899 Hay et al. 1988	CI-CV logDW = 3.24logPL - 8.51 Adult F logDW = 1.78logPL - 5.29 Adult M logDW = 2.66logPL - 5.94 Böttger and Schnack 1986	
protein content	45 %DW Acheampong 2011	48 %DW Helleland et al. 2003	52 %DW Båmstedt 1986	57 %DW Acheampong 2011	logDW = 3.05logBL + 0.99 Vijverberg & Frank 1976
lipid content	10.38 %DW Acheampong 2011	10 %DW Evjemo & Olsen 1997	12.5 %DW Peters 2006	10 %DW Evjemo & Olsen 1997	logDW = 2.51logBL + 0.22 Vijverberg & Frank 1976
carbohydrate content	3.1 $\%BW_{dry}$ Acheampong 2011				logDW = 3.29logBL + 0.15 Vijverberg & Frank 1976
energy conversion factor [J mg_{dry}]	16.99				

5.4 Results

5.4.1 Fish behaviour

In the 8.7 cm sprat size class 98.7 % had non empty stomachs in the experiments at 20 °C, while this share decreased slightly to 84.5 % at 8 °C. At 5 °C only 26.3 % of the fish had food in the stomachs at the end of experiments. The size classes 6.3 and 3.7 cm at 16 °C also showed high frequency of feeding fish from 80 to 100 %. Handling time (t_h) for an *A. salina* nauplius decreased with increasing fish size and temperature which can be described by a power function $t_h = 1.17*Length^{-0.81}$; $t_h = 3.04*Temp^{-0.96}$. Sprat with a body length of 3.7 cm TL ($t_h = 0.42$ s) needed on average twice the time to handle an *A. salina* nauplius as a 8.7 cm TL large sprat ($t_h = 0.21$ s). The effect of temperature on t_h was stronger: t_h was on average four times shorter when sprat fed at 20 °C ($t_h = 0.19$ s) than at 5 °C ($t_h = 0.77$ s).

5.4.2 Validation of observed biting rates

Observed stomach contents varied greatly between individuals within an experiment (Fig. 5.3). The mean relative standard deviations of stomach content dry weights of feeding sprat (empty stomachs were excluded) for different temperatures were 54.93 % at 5 °C, 47.41 % at 8 °C, 33.69 % at 12 °C, 65.33 % at 16 °C and 41.87 % at 20 °C. Predicted stomach contents using the biting rates from video observations were in most cases clearly higher than the observed stomach contents of the experimental fish. Predicted and observed stomach contents only matched well at experiments 8 and 9 at 12 °C (Fig. 5.3). Some sprat at 16 °C experiments (no. 1 and 4) also reached or even exceeded the stomach content predicted from the observed biting rates. Predicted stomach contents were 1.1-3.2 times higher than the mean observed stomach contents. In contrast, predicted stomach content weights using biting rates calculated by the decreasing prey concentrations in the tank over the experimental period showed a good agreement with the observed stomach contents (Fig. 5.3). Exceptions were the experiments 6 and 7 which had very high values. The difference between predicted and observed stomach content was on average only by the factor 0.62-1.46 (without experiments 6 and 7).

The deviation factor (biting rate from the video analyses divided by the biting rate calculated from the prey reduction in the tank) for the experiments with 8.7 cm sized sprat increased with decreasing prey concentration for all temperatures up to a factor of about 4 to 7 (Fig. 5.4). However, at higher prey concentrations > 50 L^{-1} 78.6 % of the deviation factors were between 0.5 and 1.5 at 20 °C and decreased to 51.5 % at 5 °C (58.3 % at 8 °C, 60.0 % at 12 °C and 62.5 % at 16 °C). The deviation factor also increased with decreasing prey concentration for smaller sprat size 6.3 and 3.7 cm TL. From a prey concentration of about 50 L^{-1} 83.7 % and 53.3 % of factors were between 0.5 and 1.5 for the size classes 6.3 and 3.7 cm TL, respectively.

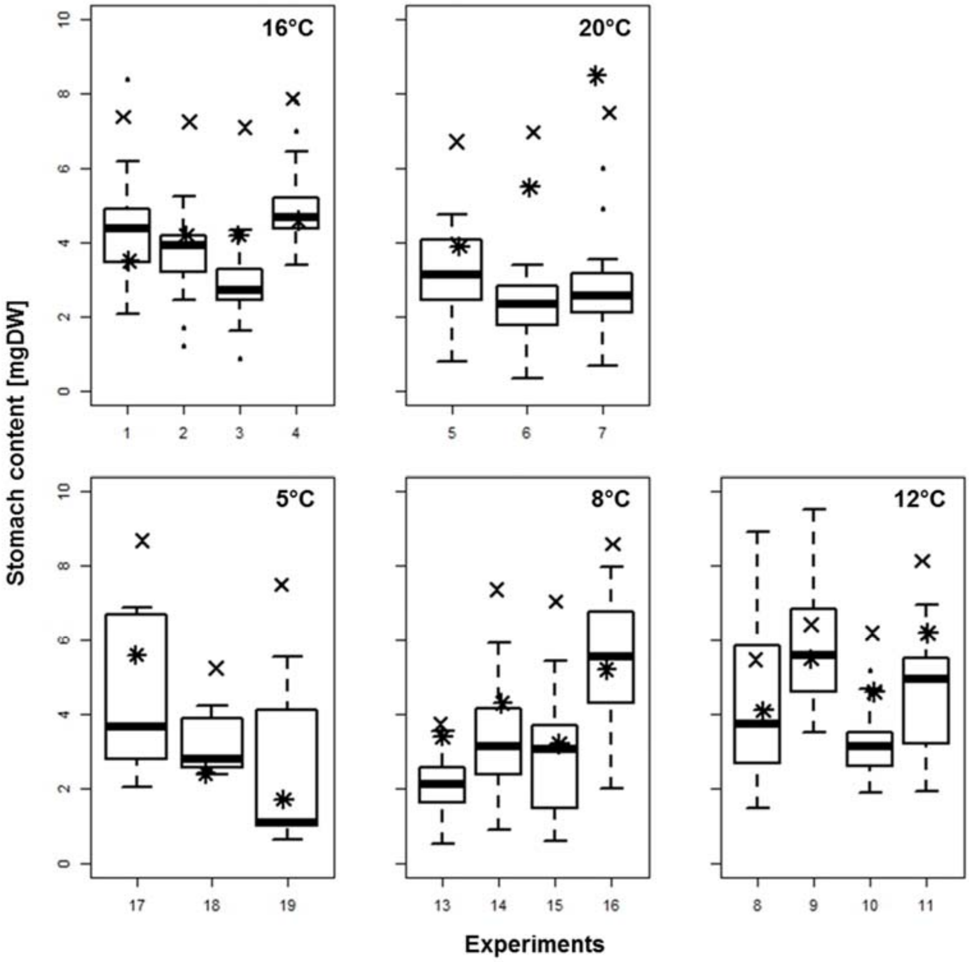

Figure 5.3: Observed and predicted stomach contents [mgDW] of feeding sprat (8.7 cm TL; without empty stomach) at different Temperatures. *Crosses represent stomach contents predicted by biting rates from the video observations, including the temperature-dependent evacuation rate of sprat. Stars represent stomach contents predicted using biting rates calculated by the decreasing prey concentrations in the tank over the experimental period, including the temperature-dependent evacuation rate of sprat.*

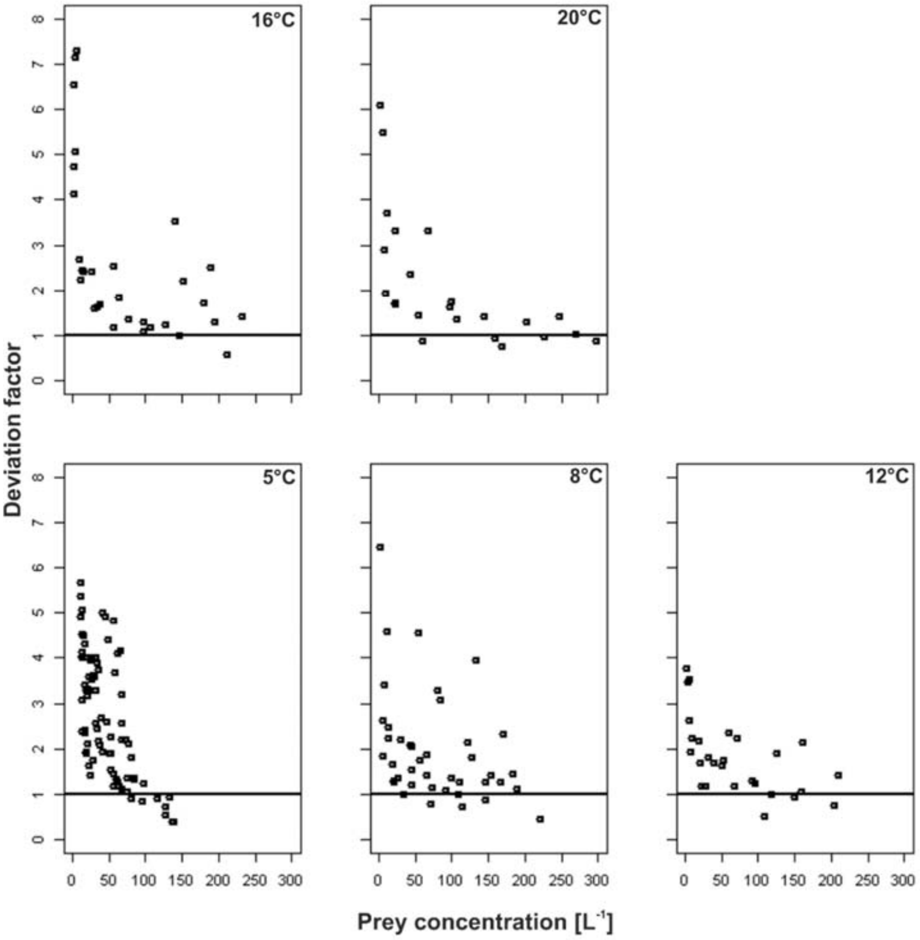

Figure 5.4: Deviation factor of biting rates estimated by two different methods in relation to prey concentration and different temperatures. *Deviation factor is obtained by dividing the biting rate from video analyses (sprat size = 8.7 cm TL) by the biting rate calculated from the decreasing of prey concentration in the experimental tank. Straight line defines the point when the biting rates obtained from both methods are equal (deviation factor = 1).*

5.4.3 Functional response

The feeding rates of sprat generally followed a Holling's type II functional response curve (Fig. 5.6 and 5.7). There was a clear fish size and temperature effect on the functional response of sprat preying on *A. salina* nauplii. *BRmax* increased with increasing temperature and fish size and asymptotically reached a maxim value of about 2.0 s^{-1} (Fig. 5.1 A and Fig. 5.2 A). The parameter *k* decreased with increasing fish size from about 41 L^{-1} for 3.7 cm TL sized sprat to a mean value of 6 L^{-1} for sprat > 7 cm TL (Fig. 5.5). Two models were developed to explain the biting rates as a function of prey concentrations of either small (< 9 cm TL, model 1 and 2) or large (> 9 cm TL, model 3 and 4) sprat (Tab. 5.2). We recommend using model 1 for small sprat because the AIC is slightly lower ($\Delta_i = 0.65$) and it is 1.4- times more likely to be the best model than model 2. Model 1 assumes a logistic function of *BRmax* for length and temperature and a linearly relationship of *k* for length (Fig. 5.1 and 5.2). In contrast to model 2, model 1 assumes a mean *k* value of 11.16 L^{-1} across the range of temperatures and not a linear dependence between *k* and temperature. For sprat > 9 cm TL we chose model 3, because it is 4.9-times more likely the best model than model 4 ($\Delta_i = 3.16$). The only difference between model 1 and 3 is that model 3 assumes a power function for the dependence of *k* with length (Fig. 5.5, Tab. 5.2). Model 1 and 3 are very similar, however, we recommend using model 1 for sprat from 4 to 9 cm TL because model 3 overestimated the *BR*s for smaller sprat (< 6 cm TL) (Fig. 5.7).

As mentioned before (Fig. 5.4), for the length class 8.7 cm biting rates calculated by the decreasing prey concentration in the tank were almost lower than the video observed biting rates (Fig. 5.6 and 5.7). This was also the case for the sprat size 3.7 cm. However, at experiments with sprat size 6.3 cm biting rates of both methods were very similar. Biting rates from decreasing prey concentration were on average by a factor 0.70 ± 0.35 lower than the biting rates predicted by our functional response model.

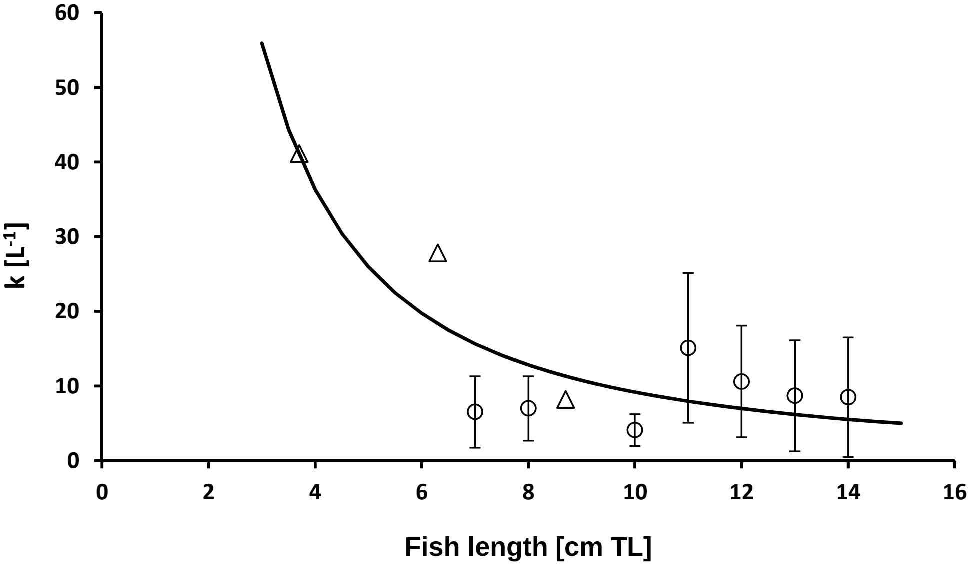

Figure 5.5: Changes of k with fish size [cm total length]. *Circles: medians of k based on stomach content data from field; error bars represent the mean deviation from median. Triangles: k based on biting rates from experiments. Solid line: power function (k = 291*$L^{-1.5}$).*

Table 5.2: Set of fitted models to explain functional response (BR; s^{-1}) of sprat preying on A. salina nauplii at various concentrations (conc; L^{-1}) in relation to different temperatures (T; °C) and fish lengths (L; cm TL)

Model	Data	L 4 to 9 cm TL	*P*	Estimate	AIC	Δ$_i$	w$_i$
1	*Exp.*	$BR = \frac{\frac{a_1}{1+b_1*e^{-c_1*T}}*\frac{a_2}{1+b_2*e^{-c_2*L}}*conc}{((a_k*L+b_k)*11.16+conc))}$	a_1	2.219	-766	0.00	0.58
			b_1	12.257			
			c_1	0.318			
			a_2	0.930			
			b_2	3258			
			c_2	2.284			
			a_k	-0.522			
			b_k	5.476			
2	*Exp.*	$BR = \frac{\frac{a_1}{1+b_1*e^{-c_1*T}}*\frac{a_2}{1+b_2*e^{-c_2*L}}*conc}{((a_k*T-b_k*L+c_k)+conc))}$	a_1	1.274	-765	0.65	0.42
			b_1	12.901			
			c_1	0.317			
			a_2	1.636			
			b_2	3258			
			c_2	2.282			
			a_k	0.172			
			b_k	5.837			
			c_k	58.708			
		L > 9 cm TL					
3	*Exp.* *field*	$BR = \frac{\frac{a_1}{1+b_1*e^{-c_1*T}}*\frac{a_2}{1+b_2*e^{-c_2*L}}*conc}{((a_k*L^{-b_k})*11.16+conc))}$	a_1	6.485	-750	0.00	0.83
			b_1	12.437			
			c_1	0.320			
			a_2	0.315			
			b_2	3258			
			c_2	17.541			
			a_k	454.062			
			b_k	2.889			
4	*Exp.* *field*	$BR = \frac{\frac{a_1}{1+b_1*e^{-c_1*T}}*\frac{a_2}{1+b_2*e^{-c_2*L}}*conc}{((a_k*L^{-b_k})*(c_k*T+d_k)*+conc)}$	a_1	3.559	-747	3.16	0.17
			b_1	12.954			
			c_1	0.319			
			a_2	0.579			
			b_2	3258			
			c_2	17.541			
			a_k	401.360			
			b_k	2.879			
			c_k	0.167			
			d_k	9.850			

Note: *P* = parameter; AIC = Akaike´s information criterion; Δ$_i$ = difference between the AIC of the best fitting model and that of model *i*; w$_i$= Akaike weight

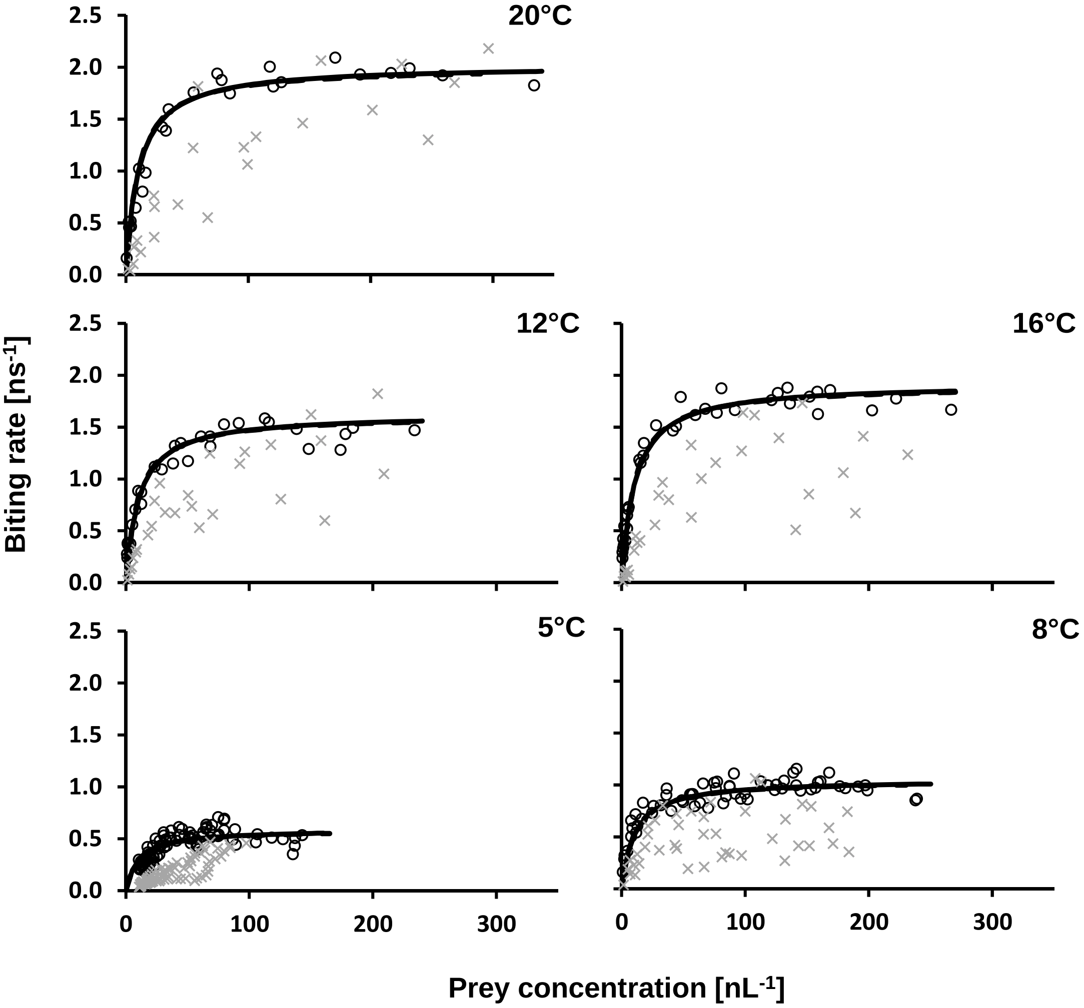

Figure 5.6: Observed biting rates from video analysis (dots) and modelled feeding rates of sprat at 16°C feeding on different concentrations of A. salina nauplii separated by fish size. *Crosses represent biting rates calculated by the decreasing prey concentrations in the experimental tank. Solid line: model 1; dashed line: model 3; for details on models see Table 5.2 and text.*

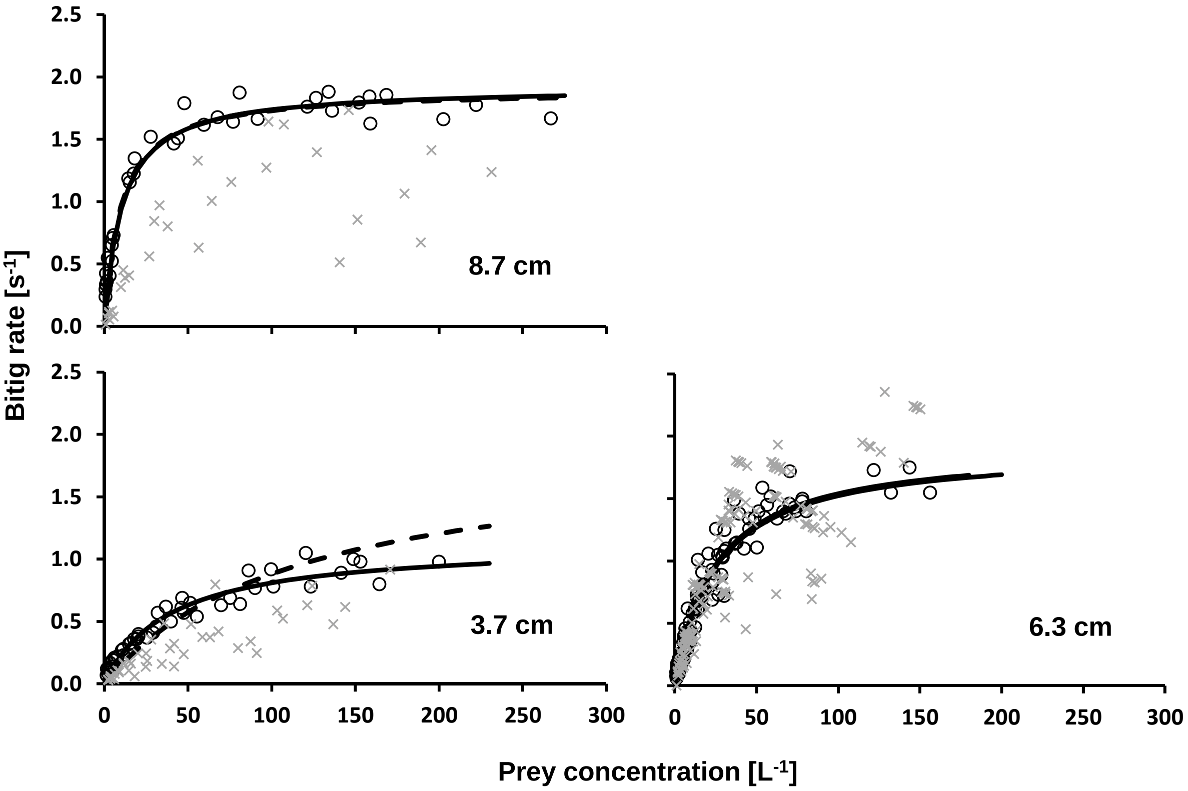

Figure 5.7: Observed biting rates from video analysis (dots) and modelled biting rates of sprat (8.7 cm TL) feeding on different concentrations of A. salina nauplii at five temperatures. *Crosses represent biting rates calculated by the decreasing prey concentrations in the experimental tank. Solid line: model 1; dashed line: model 3; for details on models see Table 5.2 and text.*

5.4.4 Field application of our functional response model

Predicted stomach content weights using our functional response model 3 were significantly higher than the observed weights. To match the observed weights predicted biting rates needed to be reduced by a factor between 0.16 and 0.42.

5.4.5 Energetic efficiency of sprat

According to our functional response models, *per capita* daily energy intake increases both with increasing fish size and temperature (Fig. 5.8 A). However, the slope of this increase decreases at higher temperatures, leading to an S-shaped relationship with an apparent asymptote. In contrast, daily energy cost also increases with warming, but following a simple exponential curve. As a consequence, sprat's energetic efficiency increases with increasing temperature, reaches an optimum and then decreases at higher temperatures (Fig. 5.8 B). The upper and lower temperature threshold is defined as the point where the daily metabolic cost of sprat can be exactly compensated by the daily energy intake (energetic efficiency = 1.0) at a given prey concentration. In summer the upper temperature threshold of an 8 cm TL sized sprat is 23.4 °C (Fig. 5.8 B). The upper temperature thresholds of smaller sprat (4 and 6 cm TL) occur outside the temperature range encountered in the field. The energetic efficiency of sprat increased with decreasing fish size (Fig. 5.8 B). At an optimum temperature of 12 °C the energy intake of sprat exceeds the metabolic cost by the factor from 2.29 (4 cm TL) to 1.15 (8 cm TL).

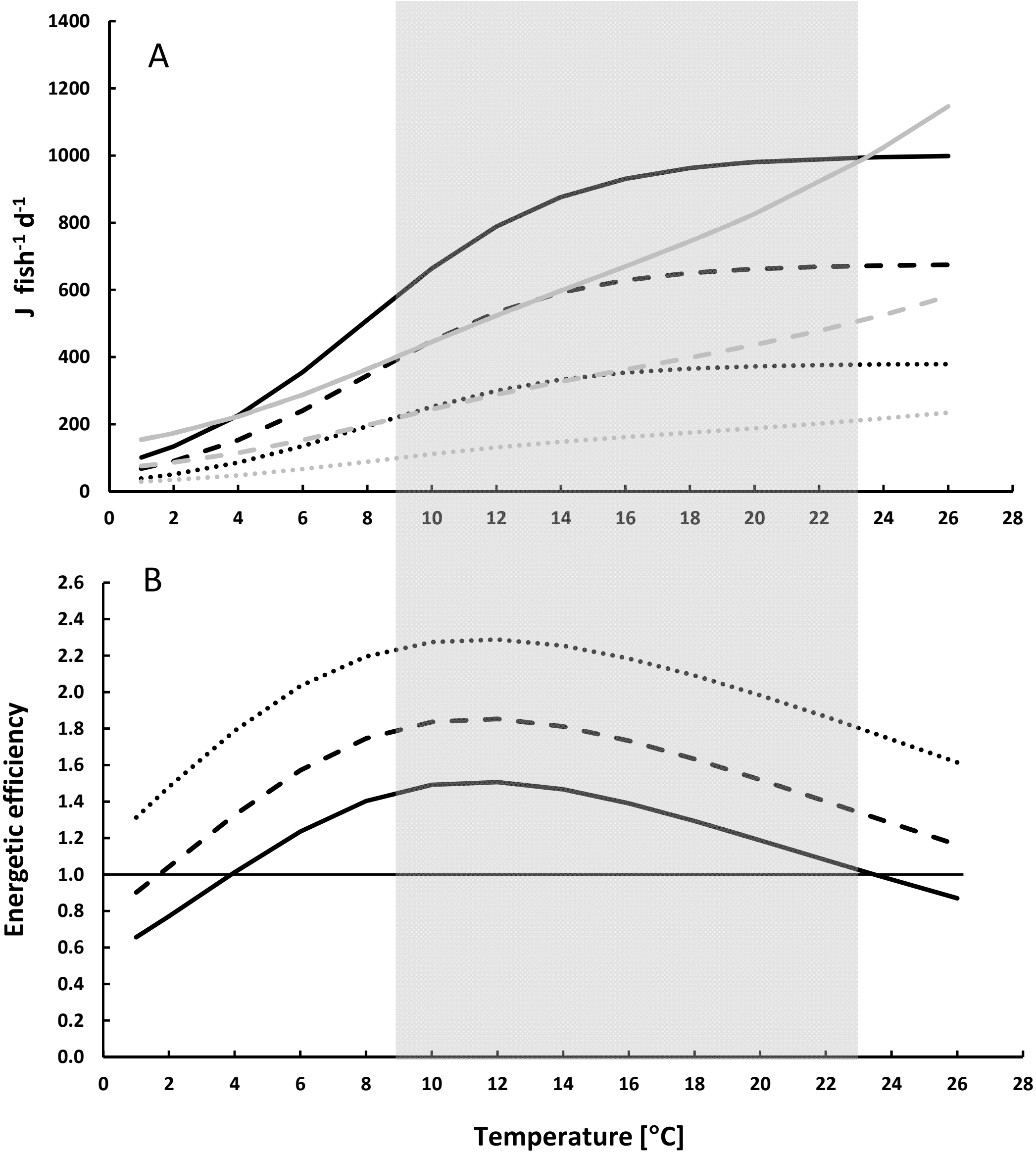

Figure 5.8: Daily energy budget of different sized sprat (solid line = 8 cm TL, dashed line = 6 cm TL and dotted line = 4 cm TL) feeding at mean prey concentration of 10 L^{-1} during summer (mean feeding period 14 hours) as a function of ambient temperature. *A: Daily energy intake (J fish^{-1}d^{-1}) (black lines) estimated from our functional response model 1 in comparison to the daily energy cost (J fish^{-1}d^{-1}) (grey lines) assessed by a temperature-dependent metabolic rate model. B: Energetic efficiency (dimensionless; per capita daily energy intake relative to energy cost by metabolism). Solid line represents the point where the energy cost is compensated by the intake. Grey bar indicates the range of relevant water temperatures during summer/late autumn throughout the entire water column at coastal area in western Baltic Sea (Kiel Lighthouse, 54°30' N, 10°16' E, July to October in 2003, BSH (2017)).*

5.5 Discussion

5.5.1 Feeding behaviour

Our experimental design allowed the measurement of feeding rates under controlled laboratory conditions that caused only minimal stress for the fish. In the present study sprat showed similar feeding behaviours as in a previous study (Brachvogel et al. 2013). Sprat swarms dissolved during feeding and sprat aligned themselves to prey items with frequent turns and changes of direction. At higher prey concentrations sprat swam in a vertical zigzag pattern, with repeated bites while swimming upwards at an angle of about 35–45°. Near the surface sprat performed a 180°-turn followed by a downward swimming movement. After another turn the next feeding sequence started immediately. These vertical zigzag patterns were also observed by an underwater camera for herring (Kils 1992) and sprat (personal observations) in the field. Thus, we assume that the observed feeding behavior in the present study reflects the normal feeding behavior of sprat.

The proportion of feeding sprat in the current experiments was high (> 80%) within the temperature range from 8 to 20°C. This corresponds to field observations made in spring and summer in the basins of the Baltic Sea (Bernreuther 2007; Möllman et al. 2004). However, at 5 °C only 26.3 % of sprat were feeding in our study. The frequency of feeding sprat for colder temperatures varies greatly in the literature from 92 to 22 % (De Silva 1973, Casini et al. 2004, Möllmann et al. 2004, Solberg et al. 2015). Last (1987) even found that immature sprat ceased to feed in December and January. Stomach content samples from the Bornholm Basin in winter/early spring seasons obtained from the GLOBEC-Germany Project in 2002 and 2003 reveal that the frequency of feeding sprat (8-9 cm) between the hauls varied greatly between 0 to 100%. The proportions of feeding sprat from our field samples in March 2012 (Kiel Bay, Baltic Sea) at about 5 °C were between 40 and 100%. Overall, the frequency of feeding sprat from the present study is in the lower range of observations made in the field. However, the mean stomach content of feeding sprat (0.018 ± 0.011 g_{WW}) from the experiments at 5°C is quite similar to the weights of 0.005 to 0.028 g_{WW} obtained from feeding sprat at colder temperatures from our field data in March 2012. Thus, we assume that feeding sprat at 5°C showed their normal feeding behaviour as they were actively searching for prey and did not seem to be stressed (e.g. not swimming against the wall of the experiment tank). However, we cannot exclude that the low frequency of feeding sprat at 5 °C from the present study was partly reflecting suboptimal conditions.

5.5.2 Interpretation of biting rates

Mean observed stomach content weights were significantly lower than the predicted weights based on the biting rates from video analysis. In contrast, predicted stomach content weights using biting rates calculated from the decreasing prey concentrations in the tank showed in almost all experiments good concordance with the observed weights (Fig. 5.3). Stronger overestimation of stomach content weights when using video observed biting rates from experiments 6 and 7 were presumably caused by uncontrolled prey loss through the overflow during the addition of prey at the beginning of the experiments. Biting rates from decreasing prey concentration were on average by a factor 0.70 ± 0.35 lower than the biting rates predicted by our functional response model. Overall, the results suggested that the biting rates from the video analysis represented the maximum possible physiological feeding response of sprat, while the lower biting rates calculated by the decreasing prey concentrations represented the average feeding response of sprat, including other behavioural patterns such as feeding gaps, or even the cease of feeding below a certain prey concentration.

If our functional response model 3 is used to predict stomach contents from observed copepod densities the true – observed – stomach contents are regularly overestimated. This might suggest that the feeding breaks observed in our experiments may actually be part of the normal feeding behaviour.

Interestingly the discrepancy between video based estimates and true biting rates was minimal at higher prey concentrations (Fig. 5.4). Below a prey concentration of about 50 L^{-1}, the deviation factor (relation between the biting rates from both approaches) increased. Satiation effects were not assumed to cause the increase of feeding gaps given the overall short feeding periods and the fact that sprat can increase their stomach contents up to as experimental time went by as laboratory investigation showed that sprat could consume at high prey densities up to 16 % of their body weight (Teich 2010). Sprat from the present study only achieved a relative stomach content weight of maximum 1.64 %. The feeding breaks may instead be interpreted in the context of optimal foraging theory (Stephens and Krebs 1986): according to the marginal value theorem (Charnov 1976) a fish should leave the patch - i.e. stop feeding - before the prey has been decimated below a certain threshold. However in our experimental tanks patchiness exists mainly in a time dimension: before the experiment the fish were fed only three times a day with higher concentrations. If fish had learned this pattern they may have decided at lower concentrations to wait for the next patch to occur.

Such a memory capacity of past feeding conditions was demonstrated for several fishes (Milinski 1994, Wildhaber et al. 1994, Warburton 2003); for example bluegill-sunfish (*Lepomis macrochirus*) use prior experiences of patch profitability to decide how long to stay in a particular food patch (Wildhaber et al. 1994). In contrast to the other sizes, both biting rates of sprat length class 6.3 cm were similar. A possible explanation for this is that, contrary to the experiments with the other length classes, the food concentration was kept constant in the first 60 minutes of experiments (Brachvogel et al. 2013). This condition may had a different trigger effect on foraging than if the prey concentration decreased exponentially from the beginning of an experiment.

The development of an additional functional response model based on the biting rates derived from decreasing prey concentrations was unsuccessful, because the discrepancy between the biting rates of both approaches revealed some stronger inconsistencies for some length class temperature combinations (Fig. 5.7). This implies that at least in some cases experimental conditions such as stress contributed to the discontinued feeding behaviour.

In conclusion, given that sprat showed their normal feeding behavior (vertical zigzag pattern) and a high proportion of them were feeding, we assume that our functional response models provide good estimates for the upper range of sprat consumption rates. However, the discrepancy between the predicted stomach content and observed content of sprat from experiments and field indicated that sprat do not perform their maximum feeding response continuously. To incorporate feeding gaps at some extent, there is an option to use the reduction factor of 0.70.

5.5.3 Functional response

The feeding rates of sprat clearly followed a type II functional response (Holling 1959, 1966) (Fig. 5.6 and 5.7), which is consistent with our previous study (Brachvogel et al., 2013). A type II response implies a high extinction risk for the prey as mortality risk per individual prey increases with decreasing prey abundance. Bernreuther et al. (2008) demonstrated that clupeids are able to store large quantities of food in their gastric caecum to optimise the exploitation in favourable situations with high prey concentrations. Thus, it appears that sprat schools are able to deplete local zooplankton patches within relatively short times due to the combination of high maximum biting rate (~2.0 s^{-1}), high storage capacity and the type II functional response. In situ observation revealed that a swarm of juvenile particulate feeding herring could deplete a micro-layer of prey with a density of 18 L^{-1} within only 25 minutes (Kils 1989 and 1992).

5.5.3.1 Prey type effect

Although *A. salina* is not a part of the natural prey composition of sprat, they are comparable with the main prey species of sprat like *T. longicornis*, *P. acuspes* and cladocerans (e.g. *Bosmina longispina maritima*) (Bernreuther et al. 2013, Van Ginderdeuren et al. 2014) in terms of their vulnerable to fish predation (Viitasalo et al., 1998 and 2001). Viitasalo et al. (1998 and 2001) demonstrated by video filming zooplankton escape response from an artificially created water flow (siphon) that *T. longicornis*, *P. acuspes* and *Bosmina* showed only a weak to even no escape response (74-100% siphon capture success). As those prey species are mainly consumed by sprat in the deep basin of the Baltic Sea (Bernreuther et al. 2013), we assume that the findings obtained from experiments with non-evasive *A. salina* can be applied to interpret the feeding of sprat in offshore areas.

In contrast, in the coastal zone during summer, 0-group sprat are largely feeding on *Eurytemora affinis* and *Acartia sp.* beside cladocerans (Arrhenius et al. 1996, Gorokhova et al. 2004, Maes et al. 2005). Both copepod species show high escape responses compared to *A. salina* (Viitasalo et al. 2001). The siphon capture success was only 9% for *E. affinis* adults (Viitasalo et al. 2001). Our previous study showed that the biting rate of sprat preying on *A. tonsa* was by a factor of 0.53 lower compared to *A. salina* (Brachvogel et al. 2013). Thus, for Baltic coastal areas we recommended to use a correction factor adjusted to prey species composition.

5.5.3.2 Fish size effect

In the present study feeding rates of sprat increased with body size (Fig. 5.7), which is in line with previous findings for other fish species (Breck and Gitter 1983; Persson 1987; Persson et al. 1998, Miller et al. 1992; Gustafsson et al. 2010). Size-related differences in capture rates can be explained by morphological and physiological constraints (Gustafsson et al. 2010). Larger sprat can realize higher absolute swimming speeds than smaller ones, so that they are able to reach the next prey item much faster than smaller sprat. In addition, improvements in vision of larger sprat increase the search volume. The size-dependent development of fish retina was demonstrated for bluegill (*Lepomis macrochirus*) (Hairstone et al., 1982) and herring (*Clupea harengus*) (Blaxter and Jones, 1967). Studies on bluegill (Mittelbach, 1981) and stickleback (Gill and Hart, 1994) also showed that handling time decreases with increasing fish size and then remains constant above a given fish size. The scaling exponent of handling time found here (-0.81) overlaps with the range of expected values (-0.66 to -1.0; Rall et al. 2012). Our results revealed that handling time for a 3.7 cm TL sized sprat was on average twice as long as for sprat with a body size of 8.7 cm TL.

We provide two different functional response models for sprat feeding on *A. salina* nauplii: model 1 for sprat between 4 and 9 cm TL and model 3 for larger sprat from 9 cm TL. For sprat smaller than 4 cm TL we do not recommend to use our functional response models, because sprat prior to metamorphoses (2.5-3 cm TL; Günter et al., 2012) show different feeding behaviour than larger sprat (Peck et al., 2012). We assume that the indirect determination of *k* values for larger sprat based on stomach content data from field provides a reasonable estimate of the relationship between *k* and length (Fig. 5.5). Despite the scattering of *k* values, the data reveal a clear trend: with increasing fish size *k* values decreased. In other words, larger sprat shows higher biting rates than smaller ones at the same prey concentrations. This trend makes sense due to the morphological and physiological improvements of larger sprat.

Our results suggest that the size effect on the feeding rate was more pronounced for smaller sprat than for larger sprat. *BRmax* increased steeply up to about 6 cm TL and then remains constant

(Fig. 5.2 A). At lower prey concentrations the influence of size on feeding rate was strong up to 8 cm TL (Fig. 5.5). As a consequence, juvenile sprat should school preferably with similar sized individuals in order to increase the foraging efficiency of individual fish. The tendency of sprat and herring of similar sizes to form mixed schools during their estuarine residency were found by Maes and Ollevier (2002). Herring-dominated schools were typically larger and contained larger-sized individuals than schools dominated by sprat.

5.5.3.3 Temperature effect

Feeding rates of sprat increased with increasing temperature (Fig. 5.6), which is consistent with other studies, e.g. on roach and perch (Bergmann 1987, Persson 1986, Linlokken et al. 2010), three-spined stickleback (Lefebure et al. 2014) and salmonids (Watz et al. 2014) . Because biochemical processes and functions of fish largely depend on temperature (Gillooly et al. 2001), handling time (time to kill and eat one prey item) is also likely to be related to ambient temperature (Sentis et al. 2012). In our study, handling time was on average four times lower when sprat fed at 20 °C than at 5 °C. Both, model 1 and 3, indicate a strong positive relationship between *BRmax* and temperature, but no temperature effect on *k*. However, at low prey concentrations biting rates of sprat also increased with increasing temperatures because the parameter *BRmax* also affect the shape of the functional response curve at lower prey concentrations (Fig. 5.6). Model 2 and 4 suggests a positive linear relation between *k* and temperature, which means that feeding rates of sprat decreased at low prey concentrations with increasing temperature (Fig. 5.1 B). We assume that these observations are artefacts and the positive trend between *k* and temperature is only caused by the small number of observations made at low prey concentrations for the 5°C experiments. A further indication that *k* more likely remains constant is the fact that the *k* values of the 8 °C ($k = 7.0$), 12 °C ($k = 8.7$) and 16 °C ($k = 8.2$) experiments were similar.

The ecological implication of increasing biting rates with increasing temperatures in the central Baltic Sea is that sprat feeding in the deep colder waters during the day have a strongly reduced feeding rates. Vertical migration into warmer upper layers may either be utilized for addition food intake or may had to an overall increased metabolic rate that also affects biting rates. The fact that the temperature increase of biting rates levels off at higher temperatures implies that at these high temperatures fish need high prey concentrations for growth because the metabolic cost show a steady increase with temperatures (Meskendahl et al. 2010).

5.5.4 Energetic efficiency of sprat

Our functional response model provides a mechanistic understanding of how prey concentrations, feeding period, fish size and temperature affect the energy intake of sprat. This knowledge combined with metabolic rate can be used to interpret growth performances among seasonal cohorts of YoY-sprat. Baumann et al. (2008) and Günther et al. (2015) analysed the fate of different seasonal cohorts and found that later born cohorts dominated among surviving recruits at the end of the year. Contrary to early born cohorts, later born cohorts experienced higher summer temperatures during larval stages, whereas juveniles grew at lower temperatures in late summer and autumn. However, no mechanistic explanation for the importance of timing and thus temperatures on seasonal cohorts has been found so far. Our results indicated that the stronger increase in metabolism compared to the energy intake with raising temperatures caused a hump-shaped energetic efficiency of sprat in relation to temperature (Fig. 5.8): the energetic efficiency increases with temperature, reach an optimum, and then decreases at higher temperatures. Similarly, the energetic efficiency decreases with increasing body size as the metabolic cost increased stronger than the energy intake by feeding as a function of fish size. As a consequence, the food demand increases with increasing temperature in order to gain energy for optimal growth. Particularly larger sprat need higher prey concentrations at higher temperatures during summer than smaller sprat for growth. Thus being born later has the advantages that the juvenile phase with larger sprat is shifted to late summer and autumn with average colder temperatures where the energetic efficiency is higher than in summer and that the risk of starvation due to unfavourable food conditions is minimize.

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6 Manuscript 3: Ignoring the vertical dimension: biased view on feeding dynamics of vertically migrating sprat (*Sprattus sprattus*)

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6.1 Abstract

Diel vertical migration (DVM) is a common behavior and often relates with the diurnal feeding periodicity. Nonetheless, sprat feeding behavior and daily ration (DR) estimation are usually based on daytime stomach contents from deeper layers. Our study provides a new approach for DR estimation, taking into consideration the DVM associated feeding periodicity. We analyzed sprat DVM by hydroacoustics and collected stomach contents in the Central Baltic Sea at different feeding depths. The main outcome is that feeding in the deep during the day represents only 15-50% of the DR. Feeding rates were on average 3.2-times higher in upper layers when compared to daytime estimates from deep waters. DRs were 1.4-times higher using our approach compared to the established approach. The underestimation by the established approach was mainly caused by ignoring the effect of higher temperatures from upper layers on the gastric evacuation rate. Our results have major implications not only for DR estimates but also on the interpretation of prey selectivity. The study emphasizes the importance of adapting the sampling design on the vertical feeding dynamics to avoid a biased picture of predator prey interactions.

6.2 Introduction

Diel vertical migration (DVM) is a common behavioral pattern for variety of organism groups ranging from phytoplankton to invertebrates and fish (reviewed by Mehner, 2012). The main proximate trigger for DVM is the diel change in light intensity – typically causing an ascent when illumination declines at dusk and a descent when light intensity increases at dawn. Additional proximate triggers are hydrostatic pressure and water temperatures (Mehner, 2012). Several ultimate causes of DVM are discussed: (i) the increase of bioenergetics efficiency by, for example, distributing at optimal temperatures to maximize growth rates or to minimize metabolic cost, (ii) the improvement of feeding opportunities by mirroring the prey daily movements and (iii) predator avoidance (Cardinale et al., 2003; Mehner, 2012; Staby et al., 2013; Solberg and Kaartvedt, 2017). There are different variants of DVM, which can vary within species depending on the region or even between juveniles and adults in the same habitat (Cardinale et al., 2003; Peltonen et al., 2004; Staby et al., 2013). The difference in DVM behavior, i.e., between different ontogenetic stages, seems to result from a trade-off between different ultimate causes like gaining energy for growth and survival (Staby et al., 2013; Solberg and Kaartvedt, 2017).

As DVM often correlates with the diurnal feeding periodicity of fish (Batty at el., 1990; Pedersen, 2000; Cardinale et al., 2003) it is particularly important to adapt the sampling design to the specific behavior pattern to avoid a biased picture of prey consumption (Pedersen, 2000). At Devil's Hole in the North Sea, for example, whiting (*Merlangius merlangus*) caught with a pelagic trawl were actively feeding on sprat and sandeel (*Ammodytes* spp.), while whiting sampled during the day with a bottom trawl were feeding on Norway pout (*Trisopterus esmaki*). Depending on the feeding depths, the prey composition and energy density of prey differed and hence also affected the estimated daily ration (DR) of whiting (Pedersen, 2000). Andersen et al. (2017) investigated the diel interaction pattern between cod (*Gadus morhua*) and sprat in the Central Baltic Sea. They analyzed the diel vertical distribution by hydroacoustics data and identified the stomach contents of cod and sprat from different depths using pelagic and bottom trawls. With a quantitative analysis of the degree of digestion of the prey items they were able to show that the predation of sprat by cod primarily took place at dusk and dawn during the ascent and descent of sprat associated with school dissolution and formation.

Planktivorous sprat (*Sprattus sprattus*) play a key role in the Baltic Sea ecosystem as they have a marked impact upon their prey communities (copepods and cladocerans) and are an important source of food for piscivorous predators, namely cod, Atlantic salmon *(Salmo salar*) and seabirds (Rudstam et al., 1994; Arrhenius, 1996; Kornilovs et al., 2001; Möllmann et al., 2004). In the deep basins of the Baltic Sea, sprat show the "normal" and widespread variant of DVM, which consists of different phases: denser sprat schools occur in deep waters during the day and ascend towards the surface at dusk and reside in upper layers by night and finally return to the deep at dawn (Cardinale et al., 2003; Nilsson et al., 2003). A similar behavior is also shown by Baltic Sea herring (*Clupea harengus*) (Cardinale et al., 2003). In contrast, in the Gulf of Finland, sprat and herring aggregate near the thermocline at night and do not ascent into surface waters (Peltonen et al., 2004). In Himmerfjärden in the Baltic Sea, herring even show a reverse DVM, staying deeper at night and, on average, shallower during the day (Jensen et al., 2011). Overwintering sprat in the Norwegian fjord carried out DVM in winter, but with a variable pattern, including both normal and asynchronous DVM (Solberg et al., 2015). Some sprat show a somewhat deeper nocturnal than daytime distribution (Solberg et al., 2015).

Numerous studies have found that sprat mainly feed during the day when light conditions are sufficient (Köster, 1994; Cardinale et al., 2003; Peltonen et al., 2004; Bernreuther et al., 2013). Cardinale et al. (2003) investigated the feeding activity of sprat and herring in the deep basin of the Baltic Sea and assumed that the visibility of prey is likely highest at the dawn and dusk when zooplankton is distributed near the surface. Köster (1994) was also able to deduce from stomach content data from 24h fisheries in the Bornholm Basin that the feeding rate of sprat was not constant during the feeding period, but increased in the first hours after sunrise. However, the actual food intake during different phases of the vertical migration has not yet been investigated.

The present study attempts to fill this gap, determining the proportions of food consumption during all phases of the DVM. This is especially important as the DR of sprat was so far mainly estimated from mean stomach content sampled during daytime in the deeper layers, with trawling depths varying between 60 and 70 m in the Bornholm Basin (Baltic Sea), in combination with a gastric evacuation model (Köster and Möllmann, 2000; Bernreuther et al., 2009). However, the gastric evacuation of sprat increases strongly with increasing temperatures

(Bernreuther et al., 2009). This temperature effect, however, was ignored based on the assumption that feeding during the day takes place mainly in the deeper water layers, consisting of colder temperatures (Möllmann and Köster, 1999; Köster and Möllmann, 2000). Furthermore, the feeding period of sprat has hitherto been regarded as the period between sunrise and sunset (Köster and Möllmann, 2000). However, field observations by an upwards-pinging echosounder showed that sprat increased their swimming speed and started to migrate already about one hour before the sunrise (Didrikas and Hansson, 2009; Solberg and Kaartvedt, 2017). This indicates that light conditions for light-sensitive sprat were sufficient for feeding already one hour before sunrise and after sunset. The additional time of feeding at upper layers can lead to further underestimation of the DR of sprat if feeding in upper water layers occurs.

A closer inspection at the vertical feeding dynamics of sprat will improve the DR estimates which is likewise essential for quantifying its trophodynamic impact and its potential scope for growth. Furthermore, if the feeding activity is different between the phases during the vertical migration, the determination of prey selectivity becomes complicated and needs to be adjusted to the DVM of the predator.

Thus, we collected data on the vertical distribution of sprat and stomach contents from shortly before sunrise to about two hours after the sunset at three stations in the Bornholm, Arkona and southern Gotland Basin in the Baltic Sea in 2015 during the main feeding season in summer. In addition, vertically resolved zooplankton samples were used to validate the feeding depth of sprat. Feeding rates of sprat at different feeding phases (FP) during the DVM were quantified by modifying the established gastric evacuation model for DR estimation. The course of sprat stomach content during the feeding period was simulated by numerical integration, whereby feeding rates within different FPs were iteratively changed in such a way that predicted contents match the observed contents from field.

6.3 Material and Methods

For the analysis of the daily pattern of feeding we collected stomach content data of sprat (n = 2740) and vertically stratified samples of zooplankton (20 hauls) from shortly before sunrise to about two hours after the sunset at 3 different stations in the Bornholm Basin (55°21.00'N 16°00.00'E), Arkona Basin (54°48.61'N 13°40.37'E) and southern Gotland Basin (56°31.79'N 18°47.78'E) in August 2015. The trawl sites at each fishing and zooplankton haul per station were located only < 1 miles apart. Information about clupeid fish densities and vertical distributions were obtained from a Simrad echosounder EK60 with a hull-mounted 38-kHz split-beam transducer. Data was processed with the Sonardata Echoview 4.9 software. A volume backscattering coefficient threshold of SV -60 dB was applied. Vertical resolution was set to 1 m, the horizontal resolution to 0.1 nmi. Results were given in nautical area scattering coefficient (NASC) values [m^2/nmi^2]. At each station a temperature profile was recorded with a CTD-probe (type ME-KMS3).

A total of 25 fishing hauls were conducted to determine the stomach contents of sprat. A mid-water trawl type PS 205 with a cod-end mesh width of 5 mm was towed for 30 min. The depth of net was adjusted to visible echoes of clupeids. From each haul, wet mass and length distributions (1 cm classes) of sprat were recorded. A total of about 30 sprat per haul and length class were preserved in 4% di-sodium-tetraborate-buffered formalin-seawater. In the laboratory, the wet mass of stomach content was determined by weighing the stomachs before and after emptying at a precision of 0.001 g. Diet analysis was conducted for 6 fish per haul and length classes from 11 to 12 cm TL for the station in the Arkona Basin. Stomach contents were initially estimated volumetrically on the proportions which are identifiable or completely digested. Identifiable organisms were determined to the lowest possible taxonomic level using a stereo microscope (magnification 16 to 80x). If a stomach contained large numbers of prey, a subsample of 200 identifiable items was analyzed. The numbers of the prey were proportionally extrapolated to the entire stomach content. A total of 90 sprat stomachs were qualified.

6.3.1 Zooplankton sampling

The vertical distributions of prey were recorded from 14:00 to 14:30 and 18:00 to 18:40 UTC (n = 4 hauls) in the Arkona Basin. Vertically stratified samples were obtained using a multiple opening-closing net (Hydro-Bios; www.hydrobios.de/) with an opening of 0.25 m^2 and a mesh size of 100 µm. Samples were taken from 22 to 41 m at 2-3 m intervals and preserved in 4% disodium-tetraborate-buffered formalin-seawater solution for later analysis in the laboratory. Mesozooplankton was identified and counted under a binocular microscope on subsamples of not less than 500 individuals per sample. Subsamples were obtained using a Kott-splitter device. Copepods were identified to species, *Pseudocalanus acuspes*, *Temora longicornis*, *Centropages hamatus*, *Oithona similis* and *Acartia* spp. (including *A. bifilosa* and *A. longiremis*). Cladocerans were not separated into species.

6.3.2 Established approach of daily ration estimation for sprat

Usually daily rations (*DR*, g_{WW}, $_{WW}$ = wet weight) of sprat were estimated using mean stomach contents and a simplified exponential or general gastric evacuation model, that incorporated temperature and fish weight as variables (Köster and Möllmann, 2000; Bernreuther et al., 2009). The evacuation rate of the stomach content (*ΔS*) can be calculated using the following equations:

$$\Delta S = \left(-R * {S_t}^{B}\right) * \Delta t \qquad \textit{Equation 6.1}$$

$$R = R'' * e^{A*T} * M^{C} \qquad \textit{Equation 6.2}$$

Where *R* = gastric evacuation constant ($g_{DW}1^{-B}$ h^{-1}; $_{DW}$ = dry weight), S_t = stomach content (g_{DW}) at time *t*, *B* = shape parameter of the gastric evacuation (0.668), *Δt* = time interval, *R''* = evacuation constant (0.0177), *A* = temperature coefficient (0.0775), *T* = mean temperature at depths where sprat remain during the daytime (°C), *M* = fish weight (g_{DW}), C = body mass exponent (0.503).

Parameters for the general gastric evacuation model were from Bernreuther et al. (2009). Following Pennington (1985), *DR*, can then be estimated as follows:

$$DR = R'' * e^{(A*T)} * W^C * S^B * D + S_t - S_0 \qquad \textit{Equation 6.3}$$

Where S = average stomach content from daytime (sunrise to sunset), D = duration of feeding period (sunrise to sunset) and S_t = average stomach content at the end as well as S_0 = average stomach content at the beginning of the feeding period. Values for S_t (144 %) and S_0 (57%) were estimated from 24 h-fisheries representing mean relative deviations from the average stomach content during daytime, 2 h before and after the food ingestion stopped and commenced, i.e. sunset and sunrise (Köster, 1994). Since the parameters by Bernreuther et al. (2009) refer to dry weights, we used a factor of 0.2 (Omori, 1969; Williams and Robins, 1982) to convert the results into wet weights.

6.3.3 New approach of daily ration estimation for sprat

The visual examination of the echograms and the evaluation of fishing depths allowed the temporal and spatial resolution of fish dispersion throughout the water column during the DVM. Due to the distribution pattern, we defined five different feeding phases (FP) during the DVM of sprat. Field observations made by Didrikas and Hansson (2009) and Solberg and Kaartvedt (2017) using an upwards-pinging echosounder showed that sprat increased their swimming speed and started to migrate already about one hour before the sunrise. Thus, we defined that the feeding period of sprat started 71 min before the sunrise (t = 0) until 71 min after the sunset (Didrikas and Hansson, 2009). The five different FP's were: FP I = feeding in upper water layers from 71 min before sunrise until the beginning of the downwards migration, FP II = feeding during the downwards migration, FP III = feeding in deeper water layers, FP IV = feeding during the upwards migration, FP V = feeding in upper water layers until 71 min after the sunset. After the FP V it was assumed that sprat show no to very little feeding activity. This can be derived mainly from the low proportion of fresh food items and the high degree of digestion of prey in the stomachs of sprat from field (Köster, 1994).

The DR (%BW) of sprat for the length classes 11 to 13 cm was estimated from the mean stomach content weight data from field and the published gastric evacuation rate by Bernreuther et al. (2009). The modified estimation of DR is based on a numerical integration of the course of stomach contents throughout different FPs during the DVM. However, to be able to model also the increase in stomach contents during the feeding period, the equation must be extended by a feeding rate term (F, g_{ww} h^{-1}). For feeding fish, the change in stomach content (ΔS) in a given time can be calculated according to Pennington (1985) as follows:

$$\Delta S = \left(F - R * {S_t}^{B}\right) * \Delta t \qquad \textit{Equation 6.4}$$

Starting with an empty stomach, we calculated the change in stomach content weights (equation 6.2 and 6.4) in 1-minute steps (dt = 0.017 h) and added it to the present stomach content weight. This stomach content weight was taken in the next step as new starting point. This procedure was repeated until the end of the feeding period. The mean ambient temperature in the equation 6.2 was changed depending on the depth range of the five different FPs. For each FP a separate feeding rate was calculated. The five feeding rates as well as the time limits of each FPs were estimated iteratively at the same time by minimising the squared differences between the observed and the simulated stomach contents at the times of sampling. For all three size classes, common time limits were determined for each FP. The DR of sprat was derived by the sum of feeding rates multiplied by feeding times from all five different FP's. DR's were finally expressed as percentage of body weight (BW, g_{ww}):

$$DR(\%BW) = \frac{DR}{BW} * 100 \qquad \textit{Equation 6.5}$$

6.3.4 Bioenergetics model

To find out if the energy balance of sprat feeding for a day in the three basins were different, we calculated a simple energy budget model for the length classes 11 to 13 cm. The energy intake resulted from the calculated DVM associated feeding rates from the numerical integration (equation 6.2 and 6.4). Feeding rates in gram wet weight from different FPs were converted in Joule per day using mean prey wet weight between 28.5 and 40.1 μg_{WW} (Hernroth, 1985) and prey energy contents between 0.042 and 0.082 J prey item^{-1}. For each FP we used a different prey weight and energy content based on the prey composition in the diet of sprat sampled in different times and depths in the present study in the Arkona basin. The energy costs were calculated separately for each FP and were defined as the sum of the respiration term for the routine metabolism ($R_{routine}$), respiration term for feeding metabolism ($R_{feeding}$) which is caused by feeding-induced swimming activity, respiration term for specific dynamic action (R_{SDA}), term for excretion (E) and term for faces (F). We assumed that $R_{feeding}$, R_{SDA}, E and F account each for 10% of the consumption (Andersen and Riis-Verstergaard, 2003; Temming and Herrmann, 2009; Meskendahl et al., 2010). The parameters for the temperature- and fish weight-dependent $R_{routine}$ of sprat came from Meskendahl et al. (2010). As mean temperatures were different between the FPs, the values for $R_{routine}$ were different for each FP. For the conversion of the results of the $R_{routine}$ in milligrams of oxygen per hour to J mgO_2^{-1}, we used the oxy-caloric factor of 13.72 by Elliot and Davison (1975). After the feeding period, the energy intake was set to zero and only the costs were taken into account. Finally, in order to determine the energy surplus, we calculated the difference between the energy intakes and costs.

6.3.5 Validation of actual feeding within the water column in relation to different feeding phases

In order to verify the actual feeding of sprat at different observed depths, we compared the mean relative abundance (%) of prey in the diet of sprat from the Arkona Basin with the mean relative abundance of zooplankton at different depths. For better comparability, numbers of prey sampled at different times were averaged into different FPs I-V. Stomach content samples of sprat sizes 11 and 12 cm were grouped in this way: FP I-II = 7:08 and 08:29 UTC, FP III = 10:26, 11:49

and 13:16 UTC, FP IV = 17:17 and 19:08 UTC. Zooplankton samples were aggregated as follows: III = 14:00 and 14:30 UTC, IV = 18:00 and 18:40 UTC.

6.4 Results

6.4.1 Feeding phases and mean ambient temperature

6.4.1.1 Bornholm Basin

The feeding period of sprat was between 2:34 and 19:29 UTC (Fig. 6.1 A). Sprat were assumed to feed near the surface (FP I) in water depths between 10 and 30 m for 2.42 hours. From 4:59 UTC on, sprat migrated downwards for 1.52 hours (FP II). In total, sprat were assumed to stay 8.02 hours in the deeper layers between 45 and 60 m (FP III). From the time of 14:31 UTC they started to migrate upwards for 4.47 hours (FP IV). The FP IV between the layers 30 to 10 m lasted 0.48 hours. Overall, sprat were supposed to feed 8.88 hours in upper water layers. This equated to 52.56 % of the total feeding period of sprat. The mean water temperature within FP I and V was 15.6°C. During the ascent, descent and residence in deeper layers sprat were exposed to mean temperatures between 5.7 to 5.8°C.

6.4.1.2 Southern Gotland Basin

Sprat were assumed to feed between 2:11 to 19:30 UTC (Fig. 6.1 B). The FP I lasted 1.10 hours between the water depths 23 to 26 m. From 5:22 UTC they started to migrate into deeper layers for 2.07 hours (FP II). Sprat stayed between the water layers 50 and 70 m for 11.62 hours (FP III). The ascent started at 17:01 to 17:59 UTC (FP IV). The FP V lasted 1.52 hours between the depths 20 and 14 m. In total, sprat were supposed to feed 5.65 hours within upper water layers, corresponding to 32.69 % of the total feeding period. Mean water temperatures for FP I and V were 13.8 and 17.6 °C, respectively. During FP II and III sprat were exposed to mean temperatures between 6.3 and 8.1 °C. In deeper layers (FP III) the temperature was on average 4.6 °C.

6.4.1.3 Arkona Basin

The feeding period of sprat started at 2:49 and ended at 19:26 UTC (Fig. 6.1 C). Sprat were assumed to feed during FP I for 3.18 hours between the depths 5 and 12 m. The descent started at 6:00 UTC for 1.97 hours. The FP III lasted 5.27 hours between the depths 35 and 38 m. The ascent began at 13:14 UTC and lasted 6.20 hours (FP IV). No FP V was assumed as sprat did not migrate during the feeding period back to layers near the surface. In total, sprat were assuemd to feed 11.35 hours within upper water layers. This corresponded to 68.30 % of the total feeding time of sprat. The mean water temperature during FP I was 17.8 °C. During the ascent and descent sprat were exposed to mean temperature of 14.8 °C. The water temperature in deeper layers was on average 8.8 °C (FP III).

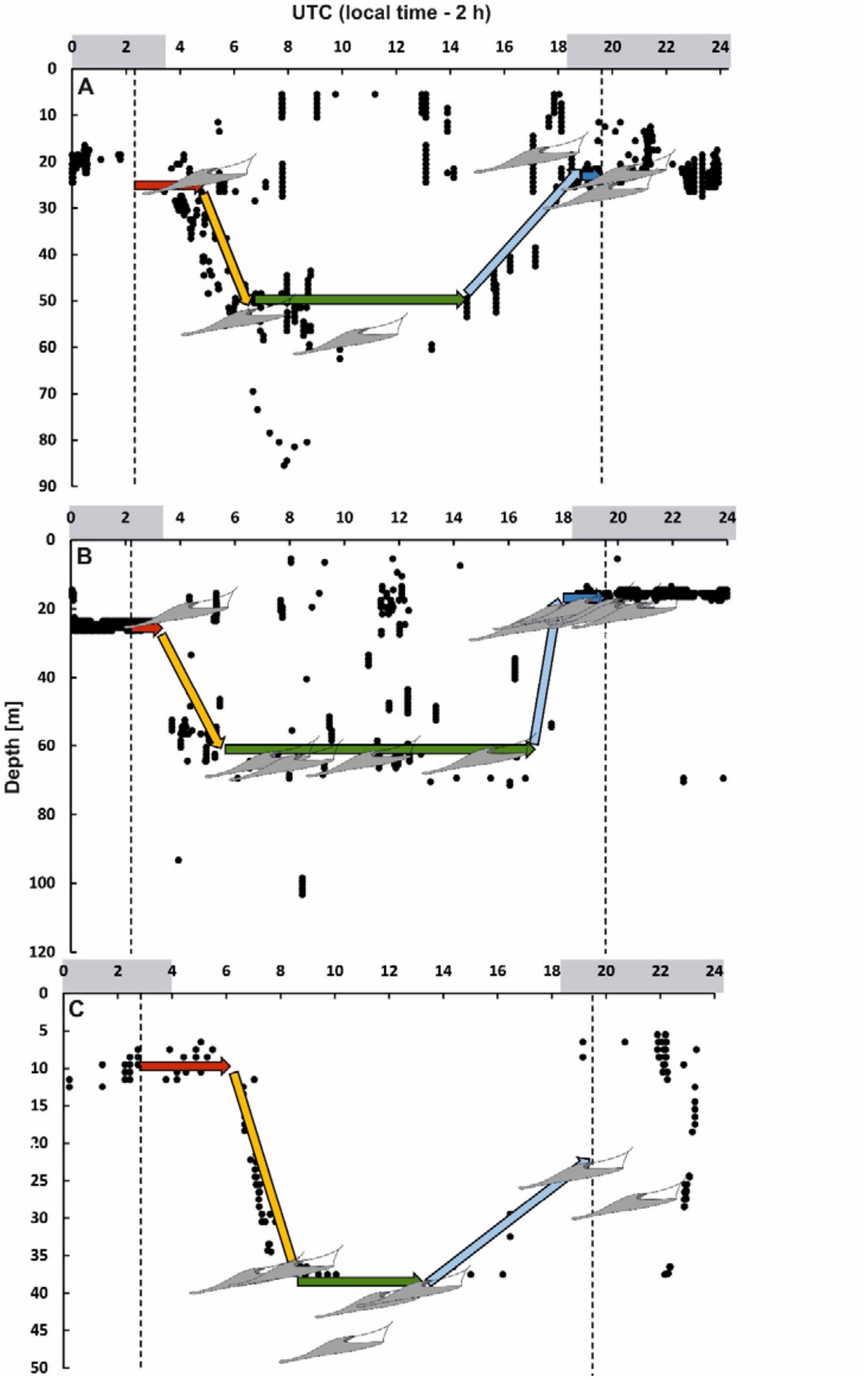

Figure 6.1: Vertical distribution of clupeids and predicted FPs during the DVM of sprat in the Bornholm (A), southern Gotland (B) and Arkona (C) Basin in August 2015. *Points represent nautical area scattering coefficient (NASC, m^2/nmi^2) higher than 200 (horizontal dimension of each profile was 0.1 n miles). Gaps represent times of day that were not covered by hydroacoustics. The colored arrows represent different FPs I-V (dark red: FP I, yellow: FP II, green: FP III, light blue: FP IV and dark blue: FP V). Dashed lines show the beginning and end of the feeding period. Undyed area in the time scale is the time from sunrise to sunset. The trawls represent the fishing depths of fishing hauls**.** The mean relative abundance of clupeids in catches were: Bornholm Basin = 90% sprat and 10% herring; Gotland Basin = 74.3% sprat and 25.7% herring; Arkona Basin = 39.6% sprat and 60.4% herring.*

6.4.2 Feeding rates and daily ration

6.4.2.1 *Bornholm Basin*

Stomach content weights of the length classes 11 to 13 cm showed the same pattern and increased with increasing time. Stomach content weights of all length classes were at the end of the FP II between 0.06 and 0.11 g_{ww} (Fig. 6.2). Feeding rates varied between 0.041 and 0.050 g_{ww} h^{-1} within FP I and between 0.012 and 0.042 g_{ww} h^{-1} within FP II (Fig. 6.5 A). During the residence in deeper water layers stomach content weight of the length class 11 cm remained almost constant. Stomach content weight of the length classes 12 and 13 cm decreased slightly to 0.07 g_{ww}. Feeding rates within FP III were between 0.010 and 0.014 g_{ww} h^{-1}. During the ascent and residence in upper water layers stomach content weights of all length classes increased again to between 0.15 and 0.21 g_{ww}. Feeding rates within FP IV were between 0.035 and 0.051 g_{ww} h^{-1} and within FP V between 0.012 and 0.095 g_{ww} h^{-1}. Sprat consumed during FPs I, II, IV and V in upper layers between 72.26 and 85.05 % of the total DR. DRs of the length classes 11, 12 and 13 cm estimated by our new approach were 3.87, 3.70 and 3.72 %BW, respectively. The DRs from the present study were 1.49 (11 cm), 1.42 (12 cm) and 1.43 (13 cm) times higher compared to the results derived from the established approach (Table 6.1). The energy budget model revealed an energy surplus of 156.20, 167.68 and 173.33 J $fish^{-1}$ d^{-1} for the length classes 11, 12 and 13 cm, respectively (Table 6.1).

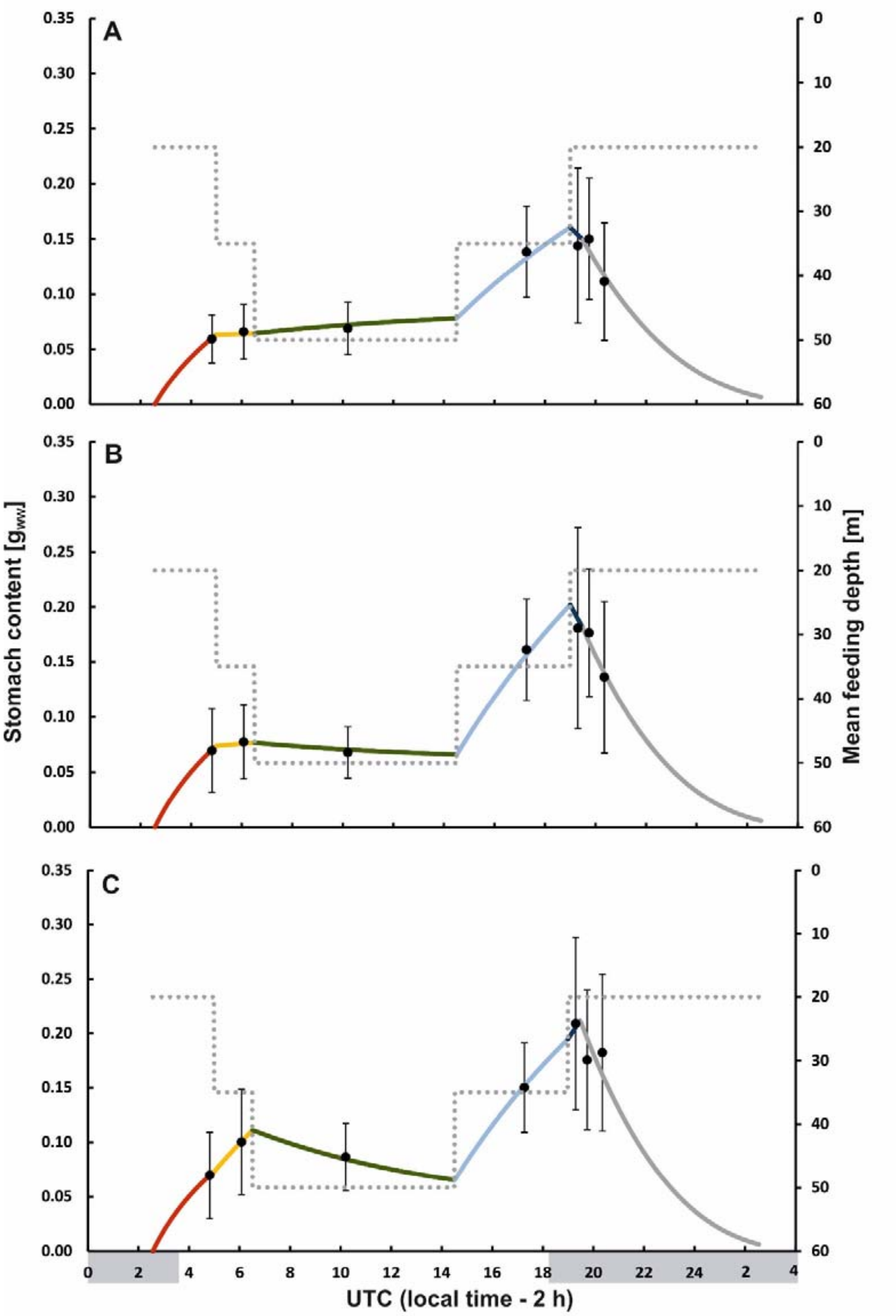

Figure 6.2: Mean observed (circle, ±SD) and predicted stomach contents (g_{WW}) of sprat feeding in the Bornholm Basin over a period of 24 hours (UTC) for the length classes 11 (A), 12 (B) and 13 (C) cm TL. *Each circle represents the mean of 14 to 30 replicate stomachs. Stomach contents were predicted using mean stomach content weights from field and a temperature- und weight-dependent model of gastric evacuation for sprat (a detailed description can be found in materials and methods). Different lines represent five different FPs: red line = FP I, yellow line = FP II, green line = FP III, light blue line = FP IV, dark blue line = FP V, grey line = time of no feeding. Pointed grey line represents the mean feeding depth (m) at different FPs. Undyed area in the time scale is the time from sunrise to sunset.*

6.4.2.2 Southern Gotland Basin

Stomach content weights of all length classes increased with increasing time during FPs I and II (Fig. 6.3). Predicted stomach content weights at the end of FP II were between 0.07 and 0.10 g_{ww}. Feeding rates during FPs I and II were between 0.021 and 0.051 g_{ww} h^{-1} (Fig. 6.5 B). Afterwards predicted stomach content weights remained almost constant during the FP III for the length classes 11 and 13 cm. In contrast, stomach content for the length class 12 cm increased to 0.11 g_{ww}. Feeding rates during FP III varied between 0.012 and 0.017 g_{ww} h^{-1}. During the upwards migration stomach contents increased and reached maximum values between 0.13 and 0.17 g_{ww}. Feeding rates of sprat were during FP IV between 0.054 and 0.104 g_{ww} h^{-1}. During the residence in upper water layers (FP V) feeding rates decreased again to between 0.014 and 0.033 g_{ww} h^{-1}. Sprat consumed during FPs I, II, IV and V between 49.85 and 59.48 % of the total DR. DRs of the length classes 11, 12 and 13 cm estimated by our new approach were 3.76, 3.59 and 3.44 %BW, respectively (Table 6.1). DVM associated DRs were 1.44 (11 cm), 1.40 (12 cm) and 1.29 (13 cm) times higher compared to the results derived from the established approach. The energy surplus for the length classes 11, 12 and 13 cm were 118.99, 117.76 and 111.85 J $fish^{-1}$ d^{-1} (Table 6.1).

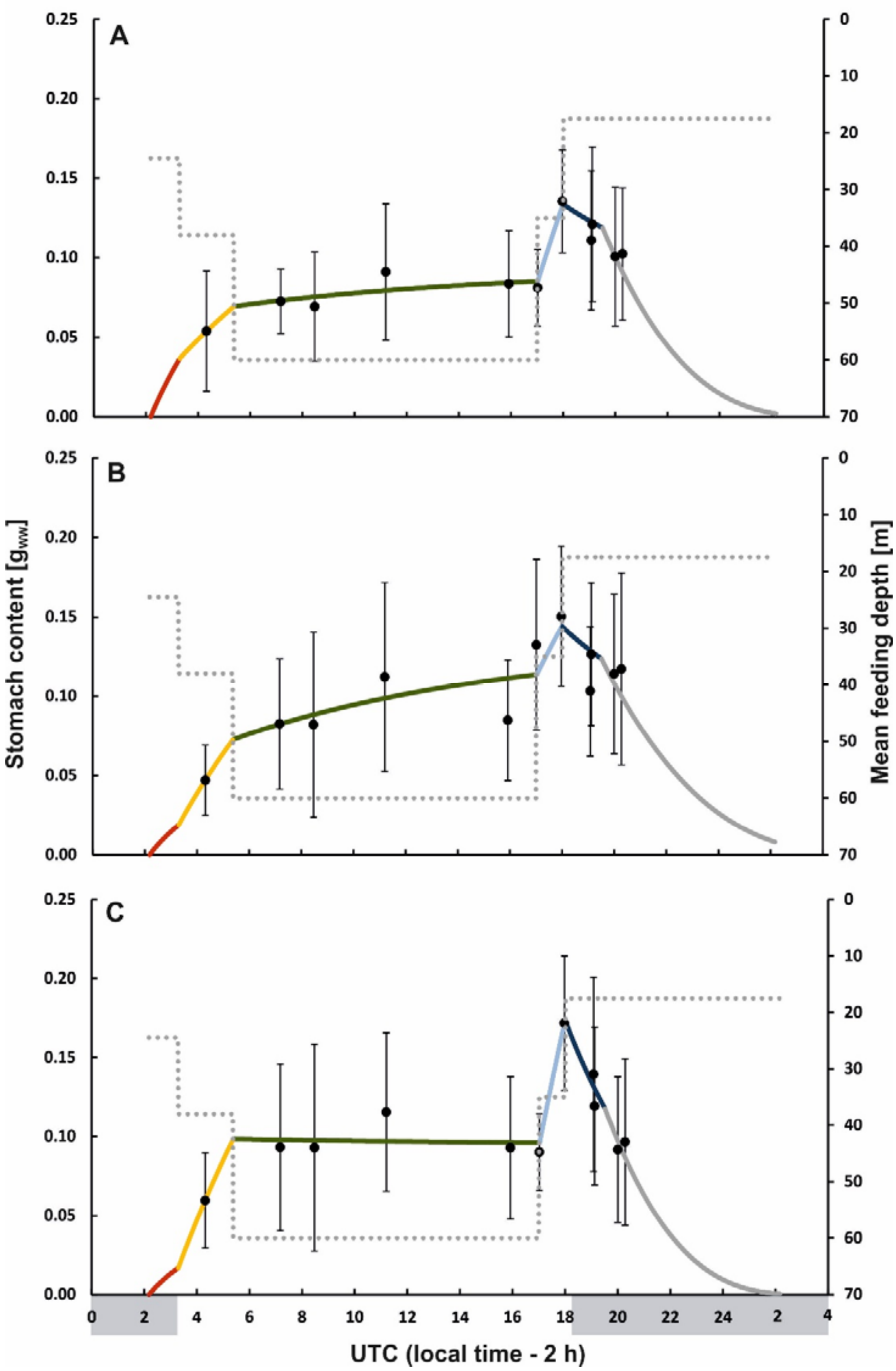

Figure 6.3: Mean observed (circle, ±SD) and predicted stomach contents (g_{WW}) of sprat feeding in the Gotland Basin over a period of 24 hours (UTC) for the length classes 11 (A), 12 (B) and 13 (C) cm TL. *Each circle represents the mean of 14 to 30 replicate stomachs. Stomach contents were predicted using mean stomach content weights from field and a temperature- und weight-dependent model of gastric evacuation for sprat (a detailed description can be found in materials and methods). Different lines represent five different FPs in accordance to DVM of sprat: red line = FP I, yellow line = FP II, green line = FP III, light blue line = FP IV, dark blue line = FP V, grey solid line = time of no feeding. Pointed grey line represents the mean feeding depth (m) at different FPs. Undyed area in the time scale is the time from sunrise to sunset.*

6.4.2.3 Arkona Basin

Predicted stomach content weights of the length classes 11 to 13 cm increased with increasing time during FPs I and II to values between 0.09 and 0.17 g_{ww} (Fig. 6.4). Feeding rates varied during the FPs I and II between 0.029 and 0.099 g_{ww} h^{-1} (Fig. 6.5 C). During the descent stomach content weights remained almost constant or decreased to weights between 0.07 and 0.11 g_{ww}. Sprat showed in deeper water layers (FP III) feeding rates between 0.011 to 0.019 g_{ww} h^{-1}. During the ascent stomach content weights remained constant or increased slightly to values between 0.08 and 0.13 g_{ww}. Feeding rates varied during FP IV between 0.024 and 0.040 g_{ww} h^{-1}. Food intake during FPs I, II, IV and V accounted for 73.12 to 84.30 % of the total DR of sprat. Predicted DRs of the length classes 11, 12 and 13 cm were 4.52, 4.77 and 4.79 %BW, respectively (Table 6.1). DRs were 1.40 (11 cm), 1.44 (12 cm) and 1.32 (13 cm) times higher compared to the results derived from the established approach. The bioenergetics model revealed an energy surplus of 118.15, 165.85 and 199.55 J $fish^{-1}$ d^{-1} for the length classes 11, 12 and 13 cm, respectively (Table 6.1).

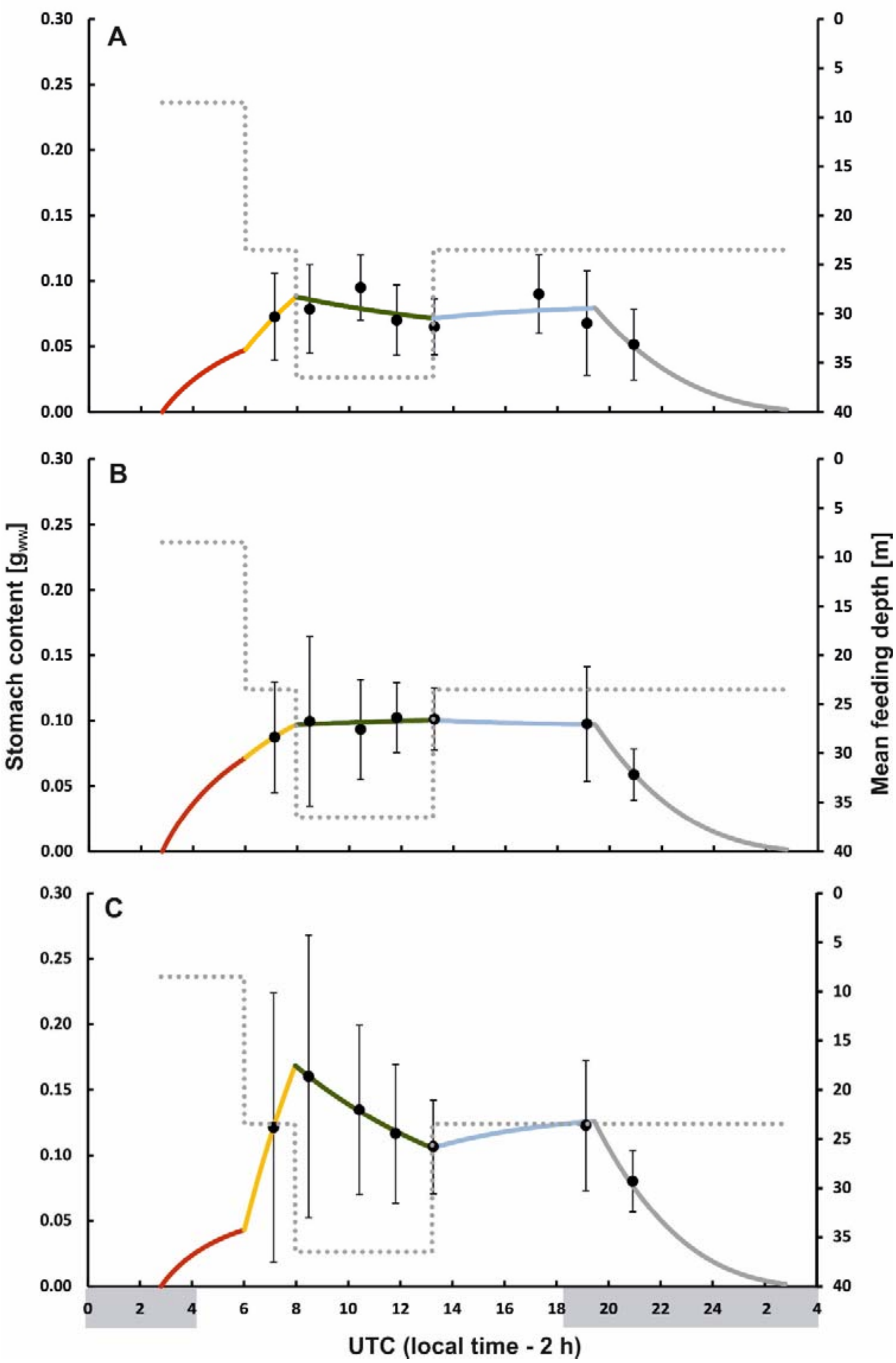

Figure 6.4: Mean observed (circle, ±SD) and predicted stomach contents (g$_{WW}$) of sprat feeding in the Arkona Basin over a period of 24 hours (UTC) for the length classes 11 (A), 12 (B) and 13 (C) cm TL. *Each circle represents the mean of 14 to 30 replicate stomachs. Stomach contents were predicted using mean stomach content weights from field and a temperature- und weight-dependent model of gastric evacuation for sprat (a detailed description can be found in materials and methods). Different lines represent five different FPs: red line = FP I, yellow line = FP II, green line = FP III, light blue line = FP IV, grey solid line = time of no feeding. Pointed grey line represents the mean feeding depth (m) at different FPs. Undyed area in the time scale is the time from sunrise to sunset.*

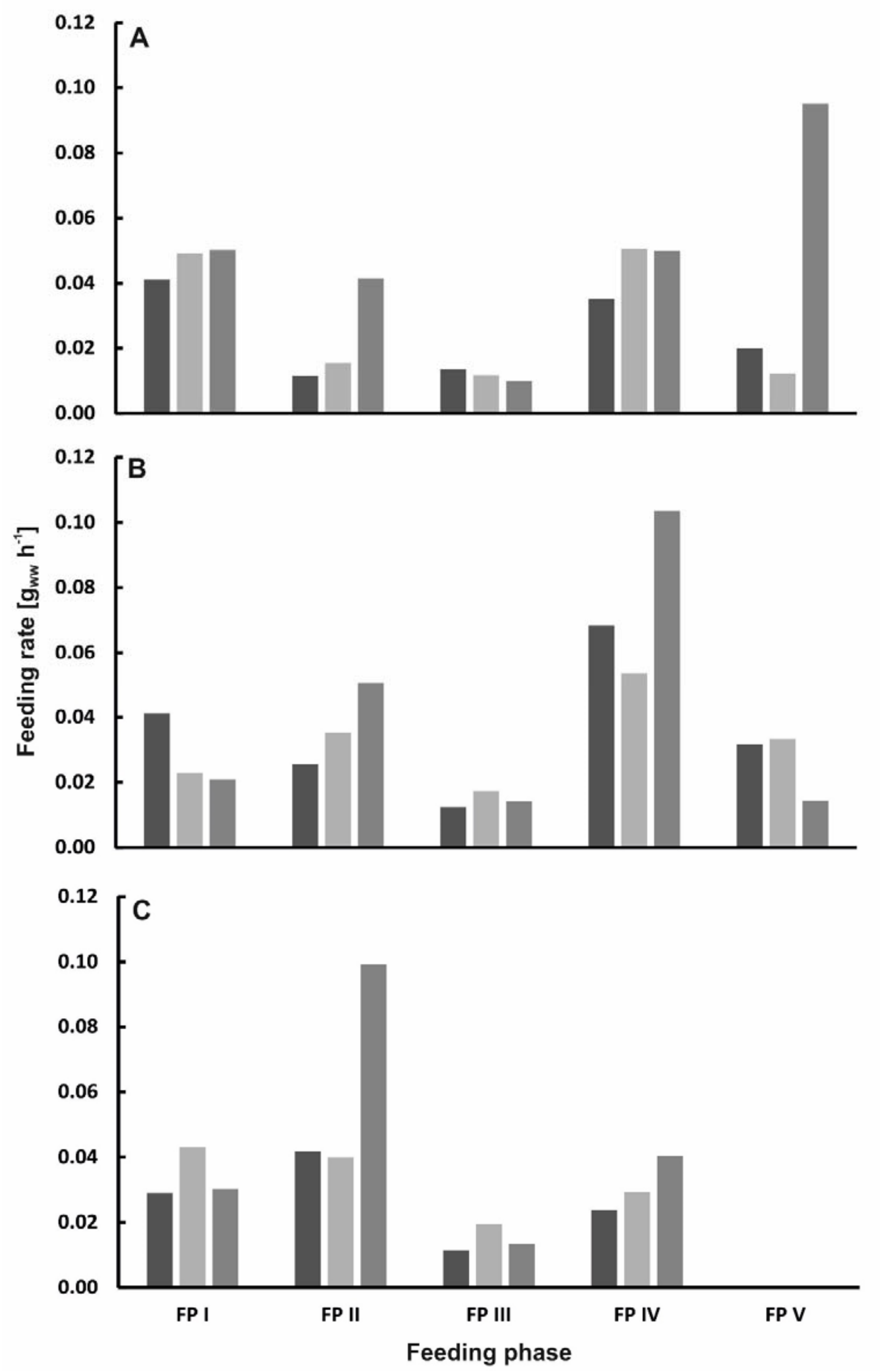

Figure 6.5: Predicted feeding rates (g_{WW} h^{-1}) of different sized sprat (left = 11 cm; middle = 12 cm; right = 13 cm) in relation to different FPs I to IV in the Bornholm (A), Gotland (B) and Arkona (C) Basin. *No FP V was defined for the Arkona Basin as sprat did not migrate back to near the surface during the feeding period.*

Table 6.1: Comparison between daily rations (%BW, body weight) estimated by our new and established approach as well as energy surpluses (J fish-1d-1) calculated by a simple bioenergetics budget model for different size classes (cm TL, total length) in different basins of the Baltic Sea. *Detailed descriptions of the two approaches and the bioenergetics model can be found in the material and methods.*

Area	**Length class [cm TL]**	**Daily ration [%BW]**		**Energy surplus [J fish^{-1} d^{-1}]**
		New approach	**Established approach**	
Bornholm Basin	11	3.87	2.60	156.20
	12	3.70	2.47	167.68
	13	3.72	2.42	173.33
Southern Gotland Basin	11	3.76	2.62	118.99
	12	3.59	2.57	117.76
	13	3.44	2.67	111.85
Arkona Basin	11	4.52	3.22	118.15
	12	4.77	3.32	165.85
	13	4.79	3.62	199.55

6.4.2.4 Simple correction formula for the established approach

We developed a simple correction formula (6.6) to reduce the discrepancy between our new and established approach. We simply divided the consumption formula 6.3 into a section for feeding within upper and deeper water layers and extended the feeding period by 2.4 hours. The first section of the formula 6.6 described the mean temperature condition during FPs I, II, IV and V. The second section described the mean condition during FP III. The following equation shows the corrected version of the established approach:

$$DR = R''{*}e^{(A+T_{upper})} * S^B * D_{upper} * W^C + R''{*}e^{(A+T_{bottom})} * S^B * D_{bottom} * W^C + S_t - S_0$$

Equation 6.6

The parameters R'', A, B, W, C, S_t and S_0 are listed in the material and methods section. S (gww) is the mean stomach weight content during the total feeding period, T_{upper} (°C) is the mean water temperature during FP I, II, IV and V, T_{bottom} (°C) is the mean water temperature during FP III, D_{upper} and D_{bottom} are the feeding times (h) during the feeding phases in the upper and bottom layers, respectively. By improving the formula 6.3 the discrepancy between the observed differences in

DRs of the new and established approach were reduced to an average value of only 4%. The term $S_t - S_0$ were kept in the corrected formula, otherwise DRs were still to low compared to the DR estimated by our new approach. The difference between the DRs without the term $S_t - S_0$ was on average 20%.

6.4.3 Validation of actual feeding within the water column in relation to different feeding phases

The comparison between the mean relative abundance of prey in the diet of sprat with vertically stratified prey data from field allowed the verification of the actual feeding of sprat at the observed water depths within different FPs. In the Arkona Basin, the mean relative abundance of cladocerans in the diet of sprat was 66.04 % within the FP I and II and decreased to 19.11 % within the FP III (Fig. 6.6). During the upwards migration and residence in upper water layers the relative abundance increased again to 57.65 % (FP IV). Compared to zooplankton data, the relative abundance of cladocerans within the FP III in the water depth of about 38 m, where sprat occurred, were only 0.66 to 1.02% (Fig. 6.7 A). In contrast, highest share of cladocerans with 48.04% was found in upper water layers of about 24 m during the FP IV (Fig. 6.7 B). Highest proportion of prey in the diet of sprat within FP III was *Temora* with 53.67% (Fig. 6.6). Zooplankton data revealed that the highest relative abundance of T*emora* with values from 23.08 to 32.69% during FP III were between the depths 29 and 38 m (Fig. 6.7 A).

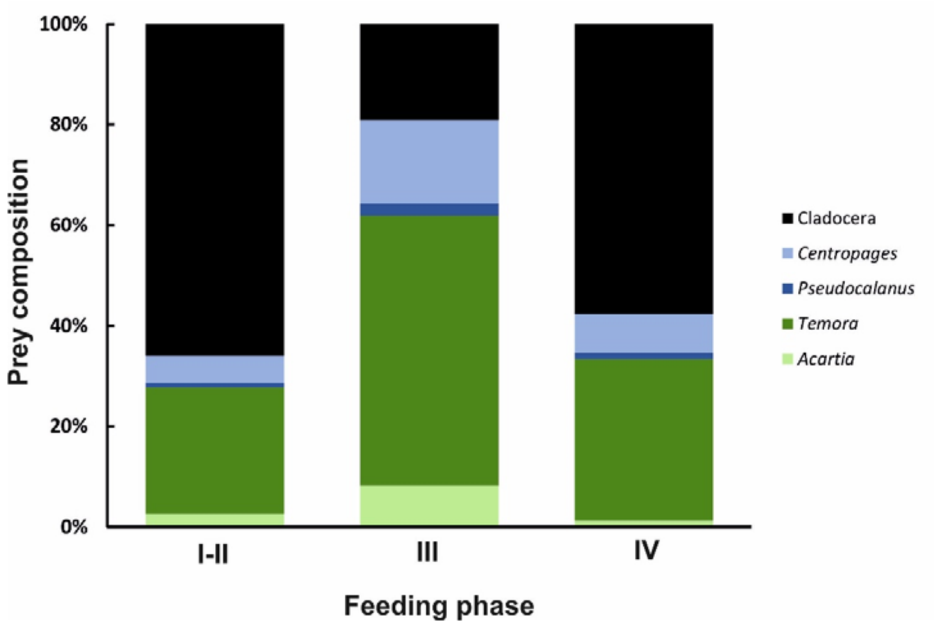

Figure 6.6: Relative abundance of prey in the diet of sprat feeding in the Arkona Basin (calculation based on number) in relation to different FPs I-IV. *Stomach content samples of sprat form the length classes 11 and 12 cm TL (n = 90) were grouped as follows: FPs I and II = 7:08 and 8:29 UTC, III = 10:26, 11:49, 13:16 UTC, IV = 17:17 and 19:08 UTC.*

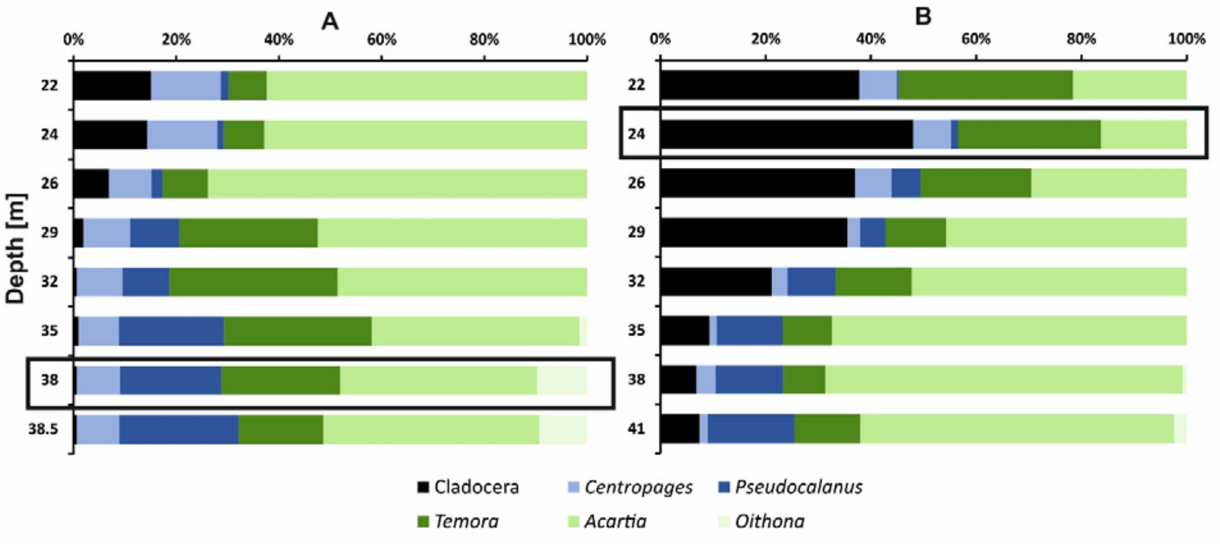

Figure 6.7: Relative abundance of prey species in field (calculation based on number) from the Arkona Basin in relation to different FPs (A = III and B = FP IV). *Zooplankton samples were aggregated as follows: FP III = 14:00 and 14:30 UTC, FP IV = 18:00 and 18:40 UTC. Black rectangles represent the average feeding depth of sprat during the FPs III or IV.*

6.5 Discussion

In the present study we estimated the DR of sprat, taking into account feeding activities prior to, during and after vertical downwards migration. The main result was that the largest share of the total DR (71.36 ± 12.71 %) was actually consumed by sprat in the crepuscular phases in the upper layers and/or during the downwards/upwards migration. Feeding rates from FPs I, II, IV and V were on average 3.16 ± 2.03 times higher than feeding rates from the FP III. Overall, these results confirmed the presumption by Cardinale et al. (2003) that feeding intensity is highest during dawn and dusk in the upper layers. However, the conventional assumption so far has been that sprat feed mainly during the day in the deep near bottom waters (Köster, 1994; Köster and Schnack, 1994). Hence, daily consumption estimates were so far based on mean stomach contents from deeper layers during the day time and lower corresponding mean temperatures (Köster and Möllmann, 2000; Möllmann and Köster, 2002; Bernreuther, 2007; Voss et al., 2011; Bernreuther et al., (in press)).

6.5.1 Implication on diet composition and prey selectivity

Prey selectivity is usually determined by comparing the relative prey composition in the diet of fish and field (Arrhenius, 1996; Bernreuther et al., 2013). However, if only the stomach contents from bottom trawling are considered without taking the vertical feeding dynamics of fish into account, incorrect conclusions might be drawn. In the present study, we compared the prey composition in the diet of sprat and field from the Arkona Basin. Highest relative abundances of cladocerans (between 57.65 and 66.04%) were found in the stomachs from morning (FP I-II), afternoon and evening (FP IV) sampling when sprat occurred in the upper layers. In contrast, the proportion of cladocerans in the stomachs of sprat sampled during the day in deeper water layers was only 19.11%. A similar temporal trend of cladocerans in the diet of sprat was also observed by Köster (1994) and Bernreuther et al. (2013) in the Bornholm Basin. Hence, cladocerans were obviously preyed in the upper layers at the beginning and end of the feeding period. In the Arkona Basin, *Temora* made up 53.67% of the relative stomach content of sprat during the FP III. This prey species occurred in the field during the day mainly at depths between 29 and 38.5 m. In contrast, *Pseudocalanus* represented only 2.39 % of the diet of sprat during FP III. During the FP

III, *Pseudocalanus* and sprat occurred at the same depths between 35 to 38.5 m. In conclusion, although there is a high spatial overlap between sprat and *Pseudocalanus* during the day in the Arkona Basin, the proportion of *Pseudocalanus* in the diet of sprat was significantly lower than *Temora*. This suggests that sprat in the Arkona Basin already filled their stomach with *Temora* during the descent. The small percentage of *Pseudocalanus* in the diet of sprat in the Arkona Basin can be explained by the fact that sprat reduced their feeding activity due to colder temperatures and lower light intensity in the deeper layers. The discrepancy between the relative abundance of *Temora* and *Pseudocalanus* in the diet of sprat and the spatial overlap between prey and predator was also observed for sprat in the Bornholm Basin (Bernreuther et al., 2013). *Temora* made up to 60% of sprat gut contents during the day. The majority of sprat in the Bornholm Basin concentrated during the day at depths between 60 and 80 m (Bernreuther et al., 2013). However, *Temora* preferentially inhabit the upper 30 m of the water column, whereas late copepodite stages of *Pseudocalanus* preferentially inhabit the halocline region (50-70 m) similar to sprat (Hansen et al., 2006; Renz and Hirche, 2006; Dutz et al., 2010). These observations indicate, that the pronounced selectivity for *Temora* that was deduced for sprat in the Bornholm Basin (Bernreuther et al., 2013), may actually be rather a consequence of the active feeding in upper water layers, where *Temora* is actually rather abundant.

6.5.2 Possible drivers for the DVM of sprat

6.5.2.1 Maximize feeding

Prey concentrations in the productive upper water layers during the main feeding period of sprat in spring and summer are higher than in the deeper layers (e.g. Ojaveer et al., 1998; Hansen et al., 2006; Dutz et al., 2010). In addition, the visibility of plankton is highest near the surface where light intensity is higher (Ryer and Olla, 1999; Vogel and Beauchamp, 1999; Cardinale et al., 2003). Many studies on fish preying on planktonic prey demonstrated that the feeding rates as well as the proportion of feeding fish increase with increasing light intensity (e.g. Holanov and Tash, 1978; Batty et al., 1990; Fraser and Metcalfe, 1997). Batty et al. (1990) found that the minimum light level threshold for particulate-feeding herring preying on large prey items (e.g. *Calanus finmarchicus*) was about 0.001 lux. However, for smaller prey items like *Artemia* *salina* nauplii (0.5 to 0.9 mm), which is comparable with the size range of natural prey of sprat in the Baltic Sea, the light level threshold was 0.01 lux (Batty et al., 1990). Similar values were found for salmonids, however, for maximum feeding rates a threshold of light intensity of approximately 3.4 lux was required (Ali, 1959; Fraser and Metcalfe, 1997). This suggest that sprat also may need higher light intensity than 0.01 lux for higher feeding rates.

Nilsson et al. (2003) investigated the DVM of clupeids in the Baltic Sea and found that sprat in the Bornholm Basin in March 2002 were exposed to light intensities between 7.3 and 1.6 lux in upper water layers and only 0.1 lux in deeper layers of about 50 m. An analysis of the light intensity in relation to water depths during the main feeding period of sprat revealed that intensities at 60 m were between 0.37 (bright summer day) and 0.07 lux (overcast summer day) (Zielinski et al., 2002; Krock et al., 2017). At night, light intensities varied between 1 (1 m) and 0.01 (20 m) lux near the surface. This estimation was based on parameters determined on Uthörn (Sylt, North Sea), which lies on the same latitude as Bornholm Basin. Although the light intensity is near the threshold of 0.01 lux and prey concentrations are relatively high near the surface at night, studies on the digestive degree of prey in the stomach contents have shown that sprat do not eat at all or only very slightly during this time (Köster, 1994; Bernreuther et al., 2013). This implies that light intensity in the deep is probably just high enough to detect prey but not to feed on it with a high rate. Furthermore, investigations on the gut fluorescence of copepods have shown that they feed particularly at night (Baars and Oosterhuis, 1984). Thus, the visibility of copepods due to filled guts is particularly high during the morning hours in the upper layers. This may increase the detection rate of copepods for sprat at dawn. Overall, the conditions in the upper layers are more beneficial for food intake for sprat than in deeper layers.

6.5.2.2 Temperature optimization

In the deep basins of the Baltic Sea, a thermal stratification with warmer surface waters and colder deep waters arises in April/May with a peak in August (Voss et al., 2012) during the most important feeding period of sprat (Möllmann and Köster, 1999). Laboratory experiments revealed that the functional response (*per capita* feeding rate as a function of prey concentration) of sprat decreased with decreasing temperature (Manuscript 2). As a consequence, feeding in deeper colder layers is unfavorable for sprat. Colder temperatures and consequently lower feeding rates, however, allow sprat to reduce their metabolic cost in the deeper layers during the day. During the night sprat are found near the surface where warmer waters will increase their digestion rate, allowing sprat to empty their guts overnight and permit feeding the following day, hence increasing the energy intake and consequently the growth rate (Neverman and Wurtsbaugh, 1994). In contrast to summer, water temperatures in the deep basins during winter are colder in the upper layers than near the bottom. Andersen et al. (2017) assumed that the ascent into upper colder layers in the dark hours may a strategy of sprat to reduce energy expenditures during winter times when sprat are food limited because of low prey densities.

6.5.2.3 Predation avoidance

With increasing light intensity at dawn on the surface, the risk of predation by visual predators like piscivorous seabirds (e.g. common guillemot *Uria aalge*) increases. By moving downwards, sprat can minimize this risk, but increases the spatial overlap with the main predator Baltic cod (*Gadus morhua*). Andersen et al. (2017) discovered that cod predation took place primarily (87.1 %) at dusk and dawn during ascent and descent of sprat associated with school dissolution and formation. The more dispersed structure of sprat swarms during the migration increases the prey catching success of individual sprat (Hawkins et al., 2012), but also reduces the protection from predation by cod. As a consequence, the duration of feeding during the ascent and descent is a trade-off between food acquisition and predation risk by cod. In contrast, during the day in the deeper layers sprat gathered together in dense compact schools (Nilsson et al., 2003). Hawkins et al. (2012) assume that the formation of large sprat schools provides a defense against visual predators but reduces feeding opportunities. Andersen et al. (2017) confirm that schooling of sprat during the day appeared to be an effective way of protection against predation because cod was not successful in preying sprat during this period.

6.5.2.4 Optimization of physiological condition for maturation

From the so far described interactions it remains unclear, why sprat do not reside in the water depths with maximum prey concentrations during the day. One possible reason for the migration into deeper layers is the higher salinity below the halocline (Voss et al., 2012). The fertilization/incubation salinity influence the buoyancy pattern of eggs and yolk sac larvae in sprat (Petereit et al., 2009). At least sprat eggs need a salinity of 5-6 PSU (Elwertowski, 1957). As the reproduction of sprat is sensitive to salinity (Ojaveer and Kalejs, 2010), the stay in deeper layers may increase the maturation and reproduction success of sprat.

In summary, the ascent into upper water layers during the main feeding period provides optimal conditions for feeding and fast digestion rate. In contrast, the descent into deeper layers leads to an increase in reproductive success and reduces the metabolic cost. Due to the fact that in winter, when prey density is low, the ascent of sprat is less pronounced compared to the main feeding period in summer (Rechlin, 1975; Andersen et al., (2017); J-P. Herrmann, pers. comm.), implies that sprat's DVM in summer is mainly driven by feeding.

6.5.2.5 Comparison with other clupeids

James (1987) also observed a higher feeding intensity of anchovy (*Engraulis capensis*) during the residence in upper layers in the southern Benguela region. The feeding periodicity in anchovy appears to be associated closely with a marked DVM and changes in shoaling behavior. During the day anchovy form dense shoals in deeper layers and ascent at dusk in a dispersed structure into layers near the surface. This ascent phase is coincides with the peak in stomach fullness. In contrast to sprat and anchovy, larger sardine (*Sardinops sagax*) (> 25gww) appear to feed continuously and show no peak of feeding activity throughout the diel cycle (van der Lingen, 1998). A possible explanation for the difference in the foraging strategy between anchovy/sprat and larger sardine can be found in the feeding behavior. While the dominant feeding mode of anchovy and sprat is size-selective particulate-feeding, sardine prefer non-selective filter-feeding (van der Lingen et al., 2006, Brachvogel et al., 2013). Therefore sardines are less dependent on light conditions than anchovy and sprat. This suggest that the effectivity of particulate-feeding strongly depends on light conditions in upper layers.

6.5.3 Comparison between DR estimated by the established and new approach

DRs estimated by our new approach were on average 1.40 ± 0.06 times higher than the results obtained by the established approach applied by Köster (1994), Möllmann and Köster (2002), Bernreuther et al. (2009) and Voss et al. (2011). The discrepancy can be explained partly by the underestimation of the gastric evacuation rate of sprat, since higher temperatures in upper water layers were not taken into account in the established approach. However, sprat feed on average 51.19 ± 17.85 % of their feeding time within upper and warmer waters. The amount of the discrepancy depends on the difference between the mean temperatures within the upper and deeper water layers. In the deep basins of the Baltic Sea, this difference increases during the most important feeding period of sprat (Möllmann and Köster, 1999) when a thermal stratification arises (Voss et al., 2012). The temperature difference between the layers in the deep basins intensifies further after major inflows with colder bottom water from the North Sea (Voss et al., 2012).

The DR estimation by the established approach tends to yield lower rations compared to bioenergetic estimates (Möllmann & Köster, 1999; Maes et al., 2005; Bernreuther, 2007). Bernreuther (2007) found that a bioenergetics model predicted 2 to 3.5 times higher DR than a gastric evacuation model for sprat in the Bornholm Basin in 2002/2003. Bioenergetics models reflect the energy intake over a longer period while the gastric evacuation method produces a point estimate at the time of sampling (Maes et al., 2005; Bernreuther, 2007). Bernreuther (2007) suggested that sprat caught later in the season in the Bornholm Basin may have fed intensively in other parts of the Baltic Sea. Nevertheless, the lower DR estimated by gastric evacuation models can also partly be explained by the fact that the vertical feeding dynamic of sprat was not take into account in the calculation. A simple way to reduce this bias is to use the presented correction formula (6.6) for the estimates produced with the established approach.

6.5.4 Comparison of regional feeding conditions

The estimated DRs of sprat in the Bornholm and southern Gotland Basin were similar with 3.77 ± 0.09 and 3.60 ± 0.16 %BW, respectively. In the Arkona Basin, mean DR of sprat was higher with 4.69 ± 0.15 %BW. A simple bioenergetics budget was calculated to estimate the effect of different temperature profiles on the metabolic cost and quantify the actual energy surplus gained in the different basins. In contrast to DRs, the mean energy surpluses of sprat feeding in the Bornholm and Arkona Basins were similar with mean values of 165.74 ± 8.73 and 161.18 ± 40.90 J fish^{-1} d^{-1}, respectively. In the southern Gotland Basin the mean energy surplus of sprat was lower with only 116.20 ± 3.81 J fish^{-1} d^{-1}. The lower energy surplus in the southern Gotland compared to the Bornholm Basin can be explained by higher energy costs due to the higher temperatures in the upper water layers. That was also the reason why in the Arkona Basin the energy surpluses of sprat were not different to the Bornholm Basin despite the higher DRs. Overall, the Arkona and Bornholm Basins seem to offer comparatively good conditions as feeding grounds, whereas in the southern Gotland Basin sprat seem to achieve lower energy surpluses compared to the other basins.

6.6 Conclusion

The sampling strategy for qualitative and quantitative analysis of feeding interactions must take into account the DVM of pelagic predators such as sprat as the feeding intensity varies between different water depths. The disregard of the vertical feeding dynamic of sprat could, one the one hand, lead to a misinterpretation of the observed diet composition and erroneously imply prey selectivity where none exists. On the other hand, this can lead to an underestimation of the DR of sprat which has a significant impact on the forecasting of the potential scope for growth and top-down effects on their prey community.

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7 General conclusions and outlook

The present thesis investigated the feeding rate of sprat (and partially herring) in order to develop an extensively parameterized functional response model for particulate-feeding planktivorous clupeids and to improve the daily ration estimation for sprat. On the one hand feeding experiments were conducted to determine the type of functional response in relation to different prey types, predator body sizes and ambient temperatures and on the other hand DVM associated daily ration of sprat from sets of ~12-h stomach content field data were estimated using mean stomach content weights sampled at different FPs and a known gastric evacuation rate of sprat. Furthermore, the energetic efficiencies of sprat were determined to advance the mechanistic understanding of how abiotic and biotic factors interact determining feeding and growth rates of early post larval juveniles.

7.1 Feeding behavior

Sprat is an obligate particulate-feeding predator, even at high prey concentrations (> 100 L^{-1}) (**Manuscript 1 and 2**). This has been reported earlier by Bernreuther (2007), but it has not been investigated systematically before. In contrast, herring exhibit both filter- and particulate-feeding modes. In our study juvenile herring (7-9 cm) started to filter feed (or gulping) at prey concentration of about >50 L^{-1}, which is similar to the observations made by Gibson and Ezzi (1985) (**Manuscript 1**). However, the dominant feeding mode of juvenile herring for all prey concentrations was particulate-feeding. This indicates that the development of filter-feeding is a continuous process during ontogeny and only larger herring (13-20 cm) are fully able to filter feed (Gibson and Ezzi 1985, 1990). Both clupeids showed two different feeding behaviors during particulate-feeding depending on prey concentrations. At low prey densities (< 15 L^{-1}) they swam mainly in a horizontal plane with only slight vertical movements and at higher concentrations they swam in a vertical zigzag pattern, with repeated bites while swimming upwards at an angle of about 35°–45° (**Manuscript 1**). However, during both feeding behaviors they attacked the prey from below. This has two benefits: to see and not been seen (Thetmeyer and Kils 1995). Thetmeyer and Kils (1995) investigated the visibility of herring and its translucent prey (mysids) in the shallow water of Kiel Fjord (Baltic Sea) by an underwater camera system from various visual angles. They found that when herring was located 30 to 90° below the mysid, the prey was fairly visible to the predator but the herring was perfectly camouflaged. In conclusion, juvenile sprat and herring developed a feeding mode optimally adapted to feed on translucent prey species (e.g. copepods, cladocerans and mysids) and they exclusively/mainly sticked to particulate-feeding, because filter-feeding is energetically more extensive than particulate-feeding (Gibson and Ezzi 1992) and thus seems to be beneficial only above a certain predator-to-prey size ratio. Durbin (1979) argued that fish particulate-feed when the prey size predator size ratio is in the range between 1:20 and 1:200, whereas filter-feeding occurs when prey size predator size ratio is in the range from 1:150 to 1:20,000. He showed that even the juveniles of obligate filter-feeding Atlantic menhaden (*Brevoortia tyrannus*) are actually particulate feeders. In the present study juvenile herring (~8 cm) only rarely filter-fed at higher prey concentrations (50 L^{-1}), corresponding to an average prey size–predator size ratio of 1:100 (prey item ~0.08 cm). In situ observations by Kils (1992) confirmed likewise that juvenile herring (38 mm mean length) attacked each copepod individually even at high prey concentrations of up to 850 L^{-1}. Clearly, distinctive filter-feeding behaviour has only been observed for larger herring (13–20 cm total length; Gibson and Ezzi 1985, 1990, 1992).

7.2 Functional response

Like many other planktivorous fish species such as kokanee salmon (Koski & Johnson 2002), percids (Bergman 1987) alewife, bloater (Miller et al. 1992) and brown trout (Gustafsson et al. 2010), sprat and herring showed a type II functional response (**Manuscript 1 and 2**). The type II is characterized by a hyperbolic curve: starting at low prey concentration on the abscissa, the feeding rate increases initially almost linearly until it gradually slows down to reach asymptotically an upper limit. Under the type II functional response predation risks for prey individuals decrease with prey abundance causing inverse density-dependent prey mortality, which can destabilized prey populations and lead to unstable boom-burst population dynamics (Sarnelle and Wilson 2008; Vucic-Pestic et al. 2010) (Fig. 3.1). In contrast to the type II, under the type III predation risks increase with prey concentrations, which can yield an effective *per capita* top-down control that often prevents unstable dynamics (see Vucic-Pestic et al. 2010) (Fig. 3.1). Slight differences in functional response parameters can thus have drastic consequences for population and food-web stability in nature ecosystems (see Vucic-Pestic et al. 2010). Most studies on the functional response have included only relatively few observations at low food density (Gibson and Ezzi 1985, Sarnelle and Wilson 2008). However, it is particularly important to investigate the feeding rates at low prey concentrations where the difference between type II and III is detectable. The experimental design in the present study ensured the fine scaled measurement of feeding rates of sprat and herring at very low prey concentrations (1 – 300 L^{-1}), allowing a reliable determination of the type of functional response.

Frame-by-frame analysis of the feeding behavior of sprat revealed that the total feeding time (search + approach + prey handling) decreased with increasing prey concentrations and asymptotically reached a minimum value (**Manuscript 1**). The relative share of handling time in total feeding time increased with increasing prey concentrations and ultimately limits the number of prey which can be consumed. Jeschke et al. (2002) criticized that most of the functional response models did not discriminate between handling and digesting prey as limitation at high prey concentrations. They postulated that digestion can indirectly prevent the predator from further searching or handling by influencing the predator’s hunger level. However, we assumed that satiation in sprat only plays a minor role as feeding experiments at high prey concentrations showed that sprat was able to feed up to 16 %BW (Teich 2010). Most observations in field, however, were significantly lower (< 2 %BW) (Möllmann and Köster 1999; Möllmann et al. 2004). Thus, we assumed that the feeding rate of sprat is primarily limited by handling time at high prey concentrations than by satiation.

The comparison of the mean stomach content weights from experimental sprat and predicted weights based on the observed biting rates from video analysis revealed that our functional response model overestimated the true observed weights (**Manuscript 2**). This indicates that the biting rates from video analysis represented the maximum physiological feeding response of sprat which, however, cannot perform by sprat continuously. At lower prey concentrations the amount of feeding breaks increased. In conclusion, we assume that our functional response model provide a good estimates for the upper range of consumption rates. To incorporate feeding gaps at some extent, there is an option to use the reduction factor of 0.70.

7.2.1 Prey type effect

Functional response was lower when sprat and herring feeding on *Artemia* nauplii (*BRmax* ~ 2 s^{-1}) than on *A. tonsa* (*BRmax* ~ 1 s^{-1}) (**Manuscript 1**). The lower feeding rates with *A. tonsa* is mainly caused by the well-developed escape response of *A. tonsa* compared to non-evasive *Artemia* (Singarajah 1969; Trager et al. 1994; Kiørboe et al. 2010). This is supported by the fact that both clupeids mostly showed an S-shaped curvation of the body before biting on *A. tonsa*, whereas this behavior was not observed with *Artemia*. Handling time for *A. tonsa* (t_h = 0.48 s) was more than threefold higher than for *Artemia* (t_h = 0.14 s). Although *Artemia* is not a part of the natural prey composition of sprat, they are comparable with the main prey species of sprat and herring like *T. longicornis*, *P. acuspes* and cladocerans (Bernreuther et al. 2013, Van Ginderdeuren et al. 2014) in terms of their vulnerability to fish predation (Viitasalo et al. 1998 and 2001). As those prey species are mainly consumed by sprat in the deep basins of the Baltic Sea we assume that the findings obtained from experiments with *Artemia* can be applied to interpret the feeding of sprat in offshore areas. The application of the functional response model for larger herring in offshore areas is difficult as they start to filter-feed at higher prey concentrations (>50 L^{-1}) and the body size effect on the functional response is, in contrast to sprat, unknown. At nursery areas in the coastal zones of the Baltic and North Sea, juvenile sprat and herring primary feed during summer on *E. affinis* and *Acartia spp*. beside cladocerans (Arrhenius 1996, Gorokhova et al. 2004, Maes et al. 2005). Both copepod species show high escape responses comparable with *A. tonsa*

(Viitasalo et al. 2001). Thus, for estimating the consumption or interpreting the feeding performance of juvenile sprat and herring at coastal areas feeding rates need to be adjusted to prey composition. For sprat, we recommend to reduce the feeding rates estimated by the extended functional response model based on *Artemia* by a factor of 0.53. For juvenile herring, the functional response model based on experiments with *A. tonsa* are assumed to provide more realistic results than the model based on experiments with *Artemia*.

Functional response models traditionally consider feeding upon a single resource even though the natural diets are usually comprised of mixture of prey species and size-classes (Gentleman et al. 2003). Studies on *Coregonus lavaretus* showed that they exhibit a functional response type II when only one prey species was available (Winkler and Moreno 1984). In contrast, the functional response type II was shifted to type III when two different prey species *Bythostrephes longimanus* and *Daphnia* were present. Moustahfid et al. (2010) also showed that the functional responses of piscivorous fish from the northern US continental shelf varied between the type II and III in relation to prey species. However, in the present study the type of functional response of sprat and herring was derived only from single-prey-species experiments. For this reason, multi-prey-species feeding experiments are needed in the future to examine whether the type is changing.

7.2.2 Temperature effect

Feeding rate of sprat increased with increasing temperatures (**Manuscript 2**). A similar increase in feeding rates was also observed for roach and perch (Bergmann 1987, Persson 1986, Linlokken et al. 2010), three-spined stickleback (Lefebure et al. 2014) and salmonids (Watz et al. 2014). This implies that feeding at colder waters within deeper layers during the DVM strongly reduces the feeding rates of sprat.

The Arrhenius equation has emerged as the preferred model for describing the temperature dependence of consumption in predator-prey models (Englund et al. 2011). The Arrhenius equation describes the temperature dependence of chemical reactions. The reaction rate (y) is given by $y = e^{-Ea/Tk}$, where T is the temperature, k is the Boltzmann's constant, and Ea is the activation energy of the reaction. Gillooly et al. (2001) argued that a universal temperature dependence exists for all ectothermic animals because all aerobic organisms share the same biochemistry. The *Ea* value should be constrained between 0.6 and 0.7 (Gillooly et al. 2006; Allen & Gillooly 2007). However, Englund et al. (2011) undertook a meta-analysis of published relationships between functional response parameters and temperature and found that the relationship between temperature and feeding rate tends to be hump-shaped rather than exponential. Feeding rate increases with increasing temperature and decreases again at a certain temperature when predators suffer from thermal stress and stop functioning normally (Englund et al. 2011, Lefébure et al. 2014). Rall et al. (2012) also emphasize that the temperature dependence of functional response is more complex than a simple Arrhenius term. Although the *Ea* of sprat with 0.68 lies between the predicted values, the relationship between the maximum feeding rate and temperature is not exponential (Fig. 7.1). Similar to the findings by Englund et al. (2011), maximum feeding rates of sprat increased with increasing temperature, but the rate of increase was progressively reduced until an asymptote was reached at high temperature of about 20 °C. Unfortunately, we cannot predict from which temperature feeding rates will decrease again as we only conducted feeding experiments up to 20 °C. Overall, the established Arrhenius equation is not applicable to sprat as it underestimates the feeding rates at lower temperatures but overestimates it at higher temperatures.

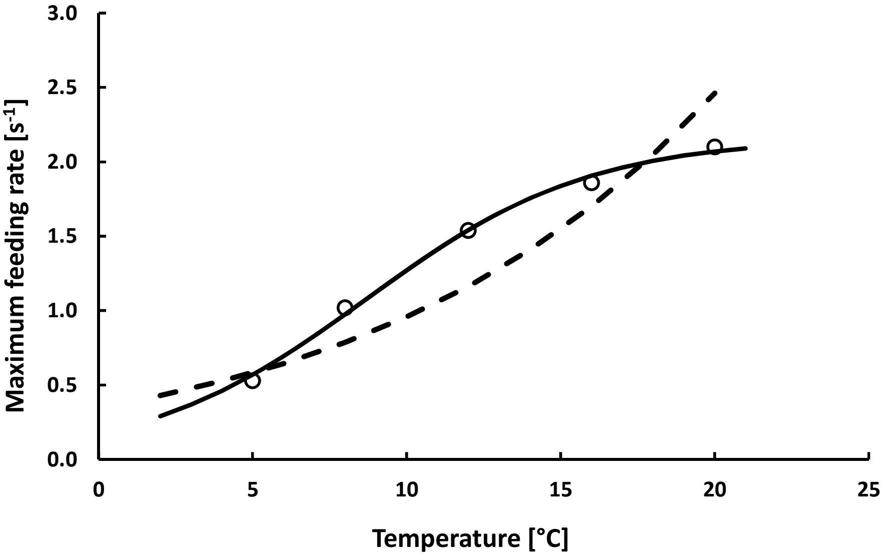

Figure 7.1: Relationship between maximum feeding rate [s^{-1}] and temperature [°C] of sprat (~8 cm) feeding on Artemia salina. *Circles = observed maximum feeding rates; solid line = S-shaped function used in our models (Manuscript 2); dashed line = Arrhenius equation.*

7.2.3 Size effect

Feeding rates of sprat increased with increasing body size, which is in line with previous findings for other fish species (Breck and Gitter 1983; Persson 1987; Persson et al. 1998, Miller et al. 1992; Gustafsson et al. 2010) and other freshwater, marine and terrestrial taxonomic groups (Vucic-Pestic et al. 2010, Rall et al. 2012). The distance between predator and prey item at which a predator responds to the presence of the prey (reactive distance) increases with increasing predator size (see Vucic-Pestic et al. 2010). In addition, handling time also decreases with increasing body size (Glazier 2010; Rall et al. 2012). The scaling exponent for handling time found in the present study (-0.81) overlaps with the range of expected values from different ecosystem and metabolic types (-0.66 to -1.0; Glazier 2010; Rall et al. 2012). Maximum feeding rates of sprat increased with increasing fish size in an S-shaped function. The gastric evacuation rate of sprat does not increase proportionally with increasing body size, but has a weight exponent of 0.503 (Bernreuther et al. 2009). As a consequence, the food intake as well as the processing of food is limited with increasing body size of sprat. In contrast, metabolic rates of sprat increase almost proportionally with body weight with a scaling exponent of 1.073 (Maeskendahl et al. 2010). This implies that larger sprat are having increasing difficulties in meeting their energy demands and are more dependent on high prey concentrations.

In conclusion, the combination of the functional response type II, high maximum biting rate (~2 s^{-1}) and the store ability of a large amount of food in their gastric caecum (Bernreuther et al. 2008), allowed sprat and herring, particularly at higher ambient temperatures (not examined for herring), to deplete local zooplankton patches within relatively short time. This is supported by strong local and temporal-limited top-down effects through sprat and herring observed in field by Hawkings et al. (2012). However, at the same time, due to the limited feeding rate at high prey concentrations and the increase of the predation risk of prey species with decreasing prey densities, it can be assumed that the heterogeneous distribution of prey and the formation of patches with high concentrations (Omori and Hamner 1982, Folt and Burns 1999) represent a evolutionarily adaptation of zooplankton to protect against the predation by planktivorous fish like sprat and herring. Many studies showed that fish predation is one of the main drivers of zooplankton patchiness and that predators are able to create patchiness in prey spatial distribution directly by removing individuals, and indirectly by eliciting avoidance or escape response (Hamilton 1971; Gliwicz et al. 2010). Pijanowska and Kowalczewski (1997) demonstrated experimentally that the aggregation of *Daphnia* was induced by kairomones of fish. In addition to the fact that the maximum feeding rate of fish is limited at high prey concentrations, the aggregation for prey offers also other protection mechanisms. The confusion and dilution effect; that is, that the predator's attention is distracted by the great number of moving and similar-looking prey items (Pijanowska and Kowalczewski 1997).

Contrary to the suggestion that swarming can be used as an anti-predation defense in prey, the individual risk of prey increases rather than decreases with increasing prey concentration for predators with a type III functional response (Gliwicz et al. 2013). Studies on roach (*Rutilus rutilus*) showed that the decline in *Daphnia* density was most dramatic in the tank with the highest prey abundance as a result of a sigmoidal functional response combined with the rapid relocation of fish to where Daphnia were most plentiful (Gliwicz et al. 2013). Since we only conducted feeding experiments separately with *Artemia* or *A. tonsa*, we do not know if the type II of sprat and herring shifts to a type III when they get multi-species diet. In the end, to find out whether the feeding behavior of juvenile sprat and herring will likely regulate, stabilize or de-stabilize prey populations, multi-prey-species feeding experiments are needed in the future.

7.2.4 Comparison between juvenile sprat and herring

Small pelagic clupeid fish species such as anchovies, sardines, sardinellas, herring and sprat are characterized by strong decadal fluctuations of biomass, which are often associated with regime shifts in marine ecosystems (Alheit et al. 2009). Consequently, small pelagics are excellent indicators of regime shifts (Alheit et al. 2009). When occurring in the same habitat, anchovy and sardine usually fluctuate out of phase (sardine- or anchovy-dominated state). The biomass of the herring stocks in the Baltic Sea declined continuously during the recent decades, while the sprat stock increased by a factor of three in the 1990s compared to the 1980s (Köster et al. 2003). Central Baltic herring landings and spawning stock biomass decreased from 1980s to 2000 by 60-

70 % (Barange et al. 2009). This raises the questions to what extent a competitive advantage in feeding efficiency of sprat might have contributed to the decline of the herring stock biomass.

The niche overlap in the diet between sprat and herring is high (65-80 %) (Bernreuther 2007; Möllmann et al. 2004). Particularly in nursery areas where 0-groups of herring and sprat form mixed schools, food competition could be a relevant factor if food resources are limited. For larger sprat and herring, competition is lower as larger herring also partially consume larger prey species such as mysidaceas and amphipods. Stepputis (2006) investigated the DVM of herring and sprat in the Bornholm Basin of the Baltic Sea by hydroacoustic and catch data. Herring and sprat showed pronounced vertical migration within diel cycle, while the timing and schooling behavior differed between both species. The downwards migration of herring started earlier in the morning without prior aggregation into schools. In contrast, sprat aggregated in surface layers before beginning their downward movement. Herring migrated earlier in the evening to the surface waters as school compared to sprat. In contrast, sprat schools dissolved before rising up. Hawkins et al. (2012) suggest that school dissolution increases the prey catching success of individual sprat. Consequently, feeding rates of sprat should be higher during the ascent than during the descent. Our results confirm this assumption as feeding rates of sprat in the Bornholm and Gotland Basin during the ascent were twice as high as during the descent (**Manuscript 3**). In conclusion, it is not clear how the time-shifted feeding activity during the DVM has an advantage for herring or/and sprat. The shift in feeding activity could potentially increase the overall intake for both clupeids as the activity is not limited to just one time window. The study of stomach contents of both clupeids during the DVM could lead to a better understanding of the time-shifted feeding activity.

Compared to Lotka-Volterra type modelling approaches, the advantage of a mechanistic theory of competition is that the competitiveness of species can be deduced from their physiological properties (Tilman 1982). For example, the comparison of the physiology of co-occurring sardine and anchovy can largely explain the species alternation (Van de Lingen 1994). Anchovy and sardine eat phytoplankton and zooplankton by filter- or particulate-feeding (van der Lingen et al. 2009). Anchovy have coarse filters, capable of retaining relatively large particles; sardine have fine filters, capable of retaining smaller particles. Anchovy use both filter- and particulate-feeding, whereas sardine primarily use filter-feeding. Overall, sardine consume smaller prey items than anchovy (van der Lingen et al. 2009). This implies that the alternation between anchovy and sardine periods may be trophodynamically mediated (van der Lingen 2006). Intermittent mixing such as upwelling leads to relatively cool temperatures in the upper water layers. This condition favors food chains dominated by diatoms and large calanoid copepods which are the main prey species for particulate-feeding anchovy. In contrast, more stable water column situations caused by relaxed upwelling and/or El Niño, lead to warmer water temperatures in the upper layers. This condition favors a flagellate-dominated food chains and a shift in the size spectrum of the zooplankton towards small-sized copepod such as cyclopoid copepod (van der Lingen 2006). Such feeding environment is particularly suitable for filter-feeding sardine.

The prediction of the outcome of a competitive situation can be made by an overlay of the two functional response curves of the competitors (Lampert and Summer 1999). The simplest situation would be the competition for one common resource. Such a graph can be provided for equally sized 0-group sprat and herring on the basis of the determined biting rates with equally sized *Artemia* (Fig. 7.2). The prey concentrations in coastal nursery areas are mainly below 50 L^{-1} (Ojaveer et al. 1998; 2009; Dzierzbicka-Głowacka et al. 2013; Paulsen et al. 2016). At these densities the main feeding mode of herring is particulate-feeding. If we compare the feeding rates of similar sizes sprat and herring (~8 cm), sprat reached significantly higher feeding rates than herring (**Manuscript 1 and 2**). Biting rate of sprat was on average 3.7 (at 1 L^{-1}) to 1.7 (at 20 L^{-1}) times higher than the biting rate of herring. As a consequence, at limited food availability the size-dependent exploitation of food is more efficiently in juvenile sprat than in herring.

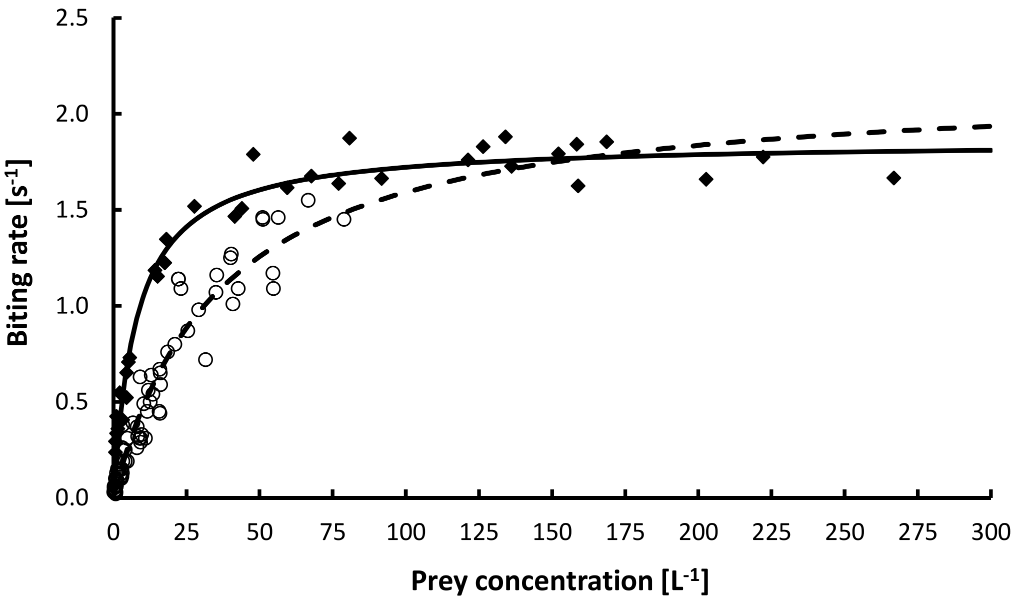

Figure 7.2: Biting rates (s^{-1}) of similar sized (~8 cm) sprat (black diamonds, solid line) and herring (circles, dashed line) feeding at 16 °C in relation to Artemia concentrations (L^{-1}). *Biting rates of herring and sprat were obtained from Manuscript 1 and 2, respectively. Sprat (BRmax = 1.9; k = 7.9); herring (BRmax = 2.17; k = 36.36).*

In the Baltic Sea, an increased competition for food was observed between sprat and herring (Möllmann et al. 2005). Particularly the reduction of the weight-at-age (WAA) of both clupeids were interpreted as consequences of competition (Cardinale & Arrhenius 2000; Cardinale et al. 2002). Since the mid-1980s, a decrease of WAA of up to 50% has been observed in herring (Cardinale & Arrhenius 2000). In contrast, the reduction of WAA in sprat started later in the middle of the 1990s (Kornilovs et al. 2001). Zooplankton data suggest that prey availability for herring and sprat declined concurrently with their WAA. Especially the decline of *P. acuspes* affected the nutritional status of herring negatively, while sprat utilizes also other copepods like *T. longicornis* and *Acartia* spp., and thus sustained a good nutritional status until density-dependent processes started to act as a consequence of the drastic increase in stock size since in the early 1990s (Möllmann et al. 2005). The increase of sprat stock was induced by the reduction of the predation pressure by cod on clupeids and also by an increased reproductive success due to warmer water temperatures and an increase of *Acartia* spp., the main food of sprat larvae (Köster et al., 2003; Voss et al., 2003; Möllmann et al., 2005). The decrease in herring stock are assumed to be mainly caused by spawning habitat destruction (Aneer 1987; Cloern 2001). Nevertheless, the drastic increase in the sprat population and the later onset of the reduction in WAA compared to herring (Casini et al. 2006), support the interpretation of the mechanistic competition model presented in the present work. Juvenile sprat are able to exploit food efficiently than juvenile herring and thus may become the dominant fish species in the Baltic Sea.

Since 2008, a severe decrease in size and body condition has also been observed in the sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) populations of the Gulf of Lions (NW Mediterranean Sea) (Brosset et al. 2016). In parallel, sprat biomass has increased tenfold in the same area. Brosset et al. (2016) suggest that changes in growth, size and condition and ultimately biomass were caused by changes in food availability and increasing potential trophic competition. Stable isotope analysis (SIA) was used to investigate the feeding habits and trophic interactions. In contrast to stomach content analysis, SIA facilitates an integrated measured of the assimilated food over the previous months depending on the variability of prey and their stable isotope rations, fractioning and the isotopic turnover (Brosset et al. 2016). The niche width was estimated by the range of $\delta^{15}N$ and $\delta^{13}C$. Before the increase of sprat's biomass, resource partitioning was found between sprat and the other species. In contrast, the isotopic niches between them have tended to overlap since 2010. Unfortunately, there are no data on the functional responses of sardine and anchovy, so that a comparison of the competitiveness is difficult. However, the strong increase in sprat's stock implies that the food intake in sprat was higher than in anchovy and sardine. Overall, although sprat is only an obligate particulate-feeder, it can probably achieve higher feeding rates at lower prey concentrations than the other clupeids. This property makes sprat especially in unfavorable food conditions to a strong competitor.

7.2.5 Energetic efficiency of sprat

Our functional response model provides a mechanistic understanding of how prey concentration, feeding period, fish size and temperature affect the energy intake of sprat. This knowledge combined with metabolic rates can be used to interpret growth performances among seasonal cohorts of YoY-sprat. The asymptotic increase in the energy intake compared to an exponential increase in metabolism with raising temperatures (Meskendahl et al. 2010) caused a hump-shaped energetic efficiency of sprat in relation to temperatures (**Manuscript 2**). Furthermore, the energetic efficiency decreased with increasing body size, indicating that smaller sprat tolerate higher temperatures better than larger ones. More precisely, larger sprat need higher prey concentrations at higher temperatures than smaller sprat to obtain enough energy for basal metabolism and growth. Thus, at limited food availability the risk of starvation for larger sprat increased with increasing temperatures. Investigations on the temperature scaling of feeding rates from various taxonomic groups also showed that feeding increases almost less strongly with temperature than metabolism (Vucis-Pestic et al. 2011, Englund et al. 2011, Rall et al. 2012). Rall et al. (2010) studied the temperature dependence of metabolism and ingestion in laboratory experiments with terrestrial arthropods (beetles and spiders). For both predator groups, warming increased metabolic rates substantially, whereas temperature effects on ingestion rates were weak. Accordingly, the energetic efficiency decreased with warming as well.

A comparison of two different years, characterised by contrasting recruitment success of sprat, highlights the importance of timing of seasonal cohorts (Baumann et al. 2008; Günther et al. 2015). Both authors found that later born cohorts had a better chance of survival than early born cohorts. In 2003 the recruitment of sprat was >3-fold higher than in 2007. In addition, growth rates of autumn-caught survivors in 2003 were among the highest observed in the field (up to ~1.0 mm d^{-1}). Due to a colder spring, the majority of survivors in 2003 were born later in the year (July): as a result, sprat larvae were able to grow at the highest summer temperatures, whereas juveniles with their higher food demand benefited from lower temperatures in late summer and autumn. In contrast, a warm spring in 2007 induced early spawning and sprat were born two months earlier (May) than in 2003. As a consequence, sprat experienced colder temperatures during the larval stage, but passed through their juvenile phase during the highest temperatures of the year. These observations are in line with the expectation based on the energetic efficiency of sprat. The risk of starvation due to unfavourable food conditions decreases and the surplus of energy increases when sprat cohorts are born later and the juvenile phase is shifted to late summer and autumn with on average colder temperatures where the energetic efficiency is higher than in summer.

Henderson and Henderson (2017) investigated the long-term change in growth, condition and survival of sprat in the Bristol Channel, UK. They found that sprat's growth is related to temperature, and has declined in recent years as late summer-autumn seawater temperatures have increased. This trend corresponds to the predictions of the energetic efficiency of sprat as well. Overall, warming generally increase the *per capita* feeding rate of sprat. Nevertheless, the stronger increase in metabolism caused decreases in energetic efficiency and hence reduces growth rates. Vucic et al. (2011) assume that the decrease in energetic efficiency with warming may dampen predator-prey oscillations thus stabilizing their dynamics. However, the severe long-term implications include predator starvation due to energetic inefficiency despite abundant resources (Vucic et al. 2011).

7.3 DVM associated daily ration of sprat

We confirmed the presumption by Cardinale et al. (2003) that feeding intensity of sprat is highest during feeding in the upper layers. Sprat consumed actually 50 to 85% of the DR in upper water layers (**Manuscript 3**). Feeding rates of sprat were on average 3.16 ± 2.03 times higher at dawn and dusk (FP I, II, IV and V) within upper layers than during the day in deeper waters (FP III). Several reasons may explain the higher feeding rates in upper layers: (1) higher availability of prey combined with (2) optimal light conditions for visual predators, (3) higher temperatures, causing higher feeding rates (**Manuscript 2**), and (4) a more dispersed structure of sprat swarm during the ascent and descent where each individual has a higher chance to capture a prey item. Investigations on the functional response of lionfish (*Pterois volitans*) showed that feeding rates was higher in blue light (crepuscular period light proxy), than in white light (daylight proxy) (South et al. 2017). That suggest that light conditions for sprat during the descent and ascent are optimal for feeding. In contrast, the downward migration into deeper layers is assumed to reduce the predation risk by seabirds. The subsequent formation of schools protects sprat from the predation by cod. In addition, colder temperatures in deeper layers during summer reduce the energy required for maintenance. Furthermore, higher salinity in the deeper layers may also increase the reproduction success of sprat (Voss et al. 2012; Andersen et al. 2017). Andersen et al. (2017) found that predation on sprat by cod took place mainly during migration at dusk and dawn when the structure of sprat swarm is more dispersed. Thus, the duration of feeding during the ascent and descent, is assumed to be a trade-off between food acquisition and predation risk by cod. During the night sprat are found near the surface where they probably selecting warmer waters to increase their digestion rate, allowing sprat to empty their guts overnight and permit feeding the following day (Neverman and Wurtsbaugh 1994). In summary, the ascent into upper water layers during the main feeding period provides optimal conditions for feeding and fast digestion rate. In contrast, the descent into deeper layers leads to an increase in reproductive success and reduces the metabolic cost and predations risks.

Energy budget models linked with a functional response model can predict the relation between energy intake and physiological costs in relation to DVM. A bioenergetics-based foraging model for kokanee salmon was developed to determine if bioenergetics and foraging constraints could explain the DVM in Nantahala Lake in North Carolina (Bevelhimer and Adams 1993; Stockwell and Johnson; 1997). In summer, the Nantahala Lake has some characteristics similar to the deep basins of the Baltic Sea: high prey concentrations in the upper layers and the water temperature decreases with increasing depths. They simulated the food consumption and growth under various vertical migration scenarios. To evaluate predictions of the model they compared the results with observed growth and DVM from hydroacoustics. For a 24h simulation, the initial input includes a vertical profile of prey densities and temperatures, size of the predator, the depths between which DVM occurs, the time spent at each depth and the time of active feeding. Energy intake was predicted by a functional response model using prey density and temperature data at the fish’s depth during that time step. The results could explain the observed pattern of kokanee’s DVM in summer, when the thermal stratification was strong. The general rule for DVM as determined from the simulation for kokanee salmon was to feed where net energy intake is maximized and reside when not feeding where energy costs are minimized and food is digested to the point that consumption during the next feeding period is not limited by the amount of undigested food remaining in the stomach (Bevelhimer and Adams 1993). They also demonstrated that bioenergetic differences among various DVM scenarios under a variety of conditions affect the growth advantages of a particular behavior. Whether DVM results in an energetic advantage depends on the ontogenetic stage of forager, seasonal and daily variation of temperature profiles and prey distribution (Bevelhimer and Adams 1993). Thus DVM varies widely among species and systems due to the variety of factors involved and the change of the relative importance of various drivers. Growth maximization is not always the main factor driving DVM (Bevelhimer and Adams 1993). However, Bevelhimer and Adams (1993) suggest that although other factors such as avoidance of predators or maximizing reproduction success are of key importance, it seems reasonable to expect that energetic considerations still influence the DVM that is exhibited within the constraints of the primary factor. Overall, the general driving forces for the DVM of kokanee seems to be very similar to those of sprat. Similarly to kokanee, a bioenergetics-based foraging model in relation to DVM could be developed in the future for sprat. Energy intake could also be estimated by the size- and temperature-dependent functional response model from the present study using fine-scaled concentration data of prey from Video Plankton Recorder. This would improve the understanding of the mechanisms behind the DVM of sprat under different environmental conditions.

DR estimate by our new DVM associated approach were on average 1.40 times higher than the DR estimated by the established model (**Manuscript 3**). The underestimation by the established model was mainly caused by ignoring the effect of higher temperatures on the gastric evacuation rate of sprat. This is particularly important if a thermal stratification occurs during the main feeding period of sprat. In addition, the feeding period of sprat has been usually only restricted from sunrise to sunset. In order to reduce the difference between our approach and the established model, we developed a simple improved gastric evacuation model.

Bernreuther (2007) estimated the DR of sprat in the Bornholm Basin in 2002/2003 using two different methods. DRs estimated by bioenergetic models derived from observed field growth exceeded those of the gastric evacuation model by a factor of two to three. Thus, Bernreuther (2007) assumed that sprat was food-limited in the Bornholm Basin in some months and that the observed energy intake required for growth of sprat was accomplished by intensive feeding in habitats outside the Bornholm Basin. However, the discrepancy would be lower if (1) higher temperatures from the upper layers, (2) an extended feeding period of sprat and (3) stomach content samples from the active FPs I, II, IV and V were included in the gastric evacuation model. Overall, the incorporation of aspects (1-3) mentioned above cannot fully explain the discrepancy between both methods as our correction factor of 1.40 is still too low to overcome the estimated difference by a factor of two to three. The feeding conditions in the Bornholm Basin in 2002/2003 were not sufficient to explain the observed growth, but probably at least be sufficient to satisfy the maintenance needs in most months.

Prey selectivity

When comparing the prey composition in the diet of sprat with that in the field, it is noticeable that sprat consumed primarily prey from the top 40 meters (cladocerans and *T. longicornis*) in the deep basins of the Baltic Sea (Dutz et al. 2010). This could be observed both in the Arkona (**Manuscript 3**) and Bornholm Basin (Bernreuther et al. 2013). In contrast, although the spatial overlap during the day in the Bornholm Basin was higher with the prey species *P. acuspes* than with *T. longicornis,* the relative share of *P. acuspes* compared to *T. longicornis* in the diet was significantly lower *(*Renz and Hirche 2006; Dutz et al., 2010; Bernreuther et al., 2013).Thus, Bernreuther et al. (2013) concluded that sprat actively prefer *T. longicornis*. Our results, however, imply that the composition of prey in the diet of sprat may not be a selection for certain prey, but simply results from the spatial overlap between sprat and their prey during the active FPs with higher feeding rates in the upper water layers. This underlines, how important it is to take the vertical feeding dynamic of sprat into account to prevent a misinterpretation of species selection.

In conclusion, the study emphasizes the importance of adapting the sampling design on the vertical feeding dynamics of sprat to avoid a biased picture of consumption and a misinterpretation of observed diet compositions. The underestimation of the DR has a significant impact on the forecasting of the potential scope for growth and top-down effects on the prey community. Our new findings can be used to improve the sampling design of stomach contents to determine more realistic DRs.

7.3.1 Sampling design

To prevent an erroneous assessment of the mean stomach content weight it is important to sample within the active FPs in the upper water layers. Furthermore, it is crucial to increase the number of samples due to the large distribution of stomach content weights per length class and haul. So far only 3 to 10 stomachs per length class and haul have been analyzed (Köster and Schnack 1994; Bernreuther 2007). This can lead to a biased picture of mean stomach content weights. To estimate the dispersion of mean contents in relation to sample sizes, we used a bootstrapping method (n = 100 per sample size) on the basis of 50 observed contents from field of the length class 13 cm (Fig. 7.3). For a sample size of only 3 contents the deviation from the true mean content can be up to 80 %. In contrast, the maximum deviation is reduced to 20 % if the sample size is increased to 30 contents as in the present study (**Manuscript 3**). An increase to 40 contents would reduce the maximum deviation from the true mean value to 10 %.

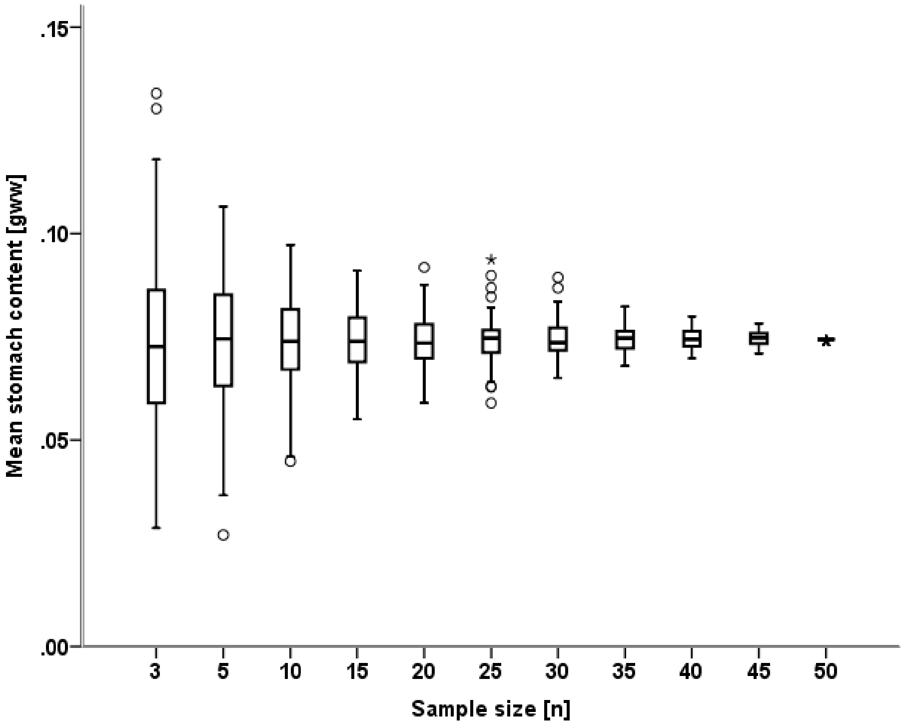

Figure 7.3: Distribution of mean stomach content weights [g_{WW}] in relation to different sample [n] sizes. *Mean stomach content weights for different sample sizes based on a random selection (bootstrapping) from 50 stomach contents of the length class 13 cm caught during November 2017. Boxplots based on 100 mean stomach contents per sample size.*

7.4 Outlook

The present study investigated the effects of prey types with different escape responses, temperatures and body sizes on the functional response of sprat and (partially) herring. However, the influence of light intensity, one of the important factor in visual predators (Ryer and Olla 1999), on the feeding rate of sprat is still unknown. Batty et al. (1990) already examined the effect of light intensities from 0.0001 to 270 lux on the feeding behavior of herring. The experiments, however, were carried out without the consideration of specific wavelengths. The spectral composition of light changes with increasing water depths: in upper water layers the full spectrum of visible light is available, but, in deeper layers only light of about 550 nm is present (Krock et al. 2017). Investigations on the spectral sensitivity of larvae showed that herring exhibited three maxima of high sensitivity (450, 520 and 600 nm) (Blaxter 1968). Anchovy larvae had their maximum at 530 nm (Bagarinao and Hunter, 1983). These maxima overlap with the wavelength which penetrate the water deeply, implying that clupeids are very sensitive to light and can catch prey at very low light levels. However, the spectral sensitivity of post-larval sprat and herring has not been investigated. First, it would be necessary to measure the light intensities and spectral composition of light in the field at different depths, where sprat and herring feed. These results, secondly, could be used to experimentally estimate the functional response at different intensities and spectrums.

The functional responses were determined in the present work with separately only one prey species (*A. tonsa* or *Artemia*) of one size class. To find out whether the type II functional response become a type III, multi-prey-species feeding experiments are needed.

To identify the vertical feeding dynamic of sprat even more accurately, it would also make sense to carry out 24-h fishing in other months than august. In addition, the sampling should be performed at more frequent intervals to determine the duration of different FPs more precisely. In addition, a bioenergetics-based foraging model in relation to DVM, as already described above, could be simulated for sprat in the future. This would require data on stomach contents, temperature profile, hydroacoustics and prey concentrations from field.

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

Manuscript 1: Functional response of juvenile herring and sprat in relation to different prey types – published in Marine Biology (2013) 160:465-478

The text writing, statistical analysis and graphical presentations were conducted by Rini Kulke (maiden name: Brachvogel) with contributions by Laura Meskendahl and under the supervision of Professor Dr. Axel Temming. All experiments were performed in equal parts by Rini Kulke and Laura Meskendahl. Jens-Peter Herrmann helped with the technical realization and was involved in the conceptual design of this study.

Manuscript 2: Temperature and size-dependent maximum functional response of *Sprattus sprattus* L. – not published

The text writing, statistical analyses and graphical presentation were conducted by Rini Kulke under the supervision of Professor Dr. Axel Temmig, who critically reviewed the manuscript. All experiments were performed by Rini Kulke and partly by Stina Kolodzey and Laura Meskendahl, who was also involved in the estimation of the energetic efficiency of sprat. Jens-Peter Herrmann helped with the technical realization and was involved in the conceptual design of this study. Claudia Günther helped to interpret the data and critically reviewed some parts of the manuscript.

Manuscript 3: Ignoring diel vertical feeding dynamics – Consequences on daily ration estimates shown for sprat (*Sprattus sprattus*). – submitted to ICES Journal of Marine Science

The text writing, analyses and graphical presentation were conducted by Rini Kulke under the supervision of Professor Dr. Axel Temmig, who critically reviewed the manuscript. All quantitative and qualitative analysis of stomach contents of sprat from the Arkona Basin were conducted out by Viola Bödewadt. The processing of all hydroacoustic data was performed by Kristin Hänselmann. Jens-Peter Herrmann conducted the sampling of the data and helped with data analysis.

Danksagungen

Zuerst gebührt mein Dank Herrn Prof. Dr. Axel Temming für die gute Betreuung, seinen Ansporn in schwierigen Zeiten, die Schaffung einer idealen Arbeitsatmosphäre sowie für die konstruktive Kritik und Entwicklung neuer Ideen.

Ein großer Dank gilt auch Jens-Peter Herrmann für die wertvollen Diskussionen und Anregungen und der Hilfe bei der Konstruktion der Versuchsanlage und Auswertung der Daten

Ich danke Prof. Dr. Christian Möllmann für seine Aufgabe als zweiter Gutachter, sowie allen Personen die sich als Gutachter für die Disputation zu Verfügung stellen.

Einen besonderen Dank gilt Dr. Laura Meskendahl für die Unterstützung bei den Experimenten, der Auswertung der Daten und das Korrekturlesen sowie für ihre Freundschaft.

Sven Stäcker und Joachim Lütke möchte ich für die Hilfe beim Fischfang, die sorgsame Pflege der Versuchstiere, den Aufbau der Versuchsanlage und die vielen netten Gesprächen danken.

Ich danke ins Besondere auch meinen lieben Freunden und Kollegen, für die schöne Zeit am IHF und deren Motivation und Stärkung. Insbesondere möchte ich mich bei Kristin Hänselmann, Dr. Rebecca Lauerburg, Dr. Claudia Günther, Andreas Teich und Sabine Eberle bedanken.

Ich möchte mich vor allem bei meiner Familie bedanken. Patrick Kulke und Lenno Kulke danke ich für deren Liebe, Rückhalt und Verständnis. Vielen Dank, für die vielen schönen und humorvollen Momente mit euch. Ebenso danke ich Noelle Brachvogel für ihre Liebe, Motivation und den vielen interessanten und sinnvollen Gesprächen. Auch möchte ich mich bei Sabine Kulke, Peter Kulke und Janette Kulke dafür bedanken, dass sie mir den Rücken freigehalten haben. Günther und Monique Brachvogel möchte ich für ihre Unterstützung danken. Ich liebe euch sehr.

Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift „Investigations on the feeding behaviour of juvenile sprat (*Sprattus sprattus* L.) and herring (*Clupea harengus* L.)“ selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Rini Kulke

Hamburg, Januar 2018

Rini Kulke

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Certification of Written English Quality

I hereby confirm that the thesis by Rini Kulke entitled "Investigations on the feeding behaviour of juvenile sprat (*Sprattus sprattus* L.) and herring (*Clupea harengus* L.)" has been prepared according to excellent written English language standards.

Sincerely,

Keith MacPherson
Founder
MacPherson Language Institute