Investigations on the feeding ecology of Baltic Sea herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.)

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English language evaluation of the Ph.D.-thesis of Matthias Bernreuther

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The quality of English grammar and the vocabulary employed by the candidate fulfills the requirement for acceptance as a Ph.D. at the University of Hamburg.

Sincerely

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Summary

The general aim of this work was to investigate the feeding ecology of the main planktivorous fish species in the Baltic Sea, herring and sprat.

Extensive diet analyses on herring and sprat in the Bornholm Basin from April 2002 to November 2003 revealed that diets of both dominant planktivores were quite similar, indicating strong potential competition for food resources, which was supported by the relatively low amount of stomach contents in comparison to other water bodies in the North-east Atlantic and Black Sea. Interestingly, there was no evidence that herring, a facultative filter-feeder, had a competitive advantage expressed as consumption in % *BW* (body weight) over sprat, a species that is an obligate particulate feeder and does not filter feed.

The results of a 24 h *in situ* prey selectivity experiment suggested that both species actively selected adult females and males (c6) and older copepodite stages (c4-5) of mainly *Temora longicornis* and *Pseudocalanus acuspes* and additionally cladocerans (*Evadne nordmanni* and *Podon* spp). Due to the stage-resolved analyses of zooplankton caught in net samples and analysed in fish stomachs and the diel observation protocol, periods were identified during which younger copepodite stages (c1-3) were actively selected. The importance of employing stage-resolved analyses in selectivity investigations was stressed by calculating an “impact factor” to quantify the bias occurring when such analyses were not included. Pooled results (that did not include resolve to stage) underestimated the feeding impact on older copepodite stages c4 and c5 and mature adult (c6) females and males.

To adequately assess the potential for top-down control, laboratory gut content analyses of herring and sprat must be combined with experiments on food consumption rates. Gaps in knowledge concerning important parameters used to derive food consumption estimates were eliminated by conducting a series of experiments that quantified: 1) the effect of temperature on metabolic rate of juvenile herring, 2) the conversion efficiency of juvenile herring, 3) the effect of temperature on the gastric evacuation in herring and sprat, and 4) the effect of body weight on gastric evacuation in sprat. The experiments demonstrated that food evacuation in herring and sprat was best described by an exponential evacuation model. The results also showed that the metabolism and gastric evacuation rates were strongly influenced by temperature and that gastric evacuation in sprat depended upon fish body weight. Additionally, an important assumption of consumption models, that fish exhibit a similar evacuation rate during feeding periods and periods in which they only evacuate food was confirmed for juvenile herring.

The results of these investigations were combined to estimate mean daily rations and the predation pressure exerted by herring and sprat on zooplankton in the Bornholm Basin. Due to the habitat preferences of specific calanoid copepods, herring and sprat appear to exert the strongest predation pressure on *P. acuspes* in spring and *T. longicornis* in summer. Furthermore, the results indicated that both clupeids were, to some extent, food limited and could not ingest sufficient food in certain time periods in the Bornholm Basin to satisfy maintenance needs. Consequently, sprat and herring were likely feeding most intensively outside of the basin, in other regions of the Baltic Sea (e.g., shallow coastal regions), a hypothesis to be tested in future investigations.

Zusammenfassung

Das generelle Ziel dieser Arbeit bestand darin, die Nahrungsökologie der wichtigsten planktivoren Fischarten der Ostsee, Hering und Sprotte, zu untersuchen.

Umfangreiche Nahrungsanalysen an Heringen und Sprotten im Bornholmbecken machten deutlich, dass die Nahrungszusammensetzungen dieser beiden dominanten planktivoren Fische von April 2002 bis November 2003 sehr ähnlich waren, was eine ausgeprägte Konkurrenz um die Futterressourcen vermuten lässt. Diese Beobachtung wurde durch die, im Vergleich zu anderen Meeresgebieten wie z.B. Nordostatlantik und Schwarzes Meer, relativ niedrigen Mageninhalte verdeutlicht. Interessanterweise wurden keine Hinweise dafür gefunden, dass sich Heringe, die fakultativ Nahrung aus dem Wasser filtern können, gegenüber Sprotten, die Nahrung nur partikelweise aufnehmen können, einen Wettbewerbsvorteil, in Form von Konsumtion als % des Körpergewichts verschaffen konnten.

Die Ergebnisse eines 24 h Feldexperiments zur Beuteselektion von Hering und Sprott deuteten an, dass beide Arten aktiv adulte Weibchen und Männchen (c6) und ältere Copepoditstadien (c4-5) von hauptsächlich *Temora longicornis* und *Pseudocalanus acuspes*, und zusätzlich Cladoceren (*Evadne nordmanni* und *Podon* spp.) selektierten. Aufgrund der stadienauflösenden Analysen des in Netzen gefangenen und in den Fischmägen gefundenen Zooplanktons und des 24 h-Beobachtungsprotokolls wurden Zeitabschnitte identifiziert, in denen zusätzlich jüngere Copepopdite (c1-3) aktiv selektiert wurden. Die Wichtigkeit der Verwendung von stadienauflösenden Analysen bei Selektivitätsstudien wurde durch Berechnung eines Einflussfaktors zur Quantifizierung der Verzerrung bei Nichtverwendung solcher Analysen hervorgehoben. Zusammengefasste Resultate (nicht stadienauflösend), unterschätzten den Fraßeinfluss auf ältere Copepodite (c4-5) und adulte (c6) Männchen und Weibchen.

Um das Potential des „Top-down“-Einflusses angemessen abschätzen zu können, müssen Mageninhaltsanalysen an Hering und Sprott mit Experimenten zu Konsumtionsraten kombiniert werden. Wissenslücken bezüglich wichtiger Parameter, die zur Quantifizierung von Konsumtionsraten benötigt werden, konnten durch eine Vielzahl an Experimenten geschlossen werden, die folgendes quantifizierten: 1) den Temperatureinfluss auf die Stoffwechselrate und 2) die Nahrungskonversionseffizienz von juvenilen Heringen, 3) den Temperatureinfluss auf die Magenleerung von Hering und Sprott, und 4) den Einfluss des Körpergewichtes auf die Magenleerung bei der Sprotte. Die Experimente veranschaulichten, dass die Magenleerung bei Hering und Sprott am besten durch ein exponentielles Entleerungsmodell beschrieben wurde. Die Ergebnisse zeigten ebenfalls, dass der Stoffwechsel und die Magenleerung durch Temperatur stark beeinflusst wurden und dass die Magenleerung der Sprotte vom Körpergewicht abhängig war. Zusätzlich konnte eine wichtige Annahme von Konsumtionsmodellen, dass Fische gleiche Magenleerungsraten während Phasen des Fressens und des Nicht-Fressens aufweisen, für juvenile Heringe bestätigt werden.

Die Ergebnisse dieser Untersuchungen wurden zur Berechnung der mittleren Tagesrationen und des Prädationsdrucks, ausgeübt durch Hering und Sprott auf das Zooplankton im Bornholmbecken, kombiniert. Aufgrund der Habitatpräferenzen bestimmter calanoider Copepoden, übten Hering und Sprott scheinbar den stärksten Prädationsdruck auf *P. acuspes* im Frühjahr und *T. longicornis* im Sommer aus. Ferner machten die Ergebnisse deutlich, dass beide Clupeiden im Bornholmbecken teilweise nahrungslimitiert waren und zu bestimmten Zeiten nicht genügend Nahrung aufnehmen

konnten um den Erhaltungsbedarf zu befriedigen. Folglich haben Hering und Sprott wahrscheinlich in anderen Bereichen der Ostsee, außerhalb des Bornholmbeckens, wie z.B. in flacheren küstennahen Gewässern, viel intensiver gefressen. Eine Hypothese, die in zukünftigen Untersuchungen getestet werden sollte.

General Introduction

Planktivorous fish

Fishes show a wide adaptive radiation in their feeding habits and occupy numerous trophic roles including being herbivores, detrivores, omnivores and carnivores. Planktivorous fish form an important link in the food chain, the connection between trophic levels (which is actually a complex food web with numerous interactions), in which material or energy accumulated at each step by either plants or animals is transferred as food to the next trophic level. Since planktivorous fish are prey for a variety of piscivores (fishes, birds, mammals and humans), they are a major conduit for channeling energy from plankton to higher trophic levels (Koski & Johnson 2002). Thus, our understanding of trophic dynamics and energy flow in marine food webs could be improved by learning more about the feeding ecology of planktivorous fish.
In the North-east Atlantic, especially the North Sea the most important clupeoids are herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.) followed by pilchards (*Sardina pilchardus*) and anchovies (*Engraulis ringens*) (Whitehead 1985). Other important planktivorous species are sandeels (*Ammodytidae*), mackerels (*Scombridae*) and horse mackerels (*Carangidae*). In the Baltic Sea, herring and sprat are the dominant species both in the commercial fishery and as zooplanktivores (Parmanne et al. 1994, Arrhenius 1996).

Sprat and herring in the Baltic Sea

The Baltic Sea is one of the worlds largest brackish water areas, with an area of about 360 000 km^2. The fish fauna is dominated by three marine species, cod (*Gadus morhua* L.), sprat and herring (Ojaveer et al. 1981) which account for 90% of the commercial catch (Thurow 1993). The surface water salinity varies from 1‰ in the north to more than 10‰ in the southwest. In the Baltic proper, with a surface area of about 200 000 km^2, a pronounced vertical salinity stratification exists with a halocline at a depth of about 60 m. Frequently, oxygen is depleted below the halocline and hydrogen sulfide (H_2S) is produced (Aneer 1985). At irregular intervals, part of the bottom water is renewed through inflows of saline North Sea water of higher oxygen content through the Belts and the Sound in the southwest. These inflows temporarily improve the situation below the halocline until the oxygen again is depleted (Jansson 1978). The frequency of inflows has drastically decreased since the early 1980´s with the last major event observed in 1993. As a consequence of the decrease of inflows the salinity and oxygen levels have decreased in the deep basins with profound effects on marine species in the brackish Baltic Sea, such as cod (Schmidt et al. 2003). Due to egg specific gravity (Nissling & Vallin 1996, Nissling 2004), cod eggs experienced low oxygen levels that resulted in a high mortality rate (Köster & Möllmann 2000). This climate-induced recruitment failure along with high fishing pressure and additional mortality due to egg consumption by herring and sprat (Köster & Möllmann 2000, Kornilovs et al. 2001) resulted in a collapse of cod stocks in the early 1990s.
The Baltic Sea fish community has therefore switched from a cod-dominated system to a clupeid-dominated system within the last decades. The highest abundance of cod caught in Baltic commercial fisheries occurred during the late 1970s to mid-1980s when spawning stock biomass reached an estimated 700 000 - 800 000 tons, followed by a drastic decline to less than 100 000 tons (Bagge et al. 1994), reaching lowest stock levels in the beginning of the 1990s and not recovering afterwards (Köster et al. 2001). The decline of cod stocks resulted in a release in predation pressure on sprat and herring and, in combination with high reproductive success and low fishing mortality, a

strong increase in sprat stock size (Parmanne et al. 1994, Sparholt 1994, Köster et al. 2001).
The increase of the sprat stock had consequences for herring and sprat condition (Cardinale & Arrhenius 2000, Cardinale et al. 2002, Casini et al. 2006). The weight-at-age (WAA) of herring has declined in the last two decades (Cardinale & Arrhenius 2000) and a similar trend has been observed for sprat (Cardinale et al. 2002, Kornilovs et al. 2001). Of the three hypotheses trying to explain the decrease of WAA (Cod predation hypothesis, Migration hypothesis, Feeding condition hypothesis, see Cardinale & Arrhenius 2000) the feeding condition hypothesis is supported by most evidence. The decrease in WAA of herring and sprat condition (Casini et al. 2006) is partly caused by an enhanced intra- and interspecific competition as a result of the increase of the sprat stock and the change in food availability, especially a decrease in population size of *Pseudocalanus* sp. (Flinkman et al. 1998, Cardinale & Arrhenius 2000, Cardinale et al. 2002, Möllmann et al. 2004, 2005). For a precise investigation concerning the trophic interactions of clupeids and zooplankton, extensive diet analyses are needed. However, the extent of intra- and interspecific competition of herring and sprat as indicated by similar diet composition has not yet been analysed on a monthly basis.

Top-down

Several studies have investigated the potential impact of herring and sprat on the zooplankton community in different parts of the Baltic Sea (Rudstam et al. 1992, 1994, Arrhenius & Hansson 1993, Arrhenius 1997, Flinkman et al. 1998, Möllmann & Köster 1999; 2002, Kornilovs et al. 2001). These studies identified both top-down and bottom-up processes in the coupling of clupeids and their zooplankton prey. Clupeids consume a large amount of the annual production of zooplankton, e.g. ~ 70% of the annual zooplankton production was estimated to be consumed by herring in the northern Baltic (Rudstam et al. 1992), having a distinct impact on the zooplankton community. Arrhenius & Hansson (1993) estimated that herring and sprat consumed between 60 and 80% of the annual zooplankton production in the Baltic Sea, whereas Arrhenius (1997) estimated that young-of-the-year herring alone consumed 30 to 60% of the zooplankton production in the northern Baltic proper. Selective predation on reproducing individuals will increase the effect that herring and sprat have on the zooplankton, by preventing these zooplankton populations from realizing their potential growth rates (Vuorinen 1982, Flinkman et al. 1992). In a Baltic coastal area, Rudstam et al. (1992, 1994) observed a simultaneous increase in planktivory and a decrease in zooplankton biomass in late summer. They identified planktivory by clupeids as a seasonally-acting top-down force. This result was supported by Möllmann & Köster (1999), who analyzed stomach content data from the Central Baltic Sea that were collected over several years. However, the general opinion is that there is a lack of unequivocal evidence that Baltic zooplankton biomass has been affected by inter-annual variation in clupeid stocks sizes (Rudstam et al. 1994, Möllmann & Köster 1999). The findings of Flinkman et al. (1998) suggested that herring feeding was not limited by the total amount of zooplankton, but rather by the availability of suitably-sized plankters.
Herring and sprat may control the structure and functioning of their prey populations by visual planktivory. Selective planktivores have been found to control the composition and functioning of pelagic lake ecosystems (Flinkman et al. 1992). Selective feeding in the Baltic is an important factor in understanding the feeding ecology of herring and sprat.

Selective feeding

The planktivores herring and sprat feed continuously on large amounts of small prey. Nevertheless, selective feeding has been observed. In these two species, both size-, season- and species-selective feeding was observed (Sandström 1980, Hansson et al. 1990, Flinkman et al. 1992, Arrhenius 1996, Viitasalo et al. 2001, Casini et al. 2004). Those investigations showed that herring and sprat tend to select late copepodite and adult stages of copepods and, in summer periods, also cladocerans. In an investigation by Sandström (1980) in Bothnian Bay, egg-sac carrying *Eurytemora* spp. were positively selected by herring, an observation that was confirmed by the findings of Flinkman et al. (1992). However, most of these studies were conducted in shallow coastal Baltic areas. Furthermore, with the exception of Hansson et al. (1990), these studies calculated selectivity indices from zooplankton sampling that integrated the water column (or parts of it) hence ignoring the differential vertical distributions of the various zooplankton species in the Baltic Sea (Hansen et al. 2006). Another shortcoming of earlier studies was the analysis protocol used, i.e., copepods were frequently not identified to developmental stage and thus a stage-resolved selectivity was missing. This is important as herring and sprat generally prefer later stages (Möllmann et al. 2004) and can prey selectively on adult female copepods and cladocerans, carrying conspicuous egg sacs (*Eurytemora affinis females*) or pigmented eggs and embryos (*Bosmina longispina* and *Podon* spp.) (Flinkman et al. 1992). Moreover, previous studies were mainly conducted during dusk or night, where the fish reside in the upper water column and in general are not feeding (Köster & Schnack 1994, Arrhenius 1998). Additionally, prey selectivity was only investigated for single months and years, and diel cycles were not examined.

Feeding mode

It was observed in a diet composition study in the Central Baltic Sea (Möllmann et al. 2004) that sprat mainly preyed upon older copepodite stages and adults, whereas herring additionally fed on smaller copepodite stages. To understand the fact that the larger species (herring) was partly preying upon smaller copepodites compared to the smaller species (sprat), preying almost exclusively on older copepodite stages, one has to take a closer look at the feeding behaviour of both species. Laboratory experiments with small schools of herring revealed three different feeding modes: biting, gulping and filter-feeding (Gibson & Ezzi 1985, 1990, 1992; Batty et al. 1990). When biting, single particles are ingested after a short directed attack at a prey, while filtering the herring swims at an increased speed with an open mouth and the amount of ingested particles depends upon the food concentration. Gulping is an intermediate feeding mode, where single particles are ingested and therefore should be considered as a type of biting (Gibson & Ezzi 1985). The type of feeding mode employed by herring depends on prey size, prey concentration, light intensity and fullness of the stomach. Herring generally switch from particulate-feeding (biting and gulping) to filter-feeding at high food concentrations. The concentrations required for the onset of filter-feeding are directly dependent on prey size (Gibson & Ezzi 1990), with e.g. the filter-feeding thresholds for *Calanus finmarchicus* being six to ten times lower than for any size of brine shrimp *Artemia* sp. Herring are not able to feed by biting in the dark, but they are able to filter-feed. Laboratory studies with clupeoids (Atlantic menhaden *Brevoortia tyrannus* and Cape anchovy *Engraulis capensis*) have shown that filter-feeding is energetically more costly than particulate-feeding (Durbin et al. 1981, James & Probyn 1989 a, Macy III et al. 1999). Optimal foraging theories assume that the forager attempts to maximize the rate of food consumption per unit time. Most models assume that the net rate of food

consumption is maximized, where net food consumption is measured as the gross energy content of the food less the energy cost of acquiring it (Wootton 1998). Herring are obviously able to maximize food consumption under certain conditions, by filter-feeding. This switch in feeding mode has not been demonstrated from field data yet. To my knowledge, no laboratory experiments have been conducted concerning the feeding behaviour of sprat at different prey and light concentrations. An extensive stomach sampling in the Bornholm Basin can be used to investigate differences in feeding modes between herring and sprat and potential consequences for their feeding ecology. For example, can situations be identified in which herring possibly were filter-feeding and thereby gaining a competitive advantage over sprat? These filter-feeding situations would be characterised by a higher fraction of younger copepodite stages in the diet, as a consequence of unselective filter-feeding, and a higher stomach fullness in comparison with sprat.

Consumption

Herring and sprat are able to affect the abundance and species composition of the zooplankton and are major predators on Baltic cod eggs (Köster & Möllmann 1997, Köster et al. 2001), and may therefore also affect ecosystem processes as nutrient cycling and primary production (Carpenter et al. 1985). These “cascading trophic interactions” need to be assessed to better understand ecosystem processes, for example responses of the Baltic Sea ecosystem to eutrophication (Rudstam 1988). For a quantification of predation rates in the clupeid-zooplankton interaction, consumption estimates (usually estimated as a daily consumption) are needed.
There are three commonly used methods to estimate daily food ration (Sainsbury 1986):
(A) Direct measurements of food consumption by fish held under laboratory conditions that imitate the natural environment (De Silva & Balbontin 1974, Boggs 1991, Richter et al. 2002). This method is often extended to provide a relationship between ration and growth in the laboratory, which is then applied to field growth data to estimate the field food ration (Kerr 1982, Durbin & Durbin 1983).
(B) Using a bioenergetics approach by determining the total energy requirements of the fish. This usually involves field estimates of growth rate and laboratory measurements of the energy utilized by metabolism and lost through faeces and excretion (e.g. Kitchell et al. 1977, Stewart et al. 1983, Stewart & Binkowski 1986, Rudstam 1988, Schaeffer et al. 1999).
(C) Estimation of food consumption from mean stomach contents in the field and knowledge of the rate of gastric evacuation (Bajkov 1935, Elliott & Persson 1978, Garcia & Adelman 1985).

Bioenergetics

Bioenergetics provides a theoretical framework for relating growth rates and feeding rates of a fish or other organisms to environmental conditions and provides some insight into causal relationships among these variables (Adams & Breck 1990). To estimate the food consumption or growth rate of fish, several bioenergetics models have been constructed for various species (e.g. Ursin 1967, Kitchell et al. 1977, Stewart et al. 1983, Rudstam 1988, Arrhenius 1995). For an individual fish, an energy budget for a defined period of time takes the basic form:

$$C = G + R + F + U, \quad (1)$$

where C is the energy content of the food consumed over the time period, G is the energy in growth (G_s = somatic growth and G_r = reproductive growth (gonads)), R is the energy lost in the form of heat produced during metabolism (M_r = standard metabolic rate, M_a = metabolic rate due to activity, SDA (specific dynamic action) = metabolic rate increase due to specific dynamic action (e.g. processing and assimilating food)), F is the energy lost in faeces and U is the energy lost in excretory products, particularly nitrogenous products such as ammonia and urea. The expansion of the energy budget results in the following equation:

$$C = (G_s + G_r) + (M_r + M_a + SDA) + F + U. \quad (2)$$

All components of the energy budget must be expressed in the same units. The units can be biomass (wet or dry weight), energy (Joules or calories), carbon or nitrogen and can be expressed as rates or as amounts gained or lost in some reference time period (Adams & Breck 1990).
Bioenergetic models for herring have been formulated by Rudstam (1988) and Arrhenius (1995), structured after Kitchell et al. (1977) and Stewart & Binkowski (1986) and parameterized using information available in the literature. Another bioenergetics model was applied to larval to juvenile herring by Kerr & Dickie (1985). The drawback with these models was that some of the parameters used were taken from other fish species like blueback herring *Alosa aestivalis* Mitchill, alewife *Alosa pseudoharengus* Wilson and Atlantic menhaden *Brevoortia tyrannus* Latrobe. This was necessary due to the fact that values for herring were not available for all bioenergetics parameters. To my knowledge, due to the fact that even fewer parameter estimates for sprat are available, no bioenergetics model has been developed for that species.

Parameters

Metabolic rates (M_r, M_a, SDA) are usually measured by oxygen consumption estimates (respirometry) at different temperatures, body sizes, feeding levels or swimming speeds, e.g. larval herring *Clupea harengus* (Kiørboe et al. 1987), Baltic herring *Clupea harengus membras* (Chekunova 1979) and Atlantic herring *Clupea harengus* (Johnstone et al. 1993).
Another method to estimate metabolic rates is by starving fish and measuring weight or energy losses. This approach was applied to, for example different tuna species *Katsuwonus pelamis*, *Euthynnus* affinis and *Thunnus albacares* (Boggs & Kitchell 1991), northern anchovy *Engraulis mordax* (Boggs 1991), juvenile perch *Perca fluviatilis* (Mehner & Wieser 1994) and Pacific sardine *Sardinops sagax* (Logerwell 2001). In fasting or starvation experiments single or groups of fish are held in experimental tanks being deprived of food. The advantages of simple starving experiments over oxygen consumption experiments are discussed by Logerwell (2001). When working with schooling clupeid fish, the starvation technique has the advantage in that fish do not need to be confined in small respiratory chambers that may stress the fish. Minimizing stress appears to be particularly important for sensitive clupeid species such as herring and sprat (*Sprattus sprattus* L.).
The metabolic demands of fish typically increase with temperature, resulting in enhanced food consumption (energy ingested) with increasing water temperature to satisfy increasing body maintenance demands (Jobling 1994). There is hardly any information available on the temperature dependency of metabolism of herring and sprat and bioenergetics models for these clupeids are provided with parameter estimates derived from related or even unrelated species (Kerr & Dickie 1985, Rudstam 1988, Arrhenius 1995).

The energy losses in faeces and as nitrogenous excretory products, mostly ammonia and urea, have not been quantified for juvenile and adult herring or sprat. In bioenergetic models usually constant values derived from species like adult menhaden (*Brevoortia tyrannus* Latrobe, Durbin & Durbin 1981) are used. The amount of energy lost in faeces and nitrogenous wastes and the costs of digestion (SDA = specific dynamic action) can be measured in growth-feeding experiments where fish are fed certain rations (in % body weight) over a defined period of time. In these experiments growth rates increase with the feeding rate. At the maintenance ration the fish neither gains nor loses weight. The net growth efficiency (NGE) measures the conversion efficiency of the food consumed in excess of the maintenance requirements (Wootton 1998). NGE integrates the energy lost in faeces and nitrogenous wastes and costs for SDA (NGE = 1 – F – E – SDA). This integrated measure of conversion efficiency combined with growth data from the field has been used to estimate food consumption rates of fish populations in the field (Temming 1995). Previously, similar feeding-growth studies were conducted on juvenile Atlantic herring (*Clupea harengus*, De Silva & Balbontin 1974), Northern anchovy (*Engraulis mordax*, Hunter & Leong 1981, Boggs 1991) and Japanese anchovy (*Engraulis japonicus*, Takahashi & Hatanaka 1960). These studies estimated the gross conversion efficiency (percentage of the ingested food material that is converted into fish flesh) with minced mussel, squid and mysids (De Silva & Balbontin 1974), trout pellets (Hunter & Leong 1981) and previously frozen euphausids (Takahashi & Hatanaka 1960 and Boggs 1991) as food. To my knowledge, measurements of net conversion efficiency in herring and sprat are lacking. Additionally, no feeding-growth studies with more realistic food like copepods or brine shrimp (*Artemia* spp.) have been performed yet except for studies examining post-larval (30 to 55 mm standard length) sprat (Baumann et al. 2005, Peck et al. In Prep.).
In the field, the bioenergetic models additionally require accurate growth estimates that are seasonally resolved in terms of e.g. energy density or body weight for the different age classes of fish. In the case of herring and sprat bioenergetic models suffer from the lack of adequately estimated parameters.

Gastric evacuation

Information on the gastric evacuation rate of prey is used to convert field data on stomach contents into estimates of feeding rate. Gastric evacuation studies have been performed on microphagous species like herring (*Clupea harengus* L., Szypula & Zalachowski 1984, Arrhenius & Hansson 1994, Darbyson et al. 2003, Maes et al. 2005), sprat (*Sprattus sprattus*, Szypula & Zalachowski 1984, Arrhenius 1998, Maes et al. 2005), sardine (*Sardinops sagax* Jenyns, Van der Lingen 1998), Cape anchovy (*Engraulis capensis* Gilchrist, James et al. 1989 b), Northern anchovy (*Engraulis mordax* Girard, Boggs 1991) and mackerel (*Scomber scombrus* L., Temming et al. 2002, Darbyson et al. 2003).
Four different methods have been used in gastric evacuation studies of planktivorous fish: 24 h-fisheries, ship-board tank experiments, cage/enclosure experiments and laboratory experiments. In 24 h-fisheries, fish are caught by diverse nets or sampled with the help of dynamite over a period of 24 hours. The rate of gastric evacuation is estimated from the depletion of the stomach contents at night (Shvetsov et al. 1983, Temming & Köster 1990, Köster 1994, Schmanns 1994, Arrhenius & Hansson 1994, Arrhenius 1998, Maes et al. 2005). In ship-board tank experiments, fish are caught by bottom or pelagic trawls and transferred to deck tanks, where sub samples are sacrificed at regular intervals and the rate of gastric evacuation is estimated from the depletion of the stomach contents (Szypula & Zalachowski 1984, Köster et al. 1990, Köster 1994, Temming 1995). Many potential problems exist in obtaining reliable gut

evacuation rate estimates from either the 24 h-fishery method or ship-board tank experiment method (Köster et al. 1990). In the case of the 24 h-fishery method, the environmental conditions are not controlled and it must be assumed that fish do not feed during the night-time sampling period and are reliably (randomly) sampled during dusk, night and dawn. Finally, it is unknown whether catches represent the same group of fish (e.g., same school with same feeding history). With ship-board tank experiments, the major drawback is the immense stress associated with capture and transfer methods and the sudden confinement within tanks. A third type of methods are enclosure experiments, where fish are enclosed by nets in their natural environment, e.g. by a purse seine or a fence trap. The fish are sampled at different times after enclosure by e.g. gillnets (Årnes et al. 2005) or dip nets and gastric evacuation is estimated from the depletion of the stomach contents with time. In this type of experimental set-up there are some doubts whether the fish actually feed during the captivity, biasing the estimates of the evacuation rate.
Laboratory experiments on gastric evacuation of clupeoids are rare. Such experiments can only be conducted using groups of fish since it is not possible to maintain species such as Atlantic herring, sprat and sardines individually. Van der Lingen (1998) conducted laboratory experiments on groups of sardine that were fed for a short period of time and subsequently sub sampled at regular intervals. A similar approach was chosen by Temming et al. (2002) for gastric evacuation experiments with Atlantic mackerel (*Scomber scombrus* L.) and by Boggs (1991) with Northern anchovy (*Engraulis mordax* Girard), two species that are also difficult to handle in the laboratory. Due to the uncertainties of the parameter estimates from 24 h-fisheries, tank and enclosure experiments, reliable parameter estimations (e.g., temperature and weight dependency) from the laboratory experiments are missing for consumption estimates of herring and sprat.

Aim of this work

The general aim of this work was to investigate the feeding ecology of Baltic Sea herring and sprat, the main planktivores in the brackish Baltic Sea. In an attempt to close the identified gaps in knowledge and available data, this study focused on the following tasks:

1. Diet composition and competition

The stomach contents from monthly and bi-monthly samplings of herring and sprat in the Bornholm Basin were analyzed to the lowest possible taxonomic level, a task that was (for the first time) accomplished over a complete seasonal cycle. The results were used to analyze the importance of the Bornholm Basin as a feeding ground for herring and sprat, to compare diets of different size groups of fish, to identify possible competitive advantages of herring through filter-feeding, and to quantify the competition for food resources. The latter task was conducted through the estimation of niche or diet overlaps based on species and within most important copepod species, based on copepodite stages (manuscript 1). These investigations formed the basis for the estimation of mean daily rations of herring and sprat in the Bornholm Basin.

2. Prey selectivity

A 24 hour *in situ* experiment in a deep Baltic basin was conducted to investigate the selective feeding behaviour of herring and sprat. Previous prey-selectivity studies have not included vertically-resolved estimates of predator and prey distributions and identification of copepods by stage. Furthermore, previous studies were mainly conducted during dusk or night, when these fish reside in the upper water column and,

in general, do not feed (Köster & Schnack 1994, Arrhenius 1998). Moreover, prey selectivity was investigated only for single months and years (Sandström 1980, Hansson et al. 1990, Flinkman et al. 1992, 1998, Arrhenius 1996, Casini et al. 2004). To better understand the selective feeding behaviour of herring and sprat, a more detailed investigation was needed. This study combined for the first time: 1) vertically-resolved zooplankton sampling, 2) diel observations of abundance, vertical distribution and stomach contents of the predators, and 3) a stage-resolved analysis of zooplankton caught in net samples and found in fish stomachs (manuscript 2).

3. Bioenergetics

Due to a lack of laboratory data, bioenergetic models for herring and sprat are currently parameterized using data from a variety of different species. In this study, laboratory experiments were conducted to evaluate the effect of temperature on the metabolic rate of juvenile herring. Additionally, the conversion efficiency of this species was estimated (manuscript 3). This was accomplished by utilizing both feeding-growth experiments and starvation experiments.

4. Gastric evacuation

The general gastric evacuation model (Jones 1974, Temming & Andersen 1994), was parameterized under controlled laboratory conditions (manuscript 4 and 5) for herring (temperature dependency) and sprat (temperature- and weight dependency). The functional response of herring feeding at different food concentrations and the role of the cecum in terms of food storage was studied (manuscript 4). A basic assumption of consumption models, based on gastric evacuation and field stomach contents, is that stomach contents are evacuated at the same rate irrespective of whether or not a fish is currently feeding. The hypothesis of Richter et al. (2002), that fish exhibited two evacuation rates, one rate while only evacuating food and a significantly enhanced rate, while feeding, was tested (manuscript 4).

5. Predator effects of clupeids on zooplankton in the Bornholm Basin

An *in situ* process study was conducted on the role of habitat heterogeneity on the vulnerability of three calanoid copepods (*Pseudocalanus acuspes*, *Temora longicornis* and *Acartia* spp.) to predation by planktivorous sprat and herring. The predatory impact of fish on the dominating zooplankton species was quantified by comparing predator consumption rates to rates of prey production. Using observations on vertical distributions of predators and prey, the hypothesis was tested that species-specific differences in hydrographic preference of prey and predators explained variability in stomach contents and vulnerability to predation (manuscript 6).

6. Are clupeids food limited in the southern-central Baltic Sea?

The parameter estimations of the gastric evacuation model (manuscript 4 and 5) and results of the diet analyses (manuscript 1) were combined to estimate mean daily rations of herring and sprat in the Bornholm Basin for the period from April 2002 to November 2003 (herring). These results were compared with estimates of maintenance rations (manuscript 3) and the estimates of mean daily ration from a bioenergetics model for sprat. In manuscript 7 the question whether or not clupeids were food limited in the Bornholm Basin is discussed.

References

Adams, S.M. & Breck, J.E. (1990). *Bioenergetics* in Methods for Fish Biology (1990). Editors: C.B. Schreck & P.B. Moyle. American Fisheries Society, 704 pp.

Aneer, G. (1985). Some speculation about the Baltic herring (*Clupea harengus membras*) in connection with the eutrophication of the Baltic Sea. Canadian Journal of Fisheries and Aquatic Sciences 42 (Suppl. 1), 83-90.

Arrhenius, F. & Hansson, S. (1993). Food consumption of larval, young and adult herring and sprat in the Baltic Sea. Marine Ecology Progress Series. 96, 125–137.

Arrhenius, F. & Hansson, S. (1994). *In situ* food consumption by young-of-the-year Baltic sea herring *Clupea harengus*: a test of predictions from a bioenergetics model. Marine Ecology Progress Series 110, 145–149.

Arrhenius , F. (1995). Feeding ecology of Baltic Sea herring (Clupea harengus L.) – field and model studies of a dominant zooplanktivor. PhD thesis. Department of Systems Ecology, Stockholm University, Sweden.

Arrhenius, F. (1996). Diet composition and food selectivity of 0-group herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.) in the northern Baltic Sea. ICES Journal of Marine Science 53, 701–712.

Arrhenius, F. (1997). Top-Down controls by young-of-the-year herring (*Clupea harengus*) in the Northern Baltic Proper. Proceedings. Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program. AK – SG – 97 – 01.

Arrhenius, F. (1998). Food intake and seasonal changes in energy content of young Baltic Sea sprat (*Sprattus sprattus* L.). ICES Journal of Marine Science 55, 319–324.

Årnes, C.B., Melle, W., Thorsen, A. (2005). Prey-specific gastric evacuation of Norwegian spring spawning herring (*Clupea harengus*). Globec International Newsletter 11, No.1, 16–17.

Bagge, O., Thurow, F., Steffensen, E. & Bay, J. (1994). The Baltic cod. Dana 10, 1–28.

Bajkov, A.D. (1935). How to estimate the daily food consumption of fish under natural conditions. Transactions of the American Fisheries Society 65, 288–289.

Batty, R.S., Blaxter, J.H.S. & Richard, J.M. (1990). Light intensity and the feeding behaviour of herring, *Clupea harengus*. Marine Biology 107, 383-388.

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

Boggs, C.H. (1991). Bioenergetics and growth of northern Anchovy *Engraulis mordax*. Fishery Bulletin 89(4), 555–566.

Boggs, C.H. & Kitchell, J.F. (1991). Tuna metabolic rates estimated from energy losses during starvation. Physiological Zoology 64(2), 502-524.

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

Cardinale, M., Casini, M. & Arrhenius, F. (2002). The influence of biotic and abiotic factors on the growth of sprat (*Sprattus sprattus*) in the Baltic Sea. Aquatic Living Resources 15, 273–282.

Cardinale, M., Casini, M., Arrhenius, F. & Håkansson, N. (2003). Diel spatial distribution and feeding activity of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the Baltic Sea. Aquatic Living Resources 16, 283–292.

Carpenter, S.R., Kitchell, J.F. & Hodgson, J.R. (1985). Cascading trophic interactions and lake productivity. BioScience 35, 634–639.

Casini, M., Cardinale, M. & Arrhenius, F. (2004). Feeding preferences of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the southern Baltic sea. ICES Journal of Marine Science 61, 1267–1277.

Casini, M., Cardinale, M. & Hjem, J. (2006). Inter-annual variation in herring, *Clupea harengus*, and sprat, *Sprattus sprattus*, condition in the central Baltic Sea: what gives the tune? Oikos 112, 638-650.

Chekunova, V.I. (1979). Energy requirements of the Baltic herring, *Clupea harengus membras*. Journal of Ichthyology 19, 118-125.

Darbyson, E., Swain, D.P., Chabott, D. & Castonguay, M. (2003). Diel variation in feeding rate and prey compositon of herring and mackerel in the southern Gulf of St Lawrence. Journal of Fish Biology 63, 1235–1257.

De Silva, S.S. & Balbontin, F. (1974). Laboratory studies on food intake, growth and food conversion of young herring, *Clupea harengus* (L.). Journal of Fish Biology 6, 645–658.

Durbin, A.G., Durbin, E.G., Verity, P.G. & Smayda, T.J. (1981). Voluntary swimming speeds and respiration rates of a filter-feeding planktivore, the Atlantic menhaden, *Brevoortia tyrannus* (Pisces: Clupeidae). Fishery Bulletin 78(4), 877–886.

Durbin, E.G. & Durbin, A.G. (1983). Energy and nitrogen budgets for the Atlantic menhaden, *Brevoortia Tyrannus*, (Pisces: Clupeidae), a filter-feeding planktivore. Fishery Bulletin Vol. 81, No. 2, 177–199.

Elliott, J.M. & Persson, L. (1978). The Estimation of daily rates of food consumption for fish. Journal of Animal Ecology 47, 977–991.

Flinkman, J., Vuorinen, I. & Aro, E. (1992). Planktivorous Baltic herring (*Clupea harengus*) prey selectively on reproducing copepods and cladocerans. Canadian Journal of Fisheries and Aquatic Sciences 49, 73–77.

Flinkman, J., Aro, E., Vuorinen, I. & Viitasalo, M. (1998). Changes in northern Baltic zooplankton and herring nutrition from 1980s to 1990s: top-down and bottom-up process at work. Marine Ecology Progress Series 165, 127-136.

Garcia, L.M. & Adelmann, I.R. (1985). An *in situ* estimate of daily food consumption and alimentary canal evacuation rates of common carp, *Cyprinus carpio* L. Journal of Fish Biology 27, 487–493.

Gibson, R.N. & Ezzi, I.A. (1985). Effect of particle concentration on filter- and particulate feeding in the herring *Clupea harengus*. Marine Biology 88, 109-116.

Gibson, R.N. & Ezzi, I.A. (1990). Relative importance of prey size and concentration in determining the feeding behaviour of the herring *Clupea harengus*. Marine Biology 107, 357-362.

Gibson, R.N. & Ezzi, I.A. (1992). The relative profitability of particulate- and filter-feeding in the herring, *Clupea harengus* L. Journal of Fish Biology 40, 577-590.

Hansen, F.C., Möllmann, C., Schütz, U. & Neumann, T. (2006). Spatio-temporal distribution and production of calanoid copepods in the central Baltic Sea. Journal of Plankton Research Vol.28, No.1, 39-54.

Hansson, S., Larsson, U. & Johansson, S. (1990). Selective predation by herring and mysids, and zooplankton community structure in a Baltic Sea coastal area. Journal of Plankton Research Vol.12, No.5, 1099–1116.

Hunter, J.R. & Leong, R. (1981). The spawning energetics of female northern anchovy, *Engraulis mordax*. Fishery Bulletin: Vol.79, No.2, 215 - 230.

James, A.G. & Probyn, T. (1989 a). The relationship between respiration rate, swimming speed and feeding behaviour in the Cape anchovy *Engraulis capensis* Gilchrist. Journal of Experimental Marine Biology and Ecology, 1989, Vol. 131: 81-100.

James, A.G., Probyn, T. & Seiderer, L.J. (1989 b). Nitrogen excretion and absorption efficiencies of the Cape anchovy *Engraulis capensis* Gilchrist fed upon a variety of plankton diets. Journal of Experimental Marine Biology and Ecology 131, 101-124.

Jansson, B.-O. (1978). The Baltic - A systems analysis of a semi-enclosed sea, 131-183. In: Charnock and Deacon [ed.]. Advances in oceanography. Plenum Publishing Corp., New York.

Jobling, M. (1994). Fish bioenergetics. Fish and Fisheries Series 13. Chapman & Hall, London. 309 pp.

Johnstone, A.D.F., Wardle, C.S. & Almatar, S.M. (1993). Routine respiration rates of Atlantic mackerel, *Scomber scombrus* L., and herring, *Clupea harengus* L., at low activity levels. Journal of Fish Biology 42, 149–151.

Jones, R. (1974). The rate of elimination of food from the stomachs of haddock *Melanogrammus aeglefinus*, cod *Gadus morhua* and whiting *Merlangius merlangus*. Journal du Conseil International pour l´Exploration de la mer 35, 225-243.

Kerr, S.R. (1982). Estimating the energy budgets of actively predatory fishes. Canadian Journal of Fisheries and Aquatic Sciences 39, 371-379.

Kerr, S.R. & Dickie, L.M. (1985). Bioenergetics of O+ Atlantic herring (*Clupea harengus harengus*). Canadian Journal of Fisheries and Aquatic Sciences 42, 105-110.

Kiørboe, T., Munk, P. & Richardson, K. (1987). Respiration and growth of larval herring, *Clupea harengus*: relation between specific dynamic action and growth efficiency. Marine Ecology Progress Series 40, 1–10.

Kitchell, J.F., Stewart, D.J. & Weininger, D. (1977). Applications of a bioenergetics model to yellow perch (Perca flavescens) and walleye (Stizostedion vitreum vitreum). Journal of Fisheries Research Board of Canada 34, 1922-1935.

Kornilovs, G., Sidrevics, L. & Dippner, J.W. (2001). Fish and zooplankton interaction in the Central Baltic Sea. ICES Journal of Marine Science 58, 579-588.

Koski, M.L. & Johnson, B.M. (2002). Functional response of kokanee salmon (*Oncorhynchus nerka*) to Daphnia at different light levels. Canadian Journal of Fisheries and Aquatic Sciences 59, 707-716.

Köster, F.W., Schober, W., Korves, A. & Schneider, R. (1990). Tank experiments on board: a useful tool for the estimation of stomach evacuation rates? ICES. C.M. 1990/G:34.

Köster, F.W. (1994). Der Einfluß von Bruträubern auf die Sterblichkeit früher Jugendstadien des Dorsches (*Gadus morhua*) und der Sprotte (*Sprattus sprattus*) in der zentralen Ostsee (Ph.D.-thesis). Christian-Albrechts-Universität, Kiel. 369 pp.

Köster, F.W. & Schnack, D. (1994). The role of predation on early life stages of cod in the Baltic. Dana 10, 179-201.

Köster, F.W. & Möllmann, C. (1997). Predation by sprat and herring on early life stages of cod and sprat in the central Baltic. Forage Fishes in Marine Ecosystems AK-SG-97-01, 41-69.

Köster, F.W. & Möllmann, C. (2000). Trophodynamic control by clupeid predators on recruitment success in Baltic cod? ICES Journal of Marine Science 57, 310-323.

Köster, F.W., Hinrichsen, H.H., St.John, M., Schnack, D. MacKenzie, B.R., Tomkiewicz, J. & Plikshs, M. (2001). Developing Baltic cod recruitment models. II. Incorporation of environmental variability and species interaction. Canadian Journal of Fisheries and Aquatic Sciences 58, 1534-1556.

Logerwell, E.A. (2001). Metabolic rate of California Pacific sardine estimated from energy losses during starvation. Transaction of the American Fisheries Society 130: 526–530.

Macy III, W.K., Durbin, A.G. & Durbin, E.G. (1999). Metabolic rate in relation to temperature and swimming speed, and the cost of filter feeding in Atlantic menhaden, *Brevoortia tyrannus*. Fishery Bulletin 97(2), 282 – 293.

Maes, J., Tackx, M. & Soetaert, K. (2005). The predation impact of juvenile herring *Clupea harengus* and sprat *Sprattus sprattus* on estuarine zooplankton. Hydrobiologia 540, 225-235.

Mehner, T. & Wieser, W. (1994). Energetics and metabolic correlates of starvation in juvenile perch (*Percha fluviatilis*). Journal of Fish Biology 45, 325–333.

Möllmann, C. & Köster, F.W. (1999). Food consumption by clupeids in the Central Baltic: evidence for top-down control? ICES Journal of Marine Science 56 Supplement, 100-113.

Möllmann, C. & Köster, F.W. (2002). Population dynamics of calanoid copepods and the implications of their predation by clupeid fish in the Central Baltic Sea. Journal of Plankton Research Vol. 24, No.10, 959-977.

Möllmann, C., Kornilovs, G., Fetter, M. & Köster, F.W. (2004). Feeding ecology of central Baltic Sea herring and sprat. Journal of Fish Biology 65, 1563-1581.

Möllmann, C., Kornilovs, G., Fetter, M. & Köster, F.W. (2005). Climate, zooplankton, and pelagic fish growth in the central Baltic Sea. ICES Journal of Marine Science 62, 1270-1280.

Nissling, A. & Vallin, L. (1996). The ability of Baltic cod eggs to maintain neutral buoyancy and the opportunity for survival in fluctuating conditions in the Baltic Sea. Journal of Fish Biology 48, 217-227.

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

Ojaveer, E., Lindroth, A., Bagge, O., Lehtonen, H. and Toivonen, J. (1981). Fishes and fisheries. In: A Voipio (ed.), The Baltic Sea. Elsevier Oceanography Series 30. Elsevier Scientific Publishing Company, Amsterdam, pp. 275-350.

Parmanne, R., Rechlin, O. & Sjöstrand, B. (1994). Status and future of herring and sprat stocks in the Baltic sea. Dana Vol. 10, 29-59.

Peck, M.A., Ewest, B., Herrmann, J.-P., Kürs, U., Temming, A. (In Prep.) Interrelationships among feeding, growth and swimming activity of post-larval *Sprattus sprattus* L. (Teleostei:Clupeidae) in the laboratory. For submission to Oecologia.

Richter, H., Lückstädt, C., Schlechtriem, C., Focken, U. & Becker, K. (2002). Evidence of violation of a basic assumption in models currently used for food consumption estimation in fish. Archive of Fishery and Marine Research 49 (3), 171–188.

Rudstam, L.G. (1988). Exploring the dynamics of herring consumption in the Baltic: Applications of an energetic model of fish growth. Kieler Meeresforschung Sonderheft 6, 312–322.

Rudstam, L.G., Hansson, S., Johansson, S. & Larsson, U. (1992). Dynamics of planktivory in a coastal area of the northern Baltic Sea. Marine Ecology Progress Series 80, 159-173.

Rudstam, L.G., Aneer, G. & Hilden, M. (1994). Top-down control in the pelagic Baltic ecosystem. Dana, vol. 10, 105 – 129.

Sainsbury, K.J. (1986). Estimation of food consumption from field observations of fish feeding cycles. Journal of Fish Biology 29, 23-36.

Sandström, O. (1980). Selective feeding by Baltic herring. Hydrobiologia Vol. 69, 3, 199-207.

Schaeffer, J.S., Haas, R.C., Diana, J.S. & Breck, J.E. (1999). Field test of two energetic models for yellow perch. Transactions of the American Fisheries Society 128, 414–435.

Schmanns, M. (1994). Zur Biologie – insbesondere Nahrungsbiologie – der im Sylter Wattenmeer auftretenden Heringe (*Clupea harengus* L.). Diploma thesis of Meike Schmanns (in German).

Schmidt, J., Möllmann, C., Temming, A., Herrmann, J.-P., Flöter, J. Sell, A. & St. John, M. (2003). Unusual water mass advection affected Central Baltic key species 2: Pseudocalanus and the winter inflow. Globec International Newsletter October 2003, 28-29.

Shvetsov, F.G., Starodub, M.L. & Sidrevits, L.L. (1983). The daily feeding rhythm of the Baltic sprat, *Sprattus sprattus balticus* (Clupeidae). Journal of Ichthyology Vol.23, no.2, 99-105.

Sparholt, H. (1994). Fish species interactions in the Baltic Sea. Dana 10, 131-162.

Stepputtis, D. (2006). The distribution of Baltic sprat, *Sprattus sprattus* L. – causes and consequences. PhD-thesis at Mathematisch-Naturwissenschaftliche Fakultät der Christian-Albrechts-Universität Kiel, Germany. 148 pp.

Stewart, D.J., Weininger, D., Rotiers, D.V. & Edsall, T.A. (1983). An energetics model for Lake Trout, *Salvelinus namaycush*: Application to the Lake Michigan population. Canadian Journal of Fisheries and Aquatic Sciences 40, 681–698.

Stewart, D.J. & Binkowski, F.P. (1986). Dynamics of consumption and food conversion by Lake Michigan Alewives: An energetics-modeling synthesis. Transactions of the American Fisheries Society 115(5), 643–661.

Szypula, J. & Zalachowski, W. (1984). Duration of food evacuation in herring, *Clupea harengus* L., and sprat, *Sprattus sprattus* (L.). Acta ichthyologica et piscatoria, Vol. 14 Fasc. 1-2, 93–102.

Takahashi, M. & Hatanaka, M.A. (1960). Experimental study on utilization of food by young anchovy, *Engraulis japonicus* Temminck et Schlegel. Tohoku Journal of Agricultural Research 11, 161-170.

Temming, A. & Köster, F.W. (1990). Stomach evacuation rates of cod and herring estimated from shipboard tank experiments and field data. ICES. C.M. 1990/G : 31.

Temming, A. & Andersen, N.G. (1994). Modelling gastric evacuation without meal size as a variable. A model applicable for the estimation of daily ration of cod (*Gadus morhua* L.) in the field. ICES Journal of Marine Science 51, 429-438.

Temming, A. (1995). Die quantitative Bestimmung der Konsumtion von Fischen. Experimentelle, methodische und theoretische Aspekte (in German). Habilitationsschrift, Universität Hamburg, Fachbereich Biologie, 235 pp.

Temming, A., Bøhle, B., Skagen, D.W. & Knudsen, F.R. (2002). Gastric evacuation in mackerel: the effects of meal size, prey type and temperature. Journal of Fish Biology 61, 50–70.

Thurow, F. (1993). Fish and fisheries in the Baltic Sea. ICES Coop. Res. Rep. 186, 20-37.

Ursin, E. (1967). A mathematical model of some aspects of fish growth, respiration and mortality. Journal of the Fisheries Research Board of Canada 24, 2355-2453.

Van der Lingen, C.D. (1998). Gastric evacuation, feeding periodicity and daily ration of Sardine *Sardinops sagax* in the Southern Benguela Upwelling Ecosystem. South African Journal of Marine Science 19, 305 - 316.

Viitasalo, M., Flinkman, J. & Viherluoto, M. (2001). Zooplanktivory in the Baltic Sea: a comparison of prey selectivity by *Clupea harengus* and *Mysis mixta*, with reference to prey escape reactions. Marine Ecology Progress Series 216, 191–200.

Vuorinen, I. (1982). Vertical migration of *Eurytemora* (Crustacea, Copepoda): A compromise between risks of predation and decreased fecundity. Journal of Plankton Research 9, 1037–1046.

Whitehead, P.J.P. (1985). FAO Species Catalogue. Clupeoid fishes of the world (Suborder clupeoidie; Part I, herrings, sardines, pilchards, sprats, anchovies and wolf-herrings. 303 pp.
Wootton, R.J. (1998). Ecology of Teleost Fishes. 2nd edition. Dordrecht: Kluwer, 386 pp.

Seasonal variation in the feeding of herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.) in the south-central Baltic Sea

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Abstract

A comprehensive study of the diet of two dominant planktivorous fish species, sprat (*Sprattus sprattus* L.) and herring (*Clupea harengus* L.), was conducted in the south-central Baltic Sea (Bornholm Basin). From April 2002 to November 2003 a total of 3097 sprat and 2821 herring stomachs were sampled and analysed in monthly or bi-monthly cruises. We did not observe an influence of sprat size on diet composition, in herring we observed an influence of fish size on diet composition in November 2003 only, where the proportion of mysids in the diet of herring increased with fish size. Our results demonstrated a high diet niche overlap between sprat and herring (in 9 out of 12 months > 80%) The proportions of feeding fish were high over the entire investigated period (> 70%). The average stomach content and fullness (sprat: ~ 0.2 to 0.4% *BW*, herring: ~ 0.1 to 0.7% *BW*) were similar to the results from other areas of the Baltic Sea proper, but low in comparison to other water bodies, indicating that sprat and herring eventually feed more intensively in e.g. coastal regions. The results of the estimations of the weighted mean copepodite stages (*WMCS*) at each sampling station did not indicate that herring were filter-feeding and thereby gaining a competitive advantage over sprat. Our results indicated that during the investigated period the Bornholm Basin was an area of intense competition for food resources between sprat and herring.

Introduction

The fish community of the southern-central Baltic Sea is dominated in abundance and production by the planktivores sprat (*Sprattus sprattus* L.) and herring (*Clupea harengus* L.) and the piscivore cod (*Gadus morhua* L.). These species make up more than 95% of the commercial catch (Sparholt 1994). The Baltic Sea fish community has switched from a cod-dominated system during the late 1970s to mid-1980s to a clupeid-dominated system from the early 1990´s until today (Kornilovs et al. 2001).

Clupeids consume a large amount of the annual production of zooplankton in the Baltic Sea, e.g. approximately 70% of the annual zooplankton production is estimated to be consumed by herring in the northern Baltic (Hansson et al. 1990, Rudstam et al. 1992). They can therefore have a distinct impact on the zooplankton community. As herring and sprat are size selective feeders (Sandström 1980), large juveniles and adults feeding mainly on older copepodite stages and adult copepods (Flinkman et al. 1992, Arrhenius 1996, Viitasalo et al. 2001), they are able to influence the seasonal development of at least two important copepod species in the Baltic Sea, *Pseudocalanus acuspes* and *Temora longicornis* (Möllmann & Köster 1999). The feeding habits of herring and sprat in different areas of the Baltic Sea have previously been studied by several authors, investigating the diet composition, diet selectivity and daily rates of food consumption (Shvetsov et al. 1983, Szypula 1985, Rudstam et al. 1992, Arrhenius 1996, Szypula et al. 1997, Kornilovs et al. 2001, Casini et al. 2004, Möllmann et al. 2004). These studies have investigated the daily feeding rhythm (Shvetsov et al. 1983) or have compared years and seasons (Szypula 1985, Rudstam et al. 1992, Szypula et al. 1997, Möllmann & Köster 1999, Kornilovs et al. 2001, Möllmann et al. 2004). Only the study of Möllmann et al. (2004) from the central Baltic Sea was copepod stage-resolved.

For a precise assessment of the potential top-down impact of clupeids on the zooplankton community knowledge about prey selectivity, diet composition and total

consumption are needed. Within the Globec-Germany programme an extensive stomach sampling programme in the Bornholm Basin, located in the south-central Baltic Sea, was performed between April 2002 and November 2003 with monthly or bi-monthly sampling. Stomach samples were taken from the major planktivores of the Baltic, herring and sprat, and analysed to the lowest possible taxonomic level, including copepodite stages of the major copepods.
The aim of this work was (1) to analyse the importance of the Bornholm Basin as a feeding ground for herring and sprat over an annual cycle, (2) to investigate upon the influence of fish size on diet composition, (3) to identify possible competitive advantages of herring through filter-feeding and (4) to quantify the competition for food resources through the estimation of niche or diet overlaps based on species and within most important copepod species, based on copepodite stages. Here we present the results of our comprehensive sampling and analysis.

Material & Methods

Sampling and content analysis

Sprat and herring were caught monthly or bi-monthly in the Bornholm Basin (ICES subdivision 25, figure 1) from April 2002 to November 2003 by pelagic trawling. The hauls were conducted during daytime only. The weights and lengths of randomly chosen sub samples of herring and sprat were measured. Sprat and herring were measured to the nearest cm below. Stomach samples were taken from these sub samples, where herring was subdivided into 2 cm-classes (14/15 cm, 16/17 cm...).

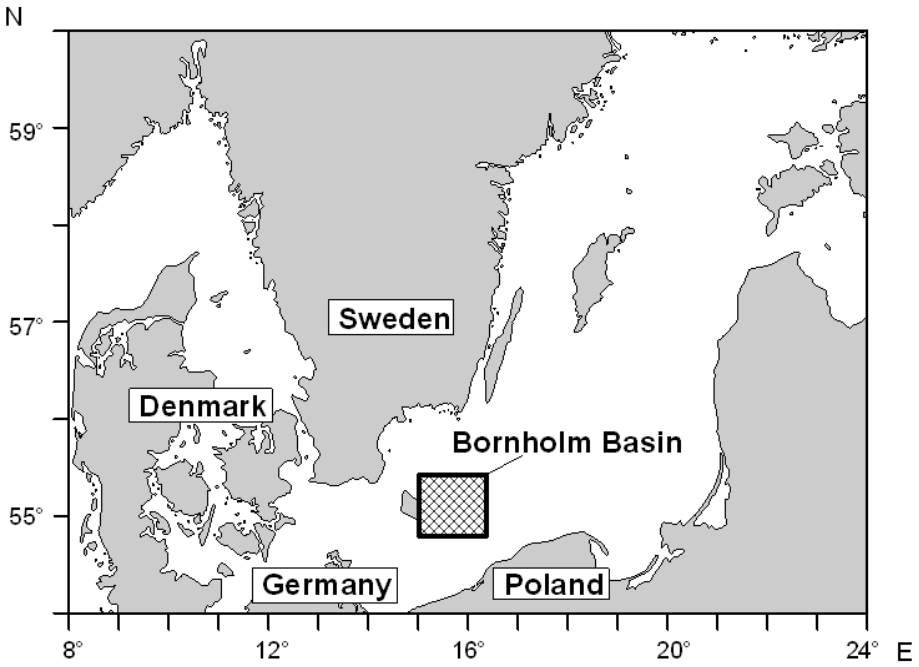

Figure 1) Map of the Baltic Sea with the study area marked by the shaded box.

The herring and sprat stomachs were analysed by the sorting centre of the Latvian Fish Resources Agency (LATFRA) in Riga (Latvia). Diet analyses were made for a minimum of 3 randomly chosen fish per sampling time and length class. Each individual stomach was cut open, and the complete content was weighed and analysed using a stereo

microscope (magnification 20–80x). Each prey item was determined to the lowest possible taxonomic level, copepods were determined to the copepodite stage, if possible. If the sample size was too large in numbers, a sub sample of at least 100 prey items was analysed. Additionally, the sample was screened for rare taxa and ichthyoplankton. A total of 2821 herring stomachs and 3097 sprat stomachs were analysed (table 1).

Table 1) Number of herring and sprat stomachs analysed per month (02 = 2002, 03 = 2003). 89% of sprat stomachs and 87% of herring stomachs were from depths of more than 50 m (Maximum: 100 m).

Month/Year	Herring	Sprat
April 02	344	223
May 02	251	483
June 02	196	201
July 02	260	188
August 02	37	86
September 02	207	228
November 02	297	275
January 03	273	255
March 03	310	318
April 03	259	300
July 03	147	294
November 03	240	246
Total	**2821**	**3097**

Data analysis

The index of stomach fullness (*ISF*) scales the weight of the stomach content to the weight of the fish and is described as a per cent of body mass:

$$ISF = \left(\frac{SC}{W}\right) * 100, \quad (1)$$

where *SC* is stomach content in g wet weight and *W* is the fish weight in g wet weight. For a description of the diet of herring and sprat the frequency of occurrence (*FO*) in per cent was estimated for each prey species by following equation:

$$FO = \left(\frac{n_i}{N}\right) * 100, \quad (2)$$

where n_i is the number of fish with food category *i* in their stomachs and *N* the total number of analysed fish. To compare the importance of prey species by numbers of herring and sprat the niche overlap was estimated. The overlap was estimated using the percentage overlap index, sometimes referred to as Renkonen index or Schoener overlap index (Krebs 1999). This measure is calculated as a percentage and is given by

$$P_{jk} = \left[\sum_{i=1}^{n}\left(\min p_{ij}, p_{ik}\right)\right]*100, \quad (3)$$

where P_{jk} = Percentage overlap between species *j* and species *k*
p_{ij} = Proportion resource *i* is of the total resources used by species *j*
p_{ik} = Proportion resource *i* is of the total resources used by species *k*
n = Total number of resource states

In order to identify situations in which herring or sprat were gaining a competitive advantage through the feeding on certain stages we estimated a weighted mean copepodite stage (*WMCS*) for each station:

$$WMCS = \frac{\left(\sum n_i * c_i\right)}{\sum n_i} \quad (4)$$

where n_i is the sum of each copepodite stage c_i consumed at each station or month. *WMCS* was estimated for the average fish size per station or month. We plotted the *WMCS* versus the weighted share for each copepod species of the stomach fullness at each station.

Results

Stomach content and fullness

Sprat

The mean stomach contents showed a similar trend for most size classes of sprat, increasing from April 2002 at approximately 0.02 g wet weight (g *WW*) to July 2002 at approx. 0.04 g *WW* with highest values of 0.064 g *WW* for 14 cm sprat (figure 2 A). The stomach contents were stable at around 0.04 g *WW* until September, subsequently declining to lowest values of around 0.007 g *WW* in January 2003. From January to July the contents increased again to similar levels as observed in July 2003.
The stomach fullness was rather constant from April to September 2003 at around 0.3% of the body weight, with a slight decrease in August (figure 2 B). Lowest values were observed in January 2003 at 0.06% *BW*. The stomach fullness decreased with increasing fish length in April, May and June 2002, whereas in the remaining months no clear trend with size was observed.
The average number of prey particles in the stomachs (figure 2 C) followed the same trend as stomach content, where highest numbers were observed in June and July 2002 with 1700 particles for size class 12 cm. Again, lowest numbers were observed in January 2003 with 100 particles per stomach.
A low number of empty stomachs was observed over the entire investigation period, meaning that most sprat were actively feeding. In January 2003 76% of the analysed stomachs had prey items in their stomachs (figure 2 A). In all other investigated months more than 94% of the fish (March 03) had prey items in their stomachs with highest levels (100%) in April, May, August and September 2002 and April and July 2003.

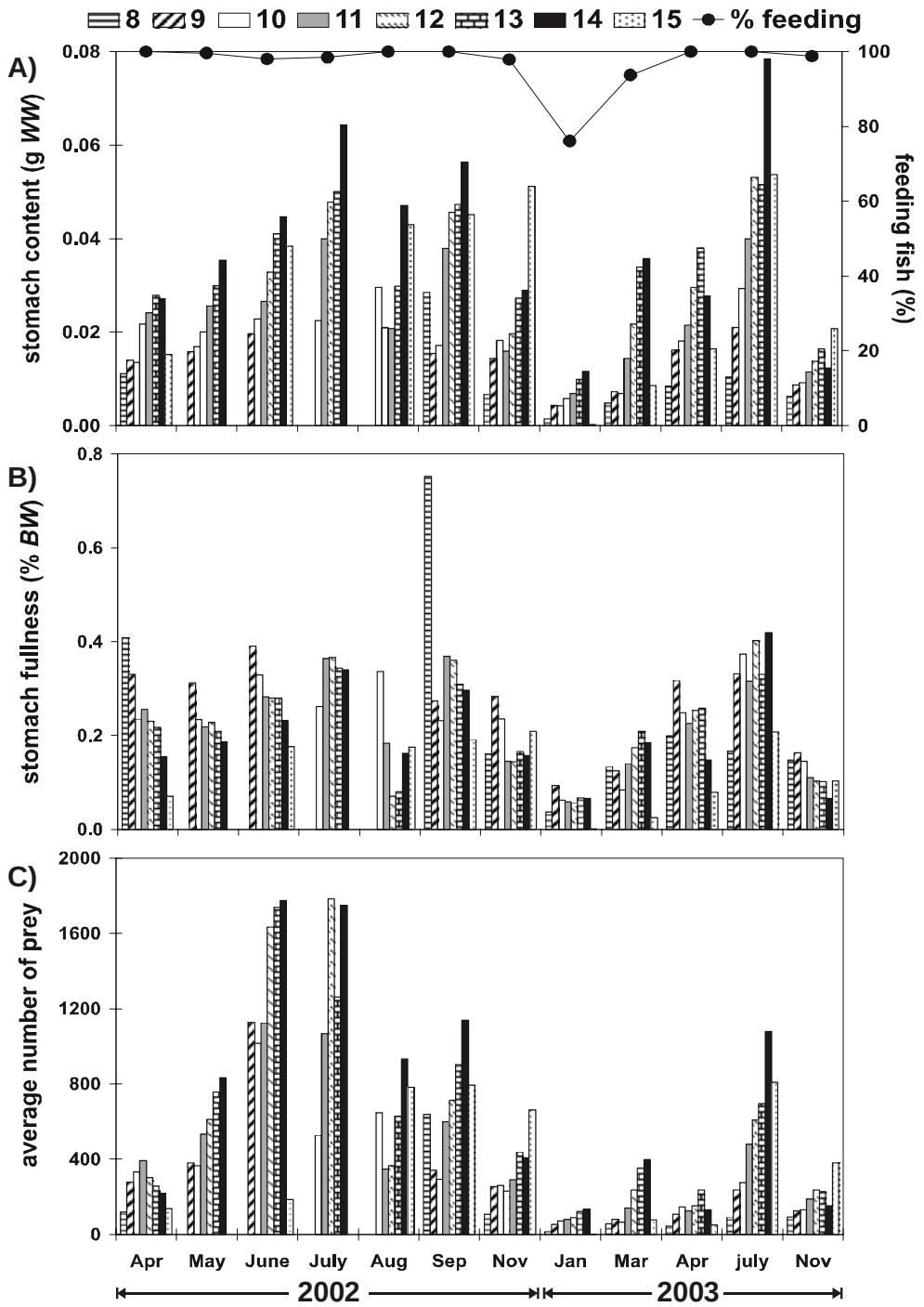

Figure 2) A) Average stomach content by size class of sprat and percentage of sprat with full stomachs. B) Average stomach fullness (*ISF*) by size class of sprat. C) Average number of prey by size class of sprat. Results are displayed per month.

Herring

In herring, more pronounced fluctuations in mean stomach content and stomach fullness were observed. The trend was similar to that for sprat though, with increasing stomach contents from April at 0.1 g *WW* to 0.3 g *WW* in July, decreasing towards the winter (figure 3 A). The stomach contents were at winter levels already in September with less than 0.05 g *WW*. Interestingly, the highest amount of food in the stomach was observed in July and November 2003 with values of 0.46 g *WW* for 22/23 cm herring.

The same trend was observed in the stomach fullness (figure 3 B) where high values were found in July 2002 at 0.7% *BW*, declining afterwards down to 0.1-0.2% *BW* in March 2003. The stomach fullness was high again at 0.4 to 0.6% *BW* in November 2003. In contrast to sprat, stomach fullness in herring increased from April to June 2002, whereas in sprat the stomach fullness was constant over that period. In April 2002 stomach fullness increased with increasing size, in comparison to sprat where the opposite case was observed.

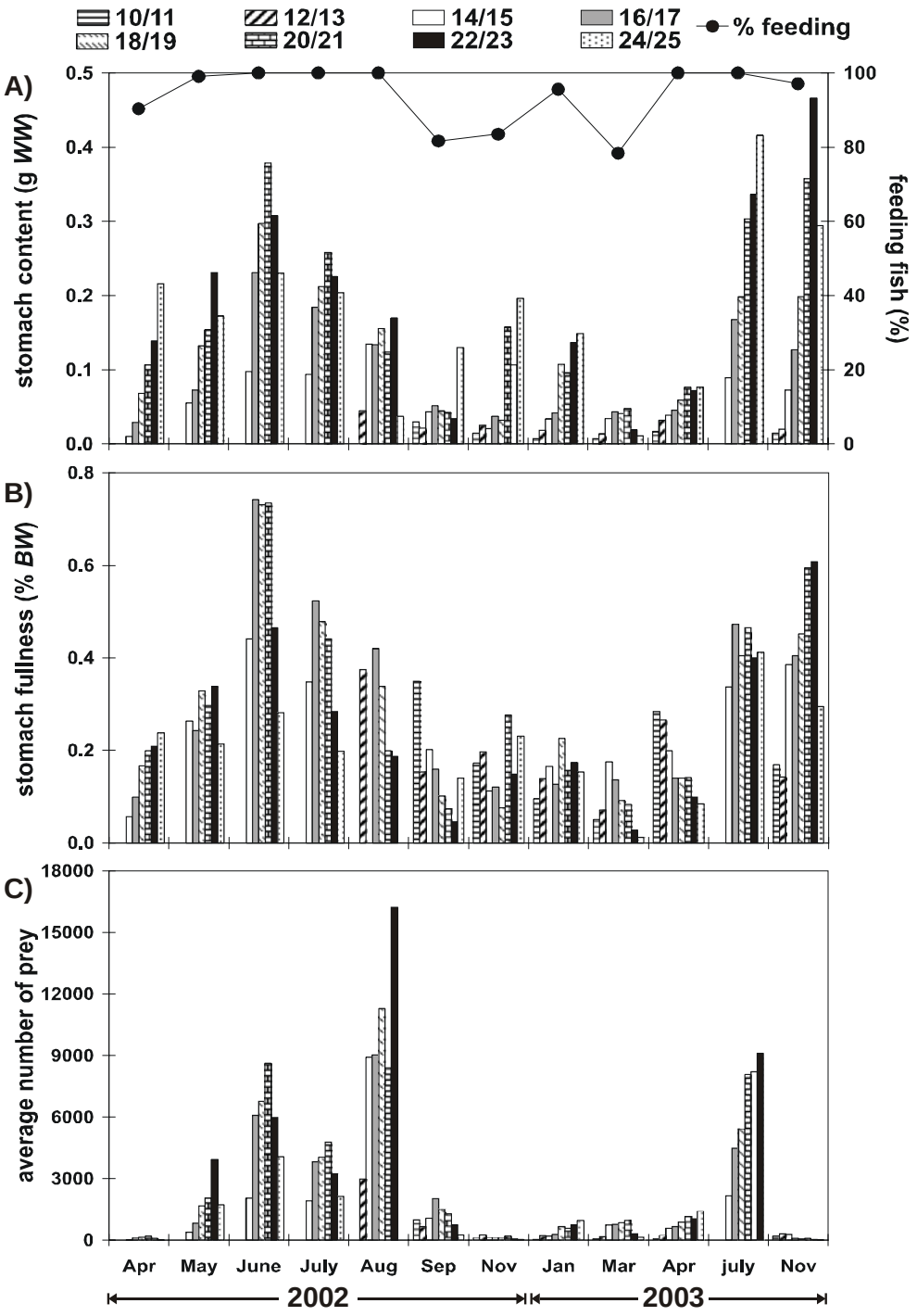

Figure 3) A) Average stomach content by size class of herring and percentage of herring with full stomachs. B) Average stomach fullness (*ISF*) by size class of herring. C) Average number of prey by size class of herring. Results are displayed per month.

The average amount of prey items in the stomachs increased from very low numbers of approx. 100 in April 2002 to highest numbers in August with 9 000 to 15 000 (figure 3 C). From September on until April 2003 the numbers were low again, with less than 1500 particles. In July 2003 high numbers of approx. 6 000 particles were observed, whereas in November 2003 below 310 (12/13 cm) particles per stomach were observed.
Low numbers of empty stomachs were observed over the entire investigation period. In June, July, August 2002 and April and July 2003 all analysed stomachs contained prey items (figure 3 A). From September 2002 to March 2003 the highest numbers of empty stomachs were observed, with lowest value of feeding fish at 78% in March 2003.

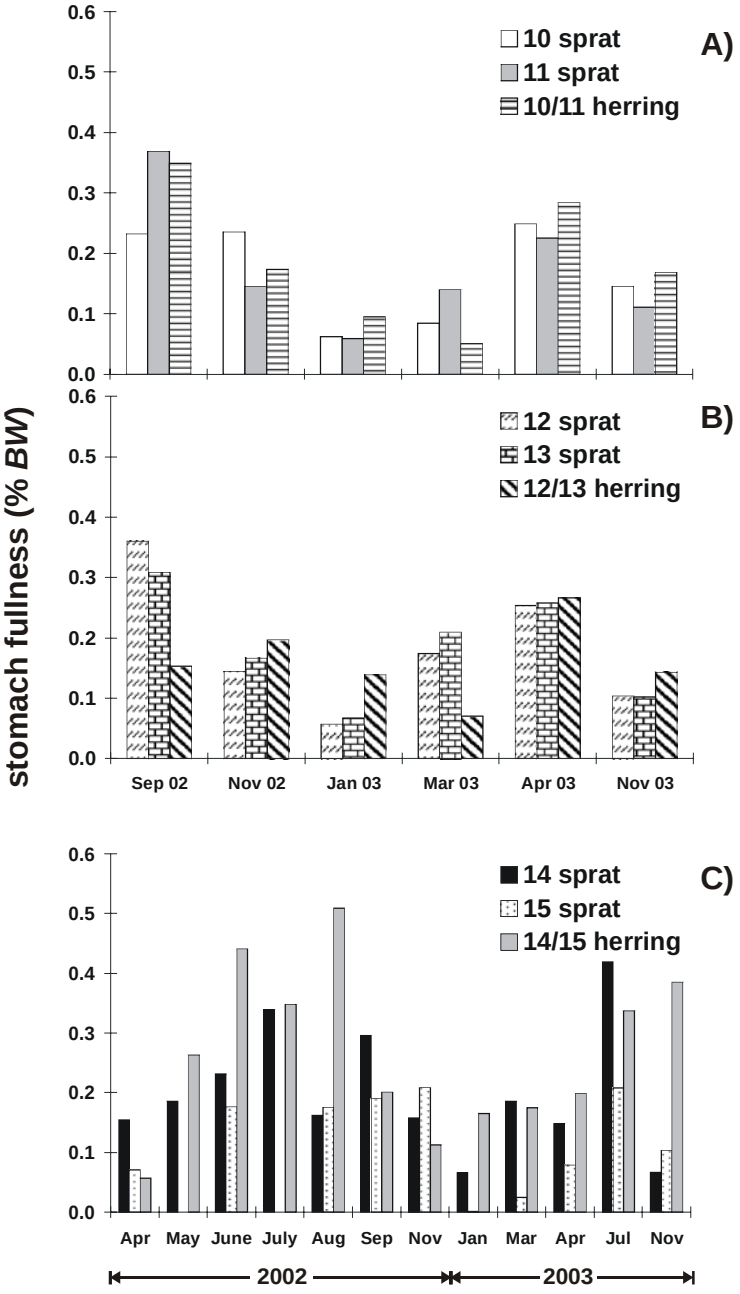

Figure 4) Comparison of stomach fullness (% *BW*) in similar sized sprat and herring. A) 10-11 cm, B) 12-13 cm and C) 14-15 cm. Corresponding numbers of analysed stomachs (n) are displayed in table 2.

Similar sized herring and sprat

A comparison of the stomach fullness of sprat and herring of similar size (10 to 15 cm) revealed a rather similar stomach fullness (figures 4 A to C). In length classes of 10 to 13 cm the stomach fullness was between approx. 0.1 and 0.35% *BW*. In 14 to 15 cm fish 0.5% *BW* was the highest observed value. In September 2002 and March 2003 the stomach fullness of 12 and 13 cm sprat was twice as high as the stomach fullness of 12/13 cm herring (figure 4 B). The numbers of analysed stomachs (n) were > 37 for 12 and 13 cm sprat and 15 in September 2002 and 37 in March 2003 for 12/13 cm herring (table 2). The stomach fullness of 14/15 cm herring was more than twice as high in June, August 2002 and January, November 2003 as the stomach fullness of similar sized sprat (figure 4 C). However, the numbers of analysed stomachs were partly low in 15 cm sprat and 14/15 cm herring, e.g. n = 7 for 14/15 cm herring in August 2002 and n = 3 for 15 cm sprat in June 2002 (table 2).

Table 2) Number of stomachs (n) analysed per length class (cm in sprat and 2 cm´s in herring) in figure 4 and month of herring and sprat.

	Sprat						Herring		
Month/year	**10**	**11**	**12**	**13**	**14**	**15**	**10/11**	**12/13**	**14/15**
April 02	54	54	54	54	53	5			15
May02	42	45	45	45	45				18
June 02	39	39	39	39	36	3			18
July 02	23	40	45	43	37				38
August 02	7	18	18	18	18	7			3
September 02	14	36	39	37	27	14	9	15	11
November 02	36	39	45	45	45	6	38	36	46
January 03	36	39	39	39	39	6	31	30	30
March 03	42	51	51	51	51	6	26	37	36
April 03	48	48	48	48	48	3	12	12	18
July 03	42	42	42	42	42	10			8
November 03	31	33	36	36	36	12	12	24	27

Diet composition

Sprat

The most important single prey species by numbers was the calanoid copepod *Temora longicornis*, followed by another calanoid copepod, *Pseudocalanus acuspes*. Except for May 2002, where only 7% of the stomach contents consisted of *T. longicornis*, more than 45% (March 2003) of the stomach contents always consisted of *T. longicornis* (figure 5 A). In most other observed months they made up 50 to over 80% of the stomach contents. *P. acuspes* was the most important prey species in May 2002 with 66% of stomach contents and March 2003 with 53% of the stomach contents. The other two important calanoid copepods *Centropages hamatus* and *Acartia* spp. (including *A. bifilosa*, *A. longiremis* and *A. tonsa*) represented only a few per cent of the stomach contents, with the exception of June 2002 where 19% of the stomach contents were made up of *C. hamatus*.

The cladocerans *Podon* spp. (including *P. intermedius*, *P. leuckarti* and *P. polyphenoides*), *Bosmina longispina maritima* and *Evadne nordmanni* were of some importance as prey in summer months, where in July 2002 up to 40% of the diet consisted of cladocerans, largely of *Podon* spp.

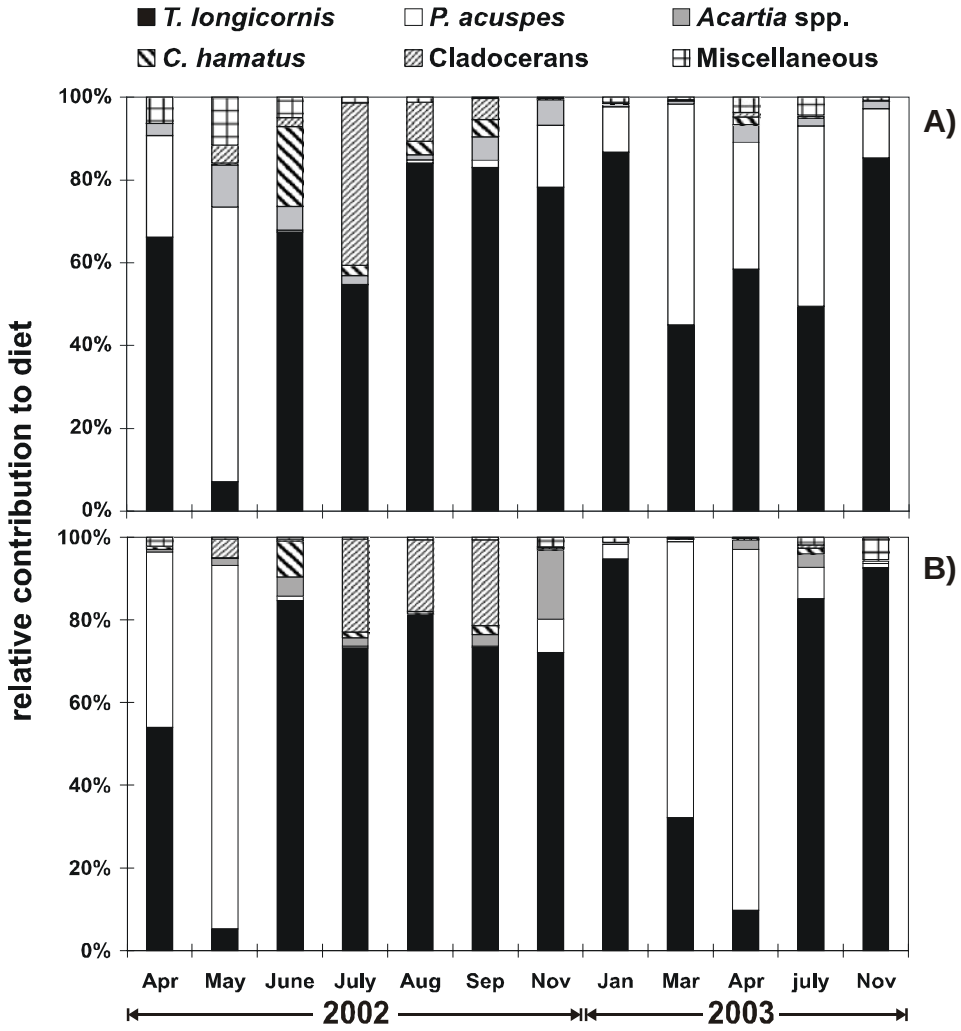

Figure 5) Seasonal development of the average diet composition (% by numbers) for sprat (A) and herring (B).

There was a clear trend towards later copepodite stages and adults in the stage-specific diet composition for the four major calanoid copepods *T. longicornis*, *P. acuspes, C. hamatus and Acartia* spp. in the stomachs of sprat (figure 6 A, C, E, G).
Almost exclusively adults (c6) and c5 copepodites of *Acartia* spp. were consumed (figure 6 A). Some c4 were consumed, but c1-3 copepodites were rarely observed. In *C. hamatus* (figure 6 B) in both years from April to August mainly c4-6 stages were consumed, whereas in winter very few adults were consumed and the proportion of c3 and c4 increased. In *P. acuspes* mainly adults and c5 were consumed from April to July (figure 6 E). From August on through the winter additionally c4 and c3 were consumed, reducing the amount of adults consumed to lowest numbers in November at 2% of the ingested *P. acuspes*. From March on 50% of the ingested stages consisted of adults. In comparison with the stage-specific copepod diet of herring a higher extent of adults were observed in *P. acuspes*. In 7 out of 12 investigated months was the relative share of adults higher in sprat than in herring.

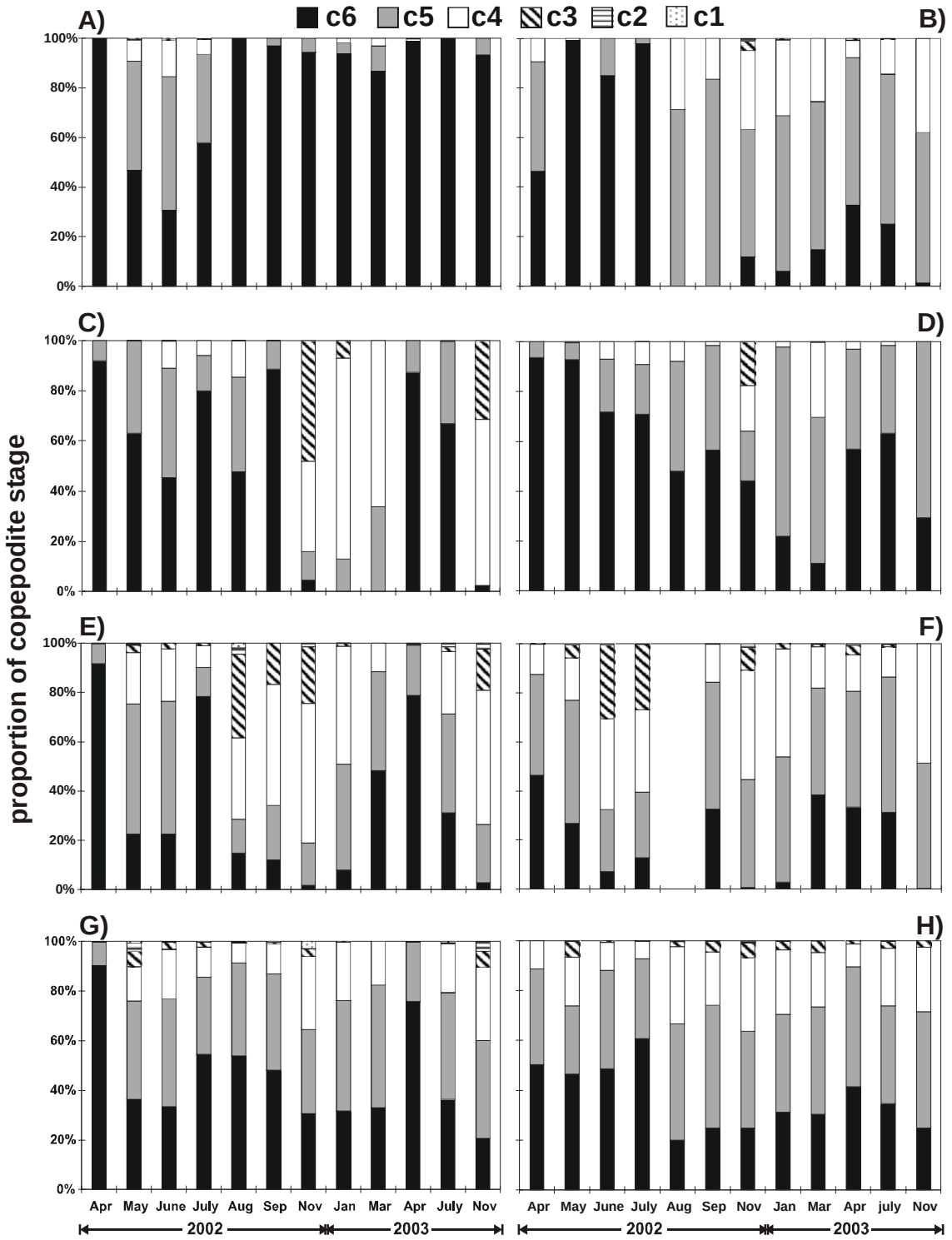

Figure 6) Seasonal development of the proportion of copepodite stages for *Acartia* spp. (A, B), *C. hamatus* (C, D), *P. acuspes* (E, F) and *T. longicornis* (G, H) in the diet of sprat (graphs on the left side) and herring (graphs on the right side).

In *T. longicornis,* adults were consumed through the entire year at values around 40 to 50% relative proportion of the ingested *T. longicornis* stages. In most months approx. 30% of the ingested *T. longicornis* stages were c5. Additionally c4 and c3 were consumed to a lesser degree. In April of both years only adults (2002: 90%, 2003: 76%) and c5 were consumed.

Mainly cod and sprat eggs were found in the stomachs of sprat (figure 10 A). The highest average number of cod eggs per stomach was 18 in July 2003, where 27% of all sampled sprat stomachs contained cod eggs. The highest average number of sprat eggs was 9 in May 2002, where 32% of all sampled sprat stomachs contained sprat eggs.
The diet composition in relation to fish size showed no clear trend (figure 8). The most important prey items were consumed irrespective of fish size, with variations that can be explained by the low numbers of analysed stomachs in smallest (8 cm) and largest (15 cm) size class.

Herring

As in sprat the most important prey species by numbers was *T. longicornis,* followed by *P. acuspes* (figure 5 B). *T. longicornis* was dominating the diet (> 70% relative contribution to diet) in 8 of 12 analysed months (from June 2002 to January 2003 and July + November 2003). In May 2002 and March + April 2003 the diet of herring consisted to a large extent of *P. acuspes* (May 02: 88%, March 03: 67%, April 03: 87%). As in sprat the diet of herring consisted of up to 22 % of cladocerans in July, August and September 2002 (mainly *Bosmina longispina maritima*). The other two calanoid copepods were of minor importance. Highest relative contribution to the diet for *C. hamatus* (9%) was reached in June 2002 and in November 2002 for *Acartia* spp. with 17%. Larger prey species were only observed in November 2002 and 2003 where mysids were consumed (1.3 and 4.4% relative contribution to diet).
As in sprat there was a trend towards older copepodite stages and adults in the stage-specific diet composition for the four major calanoid copepods *T. longicornis*, *P. acuspes, C. hamatus* and *Acartia* spp. in the stomachs of sprat (figure 6 A, C, E, G).
From April to July 2002 almost exclusively adults or c5 stages of *Acartia* spp. were consumed. From August 2002 on c5 and c4 stages were the dominating stages (figure 6 B). In comparison to sprat, the relative contribution of adults to the diet of herring starting in August 2002 was much lower. In *C. hamatus* almost exclusively adults were consumed in April and May 2002, however their share declined in proportion towards March 2003 (figure 6 D). In contrast, the proportion of consumed c5 increased over the same period. In *P. acuspes* mainly adults, c5 and c4 were consumed (figure 6 F). The highest amounts of adults were observed in April 2002 representing 46% of all ingested *P. acuspes*. In August 2002 no *P. acuspes* were found in the stomachs of herring. In November of both 2002 and 2003 nearly no adults were observed in the diet (0.7 and 0.3% respectively of all ingested *P. acuspes*). In June and July 2002 a large amount of the ingested *P. acuspes* stages were c3 with 30 and 26%, respectively. The *T. longicornis* diet consisted mainly of adults, c5 and c4. From April 2002 to July 2002 50 to 60% of the ingested *T. longicornis* stages were adults (figure 6 H). The importance of adults was lower in the following period, ranging from 20 to 40%, whereas the values for c5 ranged from 40 to 50% and the values for c4 ranged from 20 to 30% for the same period.
Mainly cod and sprat eggs were found in the stomachs of herring (figure 10 B). The highest average number of cod eggs per stomach was 115 in July 2003, where 52% of all sampled herring stomachs contained cod eggs. The highest average number of sprat eggs was 8 in June 2002, where 5% of all sampled herring stomachs contained sprat eggs. In May 2002 45% of all sampled herring stomachs contained sprat eggs with an average number of 5 eggs per stomach.
The diet composition in relation to fish size showed no clear trend for the most important prey species per month (figure 9). One exception was November 2003, where mysids were present in the stomachs of size class 14/15 cm at 0.5% relative contribution by

numbers, with an increasing percentage with increasing size to 67% in 24/25 cm herring, while in parallel the numbers for *T. longicornis* decreased.

Weighted mean copepodite stage (*WMCS*)

The weighted mean copepodite stages (*WMCS*) of the most important copepods *T. longicornis*, *P. acuspes*, *C. hamatus* and *Acartia* spp. (figure 7) ranged between 3 and 6. We plotted the *WMCS* against the weighted share (as estimated by numbers) of the copepod species of the stomach fullness (% *BW*) only for months with almost entirely consumed copepods. The highest *WMCS* was observed for sprat in April of both years 2002 and 2003, where at most stations the values varied between 5.5 and 6 for the four copepod species. The lowest *WMCS* were observed in May 2002 and in winter (November and January) where values of 3 were observed at certain stations. The highest share of the stomach fullness constituted of *T. longicornis* and *P. acuspes*. The highest values for herring were also reached in April of both years where at most stations the values outreached 5. The lowest values were observed in June 2002 where values for *P. acuspes* were as low as 3.4 and not higher than 4.7 at any station. As in sprat did the highest share of the stomach fullness constitute of *T. longicornis* and *P. acuspes*. The *WMCS* and stomach fullness of herring and sprat were rather similar for the displayed months. In April of 2002 and 2003 were both *WMCS* and stomach fullness of sprat higher than that of herring.

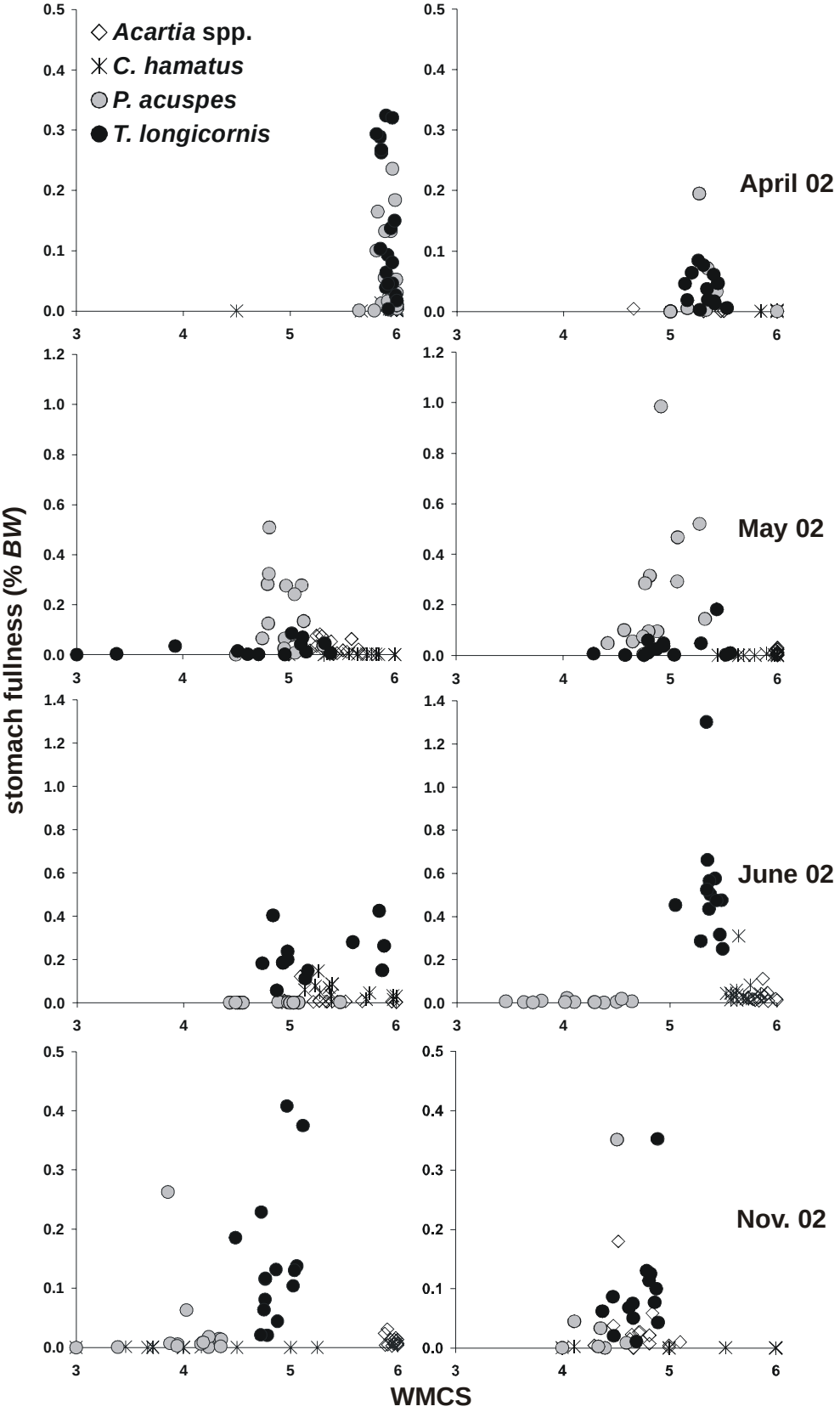

Figure 7) Monthly variation in weighted mean copepodite stage (*WMCS*) plotted versus share of stomach fullness at each sampling station for major copepods *P. acuspes* ,*T. longicornis*, *C. hamatus* and *Acartia* spp. Left column of graphs indicate results for sprat and right column for herring.

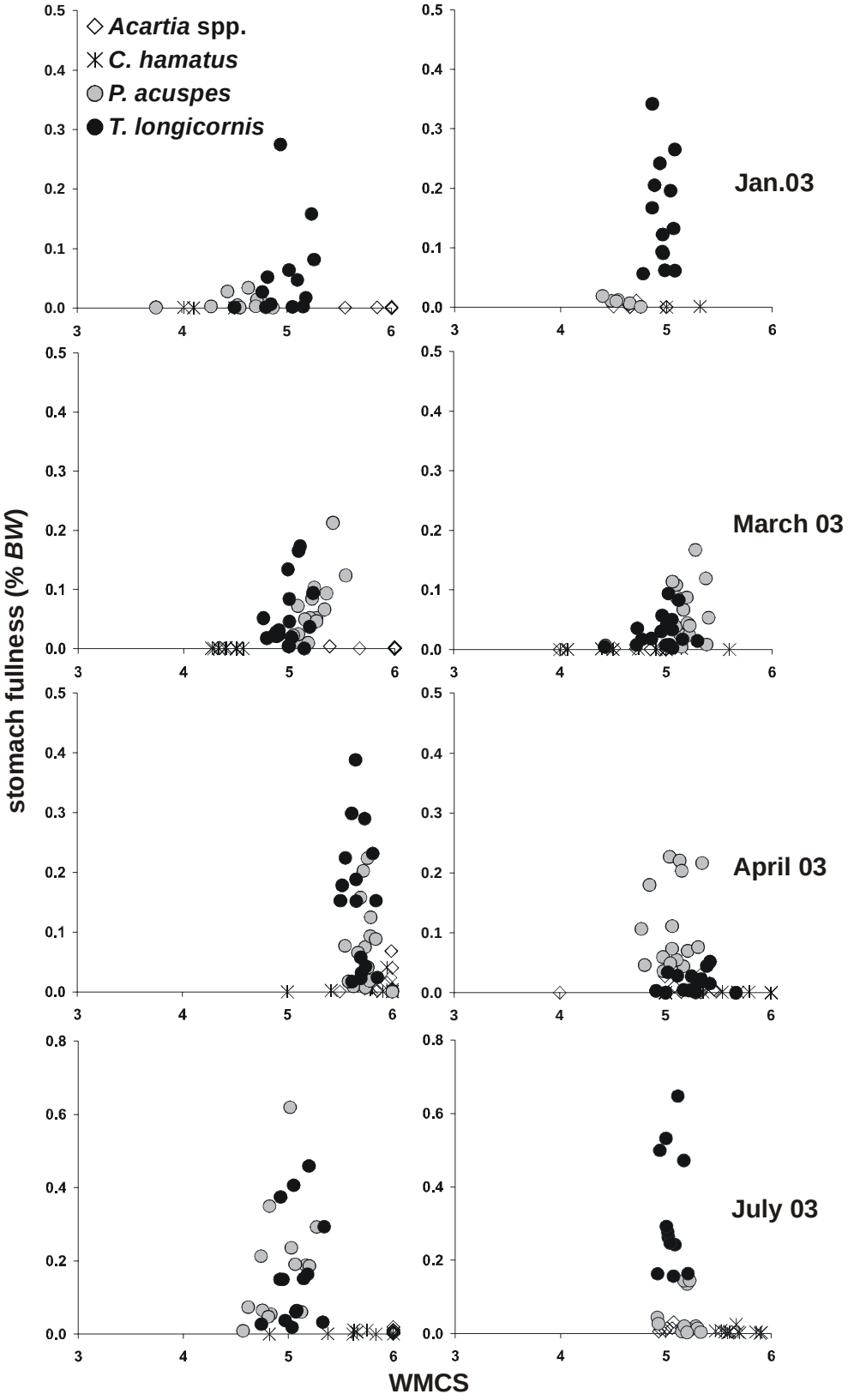

Figure 7 continued) Left column of graphs indicate results for sprat and right column for herring.

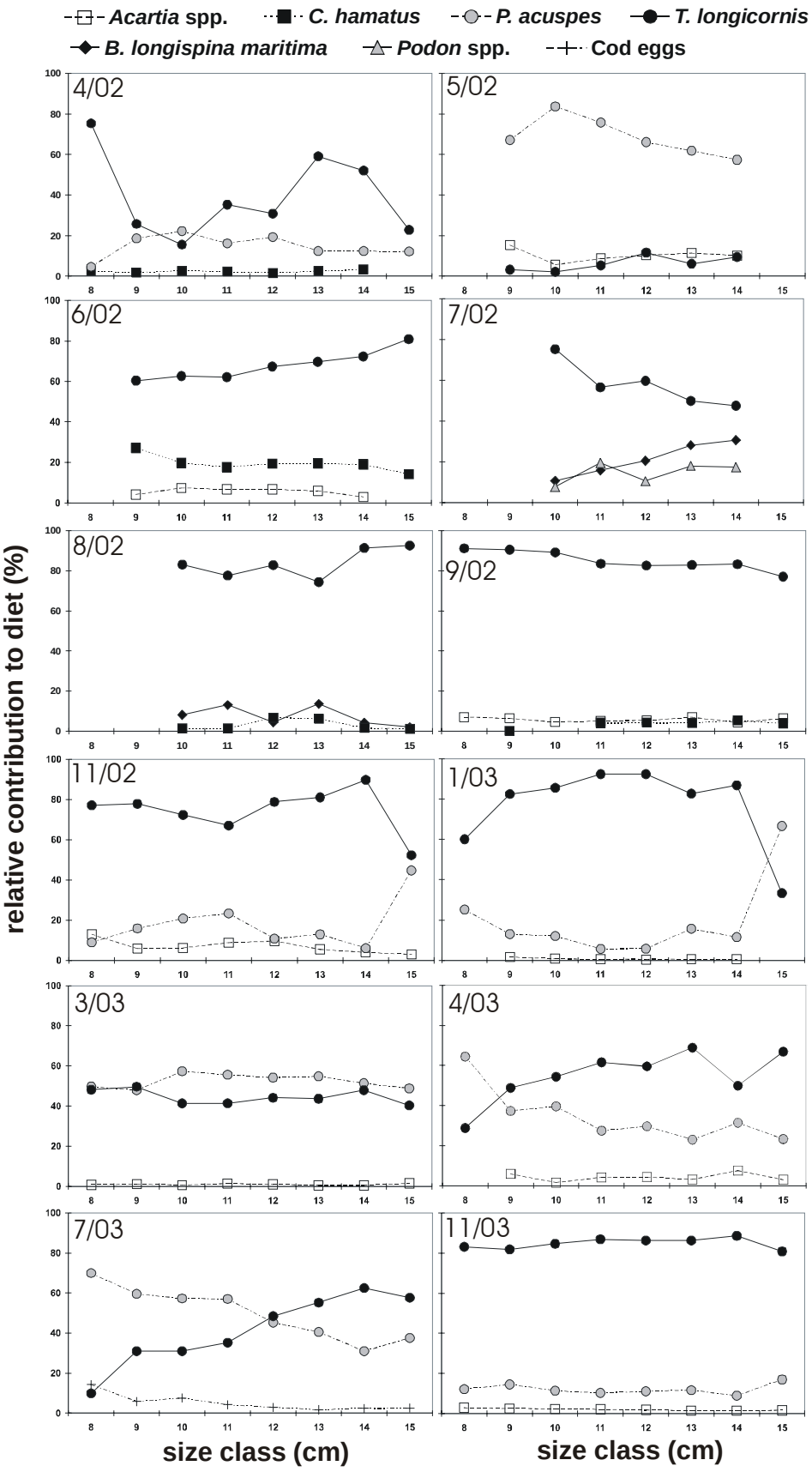

Figure 8) Relative contribution (by number of individuals) of prey species by size class of sprat. Each month (upper left corner in each graph) three species are presented that were found at highest numbers.

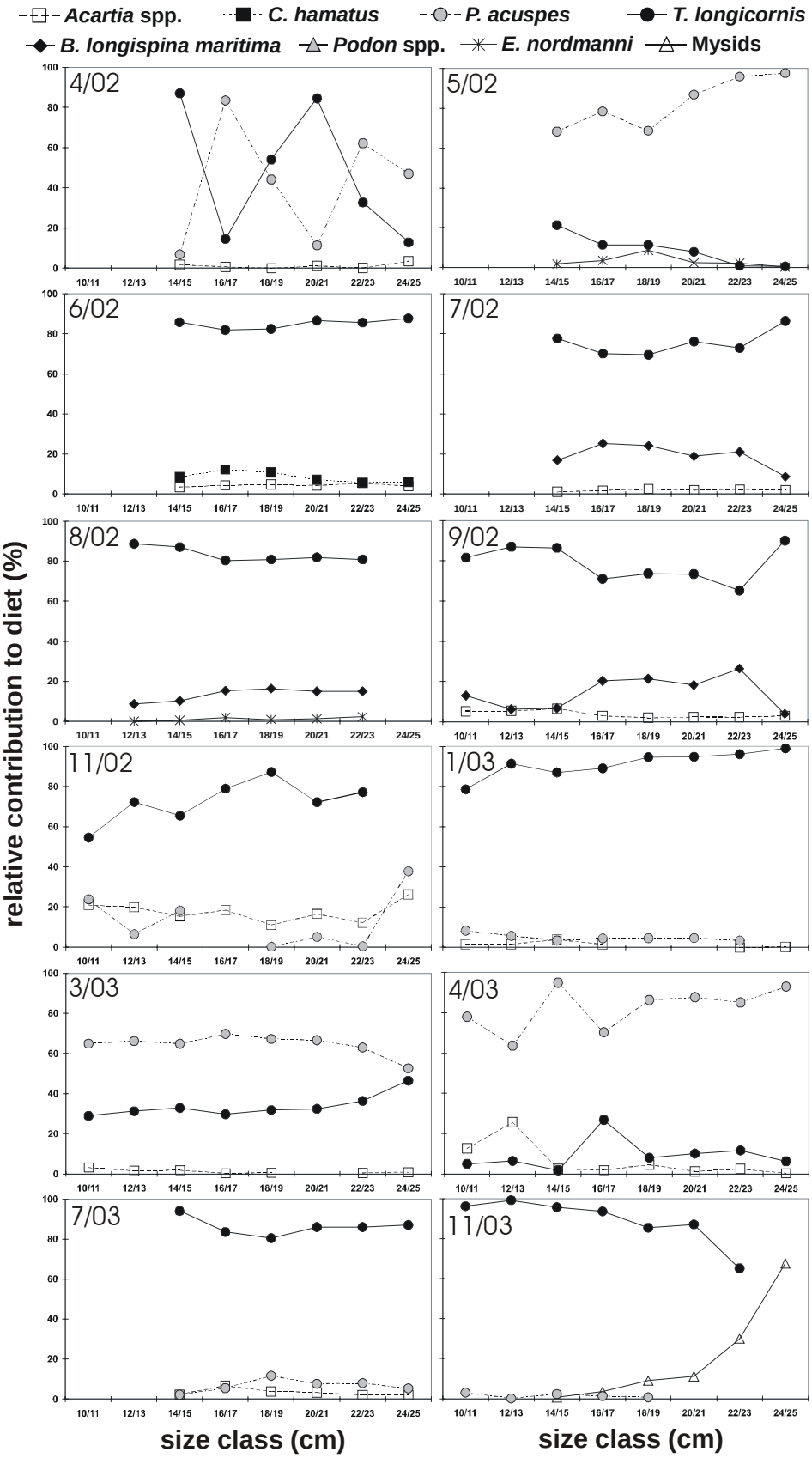

Figure 9) Relative contribution (by number of individuals) of prey species by size class of herring. Each month (upper left corner in each graph) three species are presented that were found at highest numbers.

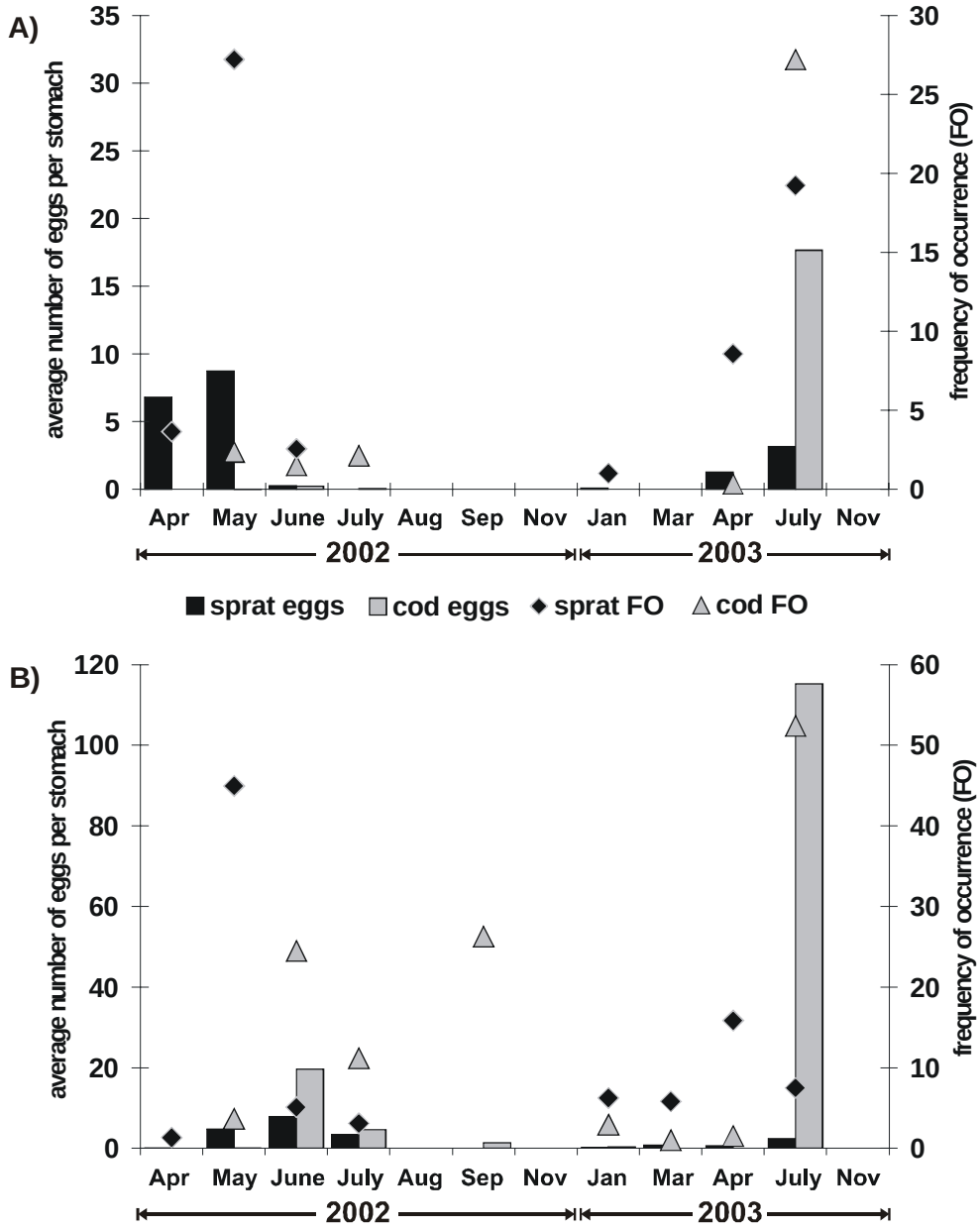

Figure 10) Average number of cod and sprat eggs per stomach and month for (A) sprat and (B) herring and frequency of occurrence (*FO*) of cod and sprat eggs in the stomachs.

Frequency of occurrence (*FO*)

Sprat

T. longicornis was found in most of the investigated stomachs (*FO* > 70%, figure 11 A), only in May and September 2002 and January 2003 *T. longicornis* was found in less than 60% of the analysed stomachs. In the other copepods more pronounced seasonal fluctuations were observed. The copepods *P. acuspes, C. hamatus* and *Acartia* spp. were found in less than 20% of analysed stomachs at some time periods. In *P. acuspes* lowest values (*FO* < 20%) were observed in June and July 2002 and highest values (*FO* > 80%) were observed in May 2002 and March, April and June 2003. In *C. hamatus* low

values (*FO* < 20%) were observed in November 2002 until March 2003 and in July and November 2003. The highest value (*FO* > 80%) was observed in June 2002. In *Acartia* spp., lowest values (*FO* < 30%) were observed in January and March 03 and highest values in September and November (*FO* > 80%).
The cladocerans *Bosmina longispina maritima*, *Evadne nordmanni* and *Podon* spp. were found in the stomachs according to a pronounced seasonal cycle with high values in July, August and September 2002 of up to 80% *FO* for *Bosmina longispina maritima* and *Podon* spp. (figure 11 C). The highest value for *E. nordmanni* was observed in June with 52%. In winter very low values (*FO* < 4%) were observed for the cladocerans.
In total, *Acartia* spp. were found in 50%, *C. hamatus* in 25%, *P. acuspes* in 65% and *T. longicornis* in roughly 80% of all analysed stomachs (figure 12). The cladocerans *B. longispina maritima*, *E. nordmanni* and *Podon* spp. were found in 15 to 20% of all stomachs. In comparison with herring, the copepods *Acartia* spp., *P. acuspes* and *T. longicornis* were found in more stomachs.

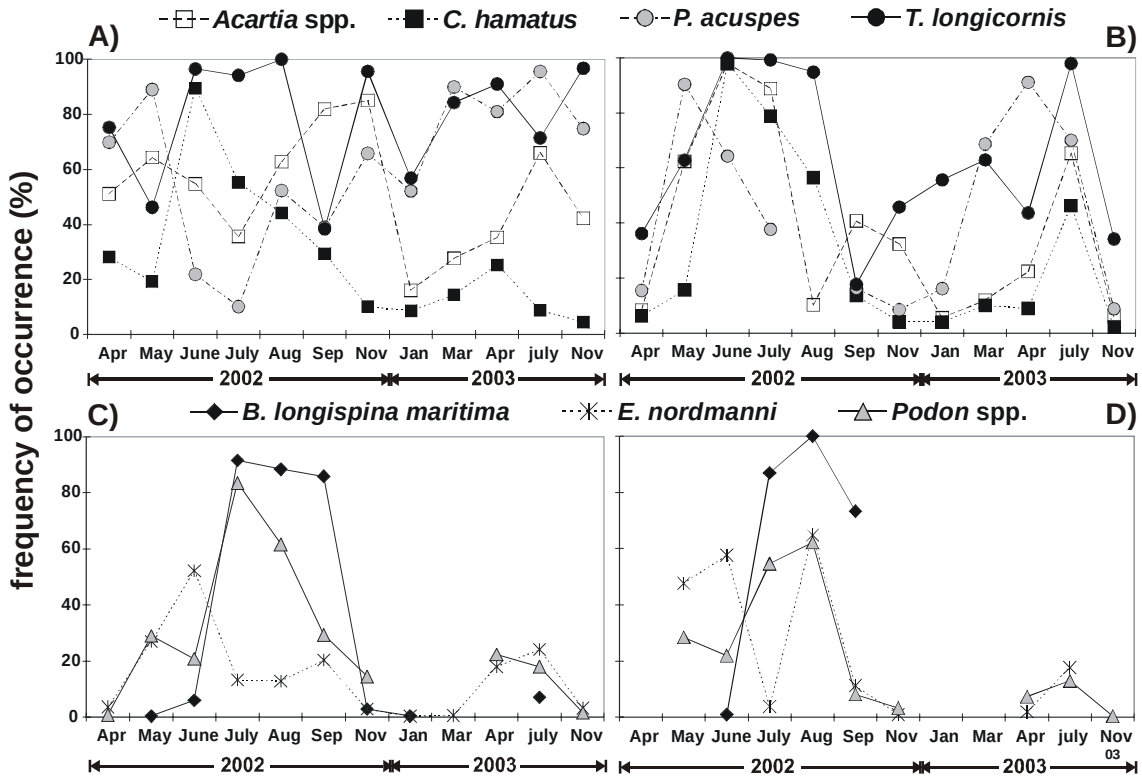

Figure 11) Frequency of occurrence (*FO*) of major copepods and cladocerans in the diet of sprat (A, C) and herring (B, D) for investigated months.

Herring

The copepod *T. longicornis* was found in most stomachs in summer (*FO* = 90-100%) and in fewest stomachs (*FO* < 20%) in September 2002 (figure 11 B). From November 2002 until April 2003 was *T. longicornis* found in roughly half of all stomachs (*FO* = 40-60%). The values for *P. acuspes, C. hamatus* and *Acartia* spp. were all relatively low in April (*FO* < 20%) and September 2002 (*FO* < 40%), whereas the values for all copepods were high in June 2002 with nearly 100% for *T. longicornis, C. hamatus* and *Acartia* spp. and 65% for *P. acuspes.*
The cladocerans *Bosmina longispina maritima*, *Evadne nordmanni* and *Podon* spp. were found in the stomachs of herring according to a similar seasonal cycle as in sprat, with highest values for *B. longispina maritima*, *E. nordmanni* and *Podon* spp. in August

2002 (figure 11 D). No cladocerans were found in any stomachs in January and March and additionally no *B. longispina maritima* were found in any stomachs in April, July and November 2003.
In total, *Acartia* spp. was found in 35%, *C. hamatus* in 25%, *P. acuspes* in 40% and *T. longicornis* in roughly 60% of all analysed stomachs (figure 12). The cladocerans *B. longispina maritima* and *E. nordmanni* were found in 10 to 15% of all stomachs. *Podon* spp. was only found in approx. 5% of all stomachs.

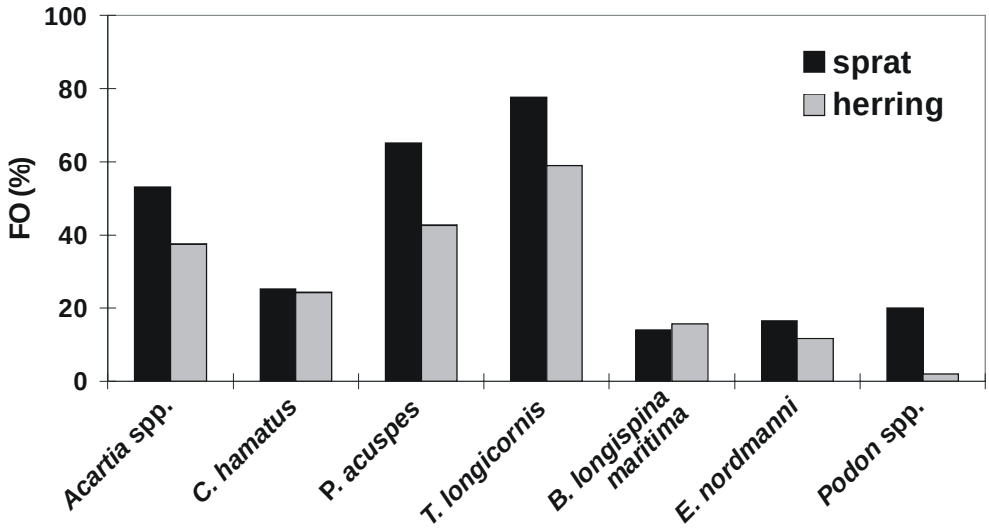

Figure 12) Frequency of occurrence (FO) of major copepods and cladocerans in the diet of sprat (black columns) and herring (grey columns) over the entire investigated period.

Niche overlap

There was a high niche overlap (*NO*) as estimated from the prey-specific diet composition between herring (small and large) and sprat in most of the sampled months, with niche overlaps of 80 to 90% (figure 13 A). In both April 2002 and 2003 the *NO* was below 50% and in July 2003 the *NO* was 60%. The highest *NO* was observed in August 2002 with 91%. The copepodite stage-specific NO between herring (small and large) and sprat for the most important calanoid copepods, as calculated from the relative proportions of copepodite stages within one species, differed depending on the species. The *NO* in *Acartia* spp. copepodites was highest in July 2002 with 60% and lowest in August 2002 with 0% (figure 13 B). The value was influenced by the very low numbers of *Acartia* spp. observed in the stomachs in August 2002. The *NO* in *C. hamatus* copepodites was over 60% except for the winter, where the *NO* was below 20% (figure 13 C). In *P. acuspes* highest *NO* was observed in May 2002 with 94%, declining to lowest *NO* in July with 34% (figure 13 D). In *T. longicornis* the *NO* was high at 84 to 94% (figure 13 E) with the exception of both April 2002 and 2003 and August 2002, where the *NO* dropped to values from 65 to 61%.
In general did the niche overlaps of sprat and smaller herring (< 20 cm) and sprat and larger herring (> 20 cm) show similar fluctuations as the niche overlaps of sprat and all herring. The *NO* of small and large herring was with few exceptions, highest during the investigated period.

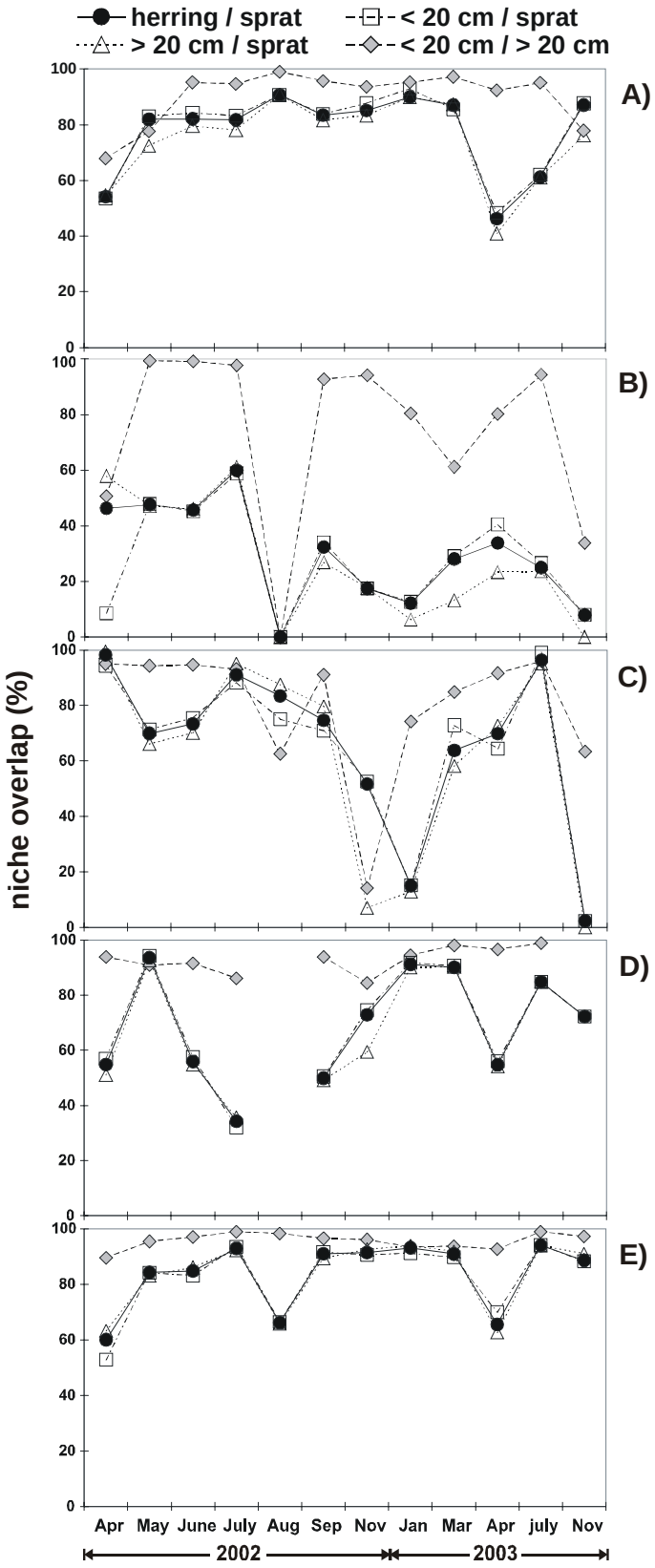

Figure 13) Niche overlap (%) of herring and sprat, small herring (< 20 cm) and sprat, large herring (> 20 cm) and sprat and of small and large herring for total diet (A) as calculated by prey species and by species-specific copepodite stages of *Acartia* spp. (B), *C. hamatus* (C), *P. acuspes* (D) and *T. longicornis* (E). Values are presented on a monthly basis.

Discussion

Bornholm Basin as a feeding ground

Proportion of feeding fish

The proportion of fish that had food in the stomachs was high, or in other words the amount of empty stomachs was low for the entire investigated period for both sprat and herring. With the exception of January and March in sprat and September to March in herring roughly 100 per cent of clupeid stomachs contained food. Similar high numbers of sprat containing food have been observed during daytime by Shvetsov et al. (1983) in the Eastern and South-Eastern part of the Baltic Sea. These numbers remain high compared to De Silva (1973), who observed that only 40 to 50% of the sampled sprat and herring at the Scottish west-coast were feeding from November to January. The results of the study of Last (1987) from the English East-coast indicated that in the winter months less than 25% of the sampled sprat were feeding, in some months all sprat ceased feeding, and that less than 50% of the sampled herring had fed.
Our results indicated that sprat and herring occurring in the Bornholm Basin nearly at all investigated periods were feeding.

Stomach content and fullness

Sprat

Despite the fact that the proportion of feeding sprat was high over the investigated period, the stomach contents and stomach fullness were similar to previous observations from the Baltic. The mean stomach content did not exceed 0.08 g wet weight (g *WW*) at any time, independent of sprat size. Working in subdivisions 26 and 28 (Gdansk deep and Gotland basin), Möllmann & Köster (1999) observed average stomach contents for sprat that ranged from 0.012 g *WW* in January 1978-1990 to 0.045 g *WW* in August 1978-1990. In comparison with the results of Köster & Möllmann (2000) from surveys from April to July for several years (1988-1995) in the Bornholm Basin our observed average stomach contents were slightly lower. In April/June 1994 the highest observed average stomach contents in sprat were approx. 0.1 g *WW* and lowest 0.01 g *WW*. The highest value observed overall was 0.14 g *WW* average stomach content in July 1991.
For a better comparison with the results of other authors and regions we need to address the stomach fullness. The stomach fullness of sprat per month rarely exceeded 0.4% *BW*. Our observed values were not low in comparison to the results from other parts of the Baltic Sea. In the Central Baltic Sea (Gdansk Deep, Gotland Basin) for the years 1977-1999, Möllmann et al. (2004) observed average stomach fullness for sprat of 0.19% in winter to 0.3% in summer. Shvetsov et al. (1983) observed an average stomach fullness in the eastern and southeastern Baltic of 0.2 to 0.7% *BW* during the day. In a 24 h-fishery within inshore areas of the Scottish coast, De Silva (1973) observed an average stomach fullness of 0.4 to 0.7 % *BW* during the day. Higher average stomach fullness (up to 2.8% *BW*) was observed in coastal areas of the Black Sea for Mediterranean sprat (*Sprattus sprattus phalericus*) by Sirotenko & Sorokalit (1979). The results of these various studies lead to the question if sprat feeds more intensively in some regions as opposed to others or whether feeding intensity is similar in most regions and differences were due temporal (decadal) changes. Möllmann et al. (2004) observed in the Central Baltic sea a decreasing average stomach fullness in sprat from the 1980´s to early 1990´s with a slightly increase from there on. Additionally,

during the same period, Cardinale et al. (2002) observed a decrease in growth of sprat in the western Baltic Sea. This decrease was related to a combination of an enhanced density-dependent competition due to an increased sprat stock (Cardinale & Arrhenius 2000, Möllmann & Köster 2002) and the effect of changing temperature and salinity levels either directly via metabolism or indirectly via changes in the structure and/or abundance of the zooplankton community. There appears to be a time trend in the stomach fullness of sprat. However, Köster & Möllmann (2000) observed no decrease in stomach contents in the Bornholm Basin from 1988 to 1995. This result suggests that sprat feed more intensively in other areas. The question of whether sprat feeds more intensively in other regions of the Baltic is not easy to answer, as few data on stomach content and fullness from coastal areas are available. Arrhenius (1998) observed stomach fullness of up to 1.7% *BW* (August) in young sprat (max. 2.0 g *WW*) in a coastal area of the Baltic Sea (subdivision 27). These fish were not longer than 50 mm and not comparable in weight with our sampled fish, but still give us a hint about areas in which feeding is more intensive. The work of Sirotenko & Sorokalit (1979) showed highest average stomach fullness for adult Mediterranean sprat in highly productive coastal areas of the Black Sea. Irrespective of the fact that the Black Sea is a different water body with differing hydrographic traits, this result leads to the conclusion that the stomach content and fullness of adult sprat needs to be studied in coastal areas to relate the results from the feeding studies in the basins to coastal areas.

Herring

The stomach contents and fullness of herring were similar to previously observed studies from the Baltic Sea. The average stomach content did not exceed 0.5 g wet weight (g *WW*) at any time, independent of herring size. The average stomach contents ranged mainly between 0.1 and 0.3 g *WW*. Similar stomach content values have been observed in the Baltic Sea. In subdivisions 26 and 28 (Gdansk Deep and Gotland Basin), Möllmann & Köster (1999) observed average stomach contents for herring that ranged from 0.036 g *WW* in January to 0.2 g *WW* in April. Data for different years (1988-1995) from the Bornholm Basin (Köster & Möllmann 2000) indicated that average stomach contents ranged between approx. 0.15 g *WW* in April and 0.54 g *WW* in July 1991. As in sprat we switch to the consideration of stomach fullness for a better comparison with the results from other studies. In our observations, average monthly stomach fullness never exceeded 0.75% *BW*, and was mainly below 0.5% *BW*. Möllmann et al. (2004), working in the Central Baltic Sea (Gdansk deep, Gotland basin) for the years 1977-1999, observed average stomach fullness for herring of 0.1% *BW* in winter to 0.2% *BW* in summer: values that are somewhat lower than our observations. Higher stomach fullness has been observed for herring in different water bodies including 0.4 to 1.2% *BW* in August in inshore waters of the west coast of Scotland (De Silva 1973). However, these numbers resulted from 24 h-fisheries, and thus do not necessarily represent mean values obtained over a month. Distinctly higher values were observed by Huse & Toresen (1996) in the Barents Sea, where herring in early summer exhibited a stomach fullness of 0.7 to 4% *BW* depending on the body length, the smaller herring having a higher stomach fullness. As in sprat the same questions concerning a possible time trend or different feeding locations have to be answered. In herring a pronounced decrease in the weight at age (WAA) between 1986 and 1996 has been observed (Cardinale & Arrhenius 2000). Of the three hypotheses attempting to explain the decrease of WAA (Cod predation hypothesis, Migration hypothesis, Feeding condition hypothesis, see Cardinale & Arrhenius 2000) the feeding condition hypothesis was the most supported by field data. The decrease in WAA of herring was partly caused by an enhanced intra- and interspecific competition as a result of the increase of

the sprat stock and the change in food availability, especially a decrease in population size of *Pseudocalanus* sp. (Cardinale & Arrhenius 2000, Cardinale et al. 2002, Möllmann et al. 2004, 2005). The stomach fullness of herring in the Central Baltic decreased from the 1980´s to early 1990´s and then slightly increasing again (Möllmann et al. 2004). However, a decrease in stomach content from 1988 to 1995 was not observed in the Bornholm Basin (Köster & Möllmann 2000). The Bornholm Basin is considered a major feeding ground for herring (Parmanne et al. 1994) that migrate to the area after spawning and stay from July to December (Aro 1989).
The diet composition and niche or dietary overlap of herring and sprat will clarify the extent of interspecific competition.

Fish size-dependent feeding

From April to June 2002 a trend in sprat stomach fullness was observed. The stomach fullness decreased with increasing length, a trend that has been observed for sprat in the central Baltic Sea (Möllmann et al. 2004) and for Mediterranean sprat (Sirotenko & Sorokalit 1979). In the other investigated months, no clear trend was observed. The same was true for herring, where no clear trend was observed over the investigated period with the exception of April 2002 and 2003 where the stomach fullness increased with increasing length (2002) and the opposite case was observed in 2003. When comparing the stomach fullness of similar-sized herring and sprat (10 - 15 cm), no distinct difference was observed from 10 to 13 cm, but stomach fullness of herring was twice that of sprat in several months for fish within the 14 to 15 cm length range. The result leads to the conclusion that young herring are able to exploit the feeding environment more effectively than adult sprat.
We did not observe size-dependent feeding in sprat, as all size-classes preyed on similar diets at similar proportions (based on numbers). In herring, size-dependent feeding was observed in November 2003 when the amount of ingested *Mysis mixta* increased with increasing body length. Casini et al. (2004) observed, that sprat and small herring (< 13 - 15 cm) were strictly zooplanktivorous and larger herring (> 15 - 20 cm) were essentially nektobenthos feeders (preying upon on *M. mixta* during autumn and amphipods and polychaetes during the winter) in the Bornholm Basin. We cannot confirm this observation, since we only observed that mysids were consumed in high numbers in November 2003. In the remaining months mysids were of minor importance. It should be noted, that the proportions of the diet compositions of sprat and herring in this study are based on numbers of prey items and not on weights. If they were based on weights, the results would to a high probability show a more pronounced switch to the feeding of nektobenthos (e.g., *M. mixta*, polychaetes and amphipods) by large herring in autumn and winter as observed by Casini et al. (2004).
Last (1989) did not find any marked differences between the diets of smaller and larger herring (10 - 34 cm) in the North Sea. Dalpadado et al. (2000) did not observe clear variations in the diet of Norwegian spring spawning herring (19 - 40 cm) with size. Last (1987) observed in coastal waters of the North Sea though, that juvenile herring and sprat had similar diets of copepods in fish up to 7 cm. Larger herring took increasingly larger food items as they grew, e.g. mysids and post-larval sprat, whereas larger sprat continued to feed on copepods.

Diet and niche overlap

We did not observe any surprising results concerning the diet composition of herring and sprat. Both herring and sprat were mainly zooplanktivorous. The most important prey species were the two calanoid copepods *T. longicornis* and *P. acuspes* over the

annual cycle along with the cladocerans *B. longispina maritima* and *Podon* spp. in summer. This observation is typical for the Central and South-central Baltic Sea, where sprat and herring mainly prey on *P. acuspes* in winter and spring, then switching to *T. longicornis* for the rest of the year and cladocerans in summer (Szypula et al. 1997, Möllmann & Köster 1999, Casini et al. 2004, Möllmann et al. 2004). *P. acuspes* is in its main reproductive period in March to May when highest biomasses are reached (Möllmann et al. 2004). The high percentage of cladocerans in the diet of sprat and herring in summer was due to the fact that cladocerans are generally at their seasonal peak in abundance in summer in the Central Baltic (Möllmann et al. 2002). Cladocerans show weak escape responses (Viitasalo et al. 2001), and are captured with greater success than copepods by visual-feeding planktivores (Drenner et al. 1978), so that a switch to consuming cladocerans in summer appears energetically beneficial.

Both sprat and herring were preying mainly on c5 and c6 of *T. longicornis* and *P. acuspes*. From late summer on to the winter additionally c4 and c3 were consumed. The observation of Möllmann & Köster (2002) that herring were forced to switch from consuming mainly c5/c6 of *P. acuspes* and *T. longicornis*, to prey on c2 of *T. longicornis* due to competition with an increased sprat stock in the Gotland Basin can not be confirmed by our results from the Bornholm Basin. The proportion of c2 in the diet of both clupeids was neglectable.

Frequency of occurrence (*FO*) data indicate the importance of a prey species to the entire population of feeding individuals. The highest values of *FO* were reached by both sprat and herring in summer for *T. longicornis* where up to 100% of the inspected stomachs contained this copepod and for *B. longispina maritima* where between 70 and 90% of the stomachs contained this cladoceran. This indicates that these species were important prey items for the entire feeding population and not only for distinct parts of the population, that may have been specialising on certain prey types.

The eggs of mainly cod and sprat were found in the stomachs of herring and sprat. The eggs of flounder (*Platichthys flesus* L.) and fourbeard rockling (*Enchelyopus cimbrius* L.) were only found sporadically. Köster & Möllmann (1997) observed that the predation on cod eggs and to a lesser extent also on sprat eggs by sprat and herring was a substantial source of mortality in the Bornholm Basin (1988 to 1995). They observed for both sprat and herring on average between 50 and 60 cod or sprat eggs per stomach in May to August. Our observed maximum was reached in July 2003, where herring stomachs contained on average 115 cod eggs and sprat stomachs on average 18 cod eggs. This is a rather high number compared to the observation of Köster & Möllmann (1997) considering that half (52%) of the analysed herring stomachs and about one fourth (27%) of the analysed sprat stomachs contained cod eggs. July 2003 was exceptional, as the second most cod eggs in the stomachs were observed in June 2002 with 0.2 on average in sprat and 20 on average in herring. In May 2002 did the sprat stomachs contain on average 9 sprat eggs and in June 2002 did the herring stomachs contain 5 sprat eggs.

It has been observed in the North Sea (Last 1989) that occasionally the diet of herring consisted up to 15% (by numbers) of fish eggs. Ellis & Nash (1997) observed in the Irish Sea in March that up to 55% (by volume) of the diet consisted of plaice eggs. High numbers of fish eggs were occasionally observed in our study, but no fish larvae were observed in the analysed stomachs.

There was a high diet niche overlap in the Bornholm Basin between sprat and herring. The overlap was in 9 out of 12 sampled months at or above 80% indicating a high similarity in the diets. Möllmann et al. (2004) estimated lower overlaps of a maximum of 65.6% for the period 1996-1999 in the Gotland Basin and Gdansk Deep. Mysids were more important in the diet of herring in that area, indicating a better availability of this prey. They estimated the highest overlaps between large sprat and small herring. We

did not find severe differences in the niche overlap between sprat/smaller herring and sprat/larger herring.
High similarity in the diet has even been observed in other areas. De Silva (1973) observed off the west coast of Scotland, that diets of 0-group herring and sprat were almost identical and also older herring and sprat fed on more or less the same food items, mainly crustaceans, with copepods contributing the major share. There was a high diet niche overlap between herring and sprat in the copepod stage-specific overlap. The copepodite stage-specific overlap in *T. longicornis* was in 9 out of 12 sampled months at or above 80%, the copepodite stage-specific overlap in *P. acuspes* was mainly varying between 50 and 90%, meaning that both sprat and herring tend to feed on the same copepodite stages of their main copepod prey species. There is only a small number of prey species available in the Baltic Sea (Postel 1996). This fact and the high qualitative overlap in the diets of sprat and herring indicate an intensive competition for food resources in the Bornholm Basin. High prey densities may cause a high diet overlap between species since there is no need to partition the available resources (Pianka 1982). However, the low stomach contents and fullness of herring and sprat in relation to other areas along with the decrease in WAA of herring and sprat in the 1990´s indicate a strong competition for food in the Bornholm Basin. One possible way to avoid this interspecific competition would be to feed at different times of the day or at different depths (De Silva 1973), but it was observed by Cardinale et al. (2003) that sprat and herring feed at the same depths, although larger herring tend to migrate closer to the bottom, and both species exhibit a similar vertical migration pattern, occurring at the same time of the 24-hour cycle at the same depths. Bernreuther et al. (In Prep.) observed in a 24 h-fishery in the Bornholm Basin that sprat and herring exhibited similar diurnal vertical migrations and feeding peaks with highest average stomach contents in the afternoon.
Sprat migrate into the Bornholm Basin in spring for spawning in the water column. They spawn and feed until they leave the basin and migrate to their over-wintering areas closer to the coast (Aro 1989). Herring migrate to the coasts in late winter and early spring to spawn in shallow waters. After the spawning the adult herring migrate back to the open Baltic to their feeding grounds. Their migrations also lead them into the Bornholm Basin, where they stay from July to December (Aro 1989). By the time the herring arrive in the Bornholm Basin, the sprat population has already been feeding intensively on adult *P. acuspes* and *T. longicornis*, as indicated by the high proportion of adults in the diet, eventually reducing an important part of the adult copepods. Spring-spawning herring are in bad condition after spawning, when they migrate to their feeding areas in deep Baltic basins, where they have to refill their energy stores (Möllmann et al. 2003). It was hypothesized by Möllmann et al. (2003) that the amount of available *Pseudocalanus acuspes* in spring is the key to the observed decrease in WAA of herring in the Baltic.
In the intensive competition for food resources would the ability to feed by filtering enhance the competitiveness of herring towards sprat?

Were herring filter-feeding?

The intention of estimating the weighted mean copepodite stage (*WMCS*) for both herring and sprat at each station and month was to identify situations in which herring possibly were filter-feeding and thereby gaining a competitive advantage over sprat. These filter-feeding situations would be characterised by a lower *WMCS*, as a consequence of unselective filter-feeding, and a higher stomach fullness in comparison to sprat. Herring are known to filter-feed depending on the prey concentration, prey size and light intensity (Batty et al. 1990; Gibson & Ezzi 1985, 1990, 1992). Sprat are

considered as particulate feeders that are unable to filter-feed, but to this day to our knowledge no laboratory studies have been conducted concerning this topic. Herring is a facultative filter-feeder and applies this feeding mode in order to maximize the energy intake. The number of filter-feeding herring in the laboratory increases with increasing prey concentration (Gibson & Ezzi 1990), depending on the prey size. The larger the prey item the lower the concentration at which 50% of experimental fish were filter-feeding (e.g. *Calanus finmarchicus*: 18 l^{-1}, medium *Artemia* sp.: 114 l^{-1}; Gibson & Ezzi 1990). The application of filter-feeding in situations of high food concentrations as in plankton patches would give herring an advantage in the exploitation of the feeding environment. We did not observe this situation as *WMCS* and stomach fullness of herring and sprat were similar and in situations where *WMCS* were lower, no increased stomach fullness was observed. The conclusion of this observation is that plankton concentrations were too low so that herring did not filter-feed or to a marginal degree, not leading to an increased stomach fullness.

Conclusions

1) The stomach contents and fullness of sprat and herring in the Bornholm Basin were similar to results from other areas of the Baltic sea proper, but low in comparison to other water bodies, indicating that, to support annual growth observed for these populations, sprat and herring must eventually feed more intensively in other regions, e.g. coastal regions.
2) We did not observe an influence of sprat size on diet composition. In herring we observed an influence of fish size on diet composition only in November 2003, where with increasing length an increasing number of mysids were observed in the stomachs.
3) The high diet niche overlap (in 9 out of 12 months > 80%) as estimated by species and stage-specific of most important copepods (*Acartia* sp., *C. hamatus*, *P. acuspes* and *T. longicornis*) indicated a very intensive competition for food resources.
4) There are indications from the estimation of the weighted mean copepodite stage (*WMCS*) that plankton concentrations were too low for herring to exhibit filter-feeding during the investigated period and therefore could not gain a competitive advantage over sprat in the exploitation of the feeding environment.
The results of this study will be used to estimate the daily consumption rates of clupeids in the Bornholm Basin.

References

Aro, E. (1989). A review of fish migration patterns in the Baltic. Rapport Procès-verbaux des Rèunion du Conseil International pour l´Exploration de la Mer 190, 72-96.

Arrhenius, F. (1996). Diet composition and food selectivity of 0-group herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.) in the northern Baltic Sea. ICES Journal of Marine Science 53, 701-712.

Arrhenius, F. (1998). Food intake and seasonal changes in energy content of young Baltic Sea sprat (*Sprattus sprattus* L.). ICES Journal of Marine Science 55, 319–324.

Batty, R.S., Blaxter, J.H.S. & Richard, J.M. (1990). Light intensity and the feeding behaviour of herring, *Clupea harengus*. Marine Biology 107, 383-388.

Bernreuther, M., Schmidt, J., Stepputtis, D. & Temming, A. (In Prep.). Vertically resolved prey selectivity of Baltic herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.) in the Bornholm Basin.

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

Cardinale, M., Casini, M. & Arrhenius, F. (2002). The influence of biotic and abiotic factors on the growth of sprat (*Sprattus sprattus*) in the Baltic Sea. Aquatic Living Resources 15, 273-282.

Cardinale, M., Casini, M., Arrhenius, F. & Håkansson, N. (2003). Diel spatial distribution and feeding activity of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the Baltic Sea. Aquatic Living Resources 16, 283-292.

Casini, M., Cardinale, M. & Arrhenius, F. (2004). Feeding preferences of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the southern Baltic Sea. ICES Journal of Marine Science, 61: 1267–1277.

Dalpadado, P., Ellertsen, B., Melle, W. & Dommasnes, A. (2000). Food and feeding conditions of Norwegian spring-spawning herring (Clupea harengus) through its feeding migrations. ICES Journal of Marine Science 57, 843-857.

De Silva, S.S. (1973). Food and feeding habits of the herring *Clupea harengus* and the sprat *C. sprattus* in inshore waters of the west coast of Scotland. Marine Biology 20, 282-290.

Drenner, R.W., Strickler, J.R. & O´Brien, W.J. (1978). Capture probability: the role of zooplankton escape in the selective feeding of planktivorous fish. Journal of Fisheries Research Board of Canada Vol. 35, 1370-1373.

Ellis, T. & Nash, R.D.M. (1997). Predation by sprat and herring on pelagic fish eggs in a plaice spawning area in the Irish Sea. Journal of Fish Biology 50, 1195-1202.

Flinkman, J., Vuorinen, I. & Aro, E. (1992). Planktivorous Baltic herring (*Clupea harengus*) prey selectively on reproducing copepods and cladocerans. Canadian Journal of Fisheries and Aquatic Sciences 49, 73–77.

Gibson, R.N. & Ezzi, I.A. (1985). Effect of particle concentration on filter- and particulate feeding in the herring *Clupea harengus*. Marine Biology 88, 109-116.

Gibson, R.N. & Ezzi, I.A. (1990). Relative importance of prey size and concentration in determining the feeding behaviour of the herring *Clupea harengus*. Marine Biology 107, 357-362.

Gibson, R.N. & Ezzi, I.A. (1992). The relative profitability of particulate- and filter-feeding in the herring, *Clupea harengus* L. Journal of Fish Biology 40, 577-590.

Hansson, S., Larsson, U. & Johansson, S. (1990). Selective predation by herring and mysids, and zooplankton community structure in a Baltic Sea coastal area. Journal of Plankton Research Vol.12, No.5, 1099–1116.

Huse, G. & Toresen, R. (1996). A comparative study of the feeding habits of herring (*Clupea harengus, Clupeidae,* L.) and capelin (*Mallotus villosus,* Osmeridae*,* Müller) in the Barents sea. Sarsia. 81, 143–153.

Kornilovs, G., Sidrevics, L. & Dippner, J.W. (2001). Fish and zooplankton interaction in the Central Baltic Sea. ICES Journal of Marine Science 58, 579-588.

Köster, F.W. & Möllmann, C. (1997). Predation by sprat and herring on early life stages of cod and sprat in the Central Baltic. Proceedings. Forage Fishes in Marine Ecosystems Alaska Sea Grant College Program. AK-SG-97-01, 41-69.

Köster, F.W. & Möllmann, C. (2000). Trophodynamic control by clupeid predators on recruitment success in Baltic cod? ICES Journal of Marine Science 57, 310-323.

Last, J.M. (1987). The food of immature sprat (*Sprattus sprattus* (L.)) and herring (*Clupea harengus* L.) in coastal waters of the North Sea. Journal du Conseil International pour l´Exploration de la mer 44, 73-79.

Last (1989). The food of herring, *Clupea harengus*, in the North Sea 1983-1986. Journal of Fish Biology 34, 489-501.

Möllmann, C. & Köster, F.W. (1999). Food consumption by clupeids in the Central Baltic: evidence for top-down control? ICES Journal of Marine Science 56 Supplement, 100-113.

Möllmann, C. & Köster, F.W. (2002). Population dynamics of calanoid copepods and the implications of their predation by clupeid fish in the Central Baltic Sea. Journal of Plankton Research Vol. 24 No. 10, 959-977.

Möllmann, C., Köster, F.W., Kornilovs, G. & Sidrevics, L. (2002). Long-term trends in abundance of cladocerans in the Central Baltic Sea. Marine Biology 141, 343-352.

Möllmann, C., Kornilovs, G., Fetter, M., Köster, F.W. & Hinrichsen, H.-H. (2003). The marine copepod, *Pseudocalanus elongatus*, as a mediator between climate variability and fisheries in the Central Baltic sea. Fisheries Oceanography 12, 360-368.

Möllmann, C., Kornilovs, G., Fetter, M. & Köster, F.W. (2004). Feeding ecology of central Baltic Sea herring and sprat. Journal of Fish Biology 65, 1563-1581.

Möllmann, C., Kornilovs, G., Fetter, M. & Köster, F.W. (2005). Climate, zooplankton, and pelagic fish growth in the central Baltic Sea. ICES Journal of Marine Science 62, 1270-1280.

Postel, L. (1996). Zooplankton. In Meereskunde der Ostsee (Rheinheimer, G., editor), 150-160. Berlin, Springer.

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

Pianka, E.R. (1982). Evolutionary ecology. New York: Harper & Row.

Rudstam, L.G., Hansson, S., Johansson, S. & Larsson, U. (1992). Dynamics of planktivory in a coastal area of the northern Baltic Sea. Marine Ecology Progress Series 80, 159-173.

Sandström, O. (1980). Selective feeding by Baltic herring. Hydrobiologia Vol. 69, 199-207.

Shvetsov, F.G., Starodub, M.L. & Sidrevits, L.L. (1983). The daily feeding rhythm of the Baltic sprat, *Sprattus sprattus balticus* (Clupeidae). Journal of Ichthyology Vol.23, no.2, 99-105.

Sirotenko, M.D. & Sorokalit, L.K. (1979). Seasonal changes in the food of the Mediterranean sprat, *Sprattus sprattus phalericus*. Journal of Ichthyology Vol. 19, no. 5, 37-51.

Sparholt, H. (1994). Fish species interactions in the Baltic Sea. Dana 10, 131-162.

Szypula, J. (1985). Comparative studies on herring and sprat feeding in the southern Baltic within 1978-1982. Acta Ichthyologica et Piscatoria Vol. XV Fasc. 2, 75-89.

Szypula, J., Wlodzimierz, G. & Wyszynski, M. (1997). Feeding of Baltic herring and sprat in the period 1986-1996 in relation to their state and biomass. Bulletin of the Sea Fisheries Institute 3 (142), 73-83.

Viitasalo, M., Flinkman, J. & Viherluoto, M. (2001). Zooplanktivory in the Baltic Sea: a comparison of prey selectivity by *Clupea harengus* and *Mysis mixta*, with reference to prey escape reactions. Marine Ecology Progress Series 216, 191-200.

Vertically resolved prey selectivity of Baltic herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.) in the Bornholm Basin

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Abstract

The prey selectivity of Baltic herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.) was studied in the Bornholm Basin in June 2001. A total of 165 sprat stomachs (10-15 cm) and 215 herring stomachs (12-30 cm) were analysed. The diurnal vertical distribution of zooplankton prey was analysed by multi net samples, clupeid distributions were estimated by hydroacoustic measurements. These measurements enabled us to describe the diurnal feeding-rhythm and to estimate vertically-resolved selectivity indices for the two most important zooplanktivores in the southern-central Baltic Sea. Diet composition of herring and sprat were similar, consisting mainly of copepods and cladocerans. Most important prey items were the copepods *Temora longicornis* and *Pseudocalanus acuspes* along with the cladocerans *Evadne nordmanni* and *Podon* spp. Sprat were strongly selecting *T. longicornis* as prey during the day and mainly *Podon* spp. during the night. Herring were also selecting *T. longicornis* during most of the entire investigated period with short phases in which *E. nordmanni, Podon* spp. and *P. acuspes* were selected. Both sprat and herring were selecting adult males and females and older copepodites, mostly avoiding younger stages. In comparison with commonly used methods, where no diel cycles were studied, we were able to show that at certain times younger copepodites (c1-3) were positively selected. The estimation of an impact factor (IF) revealed the importance of stage-resolved selectivity investigations. Grouped results were underestimating the feeding impact on older copepodite stages c4 and c5 and reproducing females and males (c6).

Introduction

Herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.) are the most abundant and commercially important planktivorous fish in the Baltic Sea. These species are dominant predators on the crustacean zooplankton and have the potential to control the Baltic Sea zooplankton community (Hansson et al. 1990, Arrhenius & Hansson 1993, Rudstam et al. 1994, Möllmann & Köster 1999, Möllmann & Köster 2002). Estimating the potential for top-down control requires knowledge on the feeding ecology, especially prey selectivity. For the latter, it is crucial that the actual feeding environment encountered by the predator is reliable known.

In the Baltic Sea, several investigations have been conducted on the selective predation of herring and sprat (Sandström 1980, Hansson et al. 1990, Flinkman et al. 1992, 1998, Arrhenius 1996, Casini et al. 2004). However, most of these studies were conducted in shallow coastal areas of the Baltic. Furthermore, with the exception of Hansson et al. (1990), these studies calculated selectivity indices from zooplankton sampling that integrated most if not all of the water column, ignoring the differences in the vertical distribution of various zooplankton species in the Baltic Sea (Hansen et al. 2006). Another shortcoming of earlier studies is the protocol used to identify gut contents and plankton composition, i.e., copepods were frequently not analysed to developmental stage and thus estimates of stage-resolved selectivity are generally lacking. This is important as herring and sprat tend to prefer later developmental stages (Möllmann et al. 2004) and prey selectively on adult female copepods and cladocerans that carry conspicuous egg sacs (*Eurytemora affinis* females) or pigmented eggs and embryos (*Bosmina longispina* and *Podon* spp.) (Flinkman et al. 1992). Furthermore, earlier studies were mainly conducted during dusk or at night, when these fish reside in the upper water column and are generally not feeding (Köster & Schnack 1994, Arrhenius

1998). Finally, in the vast majority of studies prey selectivity was investigated for single months and/or years with no analyses of potential diel cycles in prey selectivity.
We conducted a 24 h *in situ* experiment in a deep Baltic basin to investigate the selective feeding behaviour of herring and sprat. Our study included 1) vertically-resolved zooplankton sampling, 2) diel observation of abundance, vertical distribution and stomach contents of the predators, and 3) stage-resolved analyses of zooplankton caught in net samples and found in fish stomachs. Using these methods, we hoped to assess whether traditional techniques yielded reliable estimates of prey selection compared to those applied in this study.

Material and Methods

Our study was carried out in the Bornholm Basin of the Central Baltic Sea between June 4th and 6th 2001 (figure 1) using two research vessels "Walther Herwig III" and "Alkor" that made measurements in parallel. A triangular transect was sampled over a 48 h period starting point at 55°21.N, 16°00 E.

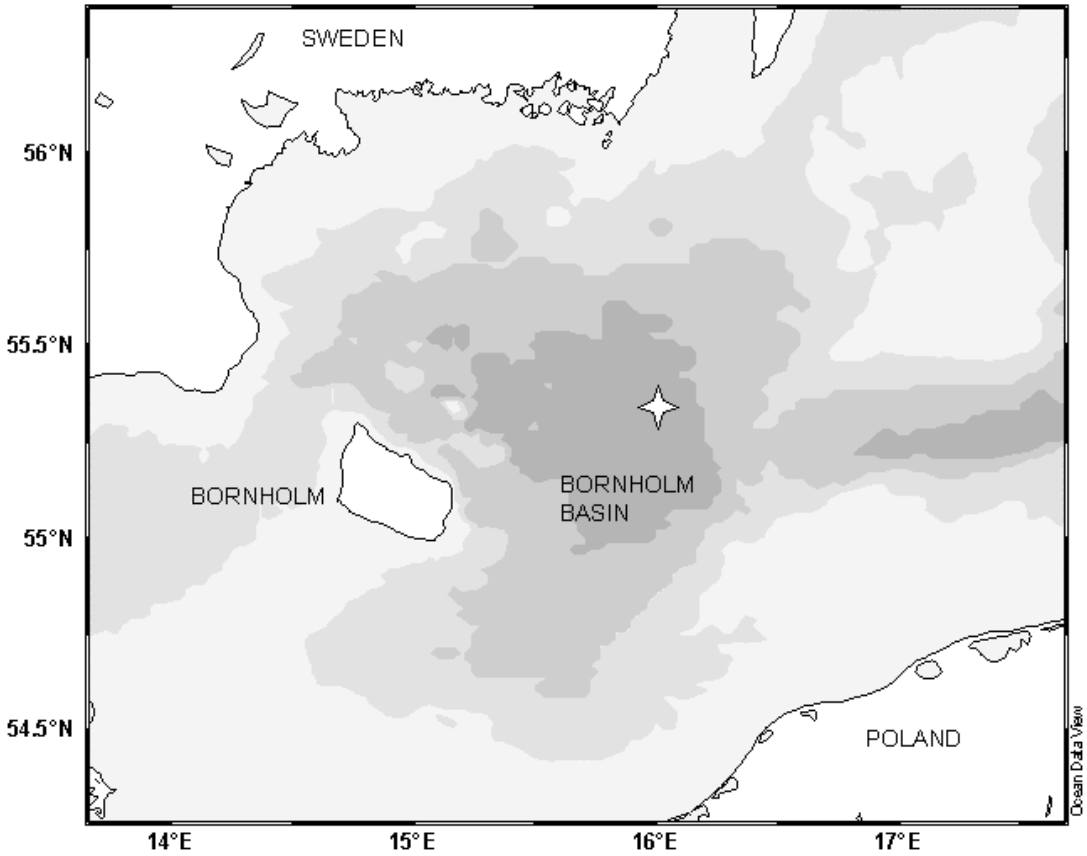

Figure 1) Map of the Bornholm Basin (Baltic Sea). 48h-station from 4-6 june 2001, Bornholm Basin 55°21.00'N, 16°00.00'E, marked by white star.

RV "Walther Herwig III" conducted hydroacoustic measurements and fishery hauls, while the RV "Alkor" conducted hydrographical measurements, zooplankton-sampling and additionally fishery hauls.

Hydrographic measurements of temperature, salinity and oxygen were performed after every fishing station with a CTD-probe (type ME-KMS3). Zooplankton was sampled at three stations during day and at three stations during night.

Hydroacoustic measurements were conducted with a SIMRAD echosounder EK500 (SIMRAD 1997) using a hull mounted split-beam-transducer (type ES38B), operating at a frequency of 38 kHz. The system was calibrated according to methods outlined for Baltic Sea hydroacoustic surveys (ICES 2001). Ship speed during the measurements was 10 knots between fishing stations and approximately 3 knots during trawling. Analysis of the data was performed using the EchoView Software (SonarData 2001). Echo-data were pooled into one metre depth layers and 0.1 nautical mile horizontal intervals from 10 m below the surface to 0.5 m above the bottom. Integration results were given as nautical area backscattering coefficient *Sa* (NASC in m² * nm^{-2}):

$$Sa = 4\pi * 1852^2 \int_{z1}^{z2} s_v dz \qquad (1)$$

after Huse & Korneliussen (2000) with z_1, z_2 being the depth and s_v the volume backscattering coefficient.
To illustrate the vertical distribution and diel migration, weighted mean depth of echoes was calculated for every echo-profile with a horizontal dimension of 0.1 nm:

$$z_c = \frac{\sum_{j=10}^{n} Sa * z_j}{\sum_{j=10}^{n} Sa_j} \qquad (2)$$

where *j* is a depth-layer of the echo-profile and z_j is the mean depth at depth-interval *j*.

A total of 15 fishery hauls was performed to identify the species composition of the echoes and for stomach sampling during the 48 h investigation period. A mid-water trawl type PS 205 with a codend mesh-width of 10 mm was towed at a speed of 3 to 3.5 knots for 30 minutes. The depth of the net was adjusted to visible echoes of the target fish species.
At every station, the weight- and size-distribution of herring and sprat were recorded into 1 cm classes for sprat and 2 cm classes for herring. A total of 3 - 10 fish (per haul and length class) was preserved in 4% di-sodium-tetraborate-buffered formalin-seawater. During stomach analysis, the wet weight of stomach contents was determined. Diet analyses were conducted for three fish per sampling time and length class. The contents were analysed using a stereo microscope (magnification 16 - 80x). Each prey item was determined to the lowest possible taxonomic level. If a stomach contained a large number of prey, a subsample of 200 identifiable items was analysed. Additionally, the sample was screened for rare taxa and ichthyoplankton. A total of 215 herring and 165 sprat stomachs was analysed.

Zooplankton sampling

Vertical distributions were recorded during daytime (12:10, 10:33 and 11:58) and during night time (22:52, 23:34 and 02:45 hours). Vertically stratified samples (10 m intervals from surface to 80 m) were obtained using a multiple opening-closing net (Hydro-Bios) with an opening of 0.25 m² and a mesh size of 100 µm. Samples were preserved in 4%

di-sodium-tetraborate-buffered formalin-seawater solution for later analysis in the laboratory. Mesozooplankton was identified and counted under a binocular microscope on sub samples of not less than 500 individuals per sample. Sub samples 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*). Copepodites were classified to developmental stages (c1 - c6), and adults (c6) to sex.

Selectivity index

Selection of prey types was estimated using a selectivity index (Krebs 1999):

$$\alpha_i = \frac{r_i}{n_i} * \left(\frac{1}{\sum_{j=1}^{k} \left(\frac{r_j}{n_j} \right)} \right) \quad (3)$$

where α_i = Manly`s α (preference index) for prey type i
r_i, r_j = Proportion of prey type i or j in the diet (i and j = 1,2,3, …,k)
n_i, n_j = Proportion of prey type i or j in the environment
k = Number of prey types possible

The α values are normalized so that

$$\sum_{i=1}^{k} \alpha_i = 1.0 \quad (4)$$

with
$\alpha_i = 1/k$ denotes unselective feeding
$\alpha_i > 1/k$ denotes that prey species i is preferred in the diet
$\alpha_i < 1/k$ denotes tha*t* prey species i is avoided in the diet

For the estimation of selectivity in feeding the plankton composition 10 m below and above the weighted mean depth of the clupeids was considered as prey field. In order to compare our method to the results of earlier studies that evaluated vertically integrated zooplankton sampling, we estimated selectivity simulating integrated plankton samples (day: 41 - 80 m, night: 0 - 40 m). In order to highlight the fluctuations in the selectivity values over the diurnal cycle, we estimated selectivity indices for the copepodite stages of *T. longicornis* and *P. acuspes* not only over the diurnal cycles, but also pooled for day and night from the average stomach contents. The progression of prey selectivity was calculated and displayed in 3-hour-intervals (00:01 - 03:00, 03:01 - 06:00, …, 21:01 - 00:00). In the graphic presentation the mid points of these intervals are displayed (01:30, 04:30,…, 22:30).

Niche overlap

The niche overlap of herring and sprat was estimated using the percentage overlap index, sometimes referred to as Renkonen index or Schoener overlap index (Krebs 1999). This measure is calculated as a percentage and is given by

$$P_{jk} = \left[\sum_{i=1}^{n}\left(\min p_{ij}, p_{ik}\right)\right]*100 \quad (5)$$

where P_{jk} = Percentage overlap between species *j* and species *k*
p_{ij} = Proportion resource *i* is of the total resources used by species *j*
p_{ik} = Proportion resource *i* is of the total resources used by species *k*
n = Total number of resource states

The percentage overlap was calculated for 3-h intervals over the 24 h period (00:01 – 03:00, 03:01 – 06:00…). A percentage overlap of 100% denoted identical prey spectrum of species j and k whereas a percentage overlap of 0% denoted that no food items in species j and k are identical.

Impact factor

The Impact factor (IF) was calculated to emphasize the importance of the estimation of a stage-resolved prey-selectivity in herring and sprat and is given by

$$IF_i = \frac{n_i}{N_i m^{-3}} \quad (6)$$

where n_i = average number of copepodite stage *i* in fish stomach
N_i = number of copepodite stage (sum) *i* in plankton samples

Results

Hydrography

The mean water depth at sampling site was 85 m and the hydrographic depth profile measured was typical for the Bornholm Basin in June (figure 2). The temperature was constant at approximately 10°C in the surface layer and decreased between 20 m and 55 m to 3.5°C. Between 55 and 80 m the temperature increased to 7°C. The salinity was constant at 9 psu in the surface layer and decreased slightly to 8 psu at 55 m. Below 55 m the salinity increased to 17 psu at 80 m. The concentration of dissolved oxygen was about 8 ml l^{-1} in the surface layer, decreased to 6 ml l^{-1} at 55 m, and declined rapidly from the upper limit of the halocline at 55 m to 0 ml l^{-1} at 80 m.

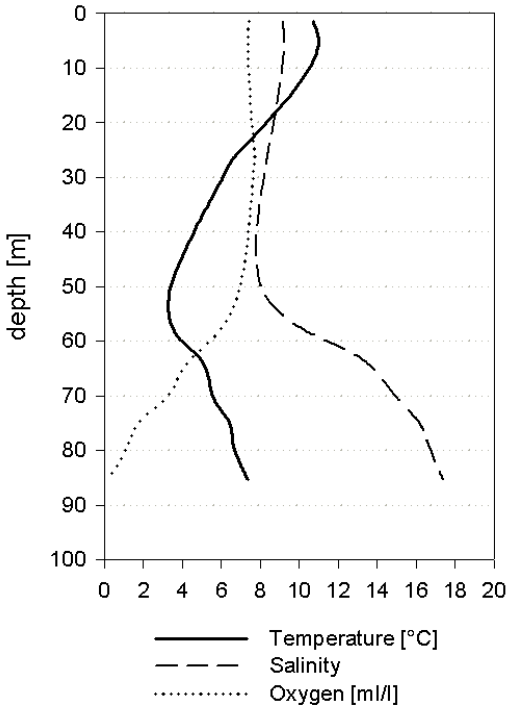

Figure 2) Vertical profiles of temperature [°C], salinity [PSU] and oxygen [ml l^{-1}]; on 5th of June 2001, Bornholm Basin 55°21.00'N, 16°00.00'E

Total global radiation was measured with a ship mounted pyranometre in Watt * m^{-2} and is presented in figure 3 together with the elevation of the sun. The elevation of the sun was computed using the freely available ”Sundi” software (V 1.1, *http://emsolar.ee.tu-berlin.de/simulation/ sundi.html*).
Global radiation (W m^{-2}) was measured onboard RV ”Alkor” and recorded at 5 minute intervals. Additionally elevation of the sun was calculated for location and time of this study (Giesen 2001§248$). The measured global radiation was in accordance with calculated elevation of the sun. Sunrise was at 04:27 h local time and sunset at 21:23 h local time.

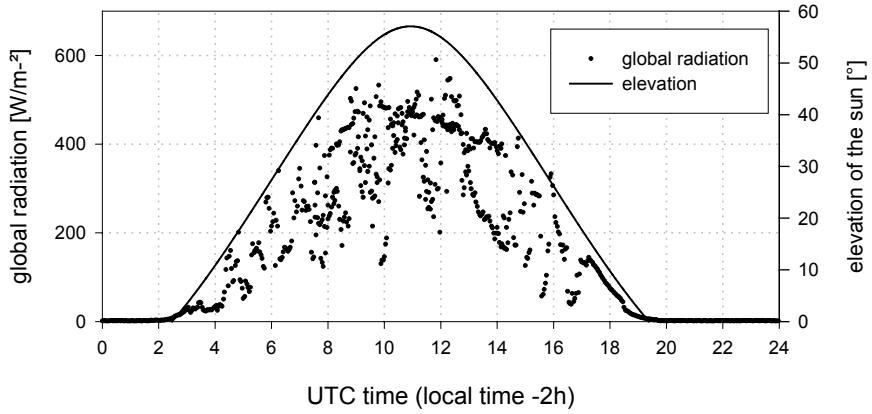

Figure 3) Elevation of the sun in 4-6 June 2001 and measured global radiation (W m^{-2}); 48 h-station from 4 - 6 June 2001, Bornholm Basin 55°21.00'N, 16°00.00'E.

Fish distribution

A distinct diurnal pattern was evident in the vertical distribution of herring and sprat. During daytime most fish were located between 60 and 80 m depth below the upper limit of the halocline. Between 18:00 hours and 21:00 hours both herring and sprat moved up in the water column to the surface layer and, between 22:00 and 02:00 hours, were concentrated at 20 m around and above the upper limit of the thermocline. At 02:00 hours the downward movement started and ended at approximately 04:00 hours when fish concentrated between 60 and 80 m again. A detailed description of this daily pattern can be found in Stepputtis et al. (In Prep.).

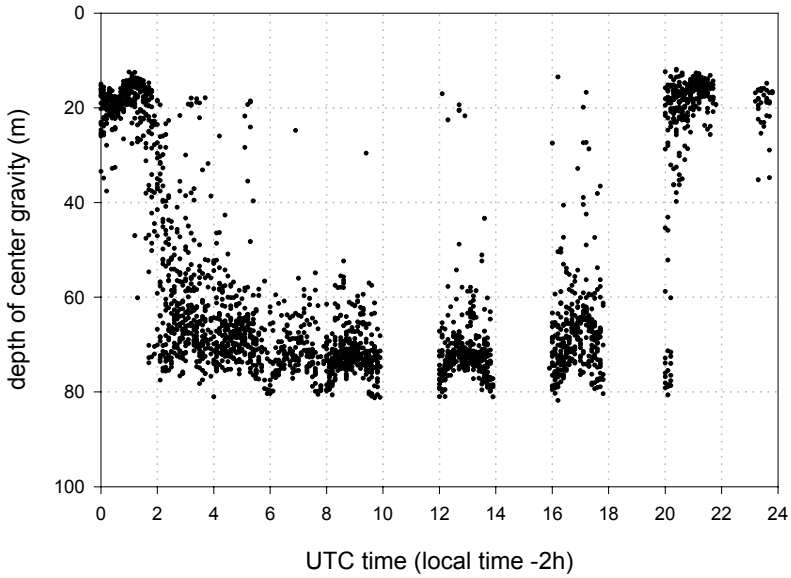

Figure 4) Vertical distribution of fish, represented as weighted mean depth of echo signals at time of day from a 48 h-station (4-6 June 2001) in the central Bornholm Basin (55°21.00'N, 16°00.00'E). Each dot represents the weighted mean depth of an echo-profile, integrated over 0.1 nm. Gaps represent times of day that were not covered by hydroacoustics.

Total stomach content weight

The mean stomach content increased steadily from the lowest value of 30 to 40 mg wet weight (*WW*) for both species during the night at 02:00 hours to a peak value in the afternoon (figure 5).

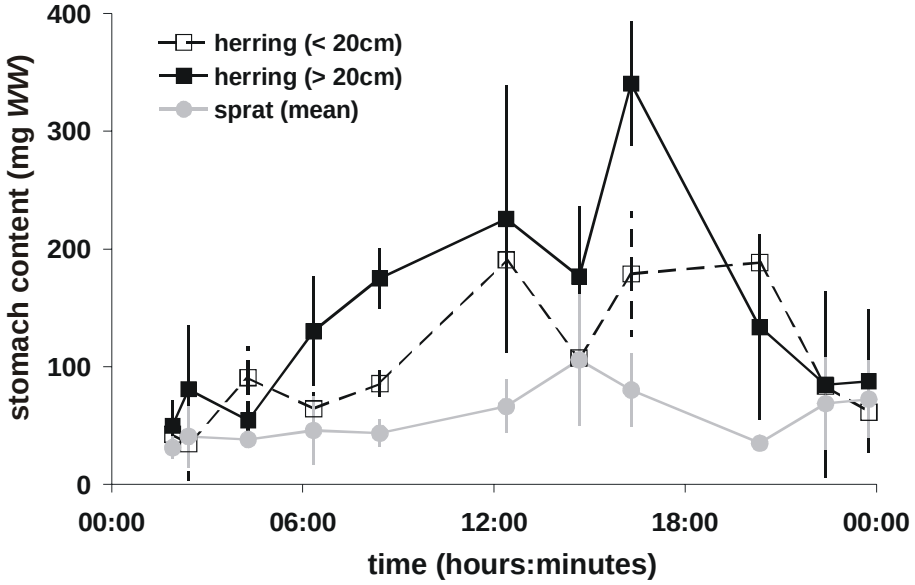

Figure 5) Mean (± standard deviation, *SD*) stomach content of herring (□ < 20 cm; ■ > 20 cm) and sprat (● mean over length classes 11-15 cm) in gram wet weight (*WW*) over the 24 hour period. Each time is the mean of 5 to 20 replicate stomachs.

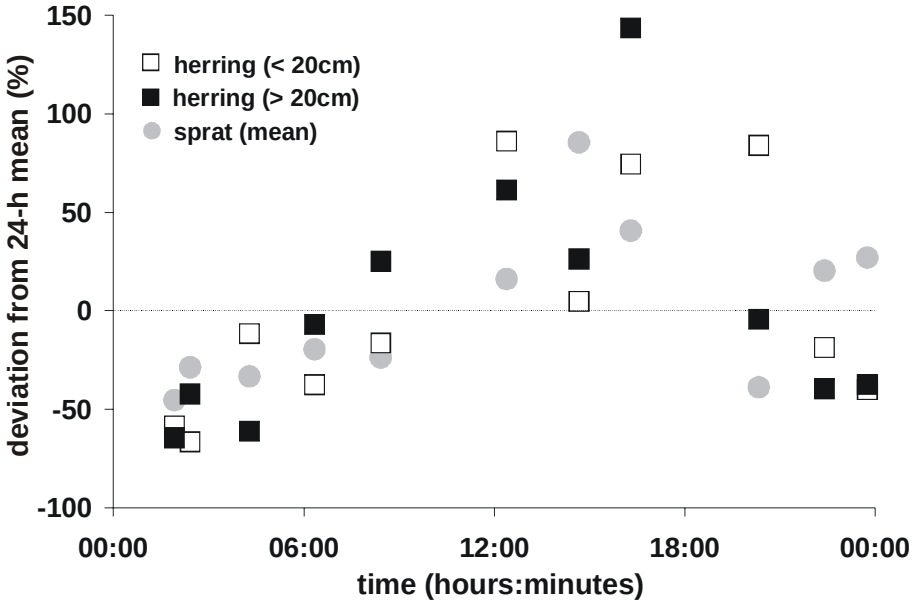

Figure 6) Diurnal variation in mean stomach content for sprat, herring (< 20 cm, > 20 cm) expressed as percentage deviation from corresponding 24-h mean (dashed line).

For sprat the increase was more moderate and the peak of 100 mg stomach content was reached earlier at 14:30 hours. The increase for small (< 20 cm) and large (> 20 cm) herring was more pronounced, reaching a peak of 190 mg *WW* at 12:30 (small

herring) and 260 mg *WW* at 16:00 hours (large herring). Following the peak in the large herring, the stomach content decreased steadily to lowest values during the night.
For both length classes of herring, a decrease in mean stomach content was observed at 14:30, co-occurring with the peak in stomach content for sprat.
The increasing positive deviations of the stomach content in relation to the 24-h mean during the day indicate that the feeding activity of both herring in sprat was related to daylight (figure 6). Two sprat feeding peaks, one in the afternoon and one close to midnight, indicated that sprat were also feeding intensively during sunset.

Food availability

The zooplankton community during the investigation was dominated by the copepods *Acartia* spp (*A. bifilosa* and *A. longiremis*), *Centropages hamatus*, *Pseudocalanus acuspes*, *Temora longicornis* and unidentified copepod nauplii. Additionally *Synchaeta* spp. were very abundant.

Table 1) Relative abundance (in percent, as estimated from mean N*m^{-3}) during the day (2:30-20:00 UTC) in 10 m intervals from multinet catches. *Acartia* spp. includes *Acartia bifilosa* and *A. longiremis*, whereas *Podon* spp. includes *P. intermedius*, *P. leuckarti* and *P. polyphenoides*. *Synchaeta* spp. includes *S. monopus* and *S. baltica.*

	0-10 m	11-20 m	21-30 m	31-40 m	41-50 m	51-60 m	61-70 m	71-80 m
Copepods								
***Acartia* spp.**	18.5	15.2	17.3	12.9	15.4	5.7	8.2	10.1
Centropages hamatus	28.7	18.6	4.2	4.2	5.9	8.0	5.2	3.7
Eurytemora affinis	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.3
Oithona similis	0.2	0.2	1.4	5.5	1.1	2.6	11.2	21.8
Pseudocalanus acuspes	11.9	11.0	29.4	35.7	16.0	20.3	23.6	37.4
Temora longicornis	5.8	12.9	12.4	7.4	7.9	8.6	9.4	4.2
Copepod unidentified	2.2	1.6	1.6	2.2	0.9	1.2	6.1	6.1
Copepod eggs	0.3	0.1	0.6	0.6	0.7	0.3	0.2	2.1
Nauplii	16.8	26.9	14.5	7.4	12.7	10.9	16.7	8.6
Cladocerans								
Bosmina longispina maritima	0.4	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Evadne nordmanni	7.0	2.8	1.4	3.2	2.8	1.0	1.3	0.4
***Podon* spp.**	0.4	1.0	0.1	0.0	0.6	0.1	0.2	0.4
Others								
Bivalvia larvae	2.8	1.9	0.1	0.2	0.9	0.2	0.0	0.2
Fish eggs	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Fritillaria borealis	0.4	0.1	0.1	1.4	1.2	1.4	0.7	1.4
***Oikopleura* spec.**	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polychaeta larvae	0.0	0.1	0.1	0.0	0.0	0.2	0.2	0.5
***Synchaeta* spp.**	4.6	7.6	16.7	19.3	34.0	39.2	17.0	2.9
sum	**100**	**100**	**100**	**100**	**100**	**100**	**100**	**100**

From the surface down to 10 m, *C. hamatus* was the most abundant species (28.7% day, 27.2% night), its abundance decreased with depth. *Synchaeta spp*. had high abundances from 20 to 60 m depth with a maximum of 63.4% relative abundance from 41 to 50 m during night. Copepod nauplii had relative abundances of 7 to 26.9% over the entire water column. The cladocerans *Bosmina longispina maritima*, *Evadne nordmanni* and *Podon* spp. were less abundant, with a maximum of 7.0% relative abundance for *E. nordmanni* from 0 to 10 m water depth during day. The highest abundances of *P. acuspes* were reached between 31 and 40 m (35.7%) and 71 and 80

m (37.4%) during the day and between 11 and 30 m (23.9-23.3%) and 71 and 80 m (27.2%) during the night. *T. longicornis* had its highest abundances during the day between 11 and 30 m (12.9-12.4%) and between 0 and 10 m (16.2%) during the night (tables 1, 2).

Table 2) Relative abundance (in percent, as estimated from mean $N*m^{-3}$) during the night (20:00-2:30 UTC) in 10 m intervals from multinet catches. *Acartia* spp. includes *Acartia bifilosa* and *A. longiremis*, whereas *Podon* spp. includes *P. intermedius*, *P. leuckarti* and *P. polyphenoides*. *Synchaeta* spp. includes *S. monopus* and *S. baltica.*

	0-10 m	11-20 m	21-30 m	31-40 m	41-50 m	51-60 m	61-70 m	71-80 m
Copepods								
***Acartia* spp.**	12.1	19.1	18.8	23.8	8.7	1.9	3.1	4.6
Centropages hamatus	27.2	6.2	4.8	6.8	1.0	0.7	2.0	2.8
Oithona similis	0.0	0.1	2.2	4.8	0.4	1.6	35.7	44.2
Pseudocalanus acuspes	11.3	23.9	23.3	19.9	7.9	21.2	20.6	27.2
Temora longicornis	16.2	7.6	6.1	5.2	1.7	0.8	1.9	3.4
Copepod unident.	1.1	1.1	1.2	1.2	0.5	1.3	2.3	1.0
Copepod eggs	0.0	0.3	0.3	0.4	2.6	13.7	9.1	2.1
Nauplii	20.0	21.3	18.4	9.8	10.2	12.0	14.9	5.9
Cladocerans								
Bosmina longispina maritima	0.2	0.0	0.0	0.1	0.0	0.1	0.0	0.0
Evadne nordmanni	3.5	5.2	4.1	3.3	0.8	1.2	2.9	1.6
***Podon* spp.**	0.3	0.3	0.0	0.0	0.0	0.2	0.0	0.0
Rest								
Bivalvia larvae	4.2	1.6	0.4	0.5	0.1	0.1	0.1	0.5
Fish eggs	0.0	0.0	0.0	0.0	0.1	0.2	0.2	0.5
Fritillaria borealis	0.7	0.4	1.6	2.7	2.7	4.6	3.8	1.5
***Oikopleura* spec.**	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polychaeta larvae	0.0	0.0	0.1	0.4	0.1	0.3	1.4	3.2
***Synchaeta* spp.**	3.0	12.9	18.6	21.2	63.4	40.1	1.9	1.5
sum	**100**	**100**	**100**	**100**	**100**	**100**	**100**	**100**

Food composition

Sprat

The most important prey items for sprat were copepods (*Temora longicornis*, *Pseudocalanus acuspes, Acartia* spp. and *Centropages hamatus*) and cladocerans (*Evadne nordmanni*, *Podon* spp. *and Bosmina longispina maritima*) (figures 7, 8). Copepod nauplii were abundant in zooplankton samples but rare in the stomachs. Other food items, (e.g. *Fritillaria borealis*, *Synchaeta* spp., fish eggs, and polychaete and bivalve larvae) occurred in only a few stomachs in low numbers.

During the day, the most important prey by numbers was *T. longicornis*, which made up to 65% of sprat gut contents (figure 7). Other important prey items were *Acartia* spp. (up to 21%), *P. acuspes* (up to 18%) and *C. hamatus* (up to 13%). The cladocerans *E. nordmanni* and *Podon* spp. were of less importance with up to 9% of the stomach contents for 11 cm sprat (figure 7). The importance of *T. longicornis* as prey increased with increasing fish length, from 34% at 11 cm to 65% relative abundance at 15 cm. Concurrently the importance of *P. acuspes* and *Acartia* spp. decreased with increasing length of sprat. The fraction of *P. acuspes* decreased from 18% relative abundance at 11 cm to 6% at 15 cm, and the proportion of *Acartia spp.* decreased from 21% to 7%.

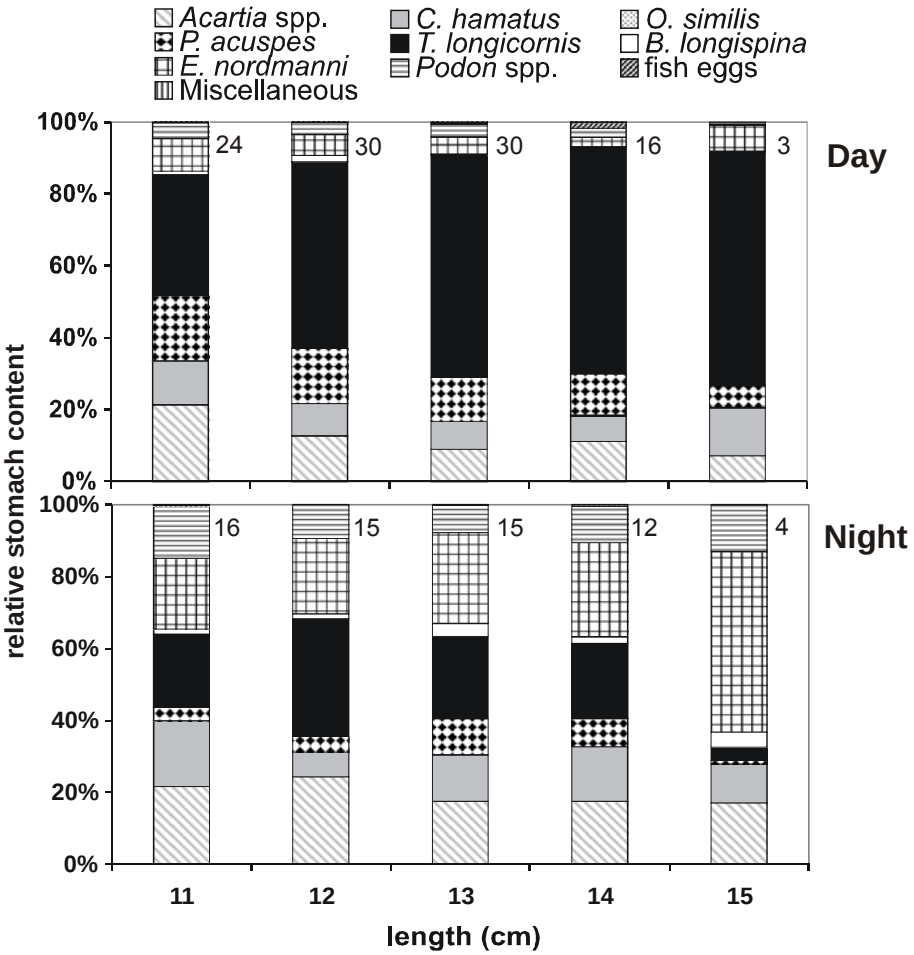

Figure 7) Diet of sprat (day) and (night). The proportions of the identified zooplankton taxa (% by numbers) are displayed. Proportions were calculated as the average of proportions in individual fish. Proportions are displayed per length class. Numbers to the right of the bars indicate total number of analysed stomachs per length class.

The different stages and sexes of each species were not equally represented in the stomachs, as shown in figure 9. In sprat stomachs, adults (c6 males and females) of *Acartia* spp. (66%) and *C. hamatus* (62%) were most abundant (figure 9). In both species slightly more females were found compared to males (37% to 30% in *Acartia* spp. and 37% to 26% in *C. hamatus*). Adults and c4-5 copepodites of *T. longicornis* were found in approximately equal abundances, 47% and 45%. Females and males (c6) were also found in approximately the same abundances with 25% and 23%. In *P. acuspes,* more c4-5 (46%) were found than adults (40%, 22% female and 18% male). The younger stages c1-3 of all four copepod species were of minor importance to stomach contents with a maximum value of 13% in *P. acuspes*.
During the night the most important prey species by numbers were *T. longicornis* (up to 33% relative abundance at 12 cm) *and E. nordmanni* (up to 50% at 15 cm). Other important prey species were the copepods *C. hamatus* and *P. acuspes*, the diet of different length classes of sprat consisted of 7 to 18% *C. hamatus* and of 1 to 10% *P. acuspes* (figure 7). Also, during the night, we observed changes in the importance of different prey species at different fish lengths. *E. nordmanni* made up to 20% of gut contents for 11 cm sprat, increasing to 50% for 15 cm sprat. *T. longicornis* made up 33% of gut contents at 12 cm, decreasing to 4% at 15 cm (figure 7).

In *Acartia* spp. adult copepods (c6 males and females) were found in highest abundances with 65% (34% females and 31% males), while in the other three copepods, c4-5 were found in higher abundances than the adults (figure 9). In *C. hamatus* 35% adults (11% females and 24% males) were found compared to 50% c4-5. In *T. longicornis* 30% were adults (14% females and 16% males), 38% c4-5 and 32% c1-3. The lowest abundances of adults were found in *P. acuspes* where only 15% were adults (9% females and 6% males). More abundant were c4-5 with 46% and c1-3 with 39% relative abundance.

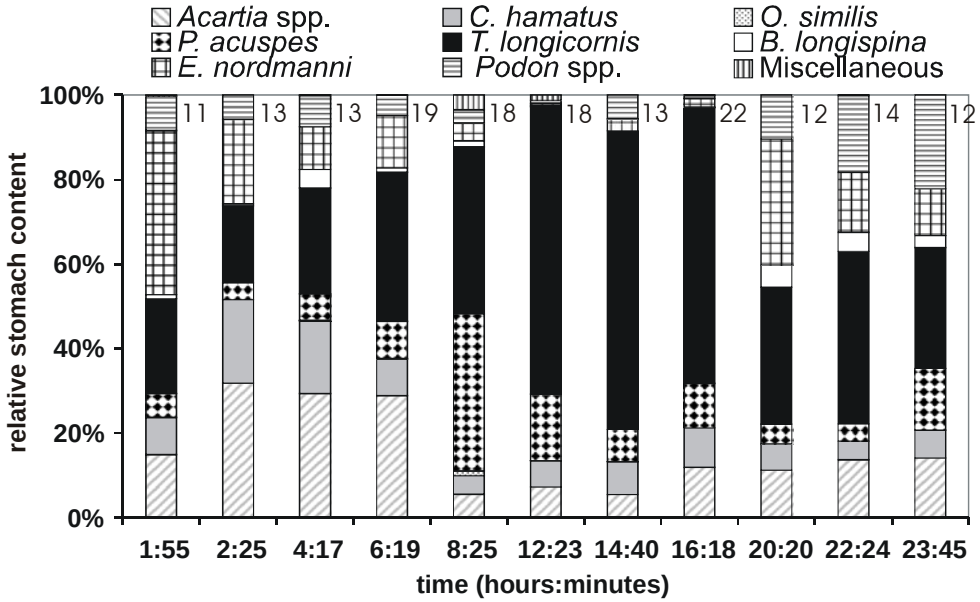

Figure 8) Diet of sprat. The proportions of identified zooplankton taxa (% by numbers) are shown as an average over length classes (11 - 15 cm). Proportions were calculated as the average of proportions in individual fish. Proportions and numbers of analysed stomachs are shown over a 24-h period. The total number of analysed stomachs per time is indicated to the right of each bar. The times presented denote the haul times. At four time periods (6:19, 8:25, 12:23 and 16:18 hours), the data from two hauls were pooled and displayed together.

During the daily cycle, the diet of 11 to 15 cm sprat (mean) was dominated by *T. longicornis* with a maximum relative abundance of 70% at 14:40 hours (figure 8). In the early morning hours from 02:25 to 06:25 UTC, *Acartia* spp. were also important as prey with 26 to 32% relative abundance, as was *C. hamatus* (up to 20%). At night the diet of sprat consisted to a high degree of the cladocerans *E. nordmanni* and *Podon* spp. (*E. nordmanni* up to 39% and *Podon* spp. up to 22%), whereas *B. longispina maritima* was found in less abundances (up to 5% at 20:20 hours). The importance of *T. longicornis* increased from 18% at 02:25 hours to 70% at 14:40 hours, being high during the day from 12:00 to 16:30 hours and decreasing thereafter. In contrast, the relative abundance of *E. nordmanni* was high during the night (39% at 01:55 hours) and decreased during the morning to reach lowest levels at 12:23 UTC with less than 1% relative abundance in gut contents. *P. acuspes* reached highest levels of relative abundance during the morning at 08:25 with 37%. Copepods of *Acartia* spp. were found in high abundance in the stomachs in the morning hours with a maximum of 32% relative abundance at 02:25 while the rest of the day the abundances were at approximately 10%.

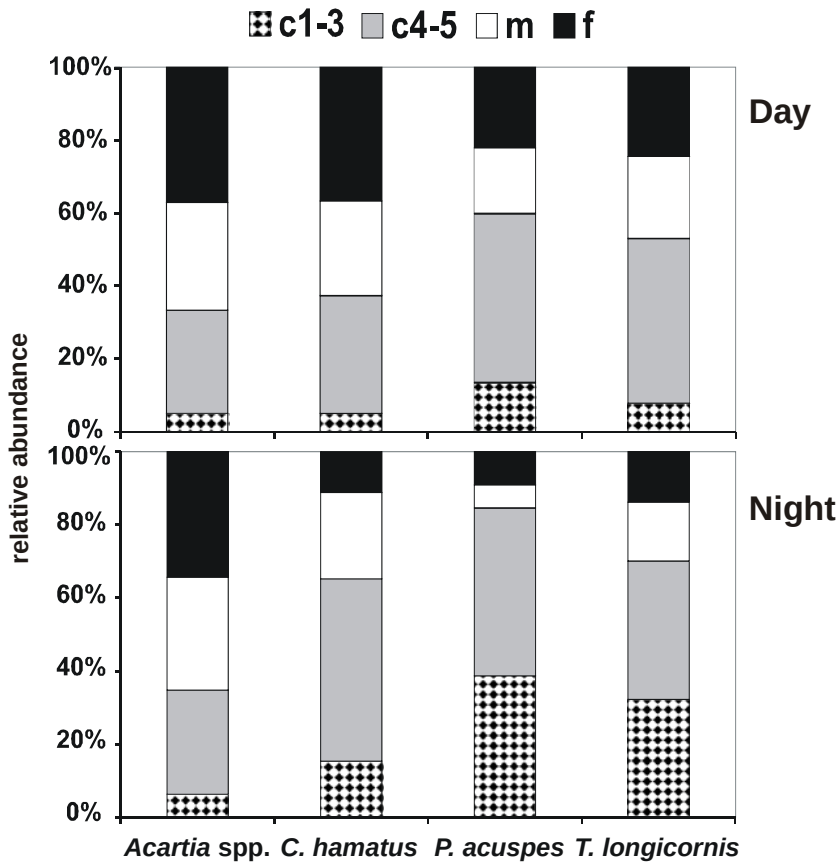

Figure 9) Copepod stages in the diet of sprat for day and night. The relative abundance of copepod stages c1-3, c4-5, c6 females (f) and c6 males (m) for *Acartia* spp., *Centropages hamatus*, *Pseudocalanus acuspes* and *Temora longicornis* are shown as an average over length classes (11-15 cm).

Herring

The diet of herring was dominated by *T. longicornis.* with stomach contents of up to 91% during the day (figure 10). Other important prey species were *P. acuspes, B. longispina maritima, E. nordmanni* and *Acartia* spp.
During the day the most important prey species were *T. longicornis* and *P. acuspes* (figure 10). Up to 91% of stomach contents in 14/15 cm herring consisted of *T. longicornis.* The relative abundance decreased with increasing length from 91% in 14/15 cm herring to 40% in 24/25 cm herring, whereas the importance of *P. acuspes* increased with increasing body length from 4% in 14/15 cm herring to 57% in 24/25 cm herring. The other species found in the stomachs were of less importance with a maximum of 3.5% of stomach contents for *E. nordmanni.*
In the smaller herring (< 20 cm) adult copepods were found in highest abundances, *Acartia* spp. (65%, 47% females and 18% males), *C. hamatus* (64%, 43% females and 21% males) and *T. longicornis* (45%, 24% females and 21% males), followed by c4-5 with 26%, 30% and 37% relative abundance (figure 12). In *P. acuspes* c5 copepodites were found in highest abundances with 56%, followed by adults with 22% (21% females and 1% males) and c4 with 20%. The copepodite stages c1 to c3 were of minor importance in all copepods.
Also in the larger herring (> 20 cm) adult copepods were found in highest abundances, *Acartia* spp. (86%, 47% females and 39% males), *C. hamatus* (59%, 40% females and 19% males) and *T. longicornis* (55%, 27% females and 28% males), followed by c4-5

with 11%, 36% and 31% relative abundance (figure 12). In *P. acuspes,* c5 copepodites were found in highest abundances with 50%, followed by adults with 23% (22% females and 1% males) and c4 with 22%. As in the smaller herring the copepodite stages c1 to c3 were of minor importance to the larger herring for all copepods.

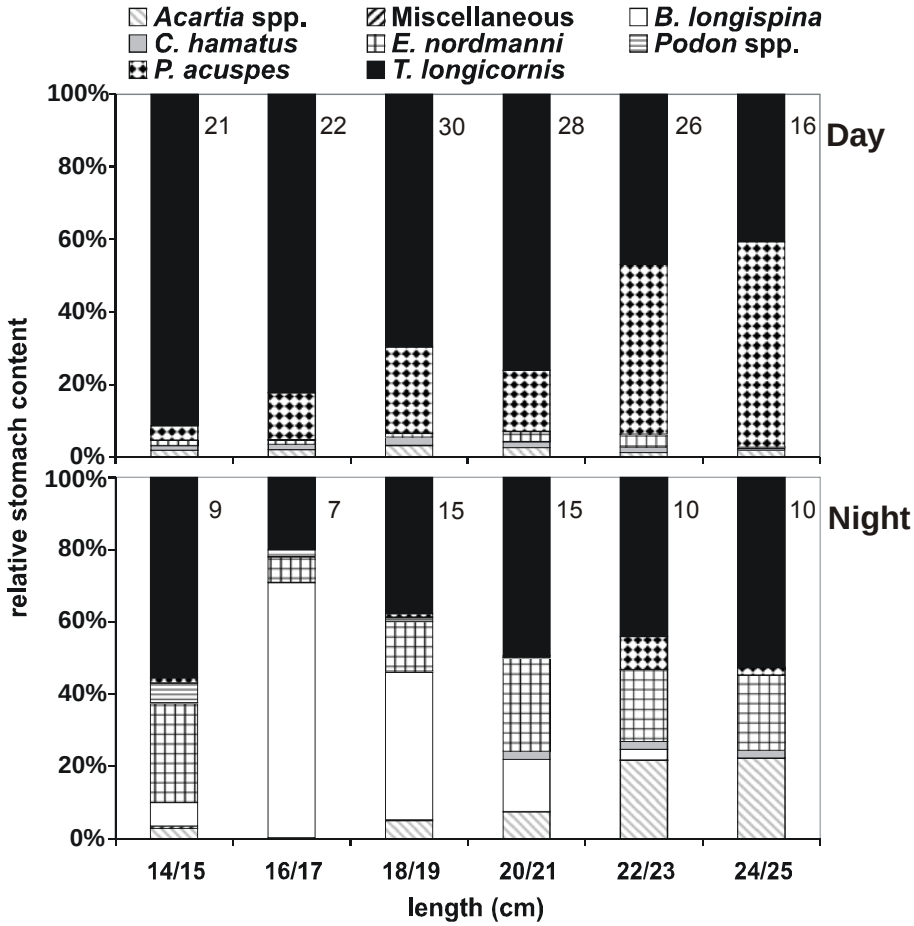

Figure 10) Diet of herring (day) and (night). The proportions of the identified zooplankton taxa (% by numbers) are displayed. Proportions were calculated as the average of proportions in individual fish. Proportions are displayed per length class. Numbers to the right of the bars indicate total numbers of analysed stomachs per length class.

During the night the most important prey species were *T. longicornis,* the cladocerans *B. longispina maritima, E. nordmanni* and *Acartia* spp. *T. longicornis* was found in highest numbers in 14/15 cm and 24/25 cm herring with 55% relative abundance each. The cladoceran *B. longispina maritima* had high abundances in the 16/17 cm herring with 70% relative abundance, decreasing in importance with increasing body weight, to not being found in the stomachs of 24/25 cm herring. The other cladoceran, *E. nordmanni* reached highest abundances in the stomachs of 14/15 cm and 20/21 cm herring with 27 and 26%. The copepods *C. hamatus* and *P. acuspes* were of minor importance in all size classes and *Acartia* spp. was only of relevance for length classes 22/23 cm and 24/25 cm (21 to 22% of stomach contents).
In the smaller herring (< 20 cm), adult copepods were found in highest abundances in *Acartia* spp. (81%, 50% females and 31% males) and *C. hamatus* (63%, 50% females and 13% males) followed by c5 (14% and 36%). In *T. longicornis* highest abundances were reached by c5 copepodites with 39% relative abundance, followed by adults with 29% (19% females and 10% males) and c4 with 20%. Copepodite stage c4 was found

in highest relative abundances with 35% in *P. acuspes* followed by c5 with 28% and c3 with 27%. Only 10% of copepodite stages found were adults. Those adults were all females, no males were found.

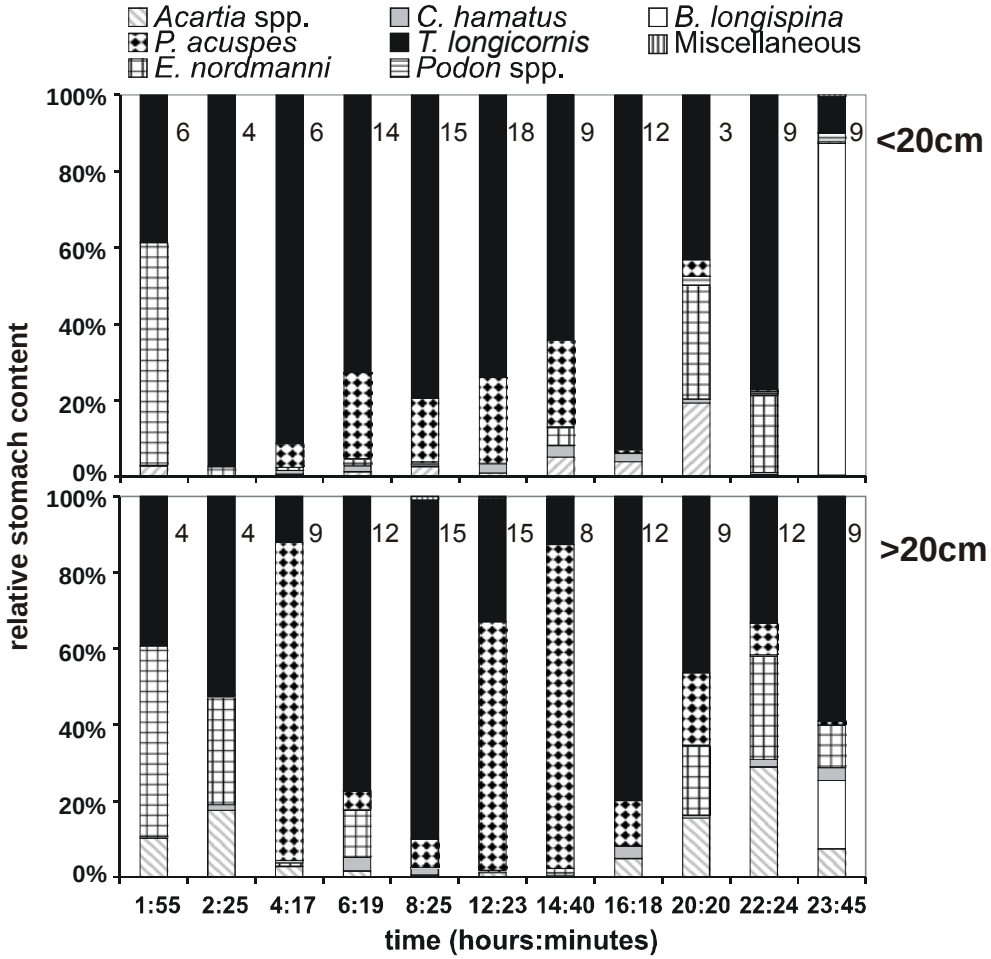

Figure 11) Diet of herring. The proportions of the identified zooplankton taxa (% by numbers) are shown as an average for small herring (< 20 cm) and large herring (> 20 cm). Proportions were calculated as the average of proportions in individual fish. Proportions and numbers of analysed stomachs are shown over a 24 hour period. Numbers to the right of the bars indicate total numbers of analysed stomachs per time. The times presented denote the haul times. The data from two hauls were pooled and displayed together at 6:19, 8:25, 12:23 and 16:18 hours.

In the larger herring (> 20 cm) adult copepods were found in highest abundances in *C. hamatus* (54%, 41 % females and 13% males) and *T. longicornis* (39%, 23% females and 16% males) followed by c5 (43% in *C. hamatus* and 32% in *T. longicornis*). In *Acartia* spp. and *P. acuspes* c5 copepodites were found in highest abundances (*Acartia* spp. 53% and *P. acuspes* 53%) followed by the adults (*Acartia* spp. 35% and *P. acuspes* 27%). While the adults in *Acartia* spp. were divided into 28% females and 7% males, the adults in *P. acuspes* consisted only of females. The younger copepodite stages c1 to c3 were found in low abundances with a maximum of 9% relative abundance of c3 in *T. longicornis*.

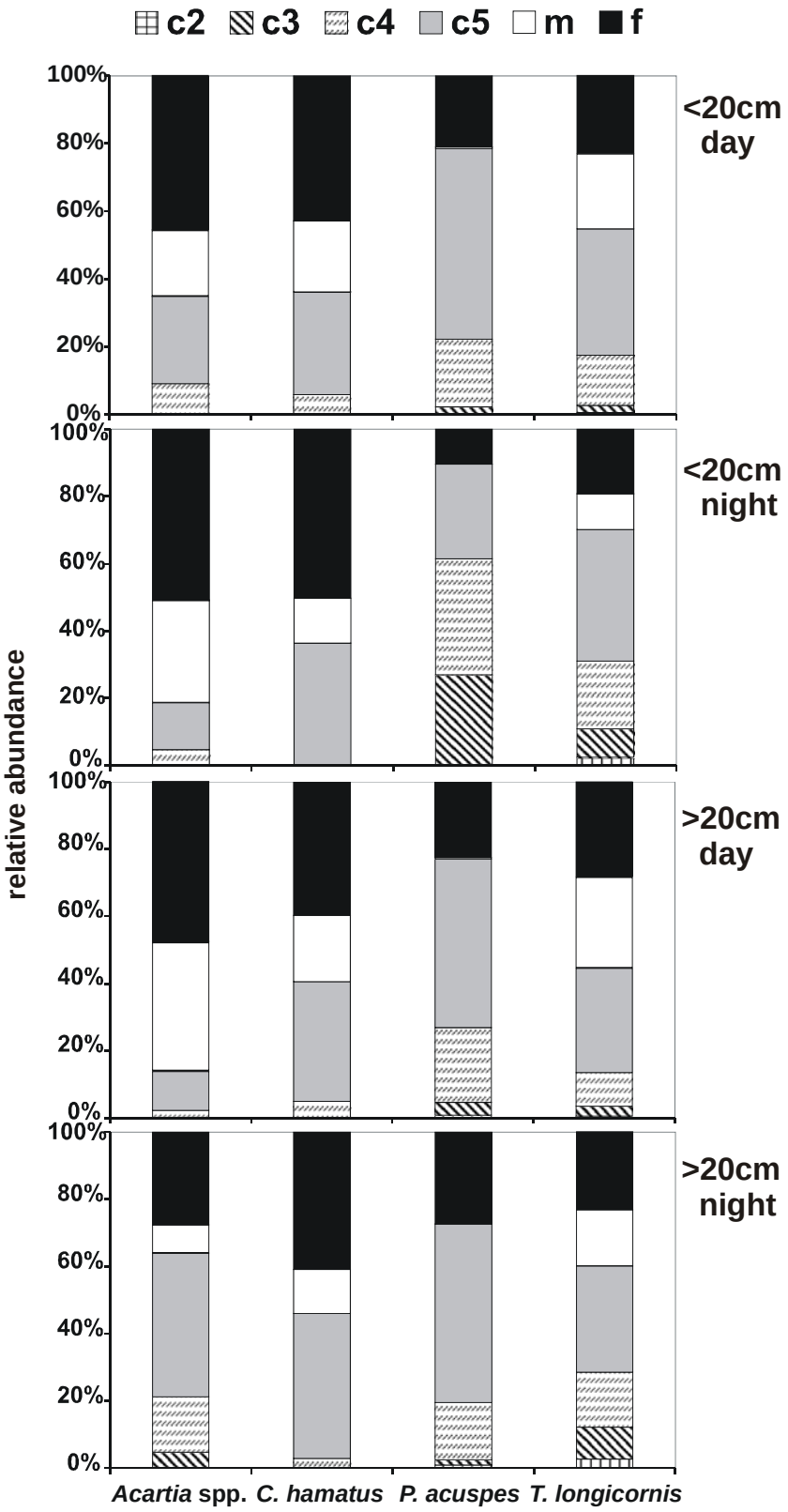

Figure 12) Copepod stages in the diet of herring at day and night. The relative abundance of copepod stages c2 to c6, c6 females (f) and c6 males (m) for *Acartia* spp., *Centropages hamatus*, *Pseudocalanus acuspes* and *Temora longicornis* are shown for small herring (< 20 cm) and large herring (> 20 cm).

In smaller herring (< 20 cm) *T. longicornis* was the dominant food item at most sampled times with highest abundances of 97% at 02:25 hours. In the middle of the night at 23:45 and 01:55 hours, *B. longispina maritima* and *E. nordmanni* reached highest abundances with 87% and 58% respectively. *P. acuspes* was found in relative abundances of approximately 22% from 06:00 to 15:00 hours.
In the larger herring (> 20 cm) both copepods *T. longicornis* and *P. acuspes* were found in highest abundances at different times. *T. longicornis* reached highest abundances in the morning at 06:19 and 08:25 hours, as well as from the afternoon at 16:18 hours into the night at 23:45 hours with maximum values of 89% relative abundance. *P. acuspes* had highest abundances at 04:17 hours with 83% and at 12:23 and 14:40 hours with 65% and 85% respectively. The cladocerans *E. nordmanni* reached highest abundances during the night with a maximum of 50% relative abundance at 01:55 hours. *B. longispina maritima* was just found at one station during the night at 23:45 hours and reached a relative abundance of 18%.

Niche overlap

The overlap of the diets of herring and sprat were ranging from a minimum of 34% from 03:00 to 06:00 hours to a maximum of 83% from 15:00 to 18:00 hours (figure 13). From this maximum value on, the overlap was decreasing over night to a minimum in the early morning, but was at 50% for the rest of the morning.

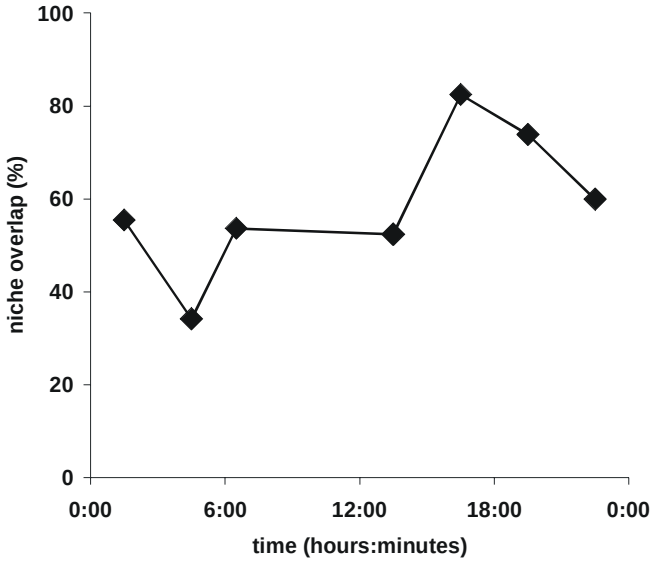

Figure 13) Niche overlap (%) of the food used by herring and sprat over the 24 hour period. The data points display the overlap in the middle of a 3 hour interval.

Selective feeding

Sprat

The copepod *T. longicornis* and the cladocerans *B. longispina maritima*, *E. nordmanni* and *Podon* spp. were the only species being positively selected by sprat (figure 14 B, black bars).
During the middle of the day we estimated the highest α-values for *T. longicornis*. This copepod was almost entirely selected between 12:00 and 15:00 (read: 13:30) by sprat (α-value: 0.63). Starting in the evening, sprat showed highest preference-values for *Podon* spp. during the night and early morning, almost exclusively selecting *Podon* spp.

from 18:00 to 00:00 hours with a maximum α-value of 0.87. During the evening and night, *T. longicornis* was negatively selected. The third species that sprat was occasionally selecting positively was *E. nordmanni*. *B. longispina maritima* was negatively selected or totally avoided through the entire diurnal cycle (figure 14 B, black bars). However, when comparing the selectivity indices from our method (black bars) and the estimation by the commonly used method (grey bars) with vertically integrated plankton samples (night: 0 - 40 m, day: 41 - 80 m) we observed different results. A striking difference was observed in *B. longispina maritima*, where as mentioned, sprat were totally avoiding this species, as estimated from our vertically resolved method, while the results from the other method indicated that sprat was actively selecting *B. longispina maritima* through almost the entire diurnal cycle (α > 0.9). The other differences in the results of the different methods are that except for *B. longispina maritima* our estimates were generally higher and at some points in time our method indicated positive selection, while the other method indicated negative selection (e.g. *T. longicornis*, *E. nordmanni* and *Podon* spp.). Both methods indicated that the other prey found in the stomachs like *Acartia* spp., *C. hamatus* and *P. acuspes* were entirely negatively selected by sprat. Nevertheless, these species were consumed in high numbers (figure 14 A). 14.1% of the diet of sprat (by numbers) consisted of *Acartia* spp., 9.7% of *P. acuspes* and 8% of *C. hamatus*.

The stage-specific selectivity of *T. longicornis* copepodites (figure 18 B) revealed that sprat was positively selecting adult females and males and c4/5 during certain periods, but also negatively selecting these stages during other periods. Another interesting observation was that in the period from 18:00 to 21:00 hours (i.e. 19:30 in figure 17 B) sprat were only selecting copepodite stages 1-3 positively (α = > 0.8), while all other stages where negatively selected. Copepodite stages c4/5 were consumed in highest numbers (figure 17 A) with 44.7% followed by females (23.8%) and males (22.1%). When comparing the estimations from our method with the results from pooled estimations (see material & methods) it became obvious that the pooled method was not able to express e.g. the observed positive selection of c1-3 (from 18:00 to 21:00 in figure 17 B), as both night and day results indicated a negative selection for c1-3.

Herring

Small herring (< 20 cm)

As in sprat only *T. longicornis*, *B. longispina maritima*, *E. nordmanni* and *Podon* spp. were positively selected by small herring (figure 15 B). While in sprat the highest selectivity indices for *T. longicornis* were observed during the afternoon, high values were observed from 0:00 to 18:00 (α > 0.7). Starting at 18:00 to midnight small herring were still positively selecting *T. longicornis*, but at much lower values as during the period mentioned before. The cladocerans *B. longispina maritima*, *E. nordmanni* and *Podon* spp. were mainly selected positively during evening or night, while they were mainly negatively selected (*E. nordmanni* and *Podon* spp.) or not consumed at all (*B. longispina maritima*) during the day. *B. longispina maritima* was somehow only selected and consumed respectively during the night from 21:00 to 0:00 (figure 15 B, 22:30). When comparing both methods, the resulting selectivity estimates were similar. Both methods indicated that the other prey found in the stomachs like *Acartia* spp., *C. hamatus* and *P. acuspes* were entirely negatively selected by small herring. Nevertheless, these species were partly found in high numbers in the stomachs (figure 15 A: *P. acuspes* 8.6%, *Acartia* spp. 3.1%)

The stage-specific selectivity of *T. longicornis* copepodites (figure 18 B) indicated that small herring were positively selecting adult females and males and c4/5 during certain periods, but also negatively selecting these stages during other periods. Females were selected at higher values during the days (α = 0.35 - 0.40) than males, which were slightly positively selected or randomly consumed. Copepodite stage c5 was positively selected through the entire investigation period, whereas c3 was only positively selected at night from 0:00 to 03:00, during the remaining times of day this stage and c2 were negatively selected. The highest abundances in numbers were observed for c5 with 34.0%, followed by females with 19.9% and males with 17.7% (figure 18 A). As in sprat, the comparison of the two estimation methods for copepodite stages revealed that the pooled method was unable to account for the positive selection of c3 during a certain period.

Large herring

In large herring *T. longicornis*, *B. longispina maritima*, *E. nordmanni* and *Podon* spp. were positively selected (figure 17 B). Additionally *P. acuspes* was positively selected from 03:00 to 6:00 and from 12:00 to 15:00. The results for *B. longispina maritima* were not displayed, as the results were similar to the results from the small herring, only selecting and consuming respectively *B. longispina maritima* from 21:00 to 00:00. *T. longicornis* was positively selected through the day with highest α-values between 15:00 and 18:00 with 0.9. During two time periods, between 3:00 and 6:00 and 21:00 and 00:00 *T. longicornis* was negatively selected or close to randomly consumed (α-values close to 1/k-line). 59.4% (by numbers) of the diet consisted of *T. longicornis*, followed by *P. acuspes* with 23.4% (figure 16 A). *Podon* spp. were only positively selected from 03:00 to 06:00, and were negatively selected during the remaining times of day. As in small herring the comparison of the two selectivity estimation measurements resulted in similar values, with few exceptions like *E. nordmanni*, where our method indicated positive selection between 12:00 and 15:00, while the other method indicated a negative selection for this time period.

As the stage-specific selectivity of *T. longicornis* copepodites was illustrated and described for small herring, we chose to display the stage-specific selectivity for *P. acuspes*, the second copepod that was positively selected by large herring at certain periods. The highest α-values were estimated for copepodite stage c5 and from 15:00 to 18:00 for c4 during the day, indicating a strong positive selection for these stages (figure 19 B). This positive selection is confirmed by the stage-specific diet composition for P. acuspes (figure 19 A), where 50% (by numbers) of the consumed stages were c5, followed by females (22.4%) and c4 (22.2%). During the same period, females were positively selected at low α-values or randomly consumed, males were only positively selected during one period (12:00 to 15:00), while being negatively selected or not consumed at all in the remaining time. Females were positively selected at night from 21:00 to 00:00 hours at similar α-values as c5 in the same time period with approx. 0.4. Copepodite stage c3 were randomly fed on, or slightly positive selected in the afternoon, while the remaining time being negatively selected or not consumed at all. Although our method indicated a weak positive selection during the day, followed by stronger selection during the first part of the night, the pooled method indicated relatively high α-values for the day and the night with 0.4 and 0.5.

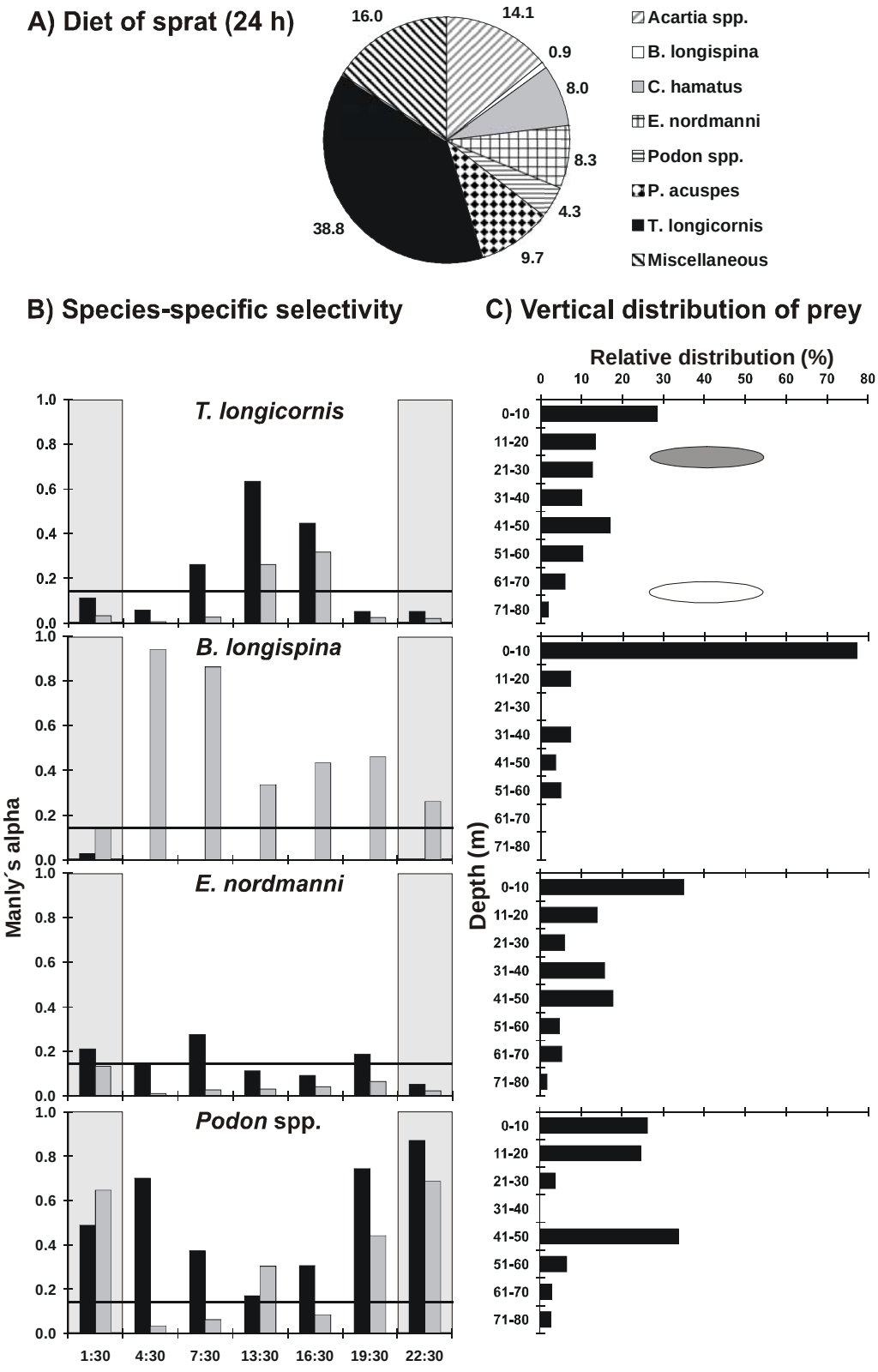

Figure 14 A) Diet composition of sprat (24 h mean). B) Species-specific selectivity indices for important prey species. Black bars indicate results from our method, grey bars indicate results from commonly used methods. Solid horizontal line indicates 1/k or random feeding. Lightly shaded grey boxes indicate night. C) Vertical distribution of prey species in left graph columns (mean over 24 h). Closed and open ellipse indicate weighted mean depth of herring and sprat during night and day.

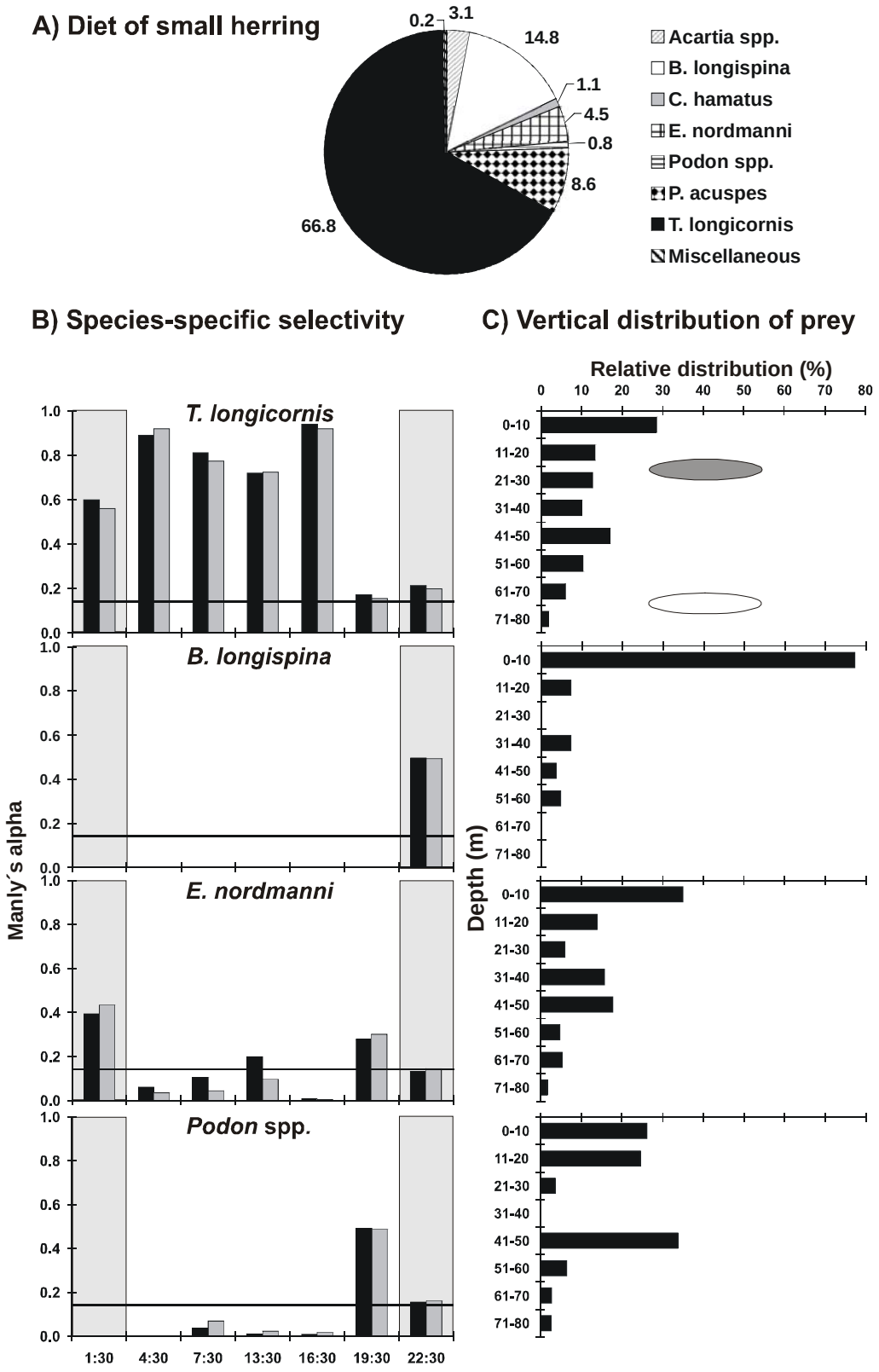

Figure 15 A) Diet composition of small herring (24 h mean). B) Species-specific selectivity indices for important prey species. Black bars indicate results from our method, grey bars indicate results from commonly used methods. Solid horizontal line indicates 1/k or random feeding. Lightly shaded grey boxes indicate night. C) Vertical distribution of prey species in left graph columns (mean over 24 h). Closed and open ellipse indicate weighted mean depth of herring and sprat during night and day.

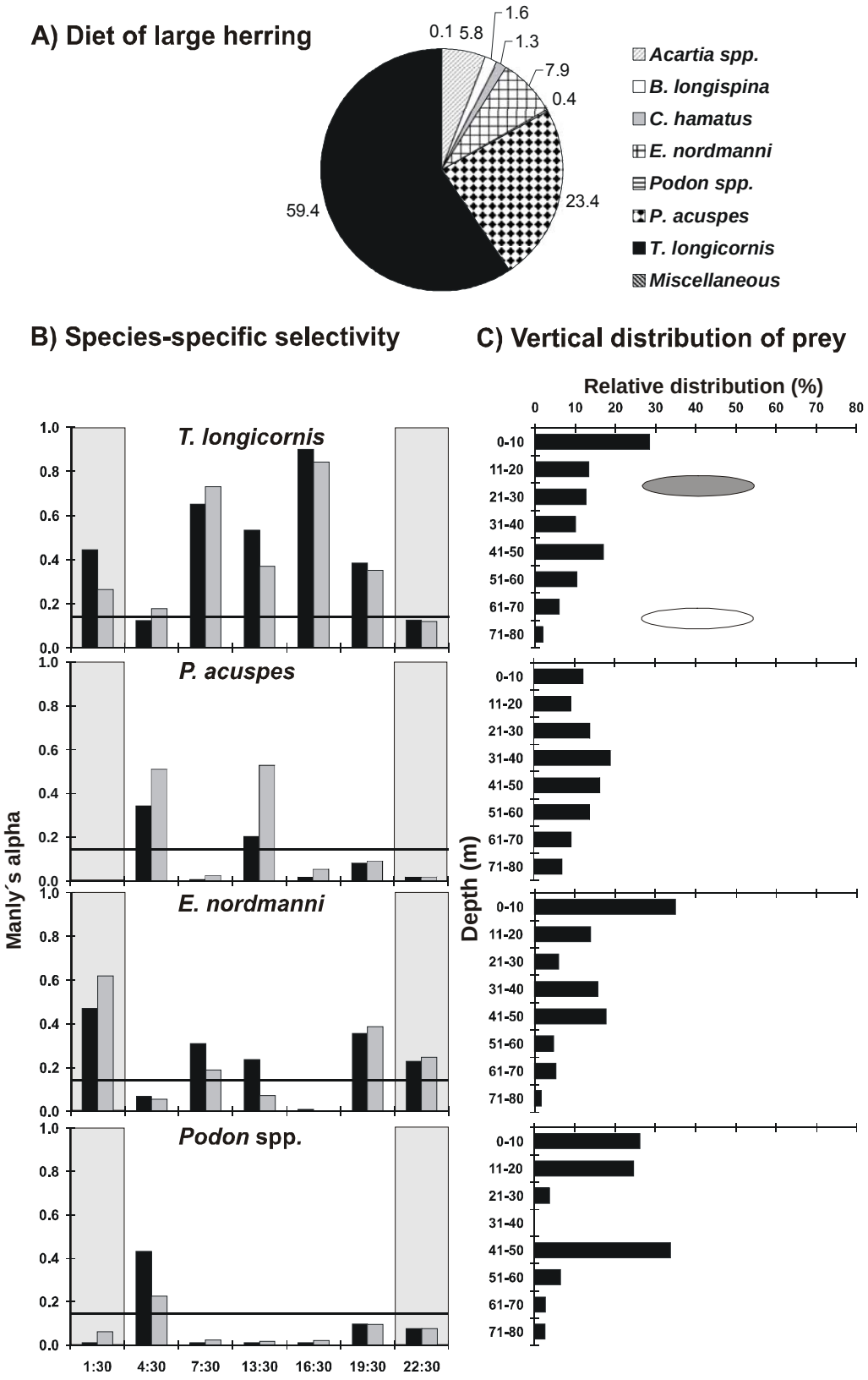

Figure 16 A) Diet composition of large herring (24 h mean). B) Species-specific selectivity indices for important prey species. Black bars indicate results from our method, grey bars indicate results from commonly used methods. Solid horizontal line indicates 1/k or random feeding. Lightly shaded grey boxes indicate night. C) Vertical distribution of prey species in left graph columns (mean over 24 h). Closed and open ellipse indicate weighted mean depth of herring and sprat during night and day.

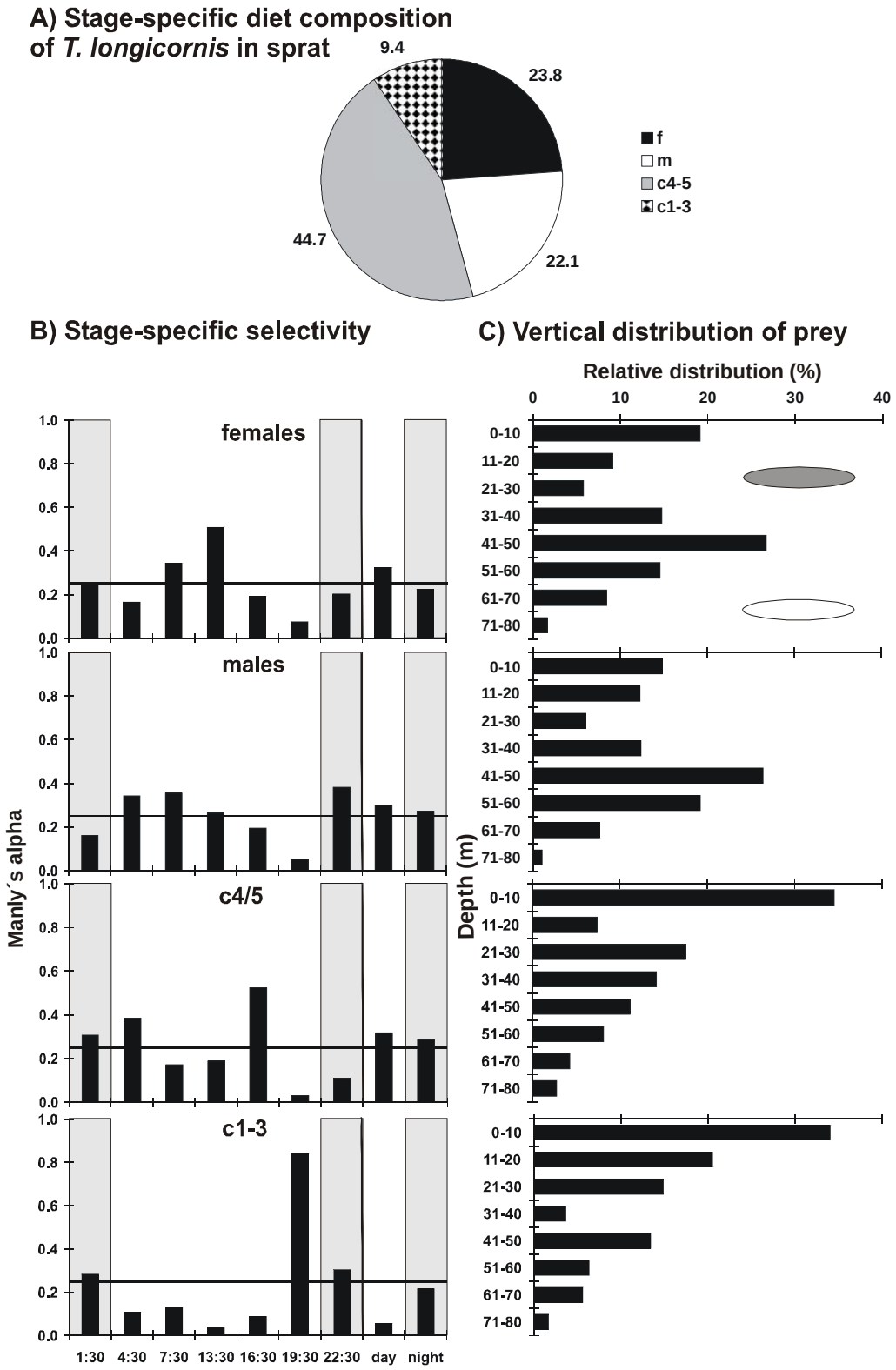

Figure 17 A) Stage-specific diet composition for *T. longicornis* in sprat (24 h mean). B) Stage-specific selectivity indices. Solid horizontal line indicates 1/k or random feeding. Lightly shaded grey boxes indicate night. The results of the selectivity estimations from the mean stomach contents during day and night are displayed by the two bars on the right side of each graph. C) Vertical distribution of copepodite stages in left graph columns (mean over 24 h). Closed and open ellipse indicate weighted mean depth of herring and sprat during night and day.

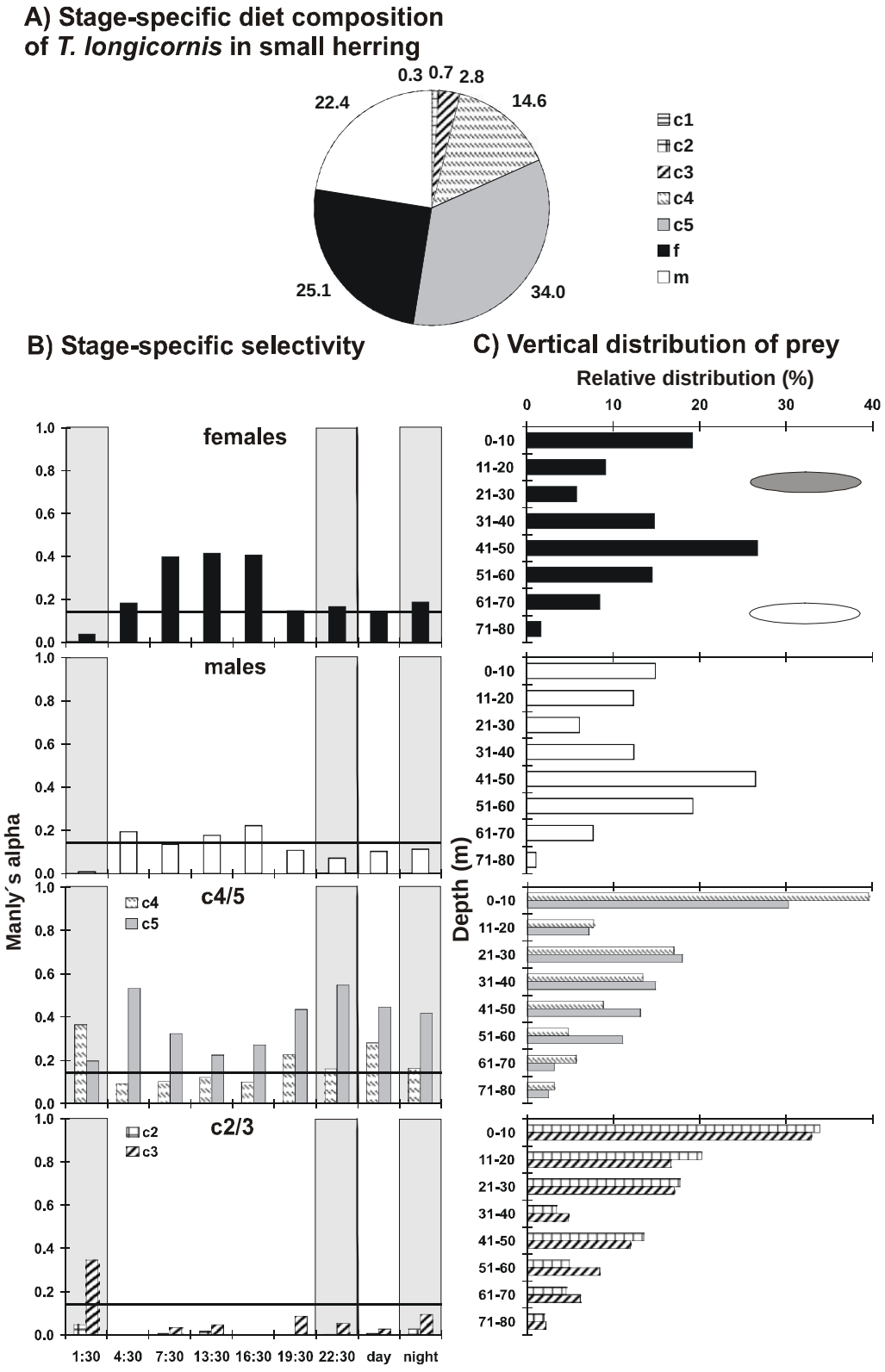

Figure 18 A) Stage-specific diet composition for *T. longicornis* in small herring (24 h mean). B) Stage-specific selectivity indices. Solid horizontal line indicates 1/k or random feeding. Lightly shaded grey boxes indicate night. The results of the selectivity estimations from the mean stomach contents during day and night are displayed by the two bars on the right side of each graph. C) Vertical distribution of copepodite stages in left graph columns (mean over 24 h). Closed and open ellipse indicate weighted mean depth of herring and sprat during night and day.

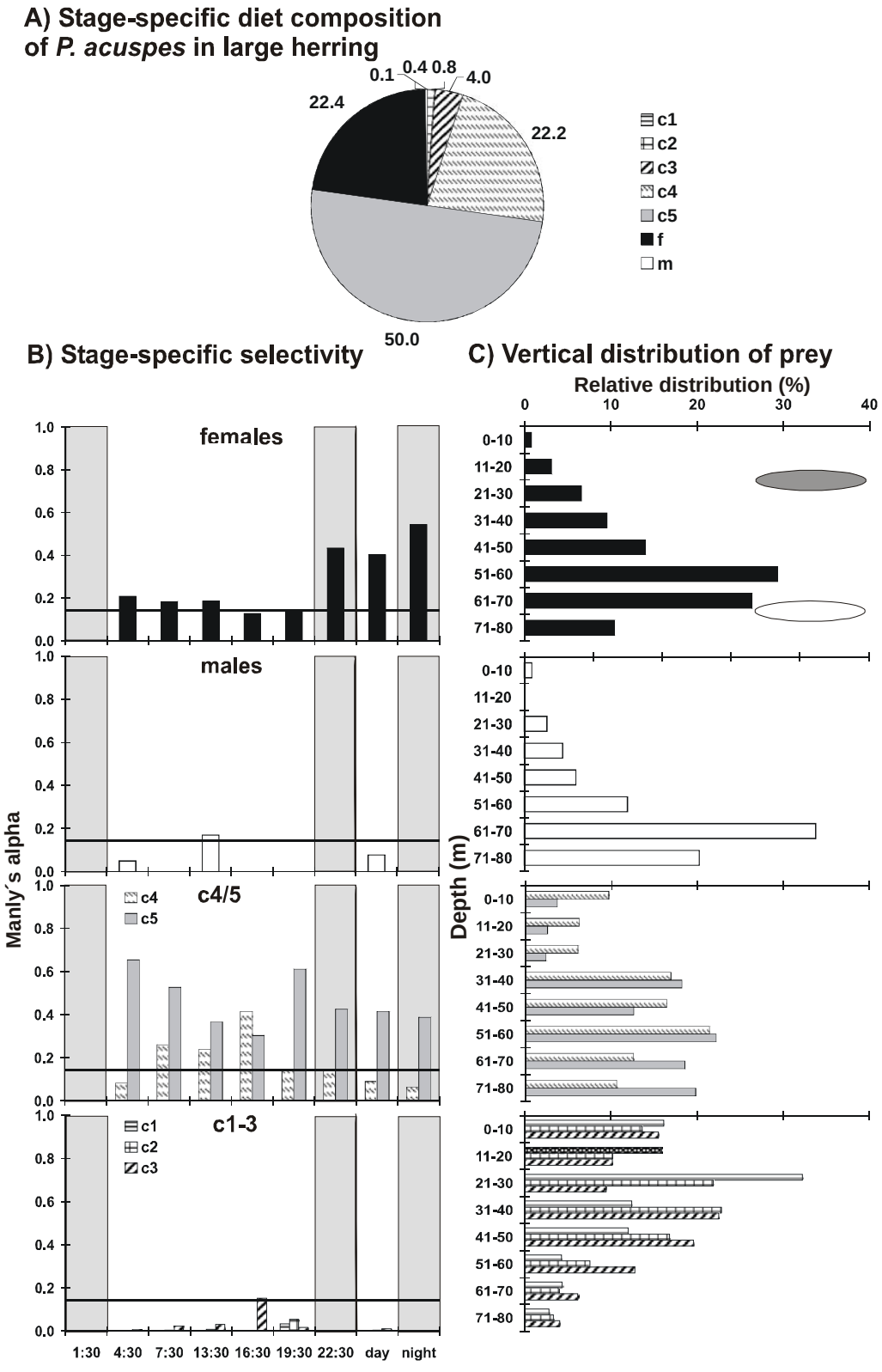

Figure 19 A) Stage-specific diet composition for *P. acuspes* in large herring (24 h mean). B) Stage-specific selectivity indices. Solid horizontal line indicates 1/k or random feeding. Lightly shaded grey boxes indicate night. The results of the selectivity estimations from the mean stomach contents during day and night are displayed by the two bars on the right side of each graph. C) Vertical distribution of copepodite stages in left graph columns (mean over 24 h). Closed and open ellipse indicate weighted mean depth of herring and sprat during night and day.

Impact factor

The results of the estimation of the impact factor for the main prey species selected (*T. longicornis* and *P. acuspes)* were similar for both herring and sprat (figure 20). The grouped impact factors, where all stages per prey species were grouped, were lower than the factors for c4-5 and c6 (females and males) in sprat and lower than the factors for c4 to c6 (females and males) in herring. The highest factor in sprat was estimated for males (m) of *P. acuspes*, where the value of 0.0034 was approx. 17 times higher than the grouped value. However, this high value is rather an artefact caused by the low numbers of *P. acuspes* males in the plankton samples. The highest factor in herring was estimated for c5 of *T. longicornis*, where the value of 0.13 was more than twice as high as the grouped value.

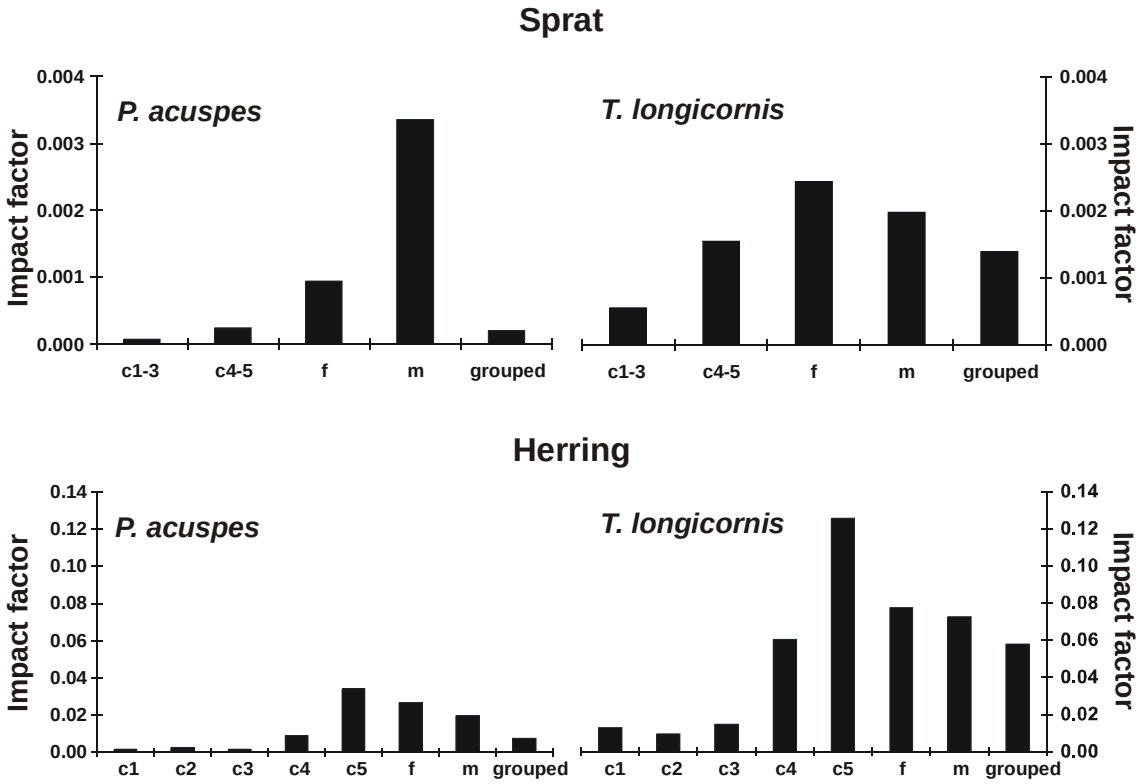

Figure 20) Impact factors for stages of *T. longicornis* and *P. acuspes* and grouped stages of both species.

Discussion

Diet composition, niche overlap and stomach fullness

In the present study, adult Baltic Sea sprat were exclusively zooplanktivorous. Herring were also mainly zooplanktivorous, with few exceptions. Mysids occurred in low numbers in only a few stomachs. These results agree with previous studies (Rudstam et al. 1992; 1994, Arrhenius 1996, Szypula et al. 1997, Möllmann & Köster 1999, Casini et al. 2004, Möllmann et al. 2004). In our study, sprat consumed, with few exceptions, only copepods and cladocerans, with *Temora longicornis, Pseudocalanus acuspes* and *Acartia* spp. being the most important copepods. The most important cladocerans in the stomachs of sprat were *Evadne nordmanni* and *Podon* spp. This is confirmed by

Möllmann & Köster (1999), Casini et al. (2004) and Möllmann et al. (2004) who observed similar patterns in the southern-central and south-eastern Baltic Sea.
The diet of Baltic herring was dominated by *T. longicornis* and *P. acuspes*. In the stomachs of smaller herring, *T. longicornis* was more abundant than in larger herring, where *P. acuspes* was fed on to a higher extent. This was also observed by Möllmann & Köster (1999), Casini et al. (2004) and Möllmann et al. (2004) in the southern Baltic Sea. Agreeing with the authors mentioned above we observed that both sprat and herring were feeding on older copepodite stages of *T. longicornis, P. acuspes*, *Acartia* spp. and *C. hamatus*. The above mentioned investigations did not analyze the diurnal fluctuations of the diet composition. In sprat, as well as in herring there was a dynamic in the prey composition over the diurnal cycle. The prey composition was altering in the course of the day. This is an important fact of the feeding ecology of sprat and herring and has implications for the calculation of daily consumption rates.
The stomach samples in the field are usually taken during the day, on the one hand due to limitations in ship operation and on the other hand due to the assumption that herring and sprat only feed during daylight hours (Köster & Schnack 1994, Arrhenius 1998). This reveals a problem, since the stomach contents represent the prey items that have been consumed during the day. The difference in the diet composition between day and night, as found in this study, would therefore result in an under representation of species consumed during evening and at night. Nevertheless, we observed peaks of mean stomach content during the day and a decreasing stomach content during the evening and night, with lowest values around 02:00 hours. We found freshly ingested prey at every fishing station and every time of day and night, indicating that both species feed at night, but to a lower extent than during the day. Batty et al. (1990) demonstrated that herring are able to filter-feed at low light intensities. Filter-feeding has not been reported in sprat. Our results suggest that sprat possibly feed in darkness, at least in June, where the nights at high latitudes in the northern hemisphere are only a few hours long. Thus, the impact of the different prey compositions between day and night should be considered in consumption estimations in certain seasons.
There was a strong niche overlap in the diets of sprat and herring, with a minimum of 34% during the early morning and a maximum of 83% in the afternoon. Besides the observed minimum, the niche overlap was above 50% during the entire investigated time range. Accordingly sprat and herring are intensive prey competitors. Möllmann et al. (2004) observed in the central Baltic Sea an increase in the niche overlap in the end of the 1990`s with highest overlaps in spring and summer at 47 to 48%. The consequences of this increased niche overlap will be discussed later.

Prey selectivity

A trend in the prey selectivity was observed for sprat over the diel cycle. During the night and early morning cladocerans were clearly preferred over copepods. The cladoceran *Podon* spp. had high α-values in this period. During the day *T. longicornis* was the most preferred prey. The vertical distribution of the fish can help to explain this observation. During the daytime the fish gathered in tight shoals between 60 and 80 m below the halocline where they were feeding, which is confirmed by the increasing mean stomach content at daytime with the highest values around 15:00 hours. At night they were dwelling above and at the upper limit of the thermocline at approx. 20 m.
Cladocerans are generally at their seasonal peak during this time of the year, occurring in high abundances of up to 230 $n*m^{-3}$ in *Podon* spp., 700 $n*m^{-3}$ in *E. nordmanni* and $13*10^3$ $n*m^{-3}$ in *Bosmina coregoni maritima* in subdivision 26 (Möllmann et al. 2002). The highest mean abundances of cladocerans were observed in our study in the upper 30 m of the water column (*B. coregoni maritima*: 26 $n*m^{-3}$, *E. nordmanni*: 666 $n*m^{-3}$ and

Podon spp.: 66 n*m^{-3}) so that the probability of encounter was low during the day when the fish dwelled mostly below 60 m (figure 14 C). The probability of sprat encountering copepods during the day, however, was high based upon the vertical distribution of copepods. The WMD of the older stages of *T. longicornis* was below 35 m (c5: 33 m, c6: 44 m) and of *P. acuspes* below 50 m (c5: 53 m, c6: 54 m). The WMD of the other two important copepods (*Acartia* spp. and *C. hamatus*) were higher in the water column with *Acartia* spp. at approx. 30 m (c5: 29 m, c6: 32 m) and *C. hamatus* above 30 m (c5: 26 m, c6: 28 m).
Although the distribution of *O. similis* was deeper in the water column (c5: 55 m, c6: 49 m) this species was rarely present in gut contents and selectivity indices could not be calculated.
Herring performed the same diurnal vertical migration as sprat (Nilsson et al. 2003, Stepputtis et al. In Prep.), dwelling below 60 m during the day and moving upward in the water column and dispersing at dusk. Consequently they encountered the same prey field at the same time as sprat.
Our results indicate that only one copepod, *T. longicornis*, was actively selected by sprat and herring. Large herring were also actively selecting *P. acuspes* at two periods during the investigated time. The other copepods were negatively selected or avoided. This agrees with the results of Shvetsov & Rudneva (1983) for the eastern Baltic, where sprat showed a positive preference for *T. longicornis*. In the southeastern Baltic Sea, the results of Patokina & Feldman (1998) indicated the importance of *P. acuspes* as prey for sprat in May/June. However, in the present study, *P. acuspes* was avoided by sprat and small herring and at most times by large herring. Möllmann et al. (2004) described a switch of both predator species from mainly older copepodites (c4-c6) of *Pseudocalanus* sp. in May to *T. longicornis* in June/July. Despite the fact that *P. acuspes* was avoided by sprat and only at two time periods was positively selected by large herring, they were consumed in high numbers due to their relatively high abundance over the entire water column (c4-6: 165 n*m^{-3}). Both *T. longicornis* and *P. acuspes,* as relatively large copepods (Hansen et al. 2006), are very important in the diet of sprat and herring. In comparison to the most important prey copepod *T. longicornis*, *Acartia* spp. were found in the diet but were negatively selected, probably because of their relatively small size and their alertness to hydrodynamic signals that results in a rapid escape response (Viitasalo et al. 2001).
Sprat and herring were partly size-selective, preferring mainly adults and older copepodites (c5 and c6), the youngest copepodites being found mostly in much smaller proportions in stomachs. The pattern of selectivity for copepodite stages of the most important copepod prey species, *T. longicornis* and *P. acuspes,* was not constant. Depending on the time of the day, herring and sprat were selecting different stages. Sandström (1980) and Flinkman et al. (1992) observed in the Baltic Sea that size and visibility of prey were both important factors in the selection of prey by herring and that generally largest food items were selected. We can confirm this, as our results indicated that older copepodite stages (c5-c6) were positively selected during most investigated periods. Sprat and herring both preferred adult females of *T. longicornis* during daytime. However, some of our results contradict their observations, specifically that both sprat and herring selected smaller copepodite stages, as indicated by higher α-values during certain time periods. There must be an additional factor that influences the selectivity of sprat and herring. One explanation may be the vertical migration of *T. longicornis* and the occurrence of older stages deeper in the water column which increases the overlap of these stages with their predators. At night, when the fish dwell at depths of ≤ 20m, they more frequently encounter younger *T. longicornis* stages. As a result of increased encounter rate, the fish may become habituated, preferring this stage over larger ones that would be more energetically profitable. A switch from snatching single particles to

filter-feeding at low light intensities, which is only known for herring (Batty et al. 1990), would explain a passive selection of the most abundant prey items, depending on different escape responses of the stages. If this was the explanation for the positive selection of younger stages it would lead to the conclusion that sprat were also able to filter-feed, as we have observed a positive selectivity for younger stages in both herring and sprat. It needs to be pointed out that, during the periods of lowest light levels during the night, the consumption was much lower than during the day, as indicated by very low stomach content during night. Therefore selectivity indices may be high, but the actual consumption is low.

Most studies investigating selective feeding by herring and sprat lack a detailed description of the prey field encountered by the predators. The plankton samples used for the estimation of selectivity indices were, with the exception of the investigation of Hansson et al. (1990), not vertically- or stage-/sex- resolved (Sandström 1980, Flinkman et al. 1992, Arrhenius 1996, Casini et al. 2004). As the knowledge about the selective feeding behaviour of predators is very important in understanding and reliably quantifying top-down processes (Carpenter et al. 1985, Carpenter & Kitchell 1993), this small-scale investigation was needed to understand in detail the selective behaviour of herring and sprat. Through our estimates of vertically-resolved prey selectivity it was possible to more thoroughly describe the dynamics of feeding and prey choice of both species. This was one of our main aims, to be able to describe the diurnal prey selectivity of sprat and herring. Another aim was to compare our vertically-resolved estimates with those obtained from commonly-used methods described above. Such a comparison could detect limitations and misleading results of both methods. The first striking observation was that the commonly-used methods, were unable to detect and illustrate diel fluctuations in the prey selectivity of herring and sprat. This was due to the fact that samples of predators and prey were taken either during the day or night over a limited time period. Sampling in this manner leads to generalizations about the selectivity of these clupeids e.g., strict size-selectivity where these fish feed mostly on egg-sac carrying females and adult copepods. Although older stages were positively selected during certain periods, at some periods these fish also positively selected (actively consumed) younger copepodite stages like *T. longicornis* c1-3 in sprat and c3 in herring. Commonly used methods would not detect this selection. Since most investigations were not copepodite stage-resolved these realities could not be observed. Our observations revealed that the process of food selection is dependent on other factors than merely size and visibility. To completely understand the feeding ecology of these clupeids, our sampling scheme appears to be the better alternative.

When comparing the results of our vertically-resolved prey selectivity with the results from the commonly used vertically pooled prey-distributions (day: 41 - 80 m, night: 0 - 40 m) we observed that in both small and large herring the tendencies of both methods were, with few exceptions, similar, meaning that the same prey was positively or negatively selected at the same time. This leads to the conclusion, that in the case of our study area with a mean depth of 85 m, the vertical resolution in the plankton samples at 10 m steps is not necessary and a pooled plankton sampling (day: 41 - 80 m, night: 0 - 40 m) is good enough to come up to reasonable results.

In the case of sprat the situation appears to be different, as we observed a striking difference in the selectivity of *B. longispina maritima* by the two methods. According to our method *B. longispina maritima* was only consumed, although negatively selected, during the night from 00:00 to 03:00, whereas according to the pooled method *B. longispina maritima* was consumed in proportion to its appearance during the same period, while this species was strongly selected during the remaining period of the diel cycle.

The answer to why *B. longispina maritima* was not at all selected and consumed, according to our method, can be given by the vertical distribution of this species. This species dwells in the surface-waters (tables 1, 2; figure 14 C) with a maximum relative distribution of more than 75% in the uppermost 10 m of the water column, and was totally absent below 60 m. As we used the 10 m plankton composition above and below the weighted mean depth of the fish, there were actually no *B. longispina maritima* present in the plankton samples, e.g. during the day, so that we were not able to estimate selectivity indices for this species, with the exception of one time period between 00:00 and 03:00 at night. As the plankton composition during the day was pooled together from 41 to 80 m in the other method, when the fish were dwelling at approx. 70 m, the result was a very low abundance of this species in the plankton samples, leading to a very high selectivity index, as *B. longispina maritima* were found in low numbers in the stomachs of discrete sprat over the entire cycle.
The fact that only 0.9% of sprat diet (by numbers) consisted of *B. longispina maritima* supports our method of estimating the selectivity. Sprat were feeding on this species at night, where it occurred at highest abundances. According to the other method sprat was feeding highly selective during the day on *B. longispina maritima*, when there were low abundances of this prey, and then at night, where there was a much better predator-prey overlap near the surface, sprat was consuming this prey in proportion to its abundance or positively selecting it at a low α-value. These α-values appear very high when bearing in mind that only 0.9% of the diet over the entire investigated period consisted of *B*. *longispina maritima*, which was at its seasonal peak.
The conclusion of the comparison of the two methods is that reasonable selectivity estimates can be obtained from pooled plankton samples only if the potential prey species are more or less evenly distributed with respect to water depth. If they are unevenly distributed the resulting selectivity estimates can be biased. In order to detect fluctuations or changes in the selectivity of herring and sprat over the diel cycle, and thereby gaining further knowledge on their feeding ecology, successive sampling over different periods of a circadian cycle are needed.

Impact factor

The results of the comparison of the grouped and stage-specific impact factor revealed the disadvantage of the estimation of non stage-specific prey-selectivity. Grouped values or selectivity estimates underestimated the effect of the predator on the older stages of copepods. Our results demonstrated that sprat and herring were size-selective feeders, which removed older copepodite stages (c5) and reproducing individuals (c6), thereby lowering the production of the zooplankton. Copepods are the main prey items of both sprat and herring in the Baltic Sea (e.g. Shvetsov et al. 1983, Möllmann & Köster 1999, Möllmann et al. 2004). Our results suggest that the extent of top-down regulation of copepods by clupeids in the Baltic Sea may not be adequately assessed when stage-resolved methods are not employed.

Conclusions

1) Most important prey species of herring and sprat by numbers were copepods *Temora longicornis*, *Pseudocalanus acuspes* and *Acartia* spp. along with cladocerans *Evadne nordmanni*, *Bosmina longispina maritima* and *Podon* spp. Niche overlap of herring and sprat was high (40 to 80%) over the investigated period.
2) Sprat strongly selected *T. longicornis* as prey during the day and mainly *Podon* spp. during the night. Small (> 20 cm) and large (> 20 cm) herring selected *T.*

longicornis during most of the investigation period with short phases in which *E. nordmanni, Podon* spp. and *P. acuspes* were selected.

3) Both sprat and herring selected adult males and females and older copepodites. During certain periods, younger stages (c1-3) were also actively selected. Commonly-used methods of estimating prey selectivity, where samples were taken during dusk or at night, and copepods were not stage-resolved, were unable to detect diurnal variations in prey-selectivity that existed in our study.

4) The use of pooled plankton samples (day: 41 - 80 m, night: 0 - 40 m) and our vertically-resolved plankton sampling resulted in similar selectivity estimates for prey species that were equally distributed at different water depths, but yielded biased estimates of selectivity in prey species with uneven vertical distributions.

5) The estimation of an impact factor (IF) revealed the importance of stage-resolved selectivity investigations. Grouped results were underestimating the feeding impact on older copepodite stages c4 and c5 and reproducing females and males (c6).

References

Arrhenius, F. & Hansson, S. (1993). Food consumption of larval, young and adult herring and sprat in the Baltic Sea. Marine Ecology Progress Series 96, 125-137.

Arrhenius, F. (1996). Diet composition and food selectivity of 0-group herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.) in the northern Baltic Sea. ICES Journal of Marine Science 53, 701-712.

Arrhenius, F. (1998). Food intake and seasonal changes in energy content of young Baltic Sea sprat (*Sprattus sprattus* L.). ICES Journal of Marine Science 55, 319-324.

Batty, R.S., Blaxter, J.H.S. & Richard, J.M. (1990). Light intensity and the feeding behaviour of herring, *Clupea harengus*. Marine Biology 107, 383-388.

Carpenter, S.R., Kitchell, J.F. & Hodgson, J.R. (1985). Cascading trophic interactions and lake productivity. BioScience 35, 634-639.

Carpenter, S.R. & Kitchell, J.F. (1993). The trophic cascade in lakes. Cambridge University Press, Cambridge.

Casini, M., Cardinale, M. & Arrhenius, F. (2004). Feeding preferences of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the southern Baltic Sea. ICES Journal of Marine Science, 61, 1267-1277.

Flinkman, J., Vuorinen, I. & Aro, E. (1992). Planktivorous Baltic herring (*Clupea harengus*) prey selectively on reproducing copepods and cladocerans. Canadian Journal of Fisheries and Aquatic Science 49, 73-77.

Flinkman, J., Aro, E., Vuorinen, I. & Viitasalo, M. (1998). Changes in northern Baltic zooplankton and herring nutrition from 1980s to 1990s: top-down and bottom-up process at work. Marine Ecology Progress Series 165, 127-136.

Giesen J (2001) Calculating the elevation of the sun with spread sheet program; http://www.jgiesen.de/SME/tk.

Hansen, F., Möllmann, C. Schütz, U. & Neumann, T. (2006). Spatio-temporal distribution and production of calanoid copepods in the central Baltic Sea. Journal of Plankton Research Vol.28, No.1, 39-54.

Hansson, S. Larsson, U. & Johansson, S. (1990). Selective predation by herring and mysids and zooplankton community structure in a Baltic Sea coastal area. Journal of Plankton Research Vol. 12 no 5, 1099–1116.

Huse, I. & Korneliussen, R. (2000) Diel variation in acoustic density measurements of overwintering herring (*Clupea harengus* L.). ICES Journal of Marine Science 57(4), 903–910.

ICES (2001) Manual for the Baltic Fisheries Assessment Working Group. ICES C.M. ACFM:18.

Köster, F.W. & Schnack, D. (1994). The role of predation on early life stages of cod in the Baltic. Dana 10, 179-201.

Krebs, C.J. (1999). Ecological Methodology. 2nd edition. Benjamin/Cummings Series. 620 pp.

Möllmann, C. & Köster, F.W. (1999). Food consumption by clupeids in the Central Baltic: evidence for top-down control?. ICES Journal of Marine Science, 56 Suppl., 100-113.

Möllmann, C., Köster, F.W., Kornilovs, G. & Sidrevics, L. (2002). Long-term trends in abundance of cladocerans in the Central Baltic Sea. Marine Biology 141, 343-352.

Möllmann, C., Kornilovs, G., Fetter, M. & Köster, F.W. (2004). Feeding ecology of central Baltic Sea herring and sprat. Journal of Fish Biology 65, 1563-1581.

Möllmann, C., Temming, A., Hirche, H.-J., Stepputtis, D., Bernreuther, M. & Köster, F.W. (2004). Fish predation control of key copepod species in the Bornholm Basin. Globec International Newsletter April 2004, 15-17.

Nilsson, L.A.F., Thygesen, U.H., Lundgren, B., Nielsen, B.F., Nielsen, J.R. & Beyer, J.E. (2003). Vertical migration and dispersion of sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) schools at dusk in the Baltic Sea. Aquatic Living Resources 16, 317-324.

Patokina, F.A. & Feldman, V.N. (1998). Peculiarities of Trophic Relations between Baltic Herring (*Clupea harengus membras* L.) and Baltic Sprat (*Sprattus sprattus balticus schneider*) in the South-Eastern Baltic Sea in 1995–1997. C.M. 1998/CC: 7 Population Biology.

Rudstam, L.G., Hansson, S., Johansson, S. & Larsson, U. (1992). Dynamics of planktivory in a coastal area of the northern Baltic Sea. Marine Ecology Progress Series Vol. 80, 159-173.

Rudstam, L.G., Aneer, G. & Hilden, M. (1994). Top-down control in the pelagic Baltic ecosystem. Dana, vol. 10, 105–129.

Sandström, O. (1980). Selective feeding by Baltic herring. Hydrobiologia Vol. 69, 199-207.

Shvetsov, F.G., Starodub, M.L. & Sidrevits, L.L. (1983). The daily feeding rhythm of the Baltic sprat, *Sprattus sprattus balticus* (Clupeidae). Journal of Ichthyology Vol.23, no.2, 99-105.

SonarData (2001) EchoView Software. www.sonardata.com

Stepputtis, D., Böttcher, U., Götze, E., Köster, F., Hinrichsen, H.H., Schmidt, J. Diel vertical migration of sprat, herring and cod in the central Baltic Sea; (In Prep.).

Szypula, J., Grygiel, W. & Wyszynski, M. (1997). Feeding of Baltic herring and sprat in the period 1986-1996 in relation to their state and biomass. Bulletin of the Sea Fisheries Institute 3 (142), 73-83.

Viitasalo, M., Flinkman, J. & Viherluoto, M. (2001). Zooplanktivory in the Baltic Sea: a comparison of prey selectivity by *Clupea harengus* and *Mysis mixta*, with reference to prey escape reactions. Marine Ecology Progress Series 216, 191-200.

Conversion efficiency and temperature dependency of metabolic rate in juvenile herring (*Clupea harengus* L.)

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Abstract

The relationship between rates of food consumption (*C*) and somatic growth (*G*) and the effect of temperature on weight loss during starvation was examined in 9 to 10 cm total length (*TL*) (1.0 to 1.5 g dry weight, *DW*) juvenile Atlantic herring (*Clupea harengus* L.) in the laboratory. One feeding-growth trial was conducted at 16°C using groups of herring feeding on known rations of brine shrimp (*Artemia* spp.) nauplii to quantify gross and net growth efficiency. Starvation weight loss trials were performed using groups of herring maintained at 9.7, 14.2 and 17.9°C to examine the influence of temperature (*T*) on starvation weight loss (a proxy for metabolic rate, *M*). Gross growth efficiency (GGE=100 * *G*/*C*) at 16°C was 25 to 30% at highest daily rations (5.8 - 6.6% body weight, *BW* (*DW*)). The maintenance ration (C_{maint} = *C* at zero *G*) was equal to 517 J * fish^{-1} * day^{-1} and 0.020 g *DW* * g *DW* $^{-1}$ * day^{-1} (2.0% day^{-1}). The net growth efficiency (100 * *G*/(*C*-C_{maint})) at 16°C was 52% (J * fish^{-1} * day^{-1}). Changes in the ratio of nucleic acids (RNA/DNA, *RD*) in herring muscle tissue were strongly related to somatic growth (*G*, % *DW* * d^{-1} = 1.88 * *RD* - 2.94, r^2 = 0.89). The effect of *T* (9.7 to 17.9°C) on *M* was described by an exponential model M = a * e ^{b*T} with b = 0.071 (Q_{10} = 2.0, J * g *DW* $^{-1}$ *day^{-1}) and b = 0.080 (Q_{10} = 2.2, J * fish^{-1} * day^{-1}). This was the first study to investigate the influence of temperature on the metabolic rate of juvenile Atlantic herring under stress-free conditions. Additionally, the first quantification of gross and net growth efficiency of juvenile herring using live food was accomplished.

Introduction

Due to a lack of detailed physiological studies conducted on Atlantic herring (*Clupea harengus*), all of the bioenergetics models previously constructed for this species (Stewart & Binkowski 1986, Rudstam 1988, Arrhenius 1995) suffer from “parameter stealing” and “species-borrowing” (Ney 1993). Herring bioenergetics models have been structured after Kitchell et al. (1977) and parameterized using data collected on a variety of other species including blueback herring (*Alosa aestivalis* Mitchill), alewife (*Alosa pseudoharengus* Wilson) and Atlantic menhaden (*Brevoortia tyrannus* Latrobe). Clearly, obtaining better estimates of the rates of specific energy budget parameters for Atlantic herring would make modeled field estimates of food consumption (or growth) more robust.

Estimates of food consumption (or growth) obtained from bioenergetics models are often particularly sensitive to parameters representing metabolic energy loss. Metabolic rates should ideally be estimated from oxygen consumption rates (respirometry) measured at different levels of activity (e.g. standard metabolic rate, metabolic rate due to activity) or feeding status (SDA = specific dynamic action) at different temperatures and fish body sizes. A number of studies have measured respiration rates of clupeid fishes including the larvae and juveniles of Atlantic herring (Chekunova 1979, Kiørboe et al. 1987, Johnstone et al. 1993) and juvenile Atlantic menhaden (*Brevoortia tyrannus)* (Macy III et al. 1999) and other pelagic fishes including horse mackerel (*Trachurus trachurus)* (Wardle et al. 1996, Herrmann & Enders 2000) and capelin (*Mallotus villosus villosus*) (Karamushko & Christiansen 2002). A second method used to estimate metabolic rates is to measure the rate of weight or energy loss in starving fish. This approach has been applied in a variety of fishes including various tuna species (*Katsuwonus pelamis*, *Euthynnus affinis* and *Thunnus albacares*) (Boggs & Kitchell 1991), northern anchovy (*Engraulis mordax)* (Boggs 1991), juvenile perch *Perca fluviatilis* (Mehner & Wieser 1994) and Pacific sardine *Sardinops sagax* (Logerwell

2001). These starvation experiments should likewise be conducted at different temperatures, fish body sizes and/or swimming speeds using either individuals or small groups.

Laboratory feeding-growth experiments that employ a wide range in feeding levels can also be used to estimate metabolic costs, here expressed as maintenance rations (C_{MAIN}, ration at zero growth). In addition these experiments reveal an estimate of the net growth efficiency (NGE). Two different definitions of net growth efficiency can be found in the literature. The first is the more commonly used ratio of growth to assimilation (100 * [*G*/*A*], Kiorboe et al. 1987) also referred to as K_2 (Wootton 1998). The second is the conversion efficiency of the food consumed in excess of maintenance requirements (100 * [*G*/ (*C* – C_{main})]), also referred to as K_3 (Wootton 1998).
Feeding-growth studies have been previously conducted on a variety of clupeid fishes including juvenile Atlantic herring (De Silva & Balbontin 1974), Northern anchovy (*Engraulis mordax)* (Hunter & Leong 1981, Boggs 1991) and Japanese anchovy (*Engraulis japonicus*) (Takahashi & Hatanaka 1960). These studies estimated gross conversion efficiency K_1 (percentage of the ingested food material that is converted into fish flesh) using a variety of diets including minced mussel, squid and mysids (De Silva & Balbontin 1974), trout pellets (Hunter & Leong 1981) and previously frozen euphausids (Takahashi & Hatanaka 1960, Boggs 1991). No feeding-growth studies have been performed with small food items such as copepods or brine shrimp (*Artemia* spp.) nauplii, which are especially relevant for planktivorous fish.
These feeding-growth studies also allow growth proxies to be calibrated such as nucleic acids (RNA-DNA ratio) (Haines 1973, Foster et al. 1993, Wang et al. 1993, Peck et al. In Prep.). The ratio of RNA-DNA in body tissues can be used to measure the recent growth in fish since it reflects the rate of protein synthesis (e.g., Haines 1973, Wang et al. 1993, Dutil et al. 1998, Peck et al. 2003). The RNA-DNA ratio of muscle tissue sample ideally increases linearly with growth rate, a trend that was observed in similar feeding-growth experiments with post-larval sprat (Peck et al. In Prep.). Fish have a highly plastic growth rate and often respond to environmental changes by changes in growth rate (Haines 1973), and if this is adequately reflected in the RNA-DNA ratio, this ratio is a useful tool in detecting favourable or unfavourable environmental conditions.

The aim of this study was 1) to perform a feeding-growth experiment with microphagous herring using realistic live food for planktivorous fish (brine shrimp, *Artemia* spp. nauplii), 2) to quantify the maintenance ration and 3) the gross (K_1) and net (K_3) growth efficiency and 4) the influence of daily ration on RNA-DNA ratios at one temperature in juvenile herring. We also quantified 5) the metabolic demands of schooling juveniles from rates of somatic energy loss of starved fish at different temperatures. These laboratory trials were conducted to provide more robust estimates of daily rations required for bioenergetics based estimates of the top-down control by clupeid fish on prey resources in the Baltic and North Sea.

Material and methods

Juvenile Atlantic herring (*Clupea harengus* L.) were caught as 0-group with a dip net in the harbours of List on the Island of Sylt (North Sea, Germany) and Havneby on the Island of Røm (North Sea, Denmark). Fish were transferred within a 700 l box with aerated seawater to an 80 m^3 recirculating aquarium facility at the University of Hamburg, Institute for Hydrobiology and Fisheries Science (Hamburg, Germany). Fish were held in large groups in circular tanks (diameter 145 cm) with capacities of 400 to 1000 l for at least six weeks prior to acclimation to experimental conditions. Fish were

fed daily rations of an artificial pelletted diet (Larviva Wean-Ex, Dana Feed AS) and brine shrimp nauplii (*Artemia* spp. INVE Aquaculture). New recirculation seawater was made at regular intervals from marine salt and tap water. Temperature was regulated with a precision of ± 0.1°C. Fish were exposed to a constant day length of 14 h, lights were dimmed from full to minimum (darkness) over a period of 20 min. The salinity was kept constant at 32 (± 0.1) ppt. The temperature and salinity in the tanks were measured daily.

Starvation experiment

The starvation experiment was performed in circular tanks (140 l water volume, 80 cm diameter). An airlift (an air-stone placed into a vertical PVC pipe) was positioned to create a circular current at the surface of the tank. Water was continuously renewed during the experiments at a rate of 2.3 l min^{-1}. Per experimental temperature two tanks were used. 20 days prior to the start of the experiment, 30 herring were transferred into each tank (table 1) and fed *ad libitum* daily rations of brine shrimp nauplii (*Artemia* spp.) and larval pelleted diet (Larviva Wean-Ex, Dana Feed AS). At the start of the experiment 10 fish were removed from each tank (20 per temperature). The fish were rapidly killed by an overdose of anaesthetic (MS-222) and the following parameters were measured: total length (0.1 mm below), weight (0.001 g accuracy) and caloric content. The caloric content was estimated using an adiabatic bomb calorimeter type IKA C4000. For the estimation of caloric content, three to four fish per tank and temperature were ground together and caloric content was estimated from three to five repeated measurements. Water temperatures were 9.7, 14.2 and 17.9 ± 0.1°C. Fish were starved for 251 to 256 deg-days (e.g., at 14.2° for 18 days = 256 deg-days).
At the end of the starvation period, all fish were killed by an overdose of anaesthetic (MS-222 at 0.28 g l^{-1}) and total length, weight and caloric content were measured. Additionally, the protein and fat contents were estimated according to Kjeldahl and Soxhlett methods, respectively. An oxycaloric equivalent of 13.6 J mg O_2^{-1} (Elliott & Davidson 1975, Brett & Groves 1979) was used for the conversion of energy losses to respiration rates.

Table 1) Starvation experiment overview.

Tank no.	Temperature (°C)	Number of fish (initially)	Days starved	Deg-days (= °C x days)
1	9.7	30	26	252
2	9.7	30	26	252
3	14.2	30	18	256
4	14.2	30	18	256
5	17.9	30	14	251
6	17.9	30	14	251

Conversion efficiency experiment

A 21-day laboratory feeding-growth experiment was conducted using groups of juvenile herring (table 5). Prior to the experiment fish were fed brine shrimp nauplii (*Artemia* spp. INVE Aquaculture) *ad libitum* 3-4 times per day over a period of two weeks. Additionally, they were fed larval pellet food sporadically. *Artemia* nauplii were also used as exclusive food in the experiment (energy density: 21502 ± 506 J g *DW* $^{-1}$ at a weight of 0.00229 ± 0.00012 mg * $ind.^{-1}$). For the experiment, groups of 18 herring were transferred into experimental tanks containing 140 l water each (diameter 80 cm). An

airlift (an air-stone placed into a vertical PVC pipe) was positioned to create a circular current at the surface of the tank. Fish were transferred two to three at a time in random order from a stock tank. In parallel, a random subsample of fish was killed by an overdose of anaesthetic (MS-222), measured (0.1 mm below), weighed (0.001 g accuracy) and caloric content was estimated in an adiabatic bomb calorimeter type IKA C4000, as described in the starvation experiment above. In the following 21 days the fish in the different tanks were provided *Artemia* nauplii at distinct rations, fed over the day (table 5). Mean concentrations of *Artemia* nauplii (no. * ml^{-1}) were determined from three counts made on each of three 1-ml subsamples of daily culture. The variability (CV) among the three counts was generally < 11% (CV = 100 * standard deviation/mean).
During the daily feeding period (14 hours), the inflow was closed to ensure that the complete ration of *Artemia* nauplii was available to the herring. At night (10 hours) tanks were switched to flow-through at a rate of 2.5 l s^{-1}. The remaining *Artemia* nauplii were flushed out of the tanks during this 10-h period, collected in a sieve and counted the subsequent morning. At high ration levels, between 80 and 90% of the daily ration was consumed. The number of nauplii in that sample was estimated using the above method. In this case the CV was generally < 20%. In tanks fed lower rations, it was often possible to count all remaining nauplii.
At the end of the experiment, all fish were killed, measured, weighed and caloric content was estimated. Wet weight (*WW*) and total length (*TL*) was measured on all fish in each group. Dry weight (*DW*) was measured on half of the fish in the group and a dorsal tissue sample was dissected from individuals from the other half of the group. Muscle tissue samples were stored at – 80 °C for nucleic acid analyses.

Nucleic acid analysis

Dorsal muscle tissue samples were freeze dried (24 h, Christ Alpha 1-4 freezedryer, – 51°C) and the mass measured (± 0.0001 mg, Sartorius microbalance SC2). The analysis of the muscle RNA and DNA content was performed by a modification of methods outlined by Clemmesen (1993) and Belchier et al. (2004). Freeze-dried muscle tissues samples between 500-700 µg were rehydrated in Tris-SDS-buffer (Tris 0.05 M, NaCl 0.01 M, EDTA 0.01 M, SDS 0.01%) for 15 min. Cells were disrupted by shaking in a cell-mill with glass beads of different sizes (0.17-0.34 mm and 2 mm diameter). The homogenate was centrifuged at 6000 rpm at 0°C for 8 min. The supernatant was used for the analysis. The amount of nucleic acids (DNA and RNA) was measured fluorometrically in a microtiter fluorescence reader (Labsystems, Fluorescan Ascent) using the fluorophor ethidium bromide. The DNA content was determined after treatment of RNase (Ribonuclease A, Serva). Nucleic acids were expressed in units of µg * mg muscle $tissue^{-1}$. RNA and DNA concentrations were determined based on calibration curves using Lambda DNA and 16S/23S ribosomal RNA (Boehringer, Mannheim). Note that the values obtained for muscle tissue in the present analysis, cannot be directly compared to values obtained for whole body measurements since different tissues and/or body parts can have different concentrations of RNA or DNA (Houlihan et al. 1988).

Results

Starvation experiment

The fish lost weight in each tank at each temperature (tables 2, 3). The lowest rates of weight loss were observed at the lowest temperature (9.7°) with 0.013 and 0.008 g g $DW^{-1}day^{-1}$ in tank 1 and 2, respectively (table 3). The highest loss rates were observed at the medium temperature of 14.2°C (tank 3) with 0.027 g g $DW^{-1}day^{-1}$ and at the highest temperature of 17.9°C (tank 5) with 0.023 g g $DW^{-1}day^{-1}$. The fish lost similarly energy in each tank at each temperature. Again, lowest loss rate was observed at the lowest temperature (9.7°) with 20 J g $DW^{-1}day^{-1}$ (tank 2) and highest loss rate at 17.9°C (tank 5) with 96 J g $DW^{-1}day^{-1}$ and 14.2°C (tank 3) with 91 J g $DW^{-1}day^{-1}$. In terms of energy loss as J $fish^{-1}$ day^{-1} and % $fish^{-1}$ day^{-1}, the lowest loss rate was 147 J $fish^{-1}$ day^{-1} (0.68 % $fish^{-1}$ day^{-1}) at 9.7°C (tank 2) and highest loss rate was 647 J $fish^{-1}$ day^{-1} (2.75 % $fish^{-1}$ day^{-1}) at 14.2°C (tank 3).

Table 2) Basic information of the starvation experiment: **A)** Initial sampling **B)** Final sampling. *TL* = total length, *WW* = wet weight, *DW* = dry weight.

Tank No.	Temperature (°C)	Days starved	n	*TL* (cm)	*WW* (g)	*DW* (g)	Caloric density (J g DW^{-1})
A	**Initial**						
1	9.7	0	10	10.67 ± 0.34	6.90 ± 0.82	1.49 ± 0.24	19992 ± 621
2	9.7	0	10	10.47 ± 0.47	6.44 ± 0.78	1.33 ± 0.17	18962 ± 243
3	14.2	0	10	10.81 ± 0.37	7.07 ± 0.69	1.53 ± 0.17	19737 ± 617
4	14.2	0	10	10.46 ± 0.43	6.64 ± 0.58	1.44 ± 0.11	19551 ± 625
5	17.9	0	10	10.41 ± 0.40	6.24 ± 0.73	1.27 ± 0.20	18568 ± 831
6	17.9	0	10	10.44 ± 0.41	6.11 ± 0.55	1.24 ± 0.13	18566 ± 725
	mean			10.54 ± 0.42	6.57 ± 0.75	1.38 ± 0.20	19229 ± 790
B	**Final**						
1	9.7	26	20	10.55 ± 0.45	5.95 ± 0.65	1.18 ± 0.20	19050 ± 1009
2	9.7	26	20	10.50 ± 0.32	5.87 ± 0.52	1.15 ± 0.15	18713 ± 485
3	14.2	18	20	10.35 ± 0.43	5.48 ± 0.71	1.03 ± 0.18	18005 ± 330
4	14.2	18	20	10.52 ± 0.35	5.84 ± 0.69	1.18 ± 0.17	18470 ± 325
5	17.9	14	12	10.42 ± 0.62	5.42 ± 0.90	0.95 ± 0.19	17227 ± 427
6	17.9	14	20	10.53 ± 0.41	5.83 ± 0.85	1.07 ± 0.18	17950 ± 375

Table 3) Rates of change in weight, energy and the metabolic rate per tank. All change rates in terms of weight are expressed as dry weight, with the exception of the metabolic rate in the last column, which relates to wet weights.

Tank No.	Temperature (°C)	Weight (g g^{-1} d^{-1})	Energy (J g^{-1} d^{-1})	Energy (J $fish^{-1}$ d^{-1})	Energy (% $fish^{-1}$ d^{-1})	Metabolic rate (mg O_2 g^{-1} h^{-1})
1	9.7	0.013	51	279	1.13	0.133
2	9.7	0.008	20	147	0.68	0.076
3	14.2	0.027	91	647	2.75	0.322
4	14.2	0.016	57	366	1.47	0.178
5	17.9	0.023	96	515	2.73	0.296
6	17.9	0.016	40	270	1.45	0.149

The initial protein contents (% dry weight) were close to 76% (75.7 to 76.6%, table 4), while the fat contents ranged from 9.3 to 11.2%. The final protein contents were close to initial contents (73.7 to 76.4%), while final fat contents ranged from 5.3 to 8.5%. The initial water content in per cent of the wet weight ranged between 78.3% at 14.2°C and

79.7% at 17.9°C, increasing to the end of the starvation period to 80.4% at 9.7°C and 82.0% at 17.9°C (table 4).

Table 4) Protein and fat contents (± s.d.) per temperature (initial and final sampling).

Temperature (°C)	Initial sampling Protein (% *DW*)	Fat (% *DW*)	Water content (% *WW*)	Final sampling Protein (% *DW*)	Fat (% *DW*)	Water content (% *WW*)
9.7	75.7 ± 0.6	11.2 ± 1.2	78.9 ± 1.2	73.7 ± 2.4	8.5 ± 2.1	80.4 ± 1.5
14.2	75.7 ± 1.0	9.3 ± 1.5	78.3 ± 0.9	75.2 ± 2.2	6.4 ± 0.9	80.6 ± 1.2
17.9	76.6 ± 2.3	10.6 ± 1.4	79.7 ± 1.2	76.4 ± 1.0	5.3 ± 1.8	82.0 ± 3.1

The effect of temperature (*T*) on the metabolic rate (M_{STARV}) as estimated by energy losses (J g *DW* $^{-1}$ day^{-1}) was described by an exponential model $M_{STARV} = a * e^{b*T}$, which resulted in b-exponents of 0.071 (Q_{10} = 2.0, figure 1) for all temperatures and 0.144 (Q_{10} = 4.2) from 9.7 to 14.2°C (table 5).

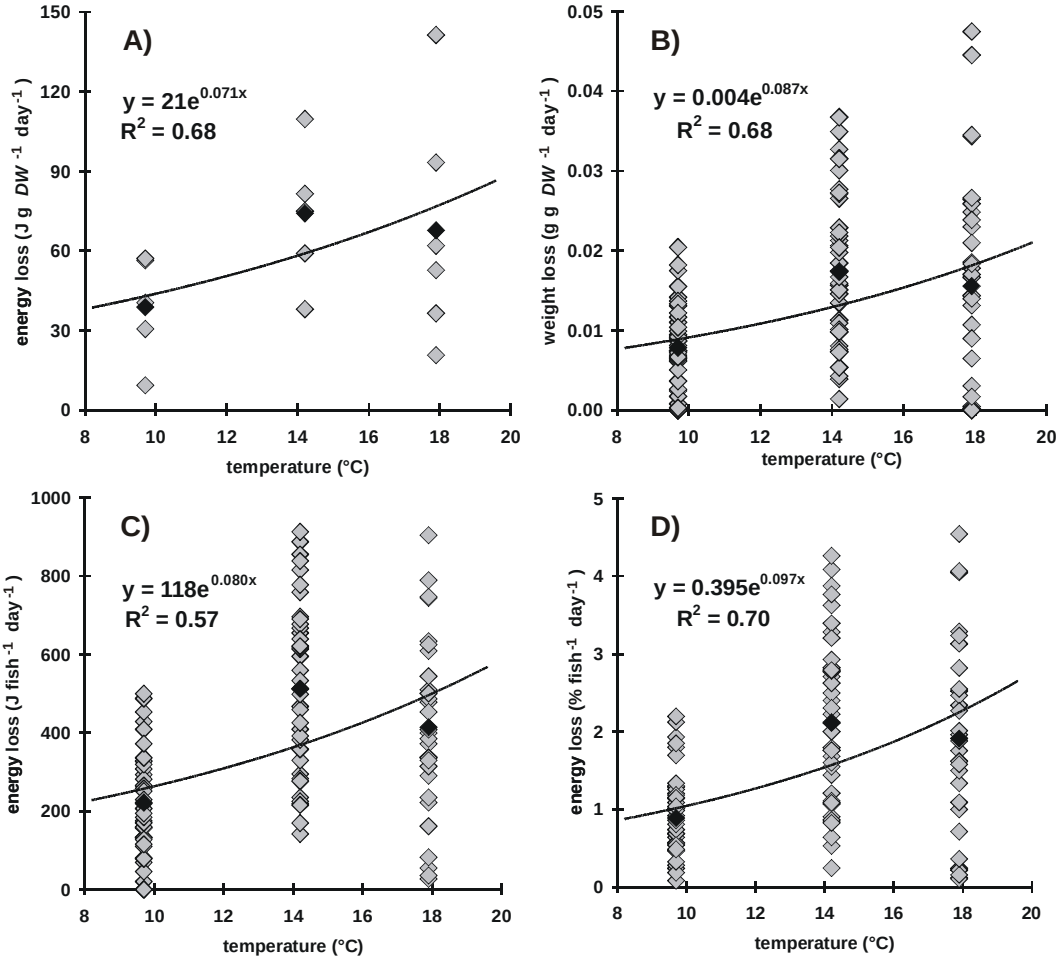

Figure 1) Energy loss in **A)** Joule g *DW* $^{-1}$ day $^{-1}$, **C)** Joule fish $^{-1}$ day^{-1}, **D)** % fish $^{-1}$ day $^{-1}$ and **B)** weight loss in g g *DW* $^{-1}$ day^{-1} versus temperature (°C). Grey rhombs indicate individual values, black rhombs indicate means.

The temperature dependency of specific growth rate (g g *DW* $^{-1}$ day^{-1}) resulted in a b-exponent of 0.087 (Q_{10} = 2.4, figure 1) for all temperatures and 0.177 (Q_{10} = 5.9) from 9.7 to 14.2°C (table 5). The regressions were also performed in terms of J fish^{-1} day^{-1} and % fish^{-1}day^{-1} (table 5), resulting in similar b-values. All in all did we observe Q_{10}-

values of 2.0 to 6.9. Since we observed a slight decrease in weight and energy losses from 14.2 to 17.9°C we aggregated the results at these temperatures and assumed the mean temperature to be 16°C (table 5). The resulting Q_{10}-values from these regressions ranged from 2.6 to 3.6.

Table 5) Parameters of the regressions (M_{STARV} = a * e $^{b * T}$) of the relative energy and weight losses per temperature (means). Regressions were performed for all temperatures together (9.7-14.2-17.9°C) or two temperatures each (9.7-14.2 denotes regression was performed between values at 9.7 and 14.2°C). For the regression from 9.7 to 16°C, values of 14.2 and 17.9 were aggregated at 16°C.

	Temperature (°C)	a	b	r^2	Q_{10}
J g *DW*$^{-1}$ d^{-1}	9.7-14.2-17.9	21	0.071	0.68	2.0
	9.7-14.2	10	0.144		4.2
	9.7-16	15	0.096		2.6
	9.7-17.9	20	0.068		2.0
g g *DW*$^{-1}$ d^{-1}	9.7-14.2-17.9	0.004	0.087	0.68	2.4
	9.7-14.2	0.001	0.177		5.9
	9.7-16	0.003	0.116		3.2
	9.7-17.9	0.003	0.084		2.3
J fish^{-1} d^{-1}	9.7-14.2-17.9	118	0.080	0.57	2.2
	9.7-14.2	37	0.186		6.4
	9.7-16	70	0.119		3.3
	9.7-17.9	106	0.076		2.1
% fish^{-1} d^{-1}	9.7-14.2-17.9	0.40	0.097	0.71	2.6
	9.7-14.2	0.14	0.193		6.9
	9.7-16	0.26	0.129		3.6
	9.7-17.9	0.36	0.094		2.6

Conversion efficiency

The growth rate in energy (figure 2 A and C) and weight (figure 2 B) increased with increasing consumption rate. Herring at high rations consumed 5.8 - 6.6% of their body weight (*BW*, in *DW*), while herring at lowest rations consumed 0.4 - 0.5% *BW* (table 6). Highest observed growth rates in J fish^{-1} day^{-1} were 963 and 1081 at high rations, while fish at lowest rations lost a maximum of 380 J fish^{-1} day^{-1}. In terms of weight, the highest growth rates were 0.024 and 0.026 g g *DW*$^{-1}$ day^{-1} at high rations and herring at low rations lost a maximum of 0.021 g g *DW*$^{-1}$ day^{-1} (figure 2 B).

Table 6) Experimental data per tank of the conversion efficiency experiment. (*TL* = total length, *WW* = wet weight, *DW* = dry weight, kJ g^{-1} = energy density, *BW* = body weight (*DW*), *GGE* = gross conversion efficiency (K_1)).

tank	*TL* (cm)	*WW* (g)	*DW* (g)	kJ g^{-1}	daily ration (% *BW*)	*GGE* (%)
Initial	9.3 ± 0.5	4.9 ± 0.9	1.09 ± 0.25	19.3 ± 0.6		
1	9.9 ± 0.4	7.1 ± 0.6	1.83 ± 0.16	22.4 ± 0.5	5.8-6.6	25
2	9.5 ± 0.6	4.5 ± 0.9	0.93 ± 0.23	19.3 ± 0.9	0.7-0.9	-101
3	9.7 ± 0.5	5.0 ± 0.8	1.02 ± 0.19	18.6 ± 0.8	1.1-1.6	-35
4	9.7 ± 0.5	5.9 ± 1.2	1.34 ± 0.31	20.9 ± 0.8	2.9-3.1	33
5	9.4 ± 0.4	4.3 ± 0.8	0.74 ± 0.33	19.4 ± 1.0	0.4-0.5	-403
6	10.1 ± 0.5	7.5 ± 1.4	1.93 ± 0.42	22.6 ± 0.4	5.8-6.6	30
7	9.7 ± 0.3	6.1 ± 0.7	1.45 ± 0.20	21.1 ± 0.9	4.2-4.6	26
8	9.6 ± 0.4	4.5 ± 0.7	0.70 ± 0.31	18.9 ± 1.0	0.4-0.5	-731

The relationship between feeding (*C*) and growth (*G*) was described by the linear equations $G = 0.44 * C - 256$ (J g *DW* $^{-1}$ day^{-1}), $G = 0.50 * C - 0.01$ (g g *DW* $^{-1}$ day^{-1}) and $G = 0.52 * C - 269$ (J fish^{-1} day^{-1}) (figure 2 A, B and C). The resulting net food conversion efficiencies (K_3), calculated as 100 * slope of the linear regression of *G* versus *C* (figure 2 A through C), were 44% in J g *DW* $^{-1}$ day^{-1}, 50% in g g *DW* $^{-1}$ day^{-1} and 52% in J fish^{-1} day^{-1}. The resulting maintenance rations (M_{RAT}), were 582 J g *DW* $^{-1}$ day^{-1}, 0.026 g g *DW* $^{-1}$ day^{-1} (2.6% day^{-1}) and 517 J fish^{-1} day^{-1}.

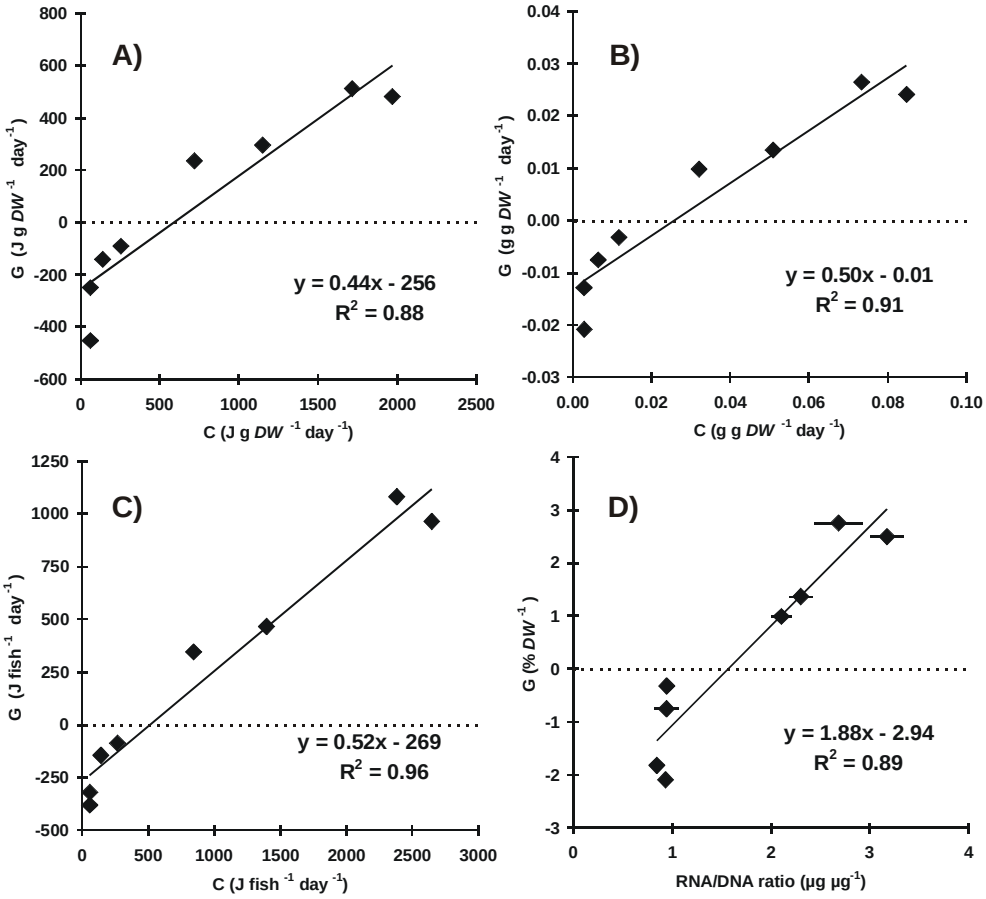

Figure 2) The effect of consumption rate *C* on the growth rate *G* in **A)** J g *DW* $^{-1}$ day^{-1}, **B)** g g *DW* $^{-1}$ day^{-1}, and **C)** J fish $^{-1}$ day^{-1} along with linear regression. **D)** Regression of mean growth rate (% *DW* day^{-1}) against RNA-DNA ratio (µg µg^{-1}).

The gross conversion efficiencies varied between 25 to 33% (table 6), when only considering positive values.

The RNA-DNA ratio increased with increasing growth rate (% *DW* day^{-1}) from a minimum value of 0.8 µg µg^{-1} at a daily growth rate of -1.8% to a maximum value of 3.2 µg µg^{-1} at a daily growth rate of 2.5% (figure 2 D).

Discussion

Starvation experiment

There is a clear advantage of performing starvation experiments as opposed to conducting oxygen consumption experiments with clupeid species such as herring and sprat (*Sprattus sprattus* L.). Although respirometry is generally used to measure metabolic rates (Jobling 1994), elevated levels of stress are associated with confining groups of schooling fish within small respirometry chambers. Elevated levels of stress clearly bias (increase) routine rates leading to overestimates of metabolic costs.
The results of the starvation experiment indicated that temperature impacted the fasting metabolism of juvenile herring. We calculated Q_{10}-values of 2.0 to 6.9 depending on the temperatures used in the regressions and the unit of measurement (e.g. weight or energy). The rates of loss of energy or weight measured at 17.9°C were not higher than those measured at 14.2°C. Rather, rates at the former temperature were slightly lower than rates at the latter. There are three possible explanations for this observation.
The first is related to variable activity patterns of herring at different temperatures and in different tanks. An indicator supporting this explanation was the difference in the mean values of energy and weight loss of fish between the two tanks at the same temperature, indicating some kind of tank effect, possibly related to different activity patterns. Very few studies have examined behavioural responses associated with starvation in a schooling planktivorous teleost species. Peck et al. (In Prep.) studied swimming activity in post-larval sprat (*Sprattus sprattus* L.) at 18°C in groups of fish experiencing constant feeding conditions as well as other groups responding to abrupt changes in prey abundance. In that study, differences were observed in the mean swimming speed of fish in separate tanks maintained at the same feeding level. We were not able to test for differences in individual activity patterns in our experiment, since we did not record fish activity, but such patterns likely occurred.
The second possible explanation is related to differences in the energy densities of herring measured at the start of the experiment at the different temperatures. The lowest energy densities were measured at the highest temperatures, indicating that these herring were not feeding at *ad libitum* (with excess food) during the temperature acclimation period. The energy losses experienced by these fish prior to the experiment biased the results of the temperature dependency of routine metabolism. This is partly reflected in the body compositions, since initial protein and fat contents were similar at all temperatures (protein: 75.7 - 76.6% *DW*, fat: 9.3 - 11.2% *DW*). However, herring in both tanks at the highest temperature (17.9°C) exhibited the lowest energy densities. The activity of fish having lower energy density may have responded differently to starvation than those having higher energy density. For example, if activity decreased during starvation, these fish may have decreased their activity more rapidly during the trial, leading to relatively lower energy losses compared to herring at other temperatures with higher initial energy densities. The variation of initial energy density at the start of starvation studies was a shortcoming that can be overcome in future experiments by providing all fish *ad libitum* food rations prior to trials. Temperatures examined in the present trials were too different for fish from one stock tank to be simultaneously transferred into all experimental tanks (see Jobling 1994 for a discussion of stress associated with inadequate temperature acclimation). The third possible explanation is that our results actually reflect the natural metabolic reaction of juvenile herring to an increase in temperature. In general, the temperature-metabolism relationship can be described by a simple exponential model (Jobling 1994). This may also be the case in our experiment with an exponential increase in the metabolic rate from 9.7 to 14.2°C, followed by a slight decrease in metabolic rate with increasing temperature.

It was suggested by Boggs (1991) and Boggs & Kitchell (1991) that the resulting estimates of metabolic rates of starvation experiments are, in most cases, comparable to those derived from oxygen uptake in respirometry experiments. For a better comparison with values found in the literature we have converted the energy losses into the corresponding oxygen consumption. The estimated oxygen consumption rates in our experiments ranged from 0.076 mg O_2 g *WW* $^{-1}$ h^{-1} at 9.7°C to a maximum of 0.322 mg O_2 g *WW* $^{-1}$ h^{-1} at 14.2°C. Hettler (1976) and Macy III et al. (1999) measured routine and standard rates of oxygen consumption by juvenile and adult Atlantic menhaden (*Brevoortia tyrannus*), a pelagic filter-feeding clupeoid, at 10 to 25°C. The routine metabolic rates of juvenile menhaden (6 to 81 g wet weight, Hettler 1976) were slightly higher (0.102 to 0.476 mg O_2 g *WW* $^{-1}$ h^{-1}) than our values and standard metabolism of larger (283 – 327 g *WW*) adult menhaden was lower (0.040 mg O_2 g *WW* $^{-1}$ h^{-1}) at 10°C. The corresponding Q_{10} values were 2.0 for juvenile menhaden and 2.2 for adult menhaden (10-20°C). Rates of routine respiration of adult Atlantic herring (25.5 to 31.0 cm) were 0.093 mg O_2 g *WW* $^{-1}$ h^{-1} at 9.3°C (Johnstone et al. 1993). This rate was similar to the estimates for our smaller (10.5 to 10.8 cm, *TL*), juvenile herring at 9.7°C (0.076 and 0.133 mg O_2 g *WW* $^{-1}$ h^{-1}), which is surprising since specific rates usually decrease with fish size (Hettler 1976). The conclusion from this observation will be discussed later. Similar routine respiration rates were measured by van der Lingen (1995), where rates of adult pilchard (*Sardinops sagax*) ranged from 0.133 mg O_2 g *WW* $^{-1}$ h^{-1} at 10°C to 0.267 mg O_2 g *WW* $^{-1}$ h^{-1} at 22°C resulting in a mean Q_{10} of 1.8 (van der Lingen 1995), presenting similar temperature dependencies (Q_{10}) as observed in our study. As specific rates usually decrease with fish size, the comparison with literature values of the same species (adult herring) or other clupeoids, indicates that oxygen consumption rates as estimated from our starvation experiment were relatively lower compared to literature values based on respiration measurements.

The lower oxygen consumption rate estimates appear with regard to the ecology of early juvenile herring meaningful. Due to the patchy distribution of their prey, their high growth capacity and high metabolic rates, post-larval and juvenile fish must possess mechanisms to cope with periods of starvation (see Wieser 1991). Such mechanisms can include the preferential use of specific metabolic substrates (Molony 1993, Arndt et al. 1996), changes in fish behaviour, including swimming activity and/or habitat use (Rudstam and Magnuson 1985, Björnsson 1993, Sogard & Olla 1996, van Dijk et al. 2002) and down-regulation of metabolism (Méndez and Wieser 1993, Wieser et al. 1992). Peck et al. (In Prep.) observed a markedly decreased swimming speed in post-larval sprat after seven days of food deprivation, which would result in lower metabolic costs. A similar reduction in activity may have occurred by the fish used in our experiments. Consequently, it is not unexpected that starved fish display relatively lower metabolic rates in comparison with fish that have been food deprived for shorter durations in respirometers. However, there may be some uncertainty whether routine or standard metabolism is measured in starvation experiments. Standard metabolism is the rate of energy expenditure by a resting, unfed fish, while the routine metabolism is the metabolic rate of an unfed fish showing spontaneous swimming (Wootton 1998). Usually standard metabolism is calculated from data obtained on swimming fish. A relationship between swimming speed and the metabolic rate of the fish is established and then the relationship is extrapolated to zero velocity (Jobling 1994). Since the experimental fish in our study were either constantly swimming or exhibited spontaneous swimming activity, we did not measure standard metabolism. However, the probability of the previously mentioned metabolic depression was high, which would result in the measurement of a “fasting metabolic rate” (see Jobling 1994) as opposed to a routine rate. The fasting metabolic rate is intermediate between standard and routine metabolism. To test a possible metabolic depression, long-term respirometry

trials could be conducted on unfed herring to see whether sudden (or gradual) significant decline(s) in respiration rate are observed.
In conclusion, a strong increase in metabolic rate was observed between 9.7 and 14.2°C (Q_{10} = 6.4, J $fish^{-1}$ day^{-1}) followed by no further temperature effect between 14.2 and 17.9°C. This observation of a high Q_{10} is in line with the change in gastric evacuation rates (Bernreuther et al. In Prep.) between 13 and 16°C where a Q_{10} of ~ 11 was observed. The increase in metabolic rate over the entire temperature range resulted in a Q_{10} of 2.2 (J $fish^{-1}$ day^{-1}). Starvation experiments are applicable in estimating the temperature dependency of the fasting metabolic rate in herring, but result in relatively lower estimates compared to the protocol commonly used in respirometry experiments measuring routine metabolism.

Conversion efficiency experiment

Net growth efficiency (K_3) is a measure of the conversion efficiency of food consumed in excess of maintenance requirements (Wootton 1998). K_3 integrates the energy lost in faeces (F) and by excretion of nitrogenous wastes (E) and costs for specific dynamic action (SDA) (K_3 = 1 – F – E – SDA), with F, E and SDA representing fractions of the ingested food that are lost. When combined with growth data from the field, K_3 has been used to estimate food consumption rates of fish populations in the wild (Temming 1995). Since feeding-growth experiments on clupeids are rare and only gross conversion efficiency has been investigated, we used literature values on energy losses due to F, E and SDA from bioenergetics models of herring to estimate K_3. Rudstam (1988) assumed losses in F, E and SDA to be 17.5, 16 and 10% of the ingested food energy. According to this rough estimate 56.5% of the ingested energy above maintenance ration would be available for somatic growth. In this study, a value of 52% was estimated based upon growth in J $fish^{-1}$ day^{-1}. This result is rather similar to the value reported by Rudstam (1988). Both values need to be discussed critically whether they actually reflect K_3 in the wild.
The question is whether the proportions lost in faeces, excretion and SDA were correct for juvenile herring, which may not be the case since the values used by Rudstam (1988) were borrowed from other species like aholehole (*Kuhlia sandvicensis*), alewife (*Alosa pseudoharengus*) and brown trout (*Salmo trutta*). A systematic error in the counting of *Artemia* nauplii may have occurred, which resulted in e.g. an overestimation of the consumed nauplii at high rations or an underestimation of the consumed nauplii at low rations, leading to a lower slope of the feeding-growth relationship. The third possible uncertainty is that fish employed different feeding modes at different daily ration levels. Herring are known to be facultative filter-feeders, switching between particulate and filter-feeding, depending on the particle size- and concentration and light intensity (Gibson & Ezzi 1985, 1990, 1992; Batty et al. 1990). Experiments on the relative profitability of particulate- and filter-feeding in herring (Gibson & Ezzi 1992) indicated that the energy cost of filter-feeding might be from 1.4 to 4.6 times higher than that of biting and particulate feeding, respectively. Therefore, a switch from particulate feeding at low rations to filter-feeding at our medium to high rations would explain the relatively low K_3. The increased metabolic costs while filter-feeding may have outweighed the increased energy intake through filtering *Artemia* spp. nauplii (which are relatively small prey for juvenile herring) from the surrounding water. The result was a decreased scope for growth at medium to high rations, and a lower slope (*G*/*C*) in the feeding-growth relationship. We observed high numbers of filter-feeding herring at medium to high rations, supporting this argument.
The gross conversion efficiencies (*GGE*, only positive values considered) in our experiment at different rations (2.9 to 6.6% *BW*) varied from 25 to 33%. Compared to

the results on the *GGE* of juvenile herring (6.1 to 18.8 g wet weight) from conversion efficiency experiments with mysids, minced mussels and squid (De Silva & Balbontin 1974), our results are high. The *GGE* for juvenile herring fed *ad libitum* rations at 14.5 (8.1 – 12.7% *BW* day^{-1}) and 6.5°C (3.5 – 5.0% *BW* day^{-1}) were 7.0 and 9.8%, respectively (De Silva & Balbontin 1974). Moreover, higher *GGE* were also observed in feeding-growth experiments with post-larval sprat fed with *Artemia* nauplii varied from 12 to 30% at 18°C (Peck et al. In Prep.). The reliability of the estimation of the conversion efficiencies (*GGE,* which is ration dependent*,* and K_3) depends to a large degree on the correct estimation of the daily rations, which was established by the counting of *Artemia* as described in the material & methods section. The precision of the counting was sometimes low (CV up to 20%) so there is some uncertainty concerning the reliability of this method.
In addition to the measurement of changes in weight and energy, we measured the RNA-DNA ratio in body tissues as a growth rate indicator. The ratio of RNA-DNA in body tissues can be used to measure the recent growth in fish since it reflects the rate of protein synthesis (e.g., Haines 1973, Wang et al. 1993, Dutil et al. 1998, Peck et al. 2003). The RNA-DNA ratio (µg $µg^{-1}$) of muscle increased linearly with growth rate (% *DW* day^{-1}) to reach the highest value at 3.2 µg $µg^{-1}$. A similar linear relationship between RNA-DNA ratio and growth rate was observed in feeding-growth experiments with post-larval sprat (Peck et al. In Prep.) where the highest ratio was ~ 2.2 µg $µg^{-1}$ at 18°C for fish with the highest growth rates. The RNA-DNA ratio adequately reflected the feeding history (21 days) of our juvenile herring, with high ratios at high rations and low ratios at low rations. Fish have a highly plastic growth rate and often respond to environmental changes by changes in growth rate (Haines 1973). If this is adequately reflected in the RNA-DNA ratio, this ratio is a useful tool in detecting favourable or unfavourable environmental conditions. However, work on juvenile Arctic charr (*Salvelinus alpinus*) (Miglavs & Jobling 1989) and other species, point to some possible shortcomings in the use of the RNA-DNA ratios as a growth index in large juvenile fish. Miglavs & Jobling (1989) reported that experimental fish responded to a change from restricted to satiation feeding by showing a growth spurt (compensatory growth). During this period of rapid growth the fish became hyperphagic and, in the days immediately following transfer from restricted to satiation feeding, showed improved food conversion efficiency compared to their counterparts raised on a liberal feeding regime. The growth rates displayed by experimental fish during the period of compensatory growth were higher than those that would have been predicted from tissue RNA-DNA ratios measured in fish permanently fed to satiation. The explanation for this was based on increased ribosomal synthetic activity (i.e., increase in protein synthesized per ribosome) occurring shortly after the transfer from restricted to satiation feeding. In adult stages, the interpretation of RNA-DNA ratios appear more difficult, since this life-stage has the ability to use energy reserves in periods of low food availability. As a result, unfavourable short-term feeding conditions are not adequately reflected in the RNA-DNA ratios. Nevertheless, in our study of 0-group fish at 16°C (a summer temperature) the feeding regime was adequately reflected in the RNA-DNA ratios. This ratio can be a useful tool in detecting favourable and unfavourable environmental conditions for 0-group (juvenile) herring.

Maintenance rations

Despite some shortcomings in terms of differences in initial energy densities in the starvation experiment and eventual drawbacks in the conversion efficiency experiment, like the limited number of experiments and the variability in the counting of the *Artemia* spp. nauplii, estimated maintenance rations at 16°C were similar in both experimental

set-ups. In terms of energy, the maintenance rations were 517 J $fish^{-1}$ day^{-1} as estimated from the conversion efficiency and 471 J $fish^{-1}$ day^{-1} as estimated from the starvation experiment. In terms of weight, the corresponding values were 0.020 g g *DW* $^{-1}$ day^{-1} (conversion efficiency experiment) and 0.019 g g *DW* $^{-1}$ day^{-1} (starvation experiment). The close agreement indicates that both methods can be applied to study the metabolic needs of schooling clupeid fish species, in this case juvenile herring

Conclusions

Starvation experiments were applied to estimate the temperature dependency of the fasting metabolic rate in herring (Q_{10} = 2.2), but resulted in relatively lower estimates of metabolic rates compared to respirometry experiments which measured routine metabolism. Care should be taken so that the experimental groups of fish at different temperatures have an identical nutritional status (i.e., energy density) at the start of the experiment. To account for the possible metabolic depression, respirometry measurements and/or swimming activity measurements should be conducted in parallel to starvation experiments.
For a complete assessment of the feeding-growth relationship in herring, experiments at different temperatures with different body sizes, incorporating groups feeding *ad libitum* and fasting groups will be necessary. Furthermore, experiments should be conducted with larger prey items, like large copepods, that can be ingested at high rates by herring through particulate feeding. These experiments should give answers to whether the net growth efficiencies in our experiments were lowered due to the energetically expensive filter-feeding.

References

Arndt, S.K.A., Benfey, T.J., Cunjak, R.A. (1996). Effect of temporary reductions in feeding on protein synthesis and energy storage of juvenile Atlantic salmon. Journal of Fish Biology 49, 247–276.

Arrhenius, F. (1995). Feeding ecology of Baltic Sea herring (*Clupea harengus* L.) – field and model studies of a dominant zooplanktivore. Dissertation, Stockholm University. 103pp.

Batty, R.S., Blaxter, J.H.S. & Richard, J.M. (1990). Light intensity and the feeding behaviour of herring, *Clupea harengus*. Marine Biology 107, 383-388.

Belchier, M. and 13 co-authors (2004). Recruitment studies: manual on precision and accuracy of tools. ICES Techniques in marine environmental Sciences, No. 33, 35 pp.

Bernreuther, M., Herrmann, J.-P. & Temming, A. (In Prep.). Laboratory experiments on the gastric evacuation of juvenile herring (*Clupea harengus* L.).

Björnsson, B. (1993). Swimming speed and swimming metabolism of Atlantic cod (*Gadus morhua*) in relation to available food: a laboratory study. Canadian Journal of Fisheries and Aquatic Science 50, 2542–2551.

Boggs, C.H. (1991). Bioenergetics and growth of northern Anchovy *Engraulis mordax*. Fishery Bulletin 89(4), 555-566.

Boggs, C.H. & Kitchell, J.F. (1991). Tuna metabolic rates estimated from energy losses during starvation. Physiological Zoology 64(2), 502-524.

Chekunova, V.I. (1979). Energy requirements of the Baltic herring, *Clupea harengus membras*. Journal of Ichthyology 19, 118-125.

Clemmesen, C. (1993). Improvements in the fluorimetric determination of the RNA and DNA content of individual marine fish larvae. Marine Ecology Progress Series 100, 177–183.

De Silva, S.S. & Balbontin, F. (1974). Laboratory studies on food intake, growth and food conversion of young herring, *Clupea harengus* (L.). Journal of Fish Biology 6, 645–658.

Dutil, J.-D., Lambert, Y., Guderley, H., Blier, P.U., Pelletier, D. & Desroches, M. (1998). Nucleic acids and enzymes in Atlantic cod (*Gadus morhua*) differing in condition and growth rate trajectories. Canadian Journal of Fisheries and Aquatic Science 55, 788-795.

Foster, A.R., Houlihan, D.F. & Hall, S.J. (1993). Effects of nutritional regime on correlates of growth rate in juvenile Atlantic cod (*Gadus morhua*): comparison of morphological and biochemical measurements. Canadian Journal of Fisheries and Aquatic Science 50, 502-512.

Gibson, R.N. & Ezzi, I.A. (1985). Effect of particle concentration on filter- and particulate feeding in the herring *Clupea harengus*. Marine Biology 88, 109-116.

Gibson, R.N. & Ezzi, I.A. (1990). Relative importance of prey size and concentration in determining the feeding behaviour of the herring *Clupea harengus*. Marine Biology 107, 357-362.

Gibson, R.N. & Ezzi, I.A. (1992). The relative profitability of particulate-and filter-feeding in the herring, *Clupea harengus* L. Journal of Fish Biology 40, 577-590.

Haines, T.A. (1973). An evaluation of RNA-DNA ratio as a measure of long-term growth in fish populations. Journal of the Fisheries Research Board of Canada Vol.30 No. 2, 195-199.

Herrmann, J.-P. & Enders, E.C. (2000). Effect of body size on the standard metabolism of horse mackerel. Journal of Fish Biology 57, 746-760.

Hettler, W.F. (1976). Influence of temperature and salinity on routine metabolic rate and growth of young Atlantic menhaden. Journal of Fish Biology 8, 55-65.

Houlihan, D.F., Hall, S.J., Gray, C., Noble, B.S. (1988). Growth rates and protein turnover in Atlantic cod, *Gadus morhua*. Canadian Journal of Fisheries and Aquatic Science 45, 951–964.

Hunter, J.R. & Leong, R. (1981). The spawning energetics of female northern anchovy, *Engraulis mordax*. Fishery Bulletin: Vol.79, No.2, 215 - 230.

Jobling, M. (1994). Fish Bioenergetics. Chapman & Hall, London. 390 pp.

Johnstone, A.D.F., Wardle, C.S. & Almatar, S.M. (1993). Routine respiration rates of Atlantic mackerel, *Scomber scombrus* L., and herring, *Clupea harengus* L., at low activity levels. Journal of Fish Biology 42, 149–151.

Karamushko, L.I. & Christiansen, J.S. (2002). Aerobic scaling and resting metabolism in oviferous and post-spawning Barents Sea capelin *Mallotus villosus villosus* (Müller, 1776). Journal of Experimental Marine Biology and Ecology 269, 1–8.

Kiørboe, T., Munk, P. & Richardson, K. (1987). Respiration and growth of larval herring, *Clupea harengus*: relation between specific dynamic action and growth efficiency. Marine Ecology Progress Series 40, 1–10.

Kitchell, J.F., Stewart, D.J. & Weininger, D. (1977). Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). Journal of the Fisheries Research Board of Canada 34, 1922-1935.

Logerwell, E.A. (2001). Metabolic rate of California Pacific sardine estimated from energy losses during starvation. Transactions of the American Fisheries Society 130: 526–530.

Macy III, W.K., Durbin, A.G. & Durbin, E.G. (1999). Metabolic rate in relation to temperature and swimming speed, and the cost of filter feeding in Atlantic menhaden, *Brevoortia tyrannus*. Fishery Bulletin 97(2), 282–293.

Méndez, G. & Wieser, W. (1993). Metabolic responses to food deprivation and refeeding in juveniles of *Rutilus rutilus* (Teleostei: Cyprinidae). Environmental Biology of Fishes 36, 73-81.

Mehner, T. & Wieser, W. (1994). Energetics and metabolic correlates of starvation in juvenile perch (*Percha fluviatilis*). Journal of Fish Biology 45, 325–333.

Molony, B.W. (1993). Effects of feeding history on mobilization and deposition of body constituents and on growth on juvenile Ambassis vachelli (Pisces: Chandidae). Marine Biology 116, 389–397.

Miglavs, I. & Jobling, M. (1989). Effects of feeding regime on food consumption, growth rates and tissue acids in juvenile Arctic charr, *Salvelinus alpinus*, with particular respect to compensatory growth. Journal of Fish Biology 34, 947-957.

Ney, J. (1993) Bioenergetics modelling today: Growing pains on the cutting edge. Transactions of the American Fisheries Society 122, 736-748.

Peck, M.A., Ewest, B., Herrmann, J.-P., Kürs, U. & Temming, A. (In Prep.). Interrelationships among feeding, growth and swimming activity of post-larval *Sprattus sprattus* L. (Teleostei: Clupeidae) in the laboratory.

Peck, M.A., Baumann, H., Clemmesen, C., Herrmann, J.-P., Kürs, U. & Temming, A. (In Prep.). Somatic-, nucleic acid-, and otoliths-based indicators of growth and condition in post-larval sprat (*Sprattus sprattus*).

Peck, M.A., Buckley, L.J. Caldarone, E.M. & Bengtson, D.A. (2003). Effects of food consumption and temperature on growth rate and biochemical-based indicators of growth in early juvenile Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). Marine Ecology Progress Series 251, 233-243.

Peck, M.A., Clemmesen, C., Herrmann, J.-P., Stäcker, S. & Temming, A. (2004). The bioenergetics of young-of-the-year juvenile sprat (*Sprattus sprattus*): 1) The effect of feeding on growth rate and growth efficiency in the laboratory. Poster. Status-seminar 2004, GLOBEC-Germany.

Peck, M.A., Buckley, L.J. & Bengtson, D.A. (2006, in press). Effects of temperature and body size on the swimming speed of larval and juvenile Atlantic cod (*Gadus morhua*): implications for individual-based modeling. Environmental Biology of Fishes 00:1-12.

Rudstam, L.G., Magnuson, J.J. (1985). Predicting the vertical distribution of fish populations: analysis of cisco, *Coregonus artedii*, and yellow perch, *Perca flavescens*. Canadian Journal of Fisheries and Aquatic Sciences 42,1178–1188.

Rudstam, L.G. (1988). Exploring the dynamics of herring consumption in the Baltic: Applications of an energetic model of fish growth. Kieler Meeresforschung Sonderheft 6, 312–322.

Sogard, S.M. & Olla, B.L. (2001). Growth and behavioral responses to elevated temperatures by sablefish *Anaplopoms fimbria* and the interactive role of food availability. Marine Ecology Progress Series 217, 121–134.

Stewart, D.J. & Binkowski, F.P. (1986). Dynamics of consumption and food conversion by Lake Michigan Alewives: An energetics-modeling synthesis. Transactions of the American Fisheries Society 115(5), 643–661.

Takahashi, M. & Hatanaka, M.A. (1960). Experimental study on utilization of food by young anchovy, *Engraulis japonicus* Temminck et Schlegel. Tohoku Journal of Agricultural Research 11, 161-170.

Temming, A. (1995). Die quantitative Bestimmung der Konsumtion von Fischen. Experimentelle, methodische und theoretische Aspekte (in German). Habilitationsschrift, Universität Hamburg, Fachbereich Biologie, 235 pp.

Ursin, E. (1967). A mathematical model of some aspects of fish growth, respiration and mortality. Journal of the Fisheries Research Board of Canada 24, 2355-2453.

Van der Lingen, C.D. (1995). Respiration rate of adult pilchard *Sardinops sagax* in relation to temperature, voluntary swimming speed and feeding behaviour. Marine Ecology Progress Series 129, 41-54.

van Dijk, P.L., Staaks, G. & Hardewig, I. (2002). The effect of fasting and refeeding on temperature preference, *activity* and growth of roach, *Rutilus rutilus*. Oecologia 130(4):496–504

Wang, S.Y., Lum, J.L., Carls, M.G. & Rice, S.D. (1993). Relationship between growth and total nucleic acids in juvenile pink salmon, *Oncorhynchus gorbuscha*, fed crude oil contaminated food. Canadian Journal of Fisheries and Aquatic Science 50, 996-1001.

Wardle, C.S., Soofiani, N.M., O`Neill, F.G., Glass, C.W. & Johnstone, A.D.F. (1996). Measurements of aerobic metabolism of a school of horse mackerel at different swimming speeds. Journal of Fish Biology 49, 854–862.

Wieser, W. (1991). Limitations of energy acquisition and energy use in small poikilotherms: evolutionary implications. Functional Ecology 5, 234–240.

Wieser, W., Krumschnabel, G., Ojwang-Okwor (1992). The energetics of starvation and growth after refeeding in juveniles of three cyprinid species. Environmental Biology of Fish 33, 63–71.

Wootton, R.J. (1998). Ecology of Teleost Fishes. 2nd edition. Dordrecht: Kluwer, 386 pp.

Laboratory experiments on the gastric evacuation of juvenile herring (*Clupea harengus* L.)

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Abstract

Laboratory experiments were conducted on groups of 9.9 to 13 cm (mean) total length juvenile herring (*Clupea harengus* L.) to describe the temperature dependency of the gastric evacuation. Experiments were conducted at 13 and 16°C. The parameters of the general model were B = 0.953 and R = 0.082 at 13°C and B = 1.323 and R = 0.843 at 16°C indicating an exponential evacuation. The evacuation constants of the exponential model were R = 0.098 at 13 and R = 0.202 at 16°C resulting in a temperature dependency parameter (A) of 0.241. The internal dynamics of the stomach and its storage capacity were studied by the use of stained copepods. Investigations on the functional response of herring to different food densities were described by the Michaelis-Menten equation. Our experimental design allowed us to test the hypothesis of Richter et al. (2002) that fish have two evacuation modes, one evacuation constant while only evacuating food and a significant higher constant while feeding, which would question the basic assumption of most consumption models, that only use one evacuation constant for consumption estimates. The experiments of Richter et al. (2002) suggested that a doubled constant would give the best match of observed feeding and estimates of consumption models. Through the results of simulations of two experiments in which we combined observed snatching rates, estimated evacuation constants and particle weights of consumed copepods, we cannot support this hypothesis. A doubled evacuation constant did not improve our simulations, on the contrary the simulations with a doubled constant gave a worse fit with our observed values.

Introduction

Atlantic herring (*Clupea harengus* L.) is a planktivorous species of great economic value to the fisheries throughout its range. It is widely distributed across the northern North Atlantic between Newfoundland and the British Isles, and also in the Arctic. It is abundant around Iceland, along the Norwegian coast and in the Baltic Sea.

Due to its large stock biomass herring is a considerable predator, having a strong impact on populations of its main prey items, mostly copepods, for example in the Baltic Sea (Last 1989, Flinkmann et al. 1991, Arrhenius & Hansson 1993). Information on the food consumption rate of herring is therefore of interest for quantifying the impact that this species has on its prey populations.

The two most commonly used methods for estimating the rate of food consumption by fish are based on either evacuation rates of food from the stomach or the energy budget of an average fish. In the field, the former requires extensive quantitative analysis of stomach contents and the latter accurate growth analysis. In addition, both methods require the estimation of the model parameters in the laboratory: either the evacuation rate as a function of body weight, temperature and food type or at least ten different parameters of energy allocation for bioenergetics model construction (Karjalainen et al. 1997).

Two different methods for the estimation of evacuation rates and constants respectively of herring have been used so far: In one method herring are caught by different nets or sampled with the help of dynamite over a period of 24 hours. The rate of gastric evacuation was estimated from the depletion of the stomach contents at night (Temming & Köster 1990, Köster 1994, Schmanns 1994, Arrhenius & Hansson 1994, Maes et al. 2005). The second method for estimating gastric evacuation rates is from ship-board tank experiments. Herring are caught by bottom or pelagic trawls and transferred to deck tanks, where sub samples are sacrificed at regular intervals and the

rate of gastric evacuation is estimated from the depletion of the stomach contents (Szypula & Zalachowski 1984, Köster et al. 1990, Köster 1994, Temming 1995).
Laboratory studies are a useful tool for obtaining comparable results to the results from these methods (24 h-fisheries and ship-board tank experiments). Many laboratory studies of food intake and gastric evacuation rate of fish have been conducted using a variety of techniques (Bromley 1994). However only a few taxonomic groups have been particularly well studied. These include the salmonids, flatfish, sunfish and the gadoids, but as yet no stomach evacuation experiments have been conducted on herring. Van der Lingen (1998) performed laboratory experiments on another clupeid, the sardine. The lack of such data for herring is largely due to the fact that herring are very sensitive to handling, making laboratory studies difficult.
The objectives of this study were:
1) to estimate under stress-free and controlled conditions the exponent B and evacuation constant R of the general evacuation model (Temming & Andersen 1994) in single-meal/short-term feeding experiments, and to investigate upon the influence of temperature on the evacuation constant.
2) to visualize the internal dynamics of the cecum, the storage part of the stomach, by the use of stained copepods
3) to investigate upon the functional response of herring feeding at different food concentrations.
4) to test the hypothesis of Richter et al. (2002), that fish exhibit two evacuation modes, one constant while only evacuating food and a significantly enhanced constant, while feeding. It was tested, whether a doubled constant, as suggested by Richter et al. (2002), gave a better fit in our simulations, than the results of our evacuation constants as estimated from fish that were only evacuating and not feeding.

Material and methods

Fish capture, transport and maintenance

Juvenile herring were caught in the German Wadden Sea in List Harbour and in Denmark in Thyborøn Harbour with a 5 m^2 dip-net and fishing tackles. The fish were dropped directly from the hooks into a 300 l aerated transport box. Fish from dip-net were only concentrated in the water and removed with buckets. They were transferred in a 700 l transport box with aerated seawater to the Institute for Hydrobiology and Fisheries Science in Hamburg.
Prior to the experiments the fish were held in large groups of 200 - 400 individuals in circular tanks with a capacity of approximately 1000 l. The aquarium was operated as a recirculation system with mechanical and biological filter units and a total capacity of 80 m^3. Exchange water was produced from marine salt and tap water to replace discarded sea water at regular intervals. Temperature was regulated with a precision of +/- 0.1 °C. In experiments 1 to 5 the temperature was held constant at 13°C and in experiments 6 and 7 constant at 16°C. Fish were exposed to a constant day length of 14 h, lights were dimmed from full to minimum over a period of 20 minutes. The salinity was kept constant at 32 ppt with a precision of 0.1 ppt. The herring were fed minced fish, copepods, euphausids and mysids twice a day.

Experimental tanks

For the gastric evacuation experiments fish were transferred into four especially designed tanks (figure 1). The outside of the tanks were covered with black tape and

cloth to minimize the stress for the fish. The tanks were circular with a conical bottom with a height of 68 cm, a diameter of 80 cm and a volume of approx. 270 l each. On one side a transparent screen was mounted for video recording of the snatching rates (figure 1 B). The design of the tanks allowed feeding and removal of the food without disturbing the fish. The aeration and the water inflow were located in a plastic pipe construction (figure 1 A). The aeration caused a permanent circular current, which continued even in the absence of water inflow. Food could be removed from the tank in approximately 20 minutes by inserting a small filter into the plastic pipe (figure 1 A).
In all experiments frozen copepods (mainly c4-6 *Cyclops* spp.) of SFM-Aquaristik were used. Prior to the experiments the copepods were thawed and suspended in seawater and then used as experimental food.

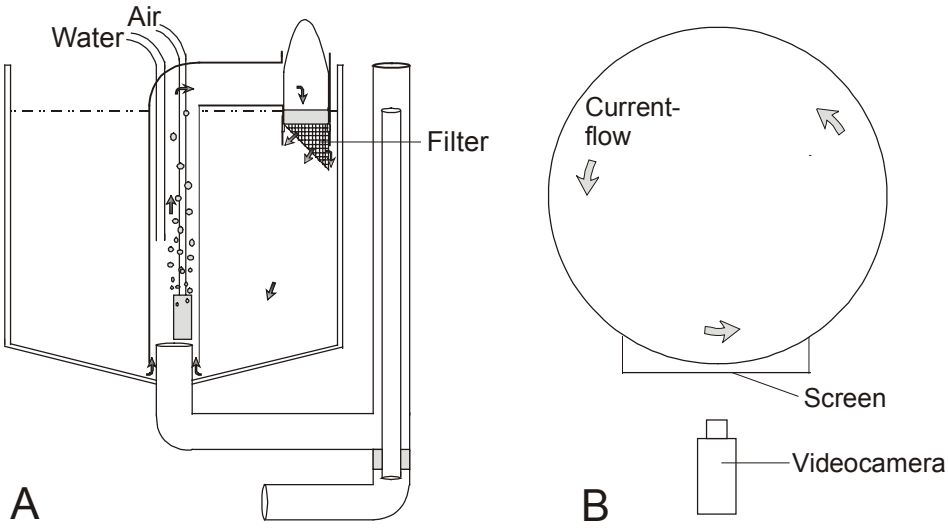


Figure 1) Experimental design. A) Side view B) Bird`s-eye view

Experimental procedure

Short-term feeding experiments

The objectives of the short-term feeding experiments were to estimate under stress-free and controlled conditions the shape parameter B and evacuation constant R of the general evacuation model (Temming & Andersen 1994). The influence of variations in meal size on the evacuation parameters were studied along with the influence of temperature on these parameters. The term “short-term feeding” refers to a single well-defined intensive feeding period, where up to 3500 copepods were eaten over a 30 min period. Short-term feeding experiments were performed at 13 and 16°C. The fish were allowed to acclimate over a period of two weeks. Experiments were only started if mortality rate was zero and fish were eagerly feeding. Prior to all experiments the fish were starved for 36 hours to avoid any food in the stomach at the start of the experiments.
In short-term feeding experiments four tanks with identical numbers of fish (20) were fed in parallel (20 g of frozen copepods were thawed in seawater) for 30 minutes whereupon the food was removed from the tanks over a 20 minute period (figure 1 A). All tanks were treated in a similar fashion. Fish from one tank were sampled immediately after the end of this feeding period to estimate the initial stomach content (= meal size). The fish were rapidly killed by an overdose of anaesthetic (MS-222 at

0.284 g l^{-1}) and the total length (mm below) and weight (0.1 g below) of each fish was determined. The stomach content in g wet weight (*WW*) was determined, then the content was dried to constant weight at 90°C and g dry weight (*DW*) was determined.
It was assumed that this initial meal size was identical in all four tanks. However the snatching rate observations made for each tank were analyzed to verify this assumption. Deviations in the mean snatching rates were then used to adjust the initial stomach contents in the three tanks from which no initial sample was taken.
The snatching rates were estimated by counting the snatching movements of the fish during the time a single herring was able to stay visible to the observer. This was conducted several times over a 5-minute period, to estimate mean snatching rates for ten, 5-minute intervals. We assumed, as it was not possible to distinguish individual fish from one another, that all fish were displaying similar feeding and activity levels.
The fish were removed from the remaining three tanks between 1 and 15 hours after the end of feeding and were treated as described above.

Long-term feeding experiments

The long-term feeding experiments served a different purpose. The first purpose was to study the influence of long-term feeding on the gastric evacuation parameters in the non-feeding phase (exp.3). The function of the caudally extending gastric cecum was investigated with regard to the internal dynamics and its storage capacity. Additionally, these experiments were conducted to test the Richter et al. (2002) hypothesis, that fish have higher evacuation constants while feeding (see “Simulation to test the hypothesis of Richter et al. (2002)”). These experiments were conducted at 13°C only.

Process sequence

Fish in all tanks were permanently offered copepods at an initial concentration of approx. 1 particle per ml for 30 min. The decrease in concentration (approx. 10% in 30 min) by feeding was replaced at the end of the 30 min feeding period by addition of a defined amount of copepods to again reach the concentration of 1 particle per ml. This sequence of 30 min feeding periods lasted for 2.5 h in experiment 6 and 8 h in experiment 7. The food was subsequently removed and green copepods (stained in malachite-green at 0.43 g ml^{-1}) were offered to the fish for 20 minutes and then these stained copepods were removed. From one tank in each experiment all 20 fish were removed directly after the removal of the stained copepods. In the other tanks the fish were offered natural (unstained) copepods. These natural copepods were offered for 1, 2 and 3 hours in experiment 6 and for 2, 4 and 6 hours in experiment 7 before being removed. For an overview see figure 2. The fish were sacrificed, dissected, the stomachs were removed, carefully cut open and digitally photographed (Olympus Camedia 3030).

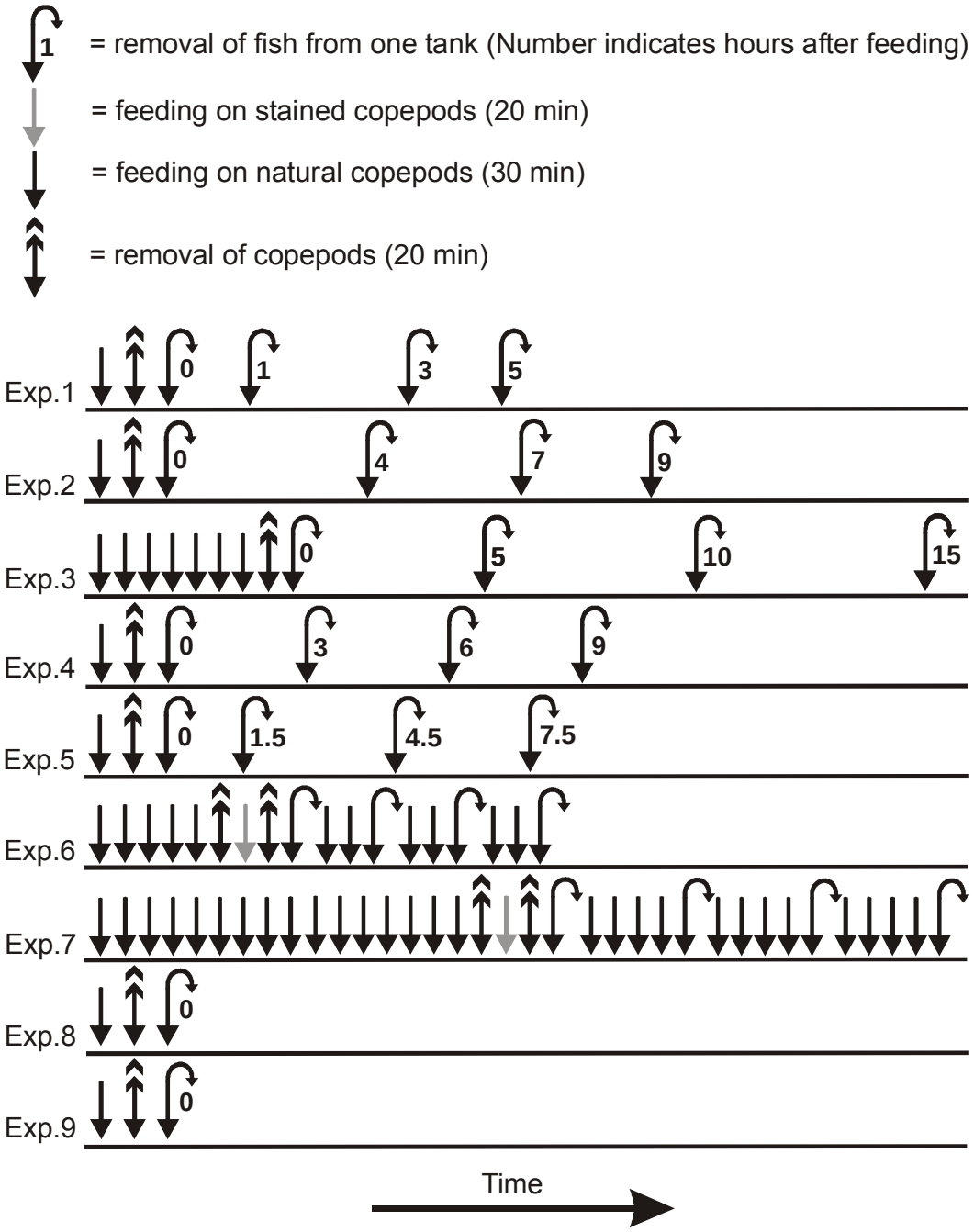


Figure 2) Schematic overview of experiments 1 to 9. From the results of experiments 1 to 5 the parameters of the gastric evacuation models were estimated.

Food density versus snatch rate

The objective of these experiments was to find a suitable food concentration for the short-term and long-term feeding experiments. We desired a food concentration at which fish were feeding by single snatches (particulate feeding) at a high rate and at which no filter feeding was observed. An additional objective was to examine the functional response of herring feeding at different food densities.
In a series of 16 experiments, different food densities (from 10 to 1600 copepods l^{-1}) were offered to 20 fish in one tank over a 30 min period. The snatching rates were estimated in three 10 min intervals as described above and means were calculated over the 30 min periods.

Verification of snatch rate

The verification of the snatching rates was conducted with the help of the short-term feeding experiments 1 and 2 at 13°C and two individual 30 min experiments at 13°C (experiment 8 and 9). The fish in the tanks were feeding on our defined experimental concentration of copepods (550 l^{-1}, see experimental procedure) for 30 min, while being videotaped. After this 30 min period the fish were removed, sacrificed and number of copepods in stomachs was counted. For the estimation of snatching rates 60 individual feeding sequences of herring were measured. In each feeding sequence a single fish was observed, time was measured and snatching movements were counted. The potential consumption of copepods was estimated from means of three ten minute intervals. The observed consumed copepods after the 30 min feeding period were compared with the potentially consumed copepods which were estimated by the observed snatch rates.

Equations for gastric evacuation

Gastric evacuation was described using the general model (Jones 1974, Temming & Andersen 1994). In this model the evacuation rate is a flexible function of the actual stomach content. The strength of the stomach content effect is modulated by an exponent (B):

$$\frac{dS_t}{dt} = -R * S_t^{B}, \quad (1)$$

with S_t = stomach content at time t after ingestion of the experimental meal (g dry or wet weight) and R = constant depending on prey type, temperature and predator weight. B = parameter determining the shape of the curve:

If	B < 0	a convex curve with increasing negative slope
	B = 0	linear, negative slope
	0 < B < 1	a concave curve, with decreasing negative slope
	B = 1	exponential decay curve
	B > 1	a concave curve, the dependence of evacuation rate on the stomach content is stronger than in exponential case. This implies higher rates at high, and lower rates at low stomach contents when compared with an exponential model

For the estimation of the constant R the integrated form of equation 1 (for B ≠ 1) was used.

$$S_t = [S_0^{(1-B)} - R * (1-B) * t]^{\left(\frac{1}{1-B}\right)} \quad (2)$$

with S_t = stomach content at time t,
and S_0 = stomach content at time 0, equals the meal size,
and R = gastric evacuation constant.

If B = 1, the integrated form of equation 1 results in the exponential function (equation 3):

$$S_t = S_0 * e^{-R*t} \quad (3)$$

Both models were fitted to the data sets of the experiments at 13°C and experiments at 16°C by means of non-linear regression as described in Temming & Andersen (1994) using the statistical software package SPSS. Additionally, equation 4 incorporated temperature as a variable:

$$R = R' * e^{A * T} \quad (4)$$

with R´= food type coefficient,
and A = temperature coefficient (T^{-1}),
and T = temperature (°C).

Simulation to test the hypothesis of Richter et al. (2002)

The snatching rates, the particle weight of the copepods and the parameter R of the exponential stomach evacuation as estimated from "single meal" experiments, were combined to simulate the trajectory of the mean stomach contents in experiments 6 and 7. The estimated mean feeding efficiency of 1.1 (see results) was used for the estimation of copepods ingested per time interval. The consumed weight of food per time interval was estimated from the copepods ingested and their particle weight (0.011 mg *DW*). The number ingested was calculated by multiplying the time interval with the snatching rate of this interval. The simultaneous evacuation in these intervals was calculated using equation 1 (with B = 1) and the estimated R-value for 13°C, and subtracted from the present stomach content. The endpoints of the simulated trajectories were compared with the observed mean stomach contents from experiments 6 and 7. It was tested whether there was a better match of the simulated and the observed stomach contents using either the estimated evacuation constant R or a doubled evacuation constant of 2R.

Results

Evacuation parameters

The evacuation parameters were estimated for two different temperatures from experiments 1 to 5. The models were applied to the medians of each experiment. An overview of the basic experimental data is given in table 1.

Table 1) Basic experimental data (SF = short term feeding, LF = long term feeding, *SR* = snatching rate, *WW* = wet weight, length = total length, Meal size = *WW* % *BW*

Experiment No.	Temp. °C	No.of fish	Mean length (cm)	Mean *WW* (g)	Meal size (% *BW*)	Experiment type
1	13	74	11.2 ± 0.5	9.0 ± 0.5	1.92 ± 1.02	SF
2	13	79	12.0 ± 0.7	11.5 ± 2.2	0.59 ± 0.47	SF
3	13	76	12.8 ± 1.0	13.1 ± 3.2	1.82 ± 0.92	LF
4	16	99	9.9 ± 0.7	6.0 ± 1.1	1.32 ± 0.44	SF
5	16	57	10.3 ± 0.7	7.0 ± 1.5	1.69 ± 0.74	SF
6	13	78	10.1 ± 0.5	6.8 ± 0.4	5.61 ± 1.51	LF
7	13	53	13.3 ± 1.0	15.8 ± 3.7	2.24 ± 1.14	LF
8	13	20	10.5 ± 0.7	7.1 ± 0.9	-	SR
9	13	20	11.3 ± 0.8	9.8 ± 1.4	-	SR

The shape parameter B of the general model was estimated as 0.95 at 13°C and 1.32 at 16°C (table 2). The temperature coefficient A was estimated to 0.245 (table 2) from the general model (equation 2).
The evacuation constants were 0.098 at 13°C and 0.202 at 16°C as estimated from the exponential model (equation 3). This resulted in a temperature coefficient A of 0.241 (table 3). These values correspond to a Q_{10} of 11.6 as estimated from the general model and a Q_{10} of 11.1 as estimated from the exponential model. A fit of the general model to all 5 short-term feeding experiments revealed a B value of 1.01 with confidence limits of 0.3 – 1.7.

Table 2) Parameters of the general model.

	Experiment No.	Value ± s.d.	Lower Confidence	Upper Confidence	r^2
13°C	1, 2, 3				
B		0.953 ± 0.408	- 0.013	1.918	0.82
R		0.082 ± 0.122	- 0.207	0.372	0.82
16°C	4, 5				
B		1.323 ± 0.534	- 0.159	2.805	0.85
R		0.843 ± 1.972	- 4.632	6.318	0.85
Temperature dependency	1, 2, 3, 4, 5				
B		1.014 ± 0.315	0.328	1.700	0.90
R´		0.004 ± 0.003	- 0.004	0.013	0.90
A		0.245 ± 0.104	0.019	0.470	0.90

Table 3) Parameters of the exponential model.

	Experiment No.	Value ± s.d.	Lower Confidence	Upper Confidence	r^2
13°C	1, 2, 3				
R		0.098 ± 0.010	0.076	0.120	0.82
16°C	4, 5				
R		0.202 ± 0.021	0.147	0.257	0.84
Temperature dependency	1, 2, 3, 4, 5				
R´		0.004 ± 0.003	- 0.003	0.012	0.90
A		0.241 ± 0.063	0.105	0.377	0.90

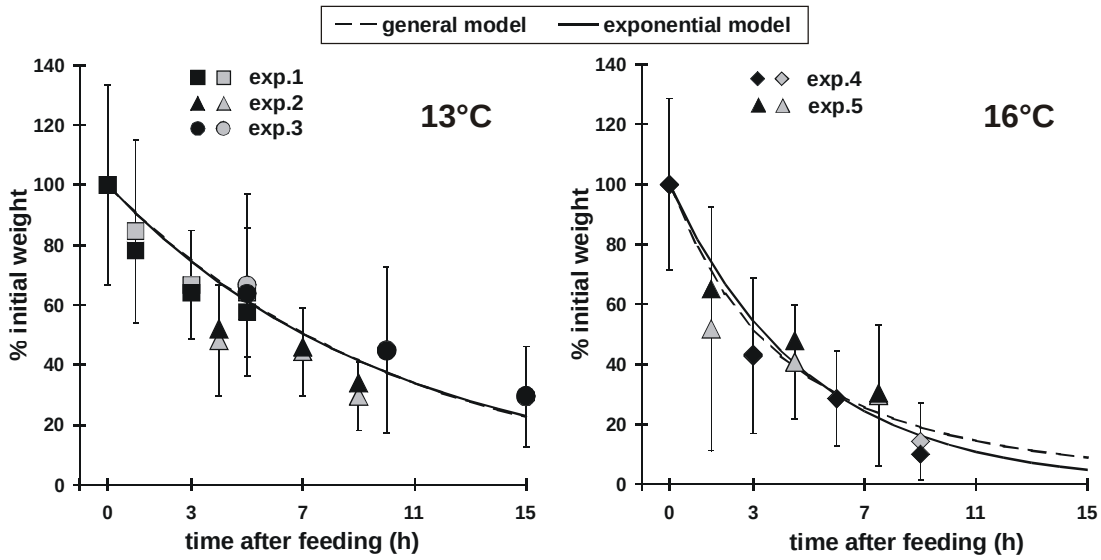


Figure 3) Relationship between dry weight as % of initial weight of copepods consumed and time after the end of feeding for the two experimental temperatures. The different experiments per temperature are labelled by different symbols. Means (± s.d.) are marked by grey symbols and medians by black symbols. The models were fitted to the medians.

Internal dynamics of herring stomach

The stained and unstained copepods could easily be distinguished. Figures 4 to 6 display examples of the dynamics of the food particles in a herring stomach for three different situations.
In all photographs the upper branch was connected to the oesophagus while the lower branch connected the stomach to the intestine via the pylorus.
In figure 4 the fish had been feeding for 2.5 hours before stained copepods were offered for 20 min. At the end of the 20 min feeding period with stained copepods the fish was removed and cut open. The stained copepods are located in the front part of the stomach and appear to have moved directly into the intestine. Hardly any stained copepods can be found in the cecum.

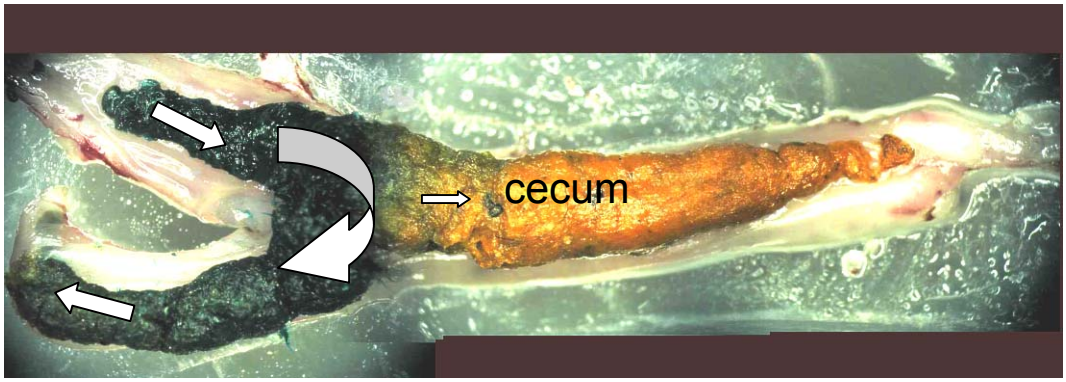


Figure 4) This fish was fed for 2.5 h natural copepods before stained copepods were fed for 20 min.

The fish in figure 5 had been feeding for 2.5 hours before stained copepods were offered for 20 min. At the end of this 20 min feeding period the stained copepods were removed and natural copepods were offered for one more hour before the fish was removed and cut open. The stained copepods are again in the front part of the stomach, where there appears to be a mixing zone of natural, freshly fed copepods and the stained copepods. Only a few dark copepods can be seen in the cecum.

Figure 5) This fish was fed for 2.5 h natural copepods before stained copepods were fed. After that natural copepods were fed for 1 h.

The fish in figure 6 was treated as the fish in figure 5 with the exception that this fish was offered natural copepods for 3 hours instead of 1 hour after being fed with the stained copepods. In the middle of the cecum a band of stained copepods is visible. It appears as if they were pushed back into the cecum by subsequent meals of copepods. The dark stripe left of this zone is an artefact that results from connecting two parts of the photo. The lighter dark area in the branch towards the intestine appears to result from a group of stained copepods that were cut off the band by subsequent ingested natural copepods.

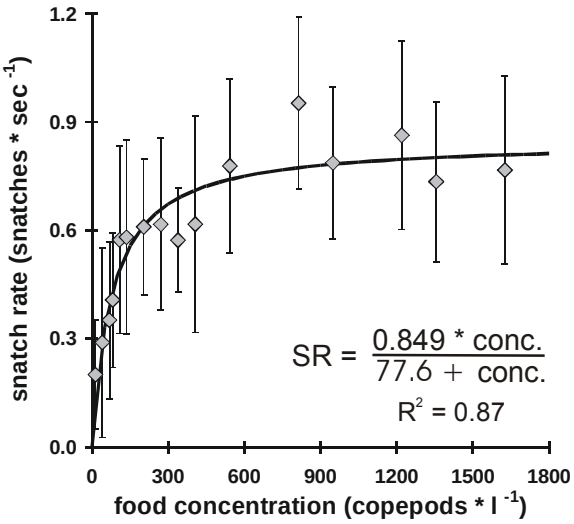
Figure 6) This fish was fed for 2,5 h natural copepods before stained copepods were fed. After that natural copepods were fed for 3 h.

Food density versus snatch rate

The mean snatching rate increased rapidly with increasing food density to a rate of approx. 0.8 snatching movements per second at 600 copepods per liter. At higher concentrations rates were between 0.7 to 0.9 and did not increase above 1.0 snatches per second. During visual observations, we did not measure the time of the gape-opening. We discriminated between particulate feeding or biting, which is a short directed attack at a prey, and filter-feeding, where the fish is swimming with a wide open mouth and a flared operculum at a markedly increased swimming speed (Gibson & Ezzi 1985, 1990). At concentrations ≥ 900 copepods * l^{-1}, we observed an increasing number of filter-feeding fish and a Michaelis-Menten-equation was fitted to the data

points (figure 7). As a result of these estimates, we chose a concentration of 550 copepods per litre for our experiments investigating the gastric evacuation rate. At this concentration the fish were feeding at high rate of close to 0.8 snatches per second and we were assured that the fish were not filter-feeding. The implications of a certain amount of filter-feeding fish on the snatching rate would have been entirely negative. This would inhibit the verification of identical meal sizes in the different experimental tanks as described in the material and methods section. Deviations in the snatching rates could not have been corrected due to the uncertainty about how many copepods were ingested per feeding movement (snatching or filter-feeding). For the simulation to test the hypothesis of Richter et al. (2002) a known snatching efficiency was needed, which could not be provided by filter-feeding fish.

Figure 7) Functional response of herring estimated from snatching rates at different food concentrations with standard deviation. The data points are means over a 30 min feeding period. A Michaelis-Menten-equation was fitted to data points. SR = Snatch rate and conc. = food concentration.



Verification of the snatching rate

The verification of the snatching rates or estimation of snatching efficiency resulted in a mean of 1.11 ± 0.14, with a maximum efficiency of 1.31.
The estimation of the snatching rates from 1 to 3 and both experiments 8 and 9 were conducted by one person, whereas the estimation of snatching rates for experiments 6 and 7 where conducted by two persons. A mean was calculated from the estimated snatching rates per 10 min interval of both persons and used for the simulation of experiments 6 and 7.

Table 4) Estimated snatching efficiency, mean and standard deviation (s.d.). Verification was performed at equal concentration (550 copepods * l^{-1}) and equal duration (30 min).

Experiment No.	Snatching efficiency (observed/estimated)
1	1.31
2	1.09
8	1.04
9	1.00
mean	1.11
s.d. (±)	0.14

Test of the hypothesis of Richter et al. (2002)

The simulated values for experiments 6 and 7 based on the estimated R = 0.098 (figure 8 A, figure 9 A) gave a better match than the simulated values based on the doubled evacuation constant R = 0.196 (figures 8 B, 9 B).

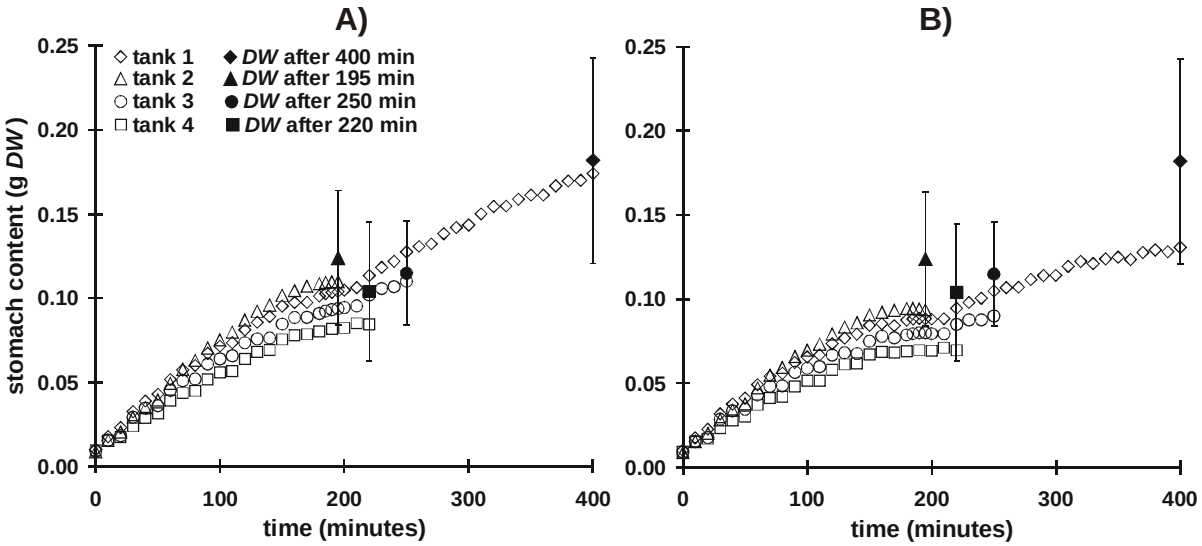


Figure 8) Simulation of experiment 6. In diagram A estimated evacuation constant R = 0.098 and in B elevated evacuation constant R = 0.196 was used to simulate progression of stomach contents. Observed stomach contents (g *DW*) are displayed with standard deviation.

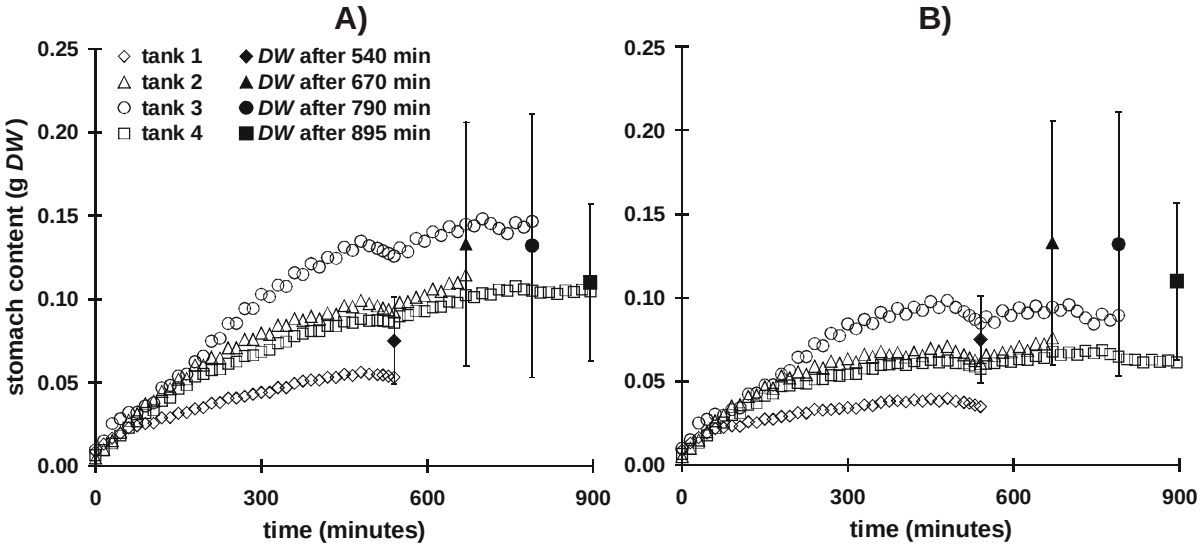


Figure 9) Simulation of experiment 7. In diagram A estimated evacuation constant R = 0.098 and in B elevated evacuation constant R = 0.196 was used to simulate progression of stomach contents. Observed stomach contents (g *DW*) are displayed with standard deviation.

In experiment 6, in all tanks (figure 8 A) the simulated values from our estimated evacuation constant were below the observed values. Nevertheless, we could observe in each tank a better match from the simulation using our estimated evacuation constant R with the observed values than with the doubled evacuation constant (figure 8 B). In experiment 7 (figure 9 A) were, with the exception of tank 3, the simulated values from

our estimated evacuation constant below the observed values. In tank 3 was the simulated value higher than the observed. When using the doubled evacuation 2R in experiment 7, all simulated values gave an inferior match than the values with R. All simulated values were below the observed values, and the result of simulation of tank 1 was not even within the observed standard deviation in that tank.

Table 5) Results of the simulation of experiments 6 and 7 with different snatching efficiencies and observed stomach contents from each tank. Simulated stomach contents resulted from estimated evacuation constant R = 0.098 and elevated evacuation constant R = 0.196. The values illustrated, display the deviation (negative or positive) in per cent of the simulated mean stomach contents in comparison to the observed mean stomach contents (g *DW*). The observed s.d. (%) indicates the standard deviation of the observed stomach contents in per cent.

Experiment 6

R = 0.098	Snatching efficiency	tank 1	tank 2	tank 3	tank 4
	1.00	-13.7	-20.2	-13.9	-26.9
	1.11	-4.4	-11.2	-4.3	-18.3
	1.31	12.6	4.8	13.0	-3.8
R = 0.196		**tank 1**	**tank 2**	**tank 3**	**tank 4**
	1.00	-35.2	-32.3	-29.6	-39.4
	1.11	-28.0	-24.2	-21.7	-32.7
	1.31	-15.4	-10.5	-7.8	-21.2
observed mean (g *DW*)		**0.182**	**0.124**	**0.115**	**0.104**
observed s.d. (%)		**33.5**	**32.3**	**27.0**	**39.4**

Experiment 7

R = 0.098	Snatching efficiency	tank 1	tank 2	tank 3	tank 4
	1.00	-33.3	-19.0	5.3	-9.2
	1.11	-25.9	-16.8	10.1	-0.8
	1.31	-12.6	6.1	37.9	19.0
R = 0.196		**tank 1**	**tank 2**	**tank 3**	**tank 4**
	1.00	-55.0	-44.9	-33.8	-45.2
	1.11	-50.0	-38.9	-26.6	-39.2
	1.31	-41.0	-27.9	-13.3	-28.2
observed mean (g *DW*)		**0.075**	**0.133**	**0.132**	**0.110**
observed s.d. (%)		**34.7**	**54.9**	**59.8**	**42.7**

We observed snatching efficiencies from 1.00 in experiment 9 to 1.31 in experiment 1 (table 4). For the simulation we used these two efficiencies and the mean snatching efficiency of 1.11. In all cases, a much better fit was observed between the simulated and observed stomach contents and our estimated evacuation constant R = 0.098 and the snatching efficiency 1.11 than when with the doubled evacuation constant R = 0.196 (table 5). The lowest deviation (%) from the observed mean stomach contents, as estimated with R = 0.098, was reached in experiment 7 in tank 4 with -0.8% (Snatching efficiency = 1.11) and the highest in experiment 7 in tank 3 with 37.9% (Snatching efficiency = 1.31). The lowest deviation, as estimated with R = 0.196, was reached in experiment 6 in tank 3 (Snatching efficiency = 1.31) with – 7.8%. The highest deviation was 55% in experiment 7 in tank 1 (Snatching efficiency = 1.00). In both experiments 6 and 7 did the results of the simulations with a doubled evacuation constant result in negative deviations, independent of the snatching efficiency (figure 10).

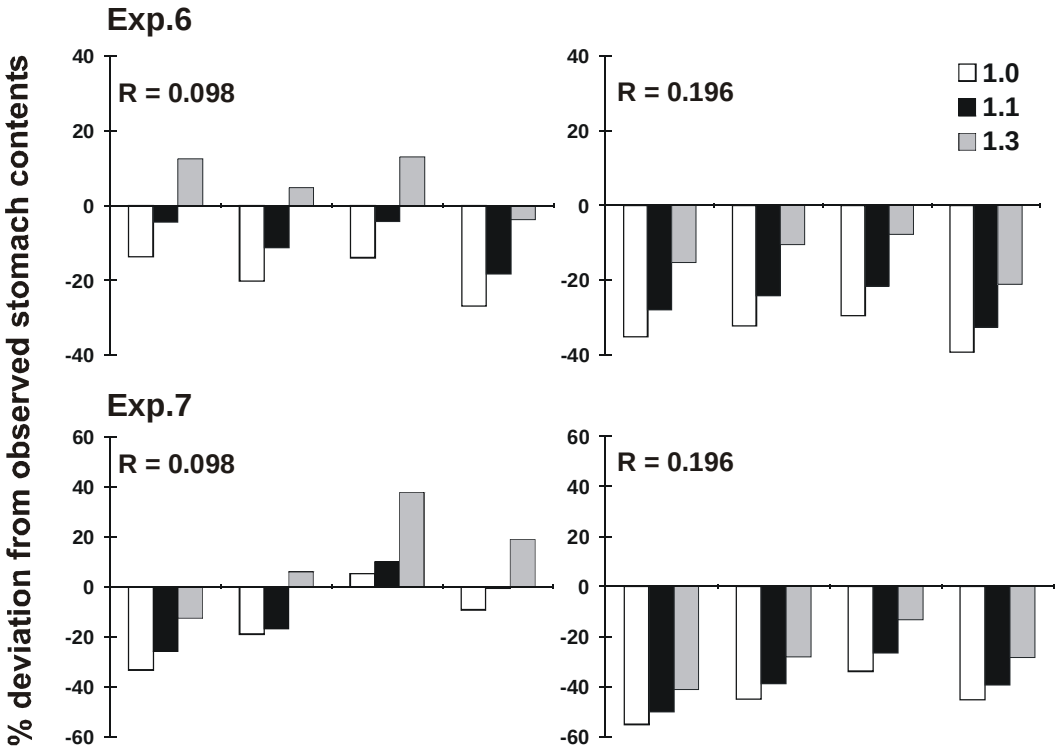


Figure 10) Graphical illustration of results in table 5. Displayed are the deviation (positive and negative) of the simulated stomach contents (with evacuation constant R and 2R) at the end point of the simulation from the observed stomach contents in the experiments 6 and 7.

Discussion

Estimation of meal size by snatching rate, a useful method ?

Microphagous fish feed on small food particles, i.e. copepods which they ingest in large numbers either by snatching for single particles or by filtering. The type of feeding method depends on the food particle size, light intensity and food concentration (Batty et al. 1990; Gibson & Ezzi 1985, 1990, 1992).
We were faced with the problem of estimating the meal size of a very sensitive fish species. Pilot experiments revealed that it was not possible to maintain herring individually, so we were forced to conduct the experiments with groups of fish. The major challenge was to estimate the meal size of herring feeding on numerous copepods. Our first approach was to measure the difference between what went into the tank and what came out. We estimated the number of copepods that were added to a tank containing no fish and estimated the amount that we were able to recover by filtering after a certain amount of time. The results were unsatisfactory, as we were not able to recover the same amount of copepods. As a result that approach was abandoned. As herring feed by biting or snatching at certain food concentrations our idea was to estimate the snatching rates of the fish in the experimental tanks, in order to be able to calculate the meal size by the mean snatching rate and the particle weight. If this was not realizable, the estimation of the snatching rates were to be used to compare the feeding in the different tanks. The basic assumption of this approach was, as in the work of Gibson & Ezzi (1992), that one particle was ingested per snatching

movement and this assumption could easily be violated by the switching between the two described modes. Carrieri & Volpato (1991) found no direct association between snatching frequency and food ingested for Nile tilapia fingerlings (*Oreochromis niloticus* L.). This conclusion was based on experiments where the tilapia were feeding on crushed pellets with varying diameters from the ground of the experimental aquaria. It was evident in this experiment that each snatching movement resulted in a different amount of food entering the jaw. Herring ingest food in the water column and do not feed off the ground, as the jaw construction makes this impossible (Blaxter & Holliday 1958).
The verification of the snatching rates was done with the help of the short-term feeding experiments 1 and 2 at 13°C and additionally experiments 8 and 9 at 13°C. We compared the observed copepods obtained from the stomachs at the end of a 30 min feeding period with the estimated from the observed snatch rates. The result for the snatch success was 1.11 ± 0.14 copepods per snatching movement. This result was expected, as the food concentration was chosen low enough so that the herring would not start to filter-feed. We can confirm the assumption by Gibson & Ezzi (1992) that one snatching movement results in approximately one ingested food particle, if copepods are offered in concentrations below 900 * l^{-1} (figure 7). To definitely exclude filter-feeding, concentrations below 600 * l^{-1} should be used. With increasing food concentration (above 900 * l^{-1}) though we were observing an increasing number of fish that were switching their feeding mode from snatching to filtering. As single filtering actions were not of a constant duration the estimation of the meal size by estimating snatching rates is not a useful method at high food concentrations. At lower concentrations (below 600 copepods * l^{-1}) the estimation of the meal size by snatching rates is a useful method.

Tank design and experimental concept

The intention with our tank design and experimental concept was to work with undisturbed herring under controlled conditions, resulting in hardly any stress on the fish. We were able to keep the herring at a constant temperature, salinity and day-length, during adaptation and experiments. The use of groups of fish in different tanks allowed us to deal with discrete fish groups without disturbing the other groups, e.g. influencing the evacuation rate by stress. The use of snatching rates enabled us to correct for minor differences in feeding on the meal size. Furthermore did we know exactly, what the fish were feeding.
The previously used methods to estimate the parameters of the gastric evacuation models in herring, 24 h-fisheries and ship-board tank experiments, have some disadvantages, resulting in uncertainty concerning the reliability of the results from these methods. In 24 h-fisheries herring are caught over a period of 24 hours. The rate of gastric evacuation is estimated from the depletion of the stomach contents at night (Temming & Köster 1990, Köster 1994, Schmanns 1994, Arrhenius & Hansson 1994, Maes et al. 2005). In this method it is difficult to obtain reliable catches during dusk and night, as herring migrate towards the upper water column, breaking up the shoals and dispersing over night (Nilsson et al. 2003). In previous mentioned studies there was a depletion of stomach contents at night, but results of experiments by Batty et al. (1986) concerning the feeding of herring at night were ignored. Batty et al. (1986) discovered that juvenile herring are able to feed by filtering at certain prey concentrations (> 70 *Artemia* sp. nauplii * l^{-1}) during darkness (= insufficient light to use for visually controlled behaviour). This disregard may lead to an underestimation of the evacuation rate. Another disadvantage is the uncertainty whether the same group of fish is sampled throughout the entire investigation period, as the same area is sampled over the

investigation period and possible migrations of the shoals are not accounted for. If the water column is stratified, then the fish will experience different temperatures, due to the diurnal vertical migrations. This will influence the evacuation rate as well.
The advantages of ship-board tank experiments is that the fish that are caught are evacuating natural prey from their feeding environment, which we were not able to provide, as the quantities of natural zooplankton and copepods respectively needed for our experiments were not obtained. After the capture, the fish are transferred to deck tanks and are sampled at certain times. The disadvantage is that these experiments are performed with heavily stressed and sometimes damaged fish. Köster et al. (1990) mention the possible causes of stress by insufficient conditions during the experiments in the tank, e.g. high densities of fish, lack of oxygen supply, high fluctuations in temperature and salinity, water turbulence, ship movements and other external disturbances. It has been observed in ship-board tank experiments that the start of the stomach evacuation was delayed by up to 3 hours (Köster et al. 1990), indicating severe stress to the fish.
In our work most of the stress factors mentioned were eliminated. The handling and transfer stress was avoided as the fish were caught, transferred to the lab and acclimated to the experimental tanks weeks before the start of the experiment. Feeding and removal of the food without causing major disturbance was also possible, due to the pipe construction and the use of filters. The lack of disturbance was evident as no escape behaviour was observed while the fish were fed or while food was removed. All in all can we state that we were able to study the gastric evacuation and feeding behaviour of juvenile herring under controlled conditions, including the minimization of stress to the fish.

Stomach evacuation

Experiments 1 to 5 were conducted to estimate parameter B and the evacuation constant R at two temperatures. The results of the general model with parameters of B = 0.953 at 13°C and B = 1.323 at 16°C indicate an exponential evacuation (special case of the general model with B = 1) in herring. Analysing experiments 1 to 5 together resulted in a value for B of 1.01. The linear evacuation (B = 0) was excluded by the confidence intervals. This is one of the first times that an exponential evacuation was observed for a fish species feeding on small particles, where the evacuation model was not determined in advance. Temming (1995) observed a B-value of 1.14 for Baltic herring (16 - 28 cm) from tank experiments. An exponential evacuation has been observed for numerous fish species feeding on small particles, e.g. perch (Perca fluviatilis, Persson 1979, 1981), ruffe (Gymnocephalus cernuus, Hölker & Temming 1996), mackerel (Scomber scombrus, Mehl & Westgård in Temming et al. 2002). In these works the exponential evacuation model was chosen in advance. In the laboratory and tank experiments with sardine (Sardinops sagax, Van der Lingen 1998) were the linear, square root and exponential function fitted to the data. The suitability of the fitted curves in describing the relationship between stomach contents and time was assessed by comparing the coefficient of determination (r^2) derived for each curve. The result was that the exponential function was the best to describe gastric evacuation in all laboratory experiments. The tank experiments were best described by the linear function, with r^2´s being marginally higher than those for the exponential function. However, the results of the tank experiments should be handled with care, bearing in mind the disadvantages of this method.
The results of the exponential model for the evacuation constant R were 0.098 at 13°C and 0.202 at 16°C. These values are comparable to the results from other authors obtained by 24 h-fisheries or tank experiments. Arrhenius & Hansson (1994 b) obtained

constants of 0.19 - 0.28 at a mean temperature of 13.2°C for herring from 6 to 7.4 cm length and constants of 0.21 and 0.27 at a mean temperature of 16.5°C for 4.5 to 5.5 cm herring from 24 h-fisheries. The constants at 13.5°C were more than doubled compared to our obtained constant at 13°C while the constants at 16.5°C were comparable to our estimated constant at 16°C. However, the constants of Arrhenius & Hansson (1994) for the two different temperatures indicate no temperature effect on the evacuation constant. This may be due to the mentioned methodical problems mentioned above in attaining enough fish at any time during the day, biasing the results. Maes et al. (2005) obtained constants of 0.14, 0.16 and 0.17 at a mean temperature of 11.9, 14.4 and 15.5°C (fish weight: 4.4 to 15.2 g *WW*) in an estuary. Temming (1995) and Schmanns (1994) estimated an evacuation constant of 0.56 at a mean temperature of 16.6°C for juvenile herring (6 – 9 cm) from a 24 h-fishery. This evacuation constant was estimated from the depletion of stomach contents during the night, associated with the problems of attaining enough fish at any time.
Another evacuation constant estimate for adult herring (mean total length = 28.6 cm) was derived from a 24 h-fishery by Darbyson et al. (2003). The resulting estimate was R = 0.397 at 14.2°C. Temming (1995) estimated an evacuation constant R of 0.51 at 13.5°C from tank experiments. The differences of these constants as compared to our constants may be explained by the weight dependency of the gastric evacuation in herring. Temming (1995) did observe small weight dependency coefficients C of maximal 0.07, indicating no or a minor influence of the fish weight on the evacuation constant. In the related species sprat (*Sprattus sprattus* L.) did Bernreuther et al. (In Prep.) observe a weight coefficient of C ~ 0.3 as estimated from gastric evacuation experiments. When applying this weight coefficient and the temperature coefficient to the herring data the evacuation constant for a 80 g herring results in R = 0.23 at 13.5°C and for a 140 g herring in R = 0.32 at 14.2°C. Van der Lingen (1998) estimated gastric evacuation constants of adult (28 – 150 g wet weight) sardines (*Sardinops sagax*) in laboratory and tank experiments that were similar to our constants. The mean evacuation constants were R = 0.09 for fish feeding on zooplankton and R = 0.27 from fish feeding on phytoplankton (temperature: 14.6 – 17.8°C).
Arrhenius (1998) estimated evacuation constants for 0-group sprat (*Sprattus sprattus*) from 24 h-fisheries that were higher with R = 0.34 – 0.38 at a mean temperature of 13.9°C. As in the study mentioned above by Arrhenius & Hansson (1994), no temperature effect was observed, which is unlikely to be the case.

Temperature effect on evacuation constant

The temperature dependency parameter A, estimated from our two experimental temperatures, was high with A = 0.241 compared to the results from the above mentioned authors. The data on herring from Arrhenius & Hansson (1994) and sprat (Arrhenius 1998) indicated high evacuation constants, but the comparison of the different temperatures did not show any temperature effect on the evacuation constant. Maes et al. (2005) estimated an exponential temperature coefficient of 0.045 for juvenile herring and Temming (1995) estimated from tank experiments an exponential temperature coefficient of 0.135 for adult herring in the Baltic Sea.
When comparing our estimated temperature coefficient with the estimates from fresh and salt water species, which were feeding on large amounts of relatively small prey, it is still high. Maes et al. (2005) estimated an exponential temperature coefficient A of 0.039 for sprat feeding on natural zooplankton, Hölker & Temming (1996) estimated an exponential coefficient A of 0.05 for ruffe (*Gymnocephalus cernuus* L.) feeding on chironomid larvae, Amundsen & Klementsen (1988) estimated an A of 0.12 for Arctic charr (*Salvelinus alpinus* L.) feeding on euphausids, Persson (1979) estimated an A of

0.14 for perch (Perca fluviatilis L.), Temming et al. (2002) estimated an A of 0.14 for Atlantic mackerel (*Scomber scombrus* L.) feeding on sprat, sandeel and krill and Mehl & Westgård (in Temming et al. 2002) estimated a rather high A value of 0.2 for Atlantic mackerel feeding on euphausiids. The latter coefficient is the closest to our value. Our temperature coefficient A = 0.241 corresponds to a Q_{10}-value of 11.1. Our temperature coefficient needs to be carefully interpreted. It resulted from experiments at two different temperatures, which can be the explanation for the estimated high coefficient. Due to the obligation to work with groups of fish, there will always be some variability, which might result in an upward shift of the estimated evacuation constant at one temperature and a possible downward shift in the other temperature. Further investigations on the temperature dependency of the gastric evacuation constant in herring are needed.

Internal dynamics of herring stomach

The functions of the stomach in fish are the storage of newly ingested food and the initiation of digestion with pepsin in an acid medium (Fänge & Grove 1979). In herring like in other clupeids does the gastric cecum extend caudally.
We observed that stained copepods were transported either directly into the intestine, without entering the cecum (figures 4, 5) or were stored initially in the cecum, identifiable as a dark area or band (figure 6). The “decision” about the path of the food particles entering the stomach is probably depending on the current stomach content of the fish. When a fish had been feeding little on the unstained copepods, before the stained copepods where offered, these freshly ingested copepods were transported or pushed into the cecum (dark area figure 6). As the cecum was not filled to its maximal capacity, subsequent feeding resulted in an additional (figure 6) stocking up of the cecum. A fish that had been feeding heavily, prior to the feeding of the stained copepods, resulting in a maximal or near maximal filling of the cecum, was likely to push the freshly entering particles directly through into the intestine (figure 4). In figure 5 a mixing zone of stained and natural coloured copepods is visible on the left side, this mixing of the food particles is probably due to muscular activity (Fänge & Grove 1979). A dynamic mixing of the stomach contents was only visible in the front part of the stomach, the contents in the cecum appeared not to be influenced by the muscular activity. Surprisingly herring appear to be able to utilize the cecum-storage, even after a prolonged feeding over 10 hours. This storing ability enables herring to optimise the exploitation of favourable feeding conditions in situations with high prey concentrations. The average relative meal size (wet weight % body weight) of experiment 6 with 5.6%, with a maximum value of 9.8% displays the whole extent of the storage ability of the herring cecum. These are impressive numbers when comparing these with observations from the field. Möllmann et al. (2004) observed average stomach contents of 0.18% for herring in summer in the central Baltic Sea.

Food density versus snatching rate

We fitted the Michaelis-Menten equation to the data of the snatching rates versus food concentrations. We observed that the snatching rates were steeply increasing with increasing food concentration reaching a maximum value at a certain concentration and remaining constant at higher concentrations. This reaction to different food concentrations is similar to a Holling type II functional response (Holling 1959). Planktivorous fish that forage in environments where prey is patchy, typically exhibit a type II functional response (Smith 1998).
The herring in our experiments were switching to filter-feeding at high food concentrations (> 900 copepods * l^{-1}). A similar observation was made by Gibson &

Ezzi (1985, 1992) in juvenile herring (*Clupea harengus* L.) feeding on different sizes of *Artemia* spp. Despite the fact that the concentrations in those experiments were lower than in our experiments, the results also suggest that filtering started when biting or snatching reached a maximum sustainable frequency. To relate these observations to the wild we can mention the results of a 24 hour study concerning the prey selectivity of herring and sprat in the Baltic Sea within the Globec-Germany program. We observed food densities of 14 to 127 prey items * m^{-3} in June 2001 in the Baltic Sea (Bornholm Basin) during the day in depths of 60 to 80 meters, where herring were feeding. We did not observe during the investigated period densities that were high enough to initiate filter-feeding. The densities needed for the onset of filter-feeding are probably only reached in plankton patches. The ability to switch to filter-feeding at high concentrations enables herring to maximize food intake by filtering at high food concentrations as in plankton patches.

Increased evacuation constant while feeding?

Richter et al. (2002) conducted consumption experiments with milkfish *Chanos chanos* (Forsskål) and tilapia-hybrids *Oreochromis niloticus* (L.) x *O. aureus* (Steindachner). The aim of these experiments was to test whether one fundamental assumption of different consumption-models (Bajkov-, Elliott-Persson-, MAXIM- and Olson-Mullen-model) turned out to be violated. The assumption that the constant at which evacuation takes place is the same in feeding and non-feeding periods. A violation of this assumption would have a severe impact on the results of these models, as they incorporate evacuation constants that were mainly estimated from single-meal experiments. This assumption was tested in the models by applying them to two feeding scenarios likely to be encountered under aquaculture conditions and comparing their consumption estimates with the quantity of food known to be taken up by the fish.
200 milkfish in a flow-through concrete tank were fed 3 mm pellets each hour from 7:55 to 11:55 (in total 3.15% of g body weight, *BW*). The fish were sampled each hour from 07:00 to 21:00 (3 fish each). The tilapia hybrids were stocked in 30 cages (60 fish each) and fed pellets in one dose at 09:00 (1.9% *BW*). Additionally, the fish had access to natural food (phytoplankton), which was of minor importance as food (< 10% of total stomach contents at any time). Subsamples of 12 fish from different tanks were taken at two-hour intervals between 05:00 and 23:00. The average consumption of the fish was estimated by the different consumption models and compared to the actual amount of food given to the fish. The result was that all consumption models were underestimating the amount of actually consumed food (1.76 to 1.81% *BW* for milkfish and 0.79 to 0.82% *BW* for tilapia). When the consumption estimates were recalculated with all models on the assumption that the evacuation constant doubles in the feeding period compared to the non-feeding phase, the model predictions increased to 2.73 to 3.58% *BW* for milkfish and 0.98 to 1.58% *BW* for tilapia. The conclusion was that fish have an elevated or doubled evacuation constant while feeding and that this observation questions the reliability of consumption estimates by most consumption models incorporating gastric evacuation constants.
This is undoubtedly an interesting result, however there are some questions concerning the results of this study. As the estimated amount of consumed food and the actual amount of food given to the fish were not similar it was concluded that either the true ingestion rate was rather lower than expected, or the real instantaneous evacuation rate must have been higher. The milkfish were fed five doses of the pellet food. It was observed and assumed that all food was consumed completely within 2 to 3 minutes. However, the tank bottom was not checked for uneaten food. The assumption that the cessation of feeding was equal to a complete consumption of the food may be

erroneous. Additionally, there might have been a pellet-effect. The pellets might have rapidly disintegrated in the stomachs leading to an elevated evacuation constant, which would not be the case with natural food.
In the tilapia experiments the cages were checked for uneaten food. The food was offered to the fish in one dose at 09:00. This is definitely a feature of a single-meal gastric evacuation experiment, from which most evacuation constant estimates are derived from. This means that the fish were feeding at a certain point in time whereupon they were only evacuating. Nevertheless, during a two hour period a doubled evacuation constant was used for the consumption estimation. The question arises why a doubled evacuation constant is needed, even for a short time, to get a better match of consumption models with actual food fed, when the evacuation constants were estimated from a single-meal experiment, and the fish were feeding a single meal? This leads to the conclusion that the quantification of the food consumed was deficient or there was a pellet effect influencing the evacuation constant.
The verification of the hypothesis by Richter et al. (2002), that fish have an elevated or doubled evacuation constant respectively was accomplished by a comparison of simulated and observed stomach contents from experiments 6 and 7. Distinct higher simulated stomach contents in comparison to the observed stomach contents would confirm the hypothesis of Richter et al. (2002).
The simulations for both experiments 6 and 7 showed a similar trend. The simulated and the observed stomach contents gave a better match with the estimated evacuation constant R than with the doubled evacuation constant 2R. If comparing the simulations (R and 2R) it is obvious that when using the estimated constant R = 0.098, with the exception of tank 3 in experiment 7, in no other tank were the simulated stomach contents at the end of the experiment higher than the observed stomach contents from the experiment. When using the elevated evacuation constant R = 0.196 all 8 simulated values were below the observed values. In two situations (exp. 7, tanks 1 and 4) were the simulated values not within the standard deviations of the observed stomach contents. If there had been an elevated or doubled evacuation constant while feeding, we could have expected that the simulations with our estimated evacuation constant R = 0.098 would have resulted in higher stomach contents than the observed contents. With one exception this is not the case, in contrary the simulated values were rather below the observed values. Even after 900 min in experiment 7 tank 4 there is a good match of the simulated and the observed values. With the doubling of the evacuation constant the simulated values are even lower. This leads to the conclusion that there was no elevation, rather a slight deceleration of the evacuation constant while feeding. A problem in working with groups is the variability between the individuals, leading to some scatter in the results as indicated by the standard deviation in the observed values. However, our experiments and simulations did not indicate a doubling of the evacuation constant while feeding, but due to the variability in the values we cannot exclude an acceleration of the evacuation constant while feeding.
There are conflicting opinions concerning the increase in the evacuation constant during feeding compared to non-feeding phases, although no study with microphagous species concerning this question has been conducted yet. The effect of an increased evacuation constant in multiple-meals was demonstrated by e.g. Jones (1974) in haddock (*Melanogrammus aeglefinus* L.), cod (*Gadus morhua* L.) and whiting (*Merlangius merlangus* L.), Talbot et al. (1984) in Atlantic salmon (*Salmo salar* L.) and Kristiansen (1998) in brown trout (*Salmo trutta* L.) and rainbow trout (*Oncorhynchus mykiss* Walbaum). The multiple-meal studies of Persson (1984) on perch (*Perca fluviatilis* L.) and roach (*Rutilus rutilus* L.), Ruggerone (1989) on coho salmon (*Oncorhynchus kisutch* Walbaum) and Dos Santos & Jobling (1992) on cod (*Gadus morhua* L.) demonstrated that the ingestion of a second meal speeds up the evacuation of the remains of the first

meal, but the evacuation of the second meal is slowed down. The experiments of Persson (1984) and Dos Santos & Jobling (1992) suggest that the total amount of food evacuated by fish in multiple-meal experiments can be predicted reasonably well using results from single-meal experiments Bromley (1994). Additional work needs to be conducted on the question of different evacuation constants while feeding and non-feeding, as the result can have a major impact on consumption estimates.

Conclusions

1) We were able to estimate the parameters of the general evacuation model under controlled and stress-free conditions. The estimated parameter B of 0.95 at 13°C and 1.32 at 16°C of the general model indicated an exponential evacuation. We applied the exponential evacuation model and estimated evacuation constants of R = 0.098 at 13°C and R = 0.202 at 16°C. The resulting temperature dependency was described by an exponential sub model with the temperature coefficient A of 0.24.
2) The use of stained copepods enabled us to visualize the internal dynamics of the herring stomach with its storage part, the cecum. The stomach enables the fish to feed on high densities of food for an extensive time (up to 10 h). The ingested food particles are either stored in the cecum for later evacuation or, depending on the fullness, can be transported directly into the intestine.
3) The functional response of herring feeding on different food concentrations was described by the Michaelis-Menten equation. This equation is similar to a Holling type II functional response (Holling 1959), where the snatching rate and food ingestion respectively is steeply increasing to reach an upper level, from where on the snatching rates and ingestion rates respectively are constant. The herring were switching from particulate feeding at higher rates (> 900 copepods * l^{-1}) increasingly to filter-feeding.
4) We were able to test the hypothesis of Richter et al. (2002) that fish exhibit two evacuation modes, one constant while only evacuating food and a significantly enhanced constant, while feeding. The results of our simulations with a doubled evacuation constant, compared to our estimated evacuation constant, indicated that the evacuation constant as estimated from single-feeding experiments is adequately used in fishes that are feeding. We did not find evidence to support the hypothesis of Richter et al. (2002), but due to the variability in the data we can not falsify it.

References

Amundsen, P.A., and Klementsen, A. (1988). Diet, gastric evacuation rates and food consumption in a stunted population of Arctic charr, *Salvelinus fontinalis* L., in Takvatn, northern Norway. Journal of Fish Biology 33, 697-709.

Arrhenius, F. & Hansson, S. (1993). Food consumption of larval, young and adult herring and sprat in the Baltic Sea. Marine Ecology Progress Series 96, 125-137.

Arrhenius, F. & Hansson, S. (1994). In *situ* food consumption by young-of-the-year Baltic sea herring *Clupea harengus*: a test of predictions from a bioenergetics model. Marine Ecology Progress Series 110: 145-149.

Arrhenius, F. (1998). Food intake and seasonal changes in energy content of young Baltic sea sprat (*Sprattus sprattus* L.). ICES Journal of Marine Science 55, 319-324.

Batty, R.S., Blaxter, J.H.S. & Libby, D.A. (1986) Herring (Clupea harengus) filter-feeding in the dark. Marine Biology 91, 371-375.

Batty, R.S., Blaxter, J.H.S. & Richard, J.M. (1990). Light intensity and the feeding behaviour of herring, *Clupea harengus*. Marine Biology 107, 383-388.

Blaxter, J.H.S. & Holliday, F.G.T. (1958). Herring (*Clupea harengus* L.) in Aquaria. II. Feeding. Marine Research 6: 1-20.

Bernreuther, M., Herrmann, J.-P. & Temming, A. (In Prep.). The influence of temperature and body weight on the rate of gastric evacuation in sprat (*Sprattus sprattus* L.).

Bromley, P.J. (1994). The role of gastric evacuation experiments in quantifying the feeding rates of predatory fish. Rev. in Fish Biol. and Fisher. 4, 36-66.

Carrieri, M.P. & Volpato, G.L. (1991). Does snatching frequency really indicate food ingestion in the nile tilapia?. Physiology & Behaviour 50, 489-492.

Darbyson, E., Swain, D.P., Chabott, D. & Castonguay, M. (2003). Diel variation in feeding rate and prey composition of herring and mackerel in the southern Gulf of St Lawrence. Journal of Fish Biology 63, 1235-1257.

Dos Santos, J. & Jobling, M. (1992). A model to describe gastric evacuation in cod (Gadus morhua L.) fed natural prey. ICES Journal of Marine Science 49, 145-154.

Fänge, R. & Grove, D.J. (1979). Fish Digestion. In Fish Physiology, Vol. VIII, Hoar, W.S., Randall, D.J. & Brett, J.R. (Hrsg.). Academic Press, New York, 161-260.

Flinkman, J., Vuorinen, I. & Aro, E. (1991). Planktivorous Baltic herring (*Clupea harengus*) prey selectively on reproducing copepods and cladocerans. Canadian Journal of Fisheries and Aquatic Sciences 49, 73-77.

Gibson, R.N. & Ezzi, I.A. (1985). Effect of particle concentration on filter- and particulate feeding in the herring *Clupea harengus*. Marine Biology 88, 109-116.

Gibson, R.N. & Ezzi, I.A. (1990). Relative importance of prey size and concentration in determining the feeding behaviour of the herring *Clupea harengus*. Marine Biology 107, 357-362.

Gibson, R.N. & Ezzi, I.A. (1992). The relative profitability of particulate- and filter-feeding in the herring, *Clupea harengus* L. Journal of Fish Biology 40, 577-590.

Holling, C. S. (1959). The components of predation as revealed by a study of small mammal predation of the European Pine Sawfly. Canadian Entomology 91, 293-320.

Hölker, F. & Temming, A. (1996). Gastric evacuation in ruffe (*Gymnocephalus cernuus* (L.)) and the estimation of food consumption from stomach content data of two 24 h fisheries in the Elbe Estuary. Archive of Fishery and Marine Research 44 (1/2), 47-67.

Jones, R. (1974). The rate of elimination of food from the stomachs of haddock *Melanogrammus aeglefinus*, cod *Gadus morhua* and whiting *Merlangius merlangus*. Journal du Conseil International pour l´Exploration de la mer 35, 225-243.

Karjalainen, J., Miserque, D., and Huuskonen, H. (1997). The estimation of food consumption in larval and juvenile fish: experimental evaluation of bioenergetics models. Journal of Fish Biology 51 (Supplement A), 39-51.

Köster, F., Schober, W., Korves, A. & Schneider, R. (1990). Tank experiments on board: a useful tool for the estimation of stomach evacuation rates? ICES. C.M. 1990/G:34.

Köster, F.W. (1994). Der Einfluß von Bruträubern auf die Sterblichkeit früher Jugendstadien des Dorsches (Gadus morhua) und der Sprotte (Sprattus sprattus) in der zentralen Ostsee. Dissertation an der Mathematisch-Naturwissenschaftlichen Fakultät der Christian-Albrechts-Universität zu Kiel. 369 pp.

Kristiansen, H.R. (1998). Effects of handling, discrete meals and body weight on the individual variation of gastric emptying parameters. Aquaculture Research, 29, 717–729.

Last, J.M. (1989). The food of herring, *Clupea harengus*, in the North Sea, 1983 – 1986. Journal of Fish Biology 34, 489-501.

Maes, J., Tackx, M. & Soetaert, K. (2005). The predation impact of juvenile herring *Clupea harengus* and sprat *Sprattus sprattus* on estuarine zooplankton. Hydrobiologia 540, 225-235.

Möllmann, C., Kornilovs, G., Fetter, M. & Köster, F.W. (2004). Feeding ecology of central Baltic Sea herring and sprat. Journal of Fish Biology 65, 1563-1581.

Nilsson, L.A.F., Thygesen, U.H., Lundgren, B., Nielsen, B.F., Nielsen, J.R. & Beyer, J.E. (2003). Vertical migration and dispersion of sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) schools at dusk in the Baltic Sea. Aquatic Living Resources 16, 317 – 324.

Persson, L. (1979). The effects of temperature and different food organisms on the rate of gastric evacuation in perch (*Perca fluviatilis*). Freshwater Biology 9, 99-104.

Persson, L. (1981). The effects of temperature and meal size on the rate of gastric evacuation in perch (*Perca fluviatilis*) fed on fish larvae. Freshwater Biology 11, 131 - 138.

Persson, L. (1984). Food evacuation and models for multiple meals in fishes. Environmental Biology of Fishes Vol. 10, No. 4, 305–309.

Richter, H., Lückstädt, C., Schlechtriem, C., Focken, U. & Becker, K. (2002). Do the fish stomach content models currently used for daily ration estimation really work? Evidence of violation of a basic assumption concerning stomach evacuation rates. Archive of Fishery and Marine Research 49 (3), 171-188.

Ruggerone, G.T. (1989). Gastric evacuation of single meals by piscivorous coho salmon, *Oncorhynchus kisutch*. Environmental Biology of Fishes 26, 143-147.

Schmanns, M. (1994). Zur Biologie – insbesondere Nahrungsbiologie – der im Sylter Wattenmeer auftretenden Heringe (*Clupea harengus* L.). Diploma thesis at University of Hamburg. 74 pp.

Smith, R.L. (1998). Elements of ecology. 4th ed. Menlo Park, California.

Szypula, J. & Zalachowski, W. (1984). Duration of food evacuation in herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.). Acta Ichthyologica et Piscatoria Vol. XIV Fasc. 1-2, 93-102.

Talbot, C., Higgins, P.J. & Shanks, A.M. (1984). Effects of pre- and post-prandial starvation on meal size and evacuation rate of juvenile Atlantic salmon, *Salmo salar* L. Journal of Fish Biology 25, 551-560.

Temming, A. & Köster, F.W. (1990). Stomach evacuation rates of cod and herring estimated from shipboard tank experiments and field data. ICES. C.M. 1990/G: 31.

Temming, A. & Andersen, N.G. (1994). Modelling gastric evacuation without meal size as a variable. A model applicable for the estimation of daily ration of cod (Gadus morhua L.) in the field. ICES Journal of Marine Sciences 51, 429-438.

Temming, A. (1995). Die quantitative Bestimmung der Konsumtion von Fischen. Experimentelle, methodische und theoretische Aspekte. Habilitationsschrift, Universität Hamburg, Fachbereich Biologie, 235 pp.

Temming, A., Bøhle, B., Skagen, D.W. & Knudsen, F.R. (2002). Gastric evacuation in mackerel: the effects of meal size, prey type and temperature. Journal of Fish Biology 61, 50-70.

Van der Lingen, C.D. (1998). Gastric evacuation, feeding periodicity and daily ration of Sardine *Sardinops sagax* in the Southern Benguela Upwelling Ecosystem. South African Journal of Marine Science 19, 305-316.

The influence of temperature and body weight on the rate of gastric evacuation in sprat (*Sprattus sprattus* L.)

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Abstract

Gastric evacuation of groups of juvenile (mean 6.3 cm total length, *TL*, 0.283 g dry weight, *DW*) sprat (*Sprattus sprattus* L.) feeding on brine shrimp (*Artemia* sp.) nauplii was studied at six temperatures (7.5, 10, 13, 16, 19.5 and 21.5°C) in the laboratory. Both a general and an exponential gut evacuation model were used to describe gastric evacuation. Although the shape parameter B of the general model varied between 0.58 at 13°C and 1.11 at 19.5°C, a B-value of 0.944 was found for the pooled analysis made below 19.5°C indicating exponential gut evacuation. The evacuation constant (R), as estimated from the exponential model, increased with increasing temperature, from 0.076 at 7.5°C to 0.179 at 19.5°C. The relationship between temperature and evacuation constant was described by three different models (exponential, a logistic and an optimum model). Additionally, the effect of mean fish body weight (range 0.286 to 1.025 g *DW*) was examined at 13°C. A simple power function ($R = R' * weight^C$) described the influence of predator weight on gastric evacuation constant where values of C were ~0.30.

Introduction

Sprat (*Sprattus sprattus* L.) is a widely distributed planktivorous fish inhabiting the Baltic Sea, the Atlantic coast of Europe from the Lofoten Islands and Tromsö in the north and Mediterranean and Black Sea in the south (Whitehead 1985, Ojaveer & Aps 2003). It is the dominant zooplanktivorous fish species in the Baltic Sea where it has a major impact on the zooplankton community structure (Rudstam et al. 1994, Arrhenius 1996, Kornilovs et al. 2001, Möllmann et al. 2004). Through its wide distribution and the seasonal changes at high latitudes, this species experiences pronounced temperature fluctuations. Knowledge about the daily ration of sprat is a prerequisite for quantifying its trophodynamic impact and for estimating its potential scope for growth in various regions. For the estimation of sprat consumption from field observed mean stomach content weights, parameters of the gastric evacuation function in relation to temperature, predator weight and prey type are needed (Karjalainen et al. 1997).

Three methods have been employed to estimate gastric evacuation rates and constants in clupeoids. First, a 24 h-fisheries method, estimates gut evacuation rates and constants from the depletion of the mean stomach content during non-feeding periods at night (Temming & Köster 1990, Köster 1994, Schmanns 1994, Arrhenius & Hansson 1994, Darbyson et al. 2003, Maes et al. 2005). Second, ship-board tank experiments have been employed in which fish captured in bottom or pelagic trawls are transferred to deck tanks, sub sampled at regular intervals and the rate of gastric evacuation estimated from the depletion of the stomach contents (Szypula & Zalachowski 1984, Köster et al. 1990, Köster 1994, Temming 1995). Lastly, groups of fish are maintained within controlled laboratory conditions and sub sampled in a similar manner as ship-board tank experiments.

Performing gastric evacuation experiments in the laboratory is a standard practice for robust fish species that can be maintained individually such as plaice (*Pleuronectes platessa* L.), Jobling (1980); turbot (*Scophthalmus maximus* L.), Bromley (1987); European perch (*Perca fluviatilis* L.), Persson (1981); whiting (*Merlangius merlangus* L.), Andersen (1999); horse mackerel (*Trachurus trachurus* L.) Temming & Herrmann (2001 a, b). Laboratory experiments on gastric evacuation of clupeoids are rare. Such experiments can only be conducted using groups of fish since it is not possible to maintain species such as Atlantic herring (*Clupea harengus* L.), sprat and sardines

(*Sardinops sagax* Jenyns) individually. Van der Lingen (1998) conducted laboratory experiments on groups of sardine that were fed for a short period of time and subsequently sub sampled at regular intervals. A similar approach was chosen by Temming et al. (2002) for gastric evacuation experiments with Atlantic mackerel (*Scomber scombrus* L.), a species which is also difficult to handle in the laboratory.
Many potential problems exist in obtaining reliable gut evacuation rate estimates from either the 24 h-fishery method (Shvetsov et al. 1983) or ship-board tank experiment method (Szypula & Zalachowski 1984 and Köster et al. 1990). In the case of the 24 h-fishery method, the environmental conditions are not controlled and it must be assumed that fish do not feed during the night-time sampling period and are reliable (randomly) sampled during dusk, night and dawn. Finally, it is unknown whether catches represent the same group of fish (e.g., same school with same feeding history). In terms of ship-board tank experiments, the major drawback is the immense stress associated with capture and transfer methods and the sudden confinement within tanks.
In the present study, the gastric evacuation of sprat was examined under controlled laboratory conditions using a similar approach as Van der Lingen (1998) and Temming et al. (2002).
The three major objectives of this study were to 1) parameterise the general evacuation model (Temming and Andersen 1994) including the shape parameter B and evacuation constant R, 2) examine the influence of temperature on the gastric evacuation function, and 3) quantify the effect of body weight on evacuation constants. Sprat were provided live zooplankton as food and a wide range in temperatures and body sizes were used in an effort to collect data that would be easily transferable to the field situation in the North and Baltic Seas, where top-down control of this predator is being investigated as part of the German GLOBEC program.

Material and methods

Experimental fish, capture and maintenance

Sprat were caught in July 2004 as 0-group with a dip net in the Kiel Bay (Baltic Sea, Germany). Fish were transferred within a 700 l box with aerated seawater to a 80 m^3 recirculating aquarium facility maintained at the University of Hamburg, Institute for Hydrobiology and Fisheries Research (Hamburg, Germany). Fish were held in large groups in circular tanks (diameter 145 cm) with capacities of 400 to 1000 l for at least six weeks prior to acclimation to experimental conditions. Fish were fed daily rations of an artificial pelletted diet (Larviva Wean-Ex, Dana Feed AS) and brine shrimp nauplii (*Artemia* spp. INVE Aquaculture). New recirculation seawater was made at regular intervals from marine salt and tap water. Temperature was regulated with a precision of ± 0.1°C. Fish were exposed to a constant day length of 14 h, lights were dimmed from full to minimum (darkness) over a period of 20 min. The salinity was kept constant at 32 (± 0.1) ppt . The temperature and salinity in the tanks were measured daily.

Experimental tanks and food

For the gastric evacuation experiments, groups of 120 sprat were transferred into 80 cm diameter experimental tanks. The tank seawater volume (never less than 140 l) was adjusted to give the school enough space to freely manoeuvre. An airlift (an air-stone placed into a vertical PVC pipe) was positioned to create a circular current at the surface of the tank. This airlift was also used to collect uneaten Artemia nauplii by sieving the surface water outflow. Tanks also had a constant water inflow (~ 10 l * min $^{-}$

[1]). The fish were kept in the experimental tanks for at least 14 days prior to the gastric evacuation experiments. During this period the fish were fed brine shrimp nauplii *ad libitum* three to four times each day. Brine shrimp nauplii were also used as food for all evacuation experiments. Two to three replicate groups (tanks) of fish were used at each combination of fish size or water temperature. Mortality was minimal during the 14 day acclimation period.

Experimental procedure

Prior to the evacuation experiments no food was offered for at least 24 h to allow a complete emptying of the stomachs. For experiments at lower temperatures (< 13°C) this time was prolonged to ensure the complete emptying.
During the experiment the water inflow was turned off and fish were offered 100 000 brine shrimp nauplii every 30 minutes (110 000 brine shrimp in experiment 14 and 15) for a period of 3.5 hours. After 3.5 hours, the water inflow was turned on and uneaten brine shrimp were flushed from the tank. Uneaten nauplii were also captured by placing a sieve over the outflow of the airlift pipe. Pre-experiments had revealed that 90% of the Artemia were removed 20 min after the start of the flushing. After 30 minutes 15 to 30 fish were carefully removed to estimate the initial meal size and 15 to 30 fish were removed every 3 to 7.5 hours thereafter. Removed fish were rapidly killed by an overdose of anaesthetic (MS-222), total length (0.1 mm below) and wet weight (0.0001 g accuracy) of each fish were measured. The fish were dissected, stomachs were removed and stomach contents in wet weight were measured (0.0001 g accuracy). The contents were dried to constant weight at 90°C and dry weights (0.0001 g accuracy) were determined.
At least two experiments were performed at each of the six test temperatures (7.5, 10, 13, 16, 19.5 and 21.5°C). A total of 13 experiments with a total of 1219 juvenile sprat was conducted in the temperature range of 7.5 to 21.5°C. Two additional experiments were performed at 13°C using larger sprat (total n = 155 fish), to study the body weight effect on the rate of gastric evacuation.

Gastric evacuation model

Gastric evacuation was described using a general model (Jones 1974, Temming & Andersen 1994) and an exponential model (Tyler 1970, Persson 1979). In the general model the evacuation rate is a flexible function of the actual stomach content. The strength of the stomach content effect is modulated by an exponent (B):

$$\frac{dS_t}{dt} = -R * S_t^{B}, \qquad (1)$$

with S_t = stomach content at time t after ingestion of the experimental meal (g dry or wet weight) and R = constant depending on prey type, temperature and predator weight. B = parameter determining the shape of the curve:

If

B < 0	a convex curve with increasing negative slope
B = 0	linear, negative slope
0 < B < 1	a concave curve, with decreasing negative slope
B = 1	exponential decay curve
B > 1	a concave curve, the dependence of evacuation rate on the stomach content is stronger than in exponential case. This implies higher rates at

high, and lower rates at low stomach contents when compared with an exponential model

For the estimation of the constant R the integrated form of equation 1 (for B ≠ 1) was used:

$$S_t = [S_0^{(1-B)} - R * (1-B) * t]^{\left(\frac{1}{1-B}\right)}, \quad (2)$$

where S_t = stomach content at time t, S_0 = stomach content at time 0, (which is equivalent to the meal size), and R = gastric evacuation constant.

When B = 1, the integrated form of equation 1 results in the exponential function (equation 3). The exponential model was used as in equation 3 and in an expanded version including temperature (equation 4) and both temperature and body weight (equation 5) as additional variables:

$$S_t = S_0 * e^{-R*t} \quad (3)$$

with

$$R = R' * e^{A*T} \quad (4)$$
$$R = R' * e^{A*T} * W^{C} \quad (5)$$

with variables

S_t = stomach content at time t after ingestion of the experimental meal (g dry weight)
S_0 = stomach content at time 0, equals the meal size (g dry weight)
t = time after ingestion (h)
T = temperature (°C)
W = predator weight (g dry weight)

and parameters

A = temperature coefficient (T^{-1})
R = gastric evacuation constant (h^{-1})
R´ = food type coefficient in equation 4, food type and predator weight coefficient in equation 5.
C = weight coefficient

Additionally to equation 4 and 5, the relation between the evacuation constant and temperature was described using a logistic model (equation 6) and Temming´s temperature optimum model (equation 7, Temming 1995).

$$R = R' + \frac{m}{1 + e^{-\left(\frac{T-T_0}{n}\right)}} \quad (6)$$

with m, n and T_0 as additional parameters.

$$R = R' * e^{a1*T} * \left(1 - \frac{1}{1 + e^{-a2*(T-T_{50})}}\right) \quad (7)$$

with a1, a2 and T_{50} as additional parameters.

Following equation 7 the optimal temperature (T_{opt}) for the gastric evacuation of sprat was estimated by the following equation:

$$T_{opt} = \frac{\ln\left(-\frac{a1-a2}{a1}\right) - a2 * T_{50}}{-a2} \quad (8)$$

All models were fitted to the data sets by means of non-linear regression as described in Temming & Andersen (1994) using the statistical software package SPSS.

Results

Shape parameter B of the general model

The shape parameter B of the general model varied between 0.58 at 13°C (experiments 3 and 4) and 1.11 at 19.5°C (table 2). At the temperatures of 7.5, 13 (experiments 14 and 15), 16 and 19.5°C the parameter B was close to 1. At 10°C and at 21.5°C the B-values were 0.61 and 0.70, respectively. Experiment 6 at 16°C was excluded from all regressions due to unusual behaviour of the fish. These fish had abnormally high swimming speeds and numerous irregular swimming bouts during the major part of the experiment. The resulting parameters of the application of the general model, including temperature (exponential model) and body weight as variables, was B = 0.94 (table 2). The upper and lower confidence limits were 1.15 and 0.74 respectively, indicating an exponential evacuation. The model was only applied to the lower temperature range of 7.5 to 16°C as the evacuation constant increased exponentially over this temperature range.

Table 1) Experimental data for all individual experiments. *TL* = total length, n = number of fish per experiment, *WW* = wet weight, *DW* = dry weight, *DW* % *BW* = the dry weight of the stomach contents (g) as a percentage of the body weight (g).

Temperature (°C)	Experiment No.	n	TL (cm)	WW (g)	DW (g)	Meal size (*DW* % *BW*)
7.5	12	102	6.55 ± 0.37	1.565 ± 0.282	0.324 ± 0.063	4.29 ± 1.36
7.5	13	90	6.62 ± 0.42	1.647 ± 0.345	0.341 ± 0.086	5.06 ± 1.50
10	1	102	6.23 ± 0.35	1.346 ± 0.261	0.274 ± 0.060	8.20 ± 2.37
10	2	92	6.22 ± 0.28	1.321 ± 0.183	0.276 ± 0.047	8.33 ± 1.76
13	3	102	6.22 ± 0.43	1.299 ± 0.269	0.263 ± 0.068	5.16 ± 1.46
13	4	85	6.22 ± 0.34	1.327 ± 0.210	0.274 ± 0.054	5.94 ± 1.32
13	14	74	8.65 ± 0.45	4.106 ± 0.737	1.036 ± 0.246	4.06 ± 1.20
13	15	81	8.70 ± 0.38	4.053 ± 0.559	1.016 ± 0.217	3.34 ± 1.10
16	5	97	6.15 ± 0.36	1.280 ± 0.244	0.260 ± 0.062	6.24 ± 2.12
16	6	87	6.19 ± 0.42	1.319 ± 0.278	0.271 ± 0.067	6.44 ± 2.20
16	7	104	6.19 ± 0.38	1.278 ± 0.232	0.255 ± 0.057	4.63 ± 1.25
19.5	8	82	6.48 ± 0.35	1.569 ± 0.289	0.339 ± 0.078	4.74 ± 1.66
19.5	9	93	6.38 ± 0.40	1.447 ± 0.303	0.299 ± 0.074	4.83 ± 1.69
21.5	10	98	6.28 ± 0.34	1.328 ± 0.238	0.269 ± 0.063	4.57 ± 2.05
21.5	11	85	6.36 ± 0.34	1.401 ± 0.257	0.282 ± 0.064	6.07 ± 2.55

Evacuation constants

The gastric evacuation constant R of the simple exponential evacuation model (equation 3) increased with increasing temperature (figures 1, 2; tables 3, 4) from 0.076 at 7.5°C to 0.179 at 19.5°C and remained approximately on that level at 21.5°C with R = 0.168. After approximately 9 hours, 50% of the initial meal was evacuated from the stomach at 7.5°C while this point was reached after approximately 4 hours at 19.5°C (figures 1, 2).

Table 2) Parameters of the general model. B and R-values for different temperatures estimated from means of gram dry weight, with 95%-confidence limits. Experiment 6 at 16°C was not included in regressions. The general evacuation model, including temperature (exponential model) and body weight as variables, was fitted for the temperature range 7.5 to 16°C.

°C	Experiment No.	Value	Lower Confidence	Upper Confidence	r^2
7.5	12, 13				
B		0.943 ± 0.451	- 0.309	2.195	0.82
R		0.058 ± 0.125	- 0.289	0.405	0.82
10	1, 2				
B		0.607 ± 0.155	0.175	1.038	0.98
R		0.015 ± 0.010	- 0.013	0.043	0.98
13	3, 4				
B		0.578 ± 0.092	0.324	0.832	0.99
R		0.014 ± 0.006	- 0.003	0.032	0.99
13	14, 15				
B		1.002 ± 0.288	0.201	1.802	0.88
R		0.177 ± 0.201	- 0.382	0.735	0.88
16	5, 7				
B		1.058 ± 0.171	0.584	1.532	0.95
R		0.223 ± 0.188	- 0.300	0.745	0.95
19.5	8, 9				
B		1.113 ± 0.251	0.417	1.810	0.94
R		0.304 ± 0.359	- 0.691	1.300	0.94
21.5	10, 11				
B		0.692 ± 0.222	0.076	1.308	0.94
R		0.038 ± 0.041	- 0.075	0.152	0.94
7.5 - 16	1-5, 7, 12-15				
B		0.944 ± 0.099	0.741	1.147	0.93
R´		0.037 ± 0.015	0.006	0.068	0.93
A		0.102 ± 0.015	0.072	0.132	0.93
C		0.327 ± 0.074	0.175	0.480	0.93

Three different models were used to describe the relation between temperature and evacuation constant (table 5) and were fitted to the evacuation constants of all experiments (exp.6, 16°C was not included) as estimated from the means. The range from 7.5 to 16°C was adequately described by a simple exponential model (upper graph, figure 2) with an explained variability of 0.93. The temperature coefficient A was estimated as 0.094 (table 5). For the description of the whole temperature range Temming´s model and the logistic model were used. Both models explained large amounts of variability, with r^2 of 0.92 for Temming´s model and 0.95 for the logistic model (table 5). With the logistic model the evacuation constant was constant at

temperatures below 7°C and above 20°C, whereas in Temming´s model the evacuation constant increased exponentially with increasing temperature in the lower temperature range and reached a maximum value at 19.5°C (T_{opt}, equation 8), after which the constant decreased with increasing temperature (lower graph, figure 2). The parameter a1 in equation 7 corresponded to the temperature coefficient A and was estimated to be 0.110.

Table 3) Parameters of the exponential model. R-values for each single experiments estimated from means of gram dry weight with 95%-confidence limits. Experiment 6 at 16°C was not included in regressions.

Temperature °C	Experiment No.	R	Lower Confidence	Upper Confidence	r^2
7.5	12	0.084 ± 0.015	0.019	0.148	0.11
7.5	13	0.072 ± 0.004	0.054	0.090	0.97
10	1	0.080 ± 0.007	0.052	0.108	0.93
10	2	0.086 ± 0.006	0.063	0.110	0.97
13	3	0.115 ± 0.008	0.082	0.147	0.97
13	4	0.110 ± 0.008	0.078	0.143	0.94
13	14	0.160 ± 0.011	0.114	0.206	0.91
13	15	0.202 ± 0.016	0.135	0.269	0.87
16	5	0.159 ± 0.011	0.114	0.205	0.94
16	6	0.108 ± 0.005	0.088	0.127	0.98
16	7	0.181 ± 0.006	0.157	0.206	0.98
19.5	8	0.179 ± 0.012	0.126	0.232	0.96
19.5	9	0.179 ± 0.017	0.107	0.250	0.88
21.5	10	0.195 ± 0.016	0.128	0.261	0.94
21.5	11	0.155 ± 0.008	0.122	0.189	0.97

Table 4) Parameters of the exponential model. R-values for different temperatures estimated from means, with 95%-confidence limits.

Temperature °C	Experiment No.	R	Lower Confidence	Upper Confidence	r^2
7.5	12, 13	0.076 ± 0.006	0.060	0.093	0.82
10	1, 2	0.084 ± 0.004	0.073	0.094	0.95
13	3, 4	0.112 ± 0.005	0.100	0.125	0.96
13	14, 15	0.175 ± 0.012	0.146	0.205	0.88
16	5, 7	0.167 ± 0.007	0.148	0.186	0.95
19.5	8, 9	0.179 ± 0.009	0.155	0.202	0.94
21.5	10, 11	0.168 ± 0.011	0.141	0.195	0.91

When body weight was included as an additional variable (equations 5 to 7) in the exponential model (equation 3), the resulting temperature coefficient A was estimated to be 0.103 with the exponential temperature model for body weight in g dry weight (*DW*) and wet weight (*WW*) (table 6). The resulting temperature coefficients from Temming´s model were a1 = 0.107 and 0.105 for g *DW* and *WW*, respectively. The temperature coefficient A = 0.094 from the exponential model corresponded to a Q_{10} of 2.6. The parameter a1 of 0.110 corresponds to a Q_{10} of 3.0.

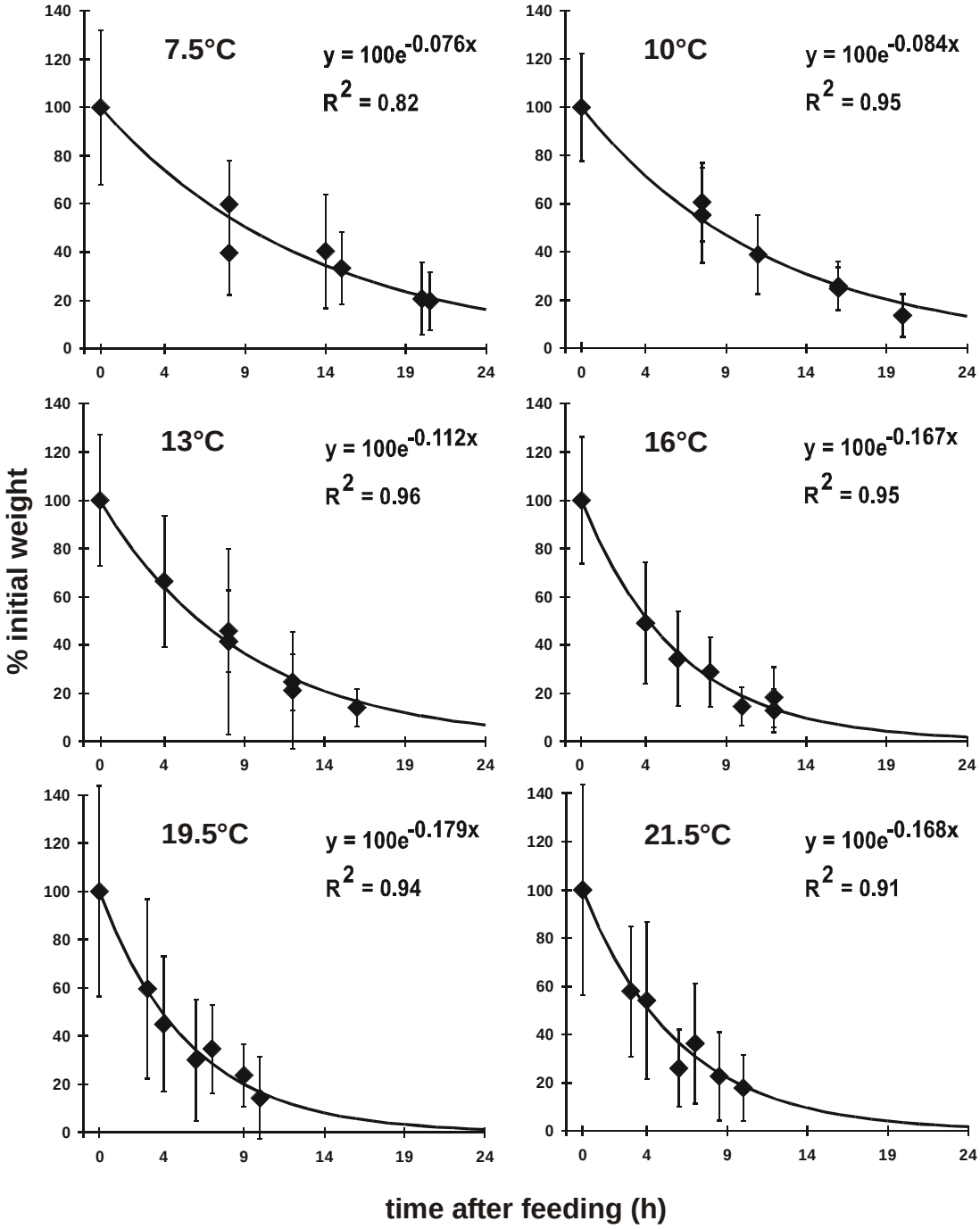

Figure 1) Relationship between mean gram dry weight as % of initial weight of stomach content with standard deviation and time after the initial meal at 6 experimental temperatures. The exponential model was applied to means.

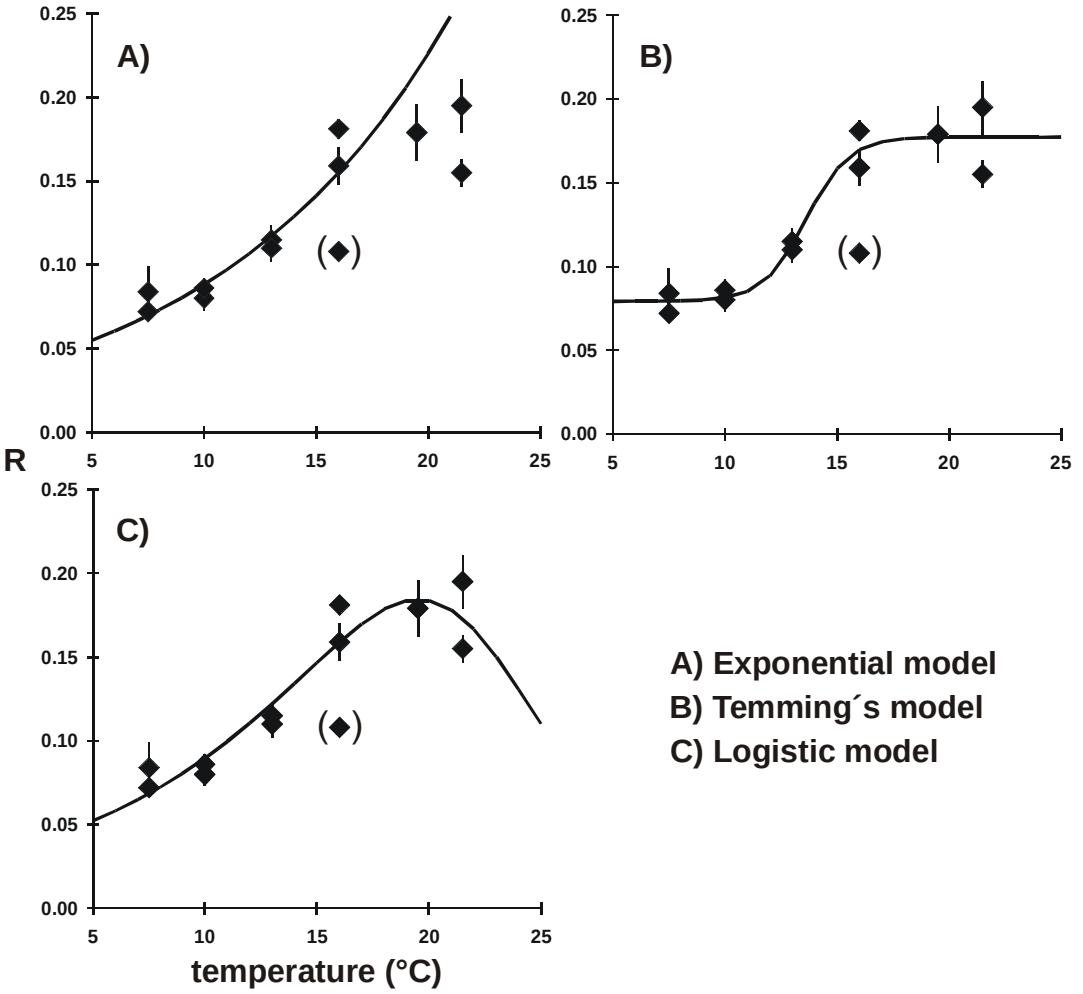

Figure 2) Evacuation constant R as estimated from the exponential model versus temperature (°C). The exponential model was fitted to temperature range of 7.5 to 16°C. The logistic model and Temming`s model were fitted to the entire temperature range of 7.5 to 21.5°C. Experiment 6 at 16°C (in brackets) was excluded from regressions.

Table 5) Temperature dependency of evacuation constant. Regressions were performed for 7.5 to 16°C (exponential model) and 7.5 to 21.5°C (logistic and Temming´s model). Confidence limits are asymptotic 95%.

model	value	lower confidence	upper confidence	r^2
exponential				
R´	0.034 ± 0.004	0.026	0.043	0.93
A	0.094 ± 0.011	0.072	0.116	0.93
logistic				
R´	0.079 ± 0.007	0.064	0.095	0.95
m	0.098 ± 0.010	0.075	0.121	0.95
n	0.956 ± 0.459	- 0.103	2.015	0.95
T_0	13.63 ± 0.47	12.55	14.71	0.95
Temming				
R´	0.030 ± 0.011	0.004	0.056	0.92
a1	0.110 ± 0.037	0.024	0.196	0.92
a2	0.384 ± 0.259	-0.213	0.982	0.92
T_{50}	21.92 ± 2.21	16.82	27.01	0.92

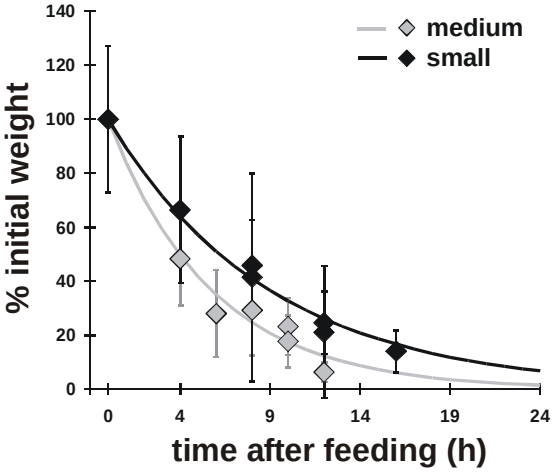

Figure 3) Relationship between mean gram dry weight as % of initial weight of stomach content with standard deviation and time after the initial meal at 13 °C. The evacuation curves from the exponential model are displayed for two size classes of sprat (small and medium). Small: $y = 100 * e^{-0.112*x}$ ($r^2 = 0.96$), medium: $y = 100 * e^{-0.175*x}$ ($r^2 = 0.88$).

Table 6) Weight and temperature dependency of evacuation constant. Regressions were performed for 7.5 to 16°C (exponential model) and 7.5 to 21.5°C (logistic and Temming´s model) with body weight as dry weight (upper part of table) and as wet weight (lower part of table). Confidence limits are asymptotic 95%.

Model	Value	Lower Confidence	Upper Confidence	r^2
Dry weight exponential				
R´	0.045 ± 0.009	0.027	0.063	0.92
A	0.103 ± 0.015	0.073	0.133	0.92
C	0.296 ± 0.049	0.196	0.397	0.92
logistic				
Y	0.105 ± 0.015	0.076	0.135	0.93
M	0.141 ± 0.025	0.089	0.192	0.93
N	1.300 ± 0.632	0.020	2.580	0.93
T_0	13.00 ± 0.63	11.73	14.27	0.93
C	0.294 ± 0.067	0.160	0.429	0.93
Temming				
R´	0.044 ± 0.013	0.019	0.070	0.92
a1	0.107 ± 0.026	0.053	0.160	0.92
a2	0.423 ± 0.293	- 0.170	1.016	0.92
T_{50}	21.92 ± 1.48	18.92	24.93	0.92
C	0.295 ± 0.052	0.191	0.400	0.92
Wet weight exponential				
R´	0.028 ± 0.004	0.019	0.037	0.93
A	0.103 ± 0.014	0.074	0.132	0.93
C	0.364 ± 0.057	0.247	0.481	0.93
logistic				
Y	0.067 ± 0.008	0.051	0.0083	0.93
M	0.092 ± 0.013	0.065	0.119	0.93
N	1.300 ± 0.614	0.056	2.544	0.93
T_0	13.00 ± 0.61	11.76	14.24	0.93
C	0.300 ± 0.079	0.140	0.461	0.93
Temming				
R´	0.028 ± 0.006	0.015	0.040	0.93
a1	0.105 ± 0.024	0.057	0.153	0.93
a2	0.450 ± 0.306	- 0.171	1.071	0.93
T_{50}	22.04 ± 1.22	19.56	24.52	0.93
C	0.363 ± 0.060	0.242	0.485	0.93

Weight dependency of gastric evacuation

The weight dependency of the gastric evacuation was estimated at 13°C from experiments performed using fish having two different body weights (figure 3, table 1, 6). At 13°C, evacuation constants (R) of 0.115, 0.110, 0.160 and 0.202 for 0.263 g, 0.274 g, 1.036 g, and 1.016 g mean *DW* sprat, respectively (table 3), were observed. Estimates for C, the weight-dependency parameter, were 0.294 to 0.364 (table 6, equations 5 - 7). When temperature and body weight (*DW*) were both included, values of C were 0.296 (eqn.5), 0.294 (eqn.6 with $weight^C$) and 0.295 (eqn.7 with $weight^C$). When body weight was expressed in wet weight C-values were slightly higher (C = 0.364 in eqn.5), 0.300 in eqn.6 with $weight^C$ and 0.363 in eqn.7 with $weight^C$) (see summary Table 7).

Table 7) Equations for the estimation of the exponential evacuation constant R with corresponding temperature range. Equations 9 – 11: temperature dependency (9 = exponential model, 10 = logistic model, 11 = Temming´s temperature optimum model). Equations 12 – 14: temperature and weight dependency (g dry weight; 12 = exponential model, 13 = logistic model, 14 = Temming´s temperature optimum model). Equations 15 – 17: temperature and weight dependency (g wet weight; 15 = exponential model, 16 = logistic model, 17 = Temming´s temperature optimum model). T = temperature (°C).

No.	Equation	Temp. range (°C)
9	$R = 0.034 * e^{0.094 * T}$	7.5 - 16
10	$R = 0.079 + \frac{0.098}{1+e^{-(\frac{T-13.63}{0.956})}}$	7.5 - 21.5
11	$R = 0.030 * e^{0.110 * T} * \left(1-\frac{1}{1+e^{-0.384*(T-21.92)}}\right)$	7.5 - 21.5
12	$R = 0.045 * e^{0.103 * T} weight^{0.296}$	7.5 - 16
13	$R = 0.105 + \frac{0.141}{1+e^{-(\frac{T-13.00}{1.30})}} * weight^{0.294}$	7.5 - 21.5
14	$R = 0.044 * e^{0.107 * T} * \left(1-\frac{1}{1+e^{-0.423*(T-21.92)}}\right) * weight^{0.295}$	7.5 - 21.5
15	$R = 0.028 * e^{0.103 * T} weight^{0.364}$	7.5 - 16
16	$R = 0.067 + \frac{0.092}{1+e^{-(\frac{T-13.00}{1.30})}} * weight^{0.300}$	7.5 - 21.5
17	$R = 0.028 * e^{0.105 * T} * \left(1-\frac{1}{1+e^{-0.450*(T-22.04)}}\right) * weight^{0.363}$	7.5 - 21.5

Discussion

Experimental procedure

Since it is not possible to maintain clupeids individually within tanks, we were forced to conduct experiments using groups of sprat. Due to the mentioned disadvantages of the commonly used 24 h-fisheries and tank experiments for the study of the gastric evacuation of clupeids, we chose to conduct our experiments in the laboratory using a method similar to those described by Van der Lingen (1998) for sardines (*Sardinops sagax*) and by Temming et al. (2002) for mackerel (*Scomber scombrus*). Compared to ship-board experiments, laboratory tank experiments imparted much less stress on the experimental animals (e.g. stress induced by catching and handling prior to the experiment, was minimal). Sprat were kept under constant conditions in the experimental tanks for a two-week acclimation period, including daily feedings of the experimental ration. Therefore, fish were well accustomed to the experimental conditions prior to the start of measurements.
The main stress induced in our experiments may have been caused by the removal of small groups of sprat from the tank. However, the impact of these irritations were considered minor, since the behaviour (swimming speed and direction) of fish in the tanks was similar prior to and shortly after fish removal. To test whether the removal of fish resulted in a deceleration of the stomach evacuation, the course of the evacuation from two experiments at the same temperature (experiments 3 and 4 at 13°C, figure 1) were compared. In experiment 3, fish were removed at 0, 4, 8 and 12 hours after feeding, while in experiment 4 the fish were removed 0, 8, 12 and 16 hours after the feeding. We tested whether the additional disturbance to fish in experiment 1 after 4 hours had an impact on the evacuation constant. Therefore we conducted a non-parametric Mann-Whitney-U-test to compare the distribution of the proportional decrease in the stomach contents 8 hours after the feeding in experiments 3 and 4. As there was no significant difference between experiments 3 and 4 (two-tailed significance level: 0.111), we concluded that the disturbance due to the removal of fish did not have an impact on the stomach evacuation.
Our experiments enabled us to measure the gastric evacuation constants in sprat under controlled laboratory conditions using techniques that caused little stress to the fish. The experiments could be improved by employing a different method to remove fish that, for the most part, would be undetected by the remaining group of fish (e.g., using underwater gates and/or corridors).

Mathematical models of the gastric evacuation

Shape parameter B of the general model

Several mathematical models have been used to describe the rate of gastric evacuation in fish (Jobling 1981, Persson 1986, Bromley 1994, Temming 1995). Linear, square root, exponential, power exponential and logistic models have been the most commonly used. The form of the model of gastric evacuation appears to be mainly dependent on prey size. Small and easily digested prey, such as zooplankton, are evacuated exponentially (B = 1) while large prey items, such as fish may be evacuated with B-values of 0.5 (square root model) or B = 0.67 (surface-area dependent model, e.g. Persson 1979, 1981; Jobling 1981,1987; Bromley 1994; Temming 1995).
As the diet of sprat almost entirely consists of zooplankton (Arrhenius 1996, Szypula et al. 1997, Möllmann et al. 2004), we tested if the exponential model was most appropriate for describing the gastric evacuation of sprat. It appears as though model

selection in many previous studies was predetermined and applied according to *a priori* expectations (e.g. Persson 1979, Talbot et al. 1984, Bromley 1988), whereas in other studies the general model was applied (Jones 1974, Temming & Andersen 1994, Andersen 1999, Temming & Herrmann 2001 a, b),
We applied the general evacuation model to our data, which included constants collected on fish fed different meal sizes. The meal sizes varied from a minimum of 3.3% of dry body weight at 13°C to a maximum of 8.3% at 10°C. Temming & Andersen (1994) discussed the importance of varying meal size in determining the shape of the evacuation curve. A model may give the best fit at a certain meal size, but may be unable to adequately predict the evacuation constants of larger or smaller meals.
The integrated analysis of all experiments from 7.5 to 16°C, including temperature (exponential model) and body weight as variables, resulted in a B-value of 0.94, strongly indicating an exponential evacuation. As a result we chose the exponential model to analyse the gastric evacuation of sprat, taking temperature and body weight as variables. The analyses at the different temperatures showed that at 7.5, 13 (experiments 14 and 15), 16 and 19.5°C the B-values varied around 1, indicating an exponential evacuation. However, there were selected cases (10°C, 13°C (experiments 3 and 4) and 21.5°C) where B-values between 0.58 and 0.69 were found. However, a B-value of 1.0 was not within the 95%-confidence limits of estimates only at 13°C. Linear evacuation was barely supported since B-values of 0 were, with the exception of experiments at 7.5°C, not within confidence limits of estimates, for the most part excluding the linear evacuation.

Exponential evacuation

Exponential evacuation has been observed for several fish feeding on high numbers of small prey items. The gastric evacuation of European perch feeding on *Gammarus pulex* (Persson 1979, 1981), the evacuation of chironomid larvae and mysidaceae by ruffe (*Gymnocephalus cernuus*) (Hölker & Temming 1996, Henson & Newman 2000), the evacuation of chironomid pupae and zooplankton in Arctic charr (*Salvelinus alpinus*), Amundsen & Klemetsen (1988), rainbow trout (*Oncorhynchus mykiss*) feeding on chironomid larvae, Hayward & Weiland (1998) and Atlantic mackerel (*Scomber scombrus*) feeding on natural plankton, Darbyson et al. (2003) were all described as exponential. In the majority of studies conducted on clupeids including sardine (*Sardinops sagax*), and Atlantic herring, mainly the exponential evacuation model has been applied (Arrhenius & Hansson 1994; van der Lingen 1998; Darbyson et al. 2003). Gastric evacuation data collected on sprat in the laboratory are generally lacking. Previous work includes evacuation rates and constants determined from collected ship-board tank experiments (Szypula & Zalachowski 1984, Köster 1994) and by 24 h-fisheries (Arrhenius 1998, Maes et al. 2005). Szypula & Zalachowski (1984) applied a linear evacuation model, whereas Köster (1994) reported exponential evacuation after applying the general model. Arrhenius (1998) and Maes et al. (2005) applied an exponential model.
The evacuation constants obtained in the present study (0.076 at 7.5°C to a maximum of 0.179 at 19.5°C) were similar to those estimated from ship-board tank experiments by Szypula & Zalachowski (1984) and Köster (1994). After re-analysing the data of Szypula & Zalachowski (1984) and applying an exponential model to the data, we estimated evacuation constants of R = 0.14 at 10°C and R = 0.19 at 16°C. However, no information was available regarding the weights of fish used in that study. Applying our weight dependency coefficient to Köster´s data, evacuation constant in that study (R = 0.23) was similar to that (R = 0.25) calculated for the same size (10 g) sprat at the same temperature (13°C) in the present study. The observed evacuation constants by

Arrhenius (1998) for sprat of 0.2 to 3.0 g wet weight (35 – 84 mm) were high with R = 0.32 to 0.38. There was no discernable temperature effect: constants at 5.8°C ranged from 0.32 to 0.34 (2.0 – 3.0 g wet weight) and at 13.9°C from 0.34 to 0.38 (0.21 – 0.59 g wet weight). The results of Maes et al. (2005) estimated from 24 h-fisheries were higher than our constants at lower temperatures (0.11 to 0.13 from 6.9 to 11.9°C) and similar to our observed constants at higher temperatures (0.15 to 0.21 from 15.5 to 23.5°C). The size range of these sprat was approx. 3 to 9 g wet weight.
Our estimated constants of gut evacuation for a 10 g sprat (R = 0.25 at 13°C) were higher than those (R = 0.098 at 13°C and R = 0.202 at 16°C) observed for juvenile Atlantic herring feeding on copepods (Bernreuther et al. In Prep.). However, constants in this study agreed well with those calculated for juvenile herring by Arrhenius & Hansson (1994). In that 24 h-fisheries study, R was 0.19 - 0.28 at a mean temperature of 13.2°C for 6 to 7.4 cm length herring and 0.21 to 0.27 at a mean temperature of 16.5°C for 4.5 to 5.5 cm herring. The comparison of the evacuation constants of sprat and juvenile herring, leads to the conclusion that both planktivorous species exhibit a comparable evacuation constant at similar fish sizes.

Evacuation constant and temperature

Temperature increased gastric evacuation constant in sprat. The relationship between evacuation constant and temperature was described by a simple exponential model over the temperature range of 7.5 to 16°C. At temperatures > 16°C, the rate of increase declined with increasing temperature, and constants were maximal and reaching a plateau at about 19°C. A similar pattern of temperature dependence was observed by Brett & Higgs (1970) working with sockeye salmon (*Onchorynchus nerka*) and by Sweka et al. (2004) for brook trout (*Salvelinus fontinalis*). In both those studies, evacuation constants stabilised near the upper limit of thermal tolerance of the species.
We used three different models to describe the relationship between evacuation constant and temperature. The results of most investigations dealing with the evacuation-temperature relationship suggest a simple exponential pattern, regardless of the model used to describe the shape of the evacuation curve. This exponential pattern was observed over the entire investigated temperature range in some studies (trout: Elliott 1972; perch: Persson 1979, 1981; ruffe: Henson & Newman 2000, burbot: Pääkkönen & Marjomäki 1997), while in others the evacuation rate increased with increasing temperature, reached a maximum and subsequently declined with further temperature increases (cod: Tyler 1970; herring: Temming 1995). Compared to our results did Maes et al. (2005) estimate a low exponential temperature coefficient A of 0.039 from 24 h-fisheries over a wide temperature range (1.9 to 23.5°C). Our estimated exponential coefficients of A = 0.094 from 7.5 to 16°C (exponential model, eqn. 4) and A = 0.110 (= a1) in Temming´s model (eqn.7) are in the middle of the range of observed temperature dependencies. Our Q_{10}-values (2.6 to 3.0) are within the middle of the range of values (1.4 to 4.3) that have been reported for a variety of fish species in previous studies: European perch, Q_{10} = 4.3 (Persson 1981); mackerel (*Scomber scombrus* L.), Q_{10} = 4.1 (Temming et al. 2002); Atlantic cod (*Gadus morhua* L.), Q_{10} = 3.7 (dos Santos & Jobling 1995); Atlantic herring, Q_{10} = 3.7 (Temming 1995); Arctic charr, Q_{10} = 3.3 (Amundsen & Klementsen 1988); brown trout (*Salmo trutta* L.), Q_{10} = 3.0 (Elliott 1972); whiting, Q_{10} = 2.1 (Andersen 1999); plaice, Q_{10} = 2.0 (Basimi & Grove 1985); ruffe, Q_{10} = 1.6 (Hölker & Temming 1996), dab (*Limanda limanda* L.), Q_{10} = 1.5 (Fletcher et al.1984); sprat, Q_{10} = 1.5 (Maes et al. 2005) and horse mackerel, Q_{10} = 1.4 (Temming & Herrmann 2001 a).
A temperature optimum of 19.5°C was estimated after applying the model of Temming (1995) to the data collected for sprat in the present study. However, due to the

variability of observed constants, the temperature optimum is likely not at this specific temperature, but is assumed to be at temperatures not < 19°C.
The estimate for sprat is higher than the optimum temperature (15°C) predicated by Tyler (1970) for Atlantic cod and the genotype-specific preferred temperatures (8.2 and 15.4 °C) for cod (Petersen & Steffensen 2003). Although sprat and cod co-occur in specific areas of the North and Baltic Seas their habitat overlap may be reduced by differences in optimal temperature and/or temperature preference. This is not unexpected due to the differences in the geographic range of these species. The North and Baltic Seas mark the northern limit of the geographic range of sprat, a species that is distributed over the whole Mediterranean and Black Sea (Whitehead 1985) whereas they mark the southern limit for cod (Cohen et al. 1990).
Concerning the choice of the appropriate model for describing the temperature effect on the gastric evacuation in sprat, different arguments have to be considered. Temming´s model is physiologically-based. Physiological processes tend to show the pattern (exponential increase, optimum, decrease) described by this model (Schmidt-Nielsen 1997). Although a decrease in evacuation constant was observed at the highest temperature (21.5°C) it is unknown whether constants would continue to decline at warmer temperature. Additional experiments are needed to test this. The logistic model provided the best fit over the range in temperatures tested. However a disadvantage of this model is that constants remain unchanged when extrapolated to lower (< 7.5°C) and higher (> 21.5°C) temperatures. This does not seem biologically reasonable. An advantage of Temming´s model is the physiological background and the possibility to compare the results with exponential models applied to evacuation constants calculated by other authors.

Evacuation constant and predator weight

The value of the weight coefficient C was ~ 0.3, and varied slightly depending upon the model employed. In all cases, a value of 0 (zero) was not included in the 95% confidence limits, indicating that the evacuation constant was positively correlated with sprat body weight. This coefficient for sprat is at the lower end of the body size coefficients discussed by Jobling (1981), which ranged from 0.23 to 0.62. However, the weight coefficient C and the shape parameter B of the general model interact. The higher the shape exponent B the lower the weight coefficient (Temming 1995). Exponential models do not explicitly need a weight effect to describe the data, as these models have an implicit weight effect. Specifically, the evacuation rate (g h^{-1}) is directly proportional to the stomach content and, since larger fish generally have higher stomach contents, the evacuation rate (g h^{-1}) is increasing accordingly with increasing fish size in the exponential model. In this perspective, the weight exponent estimated in this study is rather high. The maximal weight coefficient of Atlantic herring as estimated by Temming (1995) was C = 0.07 (< 14°C). No weight effect was observed by Elliott (1972) working with brown trout or by Persson (1979, 1981) who applied the exponential model to data collected on European perch. For a more precise estimation of the weight coefficient C, experiments with fish sizes > 10 cm total length are needed. Sprat can reach a maximum total length of 16 cm (Whitehead 1985, Ojaveer & Aps 2003) and 6 g dry weight which is approx. 6 times higher than our highest weights.

Conclusions

1) We were able to describe the gastric evacuation of sprat feeding on brine shrimp (*Artemia* spp.) under controlled (low stress) laboratory conditions. The shape parameter B of the general model was close to 1, indicating an exponential evacuation.

2) The temperature effect on gastric evacuation can be described by a simple exponential model between 7.5 and 16°C and by a logistic or a temperature optimum model (Temming 1995) between 7.5 and 21.5°C. The temperature optimum for the gastric evacuation appears to be located above 19°C.
3) The influence of the body weight on the gastric evacuation was described by a simple power function resulting in a weight coefficient C of ~ 0.3.

References

Amundsen, P.A. & Klemetsen, A. (1988). Diet, gastric evacuation rates and food consumption in a stunted population of Arctic charr, *Salvelinus fontinalis* L., in Takvatn, northern Norway. Journal of Fish Biology 33, 697 - 709.

Andersen, N.G. (1999). The effects of predator size, temperature, and prey size characteristics on gastric evacuation in whiting. Journal of Fish Biology 54, 287-301.

Arrhenius, F. & Hansson, S. (1994). In *situ* food consumption by young-of-the-year Baltic sea herring *Clupea harengus*: a test of predictions from a bioenergetics model. Marine Ecology Progress Series 110, 145 – 149.

Arrhenius, F. (1996). Diet composition and food selectivity of 0-group herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.) in the northern Baltic Sea. ICES Journal of Marine Science 53, 701-712.

Arrhenius, F. (1998). Food intake and seasonal changes in energy content of young Baltic sea sprat (*Sprattus sprattus* L.). ICES Journal of Marine Science 55, 319-324.

Basimi, R.A. & Grove, D.J. (1985). Gastric emptying rate in *Pleuronectes platessa* L. Journal of Fish Biology 26, 545-552.

Bernreuther, M., Temming, A. & Herrmann, J.-P. (In Prep.). Laboratory experiments on the gastric evacuation of juvenile herring (*Clupea harengus* L.).

Bromley, P.J. (1987). The effects of food type, meal size and body weight on digestion and gastric evacuation in turbot, *Scophthalmus maximus* L. Journal of Fish Biology 30, 501-512.

Bromley, P.J. (1988). Gastric digestion and evacuation in whiting, *Merlangius merlangus* (L.). Journal of Fish Biology 33, 331-338.

Bromley, P.J. (1994). The role of gastric evacuation experiments in quantifying the feeding rates of predatory fish. Reviews in Fish Biology and Fisheries 4, 36-66.

Brett, J.R. & Higgs, D.A. (1970). Effect of water temperature on the rate of gastric digestion in fingerling sockeye salmon, *Onchorynchus nerka*. Journal of the Fisheries Research Board of Canada 27, 1767-1779.

Cohen, D.M., Inada, T., Iwamoto, T. & Scialabba, N. (1990). FAO Species Catalogue Vol.10. Gadiform fishes of the world (order gadiformes). 442 pp.

Darbyson, E., Swain, D.P., Chabott, D. & Castonguay, M. (2003). Diel variation in feeding rate and prey composition of herring and mackerel in the southern Gulf of St Lawrence. Journal of Fish Biology 63, 1235-1257.

Elliott, J.M. (1972). Rates of gastric evacuation in brown trout, *Salmo trutta* L. Freshwater biology 2, 1-18.

Fletcher, D.J., Grove, D.J., Basimi, R.A. & Ghaddaf, A. (1984). Emptying rates of single and double meals of different food quality from the stomach of the dab, *Limanda limanda* (L.). Journal of Fish Biology 25, 435-444.

Hayward, R.S. & Weiland, M.A. (1998). Gastric evacuation rates and maximum daily rations of rainbow trout fed chironomid larvae at 7.8, 10.0 and 12.8°C. Environmental Biology of Fishes 51, 321 – 330.

Henson, F.G. & Newman, R.M. (2000). Effect of temperature on growth at ration and gastric evacuation rate of ruffe. Transactions of the American Fisheries Society 129, 552 – 560.

Hölker, F. & Temming, A. (1996). Gastric evacuation in ruffe (*Gymnocephalus cernuus* (L.)). Archives of Fisheries and Marine Research. 44(1/2), 47 – 67.

Jobling, M. (1980). Dietary digestibility and the influence of food components on gastric evacuation in plaice, *Pleuronectes platessa* L. Journal of Fish Biology 19, 29-36.

Jobling, M. (1981). Mathematical models of gastric emptying and the estimation of daily rates of food consumption for fish. Journal of Fish Biology 19, 245 - 257.

Jobling, M. (1987). Influences of food particle size and dietary energy content on patterns of gastric evacuation in fish: test of physiological model of gastric emptying. Journal of Fish Biology 30, 299-314.

Jones, R. (1974). The rate of elimination of food from the stomachs of haddock *Melanogrammus aeglefinus*, cod *Gadus morhua* and whiting *Merlangius merlangus*. Journal du Conseil International pour l´Exploration de la mer 35, 225-243.

Karjalainen, J., Miserque, D., and Huuskonen, H. (1997). The estimation of food consumption in larval and juvenile fish: experimental evaluation of bioenergetics models. Journal of Fish Biology 51 (Supplement A), 39-51.

Kornilovs, G., Sidrevics, L. & Dippner, J.W. (2001). Fish and zooplankton interaction in the Central Baltic Sea. ICES Journal of Marine Science 58, 579-588.

Köster, F.W., Schober, W., Korves, A. & Schneider, R. (1990). Tank experiments on board: a useful tool for the estimation of stomach evacuation rates? ICES. C.M. 1990/G:34.

Köster, F.W. (1994). Der Einfluß von Bruträubern auf die Sterblichkeit früher Jugendstadien des Dorsches (Gadus morhua) und der Sprotte (*Sprattus sprattus*) in der zentralen Ostsee. Ph.D. thesis. Christian-Albrecht-University of Kiel, 369 pp.

Maes, J., Tackx, M. & Soetaert, K. (2005). The predation impact of juvenile herring *Clupea harengus* and sprat *Sprattus sprattus* on estuarine zooplankton. Hydrobiologia 540, 225-235.

Möllmann, C., Kornilovs, G., Fetter, M. & Köster, F.W. (2004). Feeding ecology of central Baltic Sea herring and sprat. Journal of Fish Biology 65, 1563-1581.

Ojaveer, E. & Aps, R. (2003). Sprat, *Sprattus sprattus balticus* (Schn.). In: Fishes of Estonia, pp. 79 – 87.

Pääkkönen, J.-P.J. & Marjomäki, T.J. (1997). Gastric evacuation rate of burbot fed single-fish meals at different temperatures. Journal of Fish Biology 50, 555 – 563.

Persson, L. (1979). The effects of temperature and different food organisms on the rate of gastric evacuation in perch (*Perca fluviatilis*). Freshwater Biology (1979) 9, 99-104.

Persson, L. (1981). The effects of temperature and meal size on the rate of gastric evacuation in perch (*Perca fluviatilis*) fed on fish larvae. Freshwater Biology 11, 131-138.

Persson, L. (1986). Patterns of food evacuation in fishes: a critical review. Environmental Biology of Fishes Vol. 16. No. 1 – 3, 51 – 58.

Petersen, M.F. & Steffensen, J.F. (2003). Preferred temperature of juvenile Atlantic cod Gadus morhua with different haemoglobin genotypes at normoxia and moderate hypoxia. The Journal of Experimental Biology 206, 359-364.

Rudstam, L.G., Aneer, G. & Hilden, M. (1994). Top-down control in the pelagic Baltic ecosystem. Dana, vol. 10, 105 – 129.

dos Santos, J. & Jobling, M. (1995). Test of a food consumption model for the Atlantic cod. ICES Journal of Marine Science 52, 209-219.

Schmanns, M. (1994). Zur Biologie – insbesondere Nahrungsbiologie – der im Sylter Wattenmeer auftretenden Heringe (*Clupea harengus* L.). Diploma thesis.

Schmidt-Nielsen, K. (1997). Animal Physiology, adaptation and environment. 5th edition. Cambridge University Press. 607 pp.

Shvetsov, F.G., Starodub, M.L. & Sidrevits, L.L. (1983). The daily feeding rhythm of the Baltic sprat, *Sprattus sprattus balticus* (Clupeidae). Journal of Ichthyology Vol.23, no.2, 99-105.

Sweka, J.A., Cox, M.K. & Hartman, K.J. (2004). Gastric evacuation rates of brook trout. Transactions of the American Fisheries Society 133, 204 – 210.

Szypula, J. & Zalachowski, W. (1984). Duration of food evacuation in herring, *Clupea harengus* L., and sprat, *Sprattus sprattus* (L.). Acta ichthyologica et piscatoria, Vol. 14 Fasc. 1-2.

Szypula, J., Grygiel, W. & Wyszynski, M. (1997). Feeding of Baltic herring and sprat in the period 1986-1996 in relation to their state and biomass. Bulletin of the Sea Fisheries Institute 3 (142), 73-83.

Talbot, C., Higgins, P.J. & Shanks, A.M. (1984). Effects of pre- and post-prandial starvation on meal size and evacuation rate of juvenile Atlantic salmon, *Salmo salar* L. Journal of Fish Biology 25, 551 - 560.

Temming, A. & Köster, F.W. (1990). Stomach evacuation rates of cod and herring estimated from shipboard tank experiments and field data. ICES. C.M. 1990/G: 31.

Temming, A. & Andersen, N.G. (1994). Modelling gastric evacuation without meal size as a variable. A model applicable for the estimation of daily ration of cod (*Gadus morhua* L.) in the field. ICES Journal of Marine Science 51, 429-438.

Temming, A. (1995). Die quantitative Bestimmung der Konsumtion von Fischen. Experimentelle, methodische und theoretische Aspekte. Habilitationsschrift, University of Hamburg, Department Biology, 235 pp.

Temming, A. & Herrmann, J.-P. (2001 a). Gastric evacuation in horse mackerel I. The effects of meal size, temperature and predator weight. Journal of Fish Biology 58 No. 5, 1230 - 1245.

Temming, A. & Herrmann, J.-P. (2001 b). Gastric evacuation of horse mackerel. II. The effects of different prey types on the evacuation model. Journal of Fish Biology 58, 1246-1256.

Temming, A., Bøhle, B., Skagen, D.W. & Knudsen, F.R. (2002). Gastric evacuation in mackerel: the effects of meal size, prey type and temperature. Journal of Fish Biology 61, 50-70.

Tyler, A.V. (1970). Rates of gastric emptying in young cod. Journal of Fisheries Research Board of Canada 27, 1177-1189.

Van der Lingen, C.D. (1998). Gastric evacuation, feeding periodicity and daily ration of Sardine *Sardinops sagax* in the Southern Benguela Upwelling Ecosystem. South African Journal of Marine Science 19, 305 - 316.

Whitehead, P.J.P. (1985). FAO Species Catalogue. Clupeoid fishes of the world (Suborder clupeoide; Part I, herrings, sardines, pilchards, sprats, anchovies and wolf-herrings. 303 pp.

The role of habitat heterogeneity on the vulnerability of marine zooplankton to predation: implications for trophic cascades

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Abstract

Predator effects of planktivorous fish on marine zooplankton are generally weak, resulting in rare observations of trophic cascades in marine pelagic ecosystems. A mechanism behind the weak interaction strength might be a lacking overlap between predator and prey in the heterogeneous physical environment of marine systems. In the Baltic Sea, a strongly stratified semi-enclosed brackish area, the top-predator in the system cod (*Gadus morhua*) collapsed due to climate-induced recruitment failure and high fishing pressure. Reduced predation pressure resulted in an increased stock size of the major forage species sprat (*Sprattus sprattus*). Despite of the strong increase of the major planktivore population, the dominant zooplankton species showed differential developments. We conducted an *in situ* process-study on the role of habitat heterogeneity on the vulnerability of the calanoid copepods *Pseudocalanus acuspes*, *Temora longicornis* and *Acartia* spp. to predation by the planktivores sprat and herring (*Clupea harengus*). We first quantified the fish predation impact on the dominating zooplankton species by confronting predator consumption to prey production rates. Using observations on vertical distributions of predators and prey, we then tested the hypothesis that a variable vertical overlap due to strong hydrographic preferences of predator and prey species caused a differential vulnerability to predation. Our results show strong predator effects of the sprat population on *P. acuspes* in spring and *T. longicornis* in summer. We further showed that the vulnerability of copepod species to fish predation is modulated by preferences for different habitats leading to a differential vertical overlap.

Introduction

According to food chain theory, naturally or anthropogenically induced changes at the top of the food chain cascade down the food web eventually influencing the biomass of primary producers (Hairstone et al. 1960). Although heavily debated (Chase 2000), cascades seem to be more prevalent in water than on land (Strong 1992, Polis 1999, Halaj & Wise 2001). A cross-ecosystem comparison of the strength of trophic cascades, using meta-analyses of field manipulation experiments, revealed weakest predator effects to occur in terrestrial food webs and marine plankton (Shurin et al. 2002). Although generally zooplanktivorous predators tended to reduce herbivore abundance, the effect on marine zooplankton appeared to be weak (Shurin et al. 2002). A similar conclusion was derived from a meta-analysis of marine mesocosm experiments and long-term monitoring programmes, showing weak, statistically insignificant negative relationships between zooplanktivorous fish and mesozooplankton (Micheli 1999). Recently a few examples of cascading effects involving marine plankton in pelagic environments emerged (e.g. Daskalov 2002, Frank et al. 2005), the magnitude of evidence remains however low yet.

The pelagic ecosystem of the Central Baltic Sea provides an example for an upper trophic level cascade due to the joint effect of overfishing and climate change (Köster et al. 2003). During the early-1990s the stock of the top-predator cod (*Gadus morhua*) collapsed due to climate-induced recruitment failure and high fishing pressure (Köster et al. 2005). The main food item of cod, i.e. sprat (*Sprattus sprattus*), increased subsequently to record levels due to recruitment success and lowered predation

pressure (Köster et al. 2003, MacKenzie & Köster 2004). Sprat and herring (*Clupea harengus*) are the main planktivores in the system preying mainly on calanoid copepods (Möllmann et al. 2004). Despite the drastic increase in sprat stock size, not all mesozooplankton species declined. Rather the dominant calanoid copepods showed differential developments with *Acartia* spp. and *Temora longicornis* increasing and only *Pseudocalanus acuspes*[1] decreasing (Möllmann et al. 2000, 2003). Using time-series data from the neighbouring Gotland Basin, Möllmann & Köster (2002) showed that the increased sprat stock had a significant influence on *P. acuspes* and to a lesser degree on the *T. longicornis* population, but not on *Acartia* spp. This differential vulnerability of the copepods to predation was hypothesized to be due to differing vertical distributions (Möllmann & Köster 2002).

Generally, little is known about the processes causing variations in the magnitude of cascading effects (Borer et al. 2005). Spatial heterogeneity has been hypothesized to weaken cascades as it may provide refugia for herbivores (Polis et al. 2000). Marine environments display various physical structures which affect the spatial distribution of animals. Horizontally, marine plankton may aggregate in local frontal convergences (e.g. Taggart et al. 1989, Munk et al. 1995, Gonzales-Quiro et al. 2003) or accumulate in retentive large-scale circulation features (e.g. Falkenhaug et al. 1995, Miller et al. 1998). Vertically, planktonic animals may be concentrated at discontinuity layers, e.g. thermo- and haloclines (e.g. Harris 1988, Munk et al. 1989, Lougee et al. 2002). A consequence of these heterogeneous distribution patterns may be a spatial mismatch of herbivores with their predators, thus weaken the interactions similar to refugia.

The deep basins of the Central Baltic Sea represent an example of a highly stratified physical environment. In addition to the development of a thermocline in spring, the positive freshwater balance of this semi-enclosed sea leads to a freshening of surface waters and the development of a permanent halocline. The water column is thus in spring and summer divided into a warm surface, a cold intermediate and a saline deep water body (Voipio 1981), providing local species with different habitats to choose with pronounced consequences for trophic interactions.

Here we report on an *in situ* process-study on the role of habitat heterogeneity on the vulnerability of calanoid copepods to predation by planktivorous fish in the Bornholm Basin (Central Baltic Sea). We first quantified the fish predation impact on dominating zooplankton species by confronting predator consumption to prey production rates. Using observations on vertical distributions of predators and prey, we then tested the hypothesis that a variable vertical overlap due to strong hydrographic preferences of predator and prey species caused a differential vulnerability to predation.

Material and methods

Sampling and laboratory analyses

We conducted systematic hydrography and zooplankton grid surveys during May, June and July 2002 in the Bornholm Basin, Central Baltic Sea, with German research vessels RV ALKOR and HEINCKE. Vertical profiles of salinity, temperature and oxygen concentration (CTD-O_2) were collected on a grid of 45 stations. Zooplankton sampling was performed on a 9 station subset of the station grid (figure 1). We used a Bongo sampler (150 µm mesh-size) for double-oblique hauls to in maximum 5 m above the seafloor to record the zooplankton community integrated over the whole water column. Additionally we applied a 50 µm Multi-net resolving the water column in 10 m depth

[1] formerly called *P. elongatus*, but see Renz and Hiche (2006).

intervals, providing vertical distribution patterns of zooplankton species. Samples were preserved in a 4%-formaldhyde/seawater solution. In the laboratory copepods were identified to species and developmental stage, i.e. nauplii, copepodites 1-5 (C1-5) as well as adults (C6).

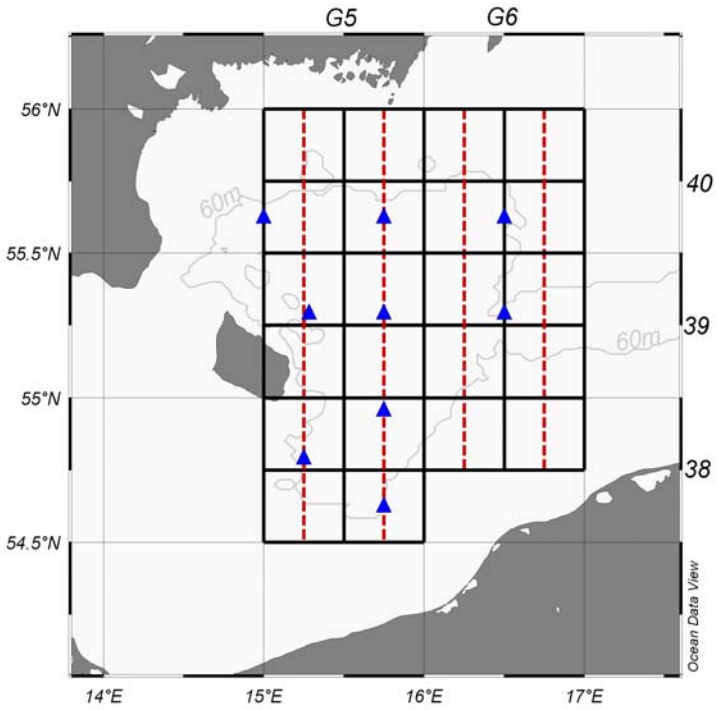

Figure 1) Study area (Bornholm Basin) with plankton sampling stations (triangles) and hydroacoustic transects (dashed lines)

We used hydroacoustic recording in combination with pelagic trawling on four transects in the Bornholm Basin with German research vessels RV ALKOR and WALTHER HERWIG III to estimate the spatio-temporal occurrence of planktivorous fish (figure 1). Acoustic measurements were conducted during the daytime feeding period of Baltic sprat and herring (Köster and Schnack 1994, Cardinale et al. 2003). A SIMRAD EK 500 echosounder was used on RV WALTHER HERWIG III, while on RV ALKOR a SIMRAD EK 60 echosounder was deployed. Calibration of the gears was performed using the standard copper-sphere method (Foote et al. 1987). The procedure and the settings of the acoustic measurements as well as the data processing were conducted according to the "Manual for the Baltic International Acoustic Survey" (ICES 2001). Digitized echograms were corrected for bottom topography and thin-echo-scattering-layers and other unwanted echoes, such as air-bubbles below the ship. Echo-data were integrated as 'nautical area backscattering coefficient' (NASC; [m²/nm²]) from 10 m below the surface to 0.5 m above bottom. We performed pelagic trawling with a Kombitrawl (Fa. Engel trawls) on the hydroacoustic transects targeting observed schools of pelagic fish. After each haul the total catch and the length-distribution of sprat and herring was recorded. Stock sizes of herring and sprat were computed for quarterly ICES (International Council for the Exploration of the Sea) rectangles (further on called rectangles, figure 1).
We collected stomachs of the clupeids for feeding analyses according to a length-stratified sampling scheme using 1 cm length–classes for sprat, and 2 cm length-classes for herring. If available, contents of 3 stomachs per length-class were analysed per trawl station, summing up to a total of 711 herring and 871 sprat stomachs. The total stomach content (in g wet weight) was measured as the difference between the full

and the empty gut. Food items were identified to species and copepods to developmental stages as described for the zooplankton samples. For the present analysis, focusing on predation effects on calanoid copepods, we grouped all other food items in one single “others” group.

Predator consumption

The average stomach fullness of herring and sprat in g wet weight (*WW*) was calculated per month and weighted according to the observed length-frequency distribution. We estimated individual daily rations (F_T) of herring and sprat per trawl station using an exponential form of the general model of gastric evacuation (Tyler 1970, Jones 1974) which incorporates the ambient temperature as a variable (Temming 1995):

$$F_T = R' \times S \times D \times e^{(A \times T)} + S_t - S_0 \qquad (1)$$

with R' a food type constant (0.108 for sprat and 0.084 for herring), S the average stomach content, D the duration of the feeding period, A a temperature coefficient (0.073 for sprat and 0.129 for herring), T the ambient temperature, and S_t the average stomach content at the end as well as S_0 the average stomach content at the beginning of the feeding period. Values for S_t (44 and 10% for sprat and herring respectively) and S_0 (43 and 52% for sprat and herring respectively) were estimated from 24 h-fisheries representing mean relative deviations from the average stomach content during daytime, 2 hours before and after the food ingestion stopped and commenced, i.e. sunset and sunrise (Köster 1994). Baltic herring and sprat form schools during daylight feeding in deeper water layers, while during night the fish disperse in surface layers showing no feeding activity (Köster and Schnack 1994, Stepputtis 2001, Cardinale et al. 2003). We thus used ambient temperatures in the observed depth of the centre of mass of herring and sprat (figure 4) during the daytime feeding period in consumption estimations. A detailed description of the evacuation model and the estimation of the parameter values is given in Möllmann and Köster (1999). Eventually we computed population consumption rates by multiplication of individual daily rations with population sizes. Consumption values per m^2 were derived using the size of the area (Möllmann & Köster 2002). Consumed mass was converted to carbon assuming the carbon content to be 5% of the wet weight (Mullin 1969).

Prey production

A comparison of the two plankton sampling gears revealed the Bongo to be the more efficient sampler for copepodites and adults of the calanoids considered here (results not shown here). Consequently, we used the results from this gear for further analyses and the production estimates. We estimated abundance ($n*m^{-2}$) of target copepod species using information on filtered volumes and water depth. Abundance was transferred to biomass (in g *WW*) using seasonal stage- and species-specific standard weights (Hernroth 1985). Mass was converted to carbon assuming the carbon content to be 5% of the wet weight (Mullin 1969). Copepod production was calculated for every zooplankton sampling station by applying a weight-specific growth rate on stage-specific biomass values (Runge & Roff 2000). We estimated weight-specific growth rates using the global models of Hirst & Lampitt (1998), providing separate equations for juvenile and adult broadcast spawning (*T. longicornis* and *Acartia* spp.) and egg-carrying copepod species (*P. acuspes*). Growth rates (g) of egg-carrying copepods were found to be solely temperature-dependent:

$$\log_{10} g = a + b[T] \quad (2)$$

with *T* the temperature in the weighted mean depth (WMD) (ºC), as well as *a* = -1.4647, *b* = 0.0358 for juvenile stages, and *a* = -1.7726, *b* = 0.0358 for adults. Growth rates of broadcast spawning copepodites were additionally dependent on body weight:

$$\log_{10} g = a[T] + b[\log_{10} BW] + c \quad (3)$$

with *BW* the body weight (mg) from Hernroth (1985), as well as *a* = 0.0111, *b* = -0.2917 and *c* = -0.6447. Growth rates of broadcast spawning adults were only dependent on body weight:

$$\log_{10} g = a + b[BW] \quad (4)$$

with *a* = -0.6516 and *b* = -0.5244.

Vertical distribution of predator and prey

We calculated weighted mean depth (WMD) as an index of the vertical orientation of the different copepods and their developmental stages (Bollens & Frost 1989):

$$WMD = \left(\sum n_i d_i\right) \Big/ \sum n_i \quad (5)$$

where n_i is the abundance (n*m^{-3}) in each depth stratum with the midpoint d_i. Vertically-resolved abundance data were derived from Multinet-sampling. We did not consider differences between day and night, because diurnal vertical migration activity is insignificant in Baltic copepods (Hansen et al. 2006, Renz & Hirche 2006). We used Analysis of Variance (ANOVA) to test for differences in WMD between the various copepods and their developmental stages. For Post-hoc tests to distinguish differences between single means, the Tukeys HSD-Test was used.
Because herring and sprat are hydroacoustically not distinguishable, we calculated a WMD for the combined sprat and herring stock using NASC-values in 1 m vertical layers.

Mean temperature and salinity of predator and prey

We calculated weighted mean temperature and salinity for both copepod species/stages and planktivorous fish to demonstrate the hydrographic preferences of predators and prey. The temperature and salinity in the WMD was computed for all copepod species/stages and every zooplankton sampling station. Mean temperature and salinity experienced by the planktivorous fish was calculated for the depth of the center of mass in every rectangle of the hydroacoustic survey. Mean monthly hydrographic parameters were weighted by the abundance of predators and prey in rectangles and on zooplankton sampling stations, respectively.

Vertical overlap between predator and prey and weighted prey density

We assessed the vertical overlap (O_i) between the pelagic fish and the copepods using the Williamson overlap index (Williamson et al. 1989, Williamson & Stoeckel 1990):

$$O_i = \left\{\sum_{z=i}^{m}\left(N_z \bullet n_{iz}\right)m\right\} / \left\{\sum_{z=i}^{m}\left(N_z\right) \bullet \sum_{z=i}^{m}\left(n_{iz}\right)\right\} \quad (6)$$

with *N* and *n* the predator and prey density, *i* the prey type (copepod species and stages), *z* a given depth stratum and *m* the number of depth strata. The index characterizes the extent to which the correlation between predator and prey deviates from a random expectation under a uniform vertical distribution. Values < 1 indicate a lower than expected overlap, values > 1 a greater than expected overlap. We assessed the significance of the overlap index using a randomization test appropriate for correlation coefficients with a similar form (Manly 1997, Garrison et al. 2000). Thereby the observed overlap value was tested against the null hypothesis of no vertical relationship between predator and prey by generating a random distribution of overlap indices. For each predator and prey pair in each month, we randomly (with replacement) selected values for the predator to prey pair with the abundance of prey *i* at each depth and calculated the randomized O_i. We randomized 5000 times with the last instance being the observed values. The significance (at a $\alpha = 0.05$ level) is the proportion of observations from the randomized distribution with deviations from 1 larger than or equal to the observed values (Garrison et al. 2000).
The choice of a prey species by a predator may depend on the relative abundances of the prey species. We thus calculated the density of each prey species available to the predators, the weighted density (WD_i):

$$WD_i = \left(n * O_i\right)/1000 \quad (7)$$

Interaction strength

We calculated consumption to production ratios (C/P) as an index of the interaction strength between the different life-stages of the target copepod species and planktivorous fish. We assigned trawl and plankton stations to individual rectangles to yield spatially-resolved C/P-values (figure 1).

Results

Predator diet, stock size and consumption

We found the diet of herring and sprat to be very similar, being dominated by the 3 target copepod species (figure 2). We further observed a clear diet change between May and the later months. In May both fish species preyed mainly upon older copepodites and adults of *P. acuspes*, while only smaller fractions of *T. longicornis* and *Acartia* spp. were found in the stomachs. Contrary, in June and July C4-6 of *T. longicornis* constituted the largest proportion of the herring and sprat diet.

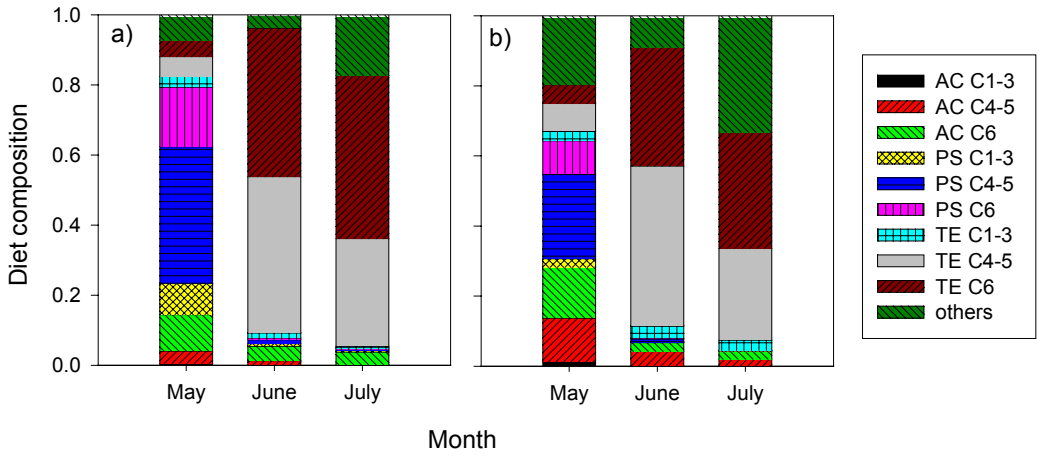

Figure 2) Diet composition of herring (a) and sprat (b); AC – *Acartia* spp., PS – *Pseudocalanus acuspes*, TE – *Temora longicornis*, C - copepodites

We found highest average stomach contents and individual daily rations of herring in June, with the latter being twice the rations in May and July (Table 1). For sprat, the mean stomach content as well as the daily individual consumption increased steadily during the observed period.
The stocks of herring and sprat showed a pronounced in- and out basin migration (Table 1). We observed the highest sprat abundance in May, decreasing during June and July. In contrast herring stock size increased over the period. In all month the pelagic fish community was numerically dominated by the sprat stock.

Table 1) Consumption and stock size of herring and sprat: D – daily feeding period (hours), T – ambient temperature (°C), S – mean stomach content (g *WW*) ± s.e., F_T – individual daily ration (g *WW*) ± s.e., and N – stock size (millions).

Month	D	T	Herring			Sprat		
			S	F_T	N	S	F_T	N
May	16.2	7.3	0.17±0.034	0.71±0.15	172	0.029±0.0037	0.118±0.012	34118
June	17.3	7.7	0.31±0.039	1.41±0.17	707	0.036±0.0038	0.163±0.019	7458
July	15.9	6.4	0.21±0.027	0.77±0.08	1368	0.050±0.0075	0.185±0.024	2080

Combining individual rations with stock sizes, we yielded daily estimates of the fish population consumption (Table 2). We found the peak sprat population consumption in May on C4-5 and C6 of *P. acuspes*. Larger consumption rates were additionally observed for the later stages of *T. longicornis* in June and *Acartia* spp. in May. Herring population consumption peaked in June and July on C4-5 and C6 of *T. longicornis*.

Prey production

We found considerable differences in stage-specific production between the 3 copepod species (Table 2). *T. longicornis* was the most productive copepod, followed by *Acartia* spp., and *P. acuspes* being the least productive. We found the same stage-specific production pattern in *Acartia* spp. in all months, with C6 having the highest production and C1-3 the lowest. In contrast, production patterns of *P. acuspes* and *T. longicornis* changed between months. *P. acuspes* C4-5 displayed the highest production in May and June, while C1-3 production was highest in July. In *T. longicornis* C1-3 production peaked in May, while in June and July C4-5 and especially C6 production was highest.

Table 2) Production of copepod species/stages and consumption by herring and sprat: WMD – weighted mean depth (m), T – temperature in WMD (ºC) ± s.e, g – daily growth rate, B – biomass (mg C * m^{-2}) ± s.e., P – daily production (mg C * m^{-2}) ± s.e., and population consumption by sprat - C_S, and herring - C_H (mg C * m^{-2}) ± s.e. PS – *Pseudocalanus* sp., TE – *Temora longicornis*, AC – *Acartia* spp.; 1-3 and 4-5 – copepodites; 6 – adults.

Species/ Stage	WMD	T	g	B	P	C_S	C_H
May							
PS1-3	42.4±8.8	4.9	0.05	54±13	2.7±0.7	0.31±0.072	0.03±0.010
PS4-5	49.3±14.9	5.2	0.05	96±42	5.1±2.3	3.45±0.997	0.21±0.082
PS6	50.4±13.7	6.0	0.06	45±63	2.5±1.3	1.44±0.414	0.09±0.034
TE1-3	15.5±4.1	8.6	0.17	142±27	23.6±4.6	0.66±0.366	0.01±0.002
TE4-5	23.6±5.7	6.4	0.12	546±78	3.9±1.0	1.11±0.519	0.01±0.007
TE6	26.6±8.1	6.1	0.03	309±74	8.8±2.1	0.76±0.312	0.01±0.004
AC1-3	15.3±3.5	9.8	0.18	13±3	2.4±0.6	0.25±0.103	<0.01±0.001
AC4-5	17.3±3.6	8.5	0.14	96±12	12.9± 1.6	1.94±0.564	0.01±0.005
AC6	22.3±6.1	6.4	0.05	368±45	18.4±2.3	2.58±0.753	0.02±0.006
June							
PS1-3	42.1±7.1	5.2	0.05	53±8	2.8±0.3	0.03±0.027	0.04±0.022
PS4-5	46.6±9.7	4.6	0.05	96±28	4.8±1.0	0.17±0.074	0.04±0.195
PS6	52.0±7.1	6.2	0.06	65±27	1.6±0.4	0.08±0.052	0.01±0.006
TE1-3	26.8±7.9	6.6	0.16	21±4	3.3±0.6	0.85±0.324	0.03±0.014
TE4-5	32.7±11.1	5.8	0.12	389±63	10.5±1.5	9.90±2.565	1.77±0.806
TE6	35.2±13.6	5.4	0.03	1052±149	30.9±4.4	6.35±2.466	1.72±0.750
AC1-3	14.2±4.0	12.4	0.20	6±1	1.2±0.2	0.06±0.031	<0.01±0.001
AC4-5	19.1±5.6	8.8	0.15	58±12	7.9±1.6	1.33±0.707	0.07±0.036
AC6	29.9±5.9	5.9	0.05	483±80	24.0±4.0	0.59±0.185	0.21±0.121
July							
PS1-3	42.2±6.4	6.2	0.05	177±63	9.6±3.4	<0.01±0.002	0.01±0.002
PS4-5	47.7±8.4	6.2	0.06	65±27	3.7±1.5	0.02±0.013	0.01±0.002
PS6	46.5±8.4	5.4	0.05	21±9	1.1±0.5	0.03±0.015	<0.01±0.001
TE1-3	27.9±5.4	8.2	0.17	8±2	1.2±0.3	0.83±0.430	0.02±0.010
TE4-5	34.1±8.8	5.8	0.12	63±17	6.3±1.5	9.37±3.314	0.74±0.186
TE6	32.8±9.9	6.4	0.03	635±136	18.6±4.0	13.20±4.944	1.00±0.235
AC1-3	19.8±6.4	14.0	0.21	2±1	0.4±0.1	0.03±0.029	<0.01±0.001
AC4-5	25.7±3.3	10.3	0.15	40±9	5.6±1.2	0.54±0.283	<0.01±0.003
AC6	29.0±5.5	7.7	0.05	184±20	9.0±1.0	0.66±0.316	0.06±0.017

Interaction strength

The strongest predation pressure was generally exerted by the sprat stock (figure 3). In May highest C/P were computed for C4-5 and C6 of *P. acuspes*, while in June and July the highest predation pressure occurred on *T. longicornis*, especially on C4-5. We estimated the sprat population to frequently consume more than the full copepod production of these copepods. Predation pressure by herring was in general very low.

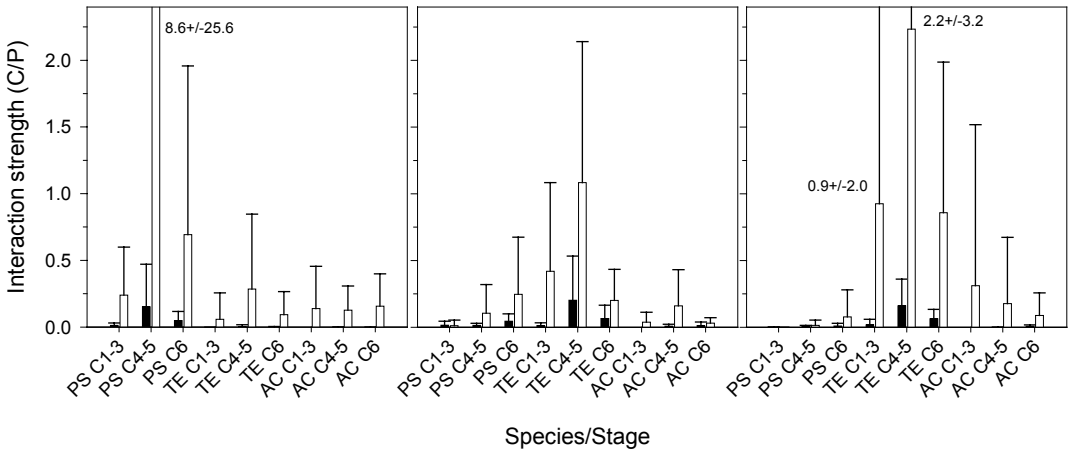

Figure 3) Interaction strength (consumption/production) between herring (black bars) and sprat (white bars), and the different copepod species/stages in May (left), June (middle) and July (right); AC – *Acartia* spp., PS – *Pseudocalanus acuspes*, TE – *Temora longicornis*, C – copepodites, error bars represent s.d. of the mean.

Hydrographic structure and vertical distribution of predator and prey

We observed mean vertical hydrographic profiles from May, June and July to match the "typical" spring/summer-stratification of the water column in a Central Baltic basin (figure 4). A thermocline separated the warm surface water from the cold intermediate water. The typical permanent halocline was observed below 60 m and separated low saline surface waters from the saline bottom-water, which has low oxygen concentrations near the bottom.
We found the habitats of the 3 dominant copepods to be vertically segregated (figure 4). *Acartia* spp. was the most surface-orientated copepod with the copepodites dwelling directly in the thermocline, while the adults are always found below the thermocline in colder water. The deepest distribution is displayed by *P. acuspes*, which dwell in the lowest part of the intermediate cold water down to the upper part of the permanent halocline. *T. longicornis* occurred always in the intermediate cold water.
Differences in the vertical distribution were supported by ANOVAs showing significant differences between the WMDs of the copepods (May: F=25.0, p<0.01; June: F=19.2, p<0.01; July: F=16.1; p<0.01). Post-hoc tests revealed no significant differences between the stages of single copepods, indicating similar habitats within a species. No significant differences in WMDs were found between all *Acartia* spp. stages and *T. longicornis* C1-3, between *Acartia* spp. C6 and *T. longicornis* C4-6 as well as between *P. acuspes* C1-3 and *T. longicornis* C4-6, indicating overlaps in vertical distribution.
We found differences in vertical orientation of copepods between May and June/July (figure 4). While the vertical position of *P. acuspes* remained stable, *Acartia* spp. and especially *T. longicornis* were found deeper in June and July, following the deepening of the thermocline. A change in vertical orientation between May and June/July was also found for herring and sprat. The planktivores occurred in May directly in the permanent halocline, while in June and July most fish were observed above the halocline in the cold intermediate water.

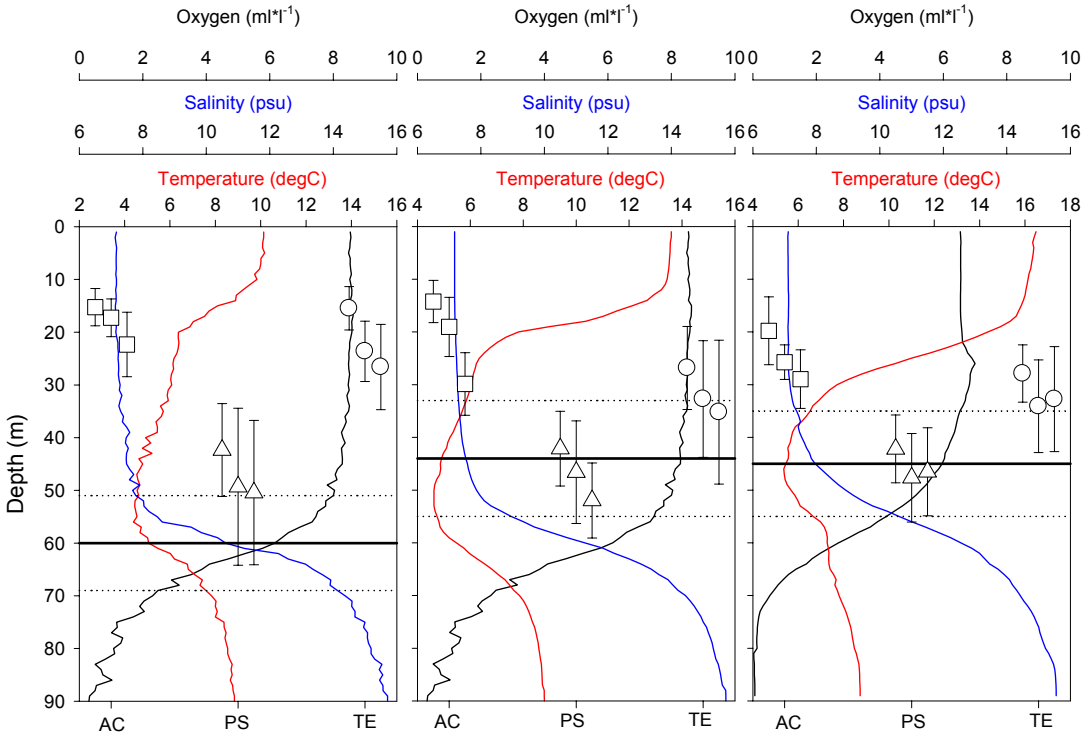

Figure 4) Hydrographic situation, and distribution of predator and prey in May (left), June (middle) and July (right); AC – *Acartia* spp., PS – *Pseudocalanus acuspes*, TE – *Temora longicornis*, C – copepodites; groups of symbols from left to right – copepodites 1-3, copepodites 4-5 and adults; error bars represent ± s.d. of the mean, solid horizontal line – weighted mean depth of herring and sprat, dotted horizontal lines - ± s.d of the mean.

Mean temperature and salinity of predator and prey

We recorded considerable differences in the average salinity and temperature preferences of the different copepod species. (figure 5). The average salinity values for *Acartia* spp. and *T. longicornis* were close to 7 psu in all months, irrespective of developmental stage. In contrast, *P. acuspes* had consistently higher average salinities with maximal values in May and lower values in June/July.
The experienced temperature range of *Acartia* spp. and *T. longicornis* was similar and relatively narrow in May, while in June and July the range was narrow for *T. longicornis*, but wide for *Acartia* spp. For the latter species a pronounced ontogenetic trend in average temperature values was found, with decreasing values for older stages. Experienced temperatures for *P. acuspes* were generally the lowest, although for later copepodites and adults as high as for the two other species
We observed the highest average salinities experienced by herring and sprat in May, while the average temperature was relatively stable, although highest in June. Mean hydrographic parameters for pelagic fish were generally similar to those of *P. acuspes*, especially in May.

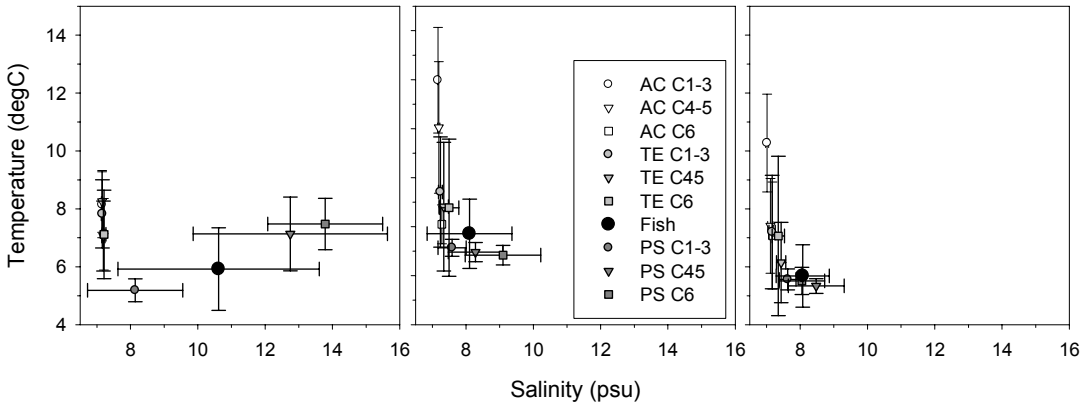

Figure 5) Mean temperature and salinity values experienced by the different copepod species/stages and the predators; AC – *Acartia* spp., PS – *Pseudocalanus acuspes*, TE – *Temora longicornis*, C – copepodites, error bars represent ± s.d. of the mean.

Vertical overlap between predator and prey and weighted prey density

We found highest vertical overlap indices between planktivorous fish and copepods in all months for *P. acuspes*, indicating a strong spatial association (Table 3). Overlap indices were significantly different from random expectation for all *P. acuspes* stages in May, for later copepodites and adults in June, and only adults in July. Overlap indices < 1 indicating negative spatial association were calculated for *T. longicornis* and *Acartia* spp. in May, however being significant for copepodites of the latter species only. Vertical overlap indices for *T. longicornis* and *Acartia* spp. changed to values > 1 in June and July, being however not significantly different from random expectation.
Weighted densities encountered by the predators were highest for *P. acuspes* in May, while insignificant for the other copepod species (Table 3). In June and July, weighted densities for all species were higher compared to May. In these months we observed early copepodite weighted densities to be highest for *P. acuspes*, while late copepodite and adult densities were highest for *T. longicornis*. Considerable weighted densities of *Acartia* spp. were only observed for adults.

Table 3) Vertical overlap indices between fish and the different copepods species/stages (O_i), and weighted density of prey species (WD_i). *, p<0.05; p values are the proportions of randomized overlap indices which have a greater deviation from 1 than the observed value.

Species/stage	O_i			WD_i		
	May	June	July	May	June	July
PS1-3	1.94*	1.44	1.71	2.46	5.03	9.40
PS4-5	2.44*	2.02*	1.82	0.53	2.24	2.61
PS6	2.32*	2.38*	1.82*	0.40	0.22	0.37
TE1-3	0.12	0.86	1.45	0.01	0.33	0.16
TE4-5	0.44	1.05	1.53	0.00	2.95	2.80
TE6	0.33	1.43	1.43	0.01	8.85	9.28
AC1-3	0.10*	0.68	1.19	0	0.01	0
AC4-5	0.12*	0.74	1.42	0	0.08	0.23
AC6	0.49	1.09	1.28	0.08	4.34	3.42

Discussion

We performed an *in situ* process-study on the role of habitat heterogeneity on the vulnerability of calanoid copepods to predation by planktivorous fish in the Bornholm Basin, Central Baltic Sea. We first quantified the fish predation impact on dominating zooplankton species. Our estimates of predator consumption in relation to prey production show that due to its presently small size the herring population was not able to control any of the copepod populations. In contrast, we found the presently abundant sprat population to exert a strong predation pressure on later stages of *P. acuspes* in May and *T. longicornis* in June/July, a result which confirms a time-series study from a neighbouring Baltic basin (Möllmann & Köster 2002). The observed pattern of predation impact was mainly determined by the diet of the clupeids, to a large degree composed of *P. acuspes* in May and *T. longicornis* in June/July. The observed diet composition of herring and sprat confirmed earlier investigations of their feeding ecology (e.g. Möllmann et al. 2004 and references therein).
We estimated the ratio of consumption to production as an index of interaction strength between planktivorous fish and the copepods. For the calculation of the daily food intake by individual herring and sprat we used a gastric evacuation model approach, which has been shown to yield in low estimates when compared to alternative bioenergetic modelling (Hansson et al. 1996, Möllmann & Köster 1999). Consequently, we consider our estimates as rather conservative and potentially underestimates of the true consumption by clupeid fish (Möllmann & Köster 2002). For the estimation of species- and stage-specific copepod production, we computed weight-specific growth rates using global models for broadcast spawning (*Acartia* spp. and *T. longicornis*) and egg-carrying species (*P. acuspes*) (Hirst & Lampitt 1998). Another common practice in the estimation of secondary production is to measure female egg production, and assume that somatic growth of the following developmental stages can be closely approximated by the weight-specific egg production (Berggreen et al. 1988, McLaren & Leonard 1995). Comparing our growth rates with rates derived from egg production experiments (EPR) in the same area (Hansen et al. 2006), showed both to be in good agreement for adults of *T. longicornis* and *Acartia* spp., but considerably higher for earlier stages of these species. EPR-derived growth rates for *P. acuspes* were slightly higher than our global model estimates for May, which is explainable by the seasonal peak egg production of this species at this time of the year (Hansen et al. 2006). Later in the season EPR-derived growth rates are lower than our global model estimates. The comparison of growth rates indicated that using EPR-derived growth rates would result on average in lower secondary production estimates than ours using global models. A reason for the potential overestimation of copepod growth rates by the global models is that these are mainly based on data derived from true marine areas (Hirst & Lampitt 1998), being potentially of limited use for the brackish condition of the Baltic Sea. Indeed, copepod egg production rates of all species in the Bornholm Basin appear to be low compared to fully marine areas, which may indicate a salinity limitation (Hansen et al. 2006). Further, copepod egg production may be food-limited, which is not considered in the global models. Consequently our estimates of copepod production rates seem to be overestimates, while our fish consumption rates seem to be underestimates of the true values, supporting the conclusion of significant fish predation effects on Baltic copepods.
Our second aim in the present study was to test the hypothesis that a differential vertical overlap due to strong hydrographic preferences of predators and prey caused the differential vulnerability to predation in the heterogeneous environment of the Baltic Sea. Highest overlap indices for later copepodites and adults of *P. acuspes* explained the dominance of this copepod in the diet of the predators in May, and thus the strong

predation pressure exerted on them. The strong vertical overlap in May was caused by the preference of both predator and prey species to high salinity, resulting in a similarly deep vertical distribution. The preference of *P. acuspes* to higher salinities and thus a deep distribution in the Central Baltic basins confirms results from other studies in the Bornholm Basin (Hansen et al. 2006, Renz & Hirche 2006). Similarly, the distribution of herring and sprat in the halocline during their daily feeding period has been reported before (e.g. Köster & Schnack 1994, Cardinale et al. 2003, Nilsson et al. 2003).

Vertical overlap indices increased for *T. longicornis* in June/July as a result of a deepening distribution of the copepod and a shallower distribution of pelagic fish. *T. longicornis* avoided obviously the warm temperatures above the deepening thermocline, which is visible in their preference of temperatures < 8ºC. Our observed vertical distribution is in accordance with observations made for *T. longicornis* in the area before (Hansen et al. 2006). In parallel to the deepening of the copepod´s distribution, we observed the clupeid fish predators in shallower waters in June/July. This shallower distribution is explainable by the annual migration of the sprat population to shallower areas of the Baltic after spawning, which usually peaks in May (Elwertowski 1960, Aro 1989). The difference in vertical distribution thus represents rather a horizontal than a vertical movement, which is not resolved by our horizontally integrated analysis.

Despite of the increased overlap between *T. longicornis* and the planktivores in June/July, the dominance of late copepodites and adults of this copepod in the diet of herring and sprat is not explained by spatial association alone. Still, overlap indices for *P. acuspes* were higher suggesting a dominance of this copepod in predator diets in June/July as well. The choice of a prey species by a predator may, however, also be dependent on the relative abundances of different prey species. Consequently we calculated weighted species-specific prey densities encountered by the predators. We showed that in June/July these values were higher for late copepodites and adults of *T. longicornis* compared to *P. acuspes*, explaining the dominance of the former copepod in the diet of the planktivorous fish.

Active prey selection of clupeid fish due to prey size, conspicuousness and escape reactions is another mechanism potentially leading to the observed feeding pattern. Size-selective feeding may thus be the reason why generally earlier copepodites constituted only very small fractions in the diets of herring and sprat, despite of high overlap indices. The selection of later and thus better visible copepodite stages by Baltic clupeid fish has been frequently demonstrated before (e.g. Flinkman et al. 1992, Möllmann et al. 2004 and references therein).

Similar to *T. longicornis*, *Acartia* spp. was found deeper in the water column in June/July compared to May, obviously avoiding the warm water above the thermocline. The continuously low fraction of *Acartia* spp. in predator diets despite of high overlap indices is explainable for early and late copepodites by low weighted densities encountered by herring and sprat. However, high weighted densities in June/July are contradictory and point towards negative selection of *Acartia* spp. by the predators. This is in agreement with a study by Casini et al. (2004), showing a selection of *P. acuspes* and *T. longicornis* over *Acartia* spp., explainable by on average a smaller size and a high escape response of *Acartia* spp. (Viitasalo et al. 2001).

We show that the vertical distribution of copepods in the Baltic Sea is largely steered by hydrographic preferences, which supports earlier findings (Hansen et al. 2006, Renz & Hirche 2006). However, other factors might have contributed to the observed spatial patterns. We found Baltic copepods to be associated to hydrographic discontinuities, i.e. the thermo- and the halocline. It is well known that in these areas of changing density, phyto- and microzooplankton food accumulates (e.g. Harris 1988, Munk et al. 1989, Roman et al. 2005). We thus cannot exclude that the observed association to hydrography is a response to a favourable feeding environment. Further, predator

avoidance has been suggested to play a major role in vertical distribution/migration of copepods (Bollens & Frost 1989). However, as no significant diurnal vertical migration has been observed for the copepods in the area (Hansen et al. 2006, Renz & Hirche 2006) and our results show a strong vertical overlap with the predators, we exclude predation as a driving force for vertical distribution.

We recorded the vertical distribution of planktivorous herring and sprat using hydroacoustic measurements. It should be noted that hydroacoustic recording cannot distinguish between these two similar fish species. However, as presently the sprat population is strongly dominating the pelagic fish community in the Baltic (Köster et al. 2003), we consider the observed vertical distribution to be mainly representative for sprat. Another flaw in our analysis may be the horizontal integration of all fish and plankton measurements to a single vertical overlap pattern. This procedure ignores variability in vertical distribution and thus overlap, an issue that needs further exploration.

In conclusion, we showed that the vulnerability of different copepod species to fish predation is to a large degree explainable by preferences for different habitats characterized by salinity and temperature. The most vulnerable species in spring is *P. acuspes* which indicates that fish predation has contributed to the decline of this species (Möllmann & Köster 2002, Möllmann et al. 2003). Our results further explain the existence of a trophic cascade in the Central Baltic involving cod, sprat and *P. acuspes*, initiated by the decline of the cod stock due to overfishing and climate change (Köster et al. 2005). The existence of the cascade on a species-level exemplifies that the trophic level abstraction in evaluating cascading interactions in ecosystems is of limited use (Polis 1999). It should, however, be considered that detrimental hydrographic conditions are another main driver for *P. acuspes* inter-annual dynamics (Möllmann et al. 2003). Further, significant predation pressure was also exerted on *T. longicornis* in summer, which is however not the primary driving force for the population dynamics of this copepod, as its abundance and biomass increased in parallel to the sprat stock (Möllmann & Köster 2002). Rather the increase in temperature during the 1990s has caused the interannual development of the *T. longicornis* population (Möllmann et al. 2003), indicating the importance of considering climate-induced environmental trends in research on cascading interactions in ecosystems (Berlow et al. 2004, Ovadia & Schmitz 2004). Finally, our study shows that *Acartia* spp. is the least vulnerable copepod due to limited overlap with the main predators, which exemplifies how spatial heterogeneity, in our case physical structures in the vertical, induce weak interactions resulting in weak trophic cascades as well. We hypothesize that limited spatial overlap between predator and prey, due to heterogeneous habitats is a major reason behind the limited evidence for trophic cascades involving plankton in the marine environment.

References

Aro, E. (1989) A review of fish migration patterns in the Baltic. Rapport Procès-verbaux des Rèunion du Conseil International pour l´Exploration de la Mer 190, 72–96.

Berggreen, U., Hansen, B., & Kiørboe, T. (1988). Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: Implications for determination of copepod production. Marine Biology 99(3), 341–352.

Berlow, E.L., Neutel, A.-M., Cohen, J.E., De Ruiter, P.C., Ebenman, B., Emmerson, M., Fox, J.W., Jansen, V.A.A., Jones, J.I., Kokkoris, G.D., Logofet, D.O., McKane, A.J., Montoya, J.M. & Petchey, O. (2004). Interaction strengths in food webs: issues and opportunities. Journal of Animal Ecology 73, 585–598.

Bollens, S.M. & Frost, B.W. (1989). Predator-induced diel vertical migration in a planktonic copepod. Journal of Plankton Research 11(5), 1047–1065.

Borer, E.T., Seabloom, E.W., Shurin, J.B., Anderson, K.E., Blanchette, C.A., Broitman, B., Cooper, S.D. & Halpern, B.S. (2005). What determines the strength of a trophic cascade? Ecology 86(2), 528–537.

Cardinale, M., Casini, M., Arrhenius, F. & Håkansson, N. (2003). Diel spatial distribution and feeding activity of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the Baltic Sea. Aquatic Living Resources 16(3), 283–292.

Casini, M., Cardinale, M. & Arrhenius, F. (2004). Feeding preferences of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the southern Baltic Sea. ICES Journal of Marine Science 53 61(8), 1267–1277.

Chase, J.M. (2000). Are there real differences among aquatic and terrestrial food webs? Trends Ecol Evol 15(10), 408–412.

Daskalov, G.M. (2002). Overfishing drives a trophic cascade in the Black Sea. Marine Ecology Progress Series 225, 53–63.

Elwertowski, J. (1960). Biologische Grundlagen der Sprottenfischerei in der östlichen und mittleren Ostsee. Fischereiforschung 3(4), 1–17.

Falkenhaug, T., Nordby, E., Svendsen, H. & Tande, K. (1995). Impact of advective processes on displacement of zooplankton biomass in a north Norwegian fjord system: a comparison between spring and autumn. In: Skjoldal HR, Hopkins C, Erikstad KE, Leinaas HP (eds) Ecology of Fjords and Coastal Waters: Proceedings of the mare Nor Symposium on the Ecology of Fjords and Coastal Aters, Tromsoe, Norway, 5-9 December, 1994. Elsevier Science, Amsterdam; Netherlands, pp 195–218.

Flinkman, J., Vuorinen, I. & Aro, E. (1992). Planktivorous Baltic herring (*Clupea harengus*) prey selectively on reproducing copepods and cladocerans. Canadian Journal of Fisheries and Aquatic Sciences 49(1), 73–77.

Foote, K.G., Aglen, A. & Nakken, O. (1986). Measurement of fish target strength with a split-beam echosounder. Journal of the Acoustical Society of America 80, 612–621.

Frank, K.T., Petrie, B., Choi, J.S. & Leggett, W.C. (2005). Trophic Cascades in a Formerly Cod-Dominated Ecosystem. Science 308, 1621–1623.

Garrison, L.P., Michaels, W., Link, J.S. & Fogarty, M.J. (2000). Predation risk on larval gadids by pelagic fish in the Georges Bank ecosystem. I. Spatial overlap associated with hydrographic features. Canadian Journal of Fisheries and Aquatic Sciences 57(12), 2455–2469.

Gonzalez-Quiro, R., Cabal, J., Alvarez-Marque. F. & Isla, A. (2003). Ichthyoplankton distribution and plankton production related to the shelf break front at the Aviles Canyon. ICES Journal of Marine Science 60(2), 198–210.

Hairstone, N.G., Smith, F.E. & Slobodkin, L.B. (1960). Community structure, population control, and competition. American Naturalist 44, 421–425.

Halaj, J. & Wise, D.H. (2001). Terrestrial trophic cascades: how much do they tickle? American Naturalist 157, 262–281.

Hansen, F.C., Möllmann, C., Schütz, U. & Neumann, T. (2006). Spatio-temporal distribution and production of calanoid copepods in the central Baltic Sea. Journal of Plankton Research 28(1), 39–54.

Hansson, S., Rudstam, L.G., Kitchell, J.F., Hilden, M., Johnson, B.L. & Peppard, P.E. (1996). Predation rates by North Sea cod (*Gadus morhua*) - predictions from models on gastric evacuation and bioenergetics. ICES Journal of Marine Science 53(1), 107–114.

Harris, R.P. (1988). Interactions between diel vertical migratory behaviour of marine zooplankton and the subsurface chlorophyll maximum. Bulletin of Marine Science 43(3), 663–674.

Hernroth, L. (1985). Recommendations on methods for marine biological studies in the Baltic Sea. Mesozooplankton biomass assessment. The Baltic Marine Biologist 10, 45 pp.

Hirst, A.G. & Lampitt, R.S. (1998). Towards a global model of in situ weight/specific growth in marine planktonic copepods. Marine Biology 132(2), 247–257.

ICES (2001). Manual for the Baltic international acoustic surveys (BIAS). ICES CM H:02:25 pp.

Jones, R. (1974). The rate of elimination of food from the stomachs of haddock *Melanogrammus aeglefinus*, cod *Gadus morhua* and whiting *Merlangius merlangus*. Rapport Procès-verbaux des Rèunion du Conseil International pour l´Exploration de la Mer 35, 225–243.

Köster, F.W. (1994). Der Einfluß von Bruträubern auf die Sterblichkeit früher Jugendstadien des Dorsches (*Gadus morhua*) und der Sprotte (*Sprattus sprattus*) in der zentralen Ostsee. Ber Inst Meereskd Christian-Albrechts-Uni Kiel 261 pp.

Köster, F.W. & Schnack, D. (1994). The role of predation on early life stages of cod in the Baltic. Dana 10, 179–201.

Köster, F.W., Möllmann, C., Hinrichsen, H.-H., Wieland, K., Tomkiewicz, J., Kraus, G., Voss, R., Markarchouk, A., MacKenzie, B.R., St.John, M.A., Schnack, D., Rohlf, N., Linkowski, T. & Beyer, J.E. (2005). Baltic cod recruitment - the impact of climate variability on key processes. ICES Journal of Marine Science 62(7), 1408–1425.

Köster, F.W., Möllmann, C., Neuenfeldt, S., Vinther, M., St. John, M.A., Tomkiewicz, J., Voss, R., Hinrichsen, H.-H., Kraus, G. & Schnack, D. (2003). Fish stock development in the central Baltic Sea (1976-2000) in relation to variability in the environment. ICES Journal of Marine Science 219, 294–306.

Lougee, L.A., Bollens, S.M. & Avent, S.R. (2002). The effects of haloclines on the vertical distribution and migration of zooplankton. Journal of Experimental Marine Biology and Ecology 278(2), 111–134.

MacKenzie, B.R. & Köster, F.W. (2004). Fish production and climate: sprat in the Baltic Sea. Ecology 85(3), 784–794.

Manly, B.F.J. (1997). Randomization, bootstrap, and Monte Carlo methods in biology. Chapman & Hall, London.

Möllmann, C. & Köster, F.W. (1999). Food consumption by clupeids in the Central Baltic: evidence for top-down control? ICES Journal of Marine Science 56, 100–113.

Möllmann, C. & Köster, F.W. (2002). Population dynamics of calanoid copepods and the implications of their predation by clupeid fish in the Central Baltic Sea. Journal of Plankton Research 24(10), 959–978.

Möllmann, C., Köster, F.W., Kornilovs, G. & Sidrevics, L. (2003). Interannual variability in population dynamics of calanoid copepods in the Central Baltic Sea. ICES Marine Science Symposium 219, 294–306.

Möllmann, C., Kornilovs, G., Fetter, M. & Köster, F.W. (2004). Feeding ecology of central Baltic Sea herring and sprat. Journal of Fish Biology 65(6), 1563–1581.

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

McLaren, I.A. & Leonard, A. (1995). Assessing the equivalence of growth and egg production of copepods. ICES Journal of Marine Science 52(3-4), 397–408.

Micheli, F. (1999). Eutrophication, fisheries, and consumer-resource dynamics in marine pelagic ecosystems. Science 285(5432), 1396–1398.

Miller, C.B., Lynch, D.R., Carlotti, F., Gentleman, W. & Lewis, C.V.W. (1998). Coupling of an individual-based population dynamic model of *Calanus finmarchicus* to a circulation model for the Georges Bank region. Fisheries Oceanography 7(3-4), 219–234.

Mullin, M.M. (1969). Production of zooplankton in the ocean: the present status and problems (RV). Oceanography and Marine Biology Annual Review 7, 293–314.

Munk, P., Kiørboe, T. & Christensen, V. (1989). Vertical migrations of herring, *Clupea harengus*, larvae in relation to light and prey distribution. Environmental Biology of Fish 26(2), 87–96.

Munk, P., Larsson. P.O., Danielsen, D. & Moksness, E. (1995). Larval and small juvenile cod *Gadus morhua* concentrated in the highly productive areas of a shelf break front. Marine Ecology Progress Series 125(1-3), 21–30.

Nilsson, L.A.F., Thygesen, U.H., Lundgren, B., Nielsen, B.F., Nielsen, J.R. & Beyer, J.E. (2003). Vertical migration and dispersion of sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) schools at dusk in the Baltic Sea. Aquatic Living Resources 16(3), 317–324.

Ovadia, O. & Schmitz, O.S. (2004). Weather variation and trophic interaction strength: sorting the signal from the noise. Oecologia 140, 398–406.

Polis, G.A. (1999). Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. Oikos 86(1), 3–15.

Polis, G.A., Sears, A.L.W., Huxel, G.R., Strong, D.R. & Maron, J. (2000). When is a trophic cascade a trophic cascade? Trends in Ecology & Evolution 15, 473–475.

Renz, J. & Hirche, H.-J. (2005). Life cycle of *Pseudocalanus acuspes* Giesbrecht (Copepoda, Calanoida) in the Central Baltic Sea: I. Seasonal and spatial distribution. Marine Biology 148(3), 567–580.

Roman, M., Zhang, X., McGilliard, C. & Boicourt, W. (2005). Seasonal and annual variability in the spatial patterns of plankton biomass in Chesapeake Bay. Limnology and Oceanography 50(2), 480–492.

Runge, J.A. & Roff, G. (2000). The measurement of growth and reproductive rates. In: Harris, R.P., Wiebe, P.H., Lenz, J., Skojdal, H.R. & Huntley M (eds). ICES Zooplankton Methodology Manual. Academic Press, London, pp 401–454.

Shurin, J.B., Borer, E.T., Seabloom, E.W., Anderson, K., Blanchette, C.A., Broitman, B., Cooper, S.D. & Halpern, B.S. (2002). A cross-ecosystem comparison of the strength of trophic cascades. Ecology Letters 5(6), 785–791.

Stepputtis, D. (2001). Räumliche/zeitliche Variabilität in der Verteilung von Sprott und Hering in der Bornholm See. Diploma thesis. University Kiel, 105 pp.

Strong, D.R. (1992). Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. Ecology 73(3), 747–754

Taggart, C.T., Drinkwater, K.F., Frank, K.T., McRuer, J. & LaRouche, P. (1989). Larval fish, zooplankton community structure, and physical dynamics at a tidal front. Rapport Procès-verbaux des Rèunion du Conseil International pour l´Exploration de la Mer 191, 184–194.

Temming, A. (1995) Die quantitative Bestimmung der Konsumption von Fischen. Experimentelle, methodische und theoretische Aspekte. Habilitation thesis. University of Hamburg, 235 pp.

Tyler, A.V. (1970). Rates of gastric emptying in young cod. Journal of Fisheries Research Board of Canada 27, 1177-1189.

Viitasalo, M., Flinkman, J. & Viherluoto, M. (2001). Zooplanktivory in the Baltic Sea: a comparison of prey selectivity by *Clupea harengus* and *Mysis mixta*, with reference to prey escape reactions. Marine Ecology Progress Series 216, 191–200.

Voipio, A. (1981) The Baltic Sea. Elsevier, Amsterdam, 418 pp.
Williamson, C.E., & Stoeckel ME (1990). Estimating predation risk in zooplankton communities: The importance of vertical overlap. Hydrobiologia 198(1), 125–131.
Williamson, C.E., Stoeckel, M.E. & Schoeneck, L.J. (1989). Predation risk and the structure of freshwater zooplankton communities. Oecologia 79(1), 76–82.

Consumption of herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.) in the Bornholm Basin: is there evidence of food limitation?

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Abstract

Mean daily rations per fish of two dominant planktivorous fish species, sprat (*Sprattus sprattus* L.) and herring (*Clupea harengus* L.) were estimated for the Bornholm Basin, a deep Baltic basin in the south-central Baltic Sea. In sprat, mean daily rations from June through November 2002 were estimated from two different consumption models, a bioenergetics and a gastric evacuation model combined with field stomach estimates. In herring, mean daily rations were estimated with a gastric evacuation model combined with field stomach estimates and compared with maintenance rations estimated from laboratory experiments from April 2002 through November 2003. The results indicated that both sprat and herring were to some extent food limited in the Bornholm Basin, since estimates of mean daily rations per fish were partly lower than maintenance rations. The discrepancy between results of bioenergetic and gastric evacuation models in sprat indicated that the observed energy intake required to fuel somatic growth of field fish was accomplished by intensive feeding in areas outside of the basin, such as shallow, coastal regions.

Introduction

The migrations of both Baltic herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.) lead these planktivores into the deep basins of the Baltic Sea in different seasons (e.g. Bornholm Basin, Gdansk Deep, Gotland Basin). Herring spawn in coastal areas during spring and subsequently migrate to the deep basins, where they occur only after May in higher concentrations in e.g. the Bornholm Basin (Aro 1989, Stepputtis 2006). In contrast to herring, sprat migrate into the deep basins in early winter concentrating below the halocline and migrate into shallower water layers of the deep basins in early summer for spawning and subsequently into areas closer to the coast (Aro 1989, Stepputtis 2006).

Due to the decline of the Baltic Sea cod (*Gadus morhua* L.) stock, the Baltic Sea fish community has switched from a cod-dominated system during the late 1970s to mid-1980s to a clupeid-dominated system from the early 1990s until today (Kornilovs et al. 2001). The decreased predation mortality due to cod caused the stock size of sprat to increase to record levels in 1994, while the herring stock size was gradually declining (Kornilovs et al. 2001). The weight-at-age (WAA) of herring has also declined in the last two decades (Cardinale & Arrhenius 2000, Kornilovs et al. 2001). Several studies hypothesized that a combination of increased density-dependent inter- and intra-specific competition for food and changes in food availability caused the changes in WAA observed in herring and, to some extent, in sprat (Flinkman et al. 1998, Cardinale & Arrhenius 2000, Cardinale et al. 2002, Möllmann et al. 2003).

The aim of the present study was to estimate mean daily rations for herring and sprat of different ages and sizes in the Bornholm Basin using two independent approaches. We estimated mean daily food rations by means of a bioenergetics- and a gastric evacuation model. Both methods were based on different, independent field data: the daily rations estimated from the gastric evacuation model were based on stomach content data collected for both species in the Bornholm Basin, whereas the daily rations estimated from the bioenergetics model were based on *in situ* growth data of sprat that

was estimated from otoliths collected in the Bornholm Basin. The primary objective was to compare the results of both methods, discuss implications of possible differences and to determine whether herring and sprat were food limited in the Bornholm Basin.

Material & methods

Field sampling

Sprat and herring were caught monthly or bi-monthly in the Bornholm Basin (ICES subdivision 25, figure 1) from April 2002 to November 2003 by pelagic trawling. The hauls were conducted only during daytime. The weights and lengths of randomly chosen sub-samples of herring and sprat were measured. Sprat and herring were measured to the nearest (lower) cm. Stomach samples were taken from these sub-samples, using sprat separated into 1-cm length classes and herring separated into 2-cm length classes (i.e. 14/15 cm, 16/17 cm). Stomachs were dissected, and contents were removed and weighed to the nearest 0.1 mg. The otoliths of sub-samples of sprat were removed for an age determination. The caloric content of different age classes of sprat was estimated in an adiabatic bomb calorimeter type IKA C4000. For the estimation of caloric content, three to four fish per cruise and age class were ground together and caloric content was estimated from three to five repeated measurements. Hydrographic measurements of temperature, salinity and oxygen were performed after every fishing station with a CTD-probe (type ME-KMS3).

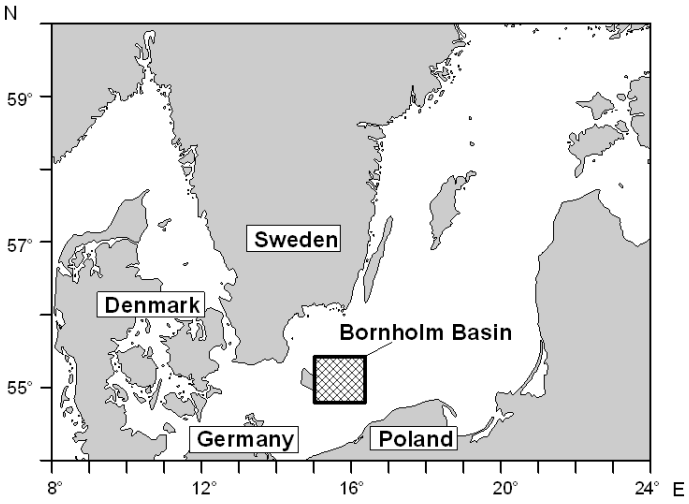

Figure 1) Map of the Baltic Sea with the study area marked by the shaded box.

Estimation of daily rations

The mean daily rations per age/length of herring and sprat were estimated by two models: a gastric evacuation model (GEM) and a bioenergetics model (BEM).

Gastric evacuation model

We estimated mean daily rations (F_T) per age/length of herring and sprat per month using an exponential form of the general model of gastric evacuation (Jones 1974) that incorporated ambient temperature and predator weight as variables (Temming 1995, Köster & Möllmann 2000):

$$F_T = R' \times S \times D \times e^{(A * T)} \times W^C + S_t - S_0, \quad (1)$$

where R' is a food type constant (0.028 for sprat and 0.017 for herring), S = average stomach content, D = duration of the feeding period, A = temperature coefficient (0.103 for sprat and 0.129 for herring), T = ambient temperature (°C), W = average fish weight, C = weight coefficient (0.364 for sprat and herring), 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 (44 and 10% for sprat and herring, respectively) and S_0 (43 and 52% for sprat and herring, respectively) were estimated from 24 h-fisheries as 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, Möllmann & Köster 2002). Since herring and sprat form dense schools and feed in deeper water layers during the day, while during night these fish disperse in surface layers and show no feeding activity (Cardinale et al. 2003, Stepputtis 2006), we used the ambient temperature in the observed depth of the centre of mass of herring and sprat during daytime feeding period in consumption estimations (Möllmann et al. In Prep.).

Bioenergetics model

Bioenergetics models allocate daily consumed energy C over metabolic processes such as respiration R and specific dynamic action SDA, waste losses due to egestion F and excretion E and growth G so that (Maes et al. 2005):

$$G = C - (R + SDA + F + E) \quad (2)$$

The growth (G) of sprat in the field was calculated from the change in the average energy density (J g^{-1} dry weight) per age class and month (figure 2). The daily ration was calculated by the following equation:

$$C = (M_r + M_a + SDA) + (F + E) + G, \quad (3)$$

with M_r = standard metabolic rate and M_a = metabolic rate increase (above standard rate) due to activity. The metabolic rates were measured through respirometry as a function of fish weight and temperature (J.-P. Herrmann, unpublished data):

$$R = \alpha \times W^{\beta} \times e^{(\rho \times T)}, \quad (4)$$

where R is respiration in g g^{-1} day^{-1}, W is wet weight (g), T is temperature in °C and α (0.057), ρ (0.087) and β (0.8) are constants. Active metabolism (M_a) was estimated from standard metabolism (M_r) by multiplying with a factor of 1.5. Sub models for waste losses were taken from Rudstam (1988) and Arrhenius (1998). Values for F, E and SDA were fixed at 0.1 each. Maintenance rations for herring at different temperatures were calculated from the results of starvation experiments at different temperatures (Bernreuther et al. In Prep. a). For these calculations the same activity multiplier (x 1.5) was used as for sprat. We assumed that the temperature dependence of metabolism in herring was adequately described between experimental temperatures of 9.7 to 14.2°C. The maintenance needs at different temperatures were described by $y = 37 * e^{0.186 * T}$ (J $fish^{-1}$ day^{-1}), with T = ambient temperature (°C). Since we have no information on the effect of weight on herring metabolism, we adopted the commonly used weight coefficient β of 0.8 (Brett & Groves 1979). Maintenance rations in sprat were calculated

from respirometry measurements and converted to wet weight (dry/wet weight factor: 0.27). Since both herring and sprat mainly feed on copepods an energy density of 20 kJ g^{-1} dry weight was assumed for the ingested prey (Mauchline 1998).

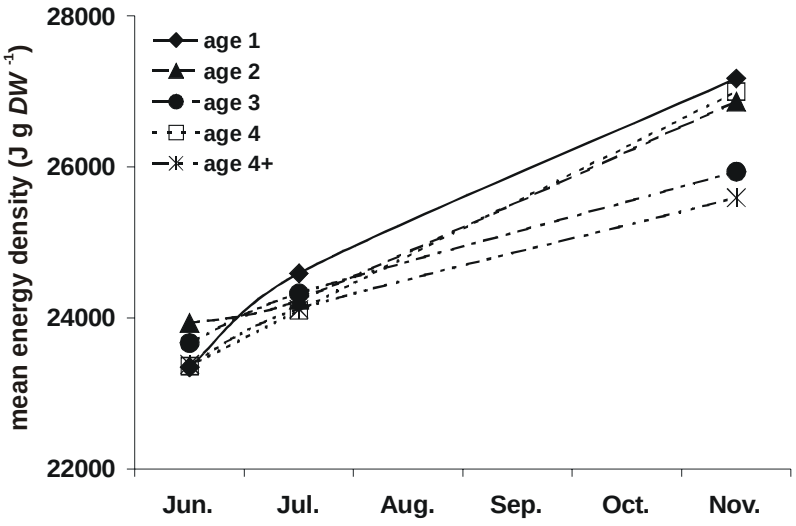

Figure 2) Energy densities (J g *DW* $^{-1}$) per age class of sprat in the Bornholm Basin from June through November 2002.

Results

Sprat

The results of the estimation of mean daily rations per age class of sprat in percent (%) wet body weight were different between the two different models (figure 3). The daily ration estimated from the bioenergetics model (BEM) was at maximum in June for age 1 sprat (3.26%) and, declined to a minimum (2.16%) at the end of November. A similar trend was observed in the age classes 2 to 4+, but the daily rations as a percentage of body weight generally decreased with increasing age. The highest daily rations estimated from the gastric evacuation model (GEM) were 1.35% wet body weight at the end of July for age 3 and age 4+ sprat. From mid June on, the daily rations increased in all age classes to reach maximum rations in the end of July, decreasing afterwards to minimum levels in the end of November with 0.40 to 0.46% for all age classes. The maintenance rations without activity costs covered (= MR) of all age classes as estimated from the standard metabolism were ~ 0.5% from mid June on to the end of July, increasing to the mid August to a maximum of ~ 0.7% and decreasing slightly afterwards again. The maintenance rations including activity cost (= 50% of standard metabolism cost) MRA exhibited a similar trend but consequently on a higher level. Highest MRA was 1.19% for age 1 at the middle of August. The daily rations estimated from BEM were constantly above the maintenance rations. The daily rations as estimated from GEM were above MR until the end of September (age 1) or the beginning of November (age 4+), whereupon the daily rations were lower than the maintenance rations. The daily rations as estimated from GEM were above the MRA until the beginning of August (age 1) and the end of August (age 4+), whereupon the daily rations were lower than MRA.

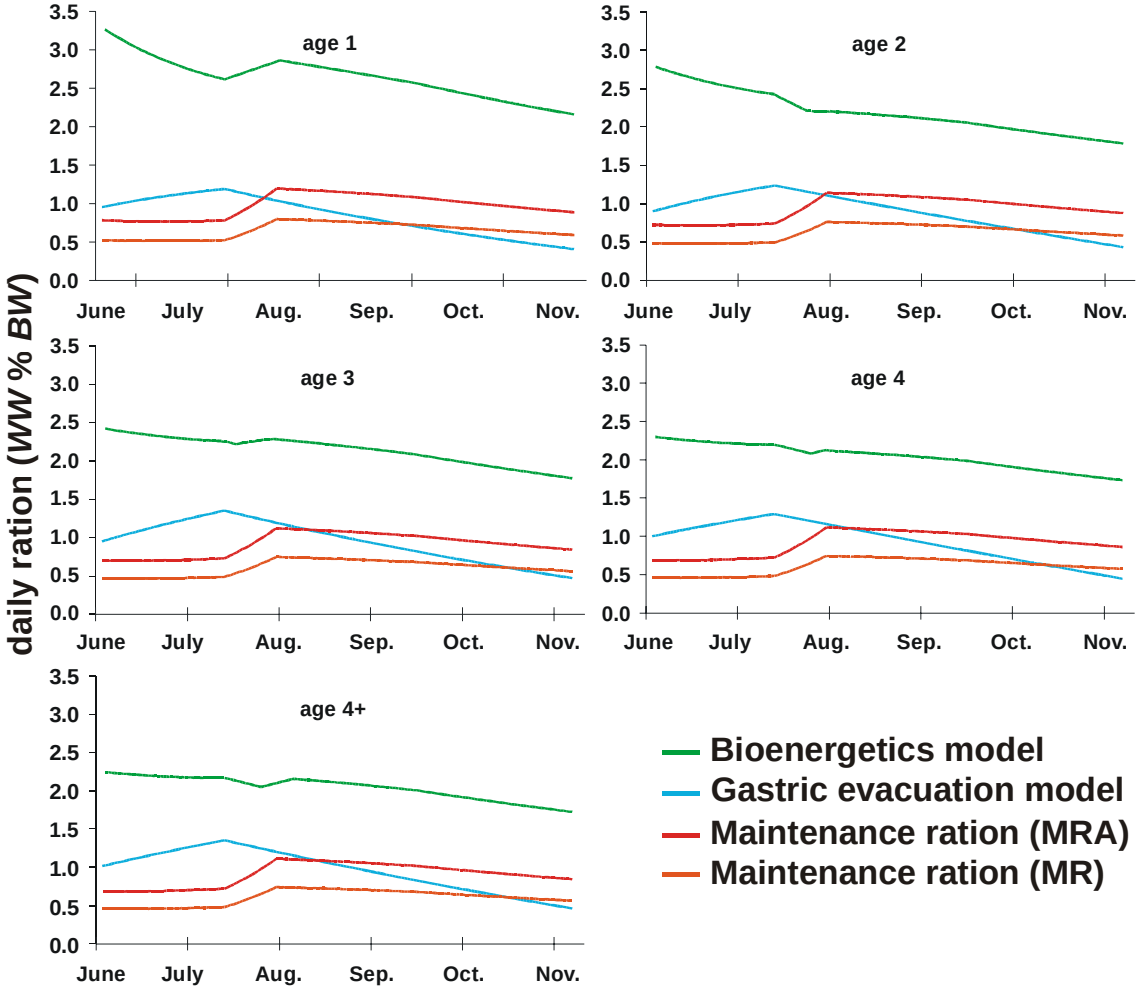

Figure 3) Mean daily ration (wet weight % body weight) per age class of sprat as estimated from a bioenergetic model and a gastric evacuation model. Additionally, the maintenance rations as calculated from respirometry are displayed. Maintenance ration MR was estimated from the standard metabolism, maintenance ration (MRA) was estimated from standard and active metabolism (MRA = 1.5 x MR).

The mean daily rations per length class and month of sprat as estimated from the gastric evacuation model varied within the seasonal cycle (figure 4). With the exception of 10 cm sprat the daily ration increased from ~ 0.6% *BW* in April 2002 to 1.0 - 1.3% *BW* in July 2002. In August 2002 the daily rations decreased and increased again in September (with the exception of 10 cm sprat). In January 2003 lowest daily rations were observed at ~ 0.1% *BW*. Daily rations in July 2003 were similar to rations in the previous year but lower in November 2002 compared to November 2003. The maintenance rations increased from April 2002 to September 2002 with highest rations of 0.9 to 1.1% *BW* in September. With the exception of 10 and 14 cm fish in April 2002 were daily rations in excess of maintenance rations from April to July and September 2002. In August 2002 daily rations were lower than maintenance rations in most length classes (exception 10 and 14 cm). During November of both years, February 2003 and partly March 2003 in most length classes, maintenance needs were higher than daily rations ingested.

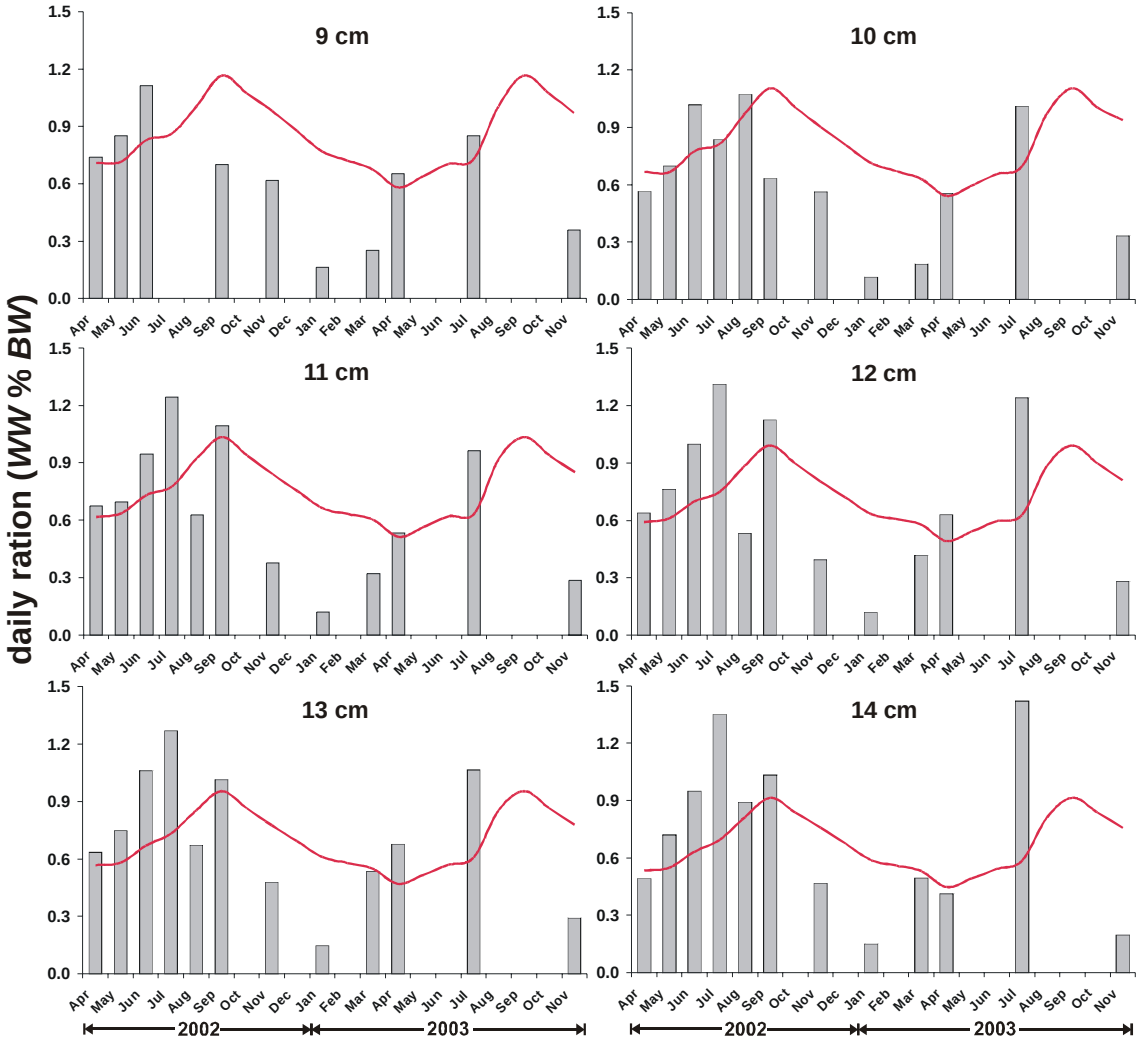

Figure 4) Mean daily ration (wet weight % body weight) per length class (cm) of sprat estimated from a gastric evacuation model (grey bars) and maintenance rations MRA (including activity, red line).

Herring

The mean daily ration per length class of herring varied with the seasonal cycle (figure 5). The daily ration increased from April 2002 to reach highest values in June and July. The highest daily rations in June (2.9% *BW*) were observed in length class 20/21 cm and lowest (< 1.4% *BW*) in length class 24/25 cm. The daily rations decreased towards autumn and winter with rations at or below 0.5% *BW*. In July and November 2003 higher daily rations of 1.0 to 2.2% *BW* were observed. The maintenance rations including activity (MRA) (*WW* % *BW*) increased from May 2002 to September 2002 to reach highest levels of 1.0 to 1.4% *BW* in September 2002, decreasing afterwards to lowest levels of ~ 0.2% *BW* in March and April 2003. The mean daily rations exceeded the maintenance needs of most length classes from April to August 2002, falling below in September and November 2002. However, the daily rations of length classes 20/21 cm to 24/25 cm were similar or exceeded maintenance rations in November. The daily rations during winter were more or less similar to maintenance rations MRA.

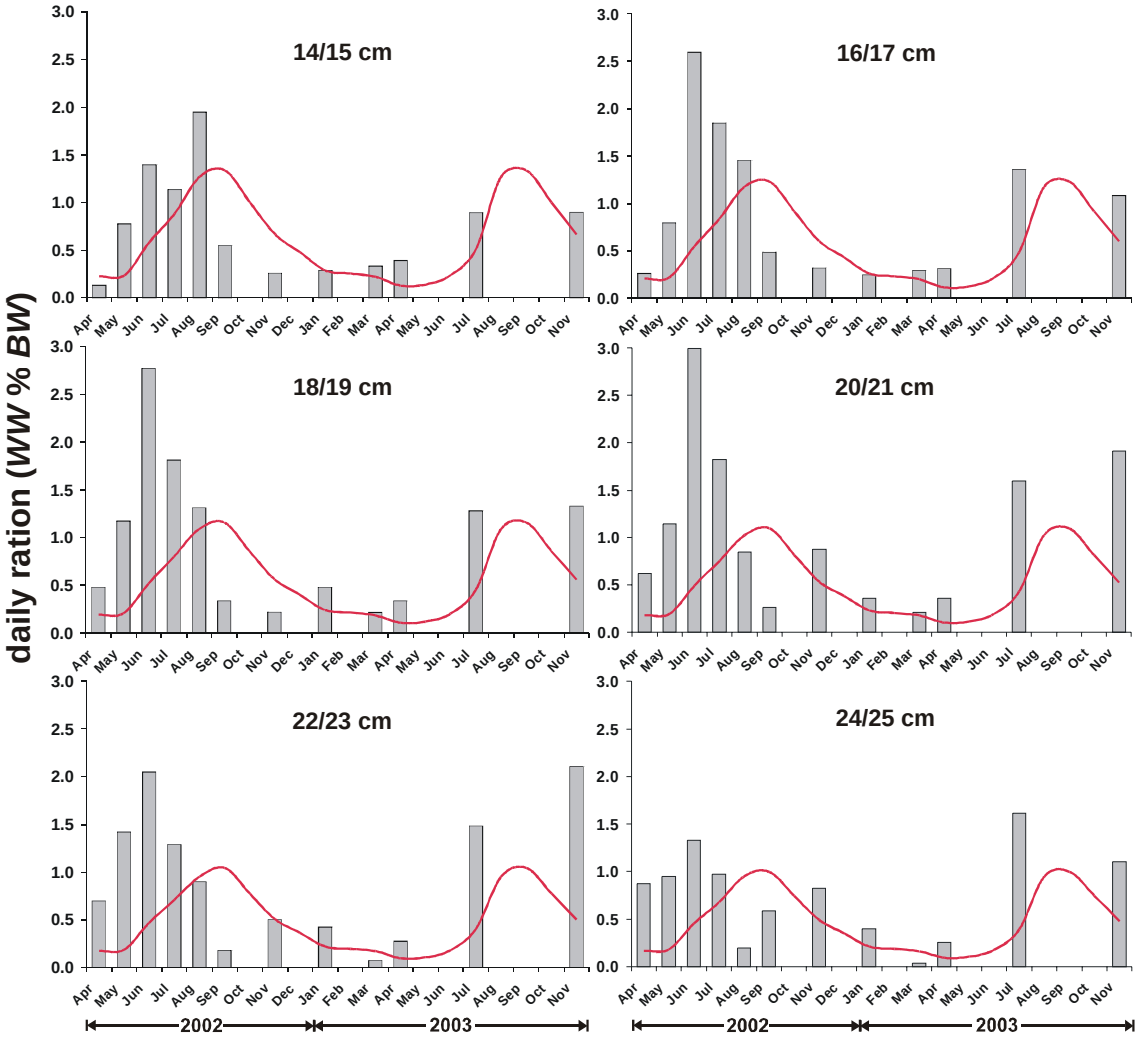

Figure 5) Mean daily ration (wet weight % body weight) per length class (cm) of herring estimated from a gastric evacuation model (grey bars). Maintenance rations MRA (red line) were calculated from energy losses in starvation experiments, adding an activity multiplier (x 1.5).

Discussion

Sprat

For the period from mid June to mid November 2002, the bioenergetics model consistently predicted higher (2 to 3.5 times) daily rations (*WW* % *BW*) than the gastric evacuation model. The discrepancy between the estimates can be explained by one or both of two reasons.
First, it is theoretically possible that one or both of the models provided erroneous estimates of daily rations. Both methods rely on a combination of field and laboratory data, so there are two independent sources of error for each approach. The results of the gastric evacuation model were based on field estimates of average stomach contents of sprat combined with laboratory experiments on the gastric evacuation in this species. Possible sources of error include: 1) incorrect estimates of field stomach contents, and 2) improper parameter estimates for the gastric evacuation model. Fishery hauls were conducted on several transects on each cruise and stomach weights

were estimated from three stomachs per length class and station. This sampling scheme may have lead to an underestimation of stomach contents, but previous studies in the same basin that used ten stomachs per station and length class yielded similar stomach contents (Köster & Möllmann 2000). We have also tested the effect of the sample size for one of the sampling periods and found no effect.

Principle doubts concerning the applicability of results from laboratory evacuation experiments were expressed by Richter et al. (2002), arguing that gastric evacuation rates measured during the non-feeding phase systematically underestimated rates in comparison to those measured during the feeding phase. This assertion was based upon food consumption experiments with milkfish *Chanos chanos* (Forsskål) and tilapia-hybrids *Oreochromis niloticus* (L.) x *O. aureus* (Steindachner) feeding on pellet food. An underestimation of the evacuation rate would lead to an underestimation of daily rations from consumption models based on gastric evacuation estimates. If this was true for sprat and herring that constantly fed during prolonged periods (during daylight hours), this would partly explain the lower estimates from the gastric evacuation model in comparison to the bioenergetic model. However, we could not confirm the findings of Richter et al. (2002) in a series of long-term laboratory feeding experiments with juvenile herring (Bernreuther et al. In Prep. b). Since herring and sprat are closely related clupeid species, we assumed that there was also no doubling or strong increase in the evacuation rate during feeding in either species and therefore assumed that our parameter estimates of the consumption model were robust.

Another question was whether the laboratory conditions during gastric evacuation experiments were comparable to the field situation for sprat (e.g., brine shrimp *Artemia* sp. nauplii versus copepods and cladocerans as food sources in the laboratory and field, respectively). The experimental food was not identical to field prey but was nearly optimal, since it was live zooplankton of a size that sprat and herring often consumed in the wild (Bernreuther et al. In Prep. c). All in all, we were the first to be able to describe the gastric evacuation of sprat feeding on brine shrimp (*Artemia* spp.) under controlled (low stress) laboratory conditions. Additionally, the evacuation rates of sprat estimated from laboratory experiments were similar to rates obtained from ship-board tank experiments (Köster 1994, Köster & Möllmann 2000) after correcting for differences in fish size.

The results of our bioenergetics model were based on field estimates of growth, combined with laboratory respirometry experiments on sprat. Possible sources of error include fish energy density that was estimated from 5 to 53 fish per age and month, and daily growth rate that was determined from linear interpolations between monthly measurements. For the estimation of daily rations by the bioenergetics model, metabolism parameters were needed for sprat. Laboratory respiration measurements were conducted, resulting in estimates of standard metabolism that were multiplied by 1.5 to account for increased activity of field fish. Generally, in herring and other coldwater fish species, the cost for activity is calculated by multiplying standard respiration rates with a swimming speed dependent function (Arrhenius 1995). Since only very few data on *in situ* swimming speeds of herring were available (Gibson & Ezzi 1985), no data on swimming speeds of sprat were available and the effect of temperature on swimming speed has not been examined for either herring or sprat, a more reliable activity multiplier can not be determined. Our activity multiplier was close to that (1.3), used by Rand et al. (1993), to represent swimming at approximately one body length per second for age-1 steelhead (*Oncorhynchus mykiss*).

Despite uncertainties concerning the activity multiplier, daily rations derived from standard + activity metabolism were more adequate than those based upon standard metabolism alone. Standard metabolism describes the energy needs of an unfed fish not expending energy for activity (even random activity), food digestion, reproductive

development, or growth. Standard metabolism, therefore, represents a state of reduced energy costs that likely occurs only very rarely for sprat in the field. To sum it up it can be said that the problem with possible errors in estimating the rations by the bioenergetics and the gastric evacuation model was rather low, leading to robust estimates of daily rations. The activity multiplier in estimation of the maintenance ration (MRA) was rather low, in comparison to the commonly used Winberg activity multiplier (x 2.0, Winberg 1956). The application of the Winberg activity multiplier would result in an even higher discrepancy between the results of the bioenergetics and the gastric evacuation models. Additionally, even the application of a lower activity multiplier would produce a discrepancy in the daily ration estimates of the two models. As a result, we conclude that the estimates of both models were robust and that there was another reason for the observed discrepancy.

The second reason for the observed discrepancy could be that both models were estimating correct daily rations, but that the results of these models need to be interpreted in different ways. The estimates of the gastric evacuation model were based on stomach contents of sprat caught in the Bornholm Basin. However, the bioenergetics model estimates were based on field growth rates for sprat that were caught in the Bornholm Basin but that had likely experienced different habitats during spawning and feeding migrations (Aro 1989, Stepputtis 2006). If both model estimates were reliable, the differences may be explained by field growth rates that were not coupled to feeding solely within the Bornholm Basin. Sprat migrate into the deep basins in early winter, move for spawning into shallower water layers of the deep basins in early summer and then migrate into areas closer to the coast (Stepputtis 2006). Hydroacoustic measurements on the distribution of sprat indicated that the majority of the sprat stock was migrating out of the Bornholm Basin after spawning in spring and early summer. Sprat were at their lowest levels of abundance in the basin from August to November 2002 (Stepputtis 2006). However, parts of the sprat population were always present in the Bornholm Basin. This part of the population was sampled for stomach contents. Sprat in the Bornholm Basin may have been facing unfavourable feeding conditions, which is indicated by the observation that sprat were not able to satisfy maintenance needs (as indicated by the maintenance rations MRA, figure 4) starting in late summer. This explains the high daily rations estimated from the bioenergetics model and low daily rations estimated from the gastric evacuation model. We conclude, therefore, that sprat were food limited during periods in the Bornholm Basin and that most of the energy required to fuel observed growth was ingested elsewhere, presumably in shallow regions closer to the coast. This assumption is supported by observations in other water bodies and a laboratory investigation on feeding intensity of sprat. Sirotenko & Sorokalit (1979) observed that adult Mediterranean sprat (*Sprattus sprattus phalericus*) exhibited highest mean stomach fullness of 2.8% *BW* in coastal areas of the Black Sea. Laboratory experiments quantified the rate of feeding by juvenile sprat (1.9 – 2.2 g *WW*) preying on *ad libitum* rations of brine shrimp (*Artemia* spp.) nauplii at different temperatures (unpublished data). At 9.5°C, a mean stomach fullness of 1.2% *BW* was reached after 1.5 h and highest mean stomach fullness was 3.6% *BW* after 4.5 h. At 16°C, a mean stomach fullness of 5.2% *BW* was already reached after 1.5 h. These results reveal the feeding potential of sprat. Unfortunately, results from diet studies in coastal areas of the Baltic are rare. Arrhenius (1998) observed in 24 h-fisheries a maximum mean stomach fullness of 0.7 to 1.7% *BW* in early juvenile sprat (0.2 – 3.0 g *WW*) in August and November. Smaller fish usually exhibit higher stomach fullness than adult fish. Nevertheless, the results of Arrhenius (1998) indicated the potential of coastal areas in the Baltic as favourable feeding areas for sprat, since highest observed mean stomach fullness of juvenile sprat was ~ 0.5% *BW* in the Bornholm Basin in the period from April 2002 to November 2003.

Herring

We estimated mean daily rations of herring in the Bornholm Basin according to the gastric evacuation method. For an evaluation of the estimated daily rations based on field stomach contents and laboratory measurements on gastric evacuation we calculated maintenance rations obtained from starvation experiments at different temperatures. Our results indicated that the daily rations of herring exceeded maintenance needs from April to July/August 2002. From August until the onset of winter, herring fed at rates that were less than or equal to maintenance levels. In general, the same possible sources of error existed for herring as were previously discussed for sprat. Due to the lack of data on the weight dependency of gastric evacuation in herring, we applied the same weight coefficient (C = 0.364) used in sprat. This weight coefficient was estimated in laboratory experiments and since sprat and herring are closely related species, we assumed this coefficient was appropriate. Maintenance rations were estimated from the results of laboratory starvation experiments. Starvation experiments measure the “fasting metabolic rate” (Jobling 1994), which is intermediate between standard and routine metabolism. The activity multiplier used for sprat (x 1.5 metabolic rate) was also used for herring, resulting in a slightly higher relative maintenance ration (MRA) compared to sprat. Additionally, we had to extrapolate the temperature dependency of the metabolic rate estimated from the laboratory experiments (9.7 to 14.2°C) to cover the slightly larger range in observed temperatures (6 - 16°C) in the Bornholm Basin. In the starvation laboratory experiments, we observed a high temperature effect between 9.7 and 14.2°C, followed by no further increase. We had to extrapolate the influence of temperature on the metabolic rate to e.g., lower temperatures. If the influence of temperature on metabolic rate was overestimated by our laboratory experiments between 9.7 and 14.2°C, this would have produced an underestimation of the maintenance ration at lower temperatures. If maintenance rations were actually higher, this would additionally downgrade the feeding situation for herring during certain periods. Nevertheless, despite these minor uncertainties concerning the weight dependency, the extrapolation of the temperature dependency and the maintenance ration, we regard our estimates as robust.

The migrations lead herring from coastal spawning grounds to feeding grounds in the deep basins in summer (Aro 1989). These migrations are regarded as feeding migrations, which may be questionable considering the low mean daily rations beginning in August. Nevertheless, peak herring abundance in the Bornholm Basin in 2002 was observed in August (Stepputtis 2006). Herring in length classes below 20 cm were able to feed in excess of their maintenance needs in August, whereas 20+ cm herring were not able to do so. After August, gastric evacuation model estimates indicated that herring rarely fed above maintenance levels. If they fed at rates above maintenance needs, the scope for growth or the replenishment of energy stores was still very low.
There are three possible explanations for this observation. The first is that herring were feeding intensely prior to their arrival in the Bornholm Basin. After spawning, herring may have spent several months intensively feeding in shallower areas of the Baltic prior to the arrival into the Bornholm Basin.
A second explanation is that the feeding migrations, which lead herring to the Bornholm Basin, may have been energetically profitable in the past, before the strong increase in the sprat stock in the 1990s. In several areas of the Baltic Sea, herring growth has been reported to be to some extent, dependent on *Pseudocalanus sp*. population size (Cardinale & Arrhenius 2000, Kornilovs et al. 2001, Möllmann et al. 2005, Casini et al. 2006), suggesting that the reduction in the size of the *Pseudocalanus sp*. population

may have reduced herring condition in the Central Baltic Sea (Möllmann et al. 2005). The large sprat stock would induce strong competition for food resources in the Bornholm Basin (Bernreuther et al. In Prep. d). Up to 60% of the food of sprat consisted of *Pseudocalanus acuspes* in the Bornholm Basin in May 2002, resulting in a strong predation pressure by sprat on this copepod species (Möllmann et al. In Prep.). As a consequence of the high sprat abundance in April and May 2002 (Stepputtis 2006) the abundance of *P. acuspes* may have declined in the Bornholm Basin resulting in unfavorable feeding conditions for the immigrating herring. Additionally, a strong predation pressure was exerted by the sprat stock on the *T. longicornis* stock in June and July 2002 (Möllmann et al. In Prep.). The result of this strong predation pressure may be that feeding in the Bornholm Basin was no longer energetically profitable for herring.
A third explanation is that herring fed on prey with a higher energy density (e.g., mysids, 23 kJ g *DW* $^{-1}$, unpublished data) during autumn and winter compared to spring and summer (e.g., copepods and cladocerans). The consequence would be rates of energy intake that were higher than those reflected in the stomach contents and daily rations estimated from data of the Bornholm Basin. However, mysids were only consumed in small amounts on single stations during autumn and winter (Bernreuther et al. In Prep. d) in the Bornholm Basin, and there was no significant correlation between the quantity of mysids in the diet of herring and the condition of these fish in the Central Baltic Sea, suggesting that mysids do not influence herring growth (Möllmann et al. 2005). We therefore suggest that feeding on mysids in autumn and winter 2002/2003 was unlikely or occurred outside of the region sampled.

Our results support the suggestion of Möllmann et al. (2005) and Casini et al. (2006) that herring condition may have declined due to the enhanced competition with sprat and the decline in *P. acuspes* stock abundance. This may have resulted in low stomach fullness in the Bornholm Basin in certain periods of the year, indicating that this basin was an unfavorable feeding area during part of the year. As was the case with sprat, mean values of stomach fullness of herring in other areas of the North-Atlantic highlight that the Bornholm Basin was not a favorable feeding area during certain periods. Atlantic herring exhibited a maximum stomach fullness of up to 4.0% *BW* (8 - 13.5 cm, *TL*) and 1.8% *BW* (16.5 - 20 cm, *TL*) in the Barents Sea (Huse & Toresen 1996) and up to 3.2% *BW* (27.7 - 35.3 cm, *TL*) in the Norwegian Sea (Prokopchuk & Sentyabov 2006). Unfortunately, feeding studies on herring from coastal areas of the Baltic are rare. In several 24 h-fisheries, Arrhenius & Hansson (1994) observed maximum mean stomach fullness of 0.8 to 2.2% *BW* in early juvenile herring (up to 8.2 cm, *TL*) a coastal area of the Northern Baltic Sea proper. Again, this gives an indication of the potential importance of coastal areas for the feeding of clupeids in the Baltic Sea. Laboratory feeding studies on juvenile herring (9.9 - 13.0 cm, *TL*, at 13°C, unpublished data) indicated that, after two, six, and ten hours of intensive feeding, herring contained stomach contents of 1.1% *BW*, 2.6% *BW* and 4.5% *BW*, respectively.

General conclusions

Apparently both herring and sprat were, to some extent, food limited in the Bornholm Basin in 2002/2003. In certain periods, mean daily rations at a given size/age of both species were not high enough to sufficiently satisfy maintenance needs. The conclusion of this study is that sprat and perhaps also herring may feed more intensively in other parts of the Baltic Sea, e.g. in coastal regions.

References

Aro, E. (1989). A review of fish migration patterns in the Baltic. Rapport Procès-verbaux des Rèunion du Conseil International pour l´Exploration de la Mer 190, 72-96.

Arrhenius, F. & Hansson, S. (1994). *In situ* food consumption by young-of-the-year Baltic Sea herring *Clupea harengus*: a test of predictions from a bioenergetics model. Marine Ecology Progress Series 110, 145-149.

Arrhenius, F. (1995). Feeding ecology of Baltic Sea herring (*Clupea harengus* L.) – field and model studies of a dominant zooplanktivore. Dissertation, Stockholm University. 103pp.

Arrhenius, F. (1998). Food intake and seasonal changes in energy content of young Baltic Sea sprat (*Sprattus sprattus* L.). ICES Journal of Marine Science 55, 319–324.

Bernreuther, M., Herrmann, J.-P., Peck, M.A. & Temming, A. (In Prep. a). Conversion efficiency and temperature dependency of metabolic rate in juvenile herring (*Clupea harengus* L.).

Bernreuther, M., Herrmann, & Temming, A. (In Prep. b). Laboratory experiments on the gastric evacuation of juvenile herring (Clupea harengus L.).

Bernreuther, M., Herrmann, J.-P. & Temming, A. (In Prep. c). The influence of temperature and body weight on the rate of gastric evacuation in sprat (*Sprattus sprattus* L.).

Bernreuther, M., Herrmann, J.-P., Möllmann, C. & Temming, A. (In Prep. d). Seasonal variation in the feeding of herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.) in the south-central Baltic Sea.

Brett, J.R. & Groves, T.D.D. (1979). Physiological energetics. In Hoar, W.S., Randall, D.J. & Brett, J.R. (eds.). Fish Physiology, Vol. 8, 279-352. Academic Press, NY.

Bromley, P.J. (1994). The role of gastric evacuation experiments in quantifying the feeding rates of predatory fish. Reviews in Fish Biology and Fisheries 4, 36-66.

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

Cardinale, M., Casini, M. & Arrhenius, F. (2002). The influence of biotic and abiotic factors on the growth of sprat (*Sprattus sprattus*) in the Baltic Sea. Aquatic Living Resources 15, 273–282.

Cardinale, M., Casini, M., Arrhenius, F. & Håkansson, N. (2003). Diel spatial distribution and feeding activity of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the Baltic Sea. Aquatic Living Resources 16, 283–292.

Casini, M., Cardinale, M. & Arrhenius, F. (2004). Feeding preferences of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the southern Baltic Sea. ICES Journal of Marine Science, 61: 1267–1277.

Casini, M., Cardinale, M. & Hjem, J. (2006). Inter-annual variation in herring, *Clupea harengus*, and sprat, *Sprattus sprattus*, condition in the central Baltic Sea: what gives the tune? Oikos 112, 638-650.

Flinkman, J., Aro, E., Vuorinen, I. & Viitasalo, M. (1998). Changes in northern Baltic zooplankton and herring nutrition from 1980s to 1990s: top-down and bottom-up process at work. Marine Ecology Progress Series 165, 127-136.

Huse, G. & Toresen, R. (1996). A comparative study of the feeding habits of herring (*Clupea harengus, Clupeidae,* L.) and capelin (*Mallotus villosus,* Osmeridae*,* Müller) in the Barents sea. Sarsia. 81, 143–153.

Jobling, M. (1994). Fish Bioenergetics. Chapman & Hall, London. 390 pp.

Kornilovs, G., Sidrevics, L. & Dippner, J.W. (2001). Fish and zooplankton interaction in the Central Baltic Sea. ICES Journal of Marine Science 58, 579-588.

Köster, F.W. (1994). Der Einfluß von Bruträubern auf die Sterblichkeit früher Jugendstadien des Dorsches (*Gadus morhua*) und der Sprotte (*Sprattus sprattus*) in der zentralen Ostsee (PhD-thesis). Christian-Albrechts-Universität, Kiel. 369 pp.

Köster, F.W. & Möllmann, C. (2000). Trophodynamic control by clupeid predators on recruitment success in Baltic cod? ICES Journal of Marine Science 57, 310-323.

Maes, J., Tackx, M. & Soetaert, K. (2005). The predation impact of juvenile herring *Clupea harengus* and sprat *Sprattus sprattus* on estuarine zooplankton. Hydrobiologia 540, 225-235.

Mauchline, J. (1998). The Biology of Calanoid Copepods. In: Advances in Marine Biology Vol.33. Academic press. 710 pp.

Möllmann, C. & Köster, F.W. (2002). Population dynamics of calanoid copepods and the implications of their predation by clupeid fish in the Central Baltic Sea. Journal of Plankton Research Vol. 24, No.10, 959-977.

Möllmann, C., Kornilovs, G., Fetter, M., Köster, F.W. & Hinrichsen, H.-H. (2003). The marine copepod, *Pseudocalanus elongatus*, as a mediator between climate variability and fisheries in the Central Baltic sea. Fisheries Oceanography 12, 360-368.

Möllmann, C., Kornilovs, G., Fetter, M. & Köster, F.W. (2005). Climate, zooplankton, and pelagic fish growth in the central Baltic Sea. ICES Journal of Marine Science 62, 1270-1280.

Möllmann, C., Temming, A., Stepputtis, D., Bernreuther, M. & Köster, F.W. (In Prep.). The role of habitat heterogeneity on the vulnerability of marine zooplankton to predation: implications for trophic cascades.

Prokopchuk, I. & Sentyabov, E. (2006). Diets of herring, mackerel, and blue whiting in the Norwegian Sea in relation to Calanus finmarchicus distribution and temperature conditions. ICES Journal of Marine Science 63, 117-127.

Rand, P.S., Stewart, D.J., Seelbach, P.W., Jones, M.L. & Wedge, L.R. (1993). Modeling steelhead population energetics in Lakes Michigan and Ontario. Transactions of the American Fisheries Society 122, 977-1001.

Richter, H., Lückstädt, C., Schlechtriem, C., Focken, U. & Becker, K. (2002). Do the fish stomach content models currently used for daily ration estimation really work? Evidence of violation of a basic assumption concerning stomach evacuation rates. Archive of Fishery and Marine Research 49 (3), 171-188.

Rudstam, L.G. (1988). Exploring the dynamics of herring consumption in the Baltic: Applications of an energetic model of fish growth. Kieler Meeresforschung Sonderheft 6, 312–322.

Sirotenko, M.D. & Sorokalit, L.K. (1979). Seasonal changes in the food of the Mediterranean sprat, *Sprattus sprattus phalericus*. Journal of Ichthyology Vol. 19, no. 5, 37-51.

Stepputtis, D. (2006). The distribution of Baltic sprat, *Sprattus sprattus* L. – causes and consequences. PhD-thesis at Mathematisch-Naturwissenschaftliche Fakultät der Christian-Albrechts-Universität Kiel, Germany. 148 pp.

Winberg, G.G. (1956). Rate of metabolism and food requirements of fishes. Journal of the Fisheries Research Board of Canada Translation Series 194 (1960), 202 pp.

General Conclusions

In both herring and sprat, a number of potential adaptations were investigated (e.g., gastric evacuation, feeding mode, diet composition and prey selectivity) that influence the rate and efficiency of exploitation of encountered zooplankton prey patches by these clupeid species in the field:

Gastric evacuation

My laboratory investigations determined that an exponential model was the most appropriate model to apply to describe gastric evacuation in these two major planktivores of the Baltic Sea (**manuscripts 4, 5**). This exponential evacuation along with the high storage capacity of the stomach (**manuscript 4**) enables herring and sprat to efficiently exploit patchy prey environments. The feeding experiments (**manuscript 4**) showed that herring was able to feed at high rates prior to obtaining maximum stomach fullness (4.5% body weight (*BW*)) after approximately 10 hours. In contrast to these laboratory studies, the highest values of mean stomach fullness in the Bornholm Basin were only 0.75% *BW* in June 2002. The high levels of stomach fullness in the laboratory resulted from an interaction between the storage capacity of the stomach and the exponential rate of gut evacuation. When feeding at a high rate, the stomach (cecum) was rapidly filled. However, as implied by an exponential evacuation, the amount of food evacuated per time unit was proportional to the amount of food present in the stomach and thus a high throughput of food was achieved even with a filled cecum. Additionally, my studies revealed a pronounced increase in the rate of gastric evacuation with increasing temperature in both herring (**manuscript 4**) and sprat (**manuscript 5**). Since high temperatures coincide with high secondary production in the Baltic Sea, this physiological mechanism allows these zooplanktivores to match their highest rates of food consumption with the timing of the summer peak in the production of their prey.
Another important aspect of my gastric evacuation studies was to test the hypothesis of Richter et al. (2002) which postulated that two different evacuation modes existed, one slow mode that occurs in non-feeding fish and a faster mode that occurs during feeding. This hypothesis was not supported by my experiments (**manuscript 4**). This is an important result since it confirmed a fundamental assumption of consumption models derived from gastric evacuation and field stomach contents, that stomach contents are evacuated at the same rate irrespective of whether or not herring or sprat are currently feeding.

Feeding mode, diet composition and prey selectivity

Herring are facultative filter-feeders and are able to apply different feeding modes: biting, gulping and filter-feeding (Gibson & Ezzi 1985, 1990, 1992; Batty et al. 1990), depending on prey concentration, prey size and light intensity. This enables herring to maximize the net rate of food consumption per unit time within a variety of different feeding situations. So far it was unknown whether sprat were able to filter-feed. However, the results of the field diet composition (**manuscript 1**) and the prey selectivity (**manuscript 2**) study indicated that sprat was strictly a size-selective feeder, leading to the conclusion that sprat, unlike herring was an obligate particulate-feeder. Additionally, we did not observe any filter-feeding in the laboratory, whether in regular feedings or in experiments with high food densities.
Using the results of our extensive field diet analyses I tried to identify situations in which herring were filter-feeding in the Bornholm Basin (**manuscript 1**). These, unselective

filter-feeding situations would be characterised by a relative high number of younger copepodite stages (i.e. c1-3) in the stomachs and possibly relatively high stomach fullness. However, we did not observe these situations in herring or sprat, indicating that plankton concentrations were too low in the Bornholm Basin to elicit a filter-feeding response in herring.

The diets of both herring and sprat were dominated by copepods and cladocerans (**manuscripts 1 and 2**) over the seasonal cycle. The most important copepods for both species were *Temora longicornis* and *Pseudocalanus acuspes*, resulting in a high diet overlap (niche overlap). In these copepods mainly adults (c6) and older copepodites (c4-5) were positively selected (**manuscript 2**). Additionally, herring were partly feeding on mysids in winter. As larger prey represent a higher energetic return per feeding action, it can be assumed that herring and sprat select mysids (mainly by herring), adult copepods and older copepodites to maximize the net rate of energy intake. Our 24 h-study, concerning the vertically-resolved prey selectivity of herring and sprat (**manuscript 2**), confirmed that both clupeids positively selected mainly adult *T. longicornis* during the day and cladocerans (*Evadne nordmanni*, *Podon* spp.) during the night and that they avoided younger copepodite stages during the major part of the investigated diel cycle. However, we were able to show that during certain periods of the diel cycle, younger copepodites (c1-3) were positively selected (**manuscript 2**). The results of this stage-specific gut content analysis revealed a very pronounced positive selection of adult stages. This implies that the estimations of predation impact on copepod populations without an explicit consideration of copepod stage will strongly underestimate the losses of reproductive females and other older, larger stages and, consequently, the potential impact of size selective predators on copepod populations.

Bioenergetics measurements in juvenile herring

Starvation experiments in which herring were deprived of food for several days to weeks (**manuscript 3**) provided robust estimates of metabolic demands (fasting metabolic rate ≈ standard metabolic rate) of schooling juveniles via rates of somatic energy loss at different temperatures. In my laboratory trials, herring were exposed to lower levels of stress compared to the commonly used technique of measuring energy losses via respirometry. In the latter, elevated levels of stress typically occur when groups of schooling fish are confined to small chambers. Despite the possibility of metabolic depression (i.e. reduced swimming activity) during starvation, this experimental approach was a better alternative than respirometry to gain estimates of the influence of temperature on the metabolic rate in sensitive species such as herring and sprat. A strong increase in metabolic rate was observed between 9.7 and 14.2°C (Q_{10} = 6.4, J $fish^{-1}$ day^{-1}) followed by no further temperature effect between 14.2 and 17.9°C.
The feeding-growth trial that used brine shrimp (*Artemia* spp.) nauplii as food for juvenile herring (**manuscript 3**) not only quantified the net growth efficiency (K_3, a measure of the conversion efficiency of food consumed in excess of maintenance requirements, Wootton 1998), but also provided an independent estimate of maintenance costs for juvenile herring. The data collected from the starvation and the feeding-growth trials, yielded similar estimates of maintenance costs indicating that both methods can be applied to study the metabolic needs of schooling clupeid fish species, in this case juvenile herring. This was confirmed by similar results from laboratory experiments made by other investigators (see discussion manuscript 3).
These bioenergetics measurements made on herring were especially important since bioenergetics models have relied upon data collected from a variety of other species including blueback herring (*Alosa aestivalis* Mitchill), alewife (*Alosa pseudoharengus*

Wilson) and Atlantic menhaden (*Brevoortia tyrannus* Latrobe). Clearly, obtaining better estimates of the rates of specific energy budget parameters for Atlantic herring will make modeled estimates of rates of food consumption (or growth) by field fish more robust. Furthermore, these estimates are needed to assess the potential for top-down control by this clupeid.

Top-down impact on the zooplankton

An *in situ* process-study on the role of habitat heterogeneity on the vulnerability of calanoid copepods to predation by planktivorous fish in the Bornholm Basin, where both zooplankton production and clupeid consumption was estimated, revealed strong predator effects (high predator consumption (C) versus prey production rate (P)) of the sprat population on *P. acuspes* in spring and *T. longicornis* in summer (**manuscript 6**). The study showed that the vulnerability of different copepod species to fish predation was, to a large degree, explainable by preferences for different temperatures and salinities, leading to differences in the vertical habitat overlap of predators and prey. The result of the predator effect was that the consumption of the sprat population frequently exceeded copepod production of *T. longicornis* during spring/summer.

Food limitation in the Bornholm Basin

The combination of the results of laboratory gastric evacuation experiments on herring and sprat and the field estimates of stomach contents revealed that herring and sprat were food limited in the Bornholm Basin in a number of months (**manuscript 7**). During these periods (starting in late summer 2002), herring and sprat could not feed in excess of their maintenance energy requirements determined from my (herring: manuscript 3) laboratory experiments (sprat: J.-P. Herrmann, unpublished data).
In sprat, mean daily rations from June through November 2002 were estimated from two approaches, a bioenergetic-based and a gastric evacuation-based method (**manuscript 7**). According to the bioenergetics model where daily rations were derived from observed field growth, sprat consumed daily food rations that exceeded those of the gastric evacuation-based method by a factor of two to three. The consumption estimates of the gastric evacuation model were based on stomach contents of sprat caught in the Bornholm Basin, whereas those of the bioenergetics model were based on field growth rates for sprat that were caught in the Bornholm Basin but that had likely experienced different habitats during spawning and feeding migrations (Aro 1989, Stepputtis 2006). Consequently, I assume that sprat was food-limited in the Bornholm Basin in some months. The discrepancy between gastric evacuation-and bioenergetics-based model results indicated that observed energy intake required to fuel somatic growth of sprat was accomplished by intensive feeding in areas outside of the basin, such as shallow, coastal regions. This may also hold true for herring.

The overall conclusion of this thesis was that the feeding ecology of both herring and sprat allows these species to efficiently exploit their feeding environment.
In spring and summer months both species, especially sprat, exerted a strong predation pressure on the zooplankton community (i.e. *P. acuspes* and *T. longicornis*) in the Bornholm Basin. However, during the majority of the time frame investigated in 2002 and 2003, this basin was a rather unfavourable feeding area for sprat and herring. This likely resulted from a strong increase in sprat stock size (Parmanne et al. 1994, Sparholt 1994, Köster et al. 2001), as a consequence of the released predation pressure on sprat and herring due to the decline of cod (*Gadus morhua* L.) stocks (Bagge et al. 1994, Köster et al. 2001), in combination with high reproductive success and low fishing

mortality in sprat. This unfavourable feeding situation presumably forced both species to feed more intensively in other regions, e.g. coastal regions, in order to gain the necessary energy for somatic as well as reproductive growth. This assumption concerning the feeding area of herring and sprat should be tested in future investigations with e.g., parallel sampling schemes in offshore areas such as the Bornholm Basin and within more shallow water, coastal locations.

References

Aro, E. (1989). A review of fish migration patterns in the Baltic. Rapport Procès-verbaux des Rèunion du Conseil International pour l´Exploration de la Mer 190, 72-96.

Bagge, O., Thurow, F., Steffensen, E. & Bay, J. (1994). The Baltic cod. Dana 10, 1–28.

Batty, R.S., Blaxter, J.H.S. & Richard, J.M. (1990). Light intensity and the feeding behaviour of herring, *Clupea harengus*. Marine Biology 107, 383-388.

Gibson, R.N. & Ezzi, I.A. (1985). Effect of particle concentration on filter- and particulate feeding in the herring *Clupea harengus*. Marine Biology 88, 109-116.

Gibson, R.N. & Ezzi, I.A. (1990). Relative importance of prey size and concentration in determining the feeding behaviour of the herring *Clupea harengus*. Marine Biology 107, 357-362.

Gibson, R.N. & Ezzi, I.A. (1992). The relative profitability of particulate- and filter-feeding in the herring, *Clupea harengus* L. Journal of Fish Biology 40, 577-590.

Köster, F.W., Hinrichsen, H.H., St.John, M., Schnack, D. MacKenzie, B.R., Tomkiewicz, J. & Plikshs, M. (2001). Developing Baltic cod recruitment models. II. Incorporation of environmental variability and species interaction. Canadian Journal of Fisheries and Aquatic Sciences 58, 1534-1556.

Parmanne, R., Rechlin, O. & Sjöstrand, B. (1994). Status and future of herring and sprat stocks in the Baltic sea. Dana Vol. 10, 29-59.

Richter, H., Lückstädt, C., Schlechtriem, C., Focken, U. & Becker, K. (2002). Do the fish stomach content models currently used for daily ration estimation really work? Evidence of violation of a basic assumption concerning stomach evacuation rates. Archive of Fishery and Marine Research 49 (3), 171-188.

Sparholt, H. (1994). Fish species interactions in the Baltic Sea. Dana 10, 131-162.

Stepputtis, D. (2006). The distribution of Baltic sprat, *Sprattus sprattus* L. – causes and consequences. PhD-thesis at Mathematisch-Naturwissenschaftliche Fakultät der Christian-Albrechts-Universität Kiel, Germany. 148 pp.

Wootton, R.J. (1998). Ecology of Teleost Fishes. 2nd edition. Dordrecht: Kluwer, 386 pp.

Individual scientific contributions to the multiple-author manuscripts

Seasonal variation in the feeding of herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.) in the south-central Baltic Sea.
All statistical analyses, the text writing and graphical presentation were conducted by Matthias Bernreuther under the supervision of Prof. Dr. Axel Temming, Jens-Peter Herrmann and Christian Möllmann. The stomach content analyses were performed by the sorting centre of the Latvian Fish Resources Agency (LATFRA) in Riga (Latvia).

Vertically resolved prey selectivity of Baltic herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.) in the Bornholm Basin.
Stomach content analyses of sprat were performed by Matthias Bernreuther, analyses of herring stomach contents were performed by the sorting centre of the Latvian Fish Resources Agency (LATFRA) in Riga (Latvia). Plankton samples were analysed by Jörn Schmidt at the Leibniz-Institute of Marine Science in Kiel, hydroacoustic measurements were conducted and analysed by Daniel Stepputtis from the Leibniz-Institute of Marine Science in Kiel. All analyses and text writing was conducted by Matthias Bernreuther under the supervision of Prof. Dr. Axel Temming and Jens-Peter Herrmann. The graphical presentation was mainly performed by Matthias Bernreuther, supported by Dr. Jörn Schmidt and Dr. Daniel Stepputtis.

Conversion efficiency and temperature dependency of metabolic rate in juvenile herring (*Clupea harengus* L.)
The starvation and conversion efficiency experiments, the text writing and graphical presentation were conducted by Matthias Bernreuther under the supervision of Prof. Dr. Axel Temming and Jens-Peter Herrmann. The measurements of the caloric density of the experimental fish were performed by Tatjana Reinke and Carmen Czerwinski.

Laboratory experiments on the gastric evacuation of juvenile herring (*Clupea harengus* L.).
All experiments, analyses, the text writing and graphical presentation were conducted by Matthias Bernreuther under the supervision of Prof. Dr. Axel Temming and Jens-Peter Herrmann.

The influence of temperature and body weight on the rate of gastric evacuation in sprat (*Sprattus sprattus* L.).
All experiments, analyses, the text writing and graphical presentation were conducted by Matthias Bernreuther under the supervision of Prof. Dr. Axel Temming and Jens-Peter Herrmann.

The role of habitat heterogeneity on the vulnerability of marine zooplankton to predation: implications for trophic cascades.
The statistical analyses, text writing and graphical presentation were conducted by Dr. Christian Möllmann in close cooperation with Matthias Bernreuther, Prof. Dr. Axel Temming, Dr. Daniel Stepputtis and Prof. Dr. Fritz Köster. All of the predation data required for calculations were provided by Matthias Bernreuther.

Consumption of herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.) in the Bornholm Basin: is there evidence of food limitation?

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