Diel Vertical Migration Patterns of Baltic Sea Copepods Analysed with a Video Plankton Recorder

Dissertation

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CONTENTS

SUMMARY

In this thesis, interspecies differences of Baltic Sea copepod diel vertical migration (DVM) are investigated with a special emphasis on drivers of these migration behaviours. Additionally, for the first time information on the spatial dimensions of Baltic Sea copepod patches are provided. Furthermore, implications of a patchy copepod distribution on feeding of clupeid fish like sprat (*Sprattus sprattus*) are elucidated. The investigations on copepod DVM and patch dimensions are based on analyses of Video Plankton Recorder (VPR) data. This unobtrusive underwater microscope system provides small- as well as large-scale information on plankton composition and hydrographic conditions. The unobtrusive nature of sampling makes the VPR the ideal gear to investigate plankton structures like copepod patches.

In the **1st chapter**: **Predator density triggered vertical migration of *Pseudocalanus acuspes* in the Baltic Sea**, VPR as well as hydroacoustic data were considered to verify the assumption that the halocline associated copepod *Pseudocalanus acuspes* shows a predator avoidance DVM in Bornholm Basin (BB), Baltic Sea. Previous findings on this topic were confirmed, by showing that ovigerous *P. acuspes* females stop their DVM during summer when feeding pressure of clupeids decreases due to low fish densities. Furthermore, evidence was provided for a possible ontogenetic migration of egg-sac carrying *P. acuspes* females into water layers above 50 m, regardless of prevailing feeding pressure or hydrographical conditions.

In the **2nd chapter: DVM patterns of thermocline associated copepods in different basins of the Baltic Sea**, VPR and hydroacoustic data delivered information on a distinct spatial overlap between copepod and clupeid depth distributions during the dawn and dusk phases of both groups' DVM. These overlaps occurred during a time of the day where clupeids exert a particularly high feeding pressure on copepods. This led to the conclusion that the thermocline associated part of the BB copepod community does not show a predator avoidance DVM, contrary to the halocline associated *P. acuspes*. Instead, an endogenous DVM driver seems more likely.

In the final and **3rd chapter: Investigating copepod patches and their implications on sprat (*Sprattus sprattus*) feeding in the Baltic Sea**, information on the spatial dimensions of Baltic Sea copepod patches are provided for the first time. This was achieved by analysing VPR data from horizontal VPR tows. Evidence was provided that copepod DVM plays a major role in the formation of patches, and that the downward migration of sprat in the morning hours is not solely driven by increasing light intensities, but also influenced by a patchy prey distribution. Moreover, it was shown that a patchy prey distribution leads to the high variability in sprat stomach content weights that is found in the field after the downward migration of these clupeids in the early morning hours.

ZUSAMMENFASSUNG

Die vorliegende Dissertation untersucht artspezifische Unterschiede der täglichen Vertikalwanderung von Copepoden in der Ostsee im Hinblick auf die verschiedenen Auslöser dieser Wanderung. Des Weiteren werden Untersuchungen zu der räumlichen Ausdehnung von Copepoden-Aggregaten (so genannten „patches“) in der Ostsee gezeigt sowie die Auswirkungen einer unregelmäßigen („patchy“) Copepodenverteilung auf das Fraßverhalten von Clupeiden wie der Sprotte (*Sprattus sprattus*) beleuchtet. Die Untersuchungen zur täglichen Vertikalwanderung der Copepoden und der räumlichen Ausdehnung von Copepoden-Aggregaten wurden in der vorliegenden Arbeit mit Hilfe eines Video Plankton Rekorders (VPR) durchgeführt. Dieses Unterwasser Mikroskop-System liefert klein- sowie großskalige Informationen über die Planktonzusammensetzung und die hydrographischen Bedingungen des untersuchten Wasserkörpers. Durch seine nicht-invasive Beprobung eignet sich der VPR besonders gut für Untersuchungen von Plankton Strukturen wie z.B. Copepoden-Aggregaten.

In **Kapitel 1: Räuberdichtegesteuerte Vertikalwanderung von *Pseudocalanus acuspes* in der Ostsee** wurden VPR- sowie hydroakustische Daten verwendet um die Annahme zu verifizieren, dass die Vertikalwanderung des im Bornholm Becken (BB) der Ostsee im Bereich der Halokline lebenden Copepoden *Pseudocalanus acuspes* eine Räubervermeidungsstrategie darstellt. Bisherige Ergebnisse zu dieser Thematik konnten dabei bestätigt werden. Es wurde aufgezeigt, dass eisacktragende *P. acuspes* Weibchen ihre tägliche Vertikalwanderung im Sommer einstellen wenn der Fraßdruck durch Clupeide aufgrund im BB sinkender Fischdichten abnimmt. Des Weiteren wurden Hinweise für eine mögliche ontogenetische Wanderung von eisacktragenden *P. acuspes* Weibchen hinein in Wasserschichten oberhalb von 50 m geliefert. Diese Wanderung wurde unabhängig von Fraßdruck oder hydrographischen Bedingungen beobachtet.

In **Kapitel 2: Vertikalwanderungsmuster von an der Thermokline lebenden Copepoden in den verschiedenen Becken der Ostsee** wurden VPR- und hydroakustische Daten genutzt um Informationen über die Tiefenverteilung von Copepoden und Clupeiden während der Dämmerungsphasen ihrer jeweiligen Vertikalwanderungen zu erlangen. Dabei wurden deutliche räumliche Überlappungen zwischen Räuber- und Beuteorganismen festgestellt. Diese Überlappungen traten zu einer Tageszeit auf, in der die Clupeiden einen besonders hohen

Fraßdruck auf Copepoden ausüben. Dies führte zu der Schlußfolgerung, dass der im Bereich der Thermokline lebende Teil der BB Copepodengemeinschaft im Gegensatz zu dem an der Halokline vorkommenden *P. acuspes* keine Räubervermeidungswanderung zeigt. Hier scheint vielmehr eine endogene Steuerung der täglichen Vertikalwanderung wahrscheinlich.

In **Kapitel 3: Untersuchung von Copepoden-Aggregaten und deren Auswirkungen auf das Fraßverhalten von Sprotten (*Sprattus sprattus*) in der Ostsee** wurden VPR-Daten aus horizontalen VPR-Hols genutzt um zum ersten Mal Informationen über die räumliche Ausdehnung von Copepoden-Aggregaten in der Ostsee zu präsentieren. Die Ergebnisse der vorliegenden Arbeit liefern Hinweise dafür, dass die tägliche Vertikalwanderung der Copepoden eine große Rolle bei der Bildung von Copepoden-Aggregaten spielt. Des Weiteren deuten die Ergebnisse daraufhin, dass die morgendliche Abwärtswanderung von Sprotten nicht ausschließlich von steigender Lichtintensität getrieben, sondern auch durch eine unregelmäßige Beuteverteilung beeinflusst wird. Abschließend wurde gezeigt, dass die hohe Variabilität der in den Morgenstunden nach der Abwärtswanderung der Clupeiden im Feld gefundenen Sprotten Mageninhaltsgewichte von einer unregelmäßigen Beuteverteilung herrührt.

GENERAL INTRODUCTION

This thesis deals with diel vertical migration (DVM) patterns of Baltic Sea copepods and the implications of these migration patterns on clupeid fish like sprat (*Sprattus sprattus*). Predator avoidance is widely acknowledged as the driver of copepod DVM, and this thesis is supposed to closer examine if this is true for different copepod species and habitats of the Baltic Sea. Furthermore, no information is available so far on the dimensions of copepod patches in the Baltic Sea. Increased knowledge about copepod migration drivers as well as copepod patches will greatly enhance our understanding of the Baltic Sea's ecosystem.

Below, the studied species are described, their behavioural characteristics as well as their habitats, and a detailed overview is given over the aim and the scope of this thesis.

THE BALTIC SEA

The Baltic Sea is an intra-continental shelf sea with an extension of 415 023 km^2 and a mean depth of 52 m (Wasmund & Uhlig 2003) located in Europe (figure 1). It is connected to the North Sea via Skagerrak and Kattegat (Møller & Hansen 1994) and represents the world's largest area of brackish water (Fonselius 1970). It shows a strong hydrographic stratification due to high input of freshwater—mainly through rivers—and water with high salinities from the North Sea (Storch & Omstedt 2008, Lindberg 2016). The deep basins of the Baltic Sea feature a permanent halocline at 50 to 75 m, as well as a thermocline in 20 to 30 m depth (Grønkjær & Wieland 1997), the latter being formed by rising temperatures in spring. These stratified conditions make the Baltic Sea, especially its deep basins, an interesting study area for vertical migration patterns of planktonic organisms. In non-stratified waters, planktonic organisms are trapped in currents and turbulences, which will drift them apart. The deep basins of the Baltic Sea are provided with water high in salinity as well as oxygen only through major inflow events from the North Sea (Naumann et al. 2016). After such an inflow event, the halocline is shifted upward due to high saline water that fills the basins from the bottom up. Also, higher oxygen levels occur not only at the bottom of the basins but higher up in the water column. Over time, salinity and oxygen levels decrease again during a stagnation period—which is the time period between two major inflow events.

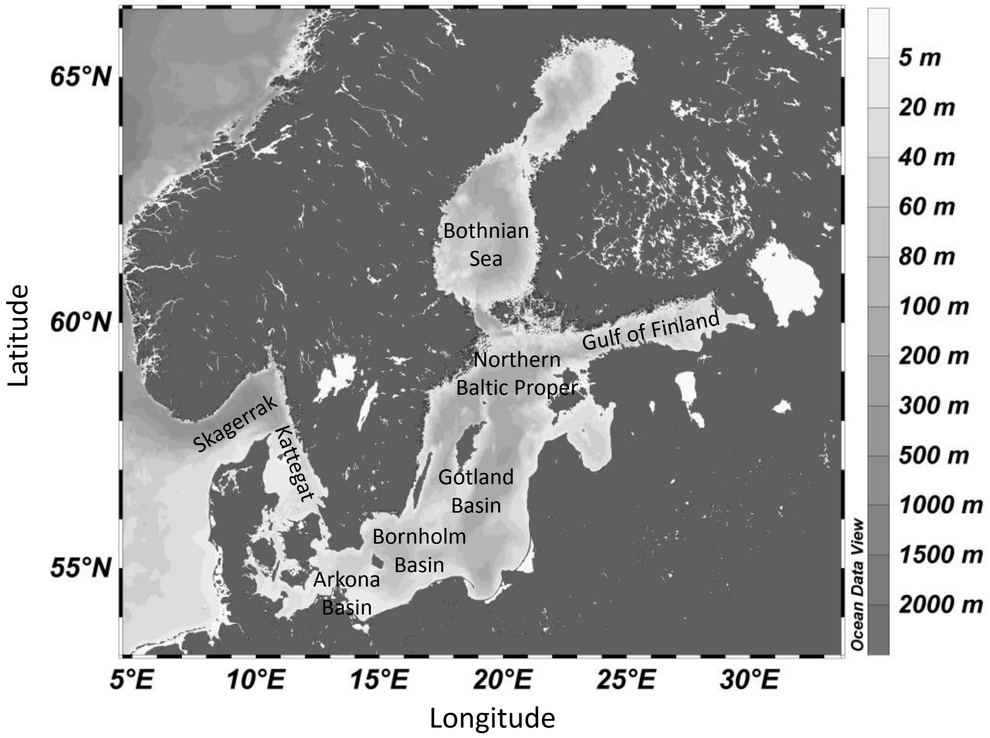

Figure 1. The Baltic Sea with its main basins and its connection to the North Sea. Colour bar on the right shows water depth.

Compared to open oceans, the Baltic Sea has a low species diversity. Reasons for this lie in the brackish water which poses a difficult habitat for a lot of aquatic species, as well as the geologically young age of the Baltic Sea and the fact that it once was a freshwater lake (HELCOM 2009). The most important heterotrophic species of the Baltic Sea are the top predator cod (*Gadus morhua*) (Casini et al. 2012), the planktivorous fish sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) (Rudstam et al. 1994), as well as four main copepod species: *Pseudocalanus acuspes*, *Temora longicornis*, *Acartia bifilosa* and *Acartia longiremis* (Möllmann et al. 2000, Hansen et al. 2006, Renz & Hirche 2006, Schmidt 2006). Since these copepods are the major prey organisms for the commercially important fish stocks of cod, sprat and herring, they represent an important link between lower and higher trophic levels of the Baltic Sea ecosystem (Arrhenius & Hansson 1993, Zuzarte et al. 1996, Möllmann & Köster 1999, Hinrichsen et al. 2002, Möllmann et al. 2003a, Voss et al. 2003, Casini et al. 2004, Bernreuther et al. 2013, Solberg & Kaartvedt 2017). Due to this important linkage, as well as the importance of *P. acuspes*, *T. longicornis* and *Acartia* spp. DVM in terms of nutrient and carbon transport (see below), the focus of this thesis is on these copepod species.

COPEPODS IN THE BALTIC SEA

In this thesis, DVM patterns and drivers of the four main copepod species of the Baltic Sea are examined. All of these species are calanoid copepods. Most species of this order of copepods are part of the pelagic plankton, and they play an important role in marine foodwebs because many of these species are herbivorous. Thereby, they build a direct link from phytoplankton to the higher trophic levels of fish (Mauchline 1998). Calanoid copepod species are small, with a body length of approximately 0.5 to 2.0 mm (Mauchline 1998). Their development (figure 2) happens in most of the species through a nauplius hatching from an egg, moulting five times until reaching nauplius stage six (NI-NVI), and from there moulting into the first copepodid stage. After five subsequent moultings (CI-CVI), the sixth copepodid or adult stage is reached (Mauchline 1998). Calanoid copepods are present in all areas of the oceans, and extend from saline to brackish and also freshwater habitats (Mauchline 1998).

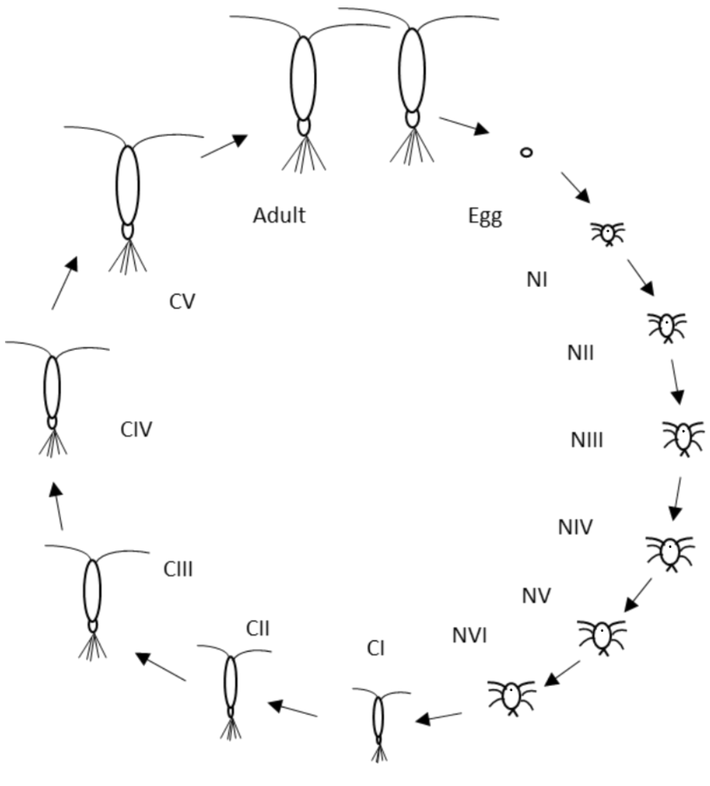

Figure 2. Schematic representation of a copepod life cycle.

As mentioned above, this thesis focuses on *P. acuspes*, *T. longicornis*, *A. bifilosa* and *A. longiremis*. These species inhabit different habitats within the water column of the Baltic Sea. *T. longicornis* is associated with the upper, less saline part of the water column and shows distinct diel vertical migration (DVM) behaviour around the thermocline (Hernroth & Ackefors 1979, Hansson et al. 1990). This species has only limited abilities to store energy, which leads to the need of constant food supply (Gentsch et al. 2009). Therefore, when phytoplankton stocks decrease in winter, *T. longicornis* is able to switch from herbivorous to omnivorous feeding until phytoplankton stocks increase again in spring (Gentsch et al. 2009). *T. longicornis* is a free-spawning species and able to produce resting eggs in the Baltic Sea (Mauchline 1998). According to Ban (1992) it is determined by the environmental conditions as well as the population density that adult copepods experienced as nauplii if they produce resting eggs.

Since the distinction of individual *Acartia* species is very difficult (Jensen 2010), organisms of this genus are referred to in this thesis as *Acartia* spp. Individuals of *Acartia* spp. are widespread over the Baltic proper and do also inhabit the upper, less saline 50 m of the water column (Hernroth & Ackefors 1979). *A. bifilosa* is thereby described to mainly occur in water layers down to 25 m, whereas *A. longiremis* is more common in layers from 25–50 m (Hernroth & Ackefors 1979). In addition, *A. longiremis* is described as psychrophilic (Mudrak & Żmijewska 2007) and as a species that avoids warm surface water layers from July–October (Hernroth & Ackefors 1979). DVM of *Acartia* spp. is described as less pronounced than that of *T. longicornis* (Hansson et al. 1990, Holliland et al. 2012). *Acartia* spp. is an omnivorous, free-spawning copepod, and at least *A. bifilosa* is known to produce resting eggs in the Baltic Sea (Viitasalo 1992, Mauchline 1998, Norrbin 2001). Resting eggs can be quiescent or diapausing (Grice & Marcus 1981). Quiescent eggs are ready-to-hatch eggs that become quiescent due to unfavourable hatching/development conditions and interrupt their development until conditions are favourable again (Grice & Marcus 1981, Katajisto 2003). Immediately after favourable conditions occur, development resumes (Grice & Marcus 1981). In contrast to that, production of diapause eggs is genetically controlled (Grice & Marcus 1981, Katajisto 2003) and those eggs are not ready-to-hatch but have to undergo a refractory phase that can last several months (Marcus 1996). During this phase, hatching cannot occur, even if environmental conditions are favourable (Grice & Marcus 1981). After this refractory phase the eggs hatch as soon as conditions become favourable again (Grice & Marcus 1981, Marcus 1996).

Together with *T. longicornis*, *P. acuspes* is the most important species in the Baltic proper (Hernroth & Ackefors 1979). In contrast to *T. longicornis* and *Acartia* spp., it is found from 50 m on downward in halocline associated layers with high salinities (Hernroth & Ackefors 1979). *P. acuspes* feeds on marine snow/detritus that accumulates at the halocline (Schmidt 2006, Renz et al. 2007, Möller et al. 2012), and depends on high salinities to ensure succesfull development, maturation and reproduction. Low salinities can cause osmotic stress and thereby lead to high energy requirements that can result in developmental failures as well as lower egg production (Möllmann et al. 2003b). *P. acuspes* shows distinct DVM behaviour into water layers below the halocline during the day (Möller 2013). Although *Pseudocalanus* spp. is described as a common herbivore (Mauchline 1998) or at least as feeding mainly herbivorous (Cotonnec et al. 2001), there are also reports of omnivorous feeding behaviour (Norrbin et al. 1990). In contrast to *T. longicornis* and *Acartia* spp., *P. acuspes* is not a free-spawning species, but carries its eggs in an egg-sac (Mauchline 1998).

Free spawning in copepods is believed to be an evolutionary adaptation to living in a pelagic environment, where visual predators like fish selectively put more predation pressure on egg-sac carrying female copepods than on individuals without an egg-sac (Webb & Weaver 1988). Thereby, free-spawning seems to be a trait-off between reducing the risk of losing ovigerous females to predation due to their higher susceptibility and enhancing the risk of losing eggs due to predation within the water column (Webb & Weaver 1988). Since free-spawning and egg-sac carrying copepods show the same maximum net reproductive and population growth rates, both reproduction strategies seem to be effective in their own ways (Kiørboe & Sabatini 1994).

COPEPOD DIEL VERTICAL MIGRATION

DVM is known from freshwater (Zaret & Suffern 1976) as well as marine (Ohman 1990) environments and throughout different geographic regions with different physical conditions. It can range from a few (Hutchinson 1967) to several hundred meters (Heywood 1996), and occurs in many different taxa—e.g. in zooplankton such as copepods (Holliland et al. 2012) or krill (Tarling 2003) and in fish such as clupeids (Cardinale et al. 2003) or basking sharks (Sims et al. 2005). There are two types of this migration behaviour. First, the “normal” or “nocturnal” DVM, with an ascent to the surface at dusk into layers with sufficient food and a descent at dawn into deep waters which provide shelter from visual predators (Bollens & Frost 1989) during the day. Second, the “reversed” DVM, with an ascent to the surface at dawn, and a descent at dusk towards deeper layers where the organisms spend the night (Hutchinson 1967, Lampert 1989, Frost & Bollens 1992, Hay et al. 2001, Sims et al. 2005). The Baltic copepods investigated in this thesis show a normal DVM.

DVM in copepods can be triggered by different cues and a combination of those cues, such as environmental factors like light and temperature, the availability of food and the presence of visual and non-visual predators (Mauchline 1998, Steele & Henderson 1998). Incident light e.g. has an effect on the visibility of copepods to visual predators, which can persuade copepods to migrate into deeper and darker water layers during the day. Different temperatures experienced by copepods while feeding in warm, food rich layers above the thermocline and resting in colder layers below the thermocline effect the metabolic rates of copepods and can result in changing bioenergetics (McLaren 1963). DVM of copepods and zooplankton in general has an important function in marine ecosystems. It contributes to the downward as well as the upward transport of nutrients through the water column and greatly to the "biological pump" (Bollens et al. 2011). The biological pump transfers carbon dioxide and inorganic nutrients in form of plant photosynthesis derived particulate organic matter from the euphotic zone to deeper layers of the ocean (Steinberg et al. 2002). Furthermore, it plays a fundamental role in regulating ocean carbon storage (Bollens et al. 2011).

PLANKTIVOROUS FISH IN THE BALTIC SEA

In the Baltic Sea, the clupeids sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) are the main planktivores feeding on copepods (Arrhenius & Hansson 1993). Together with cod (*Gadus morhua*), they also represent the most abundant fish species in the Baltic Sea (Ojaveer et al. 2010) with total landings of sprat and herring of 489 kt in 2017 (ICES 2018). They do also belong to the most important commercial fish species of the Baltic Sea (Arrhenius & Hansson 1993). Clupeids, as well as copepods, show DVM in the Baltic Sea. They descend to deeper water layers at dawn, stay there during day, ascend to surface layers at dusk and spend the night in surface waters (Orlowski 2001, Cardinale et al. 2003, Nilsson et al. 2003). Changing light conditions during the day are stated as one of the main trigger for DVM in fish, with increasing light intensities causing the downward migration and decreasing intensities causing the upward migration (Mehner 2012). On the one hand, light conditions affect the detection and resulting feeding rates of visual predators like clupeids (Eggers 1978) and on the other hand they affect the probability of clupeids falling prey to predators themselves (Mehner 2012). Temperature also seems to trigger DVM (Mehner 2012). Fish may save energy by spending the day in colder water layers, resulting in low metabolic rates, and migrating into warmer layers for feeding on zooplankton aggregated in these layers (Brett 1971). The warmer temperatures of these surface layers are also suggested to enhance digestion and thereby allow more feeding and faster growing of fish (Wurtsbaugh & Neverman 1988). For a long time it was assumed that clupeids feed mainly in deeper water layers during the day (Köster & Schnack 1994, Orlowski 2000, Nilsson et al. 2003, Stepputtis 2006), but lately Kulke et al. (2018) showed that sprat consume up to 84% of their daily ration in the upper water layers during dawn and dusk when migrating into and out of the deeper layers.

PLANKTON PATCHINESS

Planktonic organisms in the marine environment are not distributed homogeneously. Instead, they aggregate and form patches (Folt & Burns 1999). Estimates of the abundance of these planktonic organisms is traditionally based on plankton net samples like e.g. bongo nets. However, already in 1968 Wiebe & Holland (1968) described that sizes and distribution of plankton patches cause a sampling bias and significantly affect the accuracy of zooplankton abundance estimates derived by net samples. Until this day, data on patch dimensions is still scarce. Favero et al. (2015) e.g. suggest further studies on patch dimensions and the effect of sizes on multiple plankton net tows. The authors ask if it is possible that one net moves through a patch while the other does not, or that one net moves through a denser part of the patch while the other does not. It is important to gather more information on zooplankton patchiness and patch dimensions to increase the accuracy of zooplankton abundance and population estimates as well as the knowledge about effects of patchy zooplankton distributions on the whole food web (Omori & Hamner 1982). Moreover, additional information would enhance e.g. the confidence with which ecological changes can be detected (Klais et al. 2016). Since information on prey distribution is important for the assessment of fish feeding, growth as well as survival, further knowledge on patches would also enhance foraging models for larval fish (Lough & Broughton 2007).

VIDEO PLANKTON RECORDER

The Video Plankton Recorder (VPR) system is a unique gear and provides information on the interactions between biology and physics on small scales by combining sampled images of organisms from the water column with information about their specific hydrographic micro environment (Gallager et al. 2004). It hence provides higher resolution information on copepod DVM patterns than the large-scale data derived from traditional net sampling. The VPR is able to record images of plankton particles in the water column, and these images can be analysed with Visual Plankton, a Matlab application written by scientists of the Woods Hole Oceanographic Institution (Davis et al. 2005; following methods of Hu & Davis 2006). Visual Plankton is able to automatically sort the recorded images into categories of different plankton taxa. Thus, the VPR system can save an immense amount of time for sample analyses compared to traditional plankton samples—even when it is necessary to manually check the results afterwards (Benfield et al. 2007). An unobtrusive system like the VPR (Davis et al. 1992) is the ideal gear for investigating zooplankton migration behaviours and structures like copepod patches. Traditional plankton nets are not suited for patch investigations, since they are prone to problems like mesh clogging and active avoidance of the sample organisms (Yentsch & Duxbury 1956, Zhou et al. 1994). Additionally, the horizontal minimum patch scale one can detect with a plankton net equals the net tow length (Greer et al. 2016), which can lead to the loss of small-scale patch information. Besides these important advantages, only few disadvantages of the VPR system have to be considered. When the VPR is deployed off the stern of the vessel, sampling at the surface happens to be in the wake, where small-scale plankton distributions are destroyed (Davis et al. 2005). Furthermore, the VPR provides size information about organisms found within the water column only in a coarse taxonomic resolution (Davis et al. 2005) and not down to species level (Davis et al. 2004). Nevertheless, small-scale DVM behaviour like the one found in *P. acuspes* could have most likely not been detected with traditional plankton nets, and because females of this species carry one egg-sac, they are still easy to identify on digital VPR images.

AIM OF THE THESIS

The aim of this thesis was to examine the interspecies differences in the trigger of Baltic Sea copepod DVM as well as the implications of this DVM on feeding of planktivorous fish. Therefore, the focus is on the main Baltic Sea copepod species *T. longicornis*, *Acartia* spp. and *P. acuspes* from two different habitats (thermo- and halocline associated). Furthermore, this thesis aimed to test the overarching hypothesis that *in situ* systems like the VPR provide more efficient plankton sampling than traditional plankton nets. The amount of time for analyzing samples is assumed to greatly be reduced through the use of a VPR and the computer based identification of organisms (Benfield et al. 2007). Furthermore, the plankton abundances estimated by the VPR are assumed to be equivalent or even better than those derived from plankton nets (Davis et al. 2005). To test these assumptions, different VPR sampling strategies were applied and the VPR derived copepod abundance estimates were compared to multinet data. Moreover, the computer based sorting results of VPR images showing copepods were checked manually.

Three additional hypotheses were addressed in the individual chapters of this thesis. In **chapter I**, the central hypothesis was that DVM of the halocline associated copepod *P. acuspes* is a predator avoidance mechanism. No or no distinct DVM behaviour was reported for Baltic *P. acuspes* (Hansson et al. 1990, Hansen et al. 2006, Renz & Hirche 2006, Schmidt 2006), until the first evidence for a distinct migration behaviour was delivered by Möller (2013). Möller's study provided evidence that egg-sac carrying *P. acuspes* females from Bornholm Basin show a predator avoidance DVM during the day towards deeper water layers beneath the halocline. According to Möller (2013), this DVM seems to be induced by clupeid fish like sprat, which migrate from surface waters towards the halocline and spend most of the daylight hours in these deep layers. To cross check the assumption of a predator avoidance DVM, VPR derived *P. acuspes* data from low and high clupeid fish density situations as well as different hydrographical conditions were compared in this study and analysed in respect to DVM differences.

The aim of **chapter II** was to investigate the trigger of DVM in thermocline associated copepods. The central hypothesis was that species-specific factors drive DVM in copepods from halo- and thermocline associated habitats. Predator avoidance is widely assumed to trigger copepod DVM (Zaret & Suffern 1976, Lampert 1989, Ringelberg 1995). Nevertheless, the spatial overlap of thermocline associated copepods and their clupeid predators during down- and upward migration of both groups raises doubts in this regard (Schmidt 2006, Cardinale et al. 2003). Especially since Kulke et al. (2018) most recently showed that clupeids and especially sprat exert a particularly high feeding pressure on zooplankton during these migration phases, consuming up to 84% of their daily ration. To examine if DVM of thermocline associated copepods—like the one in halocline associated *P. acuspes*—is driven by predators, the relations between VPR derived copepod and hydroacoustic derived clupeid DVM data were investigated. In addition, the role of other copepod predators like jellyfish and mysids was discussed.

The central hypothesis of **chapter III** was that copepod DVM is associated with the formation of copepod patches and that this patchy prey distribution impacts the feeding behaviour of planktivorous fish like sprat. It is long known that zooplankton in the oceans is not distributed homogeneously but rather occurs in non-random aggregations. These aggregations are referred to as patches, and can range in size from several centimetres to kilometres (Haury et al. 1978, Owen 1989, Davis et al. 1992, Pinel-Alloul 1995). Zooplankton patches are assumingly formed by a combination of physical and biological processes (Mackas et al. 1985, Pinel-Alloul 1995), with DVM being named as the most powerful biological driver (Folt & Burns 1999). Knowledge about patch dimensions can help to improve zooplankton abundance and population size estimates. However, up to now no information is available on the scale of copepod patches in the Baltic Sea. Although there is a distinct spatial overlap between clupeids and their copepod prey during down- and upward migration, copepods seem not to be top-down controlled in the Baltic Sea (Bernreuther et al. 2018). A possible explanation for the underutilization of copepods by sprat might be the patchy distribution of copepods, since patchiness is described as an effective protection mechanism of prey organisms against predation (Omori & Hamner 1982, Pijanowska & Kowalczewski 1997, Folt & Burns 1999). Thus, zooplankton patches are assumed to influence predator-prey interactions (Lasker 1975, Davis et al. 1992). To investigate the dimensions of copepod patches, the influence of copepod DVM on patch formation as well as the influence of copepod patches on feeding behaviour of sprat, VPR derived copepod data were analysed in this study. Thus, measurements of copepod patches from three different basins of the Baltic Sea (Arkona, Bornholm and Gotland Basin) were estimated. Furthermore, VPR derived copepod abundances were utilized in a temperature- and size-dependent functional response model to predict sprat stomach content weights. Hereby, the implications of a patchy copepod distribution on the feeding behaviour of sprat were examined.

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Chapter I

Predator density triggered vertical migration of *Pseudocalanus acuspes* in the Baltic Sea

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ABSTRACT

This study provides a cross check situation to the findings of Möller (2013), who was the first to deliver evidence for a predator avoidance diel vertical migration (DVM) of Baltic *Pseudocalanus acuspes*. In Bornholm Basin (BB, central Baltic Sea), *P. acuspes* occurs in water layers around the halocline. In these depths, layers of marine snow and detritus provide sufficient food, and high salinities provide favourable reproduction conditions for *P. ascuspes*. During daytime, planktivorous fish (clupeids) migrate from surface waters towards the halocline, where they spend most of the daylight hours. To avoid this predation risk, the *P. acuspes* population shows DVM behaviour, wherein the individuals leave their favourable habitat and migrate towards deeper waters during the day. This study compares Video Plankton Recorder (VPR) derived data on *P. acuspes* DVM behaviour from low (2012 & 2015) and high (2002 & 2009—studied in Möller 2013) clupeid fish density situations with different hydrographical conditions (stagnation periods & post inflow situation). We can confirm the findings of Möller (2013)—predation seems to induce DVM behaviour in ovigerous *P. acuspes* females in BB. Our results show that this DVM behaviour cannot be observed in the presence of low clupeid fish densities. In addition, no indication was found that the respective hydrographical situation was influencing DVM behaviour of *P. acuspes*, although the overlap of clupeid and *P. acuspes* habitats changes with the prevalent hydrographical conditions. We further provide evidence for the occurrence of a certain share of the ovigerous *P. acuspes* female population in water layers above 50 m, regardless of the feeding pressure strength or hydrographical conditions. We consider it possible, that this behaviour might be a part of the ontogenetic migration of *P. acuspes*, in which the ovigerous females migrate half way towards the surface to release their offspring.

INTRODUCTION

The central Baltic Sea's ecosystem features a few important faunal species. In regard to fish species, these are cod (*Gadus morhua*), the top predator (Casini et al. 2012) as well as sprat (*Sprattus sprattus*) and herring (*Clupea harengus*), which are dominating the group of planktivorous fish (Rudstam et al. 1994). The main zooplankton species are *Pseudocalanus elongatus* (nowadays determined as *Pseudocalanus acuspes*—Renz 2006), *Temora longicornis* and *Acartia* spp. (Möllmann et al. 2000). Thus, members of the genus *Pseudocalanus* play an important role in the ecosystem of the Baltic Sea (Möllmann et al. 2003a, Peters et al. 2006, Renz & Hirche 2006). By being the major prey organisms for adult and larval clupeids as well as larval cod, they represent an important link between lower trophic levels and these commercially harvested fish (Zuzarte et al. 1996, Möllmann & Köster 1999, Hinrichsen et al. 2002, Möllmann et al. 2003a, Voss et al. 2003). Hence, the Baltic zooplankton community is often described as top-down controlled (Rudstam et al. 1994, Bernreuther et al. 2013). However, there are also studies, which do not find evidence for such a control on copepods (Möllmann & Köster 1999, Bernreuther et al. 2018) or even suggest that a bottom-up regulation of planktivorous fish through the zooplankton community might be possible (Flinkman et al. 1998). Likewise, the results of Möller (2013) and our study contribute relevant new information on a counter strategy allowing *P. acuspes* to defy feeding pressure by clupeid predators through diel vertical migration (DVM). DVM in zooplankton seems to be induced by different biological and physical factors or a combination of those (Zaren & Suffert 1976, Ringelberg 1995), one of them being predation. According to the predator-avoidance hypothesis, which was experimentally verified for the first time by Zaret & Suffern (1976), DVM behaviour provides shelter for prey organisms from visual predators, and its intensity should vary with the amount of predator abundance (Zaret & Suffern 1976, Lampert 1989). DVM patterns in the genus *Pseudocalanus* are highly variable, depending on geographic location, light, food, as well as predator and environmental conditions. "Normal" migration—ascent at dusk and descent at dawn—was reported e.g. by Magnesen (1989) for *P. elongatus* in Lindåspollene, western Norway, by Runge & Ingram (1991) for *P. minutus* in Hudson Bay, Canada, by Frost & Bollens (1992) as well as Dagg et al. (1998) for *P. newmani* in Dabob Bay, Washington, USA, by Niermann & Greve (1997) for *P. elongatus* in the Black Sea, by Fortier et al. (2001) for *P. acuspes* in Barrow Strait, Canada and by Daase et al. (2016) for *Pseudocalanus* spp. northeast of Svalbard. "Reverse" migration—ascent at dawn and descent at dusk—was reported e.g. by Saito & Hattori (1997) for *P. newmani* in Akkeshi Bay, Japan and no migration behaviour at all was reported by Blachowiak-Samolyk et al. (2006) for *Pseudocalanus* spp. in the Barents

Sea. In Baltic *P. acuspes*, no or no distinct DVM behaviours were observed (Hansson et al. 1990, Hansen et al. 2006, Renz & Hirche 2006, Schmidt 2006) until Möller (2013) analysed Video Plankton Recorder (VPR) derived data and described a predator avoidance DVM of ovigerous *P. acuspes* females during the day towards deeper water layers beneath the halocline. Since DVM can be triggered by several different factors, and the work from Möller (2013) is the first and only study determining DVM behaviour of *P. acuspes* as predator avoidance, our study aims to cross check Möller's findings.

For *Pseudocalanus* spp. and *P. acuspes* it is reported that naupliar and early copepodite stages inhabit warmer, food-rich surface waters, whereas late copepodites as well as adults are found in deeper, high salinity water layers around the halocline down to depths where oxygen concentrations drop below 1 mL L^{-1} (Möllmann & Köster 2002, Hansen et al. 2006, Renz & Hirche 2006, Schmidt 2006). High salinities, as found around the halocline layer, are necessary for development, maturation and reproduction of this copepod species. As Möllmann et al. (2003b) suggested, this might be due to osmotic stress caused by low salinities, which leads to higher energy requirements, resulting in developmental failures, with less offspring reaching CV-stages and less individuals being suitable for maturation. In deep water layers, the diet of *P. acuspes* consists mainly of marine snow/detritus, accumulated at the halocline (Schmidt 2006, Renz et al. 2007, Möller et al. 2012). However, waters around the halocline are not only the favourable habitat of adult *P. acuspes*, but also aggregation grounds for clupeid fish during the day, thereby exposing *P. acuspes* to severe predation pressure. These clupeids (sprat—*S. sprattus* & herring—*C. harengus*) also perform DVM in the Baltic Sea, which is explained by a combination of foraging, bioenergetics and predator avoidance behaviour (Cardinale et al. 2003). At dawn and dusk, clupeids stay in the upper water layers to feed on thermocline inhabiting zooplankton (Cardinale et al. 2003, Kulke et al. 2018). In the morning, with rising light intensities, fish migrate to deeper water layers mainly to avoid visual predators during the day in depths between 60 and 80 m around the halocline. Sprat and herring are preyed on e.g. by salmon (*Salmo salar*, Karlsson et al. 1999) or garfish (*Belone belone*, Dorman 1991). In addition, several seabirds like the common guillemot (*Uria aalge*), goosander (*Mergus merganser*) and red-breasted merganser (*Mergus serrator*) are feeding on sprat (Sparholt 1994, Österblom et al. 2006). Some of these species, as the common guillemot, are able to dive deeper than 100 m (Piatt & Nettleship 1985, Burger & Simpson 1986). Nevertheless, since this feeding pressure on sprat was described for breeding seabirds (Österblom et al. 2006), it seems unlikely to be a universal trigger for sprat DVM in different basins of the Baltic Sea as well as during different seasons. At dusk, clupeids migrate back towards the surface, whereby the schools start to dissolve. During the night, the individual fish stay above or near the thermocline (Köster & Schnack 1994, Orlowski 2000, Cardinale et al. 2003, Nilsson et al. 2003, Stepputtis 2006, Bernreuther et al. 2013) where the water is warmer. Wurtsbaugh & Neverman (1988) showed that inhabiting warmer waters during the night enhances digestion and causes higher feeding rates the following day, leading to faster growth in fish. Brett (1971) assumed that DVM was a tool for optimal transition of prey into growth.

The first observation of predator avoidance DVM in Baltic *P. acuspes* by Möller (2013) was most likely only possible due to the deployment of a VPR system. The fine depth resolution of this gear, together with its high resolution images (Davis et al. 1992, Davis et al. 2004, Davis et al. 2005, Benfield et al. 2007) makes it perfect for investigating small-scale DVM behaviour like the one found in *P. acuspes*. Most likely, this behaviour could not have been detected with traditional plankton nets. The female individuals of this copepod species carry their eggs within a sac attached to their genital opening (Renz 2006), which makes them easy to identify on digital images. Therefore, they can be used to infer species, sex and maturity stage specific migration behaviour from underwater observations with video systems like the VPR. To provide a cross check study to the work of Möller (2013), we investigated VPR derived *P. acuspes* data from summer, which is a season with low clupeid densities in Bornholm Basin (BB). During spring, this basin is inhabited by high sprat abundances, which migrated into the deeper Baltic Basins in winter (Hoziosky et al. 1989, Stepputtis 2006). In summer, large parts of the sprat population leave BB and migrate back towards coastal areas (Hoziosky et al. 1989, Köster et al. 2005, Stepputtis 2006). Although herring return from their spawning grounds to BB during summer (Aro 1989), the overall amount of clupeids during this season is still low in comparison to spring (Stepputtis 2006).

With this study, we provide evidence for the hypothesis that Baltic ovigerous *P. acuspes* females show a predator avoidance DVM behaviour that stops during summer when feeding pressure of clupeid fish decreases.

METHODS

SAMPLING AREA & STRATEGY

Pseudocalanus acuspes data analysed in this study were derived from two cruises with RV Alkor in July 2012 and August 2015 to Bornholm Basin (BB), located in the central Baltic Sea (figure I-1). The results were compared to data from two cruises in April 2002 and May 2009 to the same location (Möller 2013). Since we wanted to investigate a countercheck situation to the high fish density situations of 2002/2009, we had to compare summer samples to the spring data of Möller (2013). Video Plankton Recorder (VPR) samples were analysed in respect to migration patterns of egg sac carrying *P. acuspes* females. To determine the clupeid fish densities present during our time of sampling, hydroacoustic data were recorded and fishery hauls conducted. Fishing stations were located close to the locations of the VPR tows (figure I-1).

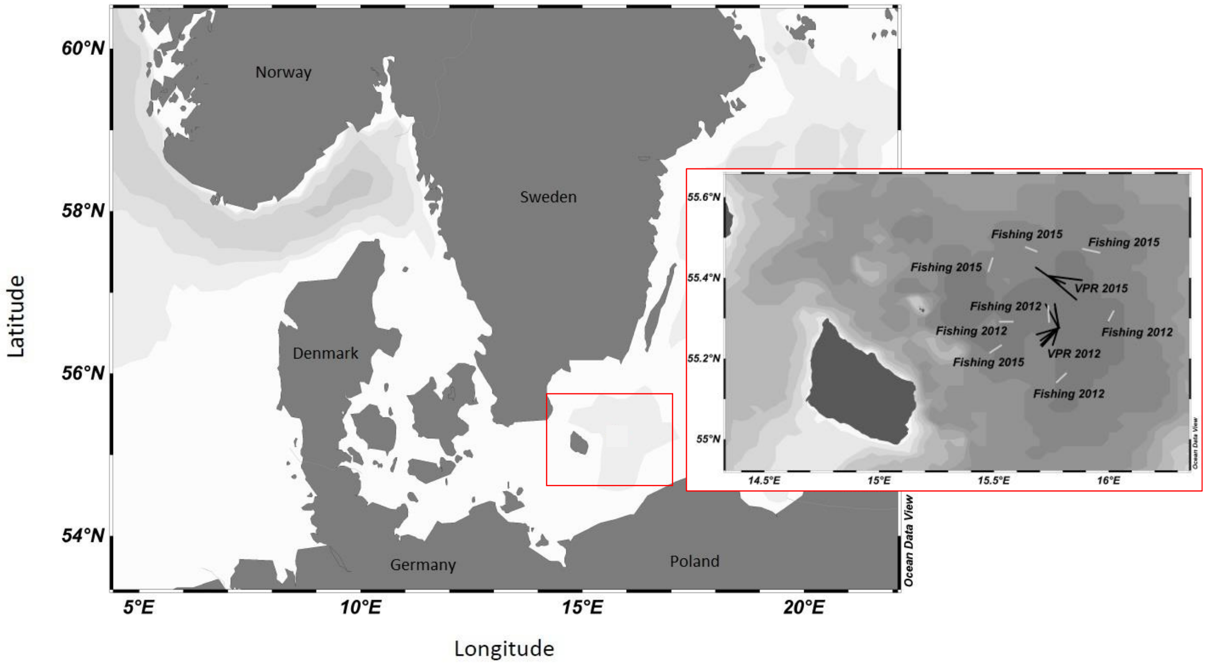

Figure I-1. Sampling area in July 2012 and August 2015, located in the central Baltic Sea (Bornholm Basin). Small map: locations of VPR tows (black) and fishing hauls (grey) in the respective years.

VIDEO PLANKTON RECORDER

Different numbers of VPR tows were conducted during the investigated cruises. Information regarding the individual VPR tows from the respective years are shown in table I-1.

Table I-1. Numbers and timeframes of VPR tows conducted in Bornholm Basin (central Baltic Sea) in the respective years.

Year	No. of VPR tows	VPR tows conducted between	
2002	1	25.04.2002, 22:55h UTC	26.04.2002, 11:32h UTC
2009	4	17.05.2009, 16:19h UTC	18.05.2009, 19:34h UTC
2012	8	29.07.2012, 14:13h UTC	30.07.2012, 11:59h UTC
2015	4	06.08.2015, 19:08h UTC	07.08.2015, 13:27h UTC

The VPR (Seascan) was attached under a V-fin and towed with three knots ship speed undulating through the water column during all tows taken into account for this study. Total sampling volumes of 28 423 L (2012) and 57 958 L (2015) were examined in comparison to 1 565 L in 2002 and 1 242 L in 2009 (Möller 2013). The large differences in sampling volumes result from the different camera settings that were used during deployment of the VPR systems. Möller (2013) used a system with real time transmission of image and sensor data to an on board unit via fiber optic cable. It was equipped with a high-resolution digital camera (Pulnix TM-1040) that took 25 image frames s^{-1}. The camera settings resulted in a field of view of 7 x 7 mm (f-zoom) and a calibrated image volume of 1.45 mL (2002) and 1.01 mL (2009). A strobe was used for illumination (Seascan/20 W Hamamatsu Xenon bulb), and additional sensors on the VPR included a CTD (Falmouth Scientific Inc.) as well as a fluorescence sensor (Seapoint Inc., model SCF). All information on these settings were taken from Möller (2013). In 2015, we deployed the same VPR system as in 2002 and 2009, except for the camera. In 2015, a Uniq UC-1800DS Color Digital CCD Camera was used. Its settings resulted in a field of view of 24 x 24 mm (S2 magnification) with a calibrated image volume of 108.23 mL. Accessory sensors on the VPR included in 2015 a FastCat 49 CTD (Sea-Bird), as well as an ECO Puck FLNTU fluorometer and turbidity sensor (WetLabs). In contrast to that, an autonomously running VPR system was deployed in 2012. There was no real time transmission of image data to an on board unit, but data were recorded internally and written to a USB key immediately after the tow. The technical settings of the VPR system used in 2012 included a one mega pixel colour camera (Bayer filter, Uniq model UC-1830CL, Pentax 12.5–75 mm F1.8 Lens) with a mean image frame rate of 14 s^{-1}, as well as a Xenon strobe (Seascan Inc., maximum rate of 30 flashes per second, one joule energy per flash). The applied camera setting enabled a field of view of 24 x 24 mm (S2 magnification) with a calibrated image volume of 34.39 mL. In 2012, the VPR included a FastCat 49 CTD (Sea-Bird).

Both VPR systems used the same data processing method: the image frames were processed with Auto Deck (Seascan Inc.), where all plankton particles visible in one image frame were extracted as regions of interest (roi) and saved as TIFF files. These rois were analysed automatically with Visual Plankton, a Matlab application written by scientists of the Woods Hole Oceanographic Institution (Davis et al. 2005; following methods of Hu & Davis 2006). To receive as accurate sorting results as possible, a training set had to be compiled prior to the actual sorting procedure. With this, a classifier was built, which in turn trained the Visual Plankton software. After classification of recorded images, this software was used to visualise the obtained data. Manually checking the automatically sorted rois was necessary because of the poor sorting results of the Visual Plankton Software for rois showing egg sac carrying *P. acuspes*.

PSEUDOCALANUS ACUSPES IMAGE DATA

Assigning VPR images to different copepod species is hardly possible from digital images, but since *P. acuspes* females are the only medium sized copepods in the central Baltic Sea carrying one egg sac, they were easy to identify (figure I-2). This provided us with the unique opportunity to generate small-scale distribution data that were not only species, but also sex and maturity stage specific. Since Holmborn et al. (2011) stated that *P. acuspes* is the only *Pseudocalanus* species living in the Baltic Sea, we assumed that all egg sac carrying individuals identified in the VPR rois were members of this species. Renz (2006) mentioned that *P. acuspes* was also referred to in older studies as *P. minutus* (Dahmen 1995), *P. elongatus* (Möllmann et al. 2000) or *P. minutus elongatus* (Hernroth 1985).

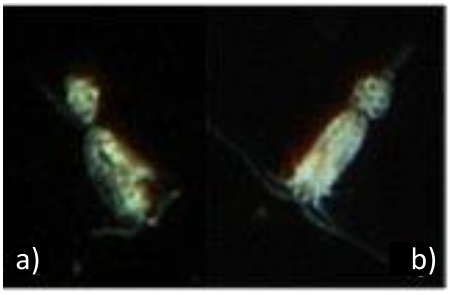

Figure I-2. Examples of egg sac carrying Pseudocalanus acuspes females from VPR tows of the cruises in July 2012 (a) and August 2015 (b); sampled at Bornholm Basin, central Baltic Sea.

CLUPEID FISH DATA

A young fish trawl net with a 5 mm mesh size codend and a vertical opening of 6 m was used for the fishery hauls. The net was towed with three knots ship speed for approximately 30 minutes per haul. Sampling was performed on detected schools of clupeid fish by pelagic trawling.

We derived the information about clupeid fish densities and vertical distributions from a Simrad echo sounder EK60 with a hull-mounted 38-kHz split-beam transducer. Hydroacoustic data were processed with the Echoview 4.9 software (Echoview Software Pty Ltd). Echograms were analysed at S_V -60 dB, which is the standard threshold for herring in the Baltic (ICES 2015). The entire water column was integrated with a horizontal resolution of 0.1 nmi and a vertical resolution of 1 m. NASC (nautical area scattering coefficient) values were calculated for every cell; results were given in m^2/nmi^2.

Since no hydroacoustic data were available for 2012, we took data from summer samples of different years (2011 & 2013, figure I-3) into account, as well as the hydroacoustic data from Möller (2013) (figure I-5, upper left panel), to locate the daytime accumulation depth of clupeid fish in relation to the halocline. Based on this information, we were able to determine the preferred daytime depth range (PDDR) of clupeids, which we applied to interpret our *P. acuspes* data from 2012. During the day (ca. 3–19h UTC), starting approximately 5 m below the beginning of the halocline, clupeid fish typically reside within a range of about 15 m below this starting point. This resulted in a preference range of 62–77 m in which clupeid fish might have been located during the day in our sample from 2012. The resulting PDDRs of clupeids for our different sampling years are listed in table I-2.

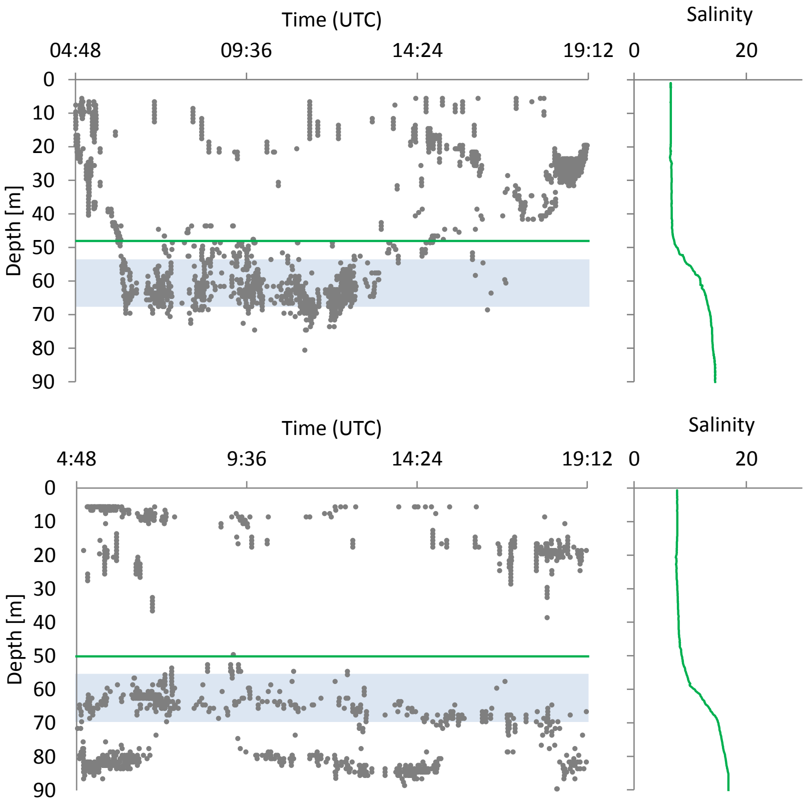

Figure I-3. Clupeid fish distribution with salinity conditions at different stations in Bornholm Basin on summer days in August 2011 (upper panels) & 2013 (lower panels). Grey dots—clupeid fish density expressed as NASC (nautical area scattering coefficient) values >50 m^2/nmi^2 (resolution of hydroacoustic data: horizontal 0.1 nmi, vertical 1 m), green line left panels—beginning of halocline (first increase in salinity), light blue rectangle—preferred daytime depth range beneath the halocline where clupeid fish were observed, green line right panels—salinity plot for the entire water column. Data points below 80 m most likely represent gadoids.

Table I-2. Observed (2002/2009 & 2015) and predicted (2012) preferred daytime depth ranges of clupeids for the different samples investigated in this study.

Sample	Depth range [m]
2002/2009	56–71
2012	62–77
2015	45–60

For the separation of data analysed in this study into “high” and “low” fish density situations, we considered hydroacoustic as well as catch data from the different years. Hydroacoustic data from Möller (2013) of May 2009 clearly showed high clupeid fish densities (figure I-5, upper left panel) with a distinct accumulation beneath the halocline during day and in surface waters during night. Catch data from spring cruises in 2002 and 2009 (table I-3) revealed that even higher amounts of sprat were caught in the first of those two years. Unfortunately, no hydroacoustic data were available for 2012, but because the samples from 2012 and 2015 were both summer samples, we compared our clupeid catch data of these cruises (table I-4). Very low numbers of clupeid fish were caught during both cruises, with even lower amounts of sprat and herring found in 2012 than in 2015. Hydroacoustic data from August 2015 (figure I-8) confirmed low densities of clupeid fish in BB during this season. No distinct accumulation of fish was visible during daytime. Comparing our hydroacoustic data from 2015 with those of Möller (2013) from 2009 resulted in higher amounts of NASC values >200 m^2/nmi^2 within the data from 2009, especially in the layers below the halocline during daytime. This indicated higher BB clupeid fish densities in spring 2009 than in summer 2015. As a result, we defined the sample from 2015 as a low fish density situation, and the even lower catch data from summer 2012 likewise confirmed low fish densities for this season.

Table I-3. Catch data for sprat (Sprattus sprattus) in Bornholm Basin, Baltic Sea (ICES Subdivision 25, Rectangle 39G5) derived from ICES reports for the years that were compared in this study.

Year	Cruise date	Research vessel	Reference	Estimated numbers [millions]	Total biomass [tonnes]
2002	03.–21.05.	Walther Herwig III	ICES 2003	4 011	42 274
2009	04.–24.05.	Walther Herwig III	ICES 2010	2 135	24 338
2012	02.–22.05.	Walther Herwig III	ICES 2013	8 543	108 151
2015	01.–21.05.	Walther Herwig III	ICES 2016	5 266	61 355

Table I-4. Clupeid fish caught in 2012 and 2015 (Sprattus sprattus—sprat & Clupea harengus—herring); stations located in Bornholm Basin close to VPR tows shown in figure I-1; results given as mean number of fish caught per 30 minute fishing activity.

Date	Time UTC [hh:mm]	Start Latitude [°N]	Start Longitude [°E]	End Latitude [°N]	End Longitude [°E]	Sprat [N/30 min]	Herring [N/30 min]
29.07.2012	04:29	55.292	15.527	55.291	15.582	0	58
29.07.2012	06:53	55.291	15.740	55.330	15.736	0	10
29.07.2012	09:10	55.290	15.995	55.318	16.021	0	13
29.07.2012	12:22	55.141	15.772	55.163	15.813	0	9
06.08.2015	04:14	55.233	15.530	55.214	15.483	119	59
06.08.2015	06:54	55.449	15.494	55.417	15.475	6	69
06.08.2015	09:30	55.466	15.685	55.476	15.637	2	21
06.08.2015	11:49	55.463	15.960	55.471	15.887	25	6

DATA ANALYSIS

To compare the day/night distributions of copepod data from 2002/2009 (Möller 2013), 2012 and 2015, we divided the available data into day and night samples (table I-5).

Table I-5. "Day" and "night" definition for VPR samples from April 2002/May 2009, July 2012 and August 2015.

Sample	"Day" UTC [hh:mm]	"Night" UTC [hh:mm]
2002/2009	04:15–16:45	16:46–04:14
2012	03:45–16:45	16:46–03:44
2015	04:00–16:45	16:46–03:59

This definition was based on the distinct copepod distribution visible in the data from Möller (2013) (figure I-4, left panels). During the day, nearly no copepods were found between approximately 56 and 71 m in a timeframe from ca. 04:15–16:45h UTC. We considered this timeframe as "day" and the remaining hours as "night" for the sample from 2002/2009. Information on sunrise and sunset, derived online from the NOAA Solar Calculator (NOAA 2017), revealed that *P. acuspes* individuals migrated out of the depth layer mentioned above about 45 minutes after sunrise and reappeared approximately 2 hours and 15 minutes prior to sunset. Subsequently, we identified sunrises and sunsets for the respective days of our samples from 2012 and 2015, and determined "day" and "night" for those samples by adding 45 minutes to the time of the sunrise and subtracting 2 hours and 15 minutes from the time of the sunset.

Our VPR tows were divided into transects for the day/night assignment—every down- and upward movement from the undulating sampling of the water column was considered a single transect. These individual transects were subsequently assigned to day or night samples. This ensured that the datasets for day/night samples solely consisted of samples of the entire water column. Hence, only 905 of the 938 copepods sampled in 2012, and 226 of the 255 from 2015 were included into subsequent data analysis.

VPR derived *P. acuspes* data from 2002 and 2009 were combined in this study for graphic representation, as done in Möller (2013).

The map in figure I-1 and the hydrographic plots of figures I-4 and I-7 were performed with Ocean Data View (Schlitzer 2018).

Hydrographic plots of figures I-4 and I-7 (oxygen, salinity and temperature) were built from data of reference CTD hauls from 2012 and 2015, respectively. In 2012, this reference haul was conducted on 29.07.2012, 08:03h UTC, and in 2015 on 05.08.2015, 01:13h UTC. The plots for 2002 were built from CTD data provided by Klas Ove Möller, as published in Möller (2013).

Salinity plots in figures I-3, I-5 and I-8 were built from CTD hauls of the respective cruises. In figure I-3 these hauls were from 16.08.2011, 00:27h UTC as well as from 04.08.2013, 01:17h UTC. Data of the salinity plot in figure I-5 were provided for 2002 by Klas Ove Möller (as published in Möller 2013) and for the sample from 2012 taken from a haul from 29.07.2012, 08:03h UTC. In figure I-8, the respective CTD haul was conducted on 05.08.2015, 01:13h UTC.

Statistical analyses were based on nonparametric Mann-Whitney tests using the statistical software R (version 3.3.1; R Core Team 2016). The tests were performed with *P. acuspes* abundance data of the investigated samples. For this, VPR tows were divided into day and night samples. Subsequently, we isolated the *P. acuspes* abundance data out of the respective clupeid PDDRs from every sample. Afterwards, we calculated a mean abundance for every single up- and downward movement of the VPR through this PDDR in every day and night tow. These mean abundance values were then tested for differences between day and night samples of the respective years.

RESULTS

Data investigated here were derived from different hydrographical conditions. These were pre inflow/stagnation periods (2002/2009 & 2012) as well as a post inflow situation (2015). To account for these hydrographical differences, we divided our results into the sections STAGNATION PERIODS and POST INFLOW SITUATION.

STAGNATION PERIODS

In April 2002 (figure I-4a), oxygen values ranged from 0.00 mL L^{-1} (from 80 m on downwards) to 8.51 mL L^{-1} (5 m). July 2012 showed higher oxygen levels in deep water layers (figure I-4b), with values ranging from 0.25 mL L^{-1} still available in 92 m to the highest value of 7.43 mL L^{-1} in 38 m. A halocline was visible in April 2002 between ca. 50 and 60 m, with salinity values increasing from 7.84 (18 m) to 18.21 (80 m) (figure I-4c). In July 2012, the halocline was located approximately between 57 and 75 m, and the salinity ranged from a minimum of 7.90 (29 m) to a maximum of 16.82 (89 m) (figure I-4d). In spring 2002, no thermocline was yet developed, and the temperatures throughout the water column were still low. They ranged from a minimum of 3.81°C (44 m) to a maximum of 8.93°C (80 m) (figure I-4e). In summer 2012 (figure I-4f), temperatures ranged from 3.85°C (61 m) to 17.87°C (5 m) with a distinct thermocline visible slightly above 30 m.

Observed ovigerous *Pseudocalanus acuspes* females numbered (in total) 912 in the data from 2002/2009 and 938 in the sample from 2012. The *P. acuspes* distribution from 2002/2009 showed almost no individuals between approximately 56 and 71 m during the day (figure I-4, left panels). High densities of clupeid fish were visible in the hydroacoustic data of this depth layer (figure I-5, upper left panel), which was therefore determined as the preferred daytime depth range (PDDR) of clupeids. At night, most of *P. acuspes* resided between 50 and 75 m with a few individuals visible in layers above 50 and below 80 m. Data from 2012 (figure I-4, right panels) showed the same overall *P. acuspes* distribution pattern—the majority was distributed between 50 and 75 m, with a few individuals visible above 50 and below 80 m. However, in contrast to the data from 2002/2009, *P. acuspes* individuals were more or less homogeneously distributed between 50 and 75 m, throughout day- as well as nighttime. They were not explicitly avoiding any depth layers in their vertical distribution during the day, not even the predicted PDDR of clupeids (figure I-5, lower left panel). Mean temperature, salinity and oxygen values for the three depth layers found in the vertical *P. acuspes* distribution pattern in the different years are shown in table I-6.

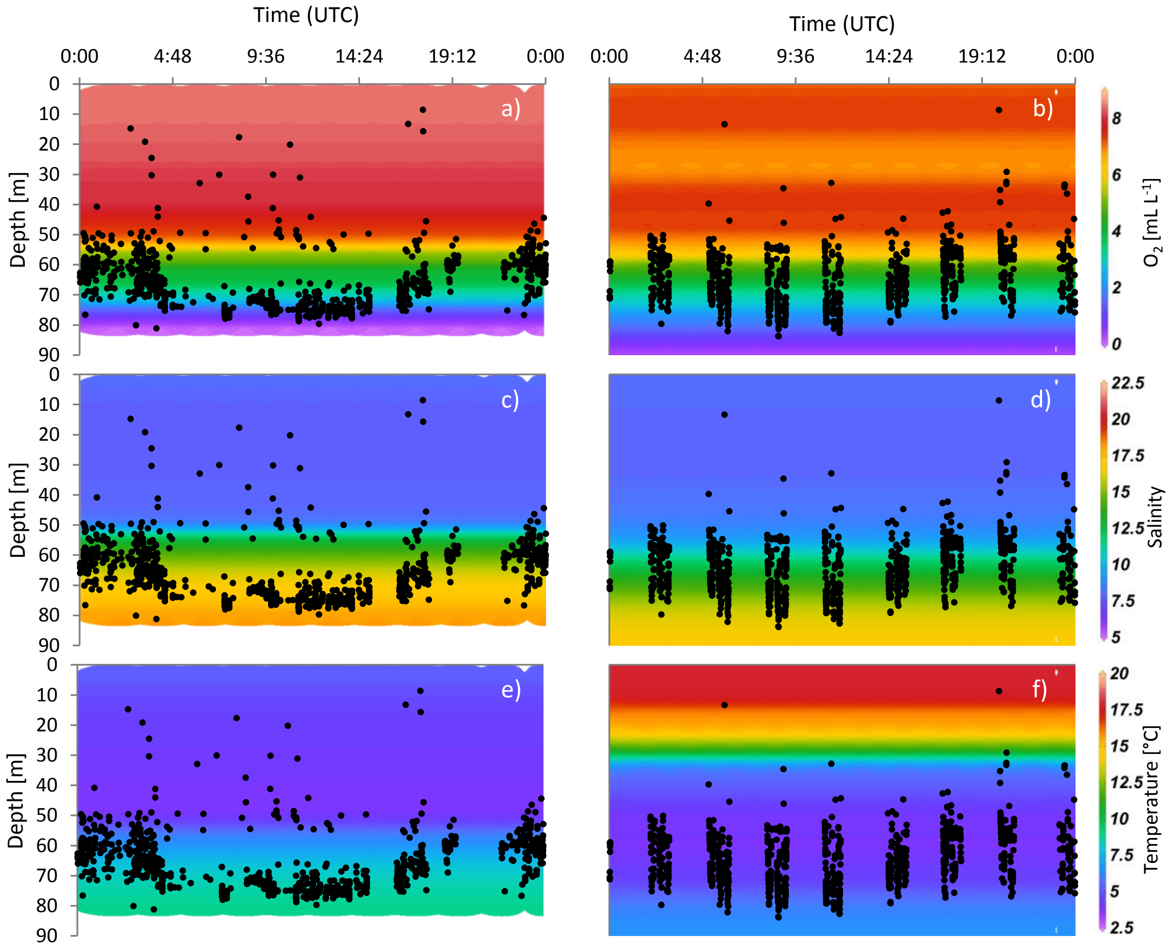

Figure I-4. Hydrographic conditions in 2002 & 2012 (Bornholm Basin, central Baltic Sea) with ovigerous Pseudocalanus acuspes female distribution of respective years. P. acuspes data plotted over the course of 24 hours. Oxygen, salinity and temperature data taken from CTD hauls of respective years; white areas: no hydrographical data; a, c, e): P. acuspes data from Möller (2013)—April 2002 & May 2009, CTD data from Möller (2013)—April 2002; b, d, f): P. acuspes data of the VPR tows from 2012, CTD data from a reference haul of 29.07.2012, 08:03h UTC; a & b): oxygen [mL L^{-1}], c & d): salinity, e & f): temperature [°C].

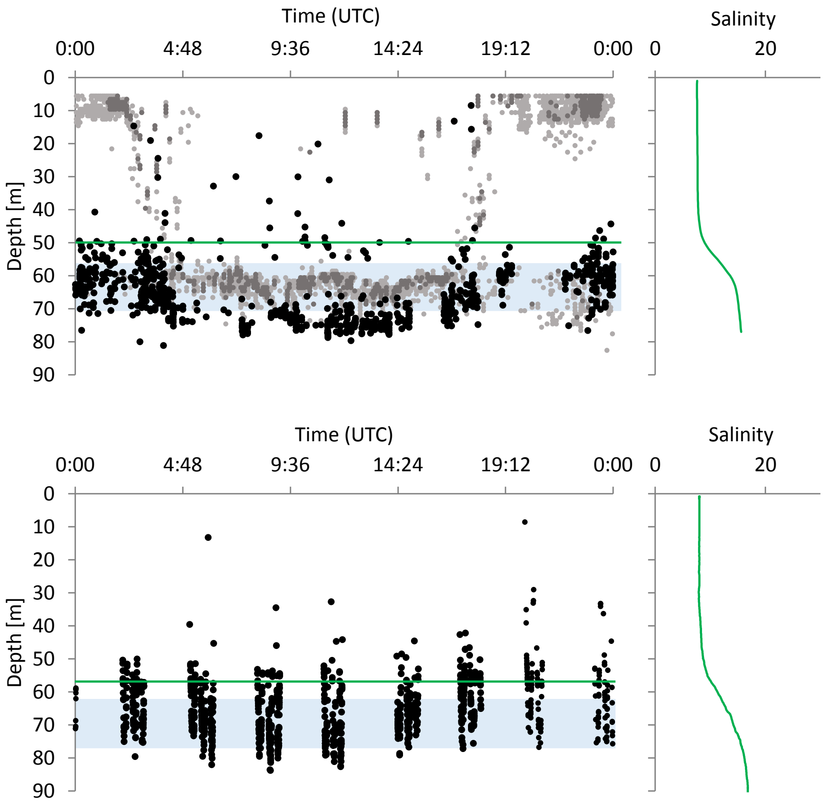

Figure I-5. Ovigerous Pseudocalanus acuspes female and clupeid fish distribution with salinity conditions for April 2002/May 2009 (Möller 2013; upper panels) & July 2012 (lower panels), sampled in the central Baltic Sea (Bornholm Basin); light grey dots—clupeid fish density expressed as NASC (nautical area scattering coefficient) values >50 m^2/nmi^2, dark grey dots—clupeid fish density expressed as NASC values >200 m^2/nmi^2 (resolution of hydroacoustic data: horizontal 0.1 nmi, vertical 1 m)—hydroacoustic data in upper panel from 2009 (Möller 2013), black dots—P. acuspes data from 2002 & 2009 in upper panel (Möller 2013) and from 2012 in lower panel, green line left panels—beginning of halocline (first increase in salinity), light blue rectangle—preferred daytime depth range beneath the halocline where clupeid fish were observed (2009) and predicted (2012), green line right panels—salinity plot for the entire water column. Hydroacoustic data of 2012 not available.

Table I-6. Mean temperature, salinity and oxygen values from the three depth layers of the vertical Pseudocalanus acuspes distribution pattern during investigated stagnation periods (2002 & 2012).

Year	Depth [m]	Temperature [°C]	Salinity	O_2 [mL L^{-1}]
2002	50–75	7.0	14.7	4.2
	<50	4.3	7.9	8.1
	>80	8.9	18.2	0.0
2012	50–75	4.2	12.0	4.7
	<50	13.1	8.1	7.2
	>80	6.6	16.7	0.5

The day/night depth distribution of ovigerous *P. acuspes* differed between 2002/2009 and the sample from 2012. The day depth distribution from 2002/2009 (figure I-6, left panel) showed the majority of *P. acuspes* below the PDDR of clupeid fish. At night, almost all *P. acuspes* individuals were visible directly within this layer. The day distribution for 2012 (figure I-6, right panel) was slightly deeper than that of the night, with a peak beneath the halocline, right within the PDDR of clupeid fish. The night distribution had its peak directly at the beginning of the halocline.

A Mann-Whitney test for differences between the *P. acuspes* abundances within the clupeid fish PDDR of day and night samples resulted in significant differences ($p<0.05$) for data from 2002/2009 as well as the sample from 2012. Data from 2002/2009 showed a day median of 0.000 *P. acuspes* L^{-1} (day mean 0.280 *P. acuspes* L^{-1}) and a night median of 0.707 *P. acuspes* L^{-1} (night mean 0.959 *P. acuspes* L^{-1}). Higher *P. acuspes* abundances were found within the PDDR at night than during the day. Data from 2012 showed the opposite—although also a significant difference was found. The day median was 0.220 *P. acuspes* L^{-1} (day mean 0.223 *P. acuspes* L^{-1}) and the night median 0.122 *P. acuspes* L^{-1} (night mean 0.119 *P. acuspes* L^{-1}). Here, even slightly higher *P. acuspes* abundances were found within the PDDR of clupeid fish during the day than during night.

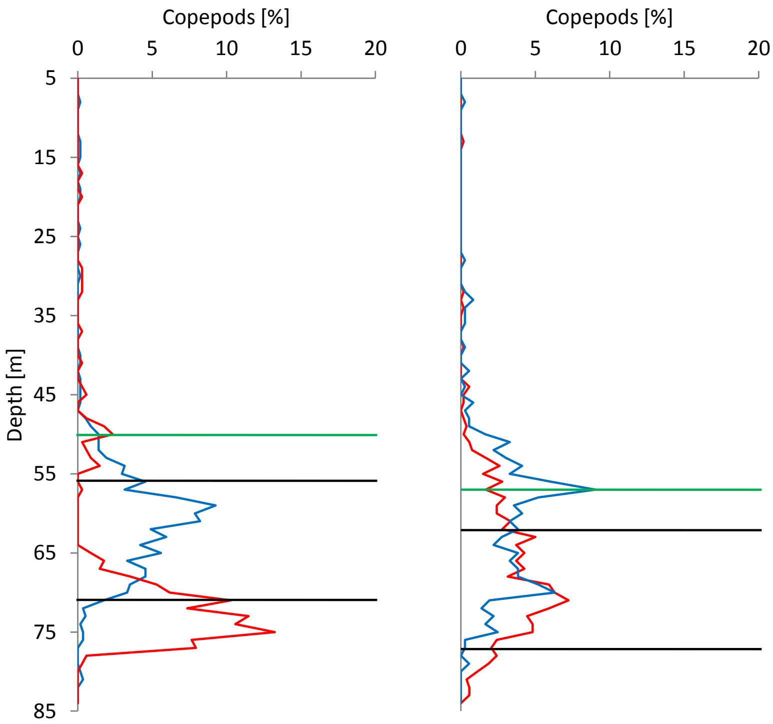

Figure I-6. Ovigerous Pseudocalanus acuspes female distribution, day (red) & night (blue), sampled in the central Baltic Sea (Bornholm Basin), shown as P. acuspes in per cent; P. acuspes in total: left panel (April 2002 & May 2009)—day: 340, night: 572, right panel (July 2012)—day: 540, night: 365; green line—beginning of halocline, black lines—preferred daytime depth range beneath the halocline where clupeid fish were observed (2002/2009) and predicted (2012).

POST INFLOW SITUATION

August 2015 featured high oxygen levels in deep water layers (figure I-7a), with values ranging from 1.36 mL L^{-1} (92 m) to 7.62 mL L^{-1} (14 m). Salinity levels were also high (figure I-7b), ranging from 7.89 (33 m) to 20.72 (92 m). A halocline was visible between ca. 51 and 65 m. Temperatures ranged from 5.50°C (50 m) to 16.70°C (1 m), and a distinct thermocline was visible slightly below 30 m (figure I-7c).

A total of 255 ovigerous *P. acuspes* females was found in this sample. Most of those individuals were visible between 50 and 75 m, with some above 50 as well as below 80 m. The mean temperature, salinity and oxygen values for these three depth layers are shown in table I-7. As in 2012, these egg sac carrying females did also show a quite homogeneous distribution throughout day as well as night, with a slightly broader distribution during the day. As in the sample from 2012, there were no depth layers explicitly avoided by *P. acuspes* during the day, especially not the observed PDDR of clupeids (figure I-8, left panel). Hydroacoustic data showed that clupeid fish densities present in Bornholm Basin (BB) (figure I-8, left panel) were not as high as in spring 2009 (figure I-5, upper left panel). Therefore, lower densities of clupeids were migrating towards the halocline during the day. While the clupeids migrated down to 70 m in the stagnation period of 2009 (figure I-5, upper left panel), the majority of fish stopped their downward movement under post inflow conditions already at around 60 m, where we determined their PDDR (figure I-8, left panel). Below that, only scattered low density readouts were visible in the hydroacoustic data from 2015.

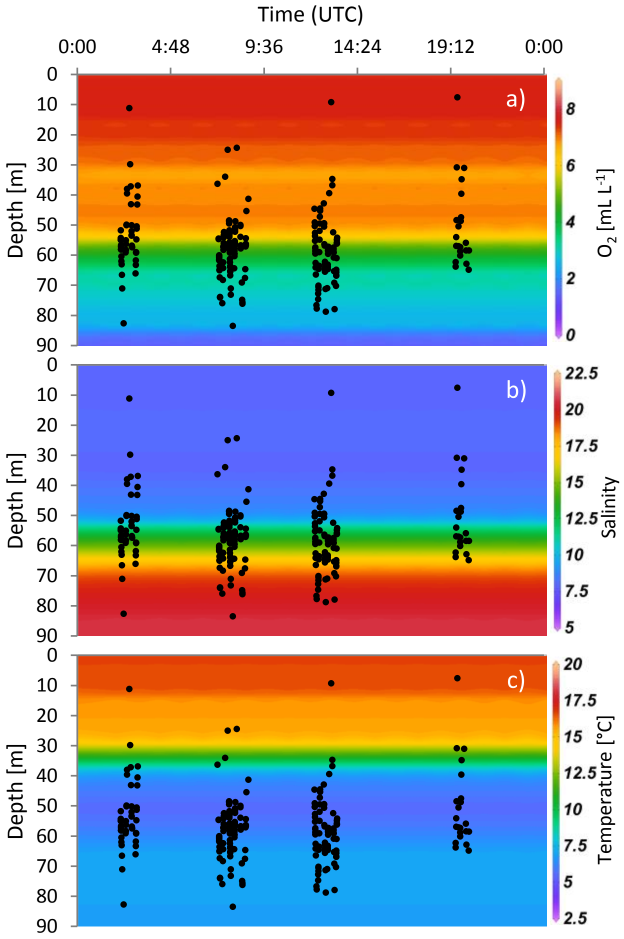

Figure I-7. Hydrographic conditions in 2015 (Bornholm Basin, central Baltic Sea) with the ovigerous Pseudocalanus acuspes female distribution of the respective year. P. acuspes data plotted over the course of 24 hours. Oxygen, salinity and temperature data taken from a reference CTD haul (05.08.2015, 01:13h UTC); a): oxygen [mL L^{-1}], b): salinity, c): temperature [°C].

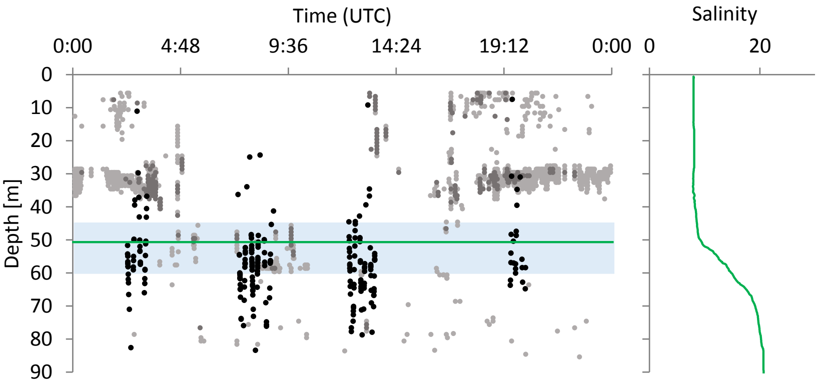

Figure I-8. Ovigerous Pseudocalanus acuspes female and clupeid fish distribution with salinity conditions for August 2015, sampled in the central Baltic Sea (Bornholm Basin); light grey dots—clupeid fish density expressed as NASC (nautical area scattering coefficient) values >50 m^2/nmi^2, dark grey dots—clupeid fish density expressed as NASC values >200 m^2/nmi^2 (resolution of hydroacoustic data: horizontal 0.1 nmi, vertical 1 m), black dots—P. acuspes, green line left panel—beginning of halocline (first increase in salinity), light blue rectangle—preferred daytime depth range where clupeid fish were observed, green line right panel—salinity plot for the entire water column. Data points below 70 m most likely represent gadoids.

Table I-7. Mean temperature, salinity and oxygen values from the three depth layers of the vertical Pseudocalanus acuspes distribution pattern during the investigated post inflow situation (2015).

Year	Depth [m]	Temperature [°C]	Salinity	O_2 [mL L^{-1}]
2015	50–75	6.5	15.6	4.2
	<50	13.1	8.2	7.2
	>80	7.0	20.6	1.8

The *P. acuspes* vertical depth distributions for day and night of 2015 (figure I-9) showed almost congruent curves, with highest values for day and night at the same depth within the halocline and also within the PDDR of clupeid fish. Again, a Mann-Whitney test for differences between day and night samples of *P. acuspes* abundances within the PDDR of clupeid fish was conducted. The result did not show a significant difference ($p>0.05$) between day and night samples. A day median of 0.058 *P. acuspes* L^{-1} (day mean 0.070 *P. acuspes* L^{-1}) and a night median of 0.045 *P. acuspes* L^{-1} (night mean 0.045 *P. acuspes* L^{-1}) were found. Slightly higher *P. acuspes* abundances were found within the PDDR of clupeid fish during the day than at night.

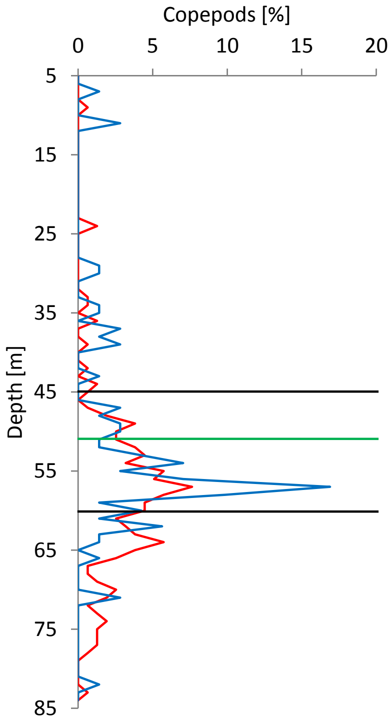

Figure I-9. Ovigerous Pseudocalanus acuspes female distribution for August 2015, day (red) & night (blue), sampled in the central Baltic Sea (Bornholm Basin), shown as P. acuspes in per cent; P. acuspes in total: day: 157, night: 71; green line—beginning of halocline, black lines—preferred daytime depth range beneath the halocline where clupeid fish were observed.

DISCUSSION

METHODS

For our clupeid fish data, no hydroacoustic data were available from 2012. Thus, we compared catch data from summer 2012 as well as 2015. The latter featured more caught clupeids. Because the hydroacoustic data from 2015 showed less clupeids than the data from 2009, we determined summer 2015—and consequently 2012 as well—as low fish density situations. This workaround was necessary because we could not directly compare catch data from 2002/2009 with those from 2012 & 2015. During the cruises of the first two years, a kombi trawl (KT) with a 10 mm mesh size codend was used (Stepputtis 2006), while the catches from 2012 and 2015 were derived with a young fish trawl (YFT) that featured a 5 mm mesh size codend. A conversion of the catch data from one trawl type into the other—based on the information about "spread between doors" (KT 111.0 m, YFT 24.7 m)—would only result in rough catch data estimates. Considering this, the indirect determination of 2012 as a low fish density situation as described above was more reliable. In addition to our catch and hydroacoustic data, several authors have confirmed summer as a season with low sprat abundances in Bornholm Basin (BB) (Hoziosky et al. 1989, Köster et al. 2005, Bernreuther et al. 2018).

RESULTS

Due to their enhanced visibility, copepod females carrying egg sacs are in general more vulnerable to predation by planktivorous fish than females without egg sacs or males (Hairston et al. 1983, Winfield & Townsend 1983). In the Baltic, this is especially true due to the spatial overlap of *Pseudocalanus acuspes* with sprat and herring during the day resulting from the vertical migration of the clupeids. Therefore, the discovery of a counter strategy (Möller 2013) to mitigate potential top-down control of Baltic ovigerous *P. acuspes* by clupeid fish represented an important step towards a better understanding of predator prey interactions in the Baltic Sea ecosystem. Here, we deliver complementary evidence for the confirmation of Möller's feeding pressure induced avoidance diel vertical migration (DVM) hypothesis of ovigerous *P. acuspes*, by showing that this migration behaviour disappears in low predator density situations. This agrees with the literature, in which the dependence of DVM behaviour strength on the prevailing predator concentrations was observed in different freshwater (Zaret & Suffern 1976) as well as marine (Ohman et al. 1983, Bollens & Frost 1989b) zooplankton communities.

Also, we can apply the three predictions of the predator-avoidance hypothesis as formulated by Lampert (1989) to our and Möller’s findings. First, ascent of the migrating organisms (here ovigerous *P. acuspes* females) happens in the evening, when predators have left the concerning depth layers, and descent is observed in the morning, when predators return. Second, avoidance DVM behaviour is witnessed in a part of the copepod population that is better detected by preying fish because of their attached egg sacs. Third, the extent of the migration itself varies with the present amount of predators—we can observe *P. acuspes* DVM when high amounts of predators are visible, and no DVM behaviour is observed during situations with low predator densities.

CLUPEID FISH DATA

The migration behaviour of clupeid fish seemed to change with the altered hydrography of stagnation periods and the post inflow situation (figure I-5, lower left panel & figure I-8, left panel). In 2015, under post inflow conditions, clupeids did not migrate as deep as in 2012 (stagnation period) and showed a shallower preferred daytime depth range (PDDR). One could assume that these migration differences resulted from the differing salinity conditions of the investigated years. Low salinities, e.g. lead to high metabolic costs for osmo- and ionoregulation (Jobling 1994, Wootton 1998, Cardinale et al. 2002). Therefore, clupeids might tend to migrate towards higher salinities during the day. In stagnation periods, these high salinity levels occur in deeper water layers, while post inflow conditions show high salinities in depth layers closer to the surface. Salinity conditions do also have an effect on sprat egg mortality. Higher salinities experienced by the eggs during fertilization result in higher egg gravity, which leads to deeper dwelling depths of the eggs with higher spatial overlap to predators as well as lower/unfavourable oxygen conditions (Voss et al. 2012). A shallower sprat migration during post inflow situations might therefore reflect more favourable spawning depths.

High (2002/2009) and low (2012 & 2015) fish density situations do not refer to the respective years featuring many or few clupeids overall, but reflect a seasonal phenomenon. This gets clear from the ICES WGBIFS reports (International Council for the Exploration of the Sea, Baltic International Fish Survey Working Group) catch data of the respective years (table I-3). These data show that even more sprat were caught in spring 2012 & 2015 than in 2002/2009. This means, that low BB summer densities of clupeids in 2012 & 2015 do reflect the seasonal migration of large parts of the sprat population out of this basin toward shallower coastal areas

(Hoziosky et al. 1989, Köster et al. 2005, Stepputtis 2006), but not years with overall low sprat densities.

Recently, Kulke et al. (2018) showed that feeding in deep water layers during day around the halocline does only account for 16–39% of the daily ration of sprat, and feeding in upper water layers results in feeding rates that are on average 3.1 times higher than those estimated for daytime feeding in deep waters. Nevertheless, the high abundances of sprat that inhabit BB during spring (Bernreuther et al. 2018) pose a distinct predation pressure on zooplankton in depths around the halocline. Furthermore, herring are known to feed more on *P. acuspes* as sprat and to prefer *P. acuspes* females over males (Flinkman et al. 1998, Bernreuther et al. 2013). Despite only low amounts of herring being present in BB during spring (Bernreuther et al. 2018), this feeding preference does add to the predation pressure on ovigerous *P. acuspes*. Therefore, the vertical migration we observed in the *P. acuspes* data from spring 2002/2009 seems to reflect the avoidance of both clupeids, herring as well as sprat.

DOWNWARD COPEPOD MIGRATION

In contrast to the clupeid migration, *P. acuspes* DVM seemed not to be affected by the changing hydrographical conditions, but triggered by predator densities only. We found almost no ovigerous *P. acuspes* females within the depth layers between approximately 56 and 71 m during the day in the high fish density situation of 2002/2009 (figure I-4, left panels). Clupeid fish migrated after sunrise into exactly this layer (figure I-5, upper left panel). There are two possible scenarios for the lack of *P. acuspes* individuals in this layer: i) fish preyed on residing *P. acuspes* and thereby removed them from this water layer, ii) residing *P. acuspes* tried to avoid predator encounter by migrating towards deeper water layers below 71 m. Since the Video Plankton Recorder (VPR) data from 2002/2009 show higher numbers of *P. acuspes* individuals below 71 m during the day than during the night (day: 248, night: 11), we suggest scenario ii as more likely.

The lack of an avoidance DVM in female *P. acuspes* during summer can be explained by results from Bernreuther et al. (2018), who showed that the low amounts of clupeids present in BB feed in August almost exclusively on *Temora longicornis* as well as cladocerans. This reduces the predation pressure on *P. acuspes* enormously. *T. longicornis* and cladocerans reside in the upper 30 m of the water column (Hansen et al. 2006, Kulke et al. 2018). Therefore, we can conclude that the low amounts of clupeids visible in the hydroacoustic data of summer 2015 (figure I-8, left panel) are mostly preying on zooplankton species which reside in the upper part of the water column, while the majority of the ovigerous *P. acuspes* females shown in our VPR data prefer deeper water layers. Thereby, the clupeids emit only low predation pressure on adult *P. acuspes*, which in turn are not forced to show an avoidance DVM towards depths below 71 m.

The day/night depth distributions of ovigerous *P. acuspes* females within the PDDR of clupeids resulted in significant differences ($p<0.05$) for spring 2002/2009 as well as summer data from 2012 (figure I-6). This does not contradict our hypothesis of an absent *P. acuspes* avoidance DVM during summer. Although the *P. acuspes* abundances within the clupeid PDDR showed statistically significant differences between day and night, more individuals were found in the day than in the night PDDR summer 2012 sample. This would not have been the case if the *P. acuspes* females had avoided the clupeid PDDR during the day, as was shown in the spring sample, where the significant differences between day and night resulted from higher *P. acuspes* abundances in the night than the day sample. The summer 2015 samples from day and night were not significantly different from each other. Slightly higher *P. acuspes* abundances were observed in the day sample. Highest abundances of day and night PDDR samples were found in the same depth layers. Therefore, ovigerous *P. acuspes* females did not avoid the PDDR of clupeids during the day in summer 2015. In addition, the vertical distribution patterns of the ovigerous *P. acuspes* females were very similar between summer 2012 and 2015. The main part of the individuals was visible between approximately 50 and 75 m. A few females were found above 50 m as well as below 80 m. In fact, the vertical distribution patterns did not differ between any of the investigated years—except for the avoided depth layer (56–71 m) during the day in spring 2002/2009. Data from these spring samples did also show the main part of ovigerous *P. acuspes* females between 50 and 75 m during the remaining time of the day, as well as single individuals above 50 m and below 80 m. The differences in the hydrographical conditions (stagnation period/post inflow situation) seemed to have no effect on the vertical distribution patterns of *P. acuspes,* since the conditions of the depth layer from 50–75 m did not differ distinctly between the investigated years (tables I-6 & I-7). Therefore, we conclude that *P. acuspes* avoidance DVM is caused by the presence of high predator densities alone, and not driven by temperature, salinity or oxygen conditions.

Möller et al. (2015) did also compare the ovigerous *P. acuspes* distribution from stagnation periods with a post inflow situation from 2003. *P. acuspes* females were found residing significantly deeper after the inflow than before, and a more than doubled vertical distribution range of *P. acuspes* was visible. Möller and colleagues linked this to the improved oxygen conditions in water layers deeper 80 m. Our post inflow situation does also show higher oxygen levels in depths >80 m than the stagnation periods (tables I-6 & I-7), but compared to the levels of the post inflow conditions from Möller et al. (2015) (>5 mL L^{-1}) they were still low. Since Naumann et al. (2016) reported that the inflow in December 2014 was stronger than the one in January 2003, the differences in oxygen levels have to be a result from the time that passed between respective inflow and sampling of VPR data. Data from Möller et al. (2015) were sampled three and four months after the inflow from 2003, while our data were taken eight months after the inflow from 2014. It seems, that during this time oxygen levels had dropped again in 2015 and resulted in a vertical distribution of ovigerous *P. acuspes* females that resembled the distribution pattern visible during the stagnation periods of 2002 and 2012.

UPWARD COPEPOD MIGRATION

In the datasets from stagnation periods as well as the post inflow situation, a few ovigerous *P. acuspes* females were observed in depths above 50 m (figures I-4 & I-7). Plankton net samples from Renz & Hirche (2006) do also show *P. acuspes* females in water layers above 50 m during day as well as night—in spring as well as summer—at the same location as the VPR sampling from 2002/2009. Results from Voss et al. (2003) show the same by describing how cod larvae actively select *P. elongatus* females as prey in the upper 45 m of BB during cruises covering the months March to October.

Möller (2013) suggested that these *P. acuspes* individuals apply a second predator avoidance strategy during the day. Individuals would either perform a downward migration towards deeper waters, or an upward migration towards the surface—according to their position within the water column relative to the encountering predator. However, when looking at the data from 2002/2009, *P. acuspes* inhabited the depths above 50 m during day as well as night. In these years, 19 individuals were found in the upper 50 m during the day, and 24 individuals at night. This does not strongly support the existence of a second predator avoidance strategy. One would expect more individuals migrating upwards into layers above 50 m during the day than during the night, because during the night there should be no reason to escape towards higher water layers since the clupeid predators already reside in surface waters at this time. In connection with our data, this second predator avoidance behaviour seems even more unlikely. We found 12 individuals in layers above 50 m during the day and 21 at night in the low clupeid fish density situation of 2012, as well as almost equal numbers of *P. acuspes* during day and night in the low predator density situation of 2015 (day—22, night—18).

Since nauplii tolerate lower salinities and higher temperatures, they are generally found in surface waters (Renz & Hirche 2006). This agrees with Kinne (1964), who reported that the salinity tolerance often differs with the different ages of an organism, and that hatched individuals seem to be less sensitive and may have a greater salinity tolerance than older, mature ones. We therefore consider it possible that the females we observed above 50 m might have migrated into those layers to release their offspring. Despite the often cited dependence of adult *P. acuspes* on high salinities (Möllmann et al. 2000, Möllmann & Köster 2002, Renz & Hirche 2006, Schulz et al. 2012), these females experienced lower salinities in the water layers above 50 m than in their usual habitat around the halocline. Hernroth & Ackefors (1979) reported the occurrence of *P. minutus elongatus* throughout the whole Baltic proper in waters with salinities as low as 6‰, as long as temperatures were below 10°C. The average salinities in the layers above 50 m of our samples (tables I-6 & I-7) do all stay above 6‰, while average temperatures reached a maximum of 13°C during summer 2012 & 2015. This means the ovigerous P. *acuspes* females in water layers above 50 m seemed to not have reached the limit of their salinity tolerance. Dzierzbicka-Glowacka (2004) reports that the growth of young *P. elongatus* stages from the Baltic Sea is half that of individuals from the North Sea—at the same temperatures—and even three times as low for adult organisms, due to the low salinities in the Baltic Sea. Therefore, the low salinities in the upper 50 m of the water column seem to very well pose unfavourable conditions concerning *P. acuspes* growth. This leads to the suggestion that the ovigerous females do not dwell in these waters for longer periods of time, but that this migration into upper water layers is a trait-off between contributing to repopulation through release of their offspring and the consequences of their temporary exposure to these unfavourable salinity conditions.

TOP-DOWN / BOTTOM-UP CONTROL

Several authors draw the conclusion that the Baltic Sea zooplankton community is subject to top-down control through planktivorous fish. In shallower areas of the Baltic Sea, 30–70% of zooplankton production are reported to be consumed by clupeids (Rudstam et al. 1992, Arrhenius 1997). Arrhenius & Hansson (1993) reported even up to 80% of the annual zooplankton production being consumed by sprat and herring. Increasing sprat stock size was assumed to prevent an increase in *T. longicornis*, as well as contributing to the decrease of *P. elongatus* (Möllmann & Köster 2002), and Casini et al. (2008) did also suggest a top-down control of sprat on zooplankton in the open Baltic Sea. Nevertheless, the fact that ovigerous *P. acuspes* females show DVM behaviour during seasons with a possible top-down control by high clupeid fish densities suggests that *P. acuspes* can actively avoid the feeding pressure emitted by these predators. Möllmann & Köster (1999) did also not find evidence for a food limitation of clupeids, which would have been expected if these fish exert a strong top-down control on zooplankton. In 2005, Möllmann et al. (2005) even reported of a parallel increase in sprat as well as *T. longicornis, Acartia* spp. and cladocerans. In addition, a recent study of Bernreuther et al. (2018) showed that the predation impact of clupeids in BB seemed not strong enough to control zooplankton dynamics.

Actually, a quite contrary control mechanism might establish in the years to come. If future changes in the hydrographical environment of the Baltic Sea ecosystem, i.e. decreasing salinity, will affect the *P. acuspes* population negatively (Möllmann et al. 2005) a bottom-up control of *P. acuspes* through the decline of an important prey source for cod larvae (Voss et al. 2003) as well as herring (Möllmann et al. 2005) might be possible.

CONCLUSION

We find that ovigerous *Pseudocalanus acuspes* females react to changes in clupeid predator densities with differences in DVM behaviour. Changing hydrographic conditions do not affect the observed migration patterns. With these adaptations to the respective predator situation, *P. acuspes* has developed a counter strategy towards a possible top-down control of the Baltic Sea ecosystem.

Furthermore, there seems to exist a share of the female *P. acuspes* population that resides in water layers above 50 m, independent from occurring predator densities. It seems possible, that this behaviour is part of the ontogenetic migration of *P. acuspes*, where ovigerous females migrate towards upper water layers in order to release their offspring. Therefore, we consider it necessary to test i) if there is an ontogenetic migration of ovigerous *P. acuspes* females into low salinity surface waters, and to further investigate ii) from which salinity levels on *P. acuspes* individuals start to experience negative effects on life cycle and reproduction. So far, experimental tests on salinity effects on reproduction and mortality have been unsuccessful due to the high mortality of *P. acuspes* under culture (Möller et al. 2015). This knowledge might play a crucial role in the future for estimations about the development of the whole Baltic Sea ecosystem, with regard to changing environmental conditions like decreasing salinities (Viitasalo et al. 2015).

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Chapter II

DVM patterns of thermocline associated copepods in different basins of the Baltic Sea

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ABSTRACT

Thermocline associated copepods (especially *Temora longicornis* and *Acartia* spp.) show distinct diel vertical migration (DVM) patterns in Bornholm Basin (BB), central Baltic Sea. Recent findings have shown that DVM of the halocline associated copepod *Pseudocalanus acuspes* clearly represents a predator avoidance strategy (chapter I of this thesis). Since this is also assumed to be the fact for the thermocline associated part of the BB copepod community but has not been verified so far, we examine here if there is evidence that DVM of these copepods is a predator avoidance behaviour against clupeid fish or other predators. Therefore, we investigated the relations between copepod and clupeid fish DVM patterns through i) Video Plankton Recorder derived data on copepod DVM patterns and ii) hydroacoustic derived data on clupeid fish migration. Our results showed a distinct overlap between copepod and clupeid depth distribution during morning and evening hours, while both groups migrated down- or upward respectively. Clupeids exert a particularly high feeding pressure on zooplankton during these time periods. Therefore, we conclude that the DVM pattern of the thermocline associated part of the BB copepod community does not represent a predator avoidance strategy against clupeids. Furthermore, we conclude that it is also not a predator avoidance mechanism against other predators like the jellyfish *Aurelia aurita*. The observed copepod DVM pattern persists in seasons where no *A. aurita* predators are visible in BB. Thus, we suggest an endogenous trigger of DVM in thermocline associated copepods.

INTRODUCTION

The Baltic Sea is an intracontinental mediterranean sea, and the largest brackish water region in the world (Fonselius 1970). It is connected to the North Sea via Skagerrak and Kattegat, from where high saline water flows in (Møller & Hansen 1994). Fresh water, brought in through precipitation and river discharges, outweighs evaporation. Therefore, a surface current of low salinity water flows out of the Baltic Sea through Kattegat and Skagerrak (Fonselius 1970). The density difference between high and low saline waters results in two distinct water layers, separated by a halocline (Fonselius 1970). This halocline lies in the deep basins of the Baltic Sea in approximately 50 to 75 m year-round, while a second cline—the thermocline—separates warmer and colder water layers in 20 to 30 m depth (Grønkjær & Wieland 1997) from spring to autumn. Due to this strong stratification and also because of its low species diversity and the resulting small amount of trophic linkages (Sandberg et al. 2000), the Baltic Sea is a very unique study area. The copepod community of the Baltic Sea consists of only four main species: *Pseudocalanus acuspes*, *Temora longicornis*, *Acartia bifilosa* and *Acartia longiremis* (Hansen et al. 2006, Renz & Hirche 2006, Schmidt 2006), which show different preferences in regard to their vertical distribution. *T. longicornis* as well as *Acartia* spp. dwell within the upper 30 m of the water column (Hansen et al. 2006) near the thermocline, whereas *P. acuspes* resides in deeper layers within the range of the halocline (Hansen et al. 2006). By providing prey for commercially important fish stocks such as clupeids (sprat—*Sprattus sprattus* & herring—*Clupea harengus*) and cod (*Gadus morhua*) copepods are an important link between lower and higher trophic levels of the Baltic Sea ecosystem (Arrhenius & Hansson 1993, Hinrichsen et al. 2002, Casini et al. 2004, Bernreuther et al. 2013, Solberg & Kaartvedt 2017).

For a long time, common knowledge regarding diel vertical migration (DVM) of clupeids and their feeding behaviour was that these planktivores form schools during dawn, migrate towards deeper water layers to avoid predators (Dorman 1991, Sparholt 1994, Karlsson et al. 1999, Österblom et al. 2006) and spend the daylight hours in deep waters feeding on zooplankton (Köster & Schnack 1994, Orlowski 2000, Nilsson et al. 2003, Stepputtis 2006). Sprat were assumed to start their migration back to the surface into warmer waters at dusk. The schools dissolve and the individuals spend the night in surface layers. Wurtsbaugh & Neverman (1988) suggested that the warmer temperatures in the surface layers would enhance digestion and enable fish to feed more and grow faster than if they stayed in cooler layers throughout day and night. Lately, however, new information and insights have emerged regarding this migration and feeding behaviour. Cardinale et al. (2003) indicated that pelagic fish feed during their down and upward migrations at dawn and dusk when encountering zooplankton aggregations, and

Bernreuther et al. (2013) were the first to provide evidence for night feeding of sprat around the thermocline. Schmidt (2006) found that sprat followed their copepod prey DVM—as Cardinale et al. (2003) also considered likely—stating that this copepod migration was not a suitable mechanism for predator avoidance and had to have other reasons. In addition, Kulke et al. (2018) showed most recently, that 61–84% of the daily ration of sprat are consumed in the upper water layers during dawn and dusk, with feeding rates on average 3.1 times higher than those of the daytime feeding in deep water layers.

DVM of zooplankton plays an important role in food web interactions and the processes that couple pelagic and benthic habitats (Berge et al. 2014). Copepods and zooplankton in general contribute to the nutrient transport in the water column through the sinking of faecal pellets into deeper water layers (Wallace et al. 2013). Furthermore, zooplankton DVM contributes greatly to the biological pump, the biologically mediated transfer of atmospheric carbon dioxide into the deep-sea (Bollens et al. 2011, Wang et al. 2015). This is due to grazing of zooplankton on phytoplankton at the surface during night and metabolizing these food particles in deeper layers during the day (Longhurst & Harrison 1988). Gaining more information on DVM patterns of different species in an ecosystem does therefore help to increase knowledge of the ecosystem structure, and to better predict vertical fluxes and carbon transport, which becomes increasingly important in an era with increasing carbon concentrations entering our oceans (Bollens et al. 2011, Wang et al. 2015). One of the main reasons for copepod DVM is believed to be predator avoidance (Zaret & Suffern 1976, Lampert 1989, Ringelberg 1995), and DVM patterns have been observed for *T. longicornis*, *Acartia* spp. as well as *P. acuspes* (Hansson et al. 1990, Hansen et al. 2006, Möller 2013). It was shown for *P. acuspes* that this migration behaviour is most likely triggered by predation pressure of clupeids (Möller 2013 & chapter I of this thesis), but for thermocline inhabiting copepods this has not been clearly shown yet. By deploying a Video Plankton Recorder we were able to closer observe the DVM patterns of this part of the copepod community. This underwater microscope system delivers fine-scale plankton data by combining zooplankton images directly with hydrographic information. With this, we were able to investigate copepod DVM patterns with a higher resolution than with the large-scale data derived by traditional plankton net sampling.

In chapter I of this thesis, we verified that DVM of the halocline inhabiting copepod *P. acuspes* in Bornholm Basin (BB) is a predator avoidance strategy. Here, we aim to investigate if the thermocline associated part of the BB copepod community does also show a predator avoidance DVM against clupeids or other predators. To increase the overall knowledge on copepod DVM in the Baltic Sea, we investigate furthermore whether these copepods show the same migration patterns in different basins, or whether our observations are limited to BB.

METHODS

SAMPLING AREA & STRATEGY

Copepod data presented in this study were derived from five different cruises with RV Alkor in May 2009, August 2014 and 2015, September 2016 and July 2017 to Arkona (AB, 2014) and Bornholm Basin (BB, 2009, 2014, 2015, 2016, 2017) in the Baltic Sea (figure II-1). Video Plankton Recorder (VPR) samples of these cruises were analysed with respect to diel vertical migration (DVM) patterns of copepods. Hydroacoustic data of the respective cruises were recorded during the VPR tows and analysed with respect to DVM patterns of clupeid fish. In 2009, hydroacoustic data were recorded one day after VPR samples were taken.

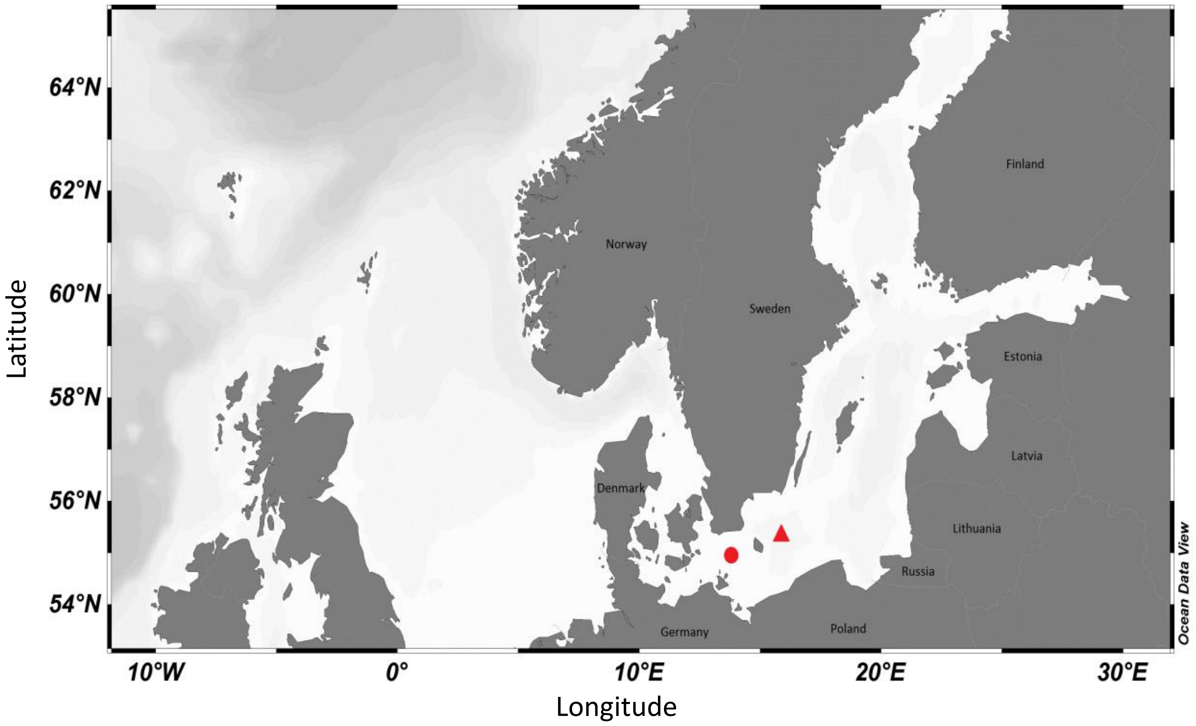

Figure II-1. Sampling area in the Baltic Sea for the investigated years; red dot—sampling location in Arkona Basin (2014), red triangle—sampling location in Bornholm Basin (2009, 2014, 2015, 2016, 2017).

VIDEO PLANKTON RECORDER

During the cruises, different numbers of VPR tows were conducted. Information regarding VPR tows from the respective years are shown in table II-1.

Table II-1. Number of VPR tows, their respective timeframes and the sampling areas where they were conducted during the investigated years; BB—Bornholm Basin, AB—Arkona Basin.

Year	Sampling area	No. of VPR tows	VPR tows conducted between	
2009	BB	4	17.05.09, 16:00h UTC	18.05.09, 20:00h UTC
2014	AB	2	06.08.14, 21:00h UTC	07.08.14, 11:00h UTC
2014	BB	5	13.08.14, 11:30h UTC	14.08.14, 04:30h UTC
2015	BB	4	06.08.15, 19:00h UTC	07.08.15, 14:00h UTC
2016	BB	5	09.09.16, 22:00h UTC	10.09.16, 19:00h UTC
2017	BB	4	27.07.17, 08:00h UTC	28.07.17, 03:00h UTC

The VPR (Seascan) was attached under a V-fin and towed with three knots ship speed. By towing the device undulating through the water column, all depth layers of the investigated Basins were sampled. Total sampling volumes of 1 417 L (2009), 10 792 L (2014, AB), 8 405 L (2014, BB), 51 139 L (2015), 45 869 L (2016) and 35 778 L (2017) were examined.

Technical settings of the VPR included a Pulnix TM-1040 camera in 2009, and a Uniq UC-1800DS Color Digital CCD camera in 2014, 2015, 2016 and 2017. The mean image frame rate was always 25 s^{-1}, as was the provision of illumination by a Xenon strobe (Seascan). The camera settings applied in 2009 provided a field of view of 7 x 7 mm (f-zoom) with a calibrated image volume of 1.01 mL. In 2014, the field of view was 14 x 14 mm (S1 magnification) with a calibrated image volume of 23.75 mL. For 2015, 2016 and 2017, the field of view was set to 24 x 24 mm (S2 magnification), resulting in calibrated image volumes of 108.23 mL (2015) and 67.95 mL (2016 & 2017). Accessory sensors on the VPR included a CTD (Falmouth Scientific Inc.) as well as a fluorescence sensor (Seapoint Inc., model SCF) in 2009. In 2014, 2015 and 2016, the accessory sensors included a FastCat 49 CTD (Sea-Bird), as well as an ECO Puck FLNTU fluorometer and a turbidity sensor (WetLabs). During the cruise in 2017, the turbidity sensor was dismounted, while the same FastCat CTD was used.

During all cruises, the deployed VPR system provided real time transmission of image and sensor data to an onboard unit via a fiber optic cable. Using AutoDeck (Seascan Inc.), all particles (plankton) recorded by the VPR were extracted as regions of interest (roi). Visual Plankton, a Matlab application written by scientists of the Woods Hole Oceanographic Institution (Davis et al. 2005) was used for the automatic analysis of these rois, following methods of Hu & Davis (2006). Manually checking the automatically sorted rois was necessary due to insufficient sorting results of the Visual Plankton software.

COPEPOD DATA

VPR data of our six different samples (BB 2009, 2014–2017, AB 2014) were analysed in regard to DVM behaviour of copepods. In this study, we focused on the migration behaviour of thermocline associated species like *Temora longicornis* and *Acartia* spp. in the upper 50 m of the water column. To verify that the copepods visible in our VPR derived rois were most likely individuals of these species, we analysed data from multinet (MSN) samples of a different cruise from the end of August 2015 (figures II-2 & II-3).

MULTINET COPEPOD DATA

Vertical distribution of the different copepod species was determined through vertically stratified samples via a multiple opening-closing net (Hydro-Bios). The opening of the net was 0.25 m^2 and a mesh size of 100 µm was used. In BB, samples were taken in 3 m intervals from 19–40 m at 14:00 and 14:36h UTC, 18:25 and 18:59h UTC as well as 03:52 and 04:27h UTC. We combined those samples for graphic display into 14h, 19h and 4h UTC. Samples from AB were taken in 2–3 m intervals from 22–41 m at 14:00 and 14:30h UTC, 18:00 and 18:40h UTC as well as 03:15 and 03:45h UTC. These were combined into 14h, 18h and 3h UTC for graphic display. For analyses later in the lab, samples were preserved in a 4% disodiumtetraborate-buffered formalin-seawater solution. Subsamples of not less than 500 mesozooplankton individuals per sample were identified and counted under a binocular microscope. Subsamples were received through splitting of the original sample with a Kott-splitter device. Copepods were identified to species level (*Acartia bifilosa*, *A. longiremis*, *T. longicornis*, *Pseudocalanus acuspes*, *Centropages hamatus* and *Oithona similis*). The *Acartia* species were combined into *Acartia* spp. for graphic display.

CLUPEID FISH DATA

Fish densities of clupeids and the appertaining vertical distribution were derived from hydroacoustic data, recorded with an EK60 echosounder (Simrad) at 38 kHz. Hydroacoustic data were processed with the Echoview 6 software (Echoview Software Pty Ltd). We analysed the echograms at S_V -60 dB, the standard threshold for herring in the Baltic (ICES 2015). During the day, single clupeid schools were detected with the school detection module within Echoview; settings for this school detection are shown in table II-2. Horizontal resolution was set to 1 nmi, while the whole water column was integrated vertically. During the night, when schools dissolve, the entire water column was integrated with a horizontal resolution of 0.1 nmi and a vertical resolution of 1 m. Results were given in nautical area scattering coefficient (NASC, m^2/nm^2) values.

Table II-2. Settings used for school detection with the Echoview school detection module.

Setting	Value [m]
Minimum total school length	1.0
Minimum total school height	0.8
Minimum candidate length	1.0
Minimum candidate height	0.5
Maximum vertical linking distance	12.0
Maximum horizontal linking distance	20.0

DATA ANALYSIS

The map in figure II-1 was created with Ocean Data View (Schlitzer 2018).

For statistical analyses, we divided our VPR tows into individual vertical transects—one transect was represented by a single down- or upward movement through the water column. Just full surface-to-bottom (and vice versa) transects were utilized in the following analyses. “Surface” and “bottom” were defined for BB tows as 5 and 85 m, and for the tows conducted in AB as 5 and 40 m. With this, we made sure that the compared transects of one basin did all have the same length. BB copepod data below 50 m were neglected in our calculations, because this study focuses on thermocline associated copepods in the upper 50 m of the water column. Below 50 m, high numbers of halocline associated species like *P. acuspes* were found, which would have influenced the DVM analyses. For data from AB, we took copepods from all depth layers (5–40 m) into account, since we know from MSN samples that *Acartia* spp. and *T. longicornis* dominate the copepod community in this basin down to deep layers (figure II-3).

All data analyses were done in the statistical and programming environment R (version 3.3.1; R Core Team 2016).

To account for nonlinear relationships, we fitted a generalized additive model (GAM) after Chambers & Hastie (1993) to our data to model the depth distribution of thermocline inhabiting copepods after equation II-1:

$$depth = s(time, k = 5) \tag{II-1}$$

where k-1 = effective degrees of freedom (edf) and time = calculated mean point in time of every vertical transect of respective VPR tow. The observed copepod depth served as the response variable, while a smoothing term on “time” was used as the explanatory variable. The VPR tows were divided into individual vertical transects to increase the sample size of observations. We set edf to 4, to account for higher non-linear effects of the copepod distribution to “time”. For modelling, we assumed a Gaussian distribution of the copepod distribution.

Due to different sample sizes of the MSN copepod data, we chose a bootstrap approach to ensure more robust results for pairwise comparisons of the groups. Therefore, we randomly selected a certain number of observations per species, which were equal to the lowest number of observations of all tested species. Then a Kruskal-Wallis test was applied due to the non-normal distribution and non-homogeneous variances of our data, followed by a dunn-test for pairwise comparison with a Benjamini-Hochberg adjustment of p-values for multiple comparisons. These tests were done 1000 times, and the results of each pairwise comparison were saved. Subsequently, an average p-value for every comparison was calculated from the saved results.

The overlap between copepod and clupeid DVM patterns was determined with a Mann-Whitney test for two samples with nonparametric data.

R package “mgcv” (version 1.8-12; Wood 2011) was used for GAM establishing, “plyr” (version 1.8.4; Wickham 2011) and “dunn.test” (version1.3.5; Dinno 2017) for data analysis and “ggplot2” (version 2.2.1; Wickham 2009) for visualization purposes.

We were not able to calculate overlaps of copepods and clupeids for morning data from 2014 and evening data from 2015 and 2017, because the VPR hauls of the respective years did not cover the time of day where the clupeid downward migration took place.

Data concerning the depth distribution of *Aurelia aurita* were only available for one basin (BB) and three years (2014, 2016 and 2017). Therefore, no analyses concerning different seasons or basins were possible.

RESULTS

MULTINET COPEPOD DATA

Our multinet (MSN) data from a cruise at the end of August 2015 (figures II-2 & II-3) did show the dominance of *Acartia* spp. as well as *Temora longicornis* in water depths of 19–40 m (Bornholm Basin—BB) and 22–38 m (Arkona Basin—AB). The copepod species composition differed only slightly between BB and AB, with small amounts of *Oithona similis* visible in AB, while no individuals of this species were found in the sample from BB.

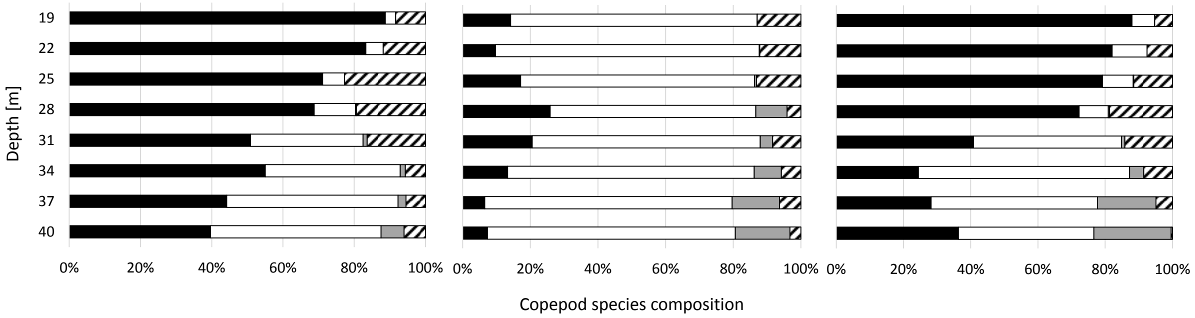

Figure II-2. Multinet data from August 2015, sampled at Bornholm Basin. Black bars—Acartia spp., white bars—Temora longicornis, grey bars—Pseudocalanus acuspes, striped bars—Centropages hamatus; left panel—14h UTC, middle panel—19h UTC, right panel—4h UTC.

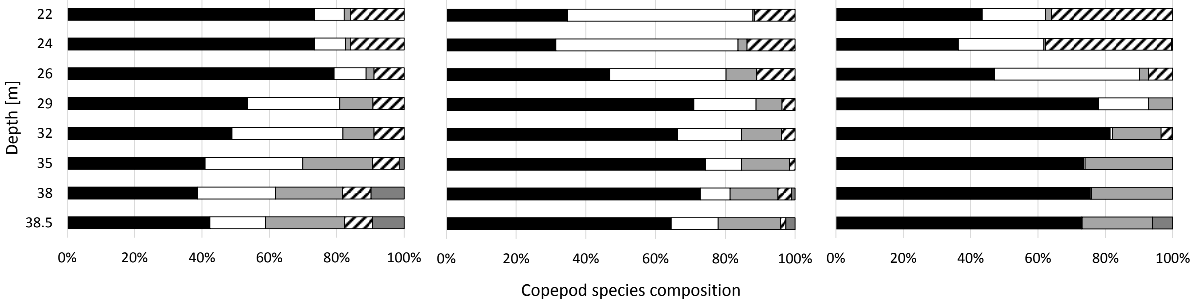

Figure II-3. Multinet data from August 2015, sampled at Arkona Basin. Black bars—Acartia spp., white bars—Temora longicornis, grey bars—Pseudocalanus acuspes, striped bars—Centropages hamatus, dark grey bars—Oithona similis; left panel—14h UTC, middle panel—18h UTC, right panel—3h UTC.

COPEPOD DVM PATTERNS

To verify that the investigated part of the copepod community in the upper 50 m of the water column did show diel vertical migration (DVM) patterns, we tested our Video Plankton Recorder (VPR) derived data with a generalized additive model (GAM). The results showed a significant correlation between the distribution of copepods in the water column and time of day (table II-3). The GAM fitted to the BB summer data showed a statistically significant relationship between copepod depth distribution and time of day for all samples (effect of smoothing term “time”: p<2e-16). The adjusted R^2 of the model was 0.092 (2014, figure II-4a), 0.204 (2015, figure II-4b), 0.132 (2016, figure II-4c) and 0.106 (2017, figure II-4d). Our BB spring sample from 2009 (figure II-4e) showed also statistically significant results (effect of smoothing term “time”: p<2e-16) with an adjusted R^2 of the model of 0.094. Samples from BB did all show the same migration pattern (down by day and up at night), with no differences between seasons. In contrast to that, the AB summer sample showed copepods distributed higher within the water column during day than at night. The GAM fitted to this AB summer data (2014, figure II-4f) showed a statistically significant relationship between copepod depth distribution and time of day (effect of smoothing term “time”: p<2e-16), but an adjusted R^2 of only 0.016.

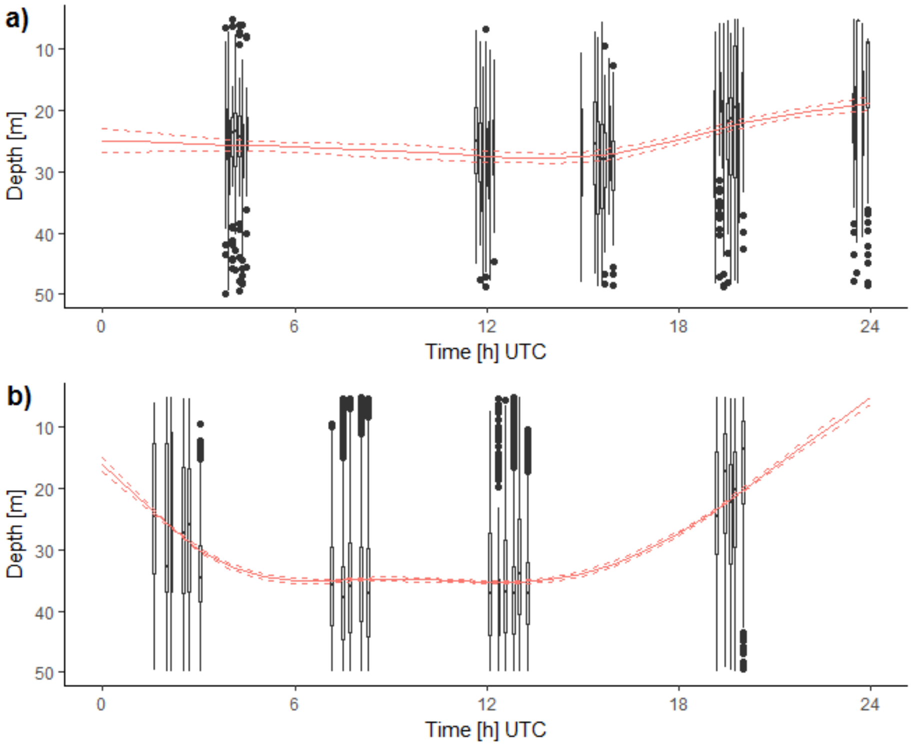

Figure II-4. Copepod depth distribution with GAM for Bornholm Basin samples of a) 13./14.08.2014, b) 06./07.08.2015, c) 09./10.09.2016, d) 27./28.07.2017, e) 17./18.05.2009 and Arkona Basin sample of f) 06./07.08.2014. Boxplots—observed copepod depth distribution (boxes represent the 25th to 75th percentiles of the data, solid black line represents the median; whiskers enclose the largest value no further than 1.5x the distance between first and third quartile to the smallest value at most 1.5x the distance between first and third quartiles; black dots show outliers), solid red line—predicted copepod depth distribution over time, dashed red lines—respective 95% confidence intervals of copepod depth distribution. Data from VPR tows were divided into individual vertical transects to increase sample size of observations.

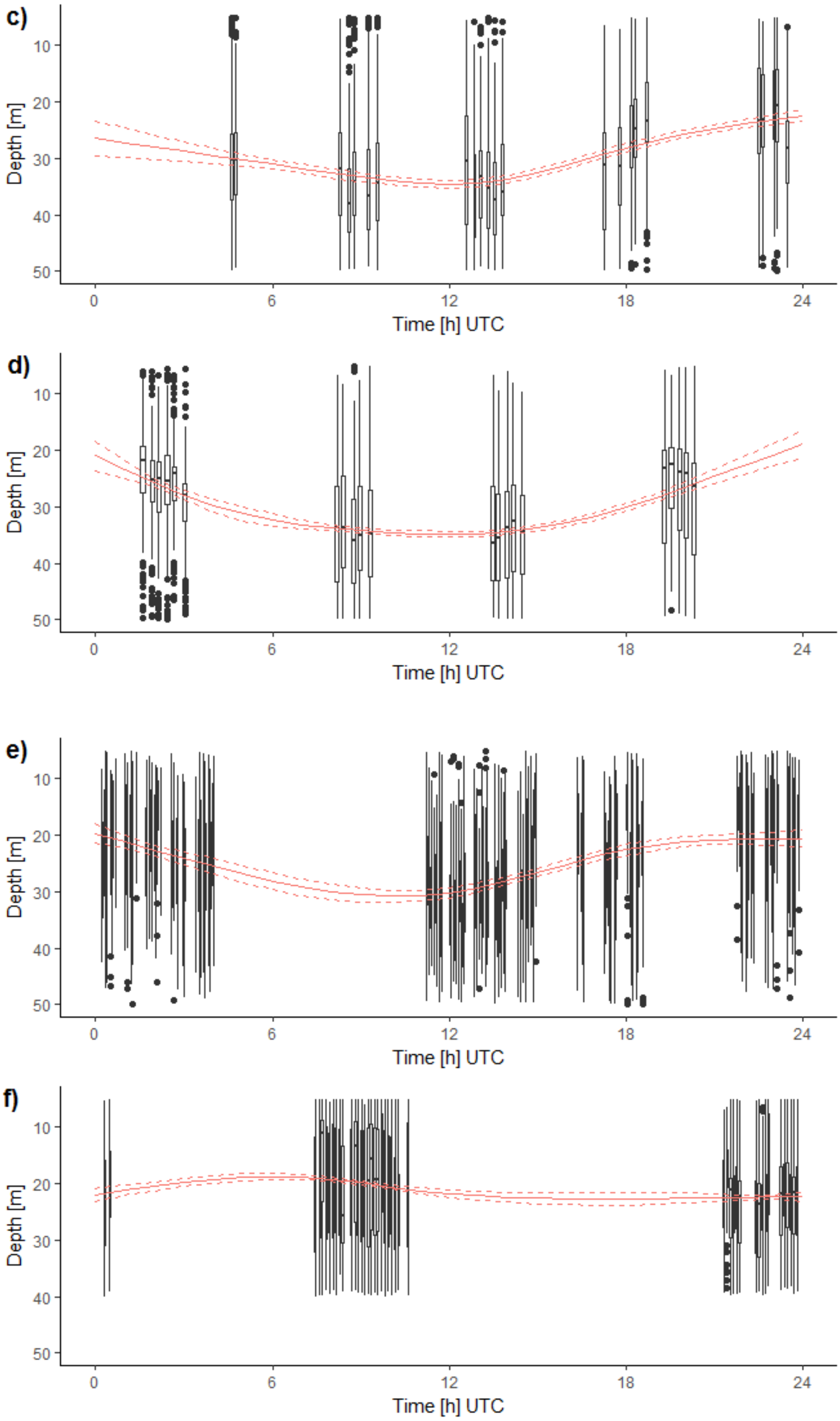

Figure II-4. (Continued)

Table II-3. Results of the generalized additive models (GAMs) fitted to the Bornholm Basin (BB) and Arkona Basin (AB) data of the investigated years.

Sampling time & area	Parameter: Intercept Estimate	Intercept SE	Intercept p-value	s(time) edf	s(time) Ref. df	s(time) p-value	adjusted R-sq.	Deviance explained
08/2014, BB	24.460	0.198	<2e-16	3.819	3.978	<2e-16	0.092	9.34%
08/2015, BB	29.927	0.064	<2e-16	3.991	4.000	<2e-16	0.204	20.40%
09/2016, BB	29.776	0.188	<2e-16	3.833	3.983	<2e-16	0.132	13.30%
07/2017, BB	32.369	0.126	<2e-16	3.742	3.939	<2e-16	0.106	10.70%
05/2009, BB	24.710	0.226	<2e-16	3.779	3.971	<2e-16	0.094	9.51%
08/2014, AB	20.599	0.102	<2e-16	3.829	3.984	<2e-16	0.016	1.66%

COPEPOD DVM PATTERNS—INDIVIDUAL SPECIES

To further investigate the differences between copepod DVM patterns in BB and AB, we took MSN data of individual copepod species from both basins into account. Depth distributions of the four most abundant copepod species from these MSN samples (*Acartia* spp., *T. longicornis*, *Pseudocalanus acuspes*, *Centropages hamatus*) were determined for depth layers from 20–40 m. A clear DVM pattern was visible for *Acartia* spp., *T.longicornis* and *C. hamatus* in the BB sample (figure II-5)—an upward migration took place in the afternoon, and a downward migration in the morning. *P. acuspes* showed only a weak shift in its depth distributions within the lower sampled depth layers over the course of the day. Nevertheless, the depth distributions of afternoon and morning differed both significantly from the evening distribution (Kruskal-Wallis rank sum test; $p<0.05$) in all of the sampled species.

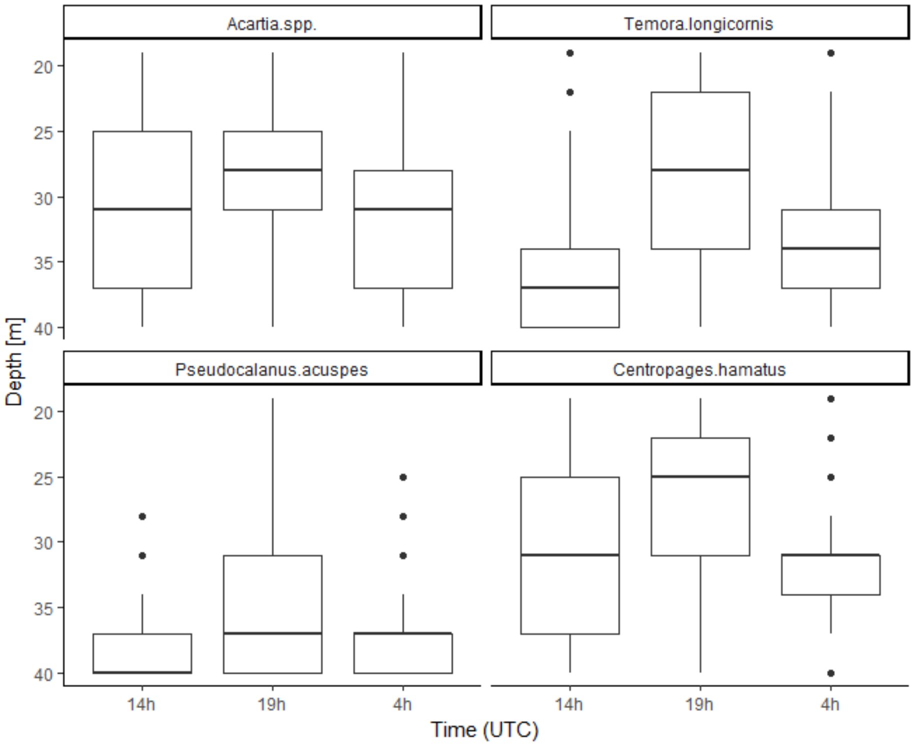

Figure II-5. Diel vertical migration patterns of individual copepod species from Bornholm Basin. Data derived from MSN samples taken on 22./23./24.08.2015. Boxes represent the 25th to 75th percentiles of the data, solid line represents the median. Whiskers enclose the largest value no further than 1.5x the distance between first and third quartile to the smallest value at most 1.5x the distance between first and third quartiles. Black dots show outliers.

In the AB sample, two different DVM patterns were found (figure II-6). While *Acartia* spp. and *P. acuspes* showed the same migration pattern as their conspecifics in BB (upward in the afternoon, downward in the morning), *T. longicornis* and *C. hamatus* migrated in a different way. Neither species did show a downward migration in our morning sample. Depth distributions of *Acartia* spp. did not differ significantly between the samples. Afternoon and morning samples of *P. acuspes* differed significantly from the evening distribution (Kruskal-Wallis rank sum test; $p<0.05$). Evening and morning samples of *T. longicornis* differed significantly from the afternoon distribution (Kruskal-Wallis rank sum test; $p<0.05$), and significant differences between all samples of *C. hamatus* were found (Kruskal-Wallis rank sum test; $p<0.05$).

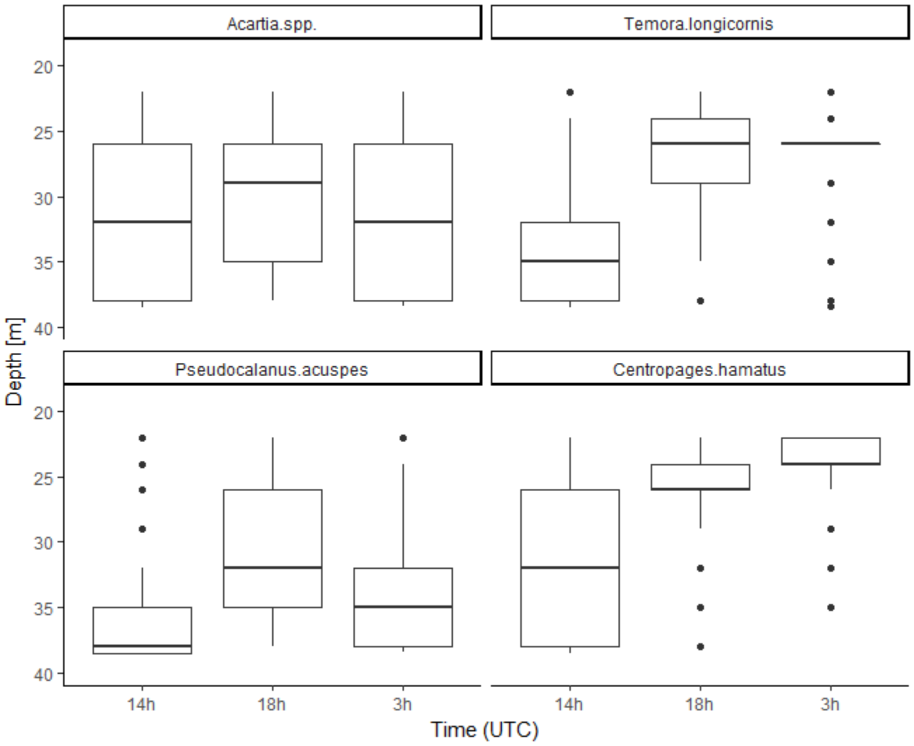

Figure II-6. Diel vertical migration patterns of individual copepod species from Arkona Basin. Data derived from MSN samples taken on 26./27./28.08.2015. Boxes represent the 25th to 75th percentiles of the data, solid line represents the median. Whiskers enclose the largest value no further than 1.5x the distance between first and third quartile to the smallest value at most 1.5x the distance between first and third quartiles. Black dots show outliers.

CLUPEID DVM PATTERNS

To find evidence for a possible predator avoidance DVM in copepods, we compared the migration patterns of copepods with those of clupeids. All samples showed the same migration pattern for clupeids, regardless of investigated season or basin: downward migration in the morning and upward migration in the evening (figure II-7). In BB, copepods stayed in the same depth layers as clupeids at night, and migrated in the same direction as their planktivorous predators during the morning and evening migrations. Oxygen levels did not seem to influence the migrations of neither copepods nor clupeids while the depth of the thermocline seemed to influence the amplitude of copepod DVM, and the location of the halocline seemed to determine how deep clupeids migrated during the day.

OVERLAP COPEPOD & CLUPEID DVM

We compared the depth distribution of copepods and clupeids during the time of the clupeid downward migration in the morning and their upward migration in the evening, to determine if the assumed predator-prey overlap between the two groups could be verified. No significant differences were found between copepod and clupeid samples from morning 2009, evening 2009, evening 2014, morning 2015 and morning 2016 (Mann-Whitney test; $p>0.05$; figure II-8 a–e). Only the samples from evening 2016 and morning 2017 showed significant differences between the copepod and clupeid depth distribution (Mann-Whitney test; $p<0.05$; figure II-8 f–g).

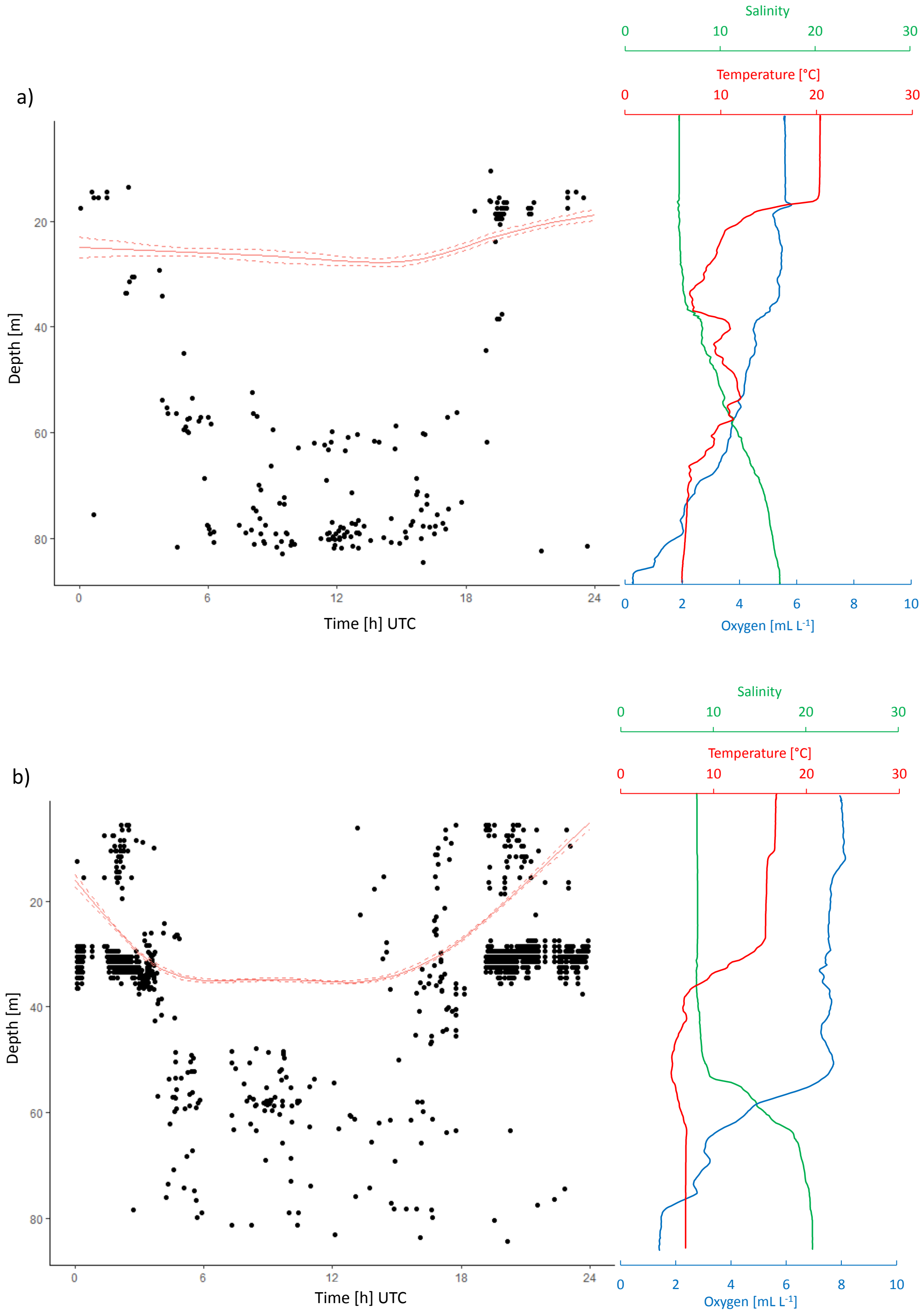

Figure II-7. Clupeid and copepod diel vertical migration patterns from Bornholm (BB) & Arkona Basin (AB) with respective hydrographical data. Left panels: black dots—clupeids, solid red line—predicted copepod depth distribution over time, dashed red lines—respective 95% confidence intervals of copepod depth distribution. Right panels: red line—temperature [°C], blue line—oxygen [mL L^{-1}], green line—salinity. A) Copepod & fish data from 13./14.08.2014, ctd data from 13.08.2014, 11:07h UTC, BB, b) copepod & fish data from 06./07.08.2015, ctd data from 05.08.2015, 00:14h UTC, BB, c) copepod & fish data from 09./10.09.2016, ctd data from 10.09.2016, 19:05h UTC, BB, d) copepod & fish data from 27./28.07.2017, ctd data from 24.07.2017, 22:15h UTC, BB, e) copepod &

fish data from 17./18.05.2009, ctd data from Möller (2013)—May 2009, BB, f) copepod & fish data from 06./07.08.2014, ctd data from 06.08.2014, 15:25h UTC, AB.

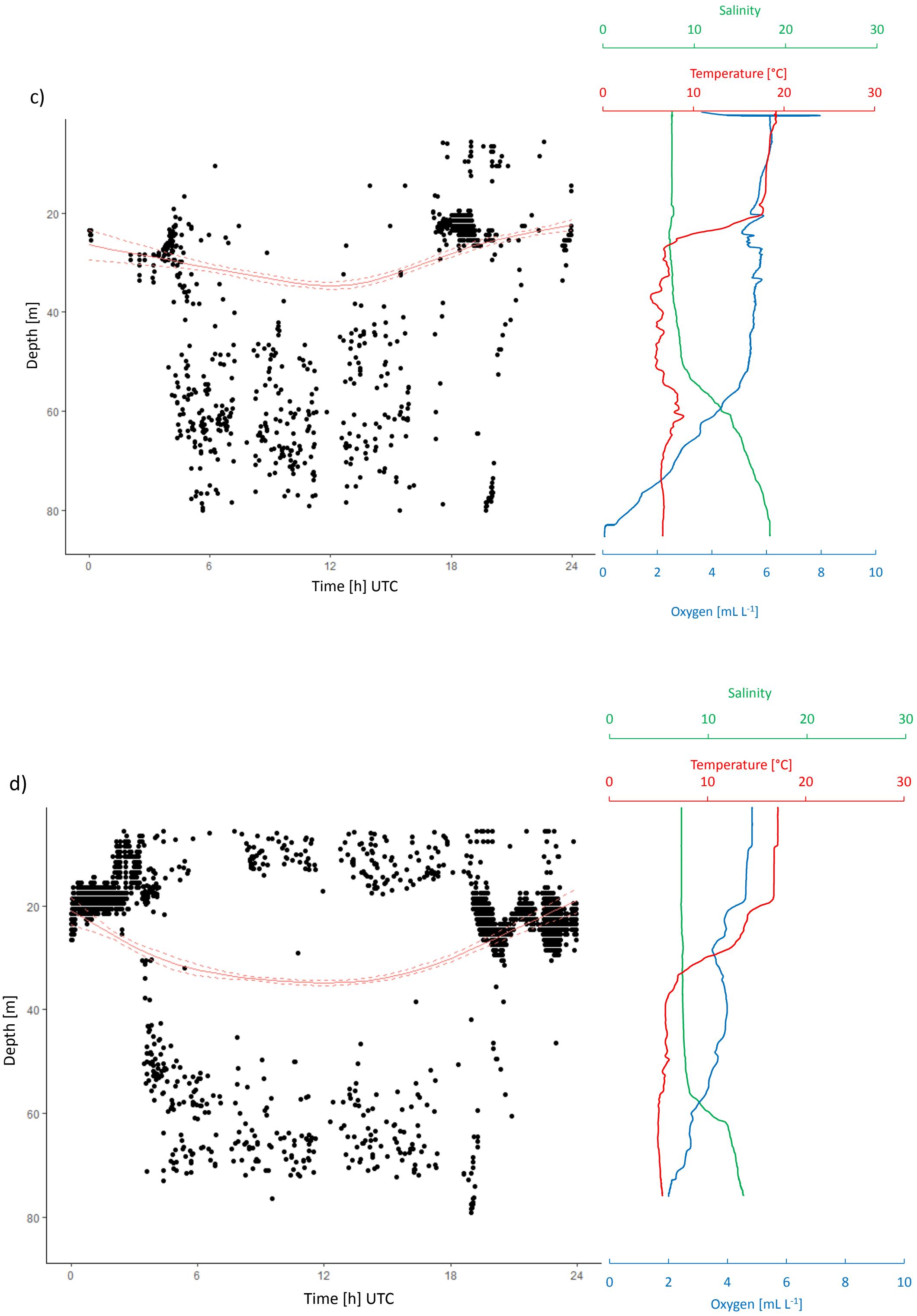

Figure II-7. (Continued)

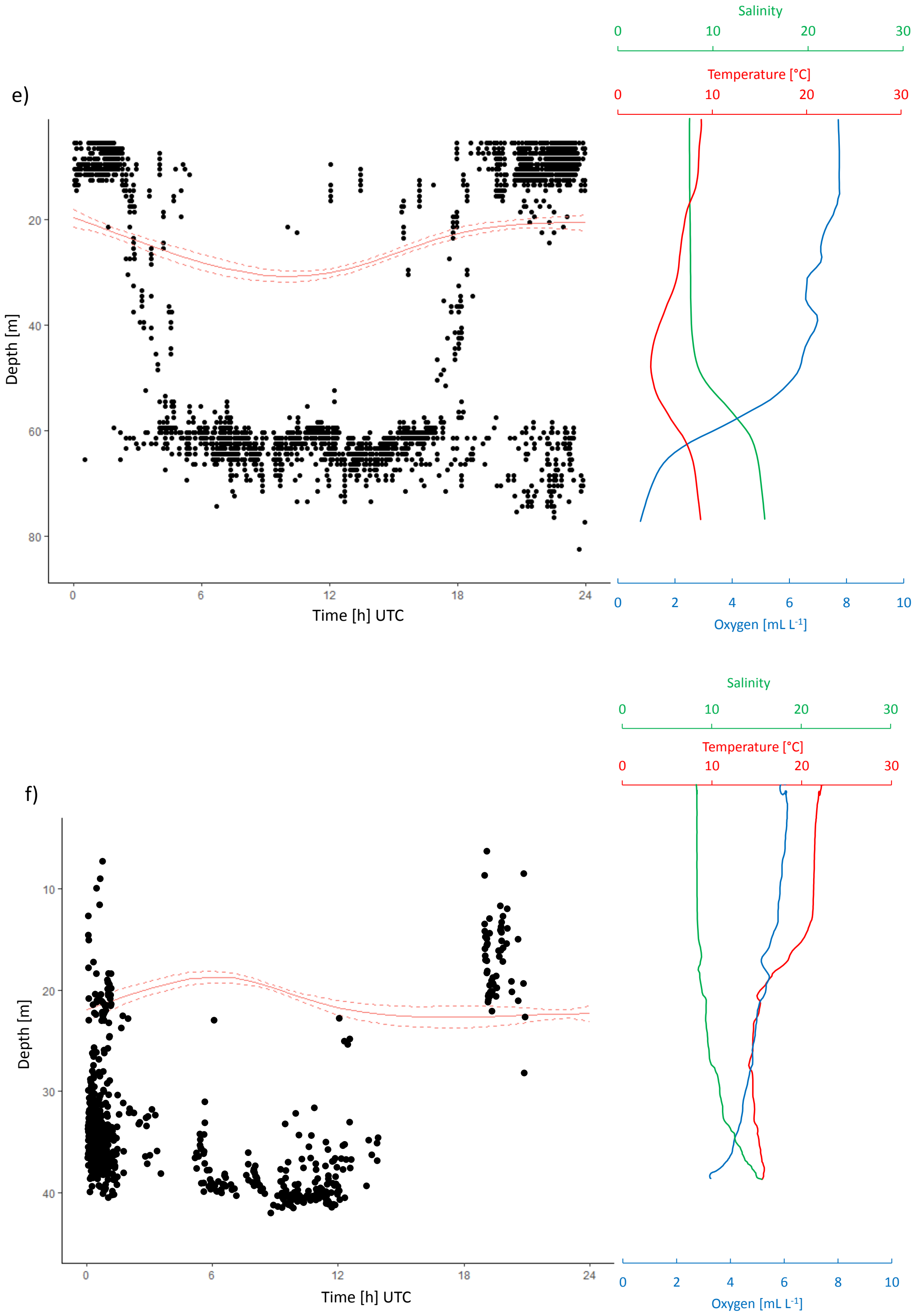

Figure II-7. (Continued)

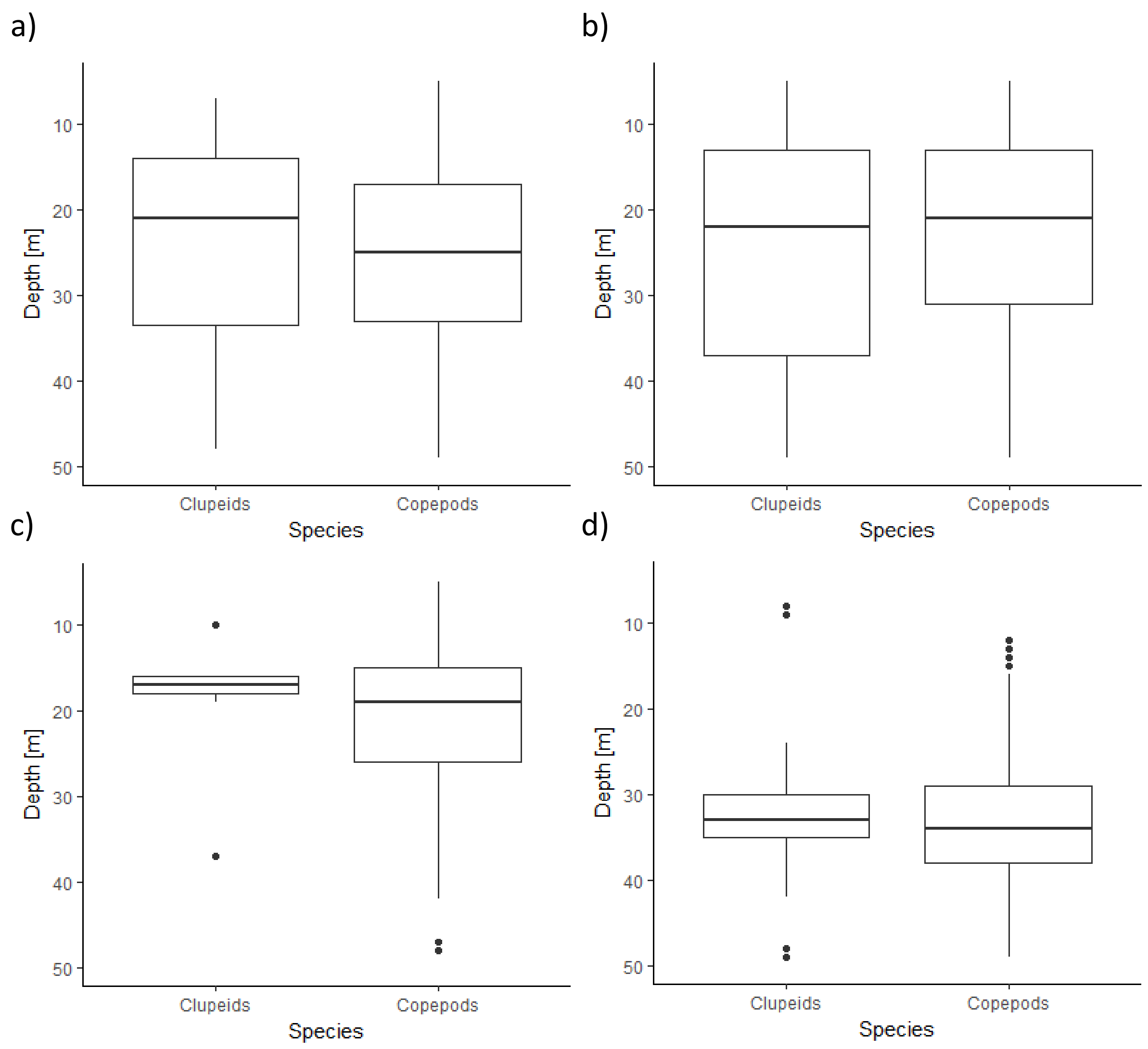

Figure II-8. Depth distribution of copepods and clupeids during the morning downward and evening upward migration of both groups within the upper 50 m of the water column in Bornholm Basin. Boxes represent the 25th to 75th percentiles of the data, solid line represents the median. Whiskers enclose the largest value no further than 1.5x the distance between first and third quartile to the smallest value at most 1.5x the distance between first and third quartiles. Black dots show outliers. A) Morning 2009, 02:24–4:48h UTC, b) evening 2009, 16:48–19:12h UTC, c) evening 2014, 17:00–19:23h UTC, d) morning 2015, 03:00–05:30h UTC, e) morning 2016, 03:00–05:30h UTC, f) evening 2016, 15:30–18:00h UTC, g) morning 2017, 03:00–05:00h UTC.

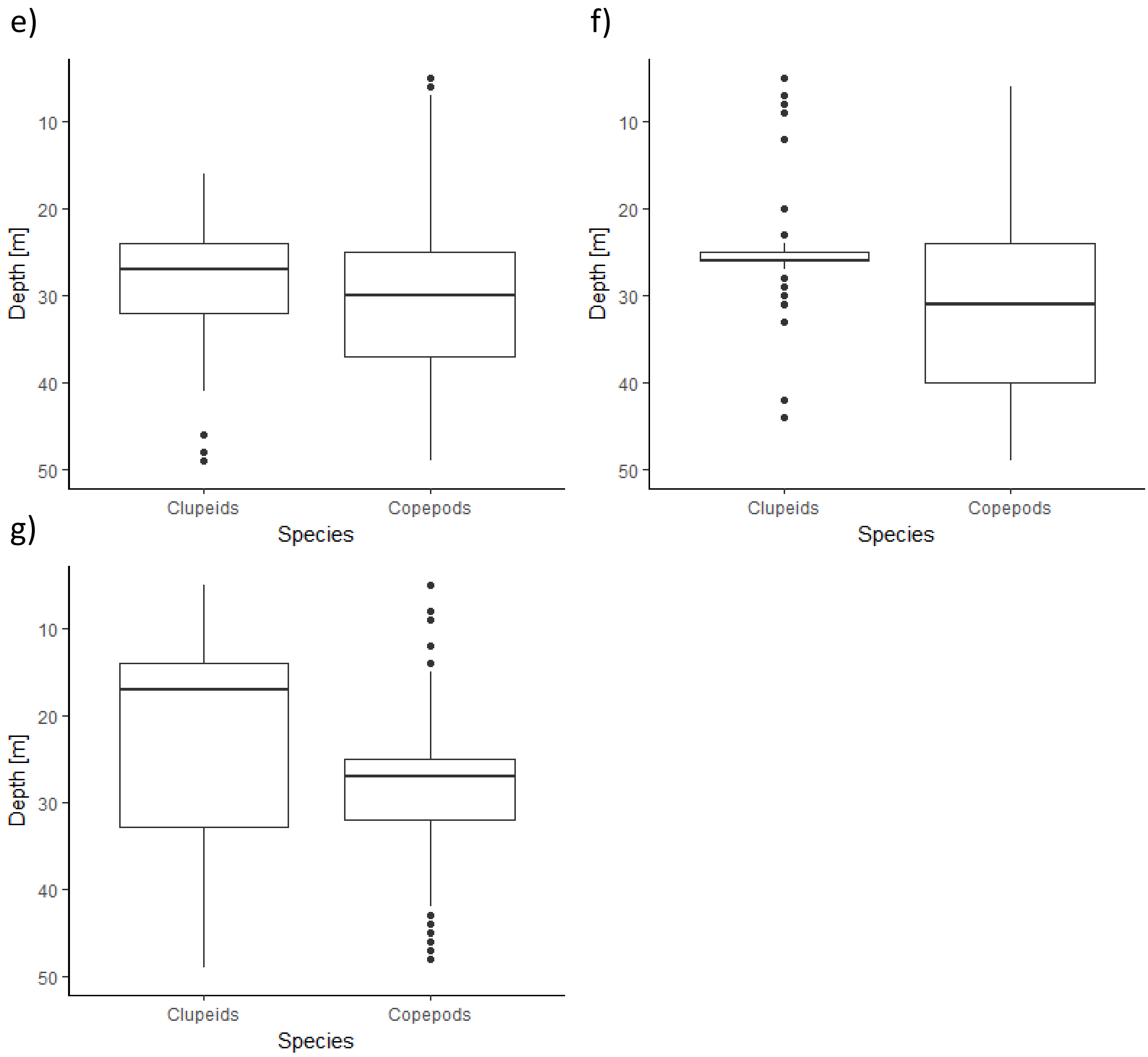

Figure II-8. (Continued)

COPEPOD & *AURELIA AURITA* DISTRIBUTION

Since other predators besides clupeids might trigger a predator avoidance DVM in copepods, we investigated the depth distribution of the moon jellyfish *Aurelia aurita* in BB. No consistent pattern was evident between the investigated years or time of day. In 2014 (figure II-9a), most of *A. aurita* were visible within the upper 20 m of the water column, throughout the day. During the investigated 24h period, no clear DVM pattern was visible. Copepods were found below *A. aurita* during the day, but migrated into shallower depth layers inhabited by jellyfish in the evening. Data from 2016 (figure II-9b) showed a more distinct *A. aurita* DVM, with a distribution deeper than 20 m in the afternoon. In this year, copepods resided again below the layers with *A. aurita* during the day, and migrated nearer to the surface and into jellyfish occupied water layers during the evening. In contrast, our third sample—from 2017 (figure II-

9c)—showed the sampled *A. aurita* within the upper 10 m of the water column during night, midday and evening, with a deeper distribution (15 m) in the morning. Here, copepods did not reach water layers with jellyfish during any time of the day.

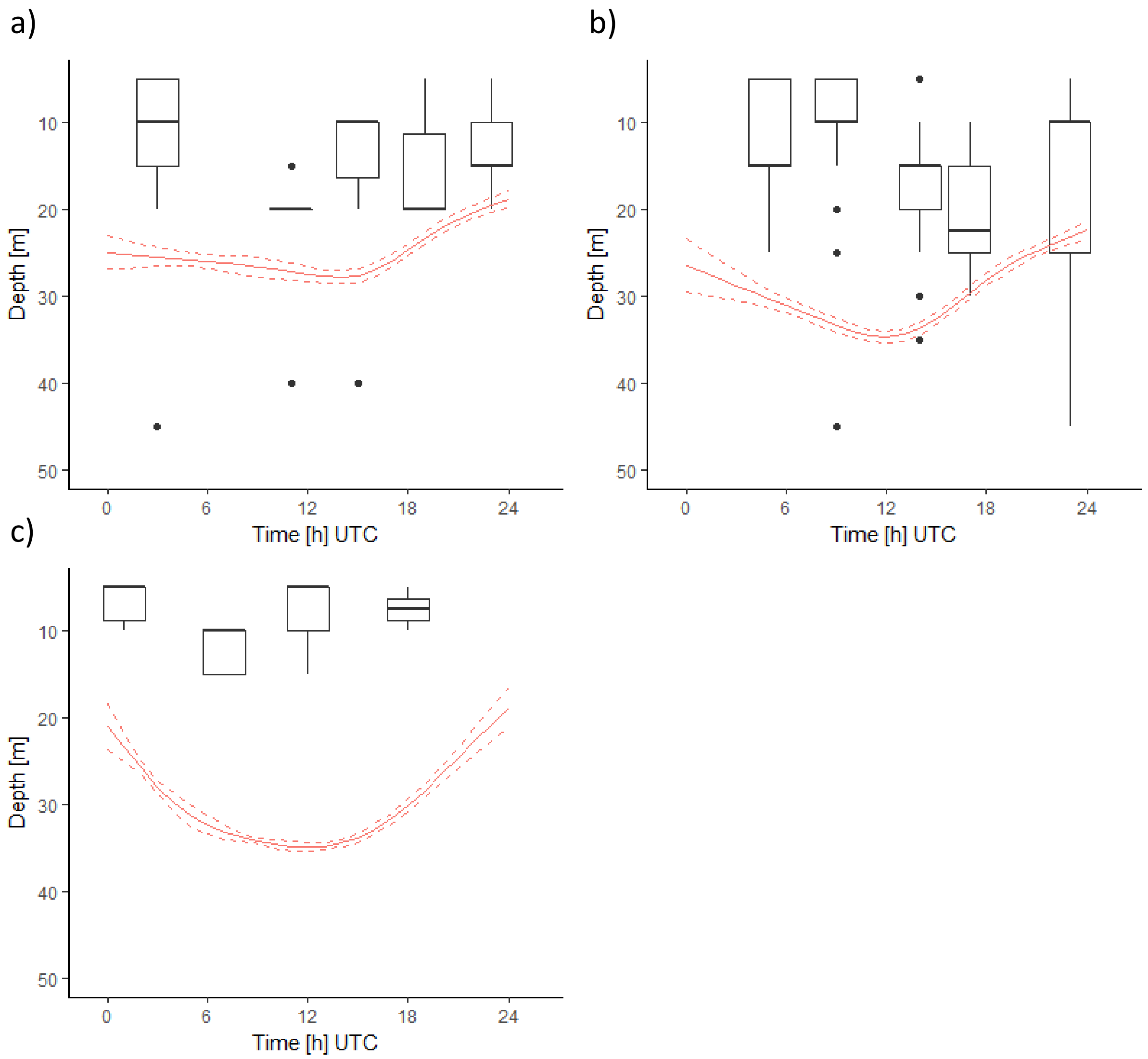

Figure II-9. Depth distribution of copepods and the moon jellyfish Aurelia aurita within the upper 50 m of the water column in Bornholm Basin. Boxes represent the 25th to 75th percentiles of the data, solid black line represents the median. Whiskers enclose the largest value no further than 1.5x the distance between first and third quartile to the smallest value at most 1.5x the distance between first and third quartiles. Black dots show outliers. Solid red line shows the predicted copepod depth distribution over time, dashed red lines show the respective 95% confidence intervals of the copepod depth distribution. A) Copepod & jellyfish data from 13./14.08.2014, b) copepod & jellyfish data from 09./10.09.2016, c) copepod & jellyfish data from 27./28.07.2017.

DISCUSSION

MULTINET COPEPOD DATA

The assumption that most of the copepods identified on our Video Plankton Recorder (VPR) derived rois belong to the species *Acartia* spp. and *Temora longicornis* was verified through the results of our multinet (MSN) samples. Here, these copepod species dominated the upper 40 m of the Bornholm Basin (BB) water column. This agrees with the literature where it is reported that *Acartia* spp. and *T. longicornis* reside in the upper 50 m of BB and the Baltic Proper water column (Hernroth & Ackefors 1979, Dutz et al. 2010 & 2012), and moreover dominate this layer together with *Centropages hamatus* during summer in BB (Bernreuther et al. 2013). The same holds true for our VPR spring sample, because Möller et al. (2012) showed for April 2002 that the upper 20 m of BB were also clearly dominated by *Acartia* spp. and *T. longicornis*.

COPEPOD DVM PATTERNS

Results from Arkona Basin (AB) have to be considered with care in terms of copepod diel vertical migration (DVM) behaviour and the overlap of copepod and clupeid DVM patterns. Only two AB samples from one investigated year were available for this study and these samples did not cover a full 24h cycle. Nevertheless, results from AB seem to hint towards different copepod DVM patterns in AB and BB. When analysing DVM behaviour of the main copepod species from MSN samples of both basins, we found two species in AB that showed a different depth distribution than the same species did in BB. At first sight these results suggest that *T. longicornis* and *C. hamatus* from AB stayed longer in shallower water layers in the morning and started their downward migration later than they did in BB. These differences could lead to the observed daytime copepod distribution in AB that was nearly twice as broad as the night-time distribution (figure II-4f). With some species starting their downward migration later than others, a part of the copepod community does already reside in deeper water layers in the morning, while the rest still lingers in shallower layers. The upward migration in the evening seemed to start for all species at the same time, resulting in a narrower distribution visible in the night sample. However, morning samples from AB and BB were not taken at exactly the same time of day. AB data resulted from a sample taken at 03:00h UTC, while data from BB were sampled one hour later. According to Tiselius & Jonsson (1990), the sinking speed of *T. longicornis* is 2.5 mm s^{-1}. This would result in a possible downward migration of 9 m in one hour. Therefore, it might be possible that the different depth distributions visible in our data result not from general differences in DVM behaviours of the individual species, but rather from the temporal differences in plankton sampling.

When further comparing our results from AB and BB, both samples showed a less pronounced DVM pattern in *Acartia* spp. than in *T. longicornis*. This agrees with data from the literature. The DVM pattern of *Acartia* spp. is described as not strong (Holliland et al. 2012) and less pronounced as in *T. longicornis* (Hansson et al. 1990).

OVERLAP COPEPOD & CLUPEID DVM

Results from BB showed that copepods and clupeids migrated into the same direction during their morning descent and evening ascent. DVM behaviour of clupeid fish, like sprat, is often explained as a predator avoidance mechanism against e.g. seabirds (Sparholt 1994, Österblom et al. 2006). Some of these birds, as the common guillemot (*Uria aalge*), are able to dive deeper than 100 m (Piatt & Nettleship 1985, Burger & Simpson 1986). Other predators that clupeids might avoid through DVM are piscivorous fish like salmon (*Salmo salar*, Karlsson et al. 1999) and garfish (*Belone belone*, Dorman 1991) as well as their main predator cod (*Gadus morhua*, Bagge et al. 1994). Besides predators, hydrographic conditions might play a crucial role in the DVM of clupeids. The depth of the downward migration in BB seems to be connected to salinity. When higher salinity levels occur in BB only in deep layers, clupeids do migrate deeper down during the day. Habitats with higher salinity levels seem to be favourable for clupeids, because they ensure that metabolic costs for osmo- and ionoregulation stay low (Jobling 1994, Wootton 1998, Cardinale et al. 2002). On the other hand, high salinity levels can negatively influence egg survival. Petereit et al. (2009) showed that higher salinities experienced during fertilization and incubation lead to lower egg buoyancy of these eggs, which in turn determines the oxygen conditions eggs experience during their development.

Only two of our samples (evening 2016; figure II-8f & morning 2017; figure II-8g) showed significant differences (Mann-Whitney test; $p<0.05$) between copepod and clupeid depth distributions during the timing of down- and upward migrations. In the morning sample from 2017, a large part of the clupeids did still reside in water layers near the surface, while the copepods—with the rest of the clupeids—had already reached layers around 30 m. In 2016, the copepods were broadly distributed from 20–50 m in the evening, while most of the clupeids had already reached shallower layers around 25 m.

We know from the literature that clupeids exert a distinct predation pressure on copepods during down- and upward migration. Just recently, Kulke et al. (2018) reported that up to 84% of the sprat total daily ration was consumed in upper layers as well as during sprat migrations. In addition, the authors found that stomachs from sprat caught directly after the downward migration in the morning consisted of up to 54% (AB) and 60% (BB) of *T. longicornis*. This means that sprat had fed during their descent extensively on a copepod species that resides in the upper 50 m of the water column. Therefore, the copepod migration pattern observed in our study does not support the assumption of a predator avoidance strategy against clupeids.

Despite this predation pressure by sprat on thermocline inhabiting copepods during dawn and dusk, the overall top-down control of copepods seems to not be very strong. Bernreuther et al. (2018) showed that only 18% of the annual *T. longicornis* and 1.4% of the *Acartia* spp. production were utilized by hering and sprat in BB.

COPEPOD & *AURELIA AURITA* DISTRIBUTION

Nevertheless, the copepod DVM investigated here might be an avoidance strategy against a predator other than clupeids—e.g. jellyfish like *Aurelia aurita.* Through their migration, copepods are protected from predation by *A. aurita* at least during the day. However, the predation impact of *A. aurita* on copepods in BB was shown to be very low. Barz & Hirche (2005) reported that during August, when *A. aurita* abundances are highest, only 0.1% of the copepod standing stock were consumed per day. A similar low impact has been reported for another potential predator—mysid shrimps. These predators do prey on copepods, especially *T. longicornis* and *Pseudocalanus acuspes* (Barz & Hirche 2009), but occur in BB only in low abundances (Salemaa et al. 1990, Margonski & Maciejewska 1999, Barz & Hirche 2009). Therefore, they do not represent important zooplankton predators in this basin. Mysids in the Baltic seem to be depending on access to the sea floor, which is not possible in the deep basins like BB due to oxygen deficiency (Barz & Hirche 2009). Barz & Hirche (2005) did also report, that *A. aurita* was found in BB from July to November, meaning it is still absent in spring. Since we know that DVM behaviour of copepods can stop when its trigger disappears (see chapter I of this thesis), the 2009 sample (figure II-4e) should show no DVM pattern if DVM of the thermocline associated copepods would represent a predator avoidance strategy against jellyfish.

OTHER CAUSES FOR DVM

Another factor assumed to be regulating DVM is the avoidance of enhanced exposure to direct sunlight (Williamson et al. 1994). Solar radiation can have lethal effects on zooplankton organisms (Huntsman 1924) living in surface waters. Natural ultraviolet radiation levels were shown e.g. to increase respiration rates in cladocerans (Fischer et al. 2006) and decrease copepod egg production (Karanas et al. 1981). However, in summer only 1% of the downward irradiance that hits the water surface of the Baltic Sea reaches depths of ca. 20 m (Dera & Woźniak 2010), while copepods migrate towards much deeper layers during the day (figure II-4). Furthermore, Dera & Woźniak (2010) (in accordance with Lampert & Sommer 1993) report that UV radiation does only reach the surface layers of the Baltic Sea, which would then not explain the deep daytime migration of copepods.

A recent study (Häfker et al. 2017) shows, that DVM in *Calanus finmarchicus* is driven by circadian clock genes, and not controlled by exogenous factors such as light or the presence of predators. An endogenous clock ensures that copepods are able to anticipate day/night cycles and adjust their behaviour—like predator avoidance migration—and their physiology accordingly (Häfker et al. 2017). The adjustment of copepod physiology includes e.g. a respiration increase prior to the energy demanding upward migration in the evening and production of digestive enzymes prior to feeding at the surface, to increase the amount of food that can be consumed in a limited time (Häfker et al. 2017). Such endogenous triggers might play a role in copepod DVM from our samples, too. The expression of circadian clock genes could on the one hand ensure that copepods leave higher water layers during the day and reduce the risk of visual predators, while saving energy in cooler water layers (Lampert 1989, Schmidt 2006) which can be used to increase fecundity (McLaren 1963). On the other hand, endogenous clock genes could ensure feeding on phytoplankton near the surface when the cells reach their highest energy content after sunset. Lampert (1989) and Lampert & Sommer (1993) stated that algal biomass and quality of the phytoplankton cells must be higher in the evening/at dusk, since photosynthesis takes place during the day and reserve substances fill the cells at dusk. Copepods that migrate toward the surface in the evening will therefore feed at elevated feeding rates on phytoplankton with higher nutritional quality after their starvation period during the day (Lampert 1989). Häfker et al. (2017) reported of the circadian clock being responsible for persistent DVM in *C. finmarchicus* despite constant darkness. An endogenously triggered DVM of thermocline associated copepods would persist in seasons with no *A. aurita* predators visible in BB, as is the case in our spring BB sample. Contrary to this internally programmed migration behaviour, DVM observed in *P. acuspes* (chapter I of this thesis) seems to be triggered exogenously, since it is only visible in situations with high predator densities. In the presence of low predator densities, DVM of *P. acuspes* stops. However, the DVM pattern visible in *P. acuspes* individuals from 2015 (figures II-5 & II-6) seems not to represent the same DVM behaviour as investigated in chapter I of this thesis. In the data from 2015, *P. acuspes* individuals were observed within the upper 50 m of the water column, and not in the usual *P. acuspes* habitat around the halocline. In chapter I of this thesis, the occurrence of individual *P. acuspes* females above 50 m was hypothesized to represent a part of the ontogenetic migration of this species. Since the MSN data used here in chapter II do not account for different copepod sexes, we have no information on whether *P. acuspes* males were also found in water layers above 50 m. However, the *P. acuspes* DVM pattern observed in data from 2015 might represent a trait-off between feeding at the thermocline, since the ususal feeding grounds at the halocline are out of reach, and an attempt to avoid warm temperatures and/or osmotic stress due to low salinities.

CONCLUSION

We conclude that DVM of the thermocline associated copepods in BB does not represent a predator avoidance strategy against clupeids, because it leads to a high overlap of copepods and their planktivorous predators during times with high predation pressure of clupeids on copepods. We also conclude that the copepods examined in this study do not show a predator avoidance strategy against jellyfish like *A. aurita* either, since the copepod DVM persists even in seasons with no *A. aurita* predators visible in BB, like spring. Instead, it seems possible that the observed DVM in thermocline associated copepods is triggered endogenously, to ensure the most effective utilization of available food and handling of metabolic needs.

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Chapter III

Investigating copepod patches and their implications on sprat (*Sprattus sprattus*) feeding in the Baltic Sea

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ABSTRACT

Zooplankton in the oceans is not distributed homogeneously but rather occurs in non-random aggregations referred to as patches. These patches can range from centimetres to kilometres in size. Nevertheless, data on plankton patch dimensions are scarce, especially for the Baltic Sea. Knowledge about the dimensions of patches can help to increase the accuracy of estimations on zooplankton abundances and population sizes. These are important information that are used in ecosystem models and for estimations on the development of fish stock biomass. In this study, we focus on the measurement of copepod patches in three different basins of the Baltic Sea (Arkona, Bornholm and Gotland Basin) through the use of a Video Plankton Recorder (VPR). To our knowledge, this is the first study on this topic conducted for the Baltic Sea. We can confirm that diel vertical migration (DVM) of copepods leads to the formation of patches. Many small patches were visible in the evening, when copepods migrate upwards through the water column towards the thermocline. In the night, we found only few but very large patches, directly below the thermocline after copepod migration. Calculated patch areas ranged from under one to several thousand m^2. Furthermore, we applied a temperature- and size-dependent functional response model to predict sprat stomach content weights with VPR derived copepod abundances from the field. Our results suggest that the high variability in sprat stomach content weights that is constantly found during fishery hauls in the early morning hours after the downward migration of clupeids is a result of a patchy copepod distribution.

INTRODUCTION

It has been known for a long time that planktonic particles aggregate in the marine environment and are not distributed homogeneously. Throughout the literature, these aggregations are described and defined in various ways. The non-random aggregation of plankton is called patchiness (Greer et al. 2016). Patches are regions that show a higher abundance of planktonic organisms than the surrounding habitat, where organism concentrations are usually twice the mean concentration, but can also be as high as 10 times the mean (Owen 1989, Folt & Burns 1999). Patches are found on different spatial scales, which range from micropatches with a few centimetres to meters (Owen 1989, Davis et al. 1992) to meso- and megascale patches that can extend for hundreds and thousands of meters (Haury et al. 1978, Pinel-Alloul 1995). Another concept for a non-homogeneous distribution of plankton particles is termed “swarms”. Swarms are dense patches wherein the individuals are not aligned in the same direction, move more or less randomly and where concentrations can be five to 1000 times higher than in normal patches (Haury & Yamazaki 1995, Leising & Yen 1997, Folt & Burns 1999). Swarms consist usually of a single species (Mauchline 1998), but can also comprise of different species (Omori & Hamner 1982) and different developmental stages of the respective organisms (Mauchline 1998). Swarm sizes can range from 0.1 m^{-3} to 60.0 m^{-3} (Omori & Hamner 1982) and feature low nearest neighbour distances of the organisms within the swarm (Mauchline 1998). If the aggregated organisms do have the same size, are spaced evenly and face the same direction, the swarm is called a “true school” (Omori & Hamner 1982). For a long time, only large-scale physical processes were supposed to lead to the formation of patches, but nowadays the contribution of biological processes is widely acknowledged (Pinel-Alloul 1995, Folt & Burns 1999, Klais et al. 2016). Nearly 50% of the spatial variation in zooplankton community structure result from behavioural processes, such as predation and food searching, thereby counteracting physical forces (Folt & Burns 1999). Consequently, zooplankton patchiness is the result from a combination of physical and biological processes (Mackas et al. 1985, Pinel-Alloul 1995). On small scales, distribution of zooplankton organisms is dominated by biological processes while on large scales physical processes are more important (Haury et al. 1978, Daly & Smith 1993). There are four main biological drivers for the formation of patches: diel vertical migration (DVM), predators/predator avoidance, food and mating (Tokarev et al. 1998, Folt & Burns 1999). DVM leads to a periodic aggregation of zooplankton in certain depths and can therefore be described as the most powerful biological driver of patchiness (Folt & Burns 1999). Predator avoidance can act as a direct as well as an indirect driver of patch formation. Either through the direct removal of prey organisms from their spatial distribution by predators or the triggering of a predator avoidance response like DVM, which leads to indirect aggregative patterns (Folt et al. 1993, Folt & Burns 1999). Food distribution can also lead to copepod patches through the response of copepods to chemical exudates (Poulet et al. 1991) and their ability to actively stay with a food patch by adjusting their swimming behaviour (Williamson 1981, Tiselius 1992). Aggregative mechanisms are also a way for zooplankton to encounter mates. Some organisms can only rely on finding mates in patches that are formed by physical processes or DVM (Folt & Burns 1999), while others—like many copepods—can track mates by chemoreception and thereby aggregate at small scales (Davis et al. 1992, Folt & Burns 1999). Zooplankton patches can have large impacts on the dynamics of marine ecosystems and their populations. This is through the influence of predator-prey interactions (Lasker 1975, Davis et al. 1992) by modifying encounter rates of predators and their prey (Davis et al. 1991) as well as the influence of trophic transfer rates (Greer et al. 2016). However, studying zooplankton patches and their dimensions is nearly impossible with traditional gear such as plankton nets. The sample volumes of these nets are difficult to control (Greer et al. 2016), mesh clogging can be a problem as well as active avoidance of the net by zooplankton organisms (Yentsch & Duxbury 1956, Zhou et al. 1994). Additionally, the minimum patch scale that can be detected horizontally matches the net tow length, which often covers hundreds of meters (Greer et al. 2016). Therefore, an unobtrusive video system like the Video Plankton Recorder (VPR) (Davis et al. 1992) that is able to continuously record data on plankton distribution along a chosen tow track is a promising alternative for this kind of investigation. The VPR provides high-resolution taxa-specific information on plankton distribution (Davis et al. 2005) on large as well as small scales, and is therefore perfect for studying plankton patchiness. Since Owen (1989) reports that stable water layers lead to greater patchiness, we chose the Baltic Sea with a stable stratification of the water column throughout the summer months as sampling location for the investigation of copepod patches. From spring to autumn, the Baltic Sea features a thermocline in 20 to 30 m depth (Grønkjær & Wieland 1997), which separates warmer surface water from colder water layers in the deep. We described the DVM patterns of copepods associated with this thermocline in chapter II of this thesis. Here, we focus now on the patches resulting from this DVM behaviour.

In the Baltic Sea, sprat (*Sprattus sprattus*) also show DVM. They spend the day in deeper water layers near the halocline and the night in surface waters (Orlowski 2000, Cardinale et al. 2003, Nilsson et al. 2003). Most of their feeding takes place in the upper water layers. Kulke et al. (2018) recently discovered that up to 84% of sprat daily ration are consumed in upper water layers during the down- and upward migration of these clupeids. While there is a distinct spatial overlap between sprat and their copepod prey during these migration phases (chapter II of this thesis), copepods seem to not be top-down controlled in the Baltic Sea (Bernreuther et al. 2018). Thus, it seems as if sprat were not able to utilize the available copepod abundances. A possible explanation for this might be a patchy copepod distribution. Patchiness of prey organisms has been described as a protection mechanism against predators (Omori & Hamner 1982, Folt & Burns 1999). This is due to two mechanisms (Pijanowska & Kowalczewski 1997). First, predators might be confused by the high amount of moving prey organisms and thus show a longer hesitation period. Second, the dilution effect lowers the risk for the individual prey organism of being captured when it is hiding among a high number of other prey organisms. In addition, a patchy prey distribution might influence the downward migration of individual sprat. The downward migration at dawn takes approximately 2 hours (Kulke et al. 2018). However, hydroacoustic data show that not all sprat migrate downward simultaneously (chapter II of this thesis). Rather, it appears that some individuals reach deep water layers very quickly, while others stay in upper waters longer. Changing light conditions are assumed to be the main driver in fish DVM (Mehner 2012). Since this driver affects all individual sprat equally, another factor has to be responsible for the different timing in the downward migration of the sprat. As stated above, this factor might be a patchy prey distribution. To address these topics, we investigated the dimensions of copepod patches from three different basins of the Baltic Sea through the use of a VPR system. Furthermore, we investigated the consequences of this patchy copepod distribution on sprat consumption and feeding behaviour.

METHODS

SAMPLING AREA & STRATEGY

We conducted Video Plankton Recorder (VPR) tows in three different basins of the Baltic Sea (Arkona Basin—AB, Bornholm Basin—BB, Gotland Basin—GB; figure III-1), to investigate copepod patches and their spatial dimensions. Samples were taken on a cruise with RV Alkor in August 2015. To generate data suitable for measuring copepod patches, we applied a different VPR sampling strategy than in chapters I & II of this thesis. We conducted horizontal VPR tows in depth layers 2–3 m apart, which enabled a better horizontal resolution of copepod patches than the usually conducted undulating VPR tows would have delivered. Fishery and multinet (MSN) hauls were conducted in every basin after the respective VPR tows, to derive information on sprat stomach content weights and prey composition, as well as information on copepod abundances in different layers of the water column.

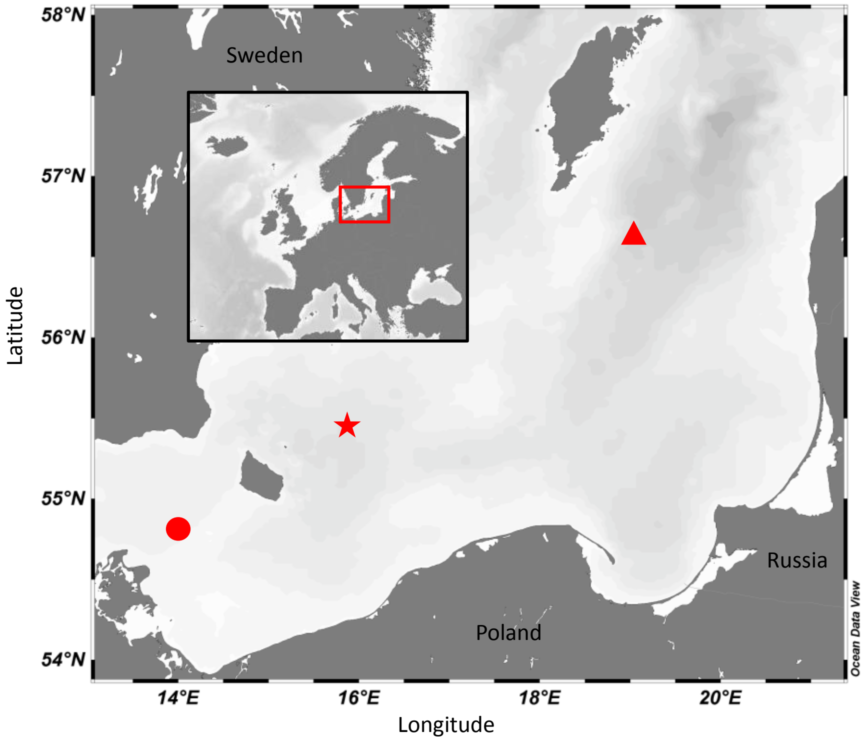

Figure III-1. Sampling area in the Baltic Sea—red rectangle in the small map; red dot—sampling location in Arkona Basin, red star—sampling location in Bornholm Basin, red triangle—sampling location in Gotland Basin.

VIDEO PLANKTON RECORDER

Three horizontal VPR tows were conducted in every investigated basin, to cover the day and night distribution of copepods and to check for daytime differences in patch formation and dimensions. These tows were scheduled from ca. 9–13h UTC (“day sample”), ca. 13–17h UTC (“evening sample”) and ca. 22–2h UTC (“night sample”). A depth range of 13–16 m directly below the thermocline was sampled in 5–6 depth layers. Exact sampling times and depth layers of the different tows are shown in table III-1.

Table III-1. Sampling times and depth layers of VPR tows in the investigated sampling areas of the Baltic Sea; AB—Arkona Basin, BB—Bornholm Basin, GB—Gotland Basin.

Sampling area	Sampling time	Sampled depth layers [m]	VPR tows conducted between	
AB	Evening	22, 24, 26, 29, 32, 35	26.08.2015, 13:14h UTC	26.08.2015, 17:00h UTC
AB	Night	22, 24, 26, 29, 32, 35	26.08.2015, 22:20h UTC	27.08.2015, 02:20h UTC
AB	Day	22, 24, 26, 29, 32, 35	28.08.2015, 09:12h UTC	28.08.2015, 13:06h UTC
BB	Evening	22, 25, 28, 31, 34, 37	22.08.2015, 13:12h UTC	22.08.2015, 16:57h UTC
BB	Night	22, 25, 28, 31, 34, 37	22.08.2015, 23:43h UTC	23.08.2015, 03:04h UTC
BB	Day	22, 25, 28, 31, 34	24.08.2015, 09:05h UTC	24.08.2015, 12:56h UTC
GB	Evening	18, 21, 24, 27, 30, 33	19.08.2015, 13:55h UTC	19.08.2015, 17:30h UTC
GB	Night	18, 21, 24, 27, 30, 33	19.08.2015, 22:12h UTC	20.08.2015, 02:17h UTC
GB	Day	18, 21, 24, 27, 30, 33	21.08.2015, 09:05h UTC	21.08.2015, 13:26h UTC

We towed the VPR (Seascan) attached under a V-fin with 1.5 knots ship speed horizontally through the different depth layers around the thermocline of the investigated basins. The total sampling volumes that were thereby examined are listed in table III-2.

Table III-2. Total sampling volumes of VPR tows from the investigated sampling areas in the Baltic Sea; AB—Arkona Basin, BB—Bornholm Basin, GB—Gotland Basin.

Sampling area	Sampling time	Total sampling volume [L]
AB	Evening	39 612
AB	Night	43 671
AB	Day	42 210
BB	Evening	46 593
BB	Night	35 391
BB	Day	43 184
GB	Evening	38 313
GB	Night	42 372
GB	Day	46 106

The technical settings of the VPR included a Uniq UC-1800DS Color Digital CCD camera with a mean image frame rate of 25 s^{-1} and a Xenon strobe (Seascan). The chosen camera settings provided a field of view of 24 x 24 mm (S2 magnification) with a calibrated image volume of 108.23 mL. The VPR did also include a FastCat 49 CTD (Sea-Bird), an ECO Puck FLNTU fluorometer as well as a turbidity sensor (WetLabs).

During sampling, a fiber optic cable transmitted images and sensor data from our deployed VPR system to an onboard unit in real time. We used AutoDeck (Seascan Inc.) to extract all particles (plankton) that were recorded by the VPR as regions of interest (roi). Subsequently, these rois were analysed automatically with the Matlab application Visual Plankton, which was written by scientists of the Woods Hole Oceanographic Institution (Davis et al. 2005), following methods of Hu & Davis (2006). Afterwards we had to check the automatically sorted rois manually due to insufficient sorting results of the Visual Plankton software.

VPR DATA

For visualisation of the copepod data, we had to calculate the distance of every sampled VPR roi from the starting point of the respective VPR tow to its individual point along the tow track. Therefore, we followed the Pythagorean Theorem for distance calculation after Kompf (2016), using equations III-1–III-3:

$$\text{distance} = \text{sqrt}(dx * dx + dy * dy) \tag{III-1}$$

where distance is the distance in km and dx as well as dy are obtained via

$$dx = 71.5 * (\text{lon1} - \text{lon2}) \tag{III-2}$$

$$dy = 111.3 * (\text{lat1} - \text{lat2}) \tag{III-3}$$

where lat1, lat2, lon1 and lon2 are latitude and longitude of the respective sampled data points in decimal degrees.

Data from the VPR tows during turns of the ship were excluded from analyses, so that all sampled depth layers of the respective tows were of the same length.

The VPR derived copepod abundances appeared to be 4 (AB), 5 (BB) and 11 (GB) times lower than the MSN derived abundances (table III-3). This resulted probably from a problem with the assumed VPR image volume. We know that clarity of the sampled water body influences the VPR image volume (Seascan Inc., personal communication). Because of the different amounts of marine snow and overall different clarity of the sampled water columns, our assumed VPR image volumes were apparently altered and led to too low copepod abundances. However, we do not have a correction factor to correct our VPR abundances for the differences in water clarity. Therefore, we increased our VPR abundances in this study to match the MSN abundances.

Table III-3. Comparison of MSN and VPR derived copepod abundances—mean abundances from all tows of one sampling area; AB—Arkona Basin, BB—Bornholm Basin, GB—Gotland Basin, STD—standard deviation.

Sampling area	MSN derived abundances [L^{-1}] ± STD	VPR derived abundances [L^{-1}] ± STD
AB	3.5 ± 1.6	0.9 ± 0.3
BB	7.0 ± 3.7	1.3 ± 0.8
GB	8.1 ± 5.7	0.7 ± 0.5

COPEPOD PATCH DEFINITION

In the literature, patches are defined as regions with higher concentration of organisms, usually twice the mean (Owen 1989). Therefore, we calculated the mean copepod abundance from all tows of all sampled basins (5 copepds L^{-1}). Thus we defined patches in our VPR samples as regions with copepod abundances ≥ 10 copepods L^{-1}.

VERTICAL INTERPOLATION OF VPR DATA

To gain information on the vertical extent of copepod patches, we had to interpolate the data points between two sampled depth layers, since the VPR data used for this study were derived from horizontal VPR tows that lay 2–3 m apart. Interpolation of this data was done with a gridding software (DIVA—Data-Interpolating Variational Analysis) integrated in Ocean Data View (ODV; Schlitzer 2018). We had to verify that the vertical interpolation did not overestimate the copepod patch heights. Therefore, we compared patch heights derived from BB data of this study, where strong vertical interpolation of the data was necessary, with a BB summer cruise in 2015, where vertical VPR tows were conducted and thus low vertical interpolation of VPR data had to be applied.

PREDICTED STOMACH CONTENT WEIGHTS

We wanted to investigate, if a patchy prey distribution can explain the high variability of sprat stomach content weights that are found in the field within fish from the same haul. Therefore, we used our VPR derived copepod abundance data, to predict stomach content weights of sprat from the 12 cm length class for each of our sampled basins. These predictions were then compared with stomach content weights from 12 cm length class sprat sampled in the field. The 12 cm length class was chosen for our analyses because it provided sufficient numbers of sprat in every haul. Field sampling of stomachs took place directly after the morning downward migration of sprat in deep waters.

For our predictions, we used copepod abundance data of VPR night tows, because these tows show a copepod distribution similar to the one that sprat experience in the early morning hours prior to their downward migration. The VPR data provided copepod abundances and temperatures in one second time bins for the duration of each respective VPR tow. These data were used to predict stomach content weights for 30 sprat after their downward migration in the morning. This is the same number of fish as analysed from the field. To predict the stomach content weights, we modelled feeding of sprat during their downward migration by dividing the morning feeding time of two hours (Kulke et al. 2018) by the number of depth layers we sampled with the VPR in each basin (AB—6, BB—5, GB—6). Thus, we received a feeding time of 20 minutes in each depth layer for AB and GB (figure III-2), as well as 24 minutes for BB, assuming a uniform descent of sprat during the downward migration.

The investigated depth layers were sampled because we wanted to investigate the effects of copepod patches on consumption and feeding behaviour of sprat, and the resulting variability in sprat stomach content weights. Therefore, we sampled depth layers from which we knew that copepods aggregate there (chapter II of this thesis). For our analyses, we focused only on copepods as sprat prey organisms, as well as the copepod share from sprat field stomach content weights. In the field, sprat feed not only on copepods, but also on cladocerans. These organisms are not included into our prey data, since they reside in water layers above the ones we sampled with the VPR, as we know from other VPR data analyses. Furthermore, the depth range below our sampled transects was not taken into account for our stomach content weight predictions. This is because sprat feeding is mainly concentrated on depth layers around the thermocline, where sprat are located when feeding starts in the morning (chapter II of this thesis). In addition, the prey composition from sprat stomachs shows that sprat mainly feed on thermocline associated copepod species during their feeding phase in the morning (chapter II of this thesis).

Feeding was modelled separately for each depth layer, and the results were added afterwards to receive stomach content weights for 30 sprat after feeding for two hours in different depth layers. To obtain these results, we let each of the modelled 30 sprat start at a different point along our VPR tow track (figure III-2). By doing so, we simulated that each fish encountered a different prey distribution while feeding. We determined the swimming activity of a sprat [body length s^{-1}] as a function of actual prey concentrations after Meskendahl (2013)—equation III-4:

$$y(x) = ø1 + (ø2-ø1) * \exp[-\exp(ø3) * conc] \tag{III-4}$$

where ø1 = 0.917, ø2 = 0.614, ø3 = -2.15 and *conc* = prey concentration (L^{-1}).

This delivered the distance a sprat was able to swim within the given feeding time. The individual starting points for feeding of the 30 sprat resulted from dividing the VPR tow track distance by the amount of modelled sprat. The end points for feeding of the 30 sprat in each depth layer were then obtained by adding the likely swimming distance within the given feeding time to the individual starting points.

We then predicted the expected stomach content weights through a series of steps. By applying a functional response model (equation III-5; Kulke 2018) to the prevailing prey concentrations and temperatures at the starting point of the individual 30 sprat, we obtained the individual feeding rate for each fish.

$$F = \frac{\frac{a_1}{1 + b_1 * e^{-c_1 * T}} * \frac{a_2}{1 + b_2 * e^{-c_2 * L}} * conc}{\left(\left(a_k * L^{-b_k}\right) * 11.16 + conc\right)} \tag{III-5}$$

where F = feeding rate (s^{-1}), *conc* = prey concentration (L^{-1}), a_1 = 3.354, b_1 = 12.859, c_1 = 0.316, a_2 = 0.619, b_2 = 3258, c_2 = 17.541, a_k = 320.114 and b_k = 2.677.

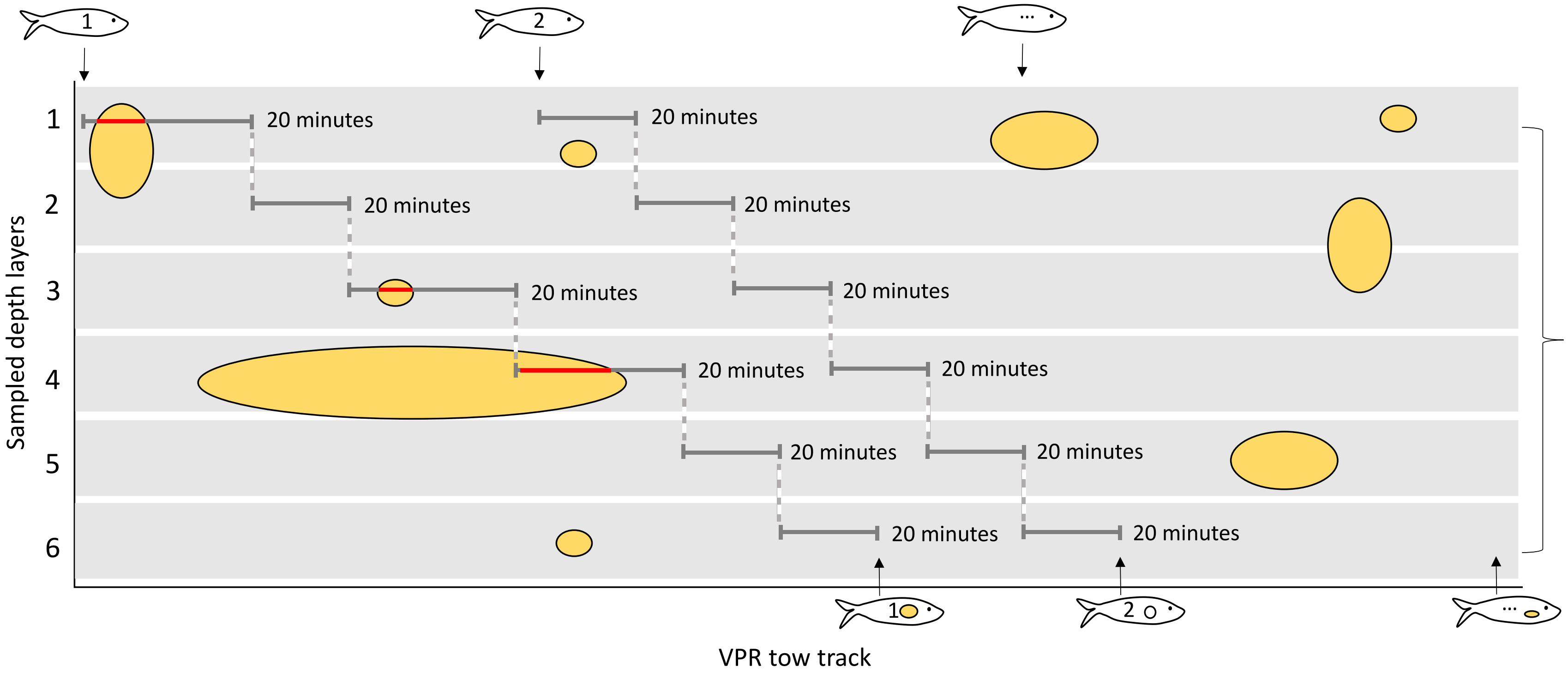

Figure III-2. Schematic representation of calculation approach to predict sprat stomach content weights for 30 sprat after a feeding time of two hours. Light grey—depth layers sampled with VPR, yellow—copepod patches, dark grey—sprat swimming distance within 20 minutes feeding time, red—sprat swimming distance within copepod patch: swimming speed increases with increasing prey concentrations until very high prey densities are reached (>500 L^{-1})—then speed decreases again (Meskendahl 2013).

Since the results obtained from the functional response model were expressed in particles per time unit, we needed a mean prey weight for the conversion into grams wet weight (g_{WW}) per time unit. Therefore, we applied a weighted mean prey weight of 32 μg_{WW} based on the relative prey composition of sprat (Bernreuther et al. 2013). Wet weights of prey were taken from Hernroth (1985). The obtained feeding rates were corrected after Kulke (2018) for feeding breaks of sprat and escape responses of certain copepod species. First, a correction factor of 0.7 was applied to account for feeding breaks observed in experimental setups with sprat. Second, we accounted for a lower feeding rate of sprat when preying on copepod species with distinct escape responses as *Acartia* spp. (Kulke 2018) by applying a correction factor of 0.53. Therefore, we took information on the copepod species composition from sprat stomach field samples into account. The share of copepod species from the stomach content weight with a strong escape response was hereby corrected with the factor of 0.53.

We were able to predict the change in stomach content *dS/dt* as the result of the corrected feeding rate and a gastric evacuation model after Bernreuther et al. (2009). The gastric evacuation constant was hereby expandet by additional variables. Ambient temperatures and predator weight were considered as variables—equations III-6 & III-7:

$$\frac{dS}{dt} = F - R * {S_t}^B \tag{III-6}$$

where F = feeding rate (F; $g_{DW}\,h^{-1}$), R = gastric evacuation constant ($g_{DW}1^{-B}\,h^{-1}$), S_t = stomach content (g_{DW}) at time t and B = shape parameter of the gastric evacuation (0.668), and

$$R = R''_{DW} * e^{A*T} * M^C \tag{III-7}$$

where R''_{DW} = evacuation constant (0.0177), A = temperature coefficient (0.0775), T = temperature (°C), M = fish weight (g_{DW}) and C = body mass exponent (0.503). As the gastric evacuation model by Bernreuther is related to dry weights, we used a factor of 0.2 (Omori 1969, Williams & Robins 1982) to convert stomach content weight from wet to dry weights.

At the beginning of each of the given feeding phases, each sprat stomach was assumed to be empty (t = 0). Then we calculated the change in stomach content weight for a time unit (1-second steps) resulting from feeding as well as evacuation and added it to the present stomach content weight. This new stomach content weight was taken as the new starting point in the next 1-second step. This procedure was repeated for the number of seconds in the respective feeding time. Finally, the stomach content weights (g_{WW}) predicted for each of the individual feeding phases in the different depth layers were added. Thus, we received stomach content weights of 30 sprat that resulted each from a total feeding time of two hours. In a second approach, we assumed an uneven descent of sprat during the downward migration and applied different feeding times for the 30 sprat in the individual depth layers (table III-4). Thereby, feeding times were based on the results we gained from stomach content predictions of the first approach. Data from AB and BB suggested that sprat in the field were feeding shorter in layers with high copepod abundances, while data from GB suggested the opposite.

Table III-4. Feeding times in second prediction approach of sprat stomach content weights from the respective sampling areas and depth layers. AB—Arkona Basin, BB—Bornholm Basin, GB—Gotland Basin. Different feeding times applied in individual depth layers, based on the assumption that sprat in AB & BB stay shorter and in GB longer in depth layers with high copepod abundances.

Sampling area	Depth layer [m]	Feeding time [min]
AB	22	10
AB	24	10
AB	26	10
AB	29	30
AB	32	30
AB	35	30
BB	22	48
BB	25	48
BB	28	12
BB	31	6
BB	34	6
GB	18	60
GB	21	60
GB	24	0
GB	27	0
GB	30	0
GB	33	0

In addition, we tested if sprat feed less when their prey particles are distributed patchy as opposed to a random prey distribution with the same mean density (Kulke 2018). Therefore, we again applied the methods of our first stomach content weight prediction approach.

However, instead of the patchy copepod distribution, we used the respective mean copepod concentrations throughout the feeding time of two hours.

SPRAT STOMACH FIELD SAMPLES

We used a young fish trawl net with a 5 mm mesh size codend for sprat sampling. This net was towed for approximately 30 minutes in every haul. Sampling was performed on schools of clupeids detected with a Furuno net sensor mounted to the head rope of the net. Sprat wet mass and length distribution were recorded, and per haul up to 30 sprat stomachs of every cm length class were preserved in a 4% disodiumtetraborate-buffered formalin-seawater solution. Subsequent to sampling, stomachs were weighed in the lab before and after emptying, to determine the wet mass of the stomach content. We conducted a diet analysis for 15 stomachs from a morning haul of every basin, where sprat were caught directly after their downward migration. The share of completely digested prey particles in the stomachs was estimated, and identifiable cladoceran and copepod individuals were counted under a stereo microscope.

To compare field and predicted stomach content weights, we decreased the field stomach weight data by the amount of cladocerans and undetermined/digested prey particles, since the predicted stomach content weight data were derived only from copepod abundances. The relative copepod shares of the total field stomach content weights that were used for the comparison are shown in table III-5.

Table III-5. Copepod, cladoceran and undetermined share of the total field stomach content weights; AB—Arkona Basin, BB—Bornholm Basin, GB—Gotland Basin.

Sampling area	Share of copepods [%]	Share of cladocerans [%]	Share of undetermined particles [%]
AB	23	42	35
BB	30	26	44
GB	70	1	29

MULTINET COPEPOD DATA

To determine the copepod abundances in the investigated basins, we used a multiple opening-closing net (Hydro-Bios) with a 0.25 m^2 opening and a mesh size of 100 µm. The samples were taken in the same depth layers as the VPR samples, directly after the VPR night tows in each respective basin. In AB, MSN samples were taken at 03:15 and 03:45h UTC, in BB at 03:52 and 04:27h UTC and in GB at 03:00 and 03:33h UTC. MSN samples were preserved in a 4%

disodiumtetraborate-buffered formalin-seawater solution and analysed later in the lab. The original samples were split into subsamples through the use of a Kott-splitter device. Per subsample, not less than 500 mesozooplankton individuals were identified and counted under a binocular microscope. For this study, we used only the mean copepod abundances of each basin derived from the MSN samples to compare those to the VPR derived abundances.

DATA ANALYSIS

Maps in figure III-1 and plots in figures III-3–III-5 were created with ODV and figures III-3–III-5 additionally with the DIVA gridding software (Data-Interpolating Variational Analysis) that is integrated in ODV.

The copepod patches we visualised with ODV were measured by determining their length from the extent along the individual tow track and their height from the extent along the sampled depth layers. Patch areas were calculated by assuming an ellipsoid shape for every patch, and applying equation III-8 to the data:

$$\text{Patch area} = a * b * \pi \tag{III-8}$$

where a = major radius, b = minor radius.

Significant differences between the frequency distributions of field and predicted stomach content weight data were determined with a Welch's t-test for two samples with parametric and a Mann-Whitney test for two samples with nonparametric data. These tests were done in the statistical and programming environment R (version 3.3.1; R Core Team 2016) using R package "car" (version 3.0.2; Fox & Weisberg 2011).

RESULTS

VALIDATING VERTICAL INTERPOLATION

Both Video Plankton Recorder (VPR) sampling strategies—horizontal and undulating—revealed patch heights of the same order of magnitude (table III-6). The vertical interpolation of VPR copepod abundances from horizontal tows resulted in calculated copepod patch heights from 0.11–10.26 m, while patches from undulating tows showed heights from 0.18–9.82 m. The only apparent difference lies in the day sample, where data from the undulating tow result in patch heights of 8.90 m maximum and data from the horizontal tow in only 1.08 m.

Table III-6. Copepod patch heights calculated from vertically interpolated data of VPR tows (Bornholm Basin) with continuous horizontal data and vertical data gaps (horizontal sampling) as well as from tows with continuous vertical data (undulating sampling).

Sampling strategy	Sampling time	Patch height [m] minimum–maximum
Horizontal	Day	0.22–1.08
Horizontal	Evening	0.31–10.26
Horizontal	Night	0.11–6.61
Undulating	Day	0.19–8.90
Undulating	Night	0.18–9.82

MEASURING COPEPOD PATCHES

In Arkona Basin (AB), only two small copepod patches were found in the evening sample (figure III-3c, d), directly at the thermocline. Day (figure III-3a, b) and night sample (figure III-3e, f) showed no copepod patches. Copepods in Bornholm Basin (BB) formed patches in all of the three samples. The day sample (figure III-4a, b) showed individual small patches below the thermocline in cooler water. More and bigger copepod patches were found in the evening sample (figure III-4c, d), where they were visible from cooler water at 38 m (ca. 5–10°C) up until directly to the thermocline at 28 m (ca. 12°C). The night sample (figure III-4e, f) finally showed very large patches directly at the thermocline with some patches stretching into warmer water (ca. 12–15°C). The copepod distribution of Gotland Basin (GB) covered all depth layers of the day as well as the evening sample. Patches were visible from cooler water at 34 m (ca. 5–10°C) up until the thermocline at 21 m (ca. 12°C) during day (figure III-5a, b) and even further into warmer water above the thermocline (ca. 15°C) in the evening (figure III-5c, d). The evening sample showed more copepod patches than the day sample. Similar to BB, few very large patches were found in the night sample, directly at the thermocline at ca. 20 m (figure III-5e, f). We cannot determine how far upward into warmer water these patches extended, due to the limited range of the sampled depth layers. The evening samples of all three basins showed most copepod patches (table III-7). In AB however, no patches were found besides the evening sample. BB and GB showed fewest copepod patches in the night samples and most patches in the evening samples. The shortest patches were found in the evening samples, while the longest patches were visible in the night samples. The night samples of both basins did also show the largest copepod patches. Patches occupied at least 0.8% (evening sample, AB) and up to 34.2% (evening sample, GB) of the respective total VPR tow tracks. Most copepod patches were found in GB, and the GB samples did also show the highest mean copepod abundances in their patches.

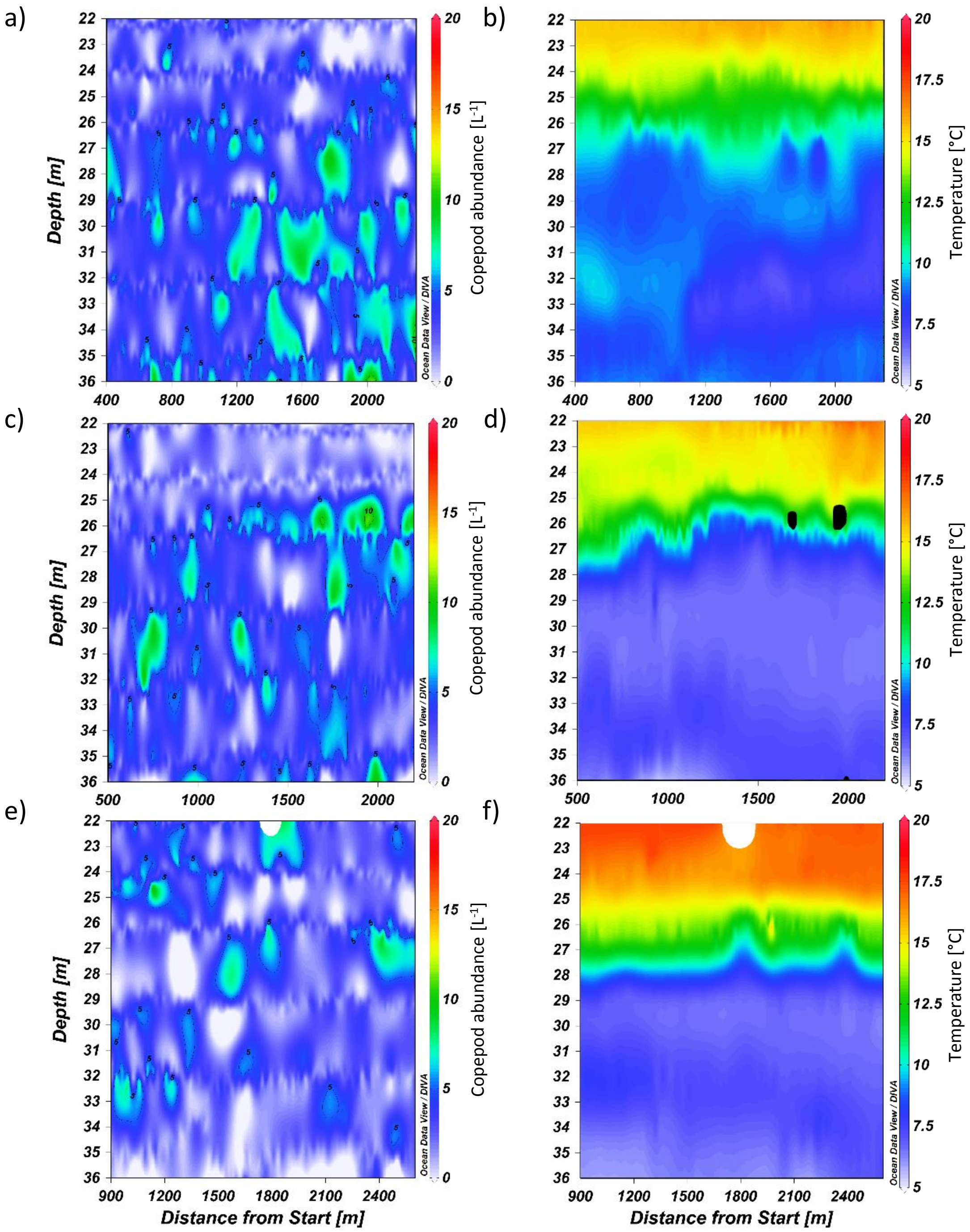

Figure III-3. VPR data from Arkona Basin. Left panels—copepod abundances L^{-1}, right panels—coloured: temperature [°C], black: copepod patches with abundances >10 L^{-1}, white: no temperature data. A) & b): VPR day tow—09:12–13:06h UTC, c) & d): VPR evening tow—13:14–17:00h UTC, e) & f): VPR night tow—22:20–02:20h UTC.

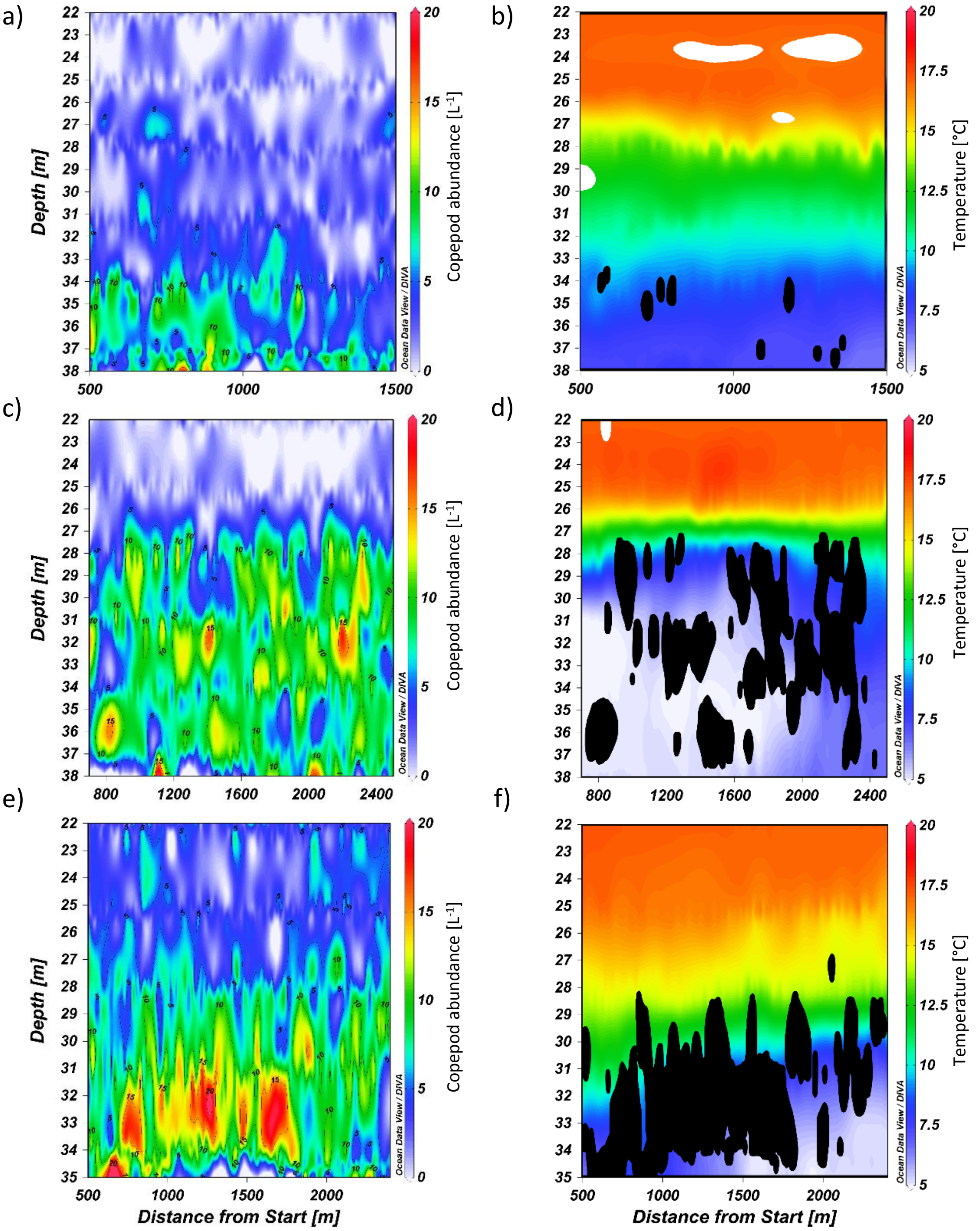

Figure III-4. VPR data from Bornholm Basin. Left panels—copepod abundances L^{-1}, right panels—coloured: temperature [°C], black: copepod patches with abundances >10 L^{-1}, white: no temperature data. A) & b): VPR day tow—09:05–12:56h UTC, c) & d): VPR evening tow—13:12–16:57h UTC, e) & f): VPR night tow—23:43–03:04h UTC.

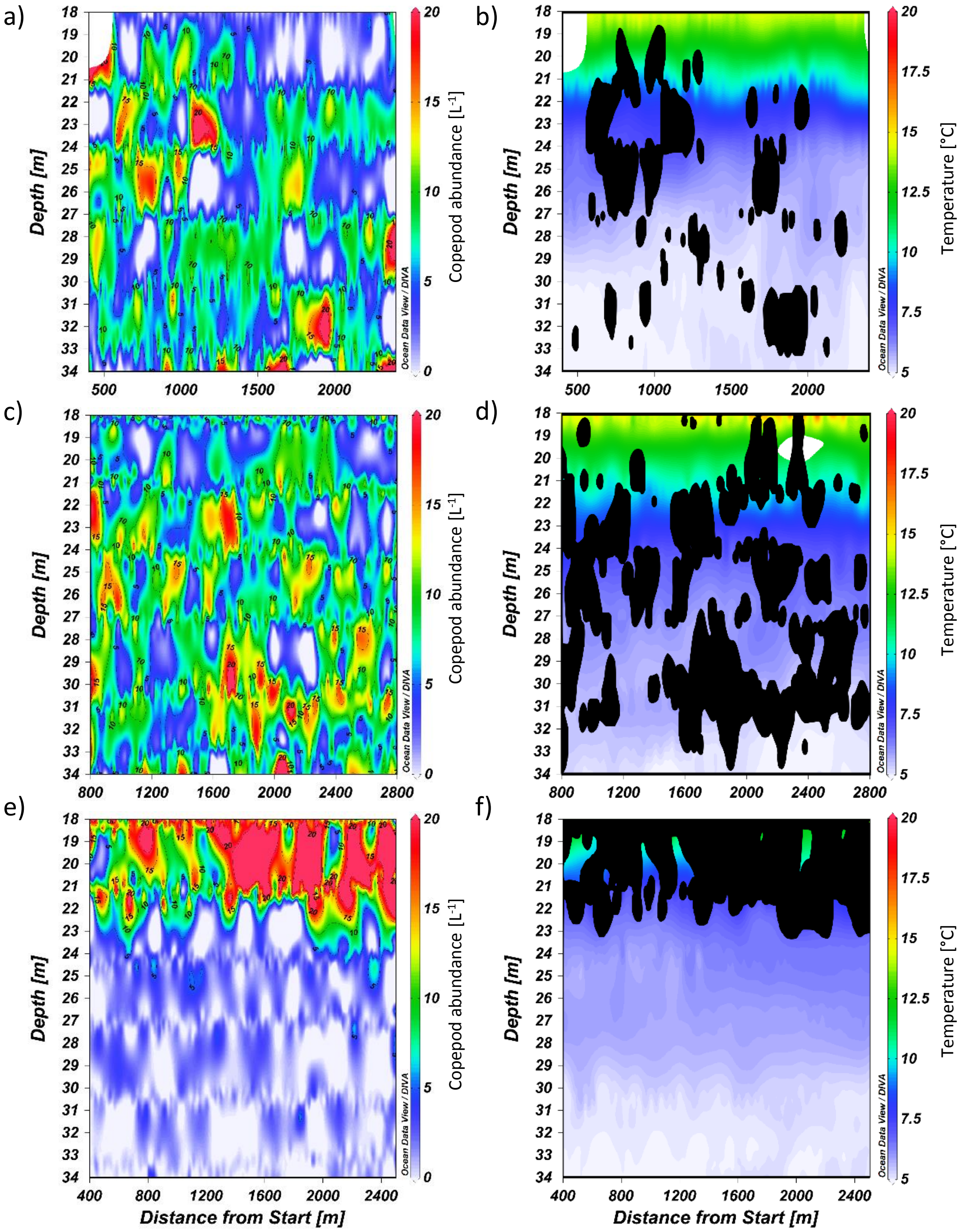

Figure III-5. VPR data from Gotland Basin. Left panels—copepod abundances L^{-1}, right panels—coloured: temperature [°C], black: copepod patches with abundances >10 L^{-1}, white: no temperature data. A) & b): VPR day tow—09:05–13:26h UTC, c) & d): VPR evening tow—13:55–17:30h UTC, e) & f): VPR night tow—22:12–02:17h UTC.

Table III-7. Numbers and measurements of copepod patches found in the investigated sampling areas; AB—Arkona Basin, BB—Bornholm Basin, GB—Gotland Basin, STD—standard deviation.

Sampling area	Sampling time	Length [m]		Height [m]		Area [m^2]		No. of patches (n/2.5h)	% of tow track occupied by patches	Mean copepod abundance L^{-1} of all patches ± STD
		min.	max.	min.	max.	min.	max.			
AB	Evening	17.83	63.72	0.29	0.60	4.11	30.16	2.00	0.80	10.41 ± 0.29
BB	Day	7.27	22.02	0.22	1.08	1.58	16.09	19.00	2.40	10.57 ± 0.49
BB	Evening	3.68	286.98	0.31	10.26	0.91	2248.41	20.00	17.60	11.67 ± 1.34
BB	Night	3.86	1290.08	0.11	6.61	0.33	6693.53	18.00	19.80	13.04 ± 2.57
GB	Day	4.07	315.83	0.09	6.04	0.29	1497.81	29.00	16.80	13.12 ± 3.03
GB	Evening	4.06	825.31	0.03	26.79	0.10	4330.34	44.00	34.20	12.45 ± 2.14
GB	Night	21.48	2100.00	0.39	5.14	6.50	8484.99	4.00	17.70	18.15 ± 6.04

PREDICTING STOMACH CONTENT WEIGHTS

The copepod share of stomach content weight data from sprat caught during early morning hours directly after their downward migration showed a high variability (figures III-6–III-8; black bars). We used VPR copepod abundance data from night samples of all three investigated basins in addition to the corresponding temperature data, to predict the copepod share of sprat stomach content weights (figures III-6–III-8; white bars). Those predicted values were compared with field data. This comparison showed an overestimation of full stomachs in the predicted data of AB and BB (figures III-6 & III-7; white bars). Predicted data of AB showed a mean stomach content weight of 0.027 g_{WW} and a median of 0.028 g_{WW}, whereas field data showed a mean stomach content weight of 0.020 g_{WW} and a median of 0.018 g_{WW}. Predicted and field data differed significantly from each other (Welch's t-test; $p<0.05$). For BB, predicted data resulted in a mean stomach content weight of 0.039 g_{WW} and a median of 0.039 g_{WW}, while field data showed a mean stomach content weight of 0.023 g_{WW} and a median of 0.022 g_{WW}. Here, predicted and field data did also differ significantly from each other (Mann-Whitney test; $p<0.05$). A different picture emerged from GB data (figure III-8). Here, much heavier stomachs were found than in AB and BB. Furthermore, predicted stomach content weight data overestimated the number of stomachs with lighter content weights (0.014–0.042 g_{WW}), while no stomachs were predicted at all for the weight classes heavier than 0.042 g_{WW} (0.056–0.140 g_{WW}). Predicted data showed a mean stomach content weight of 0.023 g_{WW} and a median of 0.023 g_{WW}, in contrast to a mean stomach content weight of 0.058 g_{WW} and a median of 0.049 g_{WW} in the field data. As in data from AB and BB, predicted and field data differed significantly from each other (Welch's t-test; $p<0.05$).

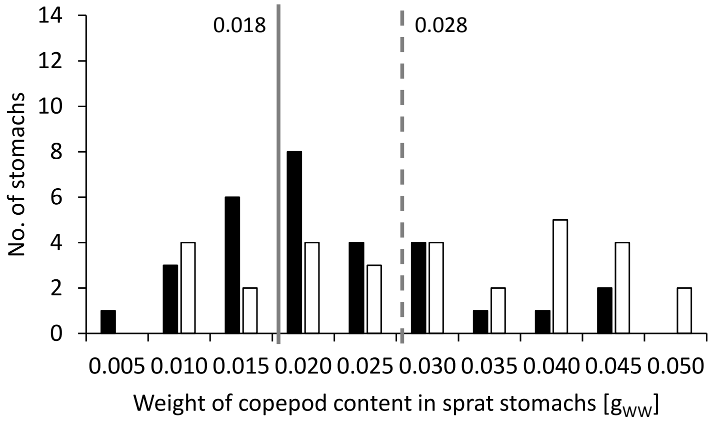

Figure III-6. Frequency distribution of copepod share in stomach content weight data [g_{WW}] from Arkona Basin. Black bars—field data from morning fishery haul after downward migration of sprat, white bars—stomach content weight data predicted with VPR derived prey concentrations and temperature data, and calculated with equal feeding time in each depth layer, solid grey line—median value of field data, dotted grey line—median value of predicted data.

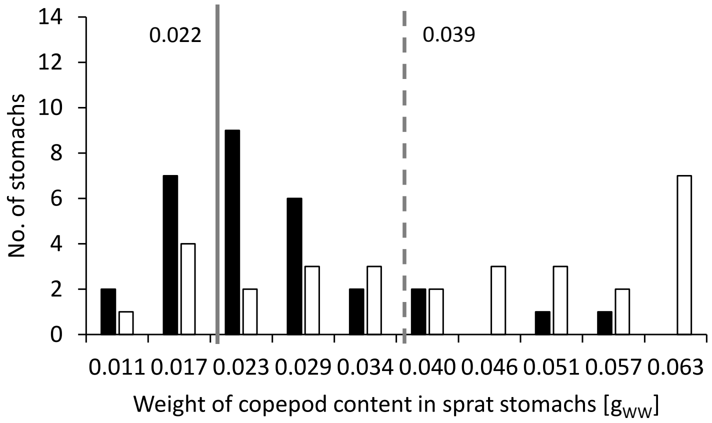

Figure III-7. Frequency distribution of copepod share in stomach content weight data [g_{WW}] from Bornholm Basin. Black bars—field data from morning fishery haul after downward migration of sprat, white bars—stomach content weight data predicted with VPR derived prey concentrations and temperature data, and calculated with equal feeding time in each depth layer, solid grey line—median value of field data, dotted grey line—median value of predicted data.

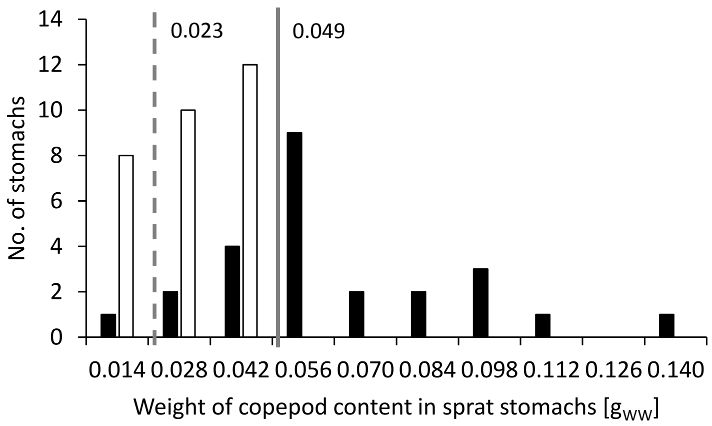

Figure III-8. Frequency distribution of copepod share in stomach content weight data [g_{WW}] from Gotland Basin. Black bars—field data from morning fishery haul after downward migration of sprat, white bars—stomach content weight data predicted with VPR derived prey concentrations and temperature data, and calculated with equal feeding time in each depth layer, solid grey line—median value of field data, dotted grey line—median value of predicted data.

In a second approach, we predicted stomach content weights by applying different feeding times for the 30 sprat in each individual depth layer. Thereby, we took results into account that emerged from the first approach with equal feeding times in each depth layer. For the second approach, we assumed shorter feeding times in layers with high copepod abundances and longer feeding times in layers with less copepods for samples from AB and BB. The opposite was assumed for the GB sample. Here, sprat feeding was limited to the two upper depth layers, which showed high copepod abundances. Predictions from the new approach did not show an overestimation of full stomachs for the AB sample anymore (figure III-9). The mean stomach content weight of these predicted data was 0.016 g_{WW}, and the median value was 0.017 g_{WW}. Thus, predicted and field data did not differ significantly anymore (Welch's t-test; $p>0.05$). Predicted data from the second approach of the BB sample (figure III-10) resulted in slightly lower stomach content weights than the ones from the first approach. Here, a mean stomach content weight of 0.033 g_{WW} and a median value of also 0.033 g_{WW} were found. Predicted and field data did still differ significantly (Mann-Whitney test; $p<0.05$). Predicted data from the GB sample did still not show full stomachs, but resulted in a lower overestimation of emptier stomachs than in the first approach (figure III-11). Mean and median stomach content weight were 0.041 g_{WW}. Predicted and field data did also still differ significantly (Welch's t-test; $p<0.05$).

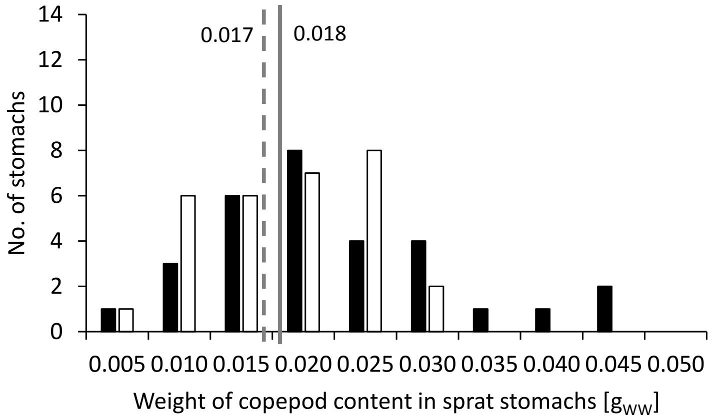

Figure III-9. Frequency distribution of copepod share in stomach content weight data [g_{WW}] from Arkona Basin; predicted data calculated with different feeding times in the individual depth layers. Black bars—field data from morning fishery haul after downward migration of sprat, white bars—stomach content weight data predicted with VPR derived prey concentrations and temperature data, solid grey line—median value of field data, dotted grey line—median value of predicted data.

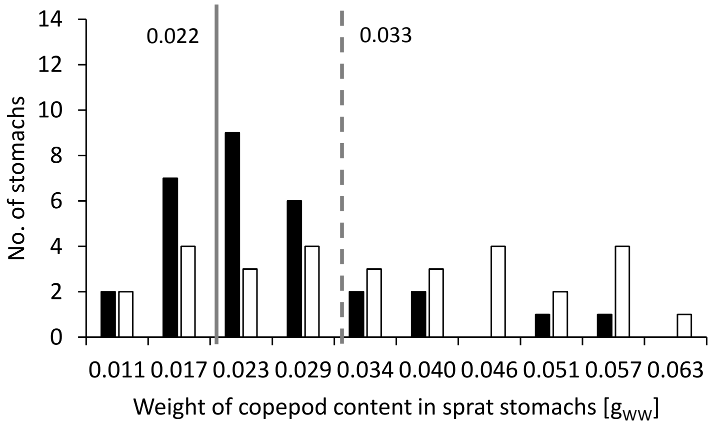

Figure III-10. Frequency distribution of copepod share in stomach content weight data [g_{WW}] from Bornholm Basin; predicted data calculated with different feeding times in the individual depth layers. Black bars—field data from morning fishery haul after downward migration of sprat, white bars—stomach content weight data predicted with VPR derived prey concentrations and temperature data, solid grey line—median value of field data, dotted grey line—median value of predicted data.

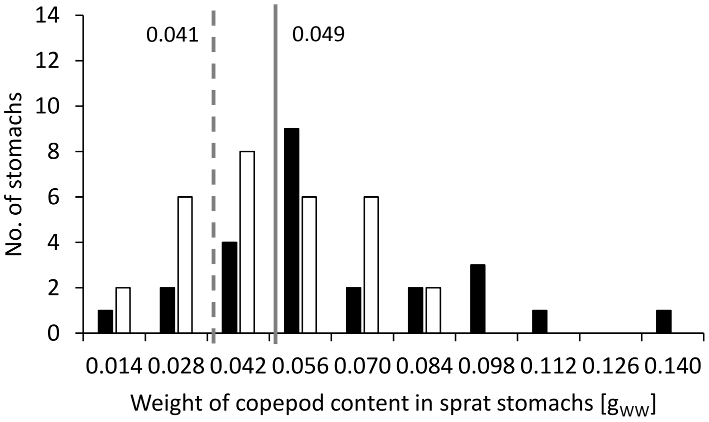

Figure III-11. Frequency distribution of copepod share in stomach content weight data [g_{WW}] from Gotland Basin; predicted data calculated with different feeding times in the individual depth layers. Black bars—field data from morning fishery haul after downward migration of sprat, white bars—stomach content weight data predicted with VPR derived prey concentrations and temperature data, solid grey line—median value of field data, dotted grey line—median value of predicted data.

When testing whether sprat feed less in an environment with a patchy or a random copepod distribution that have the same mean copepod density, we found lower mean stomach content weights resulting from the patchy prey distribution in all of the three investigated basins (table III-8).

Table III-8. Comparison of mean stomach content weights [g_{WW}] from 30 sprat predicted with VPR derived copepod abundances. Patchy prey distribution means results were predicted with patchy copepod distribution from the field, random prey distribution means results were predicted with mean prey density from the field. AB—Arkona Basin, BB—Bornholm Basin, GB—Gotland Basin, STD—standard deviation.

Sampling area	mean predicted stomach content weight [g_{WW}] patchy prey distribution ± STD	mean predicted stomach content weight [g_{WW}] homogeneous prey distribution ± STD
AB	0.027 ± 0.013	0.033 ± 0.015
BB	0.031 ± 0.015	0.036 ± 0.017
GB	0.023 ± 0.011	0.030 ± 0.015

DISCUSSION

METHODS

The comparison of vertically interpolated Video Plankton Recorder (VPR) copepod abundance data from horizontal (high vertical interpolation) and undulating tows (low vertical interpolation) revealed patch height estimates of the same order of magnitude. The only apparent differences between the results from undulating and horizontal tows were found in the day samples (table III-6). However, since the strongly interpolated data from the horizontal tow showed in this case the lower patch height, we concluded that high vertical interpolation of the data does not lead to overestimated patch heights. We therefore concluded that the vertical interpolation of horizontal VPR data used in this study had no effect on calculating patch dimensions.

To generalise the determination of patch areas, we chose to assume an ellipsoid form for each patch. This is of course a rough assumption. Figures III-3–III-5 clearly show that copepod patches have irregular forms. This implies that the actual patch areas in the field might be smaller than the ones calculated in our study.

The copepod share of sprat stomach content weights from Bornholm (BB) and Gotland Basin (GB) was predicted on the basis of copepod abundance data from a depth range that spanned 13 and 16 m respectively. Although the sprat migration does span a further 20–30 m (Kulke et al. 2018), we assumed feeding in this study to only take place in the small depth range that we sampled with the VPR as stated in the methods section. Nevertheless, our predictions are sufficient to illustrate that a patchy prey distribution can lead to the high variability of stomach content weights that is found in sprat from the field during early morning hours.

RESULTS

MEASURING COPEPOD PATCHES

We found copepod patches in all of the three investigated basins. However, in Arkona Basin (AB) these patches occurred only in the evening sample. The other AB samples did also show copepod aggregations, but with much lower abundances (figure III-3). We can clearly see the same migration pattern as in the other basins. However, it seems that copepods aggregate directly at the thermocline in the evening sample, thereby forming high abundance patches, while migrating further upwards into layers above the thermocline during the night. In the night samples of BB and GB, we found copepod patches that extended into warmer water above the thermocline. This extension into warmer layers is most likely not connected to the temperature but rather to the distribution of prey particles. Phytoplankton accumulates at the thermocline, due to associated density differences of the water column (Derenbach et al. 1979, Sharples et al. 2001, Karpowicz & Ejsmont-Karabin 2017). We found high numbers of patches with small patch sizes in the evening samples of the three investigated basins, while the night samples showed only few but large patches. Therefore, we conclude that many small patches start to form in the evening during the daily upwards migration of copepods, and subsequently aggregate into few large patches once copepods finish their migration and reach the thermocline. This interpretation agrees with Folt & Burns (1999), who stated that diel vertical migration is one of the main triggers of patchiness, as well as Tokarev et al. (1998) who link larger patches at night to vertical migration.

We did not find data on copepod patch dimensions from the Baltic Sea in the literature, but there are some studies on zooplankton patchiness from different areas to compare our results to. None of these studies did have copepod data derived with a VPR though. In addition, each of these studies' calculations are based on different patch definitions and different sampling tools. Therefore, only a few essential observations made in all of the different studies seem comparable. In our results, we found an increase in patch size at night. This agrees with Wiebe (1970), who deployed a Longhurst-Hardy plankton recorder off Guadalupe Island (Baja California) in the Pacific Ocean, to study patches of different copepod and zooplankton species. Furthermore, Tokarev et al. (1998) found also larger patches during the night. The authors used hydroacoustic as well as plankton net data from the Black Sea to investigate small-scale patchiness in zooplankton. Moreover, we found only few very large patches. This agrees with Tsuda et al. (1993), who investigated patches of the copepod *Neocalanus cristatus* from the subarctic North Pacific, by deploying an electrical particle counter as well as plankton nets. Similar to our results, the authors found that patch numbers decreased with increasing patch size. The majority of patches (75%) found by Tsuda et al. (1993) was below 500 m in length, as was the case in our study (98%).

PREDICTING STOMACH CONTENT WEIGHTS

In predicting the copepod share of sprat stomach content weights, we wanted to investigate if a patchy prey distribution results in the variability of stomach content weights found in the field. In the first approach of predicting these sprat stomach content weights, we assumed an even descent of sprat during their downward migration, and consequently equal feeding times in each depth layer. Results from AB and BB samples suggested that sprat from the field left aggregations with high prey concentrations before their stomachs were full (figures III-6 & III-7, black bars). This was assumed because our predictions showed an overestimation of full stomachs with copepod concentrations found in the field (figures III-6 & III-7, white bars). We suggest that light intensities might be the driving force behind this. Throughout their DVM fish seem to follow layers with the same light intensity (Mehner 2012). Therefore, we assumed that sprat in our case were driven by increasing light intensities and thus seemed to continuously migrate downwards, leaving patches with high copepod abundances without fully exploiting these.

Considering results of the first prediction approach from our GB sample, it seemed that sprat were staying in higher water layers for a longer period of time, thereby resisting increasing light intensities. Stomach content weights found in the field cannot be explained otherwise (figure III-8, black bars), since the lower water layers investigated by us showed almost no copepods (figure III-5e) and our predictions resulted in stomachs with only low content weights (figure III-8, white bars).

These conclusions were incorporated into our second approach of predicting stomach content weights. For the AB sample, we decreased feeding time in the upper three depth layers that showed higher copepod abundances and increased the feeding time in the lower, low copepod abundance layers. Thus, we took a migration pressure through increasing light intensities into account. Our second prediction approach verified the assumption of sprat feeding in layers with higher copepod abundances for a shorter time period by resulting in a nearly matching median value of stomach content weights from predicted and field data (figure III-9). Furthermore, our suggestion that sprat in GB prolonged their stay in upper waters in spite of increasing light intensities was also verified by our second prediction approach. By assuming that sprat fed only in the upper two high copepod abundance layers, we were able to decrease the amount of underestimated stomachs and to nearly double the median value of the predicted data (figure III-11). The fact that field data from GB showed a mean stomach content weight that was almost three times as high as the ones from AB and BB fits with our observations on copepod patches. We found the highest number of patches in GB as well as the highest mean copepod abundances in these patches. This leads to the suggestion that sprat were able to utilize the higher copepod abundances found in GB. Nevertheless, our predicted data did not result in full sprat stomachs. This might be explained by our sampling section. It does not show how copepods are distributed above 18 m, and if patches extend into the water layers above the ones sampled with our VPR. The night-time copepod distribution in GB might look similar to the one in BB, where most copepods are found directly at and above the thermocline (figure III-4e & Bernreuther et al.

2009). If that is the case, sprat would have been able to feed on high abundances of copepods in these shallower water layers, and this would explain the full stomachs found in GB field data (figure III-11, black bars).

Both of our stomach content weight prediction approaches for BB resulted in non-matching median values of predicted and field data. This might be due to the fact that none of the investigated layers showed low copepod abundances. The explanation for this might lie in the sampled depth range. In contrast to the GB sample, our VPR tows in BB covered hardly any depth layers below the thermocline. We suggest that copepod abundances drastically decline in deeper layers, as found in GB (figure III-5e). This is also suggested by Bernreuther et al. (2009), who showed for a summer situation in BB that the main part of the copepod distribution is found above 40 m during the night. This implies that sprat might be able to withstand increasing light intensities for a certain amount of time, but when they finally have to migrate further downwards, they will find only lower copepod abundances, resulting in the overall smaller stomach content weights that were found in the field data.

Results of our predicted stomach content weight data support the assumption that patchy prey distributions lead to high variability in sprat stomach content weights, although our predicted data (except BB) did not meet the fullest stomach content weights of the field data. A patchy prey distribution means that during the morning feeding phase, some sprat reach a patch of prey organisms and remain feeding in this area for a certain time, while other sprat do not encounter a prey patch and directly migrate further downward. Depending on the prey conditions sprat encounter while descending, they either interrupt this descent and start feeding or migrate further downward. Thus, some sprat are found in the field with low and some with high stomach content weights after this downward migration. This was also the case in our predicted data, where some stomachs showed lower and some showed higher content weights.

These results also support our assumption that sprat feeding concentrates mainly on depth layers around the thermocline, as investigated in this study, because our predicted stomach content weights are not distinctly lower than the field data. Even our GB results do not disagree with this, because they suggest that sprat feed even closer to the thermocline, in layers higher as the ones investigated by us.

Furthermore, our results support the suggestion of patchiness as an effective protection mechanism against predators. Kulke (2018) already showed that high prey concentrations limit the maximum feeding rate of sprat, and our results do show that a patchy copepod distribution leads to lower sprat stomach content weights than a random distribution (table III-8). However, protection against predators is in this case not due to the confusion of predators as stated in the literature (Pijanowska & Kowalczewski 1997), but rather a consequence of the handling time of a single prey organism. This handling time is limiting the maximum feeding rate of sprat in a Holling Type II functional feeding response relationship (Holling 1959, Brachvogel et al. 2013, Kulke 2018). This type II functional response is typical for particulate feeding planktivorous fish in patchy prey environments (Smith 1998) and is characterized by an asymptotic curve. The predation rate increases nearly linearly at low prey concentrations, slows down gradually with rising prey concentrations and finally reaches an upper limit at high prey concentrations (figure III-12).

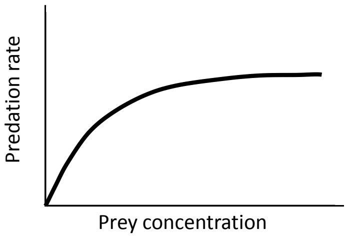

Figure III-12. Schematic representation of a functional response type II after Holling (1959) for sprat feeding. Predation rate is shown as function of prey concentration. In a Holling type II functional feeding response, prey mortality is highest at low prey concentrations.

CONCLUSION

Results of this study lead to the conclusion that DVM of zooplankton is indeed associated with patch formation, and that this patchy distribution of organisms could be an effective method of decreasing predation risk for the individual prey organism. Furthermore, we conclude that a patchy prey distribution seems to be a strong enough factor to override the need of sprat to migrate further downwards as triggered by increasing light intensities during morning hours. Since our study is the first on copepod patch dimensions in the Baltic Sea, we strongly suggest additional studies to broaden the knowledge on spatial scales of these patches. Only with this knowledge are we able to enhance the accuracy of copepod abundance and population size estimates, and to "obtain a more complete interpretation of the zooplankton biomass" as Kawamura & Hirano (1985) state.

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GENERAL DISCUSSION

The aim of this thesis was to investigate differences between copepod species in regard to drivers of diel vertical migration (DVM) and spatial dimensions of copepod patches. Furthermore, implications of a patchy copepod distribution on sprat (*Sprattus sprattus*) feeding were investigated. Here, results of the previous three chapters are discussed in the light of the following four objectives:

i) *In situ* systems such as the Video Plankton Recorder (VPR) provide more efficient plankton sampling than traditional plankton nets.

ii) DVM of the halocline associated copepod *Pseudocalanus acuspes* is a predator avoidance mechanism.

iii) Species-specific factors drive DVM in copepods from halo- and thermocline associated habitats.

iv) Copepod DVM leads to the formation of copepod patches, and patchy prey distributions impact the feeding behaviour of planktivorous fish like sprat.

EFFICIENCY OF PLANKTON SAMPLING WITH THE VPR SYSTEM

The overarching hypothesis that *in situ* systems like the VPR provide more efficient plankton sampling than traditional plankton nets was confirmed in this thesis.

As described before, it was necessary to manually sort all VPR images taken into account for the analyses conducted in this thesis. Automatic sorting carried out by the Visual Plankton software resulted in numbers of copepods that were three times lower than results obtained through manual sorting of the images (table 1). Most of the copepods were not recognised as such by the software—instead, they were sorted into the categories “unknown” and “marine snow”.

Table 1. Comparison of sorting results from Visual Plankton software and manual sorting. Percentages and ratios determined from summer VPR data as used in chapter III.

Sampling area	% of copepods found by software	% of copepods found manually	Ratio of copepods software:manual sorting
AB	7	24	01:03
BB	11	36	01:03
GB	5	13	01:03

However, manually sorting VPR images was still more efficient than having to sort traditional multinet (MSN) plankton samples (table 2). Manual sorting of all 47 VPR samples analysed in this thesis, with a total amount of 1 906 964 images, took approximately 4 months. This timeframe was estimated by dividing the amount of images by the time needed for sorting 125 000 images—which is done on average in one week á 5 days with 6 hours each. The assumed number of MSN samples required to cover the depth ranges and horizontal resolution investigated in this thesis would amount to 3336 samples. With an approximate processing time of 3 hours per sample (Rachel Harmer, personal communication), and 6 hours per day in a 5 day week, this would add up to 83 months needed for sorting these MSN samples. The investigations on copepod patches in particular (**chapter III**) would lead to an immense amount of MSN samples. When conducting horizontal VPR tows, information is gathered on the extent of copepod patches by continuously monitoring copepod abundances. This kind of information would only be achieved when individual vertical MSN samples would be conducted every few metres along the entire investigated track. Thus, 150 individual MSN hauls would be necessary along an investigated horizontal track of approximately 1500 m. Each of these hauls would have to contain 7 individual samples, to cover the investigated ca. 20 m depth range in individual 3 m layers. The amount of time needed to obtain and manually sort these samples would make a patch investigation as conducted with the VPR system in this thesis nearly impossible.

Table 2. Comparison of processing time needed for sorting the amount of VPR images analysed in this thesis and needed for sorting traditional MSN plankton samples.

Gear	No. of images / samples	Processing time [month]
VPR	1906964	4
MSN	3336	83

PREDATOR AVOIDANCE IN *PSEUDOCALANUS ACUSPES* DVM

The second hypothesis that DVM of the halocline associated copepod *P. acuspes* is a predator avoidance mechanism was also confirmed.

Chapter I showed that no DVM of ovigerous *P. acuspes* females was observed in situations with low clupeid predator densities. This agrees with results from other marine (Ohmann et al. 1983, Bollens & Frost 1989) as well as freshwater (Zaret & Suffern 1976) zooplankton communities, which showed that the strength of DVM behaviour depends on the respective prevailing predator concentrations. The summer situations where *P. acuspes* DVM stopped did not only feature low feeding pressure due to low predator densities, but also a different prey particle preference of clupeids. Bernreuther et al. (2018) showed that clupeids from Bornholm Basin (BB) favoured *Temora longicornis* and cladocerans during summer. These species reside in the upper 30 m of the water column (Hansen et al. 2006, Kulke et al. 2018), while adult *P. acuspes* females concentrate between 70 and 80 m (Renz & Hirche 2006). The hypothesis of a predator avoidance DVM was furthermore supported by the fact that—in contrast to the presence/absence of clupeids—changing hydrographical conditions had no effect on the appearance of DVM in *P. acuspes*.

SPECIES-SPECIFIC DVM DRIVERS

Furthermore, this thesis examined the hypothesis that species-specific factors drive DVM in copepods from halo- and thermocline associated habitats. Evidence was found to confirm this hypothesis.

Results from **chapter I and II** showed that there are clear differences in the factors that drive DVM in different copepod species of the Baltic Sea. As described above, DVM of halocline associated *P. acuspes* is triggered by predators (figure 3—dark grey area). Contrasting results emerged from analysing DVM patterns of thermocline associated copepods like *T. longicornis* and *Acartia* spp. in **chapter II** (figure 3—light grey area).

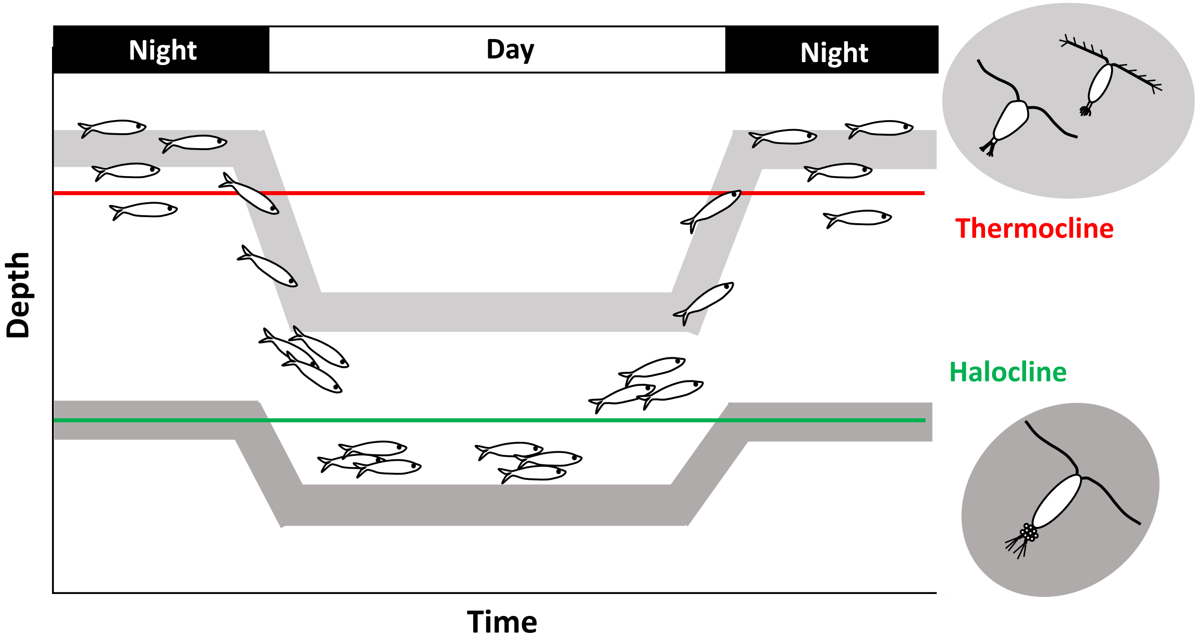

Figure 3. Schematic representation of vertical migration patterns of copepods investigated in this thesis, as well as clupeid predation as a driving factor. Light grey—vertical migration pattern of thermocline (red line) associated copepod species Acartia spp. and Temora longicornis, dark grey—vertical migration pattern of halocline (green line) associated ovigerous Pseudocalanus acuspes females.

Here, results showed a simultaneous down- as well as upward migration of predators (clupeids) and prey (copepods) during their respective DVM. Sprat consume up to 84% of their total daily ration (Kulke et al. 2018) during these phases of DVM, by feeding extensively on copepods from the upper 50 m of the water column (Kulke et al. 2018). Therefore, a copepod migration that runs in the same direction as the clupeid migration—as observed in **chapter II**—does not support the assumption of a predator avoidance DVM of copepods against clupeids. Other predators like jellyfish or mysids also fail to prove as copepod DVM drivers in the Baltic Sea. Both were shown to exert only very low predation impacts on copepods (Salemaa et al. 1990, Margonski & Maciejewska 1999, Barz & Hirche 2005 & 2009). In addition, DVM of thermocline associated copepods was visible in spring data investigated in this thesis, while the jellyfish predator *Aurelia aurita* is still absent from BB during this season (Barz & Hirche 2005).

When predator avoidance can be excluded as a copepod DVM driver, other cues have to be considered for inducing this behaviour. The assumed avoidance of sunlight (Williamson et al. 1994) does not seem a suitable explanation for copepod DVM in the Baltic Sea. UV radiation does reach only the surface layers of the Baltic Sea (Lampert & Sommer 1993, Dera & Woźniak

2010), while copepods show daytime migrations much deeper than that (**chapter II**). It seems possible that DVM in thermocline associated copepods is not at all driven by exogenous, but more likely by endogenous factors like circadian clock genes. These were shown to drive DVM in *Calanus finmarchicus,* and for being responsible for the occurrence of this DVM despite constant darkness (Häfker et al. 2017). Such an endogenous trigger could coordinate energy saving periods in cooler water layers during the day (Lampert 1989, Schmidt 2006) and feeding on high quality phytoplankton in surface layers during the night (Lampert 1989, Lampert & Sommer 1993). Thus, change of light intensities might itself not be the driving factor of DVM, but rather a synchronizing mechanism for endogenous triggers of this migration behaviour (Harris 1963, Enright & Hamner 1967, Enright & Honegger 1977). This would explain why the descent of vertically migrating organisms can be observed before changes in light intensity become visible (Harris 1963). However, although predators seem to not trigger DVM of thermocline associated copepods in the first place, this DVM behaviour leads to an indirect protection mechanism against predation. During DVM, copepod patches start to form, until these individual patches aggregate into massive patches at the thermocline (**chapter III**), and patchiness is known for its potential to act as a protection against predators (Omori & Hamner 1982, Folt & Burns 1999). Pijanowska & Kowalczewski (1997) report that this is due to the confusion of predators by high amounts of moving prey organisms and the lower risk of being captured by a predator when hiding among a high amount of other prey organisms. Nevertheless, in the situation investigated here, protection against predators through patchiness is more likely a consequence of the handling time necessary for one prey organism by the predator. Particulate feeding planktivorous fish like clupeids and specifically also sprat show a Holing Type II functional feeding response relationship (Smith 1988, Brachvogel et al. 2013, Kulke 2018). In this type II functional feeding response, the maximum feeding rate is limited by the handling time (Holling 1959). At low prey concentrations, predation risk for copepods increases because the handling time for capturing and feeding a prey organism is short enough to allow for the possible utilization of all prey organisms. On the other hand, high copepod concentrations cannot be utilized fully by sprat due to this handling time. Consequently, predation risk for the individual copepod decreases. This indirect protection mechanism might be beneficial during the simultaneous down- and upward migration of copepods and sprat. During these phases of the day, predator and prey show a high spatial overlap. Low prey concentrations would lead to high predation risk, as described above. However, since copepods gather into patches during their DVM (**chapter III**), sprat encounter high prey concentrations. Thus, handling time of prey organisms limits the amount of copepods a sprat is able to consume within the period of time where predator and prey overlap spatially. As mentioned above, this leads to a decreased predation risk for the individual copepod. Overall, both of the investigated cases (**chapter I & II**) lead to the conclusion that DVM seems to be a trait-off—in the case of *P. acuspes* between feeding at the halocline and predator avoidance (**chapter I**) and in the case of *T. longicornis* and *Acartia* spp. between feeding at the thermocline and metabolic needs (**chapter II**).

As mentioned before, copepods and zooplankton in general contribute to nutrient transport in the water column through the sinking of faecal pellets into deeper water layers (Wallace et al. 2013). Furthermore, these organisms contribute greatly to the biological pump through DVM (Bollens et al. 2011, Wang et al. 2015), by grazing on phytoplankton during night at the surface, and metabolizing this food during day in deeper layers (Longhurst & Harrison 1988). A significant fraction of the total vertical flux of particulate organic matter (POM) is thereby attributable to DVM—e.g. up to 40% of sedimenting carbon and up to 26% of sedimenting nitrogen in the North Atlantic (Morales 1999). Yet, this pathway of the biological pump remains largely unquantified in many export models (Archibald et al. 2019). However, when facing climate change and rising CO_2 levels, the abilitiy to quantify and predict vertical fluxes becomes more and more important. Knowledge about interactions of DVM and vertical fluxes are therefore highly relevant (Bollens et al. 2011). Thus, it seems especially important to quantify the amount of carbon transported into deeper water layers by copepods and their DVM in an environment that shows a trophic decoupling like the Baltic Sea (Bernreuther et al. 2018). Low feeding pressure on copepods should result in thriving copepod populations with high faecal pellet production and high numbers of organisms performing DVM, thereby contributing largely to the vertical flux of POM.

COPEPOD DVM, PATCHINESS & IMPLICATIONS ON SPRAT FEEDING

The investigated hypotheses that i) copepod DVM leads to copepod patch formation, and that ii) this patchy prey distribution impacts the feeding behaviour of planktivorous fish (e.g. sprat) were also confirmed in this thesis.

Results from the studies presented in this thesis showed that copepods from both investigated habitats (halo- & thermocline) have developed strategies to avoid feeding pressure by predators. In **chapter I**, a predator avoidance migration behaviour was verified for *P. acuspes*. This was not the case for *T. longicornis* and *Acartia* spp. in **chapter II**, but **chapter III** showed that these species apply an indirect protection mechanism through their migration behaviour. DVM leads to patchiness through the regular aggregation of organisms at a certain depth (Folt & Burns 1999), in this case the depth of the thermocline. All of the three investigated basins showed high numbers of patches with small patch sizes in the evening samples. Results from **chapter II** suggested that the upward migration of copepods takes place within this time period. During the night however, only few but large patches were found in the data from **chapter III**. This leads to the conclusion that patches start to form in the evening caused by the upward DVM of copepods. At night, the small patches subsequently accumulate to large patches once the copepods reach a certain depth—the thermocline—and aggregate there. This patchy prey distribution seems to have an impact on the feeding as well as the migration behaviour of sprat. On the one hand, results from **chapter III** showed that sprat feed less when copepods are distributed patchy in contrast to a random distribution. This is due to the handling time limiting the maximum feeding rate (Holling 1959, Brachvogel et al. 2013, Kulke 2018) as described above. On the other hand, the need of sprat to migrate further downward, as induced by increasing light intensities can apparently be overridden when migrating clupeids encounter high abundance copepod patches. It is assumed that fish follow layers with the same light intensity throughout their DVM (Mehner 2012). This would result in a continuous downward migration of clupeids with increasing light intensities, independent if high abundance copepod patches are encountered during this migration. However, results of predicted stomach content weights from **chapter III** indicate that sprat seem to modify their response to an increasing migration stimulus resulting from light intensities. It was only possible to generate stomach content weights comparable to those found in the field when sprat were assumed to feed longer in upper prey rich water layers despite increasing light intensities.

In the Baltic Sea, copepods seem not to be controlled top-down, although results from **chapter III** suggested that it is possible for sprat to feed on copepod patches for longer time periods. Möllmann et al. (2005) reported of a simultaneous increase of sprat and their prey organisms *T. longicornis*, *Acartia* spp. and cladocerans. Furthermore, Bernreuther et al. (2018) showed recently for BB that the predation impact of clupeids was not strong enough to control zooplankton dynamics. Only 18% of the annual *T. longicornis* and a meagre share of 1.4% of the *Acartia* spp. production were utilized by clupeids according to Bernreuther et al. (2018). Instead, the copepod species investigated in this thesis are controlled apparently through hydrographic conditions (Möllmann et al. 2000). Several studies report that *P. acuspes* abundance and biomass is controlled by salinity, with decreasing populations in times of decreasing salinities in the Baltic Sea (Vuorinen et al. 1998, Möllmann et al. 2000, 2003a, 2003b, 2005). In contrast, *T. longicornis* and *Acartia* spp. copepods are related to temperature, with warmer temperatures leading to an increase in both species' populations (Dippner et al. 2000, Möllmann et al. 2000, 2003a, 2005). Increasing temperatures also lead to the activation of *Acartia* spp. resting eggs, which seems to be the most important source for hatching of *Acartia* nauplii in the Baltic Sea (Möllmann et al. 2003a, Dutz et al. 2004, Alheit et al. 2005).

GENERAL CONCLUSION & OUTLOOK

Through manually sorting all VPR images used in the analyses mentioned here, and not relying on an ineffective sorting algorithm of a software, errors of these VPR data are very likely small. Furthermore, the investigations on copepod patch dimensions were only possible through the use of a VPR system. This system provides continuous plankton data on spatial scales that are challenging to cover logistically as well as financially with traditional plankton nets. This shows the potential of optical plankton sampling devices, and how vital it is to further improve methods on automatic sorting of plankton images, for example image classifiers. Copepod images manually sorted here out of nearly 2 million VPR images can contribute to these improvements by being implemented into large data training sets, thus helping to build better classifiers.

On the downside, quantifying copepods with a VPR system is highly dependent on the prevailing water clarity, as mentioned in **chapter III**. In the Baltic Sea, high amounts of marine snow lead to a high turbidity of the water column. These high amounts of marine snow might partly be caused by the trophic decoupling of mesozooplankton and planktivores that was recently described for the Baltic Sea (Bernreuther et al. 2018). Low predation impact on the zooplankton population results in a high production of faecal pellets as well as decaying biomass that disintegrates and transforms into marine snow. Thus, a method has to be developed to correct for water turbidity and to receive image volumes unaffected by these differences in water clarity, to furthermore gain accurate copepod abundances from VPR data.

Considering the results of all three chapters, there are still some aspects that warrant further investigation. First, there seems to be an ontogenetic migration of ovigerous *P. acuspes* females into low salinity water layers above 50 m in BB. It would be necessary to test if this really is a migration to release offspring half way to the surface. This migration behaviour does also raise the question from which salinity levels on *P. acuspes* individuals start to experience negative effects on life cycle and reproduction. So far, experimental tests concerning salinity effects on reproduction and mortality have been unsuccessful due to high mortality of *P. acuspes* under culture (Möller et al. 2015).

Second, predator avoidance was verified as the DVM driver in halocline associated *P. acuspes*, but factors driving DVM in thermocline associated *Acartia* spp. and *T. longicornis* are still not certain. However, predator avoidance against clupeids and jellyfish was excluded as possible DVM driver. Here, further investigations on endogenous triggers of thermocline associated copepod DVM seem appropriate.

Third, this is the first study on the occurrence and dimensions of Baltic Sea copepod patches. More knowledge about the spatial scales of these patches is needed to gain further insights into predator-prey relationships of the Baltic Sea. Therefore, regular sampling has to be conducted, and more ship time has to be devoted to measuring copepod patches. This would help to improve the vertical resolution of patch data, as well as knowledge about the high temporal dynamics of patch structures.

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Individual contributions to chapters with multiple authors

Chapter I—Predator density triggered vertical migration of *Pseudocalanus acuspes* in the Baltic Sea

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Text writing, data analyses and graphical illustrations were conducted by Kristin Hänselmann under the supervision of Axel Temming who critically reviewed the chapter. Jens-Peter Herrmann was involved in the conceptual design of this study and helped with data analysis and interpretation. Klas Ove Möller provided data included in this study. Dominik Gloe provided knowledge on processing of hydroacoustic data and critically reviewed parts of the chapter.

Chapter II—DVM patterns of thermocline associated copepods in different basins of the Baltic Sea

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Text writing, data analyses and graphical illustrations were conducted by Kristin Hänselmann under the supervision of Axel Temming who critically reviewed the chapter. Jens-Peter Herrmann was involved in the conceptual design of this study and helped with data analysis and interpretation. Steffen Funk and Rebecca Lauerburg helped with statistical analyses and data interpretation. Dominik Gloe provided knowledge on processing of hydroacoustic data and critically reviewed parts of the chapter.

Chapter III—Investigating copepod patches and their implications on sprat (*Sprattus sprattus*) feeding in the Baltic Sea

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Text writing, data analyses and graphical illustrations were conducted by Kristin Hänselmann under the supervision of Axel Temming who critically reviewed the chapter. Jens-Peter Herrmann was involved in the conceptual design of this study and helped with data analysis and interpretation. Claudia Günther provided bioenergetics information on sprat. Rini Kulke provided the temperature- and size-dependent functional feeding response model and helped with writing of the related methods section. Rebecca Lauerburg helped with statistical analyses and data interpretation.

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Eidesstattliche Versicherung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift „Diel Vertical Migration Patterns of Baltic Sea Copepods Analysed with a Video Plankton Recorder“ selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Hamburg, Juni 2019 Kristin Hänselmann

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I hereby confirm that the thesis by Kristin Hänselmann entitled “Diel Vertical Migration Patterns of Baltic Sea Copepods Analysed with a Video Plankton Recorder” has been prepared according to excellent written English language standards.

Sincerely,

Keith MacPherson

Founder

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