

Distribution patterns of Baltic sprat (*Sprattus sprattus* L.) – causes and consequences

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Still confused, but on a higher level
Enrico Fermi

Summary

This thesis shows different aspects of the distribution of adult sprat in the central Baltic Sea.

The seasonal development of the horizontal distribution of sprat was investigated in 2002/2003 under the influence of a shift in the environmental regime. During the period of investigation, several inflow events of saline and well oxygenated water into the deep Basins of the Baltic Sea were observed. This includes the first major Baltic inflow (MBI) since 1993, which occurred in January/February 2003 and dramatically changed the environmental condition in the Bornholm Basin. Prior to this MBI, a 'typical' seasonal development of the sprat abundance in the Bornholm Sea was observed. After the MBI in 2003, relatively cold temperatures were observed in the Bornholm Basin throughout the water column. It was assumed that these unfavourable conditions lead to an avoidance migration of sprat in the more eastern areas. This was supported by an increase of the sprat abundance in the Gotland Basin.

The abiotic parameters that determine the vertical distribution of sprat were investigated during several cruises, including meso-scale and small-scale investigations. Temperature and oxygen content of the water were confirmed as main driving factors for the vertical distribution of sprat, whereby the relevant thresholds were determined as 5°C and 1ml/l oxygen content. Other environmental parameters were identified to have an impact on the diel vertical migration (DVM) of sprat. Light was assumed to induce DVM of sprat, whereas the causal relationship remained unclear. Strong vertical temperature gradients can prevent DVM, if the minimum temperature, to be passed is colder than 5°C. On the other hand, cold water was crossed where the temperature gradient was relatively low. The influence of salinity and depth was found to be negligible.

The results of these investigations were used to develop two models for the vertical distribution of sprat. The first model approach bases upon the calculation of the probability of occurrence, calculated for temperature and oxygen. This simple model was successfully applied to data, derived during spawning time in spring 2002, but revealed weaknesses when applied to other seasons. Furthermore, a more complex was introduced, whereas the vertical distribution of sprat was modelled as behavioural response to external stimuli. This approach was successfully applied to model the diel vertical migration of sprat. With the latter model approach a tool is delivered to include the vertical distribution into ecosystem models and is therefore an important improvement in ecosystem research in the Baltic.

With regard to the consequences of the distribution patterns of Baltic sprat it was shown, that the vulnerability of key zooplankton species to predation by clupeids is highly influenced by the spatial overlap of predator and prey. Highest impact of sprat on zooplankton species was found for *Pseudocalanus* sp. during spring and *Temora longicornis* during summer.

Zusammenfassung

In dieser Arbeit werden verschiedene Aspekte der Verteilungsmuster adulter Sprotten in der zentralen Ostsee behandelt.

Die jahreszeitliche Entwicklung der horizontalen Verteilungsmuster wurde in den Jahren 2002 und 2003 untersucht. Während dieser Zeit haben mehrere Einströme von salz- und sauerstoffreichem Wasser in die Tiefen Becken der Ostsee zu einer gravierenden Veränderung der Umweltbedingungen geführt. Besonderen Einfluss hatte der Einstrom im Januar/Februar 2003, der der erst große Einstrom (major Baltic inflow – MBI) seit 1993 war. Vor diesem MBI wurde eine ‚typische‘ saisonale Abundanz-Entwicklung im Bornholm Becken beobachtet. Nach dem MBI im Jahre 2003 wurden im Bornholm Becken sehr kalte Temperaturen in der gesamten Wassersäule gefunden. Diese Verschlechterung der Umweltbedingungen führte zu einer Wanderung eines Großteils der Sprotten in das weiter östlich gelegene Gotland Becken.

Die abiotischen Faktoren, die die Verteilung der adulten Sprotten beeinflussen wurden während mehrerer Forschungsfahrten untersucht. Diese Untersuchungen schließen meso- und kleinskalige Verteilungsmuster ein. Temperatur und Sauerstoff wurden als entscheidende Faktoren für die Vertikalverteilung der Sprotten bestätigt, wobei 5°C und 1ml/l Sauerstoff die für die Verteilung relevanten Grenzen darstellen. Es konnte gezeigt werden, dass weitere Faktoren für die tägliche Vertikalwanderung (diel vertical migration – DVM) von Bedeutung sind, wobei nicht geklärt werden konnte auf welche Weise Licht die Vertikalwanderung steuert. Starke Temperaturgradienten können die DVM verhindern wenn die minimale Temperatur des zu passierenden Wasserkörpers kälter als 5°C ist. Andererseits werden kalte Wasserschichten durchwandert wenn der vertikale Temperaturgradient gering ist. Ein signifikanter Einfluss von Salzgehalt und Tiefe konnte nicht gezeigt werden.

Die Ergebnisse dieser Untersuchungen wurden benutzt um zwei Modelle für die Vertikalverteilung von Sprotten in der Ostsee zu erstellen. Der erste Modell-Ansatz basiert auf der Berechnung von Aufenthaltswahrscheinlichkeiten in Abhängigkeit von Temperatur und Sauerstoff. Dieses Modell konnte erfolgreich auf einen Datensatz angewendet werden, der während der Laichzeit im April 2002 gewonnen wurde. Jedoch war eine Übertragung auf andere Jahreszeiten nur bedingt möglich.

Dementsprechend wurde ein weiterer Modell-Ansatz umgesetzt, der die vertikale Verteilung durch Verhalten, ausgelöst durch externe Faktoren, simuliert. Dieses Modell wurde erfolgreich eingesetzt um die tägliche Vertikalwanderung der Sprotten zu modellieren. Damit ist nun ein gutes Werkzeug verfügbar um die Vertikalverteilung von Sprotten in Ökosystem-Modelle zu integrieren. Dieses stellt einen wichtigen Schritt in der Ökosystemforschung der Ostsee dar.

Im Hinblick auf die möglichen ökologischen Konsequenzen der beschriebenen vertikalen Verteilungsmuster, wurde der Einfluss der Sprottenpopulation auf wichtige Zooplanktonarten untersucht. Es konnte gezeigt werden, dass diese Beziehung sehr stark von der räumlichen Überlappung von Räuber und Beute abhängt. Besonders *Pseudocalanus* sp. und *Temora longicornis* waren zu bestimmten Jahreszeiten sehr stark betroffen.

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1. General Introduction

The aim of science, in general, should be the reduction of uncertainty or at least making inferences about the world that is hampered by uncertainty. While fluctuation in stock size is a well known phenomenon for several important fish stocks, the underlying principles are often poor understood. These principles are not straight forward, moreover ecosystem processes and functions are complex and variable, resulting in a high level of uncertainty.

'Natural variability, occurring over a variety of times and scales, dominates the health of complex ecosystems, regardless of fishing or other environmental pressure. We are only now beginning to compile quantitative documentation of such variability, and consequently our knowledge concerning its causes remains at the level of hypotheses. Understanding of the role of variability in the function of marine ecosystems is essential if we are to effectively manage global marine living resources such as fisheries during this period of tremendously increased human impact, and concurrent dependence, on these resources.'

GLOBEC Science Plan, 1997

This thesis was prepared in the framework of the German GLOBEC-project, which is part of the international GLOBEC. The GLOBEC-program (Global Ocean Ecosystem Dynamics) is one of the core projects of the International Geosphere Biosphere Program (IGBP) and was developed to understand the influence of physical processes on the abundance and distribution of key zooplankton and fish populations. In more general terms: GLOBEC was initiated to advance the understanding of the structure and functioning of the global ocean ecosystem, its major subsystems, and its response to physical forcing. Consequently, a capability can be deployed to forecast the responses of the marine ecosystem to global change (IGBP 1999)

GLOBEC-Germany aims to understand the interaction of zooplankton and fish under the influence of climate. Understanding of the underlying processes has to be developed through a combination of field studies, experiments and modelling exercises, including numerous subjects of marine research. The coupled biological-physical models should be a supplementation and application of knowledge, which is derived from intensive field studies (e.g. Eckmann 1994, Wiebe *et al.* 1996). The expectation was that an improved understanding of population fluctuations at short time scales could enlighten causal relationships of long-term ecosystem changes. This was studied in the Baltic and the North Sea, which have quite different oceanographic characteristics. In both seas, a similar set of species was in focus: the clupeid fishes herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.) and their main prey items *Pseudocalanus* sp., *Acartia* sp. and *Temora longicornis*, which are copepods. The scientific approach of the GLOBEC-Germany project was focused on processes that are related to the recruitment of sprat. In that context, one of the main questions is the investigation of the abundance and distribution of adult sprat (Kraus and Köster 2004, MacKenzie and Köster 2004). This information is important for several key processes influencing the sprat recruitment. These processes include (i) the distribution of spawning activity, as the environmental conditions differ between spawning sites (MacKenzie *et al.* 2000, Kraus and Köster 2004), (ii) the physiological status of adults as influenced by environmental conditions (Grauman and Yula

1989, Parmanne *et al.* 1994, Kraus *et al.* 2003) and (iii) implications for the pelagic food web, e.g. a possible top-down control of meso-zooplankton species (e.g. Möllmann and Köster 2002).

This thesis presents the work that is related to the distribution of adult sprat in the Baltic Sea and includes following tasks:

1. the identification of abiotic parameters that influence the distribution of adult sprat in the central Baltic Sea at several scales,
2. the investigation of possible implications for the (e.g. feeding) ecology of sprat and
3. the development of a habitat model for Baltic sprat.

The first task is addressed in the chapters 1, 4, 5, and 10. Investigations cover the large scale horizontal distribution and migration (chapter 1), meso-scale hydrographic patterns and their influence on the distribution of sprat, as well as small-scale (vertical) distribution patterns. The needed introduction into the Baltic ecosystem and the concepts of space, time, scale and the ecological niche were given below.

The second task is presented exemplarily in chapter 7. Since the concept of trophic cascades and top-down control is discussed in this chapter, a introduction is given below.

Models for the vertical distribution of adult sprat in the Baltic Sea (task 3) are presented in chapter 5 and 6.

The Baltic Sea

Hydrography - The Baltic Sea is the largest brackish, semi-enclosed area in the world and consists of different deep basins, which are separated by sills. The hydrography is characterized by strong thermo-haline stratification with less saline water in the upper layer and higher salinity below the halocline.

The upper water layer is influenced by river freshwater run-off and air temperature. During summer an additional thermal stratification appears near the surface (around 20m), due to heating of upper water layers (Møller and Hansen 1994). The halocline is usually found around 50-70m in the basins. Due to huge density differences, the stratification is very stable and vertical mixing between water layers is restricted. Therefore, lateral transport of inflowing saline and oxygen-rich

water from the North Sea is very important for the renewal and ventilation of the water below halocline. However, this is often hampered by the basin like bottom topography with different sills (e.g. Matthäus and Franck 1992). Salinity, temperature, oxygen content and vertical dimension of the deep-water layer depends on inflow events. Only strong inflow events will result in a renewal of deep water in the Bornholm Basin, Gdansk Deep and Gotland Basin (Börngen *et al.* 1990, Matthäus and Franck 1992, Matthäus and Schinke 1994). Due to a period of positive North Atlantic Oscillation (NAO), weather conditions have not supported strong inflows during the last decade (Fonselius and Valderamma 2003, Hänninen *et al.* 2000, Matthäus and Schinke 1999). The absence of sufficient inflow events resulted in anoxic zones in the bottom layer of the basins (Fig. 1.2 left column). A moderate inflow occurred in winter 2002/2003 and replaced the deep water of the Bornholm Basin (Fig. 1.2 right column) (Mohrholz 2006). The inflowing water was extremely cold. The implications of this inflow will be discussed in the context of sprat distribution.

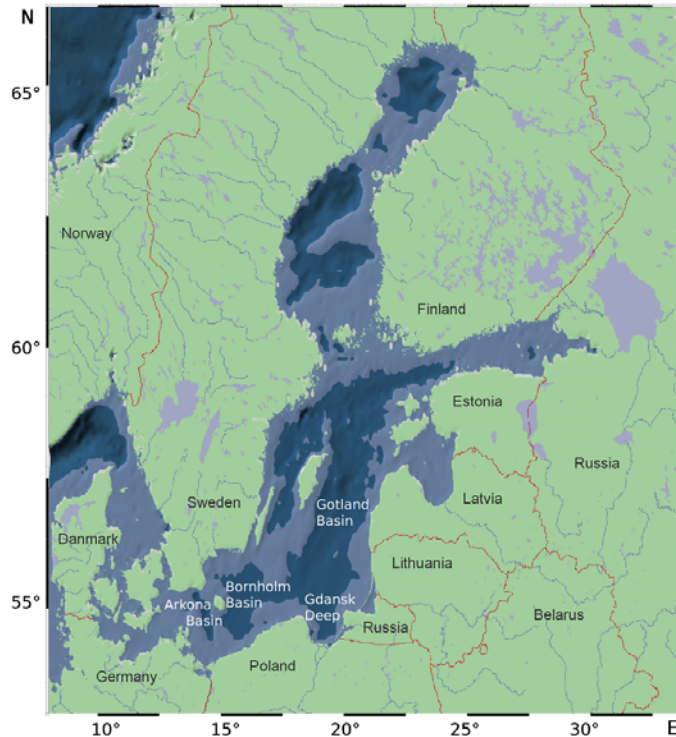


Fig. 1.1. Map of the Baltic Sea. Graph produced by Jörn Schmidt.

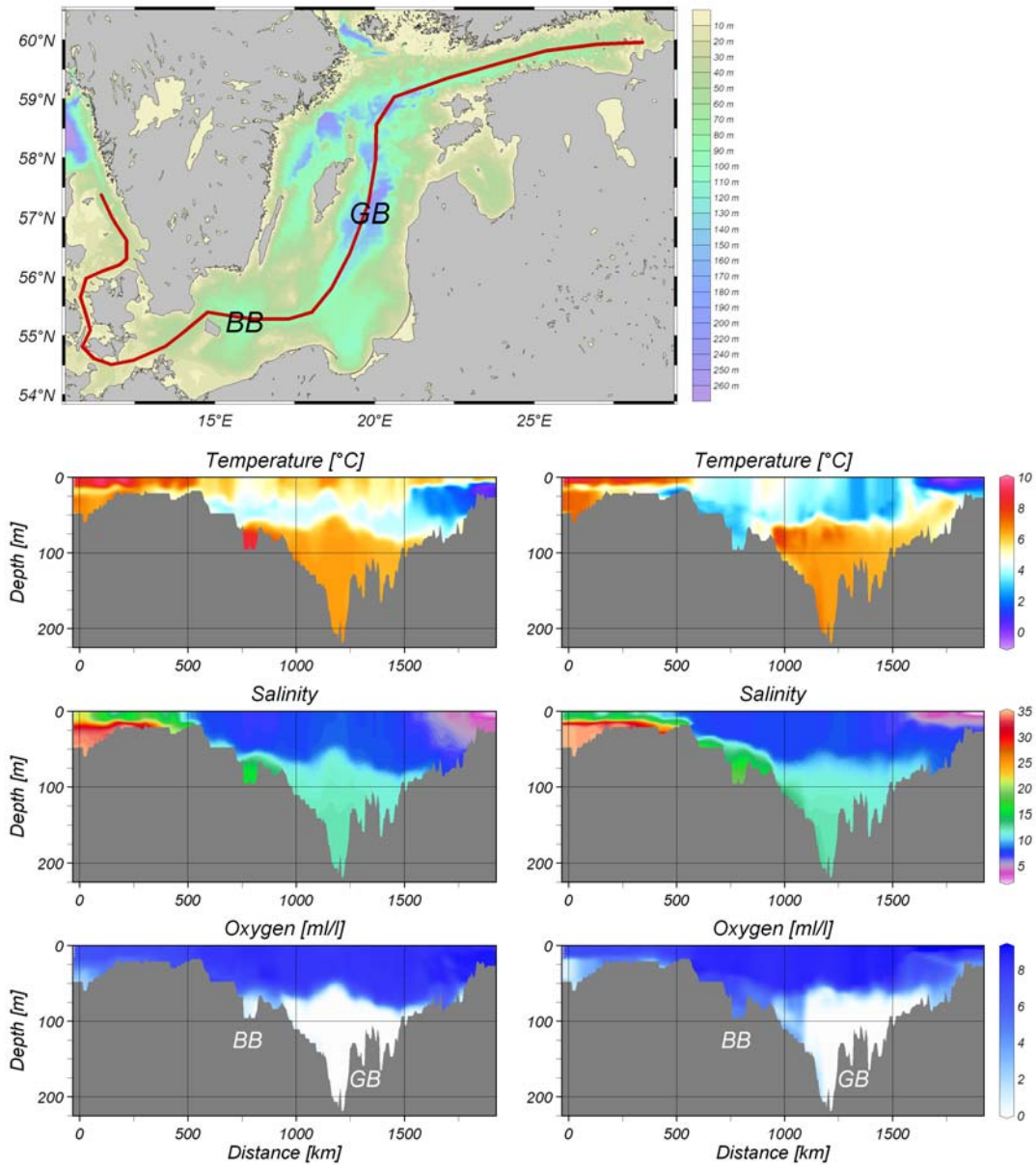


Fig. 1.2. Comparison between stagnation and post-inflow hydrography in the Baltic Sea. Shown is a slice of temperature (top), salinity (mid) and oxygen (bottom) along a transect through the Baltic Sea (see map). Bornholm Basin (BB) and Gotland Basin (GB) are marked. Left column 1st May 2002, right column 1st May 2003. Data are extracted from a hydrodynamic model by Hans-Harald Hinrichsen (Lehmann and Hinrichsen 2000a).

Baltic fish community - Sprat (*Sprattus sprattus* L.), herring (*Clupea harengus* L.) and cod (*Gadus morhua* L.) presently dominate the fish community of the Baltic Sea. These species constitute 95% of the commercial fish catches in the Baltic (Sparholt 1994). A few other pelagic species can occasionally and locally be numerous in coastal waters, like European smelt (*Osmerus eperlanus* L.), three-spined stickleback (*Gasterosteus aculeatus* L.) and vendace (*Coregonus albula* L.) (Axenrot 2005).

During the last 20 years, the structure of the Baltic fish community drastically changed from a cod- to a sprat-dominated system (Köster *et al.* 2003). The combination of climate induced recruitment failure and high fishing pressure, directed at cod, resulted in a drastically decreased cod abundance since the end of the 1980s (665.000t in 1982 to 75.000t in 1999; Bagge *et al.* 1994, Köster *et al.* 2005). As a consequence sprat abundance increased to record levels. Reasons for this increase are successful recruitment and lowered predation pressure by cod (Köster *et al.* 2003, MacKenzie and Köster 2004).

Due to the limited number of fish species (41 marine and 18 freshwater species in the central Baltic Sea, compared to 120 fish species in the North Sea; Remane 1958), the possible species interactions in the Baltic are fewer than in other marine ecosystems (e.g. North Sea), which facilitates the investigation and understanding of these relationships. The generally low number of pelagic and schooling species in the Baltic simplifies the problem of species recognition in the hydroacoustic data. Therefore, uncertainties during scrutinizing of echograms are reduced to a minimum. In a nutshell, the Baltic Sea seems to be an ideal marine environment for the investigations on habitat preferences, distributions at several scales and species interactions.

Sprat - This thesis focuses on the clupeid species sprat (*Sprattus sprattus* L.), which is a pelagic and school forming species. Sprat is one of the smallest, commercially exploited clupeid species (maximum length of 16-18cm; Rechlin 1975). In contrast to herring, sprat has pelagic eggs.

Sprat has a wide range of distribution, with subspecies being found in the North Atlantic, the Mediterranean Sea, the Black Sea and the Baltic Sea (Rechlin 1975). It is not clear whether or not the Baltic sprat population has to be divided into subpopulations (e.g. Aps *et al.* 1987, Ojaveer 1989, Shvetsov *et al.* 1995), which have to be managed as separate stock units (Rechlin 1975). Nevertheless, sprat is handled as one single unit in the stock assessment of the ICES (ICES 2005).

Clupeids (i.e. sprat and herring) represent the main fraction of fish biomass in the Baltic and are caught and consumed in large numbers by cod, salmon, marine mammals and humans. Additionally, clupeids are important predators on zooplankton (Rudstam *et al.* 1994, Parmanne *et al.* 1994, Kornilovs *et al.* 2001, Möllmann *et al.* 2004) and early life stages of fish, especially cod eggs (Köster and Schnack 1994, Köster and Möllmann 2000a). This predation on cod eggs is found to be a stabilizing factor for a sprat dominated system. Furthermore, sprat are found to be cannibalistic, preying on their own eggs (Köster and Möllmann 2000b). Trophic interactions of sprat heavily depend on the temporal and spatial overlap of predator and prey. Hence, the basis to understand such processes is the knowledge and understanding of factors which influence the distribution of organisms in space and time.

Beside inter-species relationships, other processes related to sprat are also influenced by environmental factors and consequently by the distribution of sprat. Recruitment success depends on spawning stock biomass and environmental conditions (MacKenzie and Köster 2004), because eggs and larvae have an increasing mortality rate at temperatures below 5°C

(Thompson *et al.* 1981, Nissling 2004). Additionally, the physiology of adult sprat is influenced by temperature, e.g. growth and gonadal development are lower in cold water (Grauman and Yula 1989, Parmanne *et al.* 1994). The reason could be that the Baltic sprat population (*Sprattus sprattus Balticus* S.) lives at the northern range of its distribution and is therefore vulnerable to cold temperatures. This is supported by anecdotal descriptions of several authors that it will not concentrate in water colder than 4°C (Rechlin 1975, Hoziosky *et al.* 1989). It remains unclear whether the combination of temperature or salinity sets the limit for sprat distribution.

Thus, the physical environment has a significant influence on important processes in the life of sprat. Since the interaction between physical environment and sprat biology is driven by the question ‘where is sprat at which time’, a key to quantifying such processes is the knowledge about the distribution of sprat.

Space, time, scale and the ecological niche

Pelagic ecosystems are assumed to be relatively homogeneous in space and time, compared to other ecosystems (Polis 1999, Strong 1992). Nevertheless, pronounced variability can be found herein, too. Variability in space and time, and occupation by different species has implications on the physiological status of organisms (e.g. nutritional status and fecundity) and defines the inter- and intraspecies interactions in the ecosystems. These subjects have implications for the stock dynamics and can therefore contribute to high variability in stock size and recruitment, as often observed in the field (Magnússon 1999).

Thus, the investigation of ecological niches became an important task in ecological research. The ‘niche-concept’ was introduced into ecological science almost 100 years ago (Grinnel 1917) and was primarily defined as habitat. The question was ‘where is it, when and why?’. Hutchinson (1958) expanded the concept and defined it formally as n-dimensional space, whereby every dimension describes the range of activity along an environmental factor. This includes abiotic factors, such as temperature, salinity, oxygen concentration, turbidity and light, as well as biotic factors, such as prey distribution. In this study, I will focus on those abiotic factors which likely define the habitat of Baltic sprat.

As described above, the environment to be investigated is not homogeneous in space and time. Therefore, all processes and patterns have a relative size or magnitude. This is usually understood as scale (Lovell *et al.* 2002). The basic domains of scale are time and space. Unfortunately, there is no common definition of several scale magnitudes. The terminology used in this thesis is shown in Tab. 1.1.

Tab. 1.1. Terms for magnitudes of scales, as used in this thesis.

term	spatial dimension (up to)	temporal dimension (up to)	application
small-scale	metres	hours	vertical distribution
meso-scale	few kilometres	few days	wind-induced variability
large-scale	Baltic Sea	seasons	basin-wide distribution

Argument over the appropriate, or most productive, scales of study is not new in ecology, and it still continues (Mullin 1993). Nevertheless, due to the wide range of scales in the ecosystem, ecological investigations require an adequate determination of the relevant scales, which has to be resolved (Levin 1992, Mullin 1993 (as review), Mason and Brandt 1999, Schneider *et al.* 1999, Mehner 2005). The sampling method and scheme has to be adapted to the target scale. To resolve meso-scale structures with the dimension of 0.1nm, a distance of 0.5nm between neighbouring sampling stations is virtually not sufficient. The most famous approach to define a minimum sampling rate is the sampling theorem, developed in the field of information technology (Nyquist 1928, Shannon 1948, republished: Shannon 1998). The basic declaration of this theorem defines the minimum sampling rate for digitizing a signal (i.e. the conversion of an analog, continuous signal into a discrete numeric sequence). The sampling frequency should be at least twice the maximum source-signal frequency.

Unfortunately, in contrast to many physical sampling methods, most biological sampling methods in marine research do not allow a high resolution in time and space, due to the restrictions of the sampling procedure itself and a very time consuming, often manual post-processing of samples. As example, one would like to resolve the daily vertical migration of zooplankton in the central Baltic Sea with Multinet-sampling (Hydro-Bios Kiel) at a temporal resolution of 0.5h. Assuming a vertical sampling resolution of 10m, after one diel cycle 480 samples have to be sorted, which is almost impractical. While doing the same for fish, another problem crops up. With classical fishery hauls, it is not possible to get samples of all depth strata at the desired time resolution in parallel. Therefore, it is not easy to resolve the diel migration pattern with this method alone. In that way, methods like hydroacoustics and optical methods (like VPR for zooplankton) could help.

To resolve meso-scale horizontal pattern (e.g. see chapter 4), sampling on a station basis has the disadvantage of being a very time consuming procedure of consecutive stopping of the ship to lower equipment. Here methods are very helpful, which can be deployed while the vessel steams. That is the reason why, amongst others, towed CTD equipment and hydroacoustics were used in this thesis.

In this study, I investigate the ecological niche of Baltic sprat (*Sprattus sprattus* L.), as defined by abiotic factors, at different scales. These investigations include small-scale processes, such as vertical distribution and diel migration, wind-driven meso-scale patterns of hydrography and their influence on sprat distribution, as well as the horizontal distribution of sprat over larger areas and different seasons.

Trophic cascades – top-down control

The hypothesis of top-down effect and the resulting possibility of food chain cascades, which pass changes at the upper trophic level down to lower trophic levels, was introduced in the literature by Hairstone *et al.* (1960) and later often discussed (e.g. reviews given by Shurin *et al.* 2002, Borer *et al.* 2005). Several cases of cascade effects were reported, whereby it became clear that these trophic effects are more obvious in aquatic systems (Strong 1992, Shurin *et al.* 2002 , Shurin *et al.* 2005). Field observations of trophic cascades are usually known and described for ecosystems, which have one or more of the following features: low species diversity, simple food webs and small geographic size (Shurin *et al.* 2002, Frank *et al.* 2005). This implies a dominance of observations of trophic cascades throughout the food web in freshwater systems, whereas such observations in marine areas are sparse (e.g. Estes *et al.*

1998). On the one hand, the usual high species diversity, complex food webs and larger scales could explain this. On the other hand, the marine ecosystems of the continental shelf are heavily exploited by humans, which results in a strong decline of important components of the upper trophic level such as predatory fish populations (e.g. Pauly *et al.* 1998). This could be seen as large in situ 'experiment' for initiating trophic cascades in the marine environment and therefore this should provide the most definitive test of the trophic cascade hypothesis (Steele and Collie 2004), but it didn't so far. Nevertheless, evidence for top-down control between few trophic levels has been occasionally found. Reid *et al.* (2000) found possibilities of strong interactions between different fish species and plankton in the North Sea and concluded therefore that the fishery may be an important contributor to changes in that ecosystem.

The Baltic Sea fulfils the criterion of relative simplicity and restricted area (compared to other marine systems), as given above. Therefore finding strong top-down effects is more probable than in more diverse and larger systems. Rudstam *et al.* (1994) described an upper trophic level cascade in the pelagic ecosystem of the Baltic Sea and discussed possible consequences that implied top-down control. The cascade was initiated by a combination of overfishing and climate change, which lead to a strong decrease in abundance of the main piscivore predator, cod. As a consequence, a regime shift occurred in the Central Baltic Sea from a cod dominated to a sprat dominated system (Köster *et al.* 2003).

The zooplanktivorous clupeids, herring and sprat, have some power in controlling several zooplankton species (e.g. Möllmann and Köster 1999, Kornilovs *et al.* 2001, Möllmann and Köster 2002) and eggs of their main predator cod (Köster and Möllmann 2000). In contrast, cod larvae are not significantly impacted, due to the weak spatial overlap between clupeids and cod larvae.

The abundance of species in the food web is not the exclusive driving factor for trophic interactions. Other major factors are heterogeneity and patchiness along temporal and spatial scales. The heterogeneity of the Baltic Sea in horizontal, but especially in the vertical scale, is assumed the main factor driving the interactions of different species and hence trophic cascades there. Möllmann *et al.* (in prep., chapter 7) reported consumption rates on copepods, which occasionally exceeds their production rate. The strength of this interaction is highly controlled by species overlap.

Trophic cascades are addressed in chapter 7, where the findings of previous chapters regarding the abundance and habitat-choice of Baltic sprat were employed.

Hydroacoustics

The main technical sampling devices used for this thesis were echosounders. Hence, a general introduction will be given below.

A brief history of hydroacoustics - The first known reference of underwater sound is attributed to Leonardo da Vinci in 1490 (Urick 1983). He noticed sound, emitted by ships (sailing or rowing vessels!), while holding his ear at one end of a partly immersed tube. In 1913, Dr. Alexander Behm got the first patent for an echosounder. Subsequently he founded the worlds first echosounder company in Kiel, Germany (the town where this thesis was written!). The primarily goal of these first sounders was the measurement of water depth. Kimura (1929) discovered that fish can modulate the echo transmitted and received by acoustic equipment. The first study

of fish behaviour with the echo detection method was published by Sund (1935). This was possible after the development of a paper recording echosounder by Wood. Sund (1935) described many unknown features of the distribution of Atlantic cod, *Gadus morhua* L., in the Lofoten region. His paper recordings revealed (amongst other findings) the vertical distribution of cod - namely that cod occupy a relative narrow depth range (10m) at a constant depth.

Due to technological and methodological progress, important improvements in the usage of echosounders for fisheries and fisheries research were made after World War II (Johannesson and Mitson 1983). The broad introduction of acoustics into commercial fisheries (Cushing 1963, Parrish and Horsted 1980) was an important contribution to the increase in technological fishing efficiency and therefore in fishing pressure on fish populations (e.g. McGuire 1997).

Scientists developed several approaches to measure the abundance of fish. The basic principle of echo integration, as it is used today for abundance estimation, was described by Dragesund and Olsen (1965). Of course, the development of hydroacoustical methods has progressed since these times. Advances in electronic technology induced the evolution of reliable, fast, accurate and easy to use acoustic equipment. Additionally advances in computer technology improved the processing of echo data.

Applications of hydroacoustics in biological research - As described, hydroacoustics are routinely and successfully used in fisheries research to estimate the abundances of fishes - a quantity of commercial and biological interest. (e.g. Johannesson and Mitson 1983, MacLennan and Simmonds 1992, Rivoirard *et al.* 2000). A common method to link echo energy to abundance is based on the assumption that echo energy is proportional to the product of the density of individuals and the average backscattering cross section. This assumption reveals a weak point of hydroacoustics. The precision of abundance estimation is strongly correlated with the precision of the determination of the backscattering cross section per individual. This problem has been investigated in numerous studies about the so-called target strength (TS) of species, but more research is needed.

Additionally attention is currently directed towards the investigation of behaviour, density and distribution of aquatic organisms. New hypotheses in fisheries ecology include the behaviour and the environment of fish populations. Many of the hypotheses of this ecosystem approach can be explored using hydroacoustic data, because acoustics is one of the very few methods able to provide real time, in situ and 3D field data (Massé and Gerlotto 2003). Of further interest are all aspects and factors, which can influence and enhance the results of acoustic surveys, whereby the species identification of echo targets is one of the main tasks. An overview of the acoustic methods used for studies in fish ecology is given by Nakken (1998).

During the last few decades, the application of hydroacoustics has expanded to other fields of biological research - It is very seductive to measure the distribution of lower trophic levels with hydroacoustics, as well. Several studies deal with the backscattering properties of different zooplankton taxa, which were either measured in field studies or modelled (Holliday *et al.* 1990, Chu *et al.* 1993, Stanton *et al.* 1994, Brierley *et al.* 2004, Mair *et al.* 2005). Problems occur because the zooplankton community has a wide variety of different habitus types (Stanton *et al.* 1994), whose anatomical features vary widely across species, and sometimes within species. As a consequence, there is a dramatic range of echo energy/biomass relations between species with comparable size or biomass. Due to often mixed and patchy species distribution, a

direct conversion from echo energy to biomass is very restricted. Multi-frequency approaches could help to improve plankton acoustics; as is the case for fish-species identification.

In the case of deep scattering layers (DSL), pelagic communities in the oceans are named after their acoustic properties (e.g. Krause 1971). Scattering layers are present in other areas and depth ranges, too. In the Baltic Sea, scattering layers are occasionally very prominent. Nevertheless, the source of this backscatter in the Baltic is poorly investigated (Prandke and Stips 1987). For this study, scattering layers were excluded from echo integration.

Another field of application is the acoustic seabed classification (Anderson *et al.* 2002, Wilding *et al.* 2003). Using this method, shape and physical properties of the bottom habitat can be mapped. These properties define a fundamental component of the environment for many species, including very important commercial fishery resources, such as sandeel (Holland *et al.* 2005).

Why use hydroacoustics? - The observation and sampling of fish is not an easy task in natural environments. Classical methods, such as visual observation and net sampling are often not practicable, especially in cases of high variability in space and time. The use of hydroacoustics can solve such problems, whereby the resolution of sampling in space and time is the main advantage of echosounders. The spatial resolution given by echosounders is magnitudes higher in comparison to classical net sampling. Fig. 1.3 demonstrates the possible resolution of a one-day sampling along a 60nm transect in the central Baltic Sea. Fishery hauls are often restricted to 12 hours per day onboard German research vessels. As a result, a maximum of 5 hauls (30 minutes each) can be conducted along the transect. Each covers 10m in vertical and 1.5nm horizontally. It becomes clear that spatial inhomogeneity is not adequately covered by this kind of sampling (see Fig. 1.3). In contrast, the resolution of acoustic sampling (as used in this study)

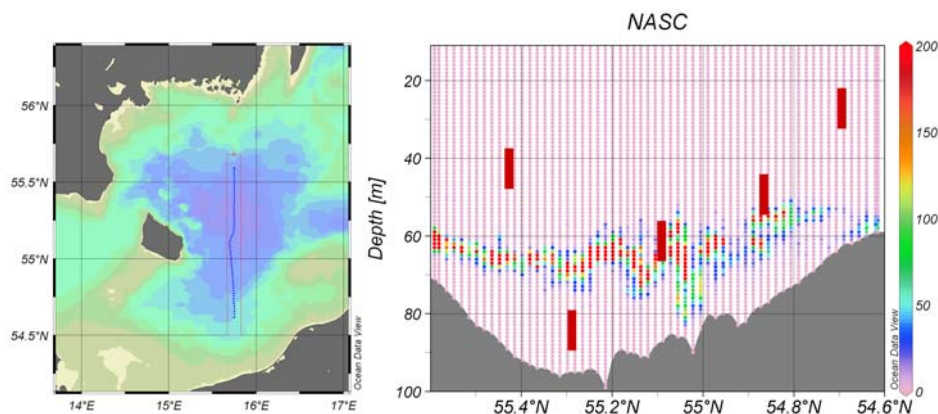


Fig. 1.3. Compared resolution of classical fishery hauls and hydroacoustics. Shown is a North-South transect through the Bornholm Basin (see map, length 60nm). Right: Section along the transect. Red rectangles mark possible (randomly distributed) fishery hauls with their horizontal and vertical dimension. Additionally integrated acoustic measurements (transect from January 2003) are represented by colour-encoded dots. Each dot is derived from the integration of a 1m depth layer over 1nm (horizontally). Therefore, each dot represents approximately 3600 single observations.

is approximately 5m in horizontal dimension and 10cm in vertical dimension at a cruising speed of 10 knots. Therefore, it is possible to sample a complete transect almost continuously over all depths. In that way, hydroacoustics solves the mismatch of resolution between high-resolution and easily-deployed physical measurements and biological sampling.

2. General Material and Methods

This chapter gives an overview of material and methods used in this thesis. If needed, additional information is given in the specific chapters.

The basic settings and the procedure of acoustic measurements, fishery sampling and data processing follows the guidelines given in the 'Manual for the Baltic international acoustic survey' (ICES 2001).

General notes

All time data are local-time in 24 hours notation. Local time is noted as Central European Time (CET; CET=UTC+1h) between last Sunday in October and last Sunday in March and Central European Summer Time (CEST; CEST=UTC+2h) otherwise.

There is no official symbol for nautical mile in the SI-system, therefore several symbols were used internationally. In this study, the symbol [nm] for nautical mile was used (not to be confused with nm, the official SI-symbol for nanometre).

Hydroacoustic measurements

For this thesis, several SIMRAD echosounders with different transducers were used on three research vessels (Tab. 2.1). The frequency used for all hydroacoustic measurements was 38kHz. The split beam transducers (type SIMRAD ES38B) onboard RV 'Walther Herwig III' (WH3) and RV 'Alkor' (AL) were hullmounted, whereas the single beam transducer (type SIMRAD 38-26) used on RV 'Heincke' was mounted on a baseframe and lowered down into the moonpool.

Tab. 2.1. Hydroacoustic equipment used for this thesis.

Research vessel	period	echosounder	transducer	Software used for recording
Walther Herwig III	total	EK500	ES38B (split beam)	Bergen Integrator 500 (BI500)
Alkor	04/2002-03/2003	EK60	ES38B (split beam)	Bergen Integrator 500 (BI500)
Alkor	04/2003 onward	EK60	ES38B (split beam)	Simrad ER60 (raw-format)
Heincke	total	EK500	38-26 (single beam)	Sonardata Echolog 500

The Calibration of acoustic equipment was conducted with the standard copper-sphere method (Foote *et al.* 1986, ICES 2001), at the beginning of each cruise. Beside calibration settings, the properties of the sound pulse, transmitted into the water, are of importance. Therefore, recommended settings (ICES 2001) were used for hydroacoustic measurements during the GLOBEC-Germany-field sampling (Tab. 2.2). Usually hydroacoustic measurements were conducted at a mean cruising speed of 10knots (10nm/hour).

Tab. 2.2. Sound-pulse settings, as used in the present study.

parameter	explanation	value
pulse rate	frequency, at which a sound pulse is transmitted into the water	1/s
max. power	maximum power transmitted into the water	2000W
pulse length	duration of the transmitted pulse	1.024ms

All acoustic data are processed with Sonardata Echoview (Sonardata 2005) at a Sv-threshold of -60dB. Digitized echograms were processed to correct bottom topography and exclude thin-echo-scattering-layers and other unwanted echoes, such as air bubbles below the ship, which are caused by high seas or ship-maneuvres. Echo-data were integrated from 10m below the surface to 0.5m above bottom. The chosen vertical resolution was 1m, whereas the horizontal resolution was usually 1nm. In chapter 5 the horizontal resolution was set to 0.1nm to get a better resolution of meso-scale patterns. Echo data were given as 'nautical area backscattering coefficient' (NASC; [m^2/nm^2]), following naming conventions given by MacLennan *et al.* (2002).

Database

Several analyses need a combined dataset of hydroacoustic and environmental data. Most field data of the German GLOBEC-project, including environmental data, are stored in the project database, called GLOBAN. Integrated acoustic data are stored in a separate database. Both databases were joined by event-time. To avoid errors in joined CTD-fish-profiles several cross-checks, such as calculating the distance between geographical positions from both datasets and the difference in bottom depth between echo-profile and CTD cast, were applied.

Abundance estimation

Abundances were calculated as described in the 'Manual for the Baltic international acoustic survey (BIAS)' (ICES 2001), except that the recommended observation time of day differed. The manual was prepared for the Baltic international acoustic survey (BIAS), which covers the whole Baltic Sea in September/October. During this season, a large fraction of fish is close to the bottom during daytime in the shallower parts of the western Baltic. Due to problems while detecting fish in the bottom dead zone, the total fish abundance would be underestimated (ICES 2001) during day. Therefore, sampling during the autumn survey should be carried out during night, when fish move upward into shallower water layers. Nevertheless, this upward movement into the surface layer can also influence the measurement by avoidance reaction of fish, caused by ship noise (Bethke and Wienbeck 1996). Additionally, comparison of abundance estimations between seasons with and without diel vertical migration would be biased, due to the depth-dependency of target-strength of clupeids, which is caused by the compression and expansion of swimbladder during vertical migration (Gorske and Ona 2003, Ona 2003).

Taking into account these potential problems, all measurements for abundance estimations presented in this thesis were carried out during daytime. This corresponds with the German and Russian spring acoustic survey in May/June, where sampling is also conducted during the daytime.

Abundances are calculated for an area with a minimum depth of 10m, which was calculated after Seifert and Kayser (1995) and summarized for ICES-rectangle in the BIAS-manual (ICES 2001).

Fishery data

To identify echoes and to allow species recognition, it is necessary to carry out fishery hauls for collecting biological data such as species composition, length-, weight- and age-distributions (MacLennan and Simmonds 1992, ICES 2001).

For abundance analyses it was attempted to sample at least 2 representative hauls per investigated ICES statistical rectangle, and sampling followed the procedure described for Baltic international acoustic surveys (ICES 2001). Fishery hauls were carried out at a standard speed of 3 to 3.5 knots for 30min. The headrope depth of the trawl was adjusted to get a representative sampling for the water column. Fishing gear differed between vessels: a pelagic trawl net PSN205 (manufacturer: ROFIA Rostock, codend-meshsize: 10mm; vertical opening 12m) was used onboard RV 'Walther Herwig III', whereas a Kombitrawl (manufacturer: Engel-Netze Bremerhaven; codend-meshsize: 10mm; vertical opening 10m) was used onboard RV 'Alkor' and RV 'Heincke'.

The catch of each haul was sorted into species and the corresponding total weight per species was measured and recorded. If mixed catches were too big to sort completely, subsamples were taken (ICES (2001)). The length distributions of all fish species were measured as total length (centimetre below). Usually the total length of clupeid fishes was measured to 0.5cm below and the length of other fishes to 1cm below, whereas during 'Alkor'-cruises prior to June 2002, clupeid measurements were done to 1cm below. For larger catches of one species, subsamples were taken for length measurements, whereby a minimum number of 200 specimens for clupeids was usually chosen.

For stomach sampling, herring was grouped into 2cm-classes and sprat in to 1cm-classes. If possible, ten individuals of each species and length group were collected. These grouped samples were weighed to get a weight distribution for clupeids.

Age distribution was only determined for every ICES statistical rectangle (Fig. 3.1) during RV 'Walther Herwig III' cruises.

Data visualization

Geo-referenced data and cruise maps are usually visualized with the free software package 'Ocean Data View' (ODV, Schlitzer 2004). Due to limitations of software packages like ODV, geographical positions are noted in two different formats. Positions are either noted as 55°30'N and accordingly 15°18'E (degree°minute'N/E) or alternatively in decimal notation as 55.5°N and 15.3°E (degree.minutes-decimal°N/E).

3. Seasonal variation in fish abundance and distribution patterns in the central Baltic Sea under the influence of major Baltic Inflows 2002 and 2003.

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3.1. Abstract

The seasonal horizontal distribution patterns of cod, herring and sprat in the Bornholm Basin (central Baltic Sea) were investigated during 2002 and 2003. In this period, several inflows of saline and oxygenated water into the Baltic occurred. Sprat was found to be the most abundant species during all seasons. The seasonal distribution patterns until autumn 2002 were typical for stagnation periods. The Major Baltic Inflow in January/February 2003 shifted well oxygenated, but very cold water into the Bornholm Basin, which replaced the old bottom water. The resulting very cold water in the Bornholm Basin throughout the water column, caused a movement of sprat into the Gdansk Deep and Gotland Basin, where warmer water below halocline was found.

3.2. Introduction

Distribution patterns of organisms are main characteristics of an ecosystem and it is therefore an important task in ecosystem research. Beside this ecosystem related point of view, the investigation of distribution patterns of fish populations also has an economic aspect. Migrations are important processes which lead to changes in the distribution of fish. Migrations (seasonal or ontogenetic) can be explained by an optimization strategy of organisms to fit their surrounding environment and their environmental needs (Aro 1989). These needs can vary over life time, daytime and season, whereby cyclical patterns are often found. Examples for such patterns are diel vertical migration (see chapter 10 on page 131) and seasonal migration between overwintering, spawning and feeding areas.

Since the exploitation of Baltic Sea fish resources has a long tradition and economic importance, there has been considerable research to answer the question 'when is the fish where'. As a result, the overall horizontal distribution patterns of Baltic fish species, caused by seasonal migrations are well known (review by Aro 1989). Aro summarized that, like many other fish populations, the investigated fish species cod, herring and sprat have seasonal spawning and feeding migrations.

Cod – Two cod stocks were separated in the assessment in the Baltic: The Western Baltic cod stock (*Gadus morhua morhua* L.) and the Eastern Baltic cod (*Gadus morhua callarias* L.). The

approximate geographical border between both stocks is the island of Bornholm (Aro 1989), where mixing occurs in the Arkona Basin and the Bornholm Basin. The spawning time of both stocks is relatively variable, with a peak in May/June (Graumann 1974, Aro 1989). The general migration pattern includes a movement of adult cod into the deep basins for spawning. After spawning an omni-directional movement into shallower feeding areas occurs.

Herring - The Baltic population of herring (*Clupea harengus membras* L.) consists of two subgroups. The more abundant group is called 'spring spawner' in contrast to the other group, which is called 'autumn spawner'. The main difference of both groups is, as the names suggest, their spawning time (Popiel 1984, Aro 1989, Parmanne *et al.* 1994). The last significant yearclass of the autumn spawning spawning stock component was recorded in 1964 (Parmanne *et al.* 1994). Although the spring spawning group is not homogeneous in terms of its structure and migration behaviour (Popiel 1984, Ojaveer 1989), the general pattern of migration of this group can be briefly summarized: spawning in coastal areas during spring followed by a migration of older herring into feeding grounds. Main feeding grounds in the southern central Baltic are the Bornholm Basin and the Gdansk Deep, where the herring arrive in July and stay until December (Popiel 1984)

Sprat - A movement into the deeper basins of the Baltic Sea (Bornholm Basin, Gdansk Deep and Gotland Basin; Fig. 1.1) in early winter characterizes the migration pattern of sprat (*Sprattus sprattus* L.). In these areas, sprat concentrate below the halocline. During early summer sprat move into shallower water layers and migrate into areas closer to the coast. Hoziosky *et al.* (1989) called this phenomenon 'two types of distribution', which are observed annually: the 'winter-spring' and the 'summer-autumn' type. The transition between both distributions takes place in June (from open sea areas toward coastal areas) and December (from shallow waters toward deeper areas). During the spawning migration into the Bornholm Basin sprat from the western Baltic (ICES Subdivision 24) enter the area via a route north of Bornholm. Additionally, a westward migration was observed for sprat of the south-eastern Baltic Sea (Aro 1989).

While the background pattern of two distribution types of sprat migration is relatively stable, migration within one type of habitat is possible. For instance, sprat could migrate between different deep basins, when local environmental conditions in one area are unfavourable. These migrations within a distribution type were assumed redistributions, since the overall sprat biomass was relatively stable over several years (Hoziosky *et al.* 1989).

The environmental conditions below halocline in the deep basins, where sprat aggregate during spring and early summer, are determined by the lateral transport of saline and oxygen rich waters from the North Sea (Nissling *et al.* 1994). Therefore, this water exchange is a process, which possibly causes migrations between basins during spawning time. Major Baltic Inflows (MBI) contribute most of the saline water for the renewal of the deep water in the Basin of the Baltic Sea. These MBI occur sporadically during autumn and winter season (Matthäus and Franck 1992). Several inflows occurred in 2002 and 2003 after a long stagnation period without sufficient inflow events (Feistel *et al.* 2003, Feistel *et al.* 2004, Meier *et al.* 2004, Mohrholz *et al.* 2006). Beside typical inflow events during the cold season, an exceptional warm summer inflow was recorded in summer 2002. Mohrholz *et al.* 2006 investigated the influence of this inflow on environmental conditions. The first MBI since 1993 (Jakobsen 1995) was observed in January/February 2003 (Feistel *et al.* 2003), Mohrholz *et al.* 2006). This MBI drastically changed

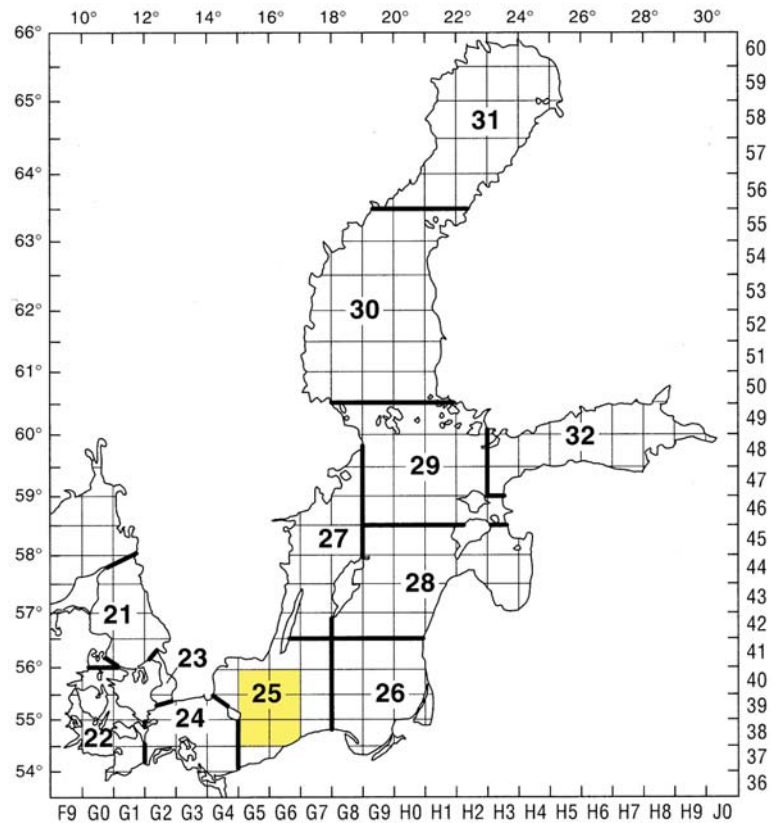


Fig. 3.1. The Baltic Sea and its sub-units, as given by ICES. Large areas bordered by thick lines, indicate ICES subdivisions (SD). Numbers in the graphic refer to the name of this SD (e.g. 25 mean SD 25 and include the Bornholm Basin). Squares indicate the area of so called ICES statistical rectangles, whereby the name is composed of the corresponding labels at the right and top side of the graph (e.g. the ICES rectangle between 55°N – 55.5°N and 15°E – 16°E is called 39G5). Yellow shaded areas indicate rectangles taken into account in this chapter. The graph is modified after ICES 1987.

the environmental conditions in the deep water layers of the Arkona Basin, Bornholm Basin and parts of the Gdansk Deep (Mohrholz *et al.* 2006, Fig. 1.2 on page 14).

The horizontal distribution during annual cycle of sprat, herring and cod in the central Baltic Sea under the influence of Baltic inflows in 2002 and 2003 will be discussed in this chapter. Since sprat is the most abundant fish species in the Baltic Sea and one of the key species to be investigated in the German GLOBEC-project, the presentation of results and the discussion will focus on that species.

3.3. *Material and Methods*

Tab. 3.1. GLOBEC-Germany research cruises, which were used for abundance estimation sampling.

cruise	ship	date of cruise	date of acoustic transects in Bornholm Basin
AL200	Alkor	2 nd -30 th April 2002	9 th -12 th April 2002
WH239	Walther Herwig III	3 rd -19 th May 2002	10 th -14 th May 2002
AL205	Alkor	11 th -23 rd June 2002	19 th -22 nd June 2002
AL207	Alkor	22 nd July-7 th August 2002	29 th July-2 nd August 2002
HE181	Heincke	11 th -29 th November 2002	19 th -24 th November 2002
HE182	Heincke	13 th -24 th January 2003	20 th -22 nd January 2003
WH251	Walther Herwig III	30 th April-16 th May 2003	13 th -16 th May 2003

The area of investigation was the Bornholm Sea, situated in the central Baltic Sea. This is a part of ICES Subdivision (SD) 25 and includes the ICES statistical rectangles 38G5, 38G6, 39G5, 39G6, 40G5 and 40G6 (Fig. 3.1)

Most data, presented in this chapter, are derived from our own measurements on several GLOBEC-Germany research cruises. These cruises were conducted at three research vessels and covered a period from April 2002 to May 2003 (Tab. 3.1). Since the cruises were used for a variety of complementary sampling programs within the project, the dates of hydroacoustic and fishery sampling within the area of investigation are also given.

The general procedure of hydroacoustic abundance estimation for sprat, herring and cod, as used for these cruises, is described in the 'Manual for the Baltic international acoustic survey (BIAS)' (ICES 2001) and in the chapter 'General Material and Method' on page 23. In contrast to the common procedure, the abundances were estimated for smaller areas, which refer to quarters of ICES statistical rectangles (Fig. 3.2). The areas of ICES rectangle quarter are given in Tab. 3.2. No calculations for these smaller rectangles are available from May 2003.

To illustrate the seasonal development in the investigation area, abundances were calculated for ICES statistical rectangles in the Bornholm Sea. These values were summarized and graphically shown. By using the larger ICES rectangles instead of formerly used quarters, a quasi area correction for uncovered quarters was accomplished. No data are available for cod in May 2003.

As described above, the analysed GLOBEC-Germany cruises only covered the Bornholm Sea during 2002 and the beginning of 2003. Therefore, information about inter-annual changes of abundance and distribution was derived from international hydroacoustic surveys and model-runs. Two data series were available for the analysis:

The international spring hydroacoustic survey, which is carried out annually by Germany, Russia and Latvia. This survey is usually conducted in May/June and covers at least SD 24, 25, 26, 28 (Fig. 3.1). Aggregated data are stored in a database, called BASS, which is hosted by Eberhard Götze at the Federal Research Centre for Fisheries in Hamburg/Germany. To identify migration between Subdivisions in May 2003, mean abundances per rectangle for ICES-SD 25, 26 and 28 were extracted from the database.

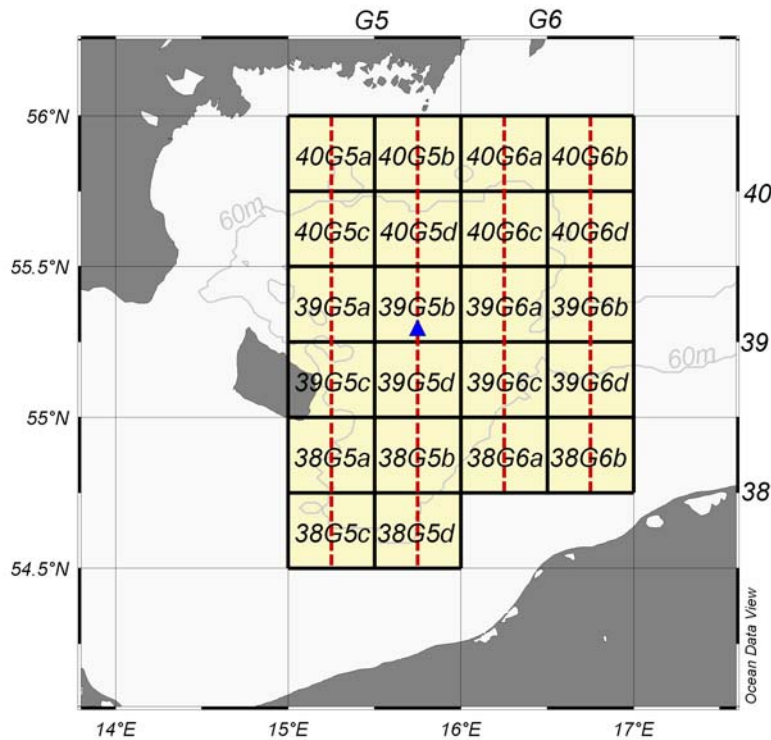


Fig. 3.2. Map of the Bornholm Sea (central Baltic Sea). The shaded area represents the area of investigation. Thick black lines surround quarters of ICES statistical rectangles (for which abundances were calculated). Red, dashed lines from North to South give a schematic presentation of hydroacoustic transects. The triangle marks the central hydrography station.

Since this joint survey does not cover the complete Baltic Sea, no total values for the whole area can be given. Therefore, total numbers and total biomass of sprat was extracted from the extended survivor analysis (XSA) model runs, published in the Report of the 2005 meeting of the Baltic Fisheries Assessment Working Group (WGBFAS) (ICES 2005). The Software used for these runs was the IFAP/Lowestoft VPA suite (see ICES 2005 for input data and settings).

A hydrographic time series for temperature and oxygen, covering the years 2002 and 2003, was compiled by Volker Mohrholz (Baltic Sea Research Institute Warnemuende). The basis for this time series were frequent measurements throughout the GLOBEC-Germany field campaign at the central station in the Bornholm Basin (station 23 at 55°17.5'N 15°45'E, see Fig. 3.2).

3.4. Results

Hydrography

Besides the usual seasonal signals, the hydrography in the Bornholm Basin during the investigation period was influenced by at least two discrete inflow events. The first inflow occurred in late summer/autumn 2002 and carried relatively warm water into the layer just

below the halocline (Fig. 3.3). This inflow was relatively weak. The second inflow event took place in the beginning of 2003. This inflow brought very cold, but oxygen rich water into the deeper Bornholm Basin and renewed the old water below halocline (Fig. 3.3). The hydrodynamic model (Fig. 1.2 on page 14) revealed that the inflow was not strong enough to replace the water in the eastern Basins. Only in parts of the Gdansk Deep and southern Gotland Basin was a slightly increased oxygen content calculated. Therefore, two contrasting situations in the deep Baltic basins were found in May 2003: The western Basins, namely the Arkona Sea (SD24), the Bornholm Basin (SD25) and parts of the Gdansk Deep (SD26), had extraordinarily cold, but oxygen rich water below the halocline, whereas in the Gotland Basin (SD28) warm, but oxygen depleted water was found.

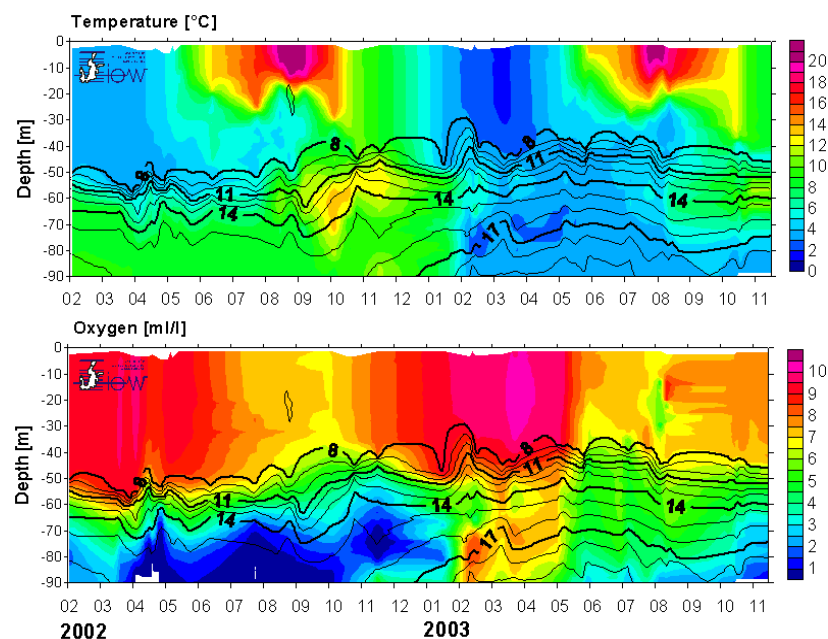


Fig. 3.3. Time series of temperature (top) and oxygen (lower panel) from February 2002 until November 2003 Both plots are overlaid with contour lines of salinity. The graph was compiled using GLOBEC-Germany measurements at the central station in the Bornholm Basin. Graph delivered by Volker Mohrholz.

Fish distribution

The dominating species by numbers in all investigated seasons was sprat, whereby a pronounced seasonality was found (Fig. 3.4). In April 2002 approximately 98.9% of all pelagic fishes in the Bornholm Sea referred to sprat with a total abundance of 56786 million specimens. After spawning time, sprat left the area. An increase in abundance was estimated for January 2003, but the extraordinary numbers as estimated for April 2002 were not found. Sprat left the basin again, resulting in relatively low abundances in May 2003. The numbers of herring were highest during summer and declined in autumn. Cod abundances followed a similar trend.

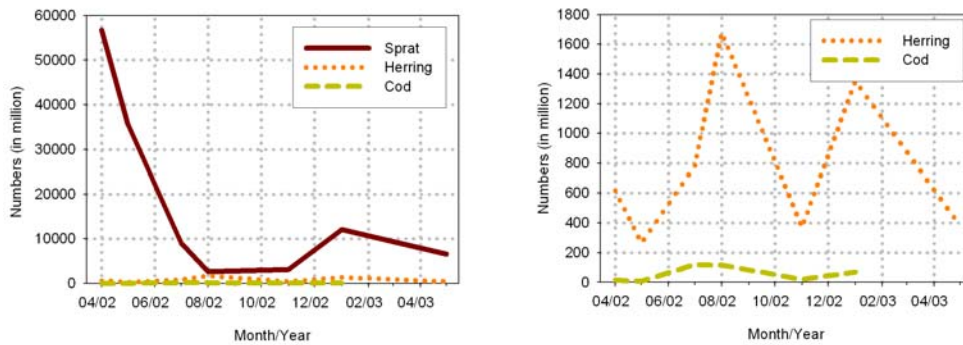


Fig. 3.4. Fish abundances in the Bornholm Sea over season. Left: All species. Right: Herring and cod abundances only (note different scaling of the y-axis).

The horizontal distribution of cod is presented in Fig. 3.5 and Tab. 3.2. Since abundances in April, May and November 2002 are very low, clear patterns are not visible. Nevertheless, in June and August 2002 and January 2003 cod preferentially occupied the area within the 60m depth-contour, with the waters close to Bornholm usually having the highest numbers. In August 2002 and January 2003 most cod were found in the south western part of the Bornholm Basin. In contrast to cod, most herring (Fig. 3.6 and Tab. 3.3) were found in shallower areas or near the slope of the Basin.

During cold seasons, where the water above the halocline was cold (April, May, November 2002 and January 2003), sprat concentrated in the deeper areas (Fig. 3.7 and Tab. 3.4). During June and August 2002 the focus of sprat distribution were shallower areas in the northern part of the investigation area.

To check whether the low abundance of sprat in spring 2003 was caused by a decline of the total stock or migration, large scale data were taken into account (Fig. 3.8). The modelled total abundance and biomass of Baltic sprat declined until 2002, followed by an increase in 2003 and 2004 (Fig. 3.8 left). This indicates that the low abundance in spring 2003, as estimated for the Bornholm Sea, was not caused by a general decline of the sprat stock.

The comparison of May abundances per ICES SD reveals that for most years the mean abundance per ICES statistical rectangle within SD 25 and 28 developed in opposite directions (Fig. 3.8 right). This is true for the period 2002 and 2003, too. The number of sprat in SD 25 decreased, whereas the abundance in SD 28 increased simultaneously. This indicates migration of stock components from the Bornholm Basin into the Gotland Basin area.

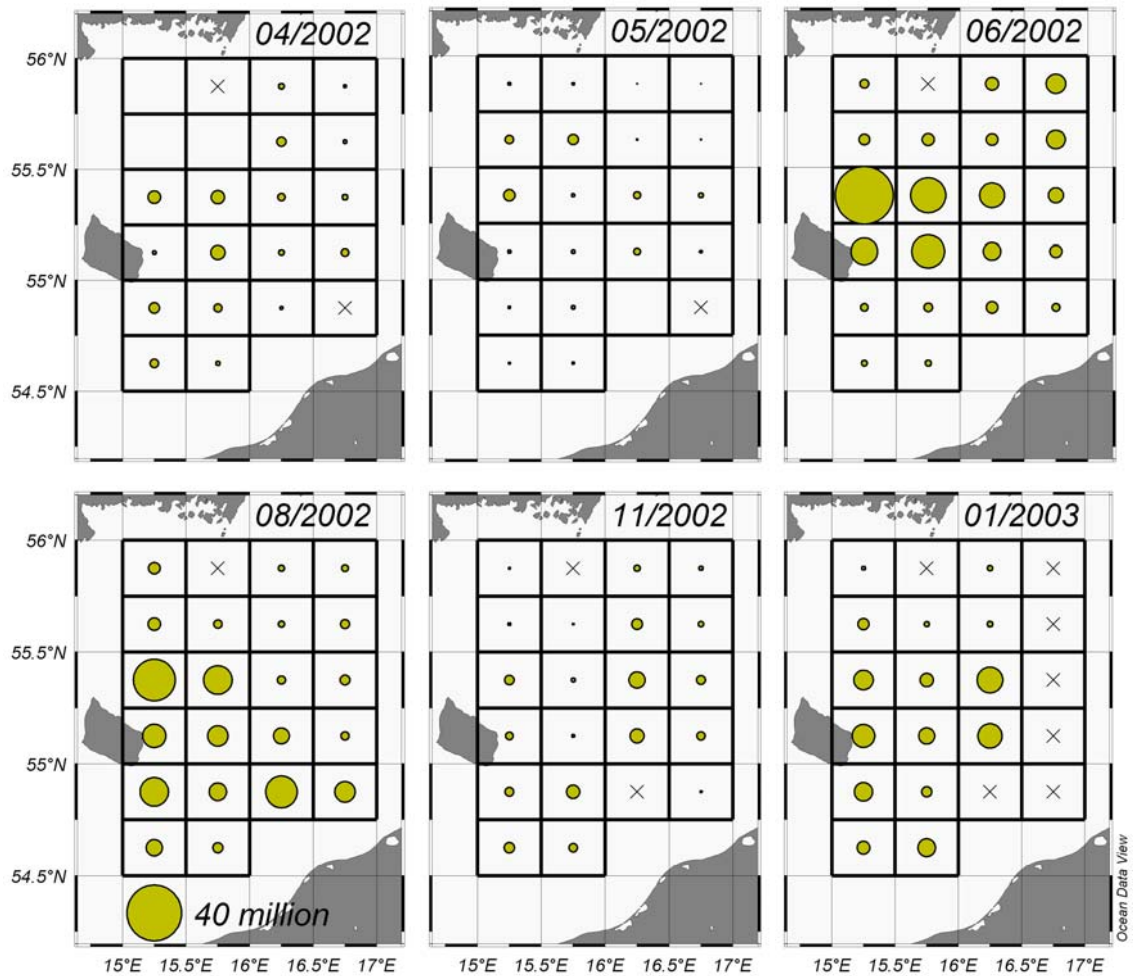


Fig. 3.5. Cod distribution over season in Bornholm Sea. Crosses indicate rectangles with no data.

Tab. 3.2. Cod abundances in Bornholm Sea (in million). The rectangles are named after Fig. 3.2.

Rectangle	area [nm ²]	April 2002	May 2002	June 2002	August 2002	November 2002	January 2003
38G5a	255.7	1.45	0.07	0.73	10.50	0.99	4.37
38G5b	258.9	0.84	0.17	0.95	3.96	2.28	1.35
38G5c	260.5	0.95	0.05	0.43	3.45	1.38	2.15
38G5d	260.5	0.24	0.07	0.48	1.33	0.93	4.11
38G6a	259.7	0.13	0.00	1.74	13.04	no data	no data
38G6b	260.0	no data	no data	0.78	5.43	0.05	no data
39G5a	255.7	2.03	1.66	42.74	22.23	1.13	4.89
39G5b	255.7	2.29	0.13	15.70	10.45	0.20	2.28
39G5c	210.3	0.18	0.13	8.99	6.97	0.74	6.69
39G5d	257.3	2.66	0.17	13.85	5.36	0.10	3.38
39G6a	255.7	0.70	0.64	7.91	0.84	3.33	8.50
39G6b	255.7	0.39	0.29	2.89	1.23	1.00	no data
39G6c	257.3	0.40	0.59	3.92	3.23	2.50	7.64
39G6d	257.3	0.75	0.08	1.90	0.85	0.87	no data
40G5a	252.5	0.00	0.10	0.97	1.69	0.04	0.18
40G5b	252.4	no data	0.08	no data	no data	no data	no data
40G5c	254.1	0.00	0.89	1.45	1.99	0.10	1.60
40G5d	254.1	0.00	1.36	1.84	0.88	0.03	0.33
40G6a	252.5	0.41	0.00	2.08	0.47	0.49	0.36
40G6b	252.5	0.12	0.00	4.77	0.57	0.21	no data
40G6c	254.1	1.10	0.02	1.75	0.49	1.42	0.39
40G6d	254.1	0.18	0.01	4.44	1.01	0.38	no data
total		14.82	6.52	120.31	95.96	18.20	48.21

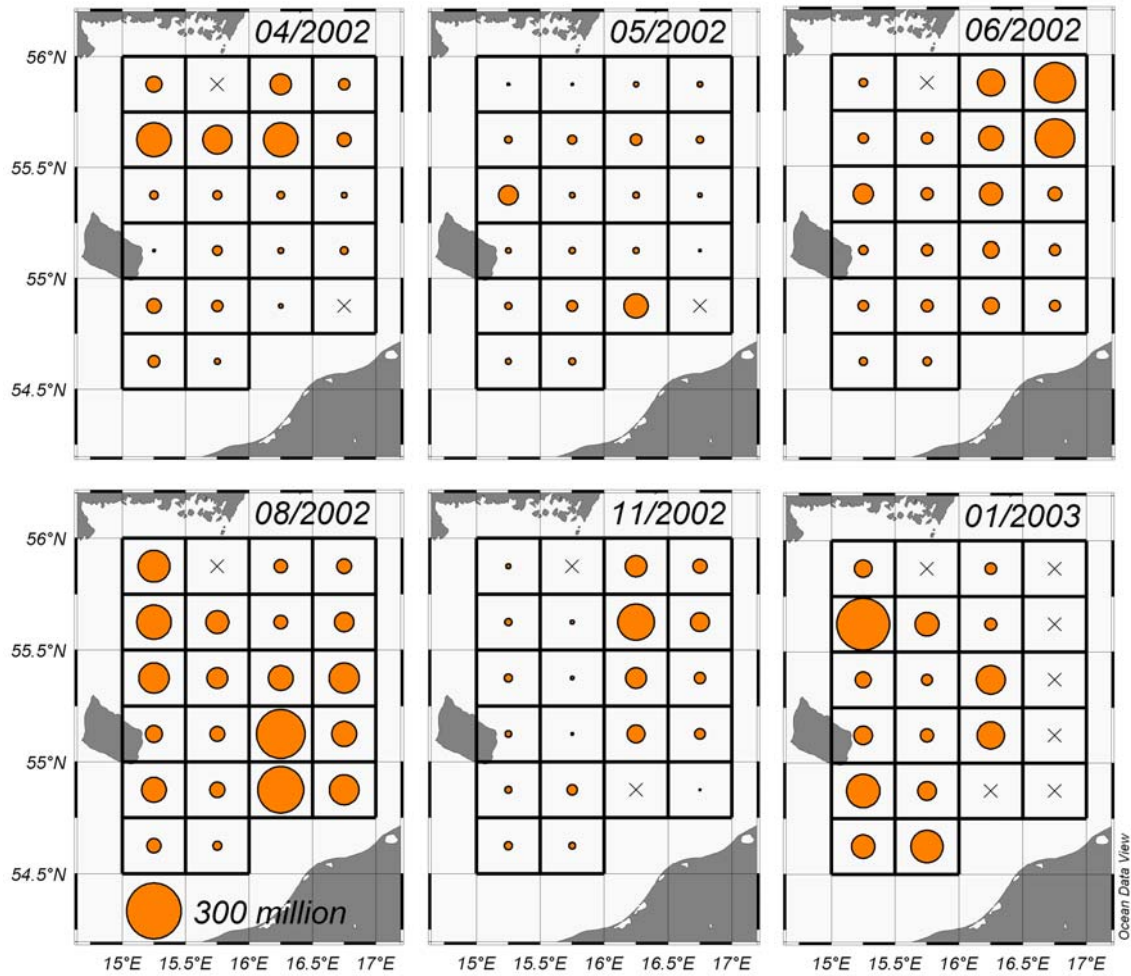


Fig. 3.6. Herring distribution over season. Crosses indicate rectangles with no data.

Tab. 3.3. Herring abundances in Bornholm Sea (in million). The rectangles are named after Fig. 3.2

Rectangle	area [nm ²]	April 2002	May 2002	June 2002	August 2002	November 2002	January 2003
38G5a	255.7	20.79	4.69	10.70	59.91	4.42	109.04
38G5b	258.9	12.01	11.41	13.91	22.59	10.22	33.56
38G5c	260.5	13.60	3.22	6.39	19.71	6.19	53.56
38G5d	260.5	3.42	4.59	7.02	7.58	4.17	102.46
38G6a	259.7	1.79	56.67	25.63	207.70	no data	no data
38G6b	260.0	no data	no data	11.48	86.45	0.21	no data
39G5a	255.7	6.74	36.53	38.26	88.09	6.05	24.23
39G5b	255.7	7.61	2.87	14.05	41.41	1.09	11.32
39G5c	210.3	0.60	2.82	8.05	27.61	3.96	33.19
39G5d	257.3	8.84	3.76	12.40	21.23	0.54	16.74
39G6a	255.7	5.37	3.82	49.48	59.30	40.82	79.70
39G6b	255.7	3.05	1.74	18.08	87.22	12.29	no data
39G6c	257.3	3.09	3.50	24.55	229.03	30.67	71.62
39G6d	257.3	5.83	0.50	11.92	59.92	10.70	no data
40G5a	252.5	24.13	0.57	6.57	96.10	2.13	28.77
40G5b	252.4	no data	0.47	no data	no data	no data	no data
40G5c	254.1	113.58	5.00	9.79	113.22	4.73	262.28
40G5d	254.1	80.05	7.61	12.48	49.85	1.51	53.61
40G6a	252.5	42.11	2.45	68.03	16.69	42.98	12.37
40G6b	252.5	12.04	2.65	156.01	20.39	18.58	no data
40G6c	254.1	111.71	12.32	57.08	17.60	125.51	13.44
40G6d	254.1	18.21	4.79	145.09	36.01	33.55	no data
total		494.56	171.99	706.98	1367.60	360.30	905.90

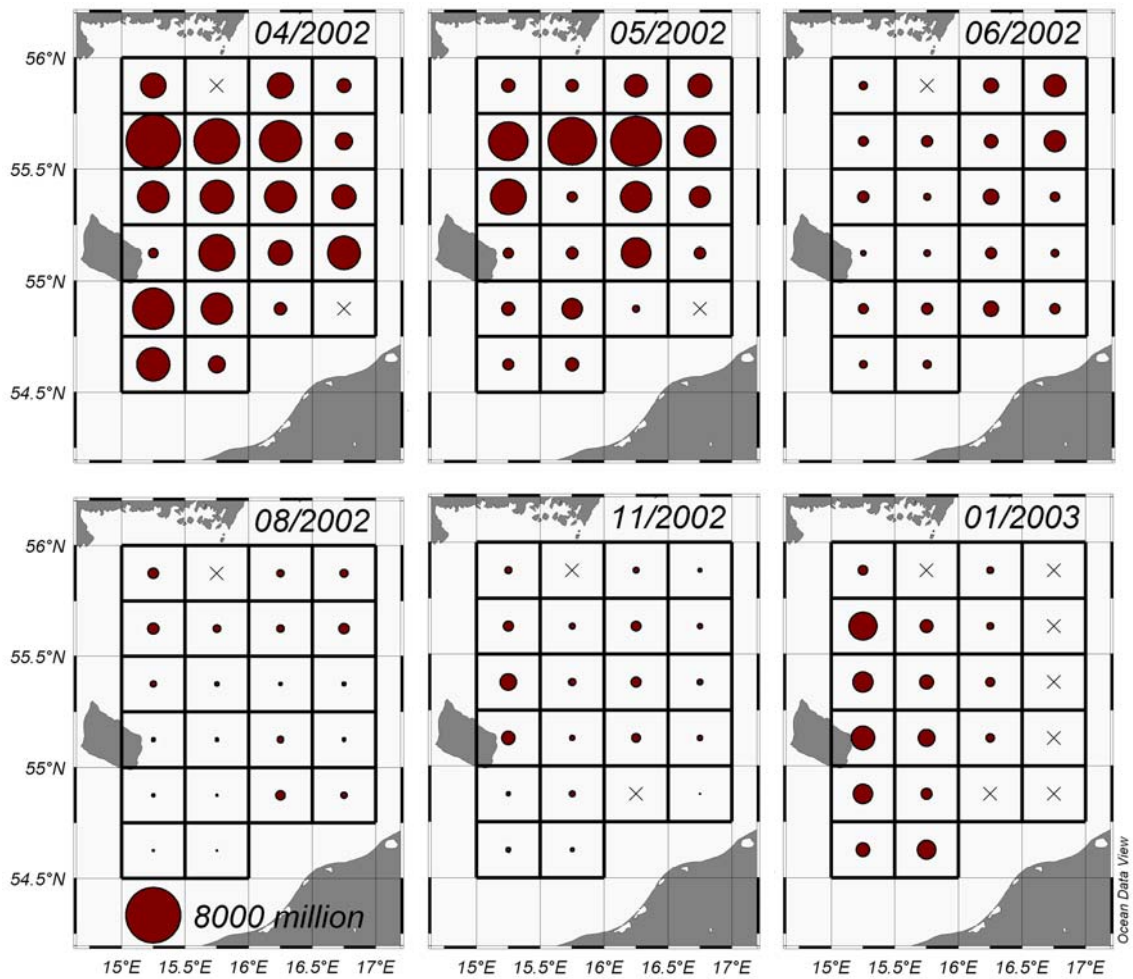


Fig. 3.7. Sprat distribution over season in Bornholm Sea. Crosses indicate rectangles with no data.

Tab. 3.4. Sprat abundances in Bornholm Sea (in million). For the naming of rectangles see Fig. 3.2

Rectangle	area [nm ²]	April 2002	May 2002	June 2002	August 2002	November 2002	January 2003
38G5a	255.7	4353.85	433.07	238.89	21.02	34.85	957.47
38G5b	258.9	2515.76	1053.33	310.47	7.92	80.64	294.70
38G5c	260.5	2849.52	297.32	142.55	6.91	48.86	470.29
38G5d	260.5	715.84	423.55	156.76	2.66	32.88	899.74
38G6a	259.7	374.95	117.08	572.18	220.73	no data	no data
38G6b	260.0	no data	no data	256.32	91.88	1.67	no data
39G5a	255.7	2498.56	3190.97	306.27	86.73	674.45	1023.21
39G5b	255.7	2822.50	250.82	112.47	40.77	121.85	478.09
39G5c	210.3	221.85	246.63	64.46	27.19	441.11	1401.42
39G5d	257.3	3279.71	328.75	99.24	20.90	59.81	706.78
39G6a	255.7	2540.53	2401.81	584.05	23.57	243.29	189.64
39G6b	255.7	1442.81	1095.78	213.47	34.67	73.25	no data
39G6c	257.3	1459.70	2201.34	289.75	91.03	182.84	170.42
39G6d	257.3	2756.53	313.58	140.69	23.82	63.77	no data
40G5a	252.5	1566.64	428.39	153.53	265.30	109.19	214.50
40G5b	252.4	no data	356.25	no data	no data	no data	no data
40G5c	254.1	7374.17	3781.87	228.77	312.56	242.48	1955.45
40G5d	254.1	5197.33	5749.09	291.75	137.64	77.49	399.68
40G6a	252.5	1640.43	1265.11	526.16	122.37	77.57	99.02
40G6b	252.5	469.10	1363.77	1206.61	149.53	33.54	no data
40G6c	254.1	4351.33	6349.66	441.46	129.08	226.54	107.59
40G6d	254.1	709.39	2469.44	1122.09	264.11	60.55	no data
total		49140.49	34117.61	7457.92	2080.37	2886.62	9368.00

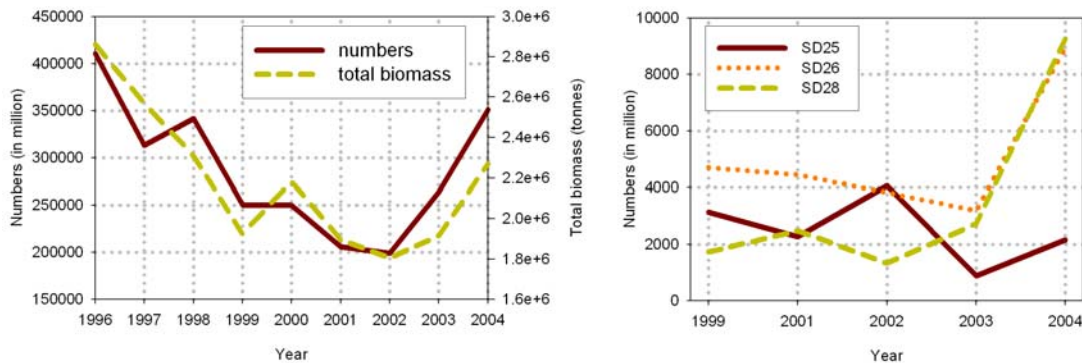


Fig. 3.8. Sprat abundances over years. Left: Abundance and biomass of sprat in the Baltic Sea (SD 22-32) as output from XSA-runs of ICES WGBFAS 2005. Right: Mean abundance per rectangle for ICES SD25, 26 and 28 as estimated by the international spring hydroacoustic survey.

3.5. Discussion

The abundances of sprat (*Sprattus sprattus* L.), herring (*Clupea harengus* L.) and cod (*Gadus morhua* L.) in the Bornholm Sea were estimated with hydroacoustics. Until winter 2002/2003 the development of abundances in the Bornholm Sea are in good agreement with known migration patterns, as reviewed by Aro (1989).

During all seasons, sprat was the most abundant species. In April 2002, very high numbers of sprat were found in the deeper Bornholm Basin, where sprat was captured between cold intermediate water and oxygen depletion zone (Fig. 5.11 on page 68). The resulting aggregation between both distributional limits was very dense. This is best illustrated by an anecdote as happened on the cruise in April 2002. Parallel to the hydroacoustic sampling onboard RV 'Alkor', colleagues from the Baltic Sea Research Institute Warnemuende deployed a towed CTD-system (Scanfish) onboard of RV 'Prof. Albrecht Penck' in the same area. They were hesitant to slack their towed CTD-equipment beneath this unusual 'bottom' seen in the echosounder. Therefore, the colleagues contacted the RV 'Alkor' to get more information about this 'strange bottom'. This 'bottom' was the dense echo-layer of sprat.

After spawning season, sprat left the deeper Bornholm Basin and the abundances of herring and cod increased during that time. This reduction of the strength of the spatio-temporal overlap between sprat on the one hand and herring and cod on the other hand has important implications on interaction between these species. Sprat influences the recruitment of cod by predation on cod eggs (Köster and Schnack 1994, Köster and Möllmann 2000b). The vulnerability of cod to predation depends on spatial overlap between sprat and cod eggs (Köster *et al.* 2001, Andersen and Möllmann 2004). The effect of the vertical overlap is discussed in chapters 5 and 6. This overlap is influenced by general hydrographic situations, i.e. periods of stagnation and inflow events in the deep basins of the Baltic Sea (Köster and Möllmann 2000b). The seasonal overlap between sprat and cod eggs is influenced by the spawning times of sprat and cod. As discussed above, sprat usually leaves the deeper basins after spawning in spring

(Aro 1989, Köster and Möllmann 2000b). This spawning time seems to be stable over the years, whereas spawning during winter time was observed after the unusual warm water inflows in autumn 2002 (Kraus *et al.* 2003, Mohrholz *et al.* 2006). In contrast a shift in spawning of cod from spring to summer occurred in the 1990s (Wieland *et al.* 2000). When comparing the sprat abundances between April 2002 (56786 million in the Bornholm Sea) and June 2002 (9078 million) the number of sprat, potentially preying on cod eggs was 6.3 time higher in spring 2002. These numbers illustrate the possible effects of the change of cod spawning time on the predator induced natural mortality of cod eggs. The area-disaggregated multispecies virtual population analyses (MSVPA) (Köster *et al.* 2001) incorporates the spatial dynamics of the sprat and cod population with a resolution of ICES subdivisions. Assuming a migration within subdivisions (e.g. from open sea to coastal areas), the found seasonal changes of the spatial overlap of sprat and cod are not covered by the MSVPA.

The spatial overlap between sprat and herring can result in food competition. The rapid increase of the Baltic sprat stock and a resulting higher food competition between herring and sprat was hypothesised as a driving factor for a strong decline of weight at age of Baltic herring (Cardinale and Arrhenius 2000, Möllmann *et al.* 2004). The weight at age of herring declined by more than 50% in all age-groups since the beginning of the 1980s (ICES 2000).

In the beginning of 2003, the sprat abundance in the Bornholm Sea was low compared to values calculated for spring 2002. Some indications for a climate-induced shift of sprat biomass toward the eastern Baltic Sea were presented. After the major Baltic inflow (MBI) 2003 very cold water (maximum temperature = 3.6°C) was found throughout the water column in the Bornholm Basin in April 2003. In contrast, relative warm water was still found in the Gotland Basin below the halocline (Fig. 1.2 on page 14). The unfavourable conditions in the Bornholm Basin probably induced an eastward migration of a large fraction of sprat. This supports the findings Hoziosky *et al.* (1989), who hypothesised a migration within a type of distribution in the case of an unfavourable environment.

The MBI in 2003 started at the Darss Sill between 16th and 25th January 2003 (Meier *et al.* 2004). The abundance estimates for January 2003 (sampling date 20th to 22nd January 2003) are assumed as pre-inflow abundances, since first effects for the Bornholm Basin were estimated for the 28th January 2003 (Meier *et al.* 2004).

Seasonal abundance estimations from survey cruises are quite laborious. Therefore the presented investigation delivers a unique dataset for the seasonal abundance development of the main fish species (sprat, herring and cod) in the Bornholm Sea. This dataset is the basis for further analyses regarding the ecology of Baltic sprat, especially during the Baltic field campaign of the German GLOBEC-project. An example is presented in chapter 7.

4. Meso-scale hydrographic features in the central Baltic Sea and their influence on the distribution and vertical migration of sprat

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4.1. Abstract

A wind-driven meso-scale pattern in temperature, salinity and oxygen was found along a transect in the northern Bornholm Basin (central Baltic Sea). Strong winds caused currents, which shifted the cold intermediate water (down to 3.6°C) towards south. The transect was sampled with a towed CTD-system and hydroacoustics in parallel. This allowed the investigation of the sprat distribution in relation to the observed meso-scale pattern. In those parts of the transect, where the cold intermediate water was persistent, the vertical distribution of sprat was restricted to water layers below the halocline. In other parts of the transect, sprat moved into shallower waters and occupied a wider depth range. This identified temperature as the important factor, setting the upper limit of sprat distribution. The development of hydrography, as measured in the field, was evaluated with a hydrodynamic model.

4.2. Introduction

The meso-scale includes distances from tenths to tens of kilometres (Mullin 1993). A more objective definition is given in oceanography: phenomena within the dimension of the baroclinic Rossby radius are usually referred as meso-scale (Reißmann 2005). The first internal Rossby radius in the investigation area (Bornholm Basin / Baltic Sea) is approximately 5 to 8km (Fennel *et al.* 1991, Mohrholz *et al.* 2006). Good examples for relevant structures in the pelagic zone at this scale are shelf fronts (Le Fevre 1986) and isolated anomalies – eddies.

Several processes can cause meso-scale pattern in the Baltic. Some examples are connected to the thermo-haline circulation, i.e. transport of North Sea water into the deep Basins of the Baltic Sea. For example, the inflowing high saline water often forms tongues of saline water, when it overflows the shallow sills (Zhurbas and Paka 1997, Schmidt *et al.* 1998). Furthermore, the saline deep water was found to be partially populated with mesoscale eddies, which have a diameter of 10 to 30km and a vertical extent of up to 40m (Zhurbas and Paka 1997, Reißmann 2005). Wind driven processes can cause meso-scale patterns in the Baltic Sea. Lehmann *et al.*

(2002) described the mean circulation pattern in the Baltic and its modification caused by local wind forcing. These processes result in a variety of meso-scale patterns, such as coastal up and down welling. Patches of river-water or anomalies of precipitation and evaporation cause meso-scale patterns in the surface layer.

It is known, that meso-scale patterns can influence the distribution of organisms, including fish (Le Fevre 1986, Fiedler and Bernard 1987, Mullin 1993, Casotti *et al.* 2000, Garçon *et al.* 2001). Most studies of the ecosystem effect of meso-scale patterns were conducted at frontal systems, since fronts are often persistent over longer time periods and partially predictable. Such fronts are typical in the North Sea, where Munk *et al.* 1995 found an aggregation of juvenile cod within a narrow band along the front. In contrast to frontal systems, eddies and wind-driven meso-scale variability are difficult to detect and predict. Therefore, the measurement and quantification of their effect on the pelagic ecosystem is a formidable challenge (Garçon *et al.* 2001).

Former investigations of pelagic fish distributions in relation to hydrography in the Baltic Sea were restricted to small-scale processes (e.g. vertical distribution) or large-scale phenomena (e.g. basin-wide horizontal distributions). This is promoted by the unique hydrography of the Baltic Sea, which offers a good environment for investigations on these scales due to the relative stable stratification along the vertical axis and over larger horizontal distances. On the other hand, we are not aware of examples for the influence of meso-scale patterns on fish distributions in the Baltic.

Physical parameters relevant for the distribution of Baltic sprat (*Sprattus sprattus Balticus* S.) are temperature, salinity and oxygen. Some authors supposed temperature and oxygen as ultimate limiting factors (Hoziosky *et al.* 1989, Rechlin 1975). The reason could be that the Baltic sprat population lives at the northern range of its distribution and is therefore vulnerable to cold temperatures. This is supported by anecdotal description of several authors, that sprat will not concentrate in water colder than 4°C (Hoziosky *et al.* 1989, Rechlin 1975). Since temperature and salinity are often correlated below the halocline in the deep Basins of the Baltic, it remained unclear whether salinity or temperature is the leading factor for the upper limit of the sprat distribution.

The aim of this chapter is to describe the hydrography and the development of a mesoscale pattern, which was found in May 2002 and its effect on the sprat distribution.

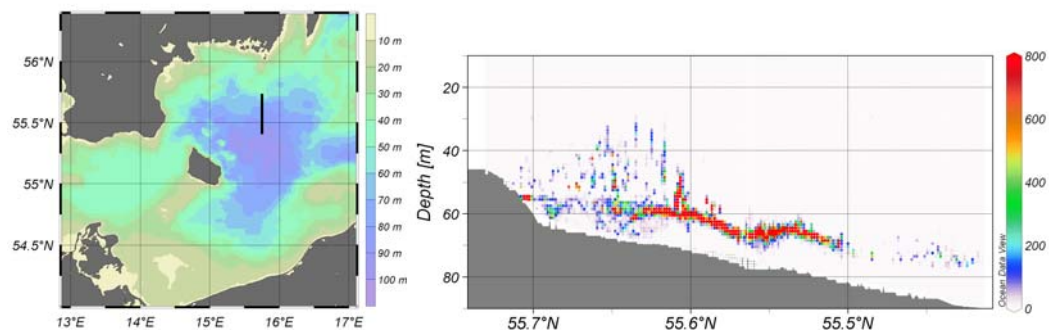


Fig. 4.1. Left: Map of the sampling site in the central Baltic Sea (Bornholm Basin). The line marks the sampled transect, which was sampled with hydroacoustics and towed CTD. Right: Fish distribution as found during regular daytime acoustic work marked by interesting pattern.

4.3. *Material and Methods*

Study area and time

The study was conducted at 11th May 2002 in central Baltic Sea onboard the German federal research vessel 'Walther Herwig III'. During the regular hydroacoustic spring-survey which is directed towards abundance estimation of Baltic sprat, an unusual inhomogeneous pattern of vertical fish distribution along a transect was recorded with hydroacoustics. This was assumed as a hint on a locally limited, meso-scale pattern of hydrography. To resolve finer structures of hydrography and to investigate the influence of this phenomenon on the behaviour of pelagic fishes in the central Baltic Sea, the area of interest was resampled during night with a towed undulating CTD-system and hydroacoustics in parallel.

The transect of investigation was directed along 15°45'E between 55°27'N and 55°42'N (across the northern slope of the basin), with an approximate length of 15nm (Fig. 4.1). The bottom depth decreased from 90m at the southern end of the transect to 47m at the northern endpoint.

Hydroacoustic measurements

Hydroacoustic measurements along this transect were conducted at the transect-work during daytime (from South to North; 15:42h-18:32h), during sunset/dusk (from North to South; 20:47h-22:39h) when steaming back to the start position of the CTD-transect and simultaneously to the CTD-tow during night time (from South to North; 22:39h-02:35h). The Simrad echosounder EK500 in combination with a hull mounted split beam transducer ES38B, working at a frequency of 38kHz, was used for acoustic measurements. For detailed description of acoustic data acquisition, please refer to chapter 1. In contrast to the standard procedure, the horizontal resolution of echo-integration was set to 0.1nm. Mean sprat density was calculated for the corresponding ICES-statistical square (40G5 – see Fig. 3.1 on page 29) and downscaled to numbers per square nautical mile (N/nm²). For this calculation, only echo recordings derived during daytime (6 to 20 o'clock) were used.

Fishery data

To identify echoes, pelagic trawl hauls were carried out during daytime. The pelagic trawl net PSN205 with a codend mesh-size of 10mm was used. The headrope depth of the trawl was adjusted to get a representative sampling of the main echo-layer. Trawling was carried out at a mean speed of 3.5knots for 30minutes per haul. Processing of fish samples followed standard procedures (ICES 2001, chapter 1). Subsequently, species composition and length-distribution were estimated from trawl haul data.

Hydrographic data

The meso-scale structure of hydrography along the transect was investigated using an ADM-CTD-system (Analoge und digitale Messsysteme GmbH), mounted on a Gulf III sampler frame. It was deployed in U-tows from 25m below the surface to approximately 6m above the bottom at a cruising speed of 5knots. Slack and heave speed of the winch was 0.5m/s. It was known from daytime vertical CTD-casts, that the upper water-layer was relative homogeneously than deeper water layers. Therefore the water layer above 25m depth was not covered during night, to get a better coverage and resolution of the hydrographic structures in mid- and bottom water.

For analyses slack and heave profiles were used. The vertical resolution of the hydrographic data was 0.25m, while in the horizontal one U-tow represents between 0.5 and 0.8nm (depending on bottom depth).

Wind direction and speed were recorded onboard RV 'Walther Herwig III' and averaged for hourly intervals.

Hydrodynamic model

To evaluate and understand the formation of the meso-scale hydrographic structure found during this study, a hydrodynamic model was used. The model should enlighten underlying processes, such as currents, which contribute to the water mass formation in the observed pattern.

The hydrodynamic model is based on the free surface Bryan-Cox-Semtner model (Killworth *et al.* 1991). A detailed description of the equations and modifications made, necessary to adapt the model to the Baltic Sea, can be found in Lehmann (1995) and Lehmann and Hinrichsen (2000a). Analyses of the Baltic Sea circulation has been performed by Lehmann and Hinrichsen (2000b) and by Lehmann *et al.* (2002).

The model domain includes the entire Baltic Sea (including Gulf of Bothnia, Gulf Finland and Gulf of Riga) and adjacent waters (Belt Sea, Kattegat and Skagerrak). The horizontal model-resolution is 5km and 60 vertical levels are defined, whereas the broadness of each level is chosen to best suitable for different depths of sills in the Baltic Sea. Forcing data for the model

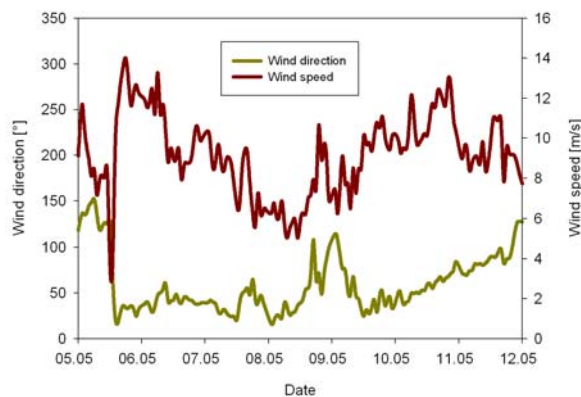


Fig. 4.2. Prevailing wind, prior to the investigation, carried out at 11th May 2002 in the central Baltic Sea, measured onboard RV 'Walther Herwig III'.

are delivered by atmospheric data as provided by the Swedish Meteorological and Hydrological Institute (SMHI: Norrköping, Sweden) and by river runoff data extracted from a runoff database (Bergström and Carlsson 1994). The model delivers prognostic variables, such as baroclinic current fields and a 3D distribution of temperature, salinity and oxygen, which are used for this study. Comparison of model-calculations with circulation features and observed physical properties showed a good agreement in previous studies (Lehmann 1995; Hinrichsen *et al.* 1997, Lehmann and Hinrichsen 2000a).

Modelled velocity fields and distributions of temperature, salinity and oxygen were extracted at 6 hours intervals.

4.4. Results

Wind

Relatively strong, easterly winds were recorded prior to the sampling date (Fig. 4.2). With the exception of the 8th May, mean wind strengths of 5 to 6 Beaufort (Bft) were measured, which correspond to 8-13.8m/s. Lowest wind speed were measured during the 8th May 2002, when wind decreased down to 3-4 Bft (down to 5.0m/s).

Hydrography

Observed data

Small-scale resolving measurements of hydrography showed a highly variable structure (Fig. 4.3). Along the transect a clear haline stratification, as typically for the deep basins of the Baltic Sea, was found. Down to approximately 50m water salinities of less than 8 were measured. Below this depth, salinity increased rapidly in the halocline. Maximum values of 15.5 were measured in the saline bottom layer. Oxygen showed an opposite pattern. Down to the

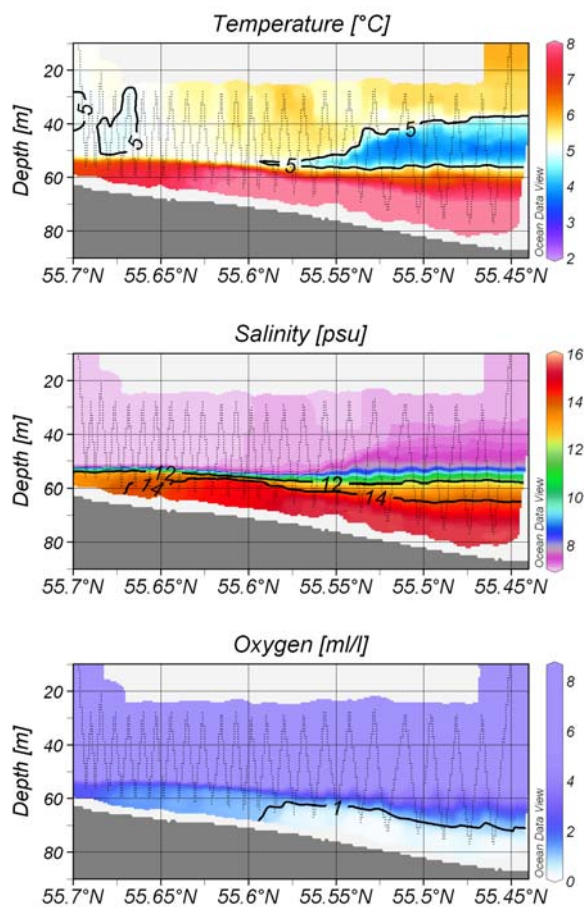


Fig. 4.3. Section plots of the distribution of physical variables along the sampled transect (Fig. 4.1 left). Relevant iso-lines are drawn for each variable. Sample points of the CTD were marked by small dots, showing the undulating sampling. The wave-like pattern of temperature and oxygen at 60-70m depth are artefacts from the sampling process, because different time constants of used sensors were not taken into account.

beginning of the halocline, the oxygen content of the water was slightly above 8ml/l and decreased rapidly with depth below the halocline. Temperature profiles along the transect (Fig. 4.4 upper panel) are more different than profiles of salinity and oxygen. Most differences were found in midwater between 35m to 55m depth. The water from the surface down to 35m had a relatively constant temperature between 5 and 6°C. Temperature increased below the halocline to 8.5°C in maximum.

Due to differences in the physical features, caused by relatively high meso-scale variability, it is possible to distinguish between three parts of the transect:

1. From the southern most point of the transect to approx. 55.5°N a typical spring/early summer situation with a warming of the upper water column and cold intermediate water was found. Minimum temperature of the cold intermediate water was 3.62°C. An oxygen-depletion zone was found above bottom. The cold intermediate water had a higher salinity compared to the intermediate water in the northern part of the transect.
2. From the northern most point of the transect to approximately 55.6°N the cold intermediate water was completely absent. Instead, warmer (minimum temperature = 4.92°C) and less saline water was found in exchange.
3. Between the northern and the southern part, a transition part was found, where the

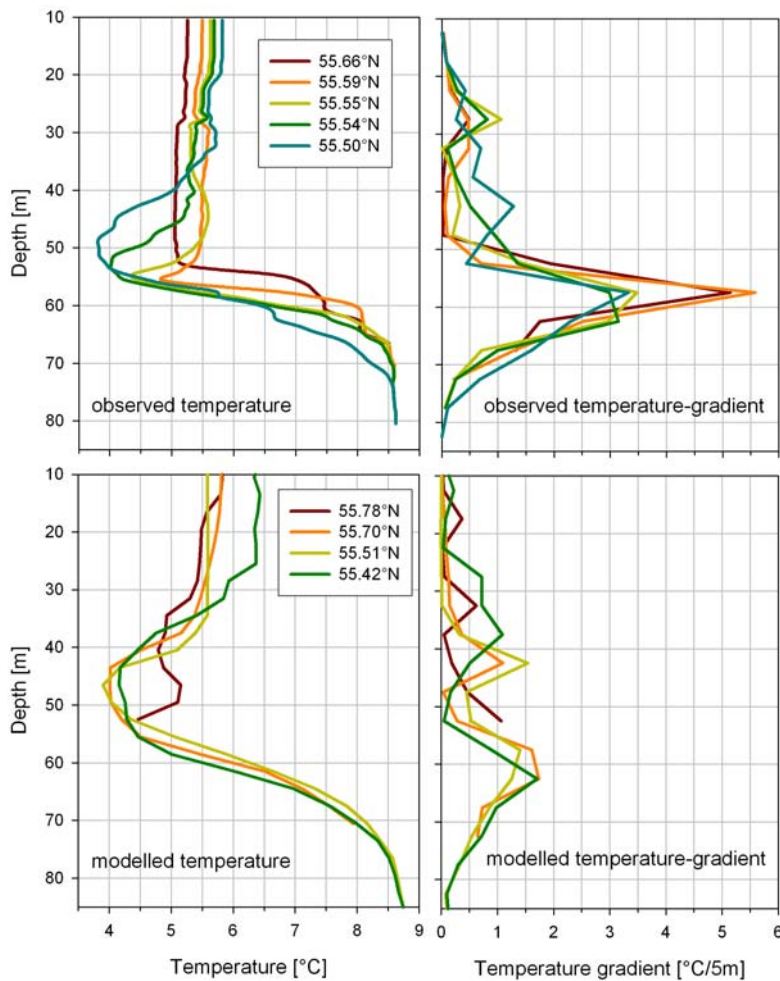


Fig. 4.4. Selected temperature profiles of the North-South-transect along 15°45'E (equal to 15.75°E), as observed in the night from 11th to 12th May 2002 (upper panel) and as model output for 11th May 24 o'clock (lower panel). Left: Temperature profiles showing the transition between parts of the transect with and without cold intermediate water. Right: Profiles of vertical temperature gradients as maximum values of 5m depth-intervals.

displacement of cold intermediate water took place. The thickness of the cold intermediate water layer (marked by 5°C isotherme) decreased rapidly from south to north (Fig. 4.4), resulting in a thin tongue of cold water. Additionally, the 1ml/l iso-oxygene turns towards the bottom and reached the bottom at approx. 55.6°N (Fig. 4.3).

It should be noted, that the vertical temperature gradients between the high saline bottom water and the midwater were relative high in all parts of the transect. The thermocline between the deep water and the midwater was strongest in the North, whereas in this area the minimum temperature was around 5°C.

Modelled data

The goal of using the hydrodynamic model was to understand the development of the hydrographic situation, observed during the field study at the 11th/12th May 2002. The evolution of temperature and flow fields is illustrated in Fig. 4.6. It can be seen how dramatically the hydrography of the northern Bornholm Basin changed during the 10 days prior to the field-observations at 11th/12th May 2002. The warming of water above 40m started slightly at the 2nd May and proceeded during the following days. As a result, the depth range of the water layer colder than 5°C decreased until the 12th May 2002. It is not very plausible, that the high horizontal variability of the observed pattern, was only caused by warming of the upper water layer. Relatively permanent currents below 20m depth from north to south can be seen in the

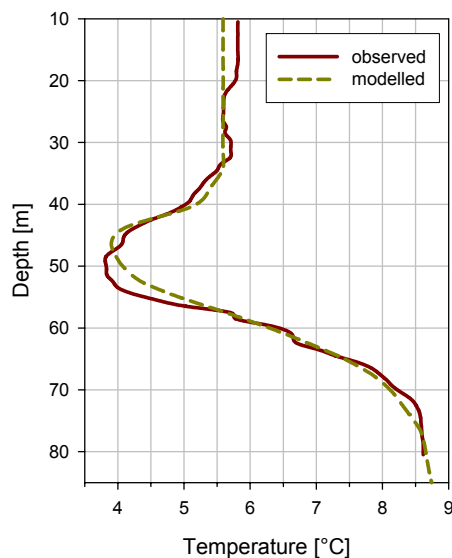


Fig. 4.5. Modelled and observed temperature profile for 55°30'N (55.5°N), 15°45'E (15.75°N) in the night of 11th to 12th May 2002.

modelled flow field (Fig. 4.6 mid panel) since the 8th May 2002. The east-west-component of the mid-water flow field does not show such a consistent pattern.

The most obvious changes in hydrography were found for temperature (Fig. 4.6 left panel). A total accordance between modelled and observed data was not expected. Nevertheless, main common features can be seen in both data sets for the night of the 11th to the 12th May 2002 (corresponds to the 11th May 2002 24:00h for modelled data), which are shown as cross sections in Fig. 4.3 (top panel) and Fig. 4.6 (lower left panel) and as temperature profiles along the transect in Fig. 4.4. In both datasets, a warmer upper water layer and increasing temperature below the halocline was found, whereas the temperature of the upper water layer was slightly higher in the southern part of the transect and decreased northwards. Main differences were found in the water layer between 30 to 60m. Although very high variability of the intermediate water layer, colder then 5°C, was noticed in the model, a complete displacement of

this water in the northern part of the transect wasn't found. However, the thickness of the cold intermediate water layer decreased from south to north, as it was found in the field

observations. While finding important differences north of 55.5°N, the data sets are almost identical in the southern part of the section (Fig. 4.5).

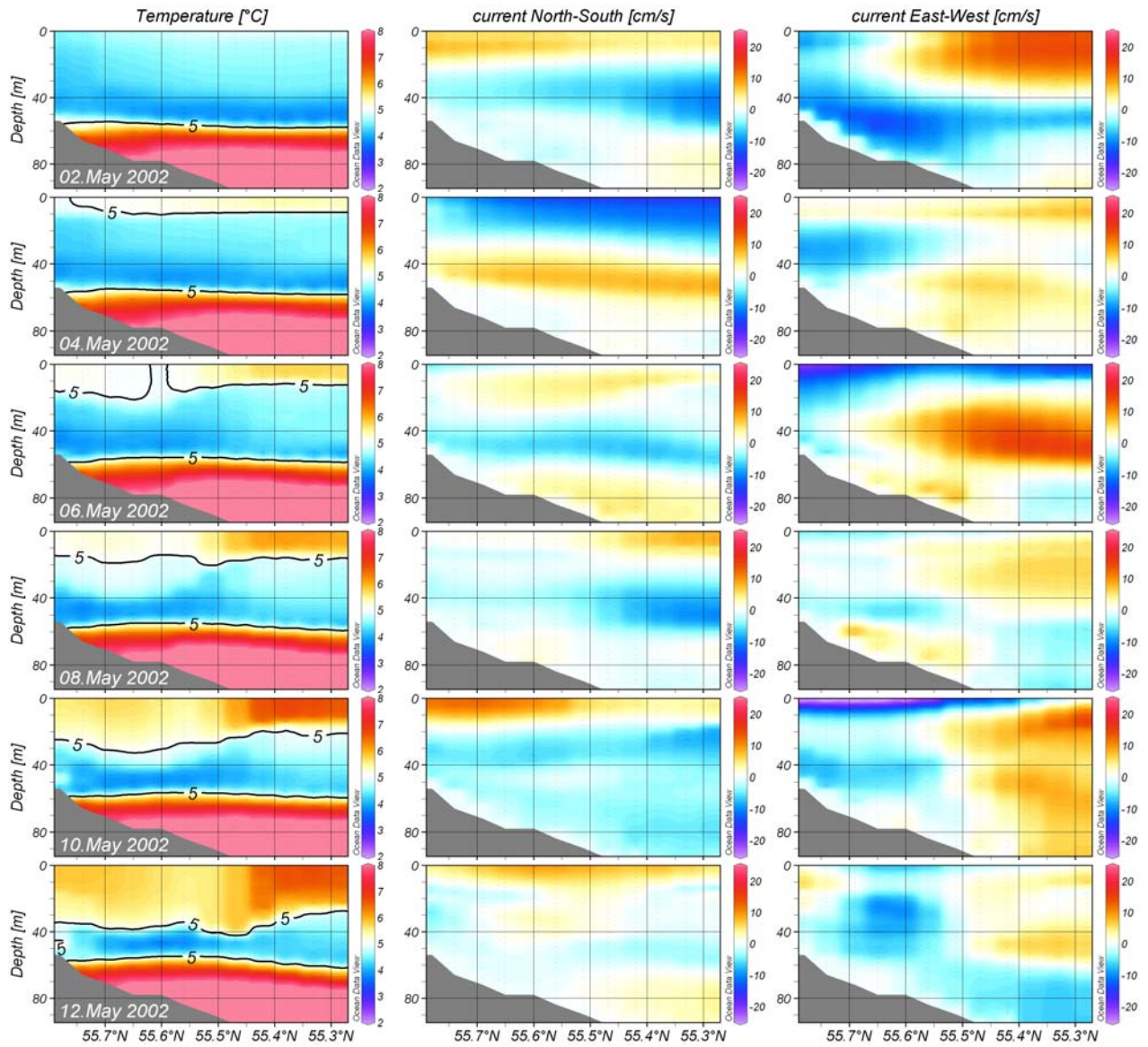


Fig. 4.6. Model snapshots of the investigated transect along 15°45'E (equal to 15.75°E) of temperature, and the speed of direction-components of the water currents (north-south and east west). Snapshots were taken every two days from the 2nd May to the 12th May 2002 at midnight (00:00a.m.). Values of the velocity indicate the direction of the current: For the north-south-component, positive values indicate a northward current, whereas negative values indicate a southward flow. Correspondingly, for the east-west-component, positive values indicate an eastward current, whereas negative values indicate a westward current.

Fish distribution

Catch data and abundances

Sprat was the dominant species in the investigation area (Tab. 4.1). Almost 99.8% of all fishes by numbers, or 97.2% of total caught fish-biomass were sprat. The estimated abundances reflect the dominance of sprat in the reference catches. The contribution of each species to recorded fish echoes was calculated by taken into account the length dependency of acoustic backscatter and the species composition. About 99% of all fish echoes can be allocated to sprat. Due to this superiority of sprat, it is legitimate to neglect herring and cod in subsequent discussions.

Tab. 4.1. Information about the fish fauna in the investigation area (northern Bornholm Basin). The species-composition was derived from a reference haul at 55°33'N 15°46'E conducted at 15:51h of 11th May. The abundances were calculated for the corresponding ICES-statistical rectangle 40G5 and downscaled to numbers per square nautical mile. Furthermore, the contribution of each species to the total fish echo was calculated.

species	weight per catch [kg]	fraction by weight	number per catch	fraction by number	abundance [million/rectangle]	abundance [million/nm ²]	relative contribution to total fish echo
sprat	1612.3	0.9716	152948	0.9982	11723.8	11.575	0.9904
herring	11.0	0.0066	204	0.0013	15.5	0.015	0.0041
cod	36.1	0.0218	67	0.0004	2.8	0.003	0.0055

Meso-scale distribution of sprat

The meso-scale distribution of sprat was highly variable along the sampled transect, as demonstrated in Fig. 4.8. This includes an inhomogeneity in horizontal scale, as well as of the vertical distribution. The distribution of sprat seems to be highly connected to meso-scale hydrographic structures, as described above. Before describing features of this biological-physical interaction, it should be noted that there is a time lag between acoustic measurements during daytime and dusk on the one hand and CTD-measurements on the other hand. Taken into account the relative fast evolution of hydrography in the sampling period (Fig. 4.6), a slightly misfit between acoustic and hydrographical measurements could be possible for day and dusk sampling.

Daytime distribution - Two contrasting patterns of the sprat vertical distribution were found during light hours at the 11th May 2002. South of 55.6°N, a vertical distribution of sprat, typical for spring/early summer (please refer to chapter 5), was found. The distribution of sprat is restricted to lower depths. Sprat is trapped below the cold intermediate water and hence below the permanent halocline. Although the sprat distribution and the relevant 1ml/l iso-oxygene do not show a very strong correlation during daytime (in contrast to dusk and night, probably due to time lag between samplings), it can be expected that the lower boundary for the sprat distribution is given by the oxygen depletion zone above the bottom. This results in a fish-free zone above the bottom. North of 55.6°N, sprat are no longer trapped by the cold intermediate water and occupy a wider depth range. This vertical distribution of sprat is typical for summer/autumn (please refer to chapter 5). It is important to note, that the strong temperature gradient in that area does not prohibit a spreading into shallower water layer.

Dusk distribution - A clear lower boundary of the sprat distribution, caused by the oxygen depletion zone, was found during dusk (Fig. 4.8 mid panel). This relationship becomes more obvious due to a better agreement of the fish-free zone and oxygen contours. There were two

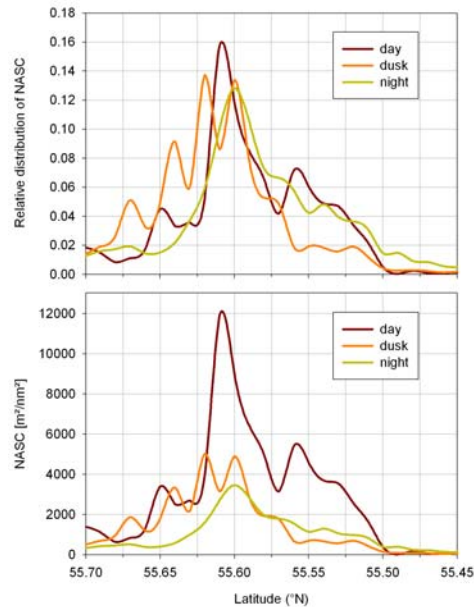


Fig. 4.7. Horizontal distribution of sprat echoes along the transect sampled at 11th/12th May 2002 in Northern Bornholm Basin. Top panel: Relative distribution; Lower panel: Total echoes as nautical area backscattering coefficient.

echo layers. On the one hand, one part of the fishes were found below the halocline, on the other hand, a large fraction migrated upwards into shallower water layers. This upper fraction of sprat seems to be higher located in the water column towards south. Hydroacoustic measurements during dusk (from 20:47-22:39h) captured the upward vertical migration of sprat. Therefore, this pattern of the sprat distribution is a result of capturing different stages (in time) of the daily vertical migration of sprat. South of 55.6°N, only very sparse echoes were found in this upward migrating fraction of sprat, which indicate an inhibition of upward migration of sprat where cold intermediate water was present.

Nighttime distribution - Measurements of acoustics and hydrography were conducted in parallel from south to north. The recorded echo distribution has some similarities to recordings during dusk, whereas upward migration of sprat was finished. A slight transition between the echo layer below the halocline and the echo layer in the upper water column was found. This excludes the cold intermediate water, where almost no echoes were recorded.

The horizontal distribution of sprat along the transect was not homogeneous. Acoustic data of all three consecutive samplings periods show comparable patterns of the horizontal distribution of sprat (Fig. 4.7 top), whereas the amount of measured echoes was higher during light hours (Fig. 4.7 bottom). South of 55°30'N (55.5°N), measured echoes were very weak. Following the transect northwards, the echo values increased and reached a maximum at 55°36'N (55.6°N) and decreased again towards north. Therefore, the abundance of fish (i.e. sprat) is highest in parts of the transect, where the transition between hydrographic features (with and without cold intermediate water) was found.

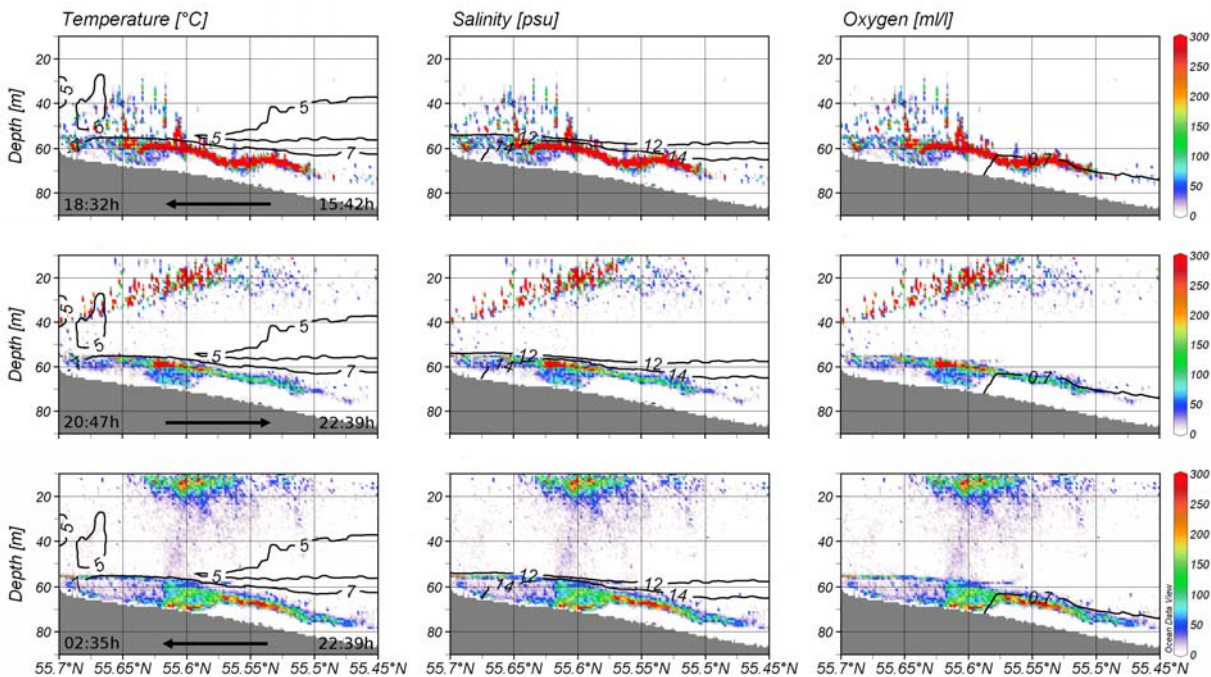


Fig. 4.8. Condensed echograms along a transect in Northern Bornholm Basin at different times of the day overlaid by contour lines of hydrographical parameters. The direction and the start- and end-time of the hydroacoustic measurements are noted in the left column. Given are integrated echo-values (NASC – nautical area backscattering coefficient [m^2/nm^2]). The environmental parameter temperature, salinity and oxygen (from left to right) were sampled in parallel to night time acoustic measurements.

4.5. Discussion

It was shown in this study, that hydrographic features at meso-scale dimension directly influence the distribution of Baltic sprat. The situation found in May 2002, offers interesting insights into the behaviour and habitat-preferences of sprat.

It has to be pointed out, that the presence of such mesoscale pattern of hydrography was assumed during the observation of the fish distribution pattern, which was derived from hydroacoustic measurements. I.e. the distribution of fish was a cue for hydrography.

The field observations itself did not explain the evolution of the hydrographic situation, observed during the field sampling. It is common knowledge in oceanography, that steadily winds induce water mass transport, which is often described as Ekman transport. At the northern hemisphere, the wind-induced surface current will theoretically directed 45° to the right of the wind direction. In the open ocean, the direction of the current will change with depth. However, the water transport in the Baltic Sea is strongly influenced by bottom topography and coastlines (Krauss and Brüggge 1991, Lehmann *et al.* 2002). Therefore, simple explanations for the development of the observed hydrographic pattern, derived solely from field observations,

cannot be given. Hence, a hydrodynamic model was used to investigate the processes that lead to the observed high meso-scale variability of the physical parameters.

The hydrodynamic model did not fully reflect the complete removal of cold intermediate water in the northern part of the sampled transect (Fig. 4.3 compared to Fig. 4.6). Nevertheless, the modelled hydrography is in good agreement with observations (Fig. 4.4 and Fig. 4.5). Additionally, the model offered a good explanation for the temporal evolution of the measured hydrography. During the days prior to the field sampling, relatively constant and high wind speeds were measured onboard RV 'Walther Herwig III'. The resulting wind stress acted upon the sea surface and induced an transport of water masses (Hinrichsen *et al.* 2003), which is indicated in Fig. 4.6 by strong (mainly) north-westerly currents of the surface layer. This is in good agreement with theoretical Ekman transport caused by winds from easterly directions. The movement of near-surface water masses is compensated by a return flow, which is assumed to be strongly influenced by the basin-like topography of the Baltic Sea (Krauss and Brügge 1991, Lehmann *et al.* 2002). The midwater return flow was of southerly directions (see Fig. 4.6), shifting warmer, but less saline water towards south. This resulted in a replacement of the cold intermediate water, which in turn influenced the distribution of pelagic fish.

The biological implications of wind-driven currents were shown for egg and larval transport of Baltic cod (e.g. Voss *et al.* (1999), Hinrichsen *et al.* 2003, Voss and Hinrichsen 2003), Baltic sprat (Baumann *et al.* 2004, Hinrichsen *et al.* 2005) and zooplankton species (Schmidt 2006). All these examples were described as passive processes, acting on planktonic species (e.g. copepods) or drifting early-life stages of fish (ichthyoplankton). An active reaction of organisms, which was induced by wind-driven meso-scale variability in hydrography, was not shown so far in the Baltic Sea. However, horizontal hydrographic features, such as frontal systems, are known to influence the distribution of adult fish. The congregation of fish is induced by the aggregation of lower trophic levels in high productive regions of the front. I.e. the phytoplankton production increases due to high nutrient availability in upwelling or convergence zones (Beardall *et al.* 1982). This leads subsequently to a successive aggregation of zooplankton, planktivorous fish, piscivorous fish and seabirds (Pingree *et al.* 1974, Fiedler and Bernard 1987, Royer *et al.* 2004), i.e. from lower to higher trophic levels.

In contrast to large frontal systems, which are often persistent over a longer time period, the meso-scale pattern, as described in this chapter, is expected to be a short-term event. Therefore, a response of fish to changed distribution patterns or productivity of phytoplankton and zooplankton cannot be assumed, which indicate a solely influence of variable hydrography on the behaviour of sprat.

The described parts of the transects have characteristics of different seasons. The southern part represents a typical spring situation in open basins (with cold water above the halocline), whereas in the northern part the very cold intermediate water was replaced. Water temperatures above 5°C in midwater are more typical for summer situation. But in contrast to a 'typical' summer situation, the summer thermocline in the upper 20m was not found.

Due to the different vertical distribution patterns of sprat, caused by contrasting hydrographic situations, we got insights into the process of habitat selection of sprat. Until now, it was not clear, whether the occupation of different depth ranges at different seasons is caused by seasonal changes of hydrography or physiological rhythms, such as the spawning status.

In this chapter, it is demonstrated that low temperature limits the spreading of sprat into shallower water layers.

Additionally, a connection between the lower boundary of the sprat distribution and the oxygen depletion zone, represented by the 1ml/l iso-oxygene was found. An influence of other abiotic factors (salinity, light, temperature gradient) was not found in this dataset, whereas strong temperature gradients (5.5°C/m) in the halocline were found. Temperature gradients are discussed as barriers for vertical migration (Blaxter and Holliday 1963), whereas given thresholds vary. Therefore, it can be concluded, that either a gradient of 5.5°C/5m does not influence the migration behaviour at all, or the effect depends on the temperatures within the gradient, e.g. if minimum temperature is above 5°C, the gradient is not influential.

The implications of a variable environment in the context of habitat preferences of Baltic Sprat are discussed in more detail in chapter 5.

5. Observed and modelled vertical distribution of Baltic sprat

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5.1. *Abstract*

This study aims to identify those environmental factors, which determine the vertical distribution of adult sprat during spawning time. The investigation was carried out with a dataset from April 2002, since almost 100% of all fish echoes were caused by sprat and the hydrographical situation was typical for early spawning time in stagnation periods. In a first step, temperature, salinity and oxygen were identified as potential limiting factors, whereby it was not clear whether salinity or temperature is the leading factor for the upper limit of distribution. A unique hydrography, found in May 2002, with high mesoscale variability revealed temperature as the driving factor. Sprat avoided temperature colder than 5°C and oxygen content lower than 1ml/l. With these findings a simple distribution model was parameterized, which lead to an excellent agreement between modelled and observed data. The minimization of differences between modelled and observed profiles, supported the found limits. Nevertheless, the application of the model to other seasons offered discrepancies. Therefore, it has to be concluded, that more environmental factors should be taken into account during other seasons. Nevertheless, the model can be applied to spawning time during stagnation periods, and is an enhancement to previous approaches.

5.2. Introduction

The distribution of pelagic fish usually does not cover the entire water column (Magnuson 1985). In fact, pelagic fish are often concentrated within a certain depth range, which is confined by the combined influence of several environmental factors defining the habitat. The identification of relevant environmental factors will improve the understanding of population biology and dynamics, because the habitat-choice influences important processes, such as inter- and intraspecific interactions and many physiological processes like metabolism, digestion and gonad ripening (e.g. Grauman and Yula 1989, Parmanne *et al.* 1994, (Rudstam *et al.* 1994)

In this study, the principles behind the habitat-choice of Baltic sprat were investigated. Because spawning is a key process for the stock development of fish species, the investigation were focussed on spawning area and time, in which sprat accumulate in the Basins of the Baltic Sea (Aro 1989).

These basins are characterized by pronounced and stable vertical thermo-haline stratification (Matthäus and Franck 1992), whereby salinity increases with depth below approximately 50-70m. Above the halocline, salinity varies between 7 and 8 in the central Baltic Sea. The profiles of temperature and oxygen are more variable over time than the salinity profile. In years with no sufficient inflow of oxygen-rich North Sea water, i.e. stagnation years, the oxygen content decreases below halocline and an oxygen depletion zone occurs above bottom (Börngen *et al.* 1990, Matthäus and Franck 1992, Matthäus and Schinke 1994). Temperature above the halocline shows distinct changes during the annual cycle (Møller and Hansen 1994), whereas temperature below halocline is often relatively stable and warm, but influenced by sporadically inflowing North Sea water. For instance, very cold water (approx. 3°C) replaced the warmer water layer below halocline in the Bornholm Basin during winter/spring 2003 (Feistel *et al.* 2003, Meier *et al.* 2004) (Fig. 1.2).

This high vertical heterogeneity of potentially habitat-defining parameters provides a good basis for the investigation of the relevant physical parameters and physical-biological interactions, which influence the vertical distribution of sprat during spawning time.

The approximate vertical distribution of Baltic sprat was occasionally described (Orlowski 1991, Gröhsler *et al.* 2000), but a study to identify the potentially limiting factors and thresholds was not published so far.

The determination of habitat-defining environmental factors is the basis for the parameterization of distribution models. Such model predictions can be regarded as null hypothesis, which states that the vertical distribution of sprat is dependent exclusively on identified parameters relevant for distribution. To support this hypothesis, the model was tested against the observed vertical distribution of sprat.

Experiments with freshwater fish revealed, that several fish species have a temperature preferendum (Reynolds and Casterlin 1979). These findings were ratified in the field for some species (Neill and Magnuson 1974), whereas the basic response, as initialized by a preferred temperature range, can be modified by other factors, such as low oxygen level (illustrated in

Fig. 5.1 left) or food supply (Javaid and Anderson 1967). Experiments with adult clupeids are restricted by technical reasons, e.g. low survival rates in captivity. Therefore, it is not possible to clarify experimentally whether sprat has a preferred temperature, or not. Hence, it is possible to identify the relevant parameters, which define limit the habitat of sprat, but the type of response (either one-sided as limiting function or two-sided as optimum curve) may remain unclear due to restrictions of field sampling. However, a simple approach was chosen, which assumes an ordinary limiting response for temperature, too (Fig. 5.1 right). If this assumption do not lead to biased model results, it can be stated, that either they do not have a temperature preferendum, or the second limiting threshold of temperature is not prevalent in the environment.

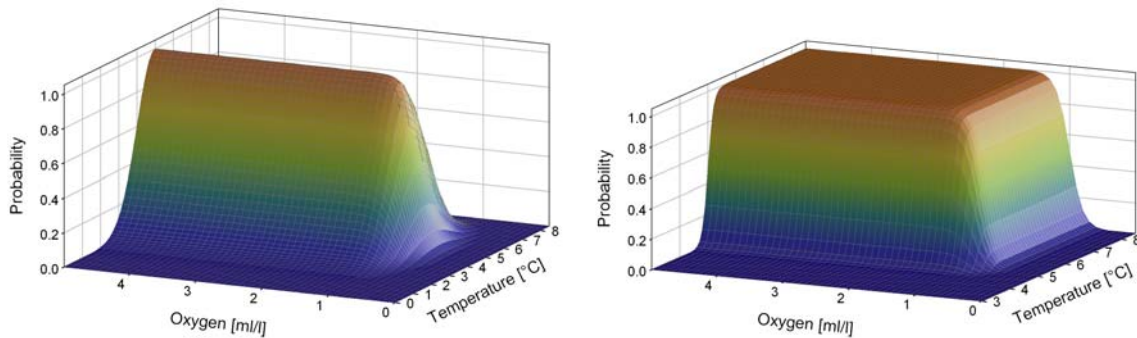


Fig. 5.1. Combined temperature-oxygen response surface. The z-axis values indicate the relative probability of occurrence of sprat in a given temperature-oxygen combination, whereas the most preferred habitat was set to 1. Right: Response surface calculated for sprat, as used in this chapter. Left: Schematic drawing of response surface with a temperature optimum, as used by Rudstam and Magnuson (1985) for freshwater fish.

Tab. 5.1. Summary of used datasets. Cruise names indicate the used research vessel. AL=RV 'Aikor', WH=RV 'Walther Herwig III'.

month	cruise	used for...	figure
04/2002	AL200	abundance estimation	Fig. 5.4
		definition of habitat preferences	Fig. 5.6; Fig. 5.5; Fig. 5.8; Fig. 5.9; Fig. 5.11; Fig. 5.12
		modelling of vertical distribution	Fig. 5.13; Fig. 5.14
05/2002	WH239	estimation of oxygen threshold	Fig. 5.7
		meso-scale investigation	Fig. 5.10
		modelling of vertical distribution	Fig. 5.15
08/2002	AL207	estimation of oxygen threshold	Fig. 5.7
		typical summer vertical distribution	Fig. 5.9
04/2003	AL219	vertical distribution after winter inflow	Fig. 5.16; Fig. 5.17

In this chapter, investigations on the vertical distribution of sprat in the central Baltic Sea are presented. The focus will be 1) the identification and calculation of environmental thresholds for the vertical distribution of sprat and 2) the application of these thresholds in a simple model, which describes the vertical distribution of sprat during spring and early summer. The applied model should support our findings by comparison with observed data.

5.3. Material and Methods

Sampling

For the presented analyses, data from several cruises were used. Field investigations were carried out April, May and August 2002 as well as April 2003 in the central Baltic Sea onboard the German federal research vessels 'Walther Herwig III' and 'Alkor' (see Tab. 5.1).

April 2002

The primary dataset, used in this study was collected in April 2002 onboard RV 'Alkor'. This dataset was used to calculate environmental thresholds for vertical distribution of sprat during early spawning season. This cruise was chosen, because it covers the beginning of sprat spawning time and additionally the proportion of other fish species (i.e. herring and cod) was negligible in Bornholm Basin.

May 2002 and August 2002

Data from May 2002 (RV 'Walther Herwig III') and August 2002 (RV 'Alkor') were used to get a further estimation for the oxygen threshold, which defines the lower boundary of sprat distribution.

Additionally, in May 2002 the sprat distribution in relation to meso-scale hydrographical features was investigated. During the regular hydroacoustic spring-survey, directed toward Baltic sprat, locally limited high meso-scale variability of fish distribution were noted at transect work. To resolve underlying physical structures, the area of interest was resampled during night with a towed undulating CTD and hydroacoustics in parallel. The sampled transect along 15°45'E started at 55°27'N and ended at 55°42'N, resulting in an approximate length of 15nm. Bottom depth decreased from 90m at the southern end of transect to 47m at the northern endpoint. For more details, refer to chapter 4.

April 2003

This cruise represents a contrary hydrographical situation, compared to previous cruises. In winter 2002/2003 a strong Baltic inflow occurred, which replaced the water in the bottom layer with very cold, but oxygen rich water (Fig. 1.2 right column).

Hydrographic data

Hydrography profiles were measured on a 10nmx10nm station grid during the Baltic sampling programme of the German GLOBEC programme onboard RV 'Alkor' or along regular transect work at the spring hydroacoustic survey onboard RV 'Walther Herwig III'. An ADM-CTD-system, equipped with an oxygen probe, was used for vertical profiles of hydrography. Samples for salinity and oxygen calibration were taken at random stations and depths throughout the surveys.

The meso-scale structure of hydrography along the transect in May 2002 was investigated with an ADM-CTD, mounted on a base frame. This system was deployed in U-tows from 25m below

surface to approximately 6m above bottom at a cruise speed of 5knots. The water layer above 25m depth was not covered to increase the sample resolution in mid- and bottom water.

Slack and heave profiles were used for analyses and were plotted with the free software package 'Ocean Data View' (ODV, Schlitzer 2004).

The general procedures of hydroacoustics and biological sampling, as well as the combination of acoustic and hydrographic databases are described in chapter 1.

Data processing and statistics

Cumulative frequency distribution plots

Cumulative frequency distributions (D'Amours 1993, Perry and Smith 1994, Tomkiewicz *et al.* 1998) were calculated to illustrate the range of environmental variables at which sprat occur, whereby depth, temperature, salinity and oxygen were included. First, the empirical cumulative frequency distribution for habitat variables ($f(t)$) was calculated:

$$1) \quad f(t) = \frac{\sum_{i=1}^L \sum_{j=10}^{n_i} I(t_{ij})}{\sum_{i=1}^L \sum_{j=10}^{n_i} 1} \quad \text{with indicator function: } I(t_{ij})=1, \text{ if } t_{ij} \leq t; 0 \text{ otherwise}$$

Here, L is the number of stations, taken into account and n_i is the maximum depth at station i . The cumulative frequency distribution was calculated for discrete bins (t) of the environmental variable, whereby an increment width =0.1 was chosen, which covers the range of the physical factor. The measured value of the variable at station i and depth j is noted as t_{ij} . The cumulative distribution function derived from equation 1) can be used to identify the proportion within any range of the habitat variable during the survey, i.e. the range of temperature that occurred in the central 50% (between 25th and 75th percentiles).

The cumulative frequency distribution of measured sprat echoes in relation to the environmental factor $g(t)$ was calculated thereafter. The used echo-values were calculated for every depth in relations to the total echo measured at this station (Y_{ij}), i.e. the sum over all depth of a given station is 1. As result, stations were weighted equally.

$$2) \quad g(t) = \frac{\sum_{i=1}^L \sum_{j=10}^{n_i} Y_{ij} * I(t_{ij})}{\sum_{i=1}^L \sum_{j=10}^{n_i} Y_{ij}} \quad \text{with indicator function: } I(t_{ij})=1, \text{ if } t_{ij} \leq t; 0 \text{ otherwise}$$

For every cumulative frequency distribution of sprat the corresponding threshold values were determined as 5% limits (5% echoes at one side of the threshold and 95% on the other side).

Therefore, both thresholds per environmental variable include the central 90% of all measured sprat echoes.

Correlation-matrix

The correlation matrices and the scatter-matrix-plots were calculated and displayed with the freely available statistic package R (R Development Core Team 2005). Fitting curves were calculated as least-square method and as smooth of the data.

Quotient plots

Single parameter quotient analysis in combination with a randomization test (van der Lingen and Castro 2004 and ICES 2005) was used to characterize the habitat of sprat. The environmental parameters, taken into account, were sample-depth, temperature, salinity and oxygen. As response variable the standardized echo distribution was chosen, i.e. the values of the probability density function (pdf) of each profile. Without this standardization, the echo profiles with high total NASC would overlay the effect of weaker profiles. The analysis was conducted for discrete bins of each environmental variable.

The quotient analysis delivers a value per bin, which indicates the selection of the habitat. Values above 1 indicate positive selection and vice versa. The randomization procedure estimates the 95% confidence limits for rejecting the null hypothesis, which states that the observed quotient within a particular discrete bin of the environmental variable can be obtained by pure random alone.

The software package to calculate this analysis was prepared by Miguel Bernal (Bernal 2005) and delivered as an additional package, called '*shachar*' for the R-software (R Development Core Team 2005).

Modelling the vertical distribution of sprat in April 2002

Using the results from investigations, as described above, a vertical distribution model for sprat in early spawning time was developed. Due to the identification of only two variables (temperature and oxygen), which control the vertical distribution of sprat in early spawning time, a quite simple model was chosen. Consequently, if other factors, such as light, prey availability or predator avoidance are of importance, this model will fail.

The model output should be a probability distribution function (pdf), which gives the relative vertical distribution of sprat.

Response functions

For oxygen, as well as for temperature, lower thresholds were found, which limit the vertical distribution of sprat. However, no upper levels and consequently no optimum curves for both parameters were found in the field. Therefore, simple response-functions were applied for both parameters (illustrated in Fig. 5.1 right). To avoid sharp transitions of both curves, sigmoid functions were applied, whereby the point of a 50% response was set to the limiting threshold of each parameter. The output of the response-function can be interpreted as probability of occurrence, relative to the optimum environment, which was set to one.

$$3) \quad \text{resp}(x_z) = \frac{1}{1 + \exp(-\alpha * (x_z - x_{50}))}$$

with:

$\text{resp}(x_z)$...response function for one environmental factor, i.e. temperature or oxygen
x_z	...value of environmental parameter at depth z, i.e. Ox_z or T_z
x_{50}	...threshold value of x, with probability of occurrence=0.5
α	...steepness of sigmoid function

According to the identified thresholds, the initial x_{50} -parameters of the model are $Ox_{50} = 1\text{ml/l}$ for oxygen and $T_{50} = 5^\circ\text{C}$ for temperature, whereby a steepness $\alpha = 10$ was chosen.

The combination of the response function for temperature and oxygen, results in a response surface, depending on both parameters ($\text{respsurf}(Ox_z, T_z)$ - see Fig. 5.1 right).

$$4) \quad \text{respsurf}(Ox_z, T_z) = \text{resp}(Ox_z) * \text{resp}(T_z)$$

Calculation of vertical distribution

After defining the response surface (Fig. 5.1 right), the calculation of the probability density function (pdf) needs two more steps. At first, for every depth interval of a given hydrography profile, the corresponding value of the response surface ($\text{respsurf}(Ox_z, T_z)$) has to be calculated. Since a probability density function has an integral equal to 1, these values have to be standardized.

$$5) \quad \text{pdf}(z) = \frac{\text{respsurf}(Ox_z, T_z)}{\int \text{respsurf}(Ox_z, T_z)}$$

Optimization of model parameter

The optimum values of the response function parameters Ox_{50} and T_{50} were estimated by minimizing the differences between modelled and observed vertical distribution of sprat for every echo profile. The minimization of the total error for all profiles of a given cruise was conducted using the 'fminsearch'-function in Matlab (The Mathworks 2005). Alternatively, an error-matrix was calculated for combinations of the initial parameters Ox_{50} and T_{50} . From this error-matrix the lowest error and the corresponding parameter combination can be easily extracted. The calculated error-matrix is shown in Fig. 5.14.

5.4. Results

General hydrography in April 2002

In April 2002, hydrography was characterized by strong vertical gradients in salinity, temperature and oxygen. Salinity above halocline ranged between 7 and 8 at a temperature around 4°C. At approximately 50m depth salinity increased sharply up to 16 and temperature increased to 9°C. Oxygen decreased below halocline rapidly to 0 ml/l at approximately 80m (Fig. 5.2). This clear structure of the water column is reflected by high correlation between physical parameters (Tab. 5.2, Fig. 5.3). The relationships between temperature and other environmental parameters had the weakest correlation coefficients, but correlation was evident.

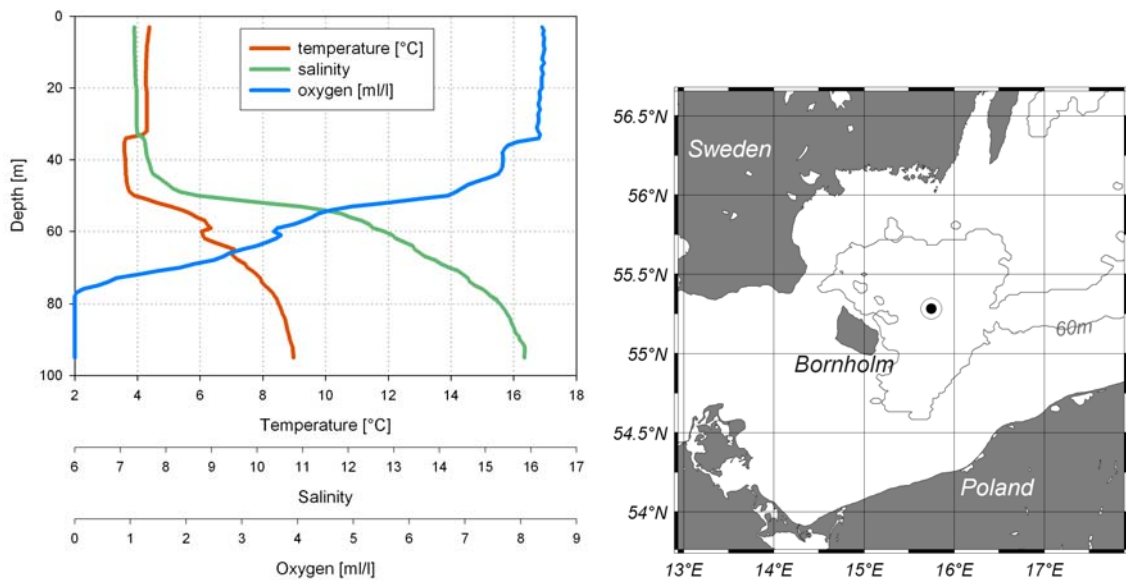


Fig. 5.2. Left: Profile of hydrography in April 2002 Bornholm Basin at central station; Right: position of central station (GLOBEC-station 23).

Tab. 5.2. Correlation matrix of environmental parameters and echo-values. Given is the Spearman's rank correlation coefficient.

	depth	oxygen	salinity	temperature	NASC relative
depth	1	-0.8982727	0.9659280	0.6740604	0.6855895
oxygen		1	-0.8949519	-0.7981667	-0.6985718
salinity			1	0.7103566	0.6814142
temperature				1	0.6470738
NASC relative					1

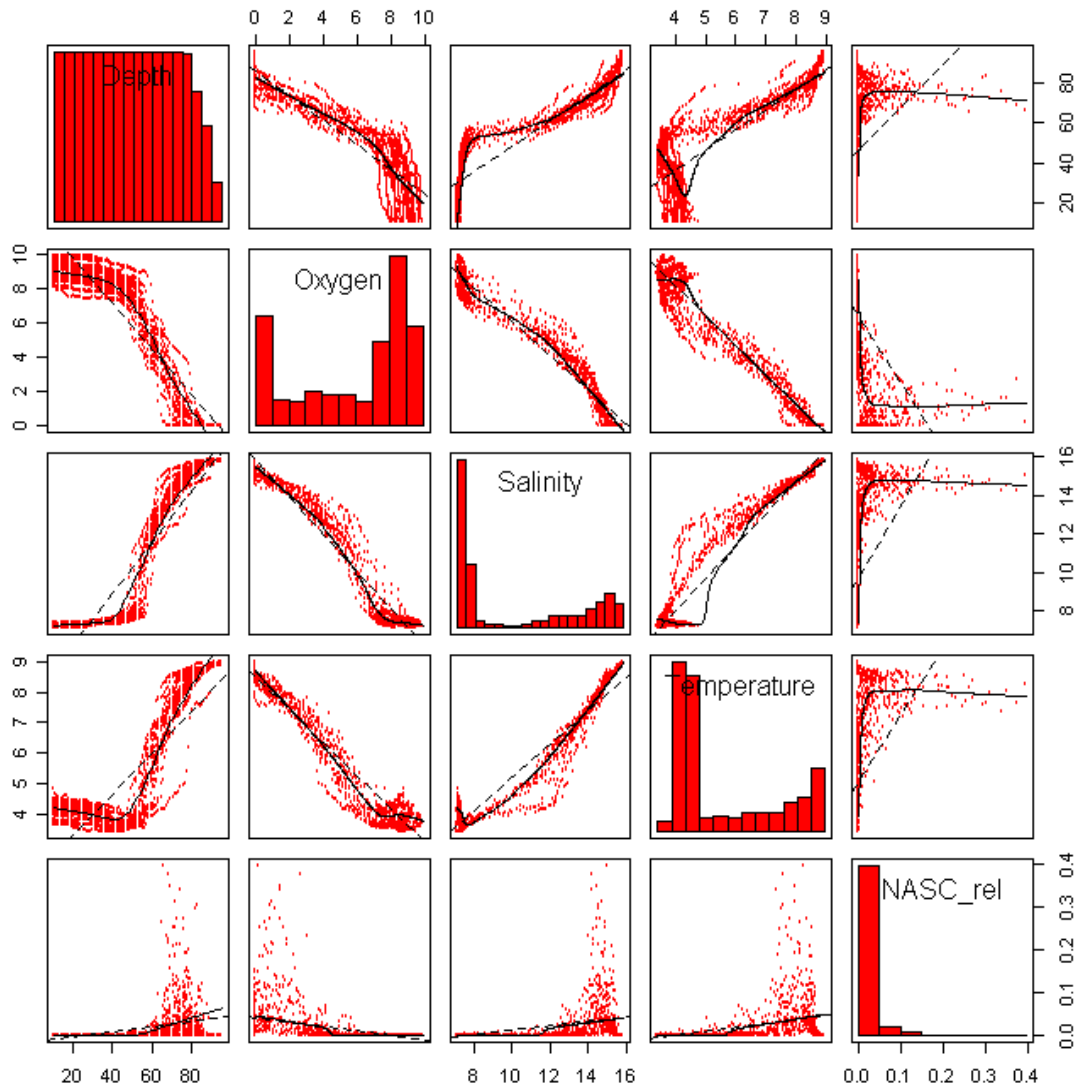


Fig. 5.3. Scatterplot matrix of environmental and echo data in April 2002. In the boxes along the diagonal, histograms of frequencies for every bin of analysed parameter are shown. The scatterplots contain fitting curves. The dashed line is calculated with the least-square method, whereby the solid line represents a smooth of the scattered data.

Horizontal distribution and abundance in April 2002

A detailed description of the fish abundance in April 2002 is given in chapter 1. The abundance of sprat in the Bornholm Basin was very high, whereas abundances of herring and cod were negligible compared to sprat (Fig. 5.4; Tab. 5.3). Therefore, around 97% off all echoes can be assigned to sprat (Tab. 5.3), whereby this is not a simple relationship derived from the relation

of abundances. In fact, the diverse acoustic properties of different species and the fish-length dependency of sound backscatter were taken into account. The three fish species were concentrated in the Bornholm Basin, with water depth deeper than 60m. Highest concentration of sprat and herring were found in the northern Bornholm Basin, whereas cod was mostly found in the central Basin.

Tab. 5.3. Abundance (in million) and proportion of total echo of sprat, herring and cod in ICES subdivison 25 in April 2002.

	sprat	herring	cod
abundance in SD25	56.786	617	15
relative proportion of total echo	96.7%	2.5%	0.8%

Due to the very low proportion of cod and herring born echoes (Tab. 5.3), all measured echoes in April 2002 were treated as they are sourced from sprat in the following analysis.

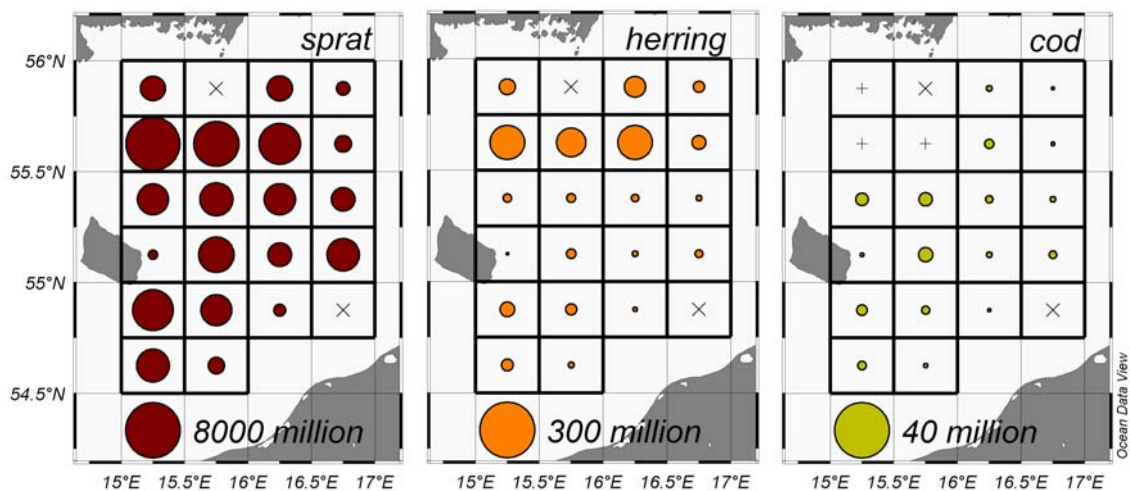


Fig. 5.4. Distribution and abundances of main fish species (sprat, herring and cod) in Bornholm Basin in April 2002, as estimated using hydroacoustics.

Vertical distribution of sprat in April 2002

Sprat was concentrated in a narrow and dense layer in the deeper Bornholm Basin (Fig. 5.9 left). The cumulative frequency plots, calculated for April 2002 (Fig. 5.6) give an idea about the environmental range, where most of the fish echoes (90% within dashed vertical lines) were recorded. The values of 5% thresholds are given in Tab. 5.4. Some of these thresholds are marked as potential limits of the vertical distribution of sprat. Since, oxygen depletion is a common phenomenon of the bottom water in the Baltic Sea, the identification of low oxygen content as lower limit for the vertical distribution of sprat is obvious. In contrast, the limiting factor at the upper boundary of distribution is not that clear, because, as described above, temperature and salinity increased simultaneously below 50m. Therefore, it is not self-evident until now, whether the fish distribution in April 2002 is limited above by low salinity (12.8) or low temperature (5.1°C).

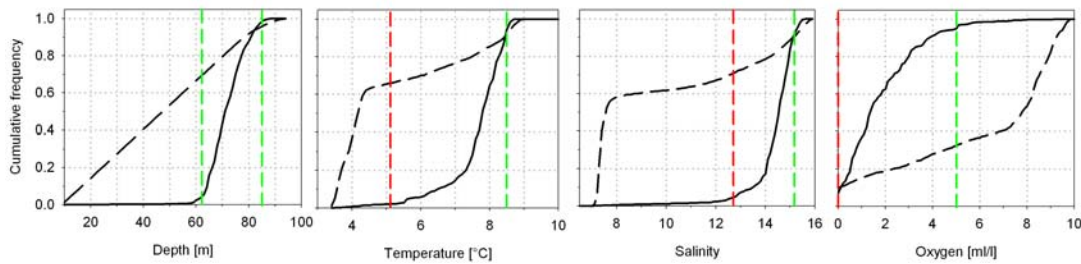


Fig. 5.6. Cumulative frequency plots of integrated fish-echoes (solid black lines) in relation to selected environmental parameters (dashed black lines). Shown are data from April 2002. Vertical dashed lines represent 5% thresholds for the cumulative frequency of integrated echoes, i.e. 90% of all fish echoes are between both vertical lines (Tab. 5.4). Thresholds, which are potentially limiting factors for the vertical distribution of sprat, are marked as red dashed lines.

The lower threshold for oxygen, found in April 2002, is not reasonable, as roughly 10% of all measured fish-echoes are found in water layers with no dissolved oxygen. It is assumed, that this is a sampling artefact.

The reason could be a relative high variability of the lower boundary of sprat distribution at some station in April 2002 (Fig. 5.5 left), probably caused by high variation of the depth at the beginning of the oxygen depletion zone. This will potentially result in a misfit between corresponding CTD casts, which are point measurements, and horizontal integrating echoes (integrated over 1nm). In addition, the oxygen content of the water decreased very rapidly at some stations. For example, the oxygen content of water at the station, shown in Fig. 5.5 (right), will rise acceptable limits shortly above the 0ml/l iso-oxygene. 4m above 0ml/l level, sufficient 1.4ml/l and 2m higher, 4ml/l oxygen were found. Briefly, oxygen values range from deadly to acceptable conditions within very few metres. Due to this steep decrease of oxygen-content, a mismatch of both profiles (echo and hydrography) of only few meters can result biased

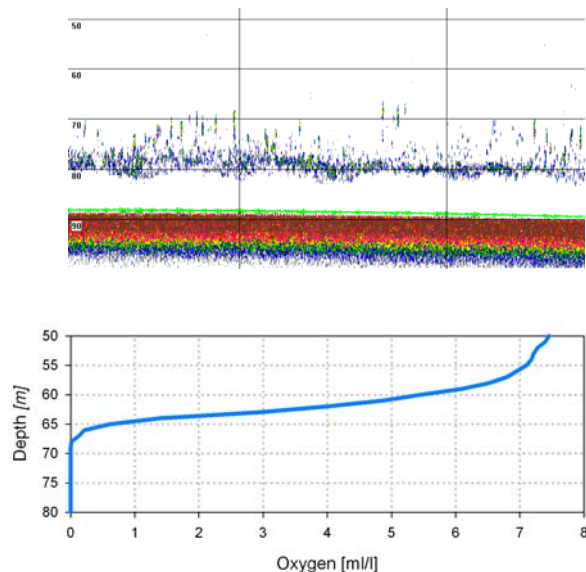


Fig. 5.5. High variability of depth of occurrence of oxygen depletion zone, as indicated by the lower boundary of sprat distribution. Upper panel: Echogram, showing the high variability in lower boundary of sprat distribution, as found on some stations in April 2002. Vertical lines are drawn every 1nm. Lower panel: Example of a vertical oxygen-profile, showing the steep decrease of oxygen content.

estimates for oxygen threshold. At other cruises, this high variability was not found. Therefore, the estimation of the lower boundary of sprat distribution is much more reliable and will be presented here, too.

As examples for such cruises, cumulative frequencies of May and August 2002 are shown (Fig. 5.7). The lower 5%-oxygen-

thresholds was estimated at 1.0ml/l for both cruises, which is in good accordance with most other cruises conducted during the GLOBEC-field phase.

The habitat selection as demonstrated with quotient plots (Fig. 5.8) serves the findings derived from cumulative frequency plots. The quotient-value is below the lower confidence interval, when habitat is (statistically) avoided. Therefore, the limits for distribution can be determined as

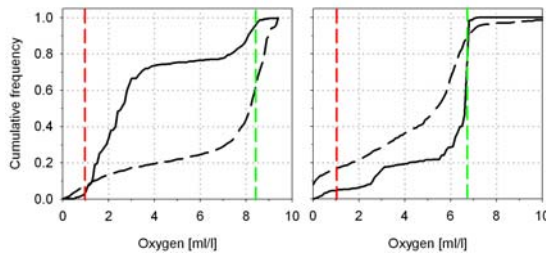


Fig. 5.7. Examples for ‘typical’ cumulative frequency plots of integrated fish-echoes (solid black lines) and oxygen (dashed black lines). Shown are data from May 2002 (left) and August 2002 (right). The vertical dashed lines represent 5% thresholds for the cumulative frequency of integrated echoes, i.e. 90% of all fish-echoes are between both vertical lines. Red dashed lines represent limiting oxygen thresholds for the distribution of sprat (in both cases 1.0ml/l).

Tab. 5.4. 5% thresholds of the cumulative frequency distribution as shown in Fig. 5.6. Potentially important limits are marked by (*).

	lower threshold	upper threshold
depth [m]	62	83
temperature [°C]	5.1*	8.5
salinity	12.8*	15.1
oxygen [ml/l]	0*	5

values of environmental parameters, were the quotient line crosses the lower confidence interval. In other words: The range of an environmental parameter can be defined as selected habitat, when the quotient-value of echoes at a given bin lies above the lower dashed, red line. If the quotient-value is above the upper dashed, red line, adult sprat prefer this habitat at a confidence level of 95%. Of course, the quotient plot related to oxygen suffers sampling problems, as discussed above, too.

So far, it can be summarized; that lower boundary of sprat distribution is defined by low oxygen-content of water (1.0 ml/l). The upper boundary could be salinity (12.8) or temperature (5.1°C), whereas it is not distinguishable, until now, which of these limits is relevant for sprat.

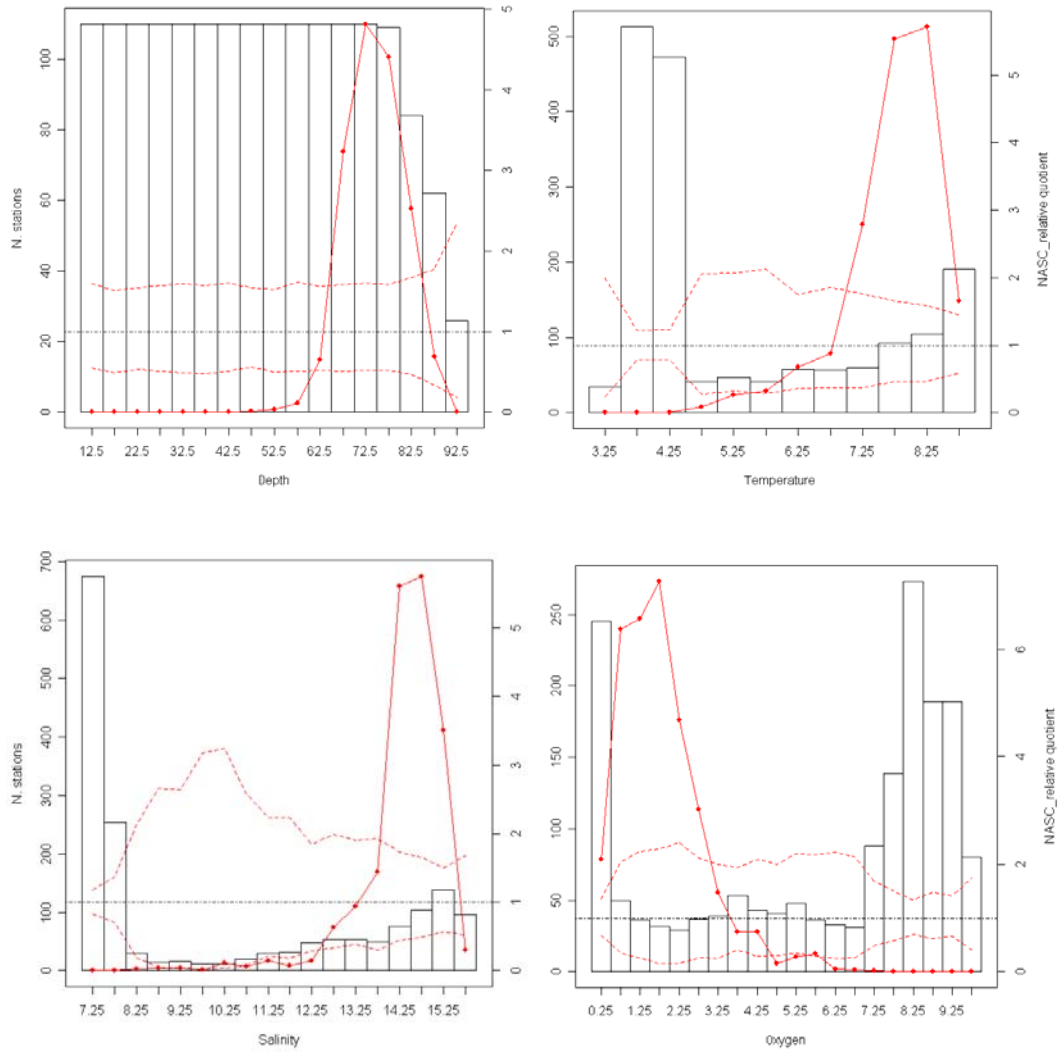


Fig. 5.8. Quotient plots of integrated fish echoes (solid red lines) in relation to the number of samples within a given bin of the environmental parameter (bar charts). Shown are data from April 2002. Quotient values above 1 (dashed horizontal lines) indicate selection of this habitat, and vice versa. Additionally the confidence intervals, derived from randomization procedure, were drawn (red dashed lines). Quotient values outside the confidence interval cannot be obtained by pure random alone at a 95% confidence level.

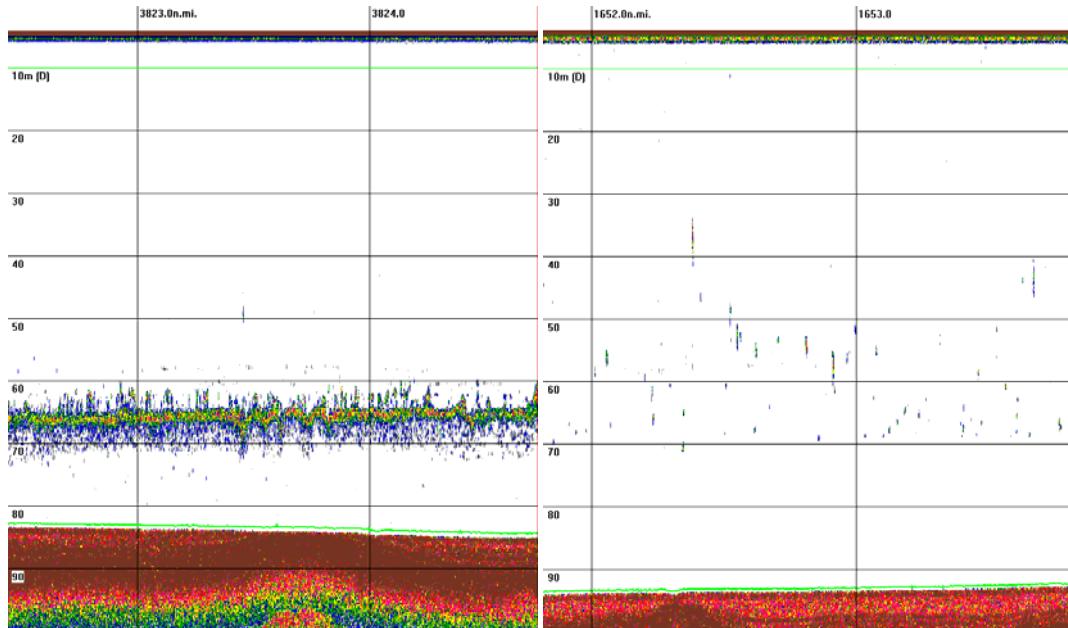


Fig. 5.9. Vertical distribution of clupeids in the central Baltic Sea - the season-factor. Shown are representative echograms from April 2002 (left) and August 2002 (right). Please note the dense layer of sprat between 60 and 70m in April 2002 and the much broader depth-range of distribution in August 2002. Red area below 80m represents the bottom. Vertical lines are drawn every 1nm, horizontal lines every 10m depth.

The relevant parameter for vertical distribution - temperature or salinity?

The pattern of vertical distribution of sprat changes between seasons (Fig. 5.9). In late summer (Fig. 5.9 right), the upper limit for vertical distribution is no longer relevant for sprat and sprat occupy a wider depth range, compared to spring. It is not clear whether this is due to changes in hydrography, spawning status, food supply or other seasonal changes in behaviour. Both distribution patterns are needed simultaneously to exclude seasonal effects. In May 2002 this situation was found at regular transect work during the German spring acoustic survey in northern Bornholm Basin (Fig. 5.10). A detailed description is given in chapter 4. Therefore, only the key-facts, necessary for the actual question are presented here.

Small-scale resolving measurements of hydrography showed a highly variable structure (temperature is shown in Fig. 5.10 mid). Along the transect a clear haline stratification was found with no extraordinary features, whereas for temperature and oxygen it is possible to distinguish three parts of the transect:

At the southern part of the transect, from the southern most point of the transect to 55.5°N a typical spring/early summer situation can be found with a warming of surface layers, cold intermediate water and increasing temperature below halocline. An oxygen-depletion zone was found above bottom. At the northern part of the transect, from the northern most point of the transect to 55.6°N the cold intermediate water is completely replaced by warmer and less saline

water. This displacement was caused by strong and persistent northerly winds during preceding days. An oxygen depletion was not found in this part of the transect. Between the northern and the southern part, an intermediate part was found, where the thickness of the cold intermediate water (marked by 5°C isotherm) decreased rapidly from south to north. Additionally the 1ml/l iso-oxygen turned toward bottom and reached it at approx. 55.6°N.

Distribution of fishes is highly connected to these meso-scale hydrographical structures. In those parts of the transect, where any of the cold intermediate water was left, the spreading of sprat into shallower water layers was inhibited by cold temperatures (Fig. 5.10 right). Therefore, it is shown, that temperature is the leading factor, which defines the upper distribution limit in early spawning time.

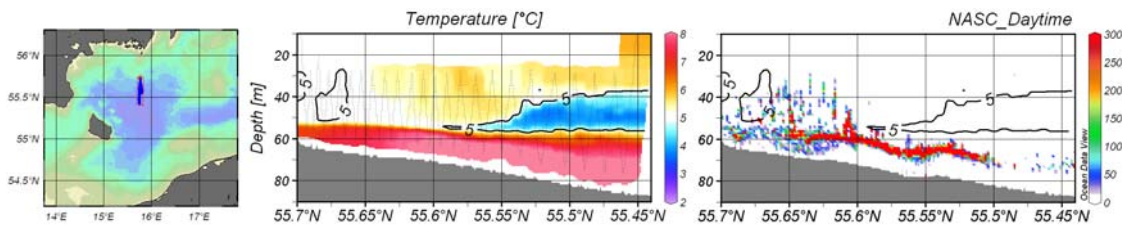


Fig. 5.10. Temperature prevents spreading of sprat into higher water layers. Temperature and corresponding condensed echogram along a transect in the Northern Bornholm Basin in May 2002 (cruise: WH239). Left: Map of the sampled transect; Mid: Temperature along the transect-slice, marked is the cold intermediate water in the southern part of the transect; Right: Condensed echogram during daytime, overlaid with 5°C-isotherme. Given are integrated echo-values (NASC-nautical area backscattering coefficient). Note the narrow band of fish echoes (mainly sprat) in the southern (right) part of the transect and the spreading in the northern part. For more detail, please refer to chapter 4.

Implications for sprat distribution in April 2002

Applying 5°C temperature and 1ml/l oxygen content as limiting parameter to the basin wide distribution of pelagic fishes (98% sprat) in April 2002 it becomes clear, that sprat were trapped between cold intermediate water and oxygen-depletion zone (Fig. 5.11). This becomes very clear at the margins of the basin, where isotherms contacted the slope of the basin (Fig. 5.12). This capture of sprat in the deep basin, caused by low temperatures in the mid water, is reflected by the horizontal distribution shown in Fig. 5.4. The majority of sprat was found in the rectangles, which cover to deeper Bornholm Basin.

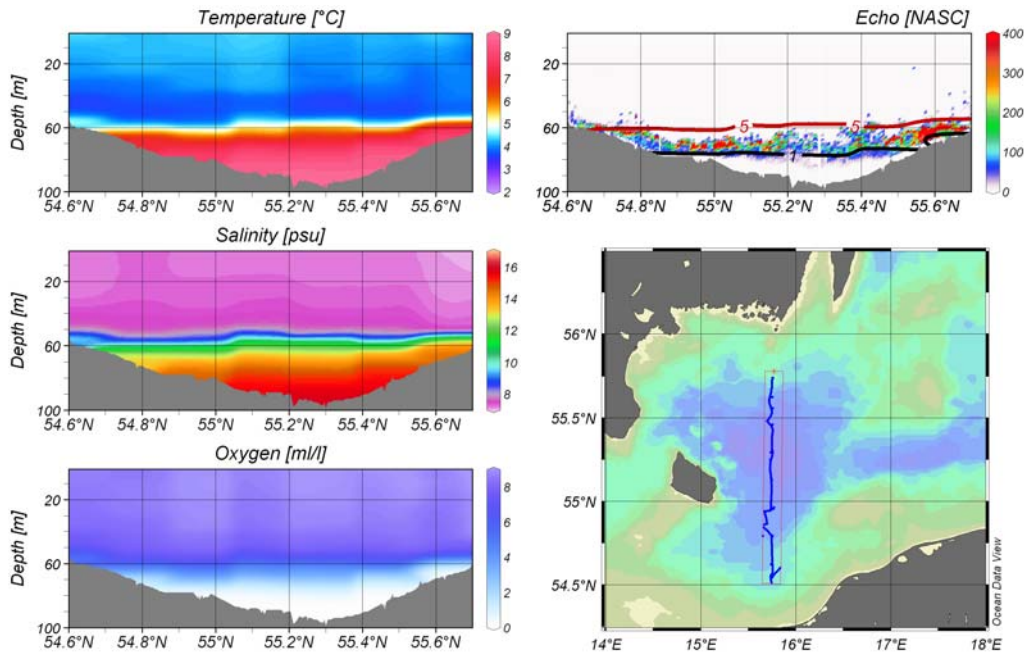


Fig. 5.11. Slices of hydrography and the corresponding condensed echogram in April 2002 (during daytime) along a transect, crossing the Bornholm Basin (see Map). Left panels: Hydrography; Right panel: Condensed echogram, overlaid with contour lines of limiting parameters (temperature: 5°C and oxygen: 1ml/l). Given are integrated echo-values (NASC – nautical area backscattering coefficient [m^2/nm^2]).

Modelling the vertical distribution of sprat

The developed model for the vertical distribution of sprat was applied to the data of April 2002 (Fig. 5.13). Modelled and measured vertical distribution are in good agreement, hence the model adequately describes the overall pattern of sprat vertical distribution in early spawning time. During the optimization of the model (Fig. 5.14) minimum differences between real and modelled vertical distribution were found at a temperature-threshold $T_{50}=5.1^\circ\text{C}$ and oxygen content $Ox_{50}=0.9\text{ml/l}$. This strongly supports the findings of the investigations regarding habitat selection. Despite a good model-fit for the hydrographic situation in spring, the predicted vertical distributions for other seasons differ from observed patterns. Fig. 5.15 shows examples for May 2002, when summer thermocline developed in the surface layer. Since temperature in this layer was higher than 5°C, the model predicts a partial moving of sprat into the warm surface waters.

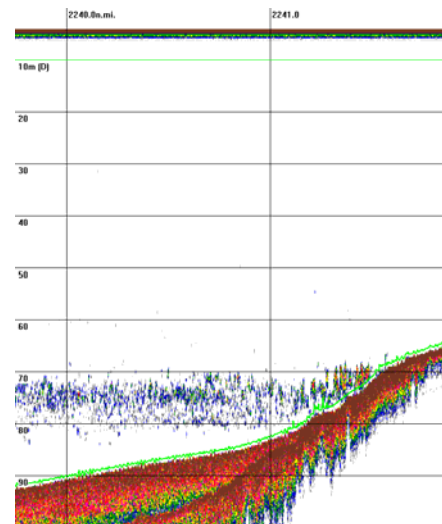


Fig. 5.12. Sprat is trapped below the cold water: Shown is an example echogram from the margin of the Bornholm Basin in April 2002. Vertical lines are drawn every 1nm.

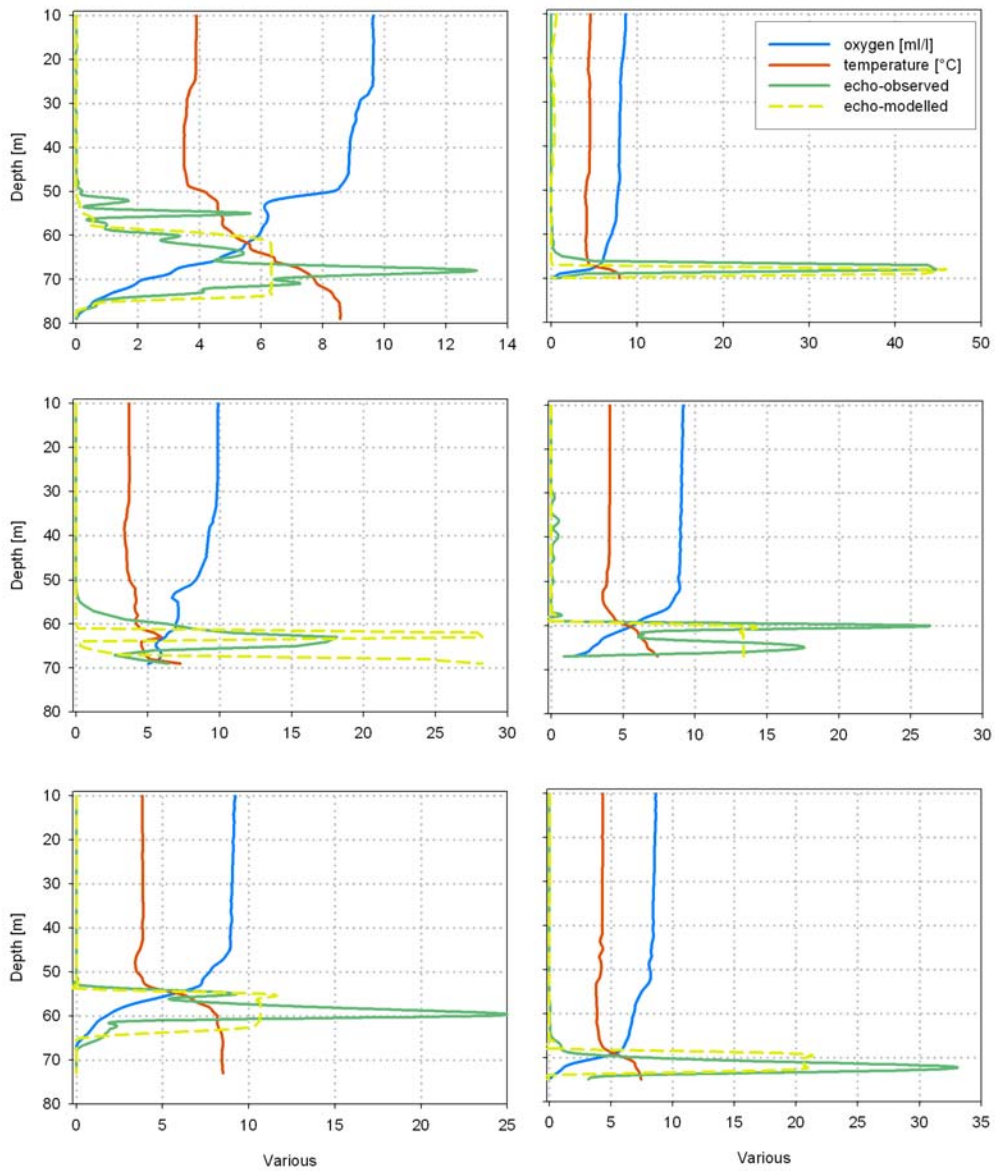


Fig. 5.13. Modelled and observed vertical distribution of sprat in relation to temperature and oxygen. Shown are six profiles from deeper Bornholm Basin in April 2002 (cruise: AL200). Echo profiles are relative measures.

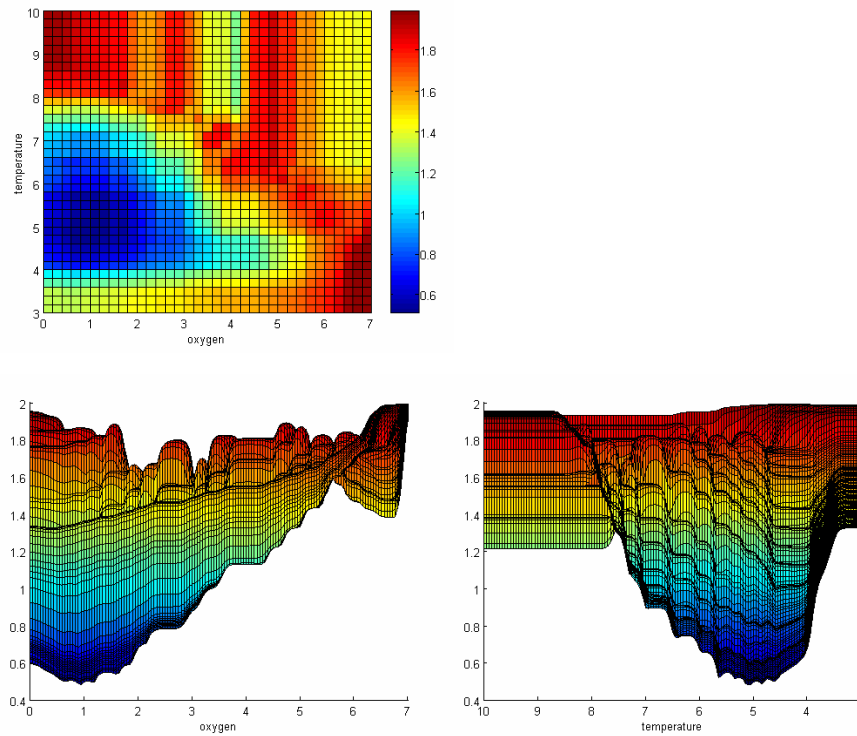


Fig. 5.14. Visualisations of the model-optimization, shown is an error index, calculated from the difference between observed and modelled vertical distribution of adult sprat in April 2002. Top: 2D-contour plot; Lower panel: 3D-side-views along the temperature and oxygen-axis.

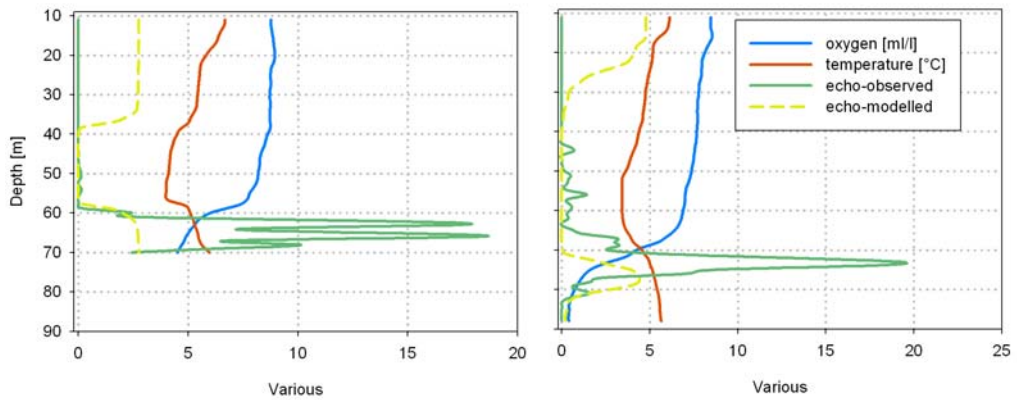


Fig. 5.15. Modelled and observed vertical distribution of sprat in relation to temperature and oxygen. Shown are profiles from deeper Bornholm Basin in May 2002 (cruise: WH239). These profiles are chosen to illustrate the limitation of the used simple model-approach (see text for details).

5.5. Discussion

The aim of the present study was to investigate, which environmental parameters influence the vertical daytime-distribution of sprat in the central Baltic Sea. For that purpose, hydroacoustic measurements were combined with profiles of hydrography, resulting in a unique data set of vertical distribution pattern directly connected to hydrography. The findings were used to develop a simple model of the vertical distribution of sprat during early spawning time in stagnation periods.

Habitat thresholds for adult sprat were estimated using a dataset from spring (April 2002), since the abundance of other pelagic fish species in Bornholm Basin was almost negligible during that season. The largest fraction of the herring population concentrates at coastal areas during that time, whereas cod have not started migration into the deep basins for spawning (Aro 1989). Later in the season, herring and cod considerably occupy the deep Basins of the Baltic for feeding (herring) or spawning (cod) and a substantial fraction of sprat migrate into shallower waters (Aro 1989, Hoziosky 1989). Consequently, the proportion of sprat echoes will decrease and echoes, not caused by sprat, may bias the investigation of sprat vertical distribution derived by hydroacoustics.

The overall hydrographical situation during the investigation was typical for the Bornholm Basin in stagnation periods (except for April 2003, see description below) with a clearly distinguishable halocline and decreasing oxygen content with depth, resulting in an oxygen-free layer above the bottom (Matthäus and Franck 1992). The temperature-profiles varied between cruises, but were consistent with previous observations of thermal mixing above halocline, due to the cooling of surface waters in winter, followed by re-establishing of thermal stratification during spring and summer (Møller and Hansen 1994, Tomkiewicz *et al.* 1998, Gröhsler *et al.* 2000).

As known from previous investigations (e.g. Orłowski 1991, Gröhsler *et al.* 2000, Szczucka 2000, Neuenfeldt and Beyer 2002) clupeids stay below the halocline during daytime. However, environmental factors are often correlated. For example, oxygen usually decreases with depth, which suggests that the avoidance of a certain depth range may also be caused by an avoidance of low oxygen conditions. In our case (April 2002), temperature and salinity increased simultaneously below the halocline, whereby it was not obvious whether salinity or temperature defined the upper boundary for the distribution. In this study, the influence of temperature on the vertical distribution of sprat was confirmed.

Additionally, the limiting influence of low oxygen-content was demonstrated and ratified. It was shown before, that clupeids are capable to inhabit water with very poor oxygen content. Dommasnes *et al.* (1994) found high concentrations of Norwegian spring-spawning in areas with only 1-2ml/l dissolved oxygen. Additionally several authors reported about a limitation of sprat habitat by 1ml/l to 1.5ml/l (e.g. Rechlin 1975), however these statements are only anecdotal.

The modelled vertical distribution of sprat is in good agreement with the observed distribution in April 2002. Despite its simplicity, the developed model is able to give a realistic sketch of sprat vertical distribution at spawning times, at least in stagnation years. Therefore, it is an improvement to previous model approaches of sprat vertical distribution, e.g. to Andersen and Möllmann (2004), who assumed a fixed depth range right above the oxygen depletion zone.

They do not taken into account possible environmental variables which defining the upper limit of distribution.

Nevertheless, the presented model only uses oxygen and temperature as input variables. If these are the solely relevant parameters, the application to other hydrographical situations should deliver meaningful results, too. If this fails, other parameter, which modify the proposed temperature response should be taken into account.

Often it is assumed that fish distribution usually follow a temperature optimum (Magnuson and Beitinger 1985; Rudstam and Magnuson 1985), while other factors can force the fish to inhabit other temperatures (Fig. 5.1). These factors could be light, oxygen and social interactions. The optimal method to define such preferred ranges are experiments, where only one parameter is modified and the organisms of interest have to choose their preferred range of occurrence (i.e. temperature gradient chamber). Unfortunately, it is not easy to extract the preferred ranges of a given parameter from field investigations, because the interaction with several parameters influences the distribution of fish. An experimental approach to test for a preferred temperature of clupeids is not trivial, due to their sensitivity and extremely high mortality rate in captivity.

The modifications of a possible temperature preference can be seen when data from other seasons and years were taken into account. For example, in May 2002 when the upper water layer began to warm up, a pure temperature-driven sprat population should inhabit this upper water layer, too (Fig. 5.15). However, they did not. Another example from April 2003 is characterized by a completely different hydrographic situation (Fig. 5.16), while it is in the same season. In Winter 2002/2003 a major Baltic inflow of haline and oxygen-rich, but very cold water occurred. As a result, no oxygen limitation of sprat distribution and very low temperatures over the whole water column were found. The temperature ranged between 3.6 and 2.6°C, whereby highest temperatures were found in the upper water layer and right above the bottom. This situation had two effects on the sprat population: On the one hand, the abundance in the Bornholm Basin was much lower, compared to 2002 (see chapter 1). A later cruise (in May 2003) with RV 'Walther Herwig III' revealed a decrease in Bornholm Basin sprat abundance and an increase of the sprat abundance in the Gotland Basin and Gdansk Deep (Böttcher and Götze 2004), where higher temperatures below halocline were measured (Fig. 1.2). On the other hand, the fraction of the sprat population, which remains in the Bornholm Basin, was confronted with temperatures lower than 5°C, which was determined as distribution limit. This indicates that sprat is able to live outside a preferred temperature, if necessary. Interestingly sprat occupied again the deeper water layers (Fig. 5.17).

For the given examples of May 2002 and April 2003, the model implementation failed. This strongly indicates that other factors should be included.

The most obvious candidate factor is light, whereby two different processes of the influence of light on behaviour were discussed. Several author assumed, that fish follows a given light level (preferendum) (e.g. Woodhead 1966, Nilsson *et al.* 2003), whereas others supposed an influence of changing light intensities, which can be found (e.g.) during sunset and sunrise. The concepts of light as trigger for vertical migration will be discussed in more detail in chapter 6.

The factors, which are described until now, influence behaviour in a direct manner. For instance, when fish follow a given light level or move toward a temperature optimum. In

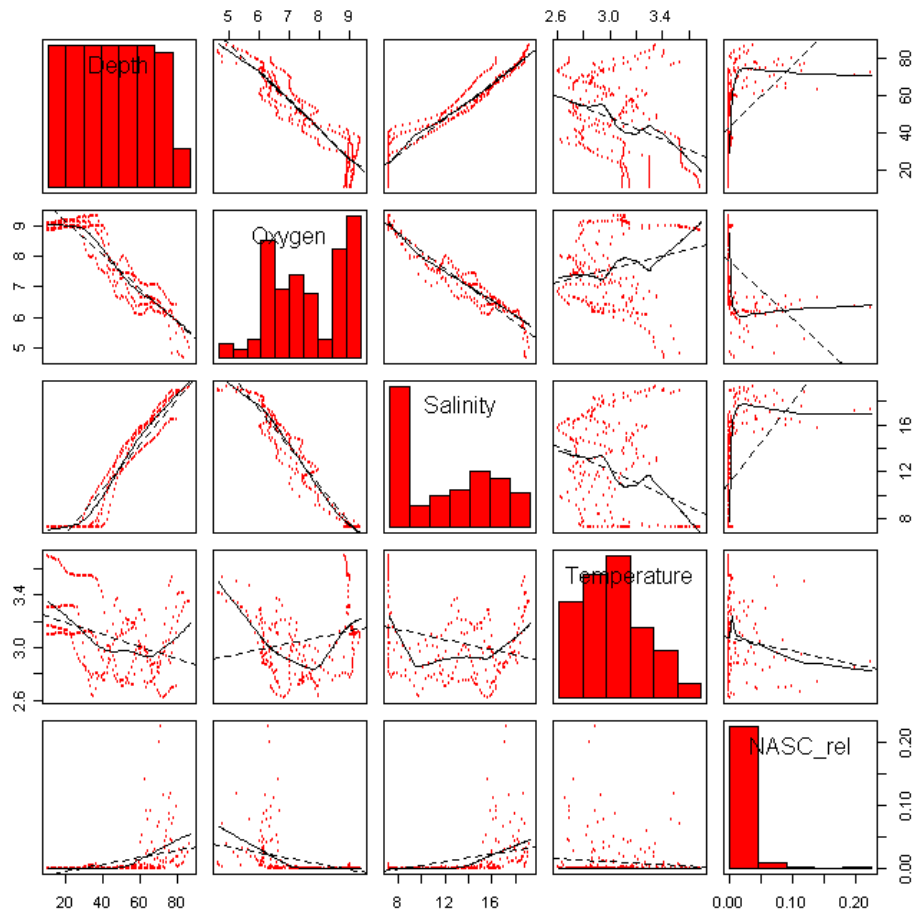


Fig. 5.16. Scatterplot matrix of environmental and echo data in April 2003. In the boxes along the diagonal, histograms of frequencies for every bin of analysed parameter are shown. The scatterplots contain fitting curves. The dashed line is calculated with the least-square method, whereby the solid line represents a smooth of the scattered data.

contrast, the temperature gradient cannot induce a migration behaviour, nevertheless it acts while preventing behaviour induced by other factors. Schubert (1950) reported that the upward movement of North Sea herring through thermoclines is inhibited by a temperature gradient of $6^{\circ}\text{C}/3\text{m}$ ($=10^{\circ}\text{C}/5\text{m}$), whereas no effect was registered at $2^{\circ}\text{C}/3\text{m}$ ($=3.3^{\circ}\text{C}/5\text{m}$). Other authors approved an influence of the thermal stratification on the migration behaviour of clupeids (e.g. Richardson 1952). Nevertheless, the herein presented data do not allow to determine the influence of the temperature gradient. This task is discussed in chapter 4.

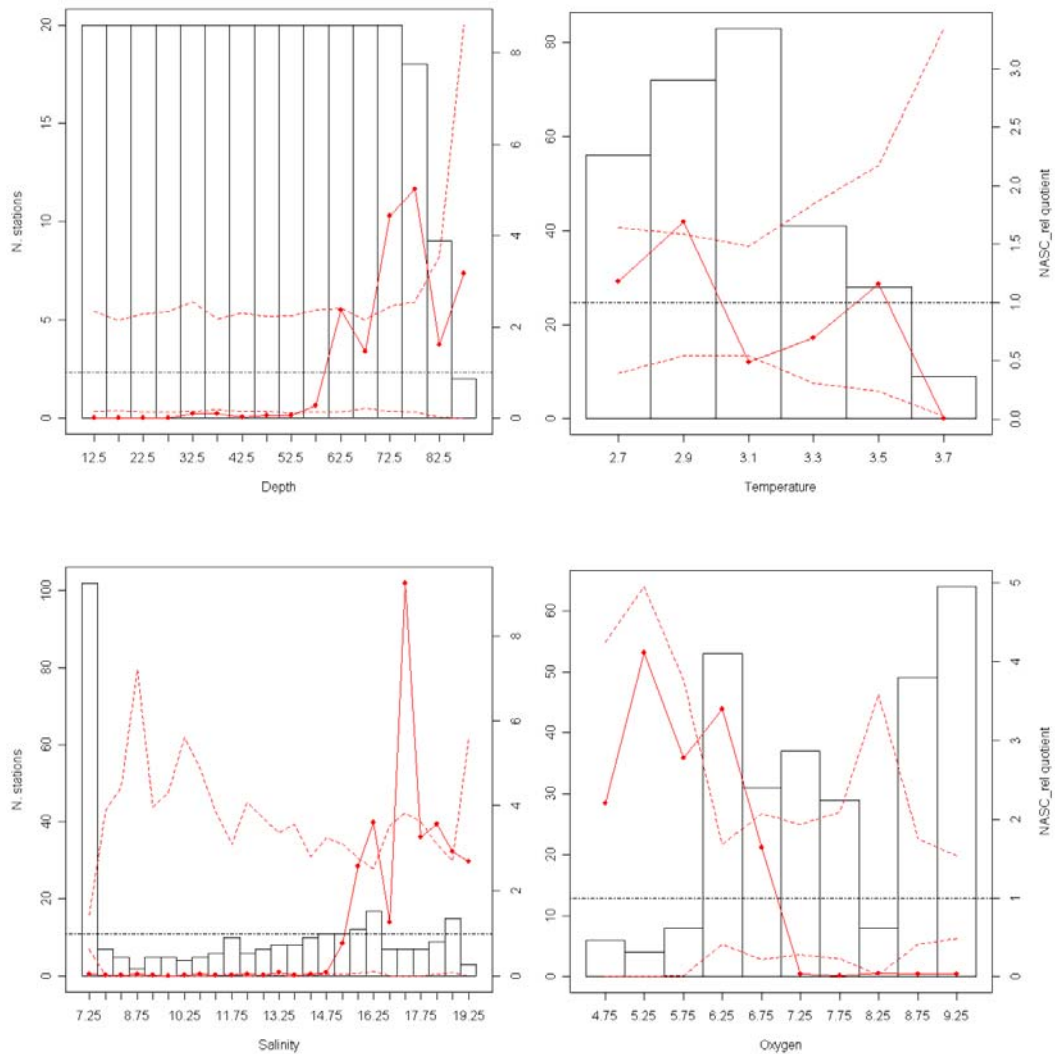


Fig. 5.17. Quotient plots of integrated fish echoes (solid red lines) in relation to the number of samples within a given bin of the environmental parameter (bar charts). Shown are data from April 2003. Quotient values above 1 (dashed horizontal lines) indicate selection of this habitat, and vice versa. Additionally the confidence intervals derived from randomization procedure were drawn (red dashed lines). Quotient values outside the confidence interval cannot be obtained by pure random alone at a 95% confidence level.

Beside shown limitations of the applied model, the findings of this study provide an essential basis for the understanding of the vertical distribution of adult sprat, which has ecological implications, too. Due to a strong stratification of the Baltic Sea, environmentally defined thresholds and preferences for occurrence can determine the distributional overlap of species (Möllmann and Köster 1999, Köster and Möllmann 2000). The habitat of sprat, as found in this study, heavily overlaps with the potential habitat of Baltic cod. The environmental thresholds of cod are determined by oxygen and salinity (Neuenfeldt 2002, Neuenfeldt and Beyer 2002) whereupon the upper limit of sprat distribution is defined by temperature. This implies that sprat

is potentially heavily exposed to its main predator cod when water above halocline is too cold to allow a spreading of sprat into shallower water. Whereas later in the season, the predator-prey overlap will decrease due to an upward movement of sprat.

The possible influence of other environmental factors has to be investigated in following field studies. Additionally, a more complex model has to be developed to include other parameters than temperature and oxygen. With such a kind of model, the influence of other potentially important factors could be confirmed.

5.6. *Acknowledgements*

I like to thank Miguel Bernal from the IEO (Instituto Español de Oceanografía) for supplying the R-package 'shachar' and the support on it.

6. Modelling the vertical distribution of adult sprat in the central Baltic Sea

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6.1. Abstract

In this chapter, a model approach was introduced, which aims to describe the vertical distribution of adult sprat. The behaviour of sprat was parameterized by behavioural rules, which are calculated for every external stimuli, taken into account. Different migration behaviour, estimated for environmental factors, were weighted by their relative importance, using so-called evaluation functions. Physical properties, used for this model approach, were temperature, temperature gradient, oxygen and light, whereby the implementation of light induced behaviour is discussed in detail.

To test the model, simulations were carried to compare model results with real vertical distribution pattern, as derived from field observations. A dataset, which describes the diel vertical migration in May 2001, was used for this purpose. The modelled vertical migration showed very good agreement with observed patterns. Minor discrepancies were noted, but are probably caused by problems when calculating the surrounding light levels. This model has to be ratified by comparison with other observations. Nevertheless, it became clear, that this approach has high potential, due to its good parameterization and straightforward implementation. In that way, it should be incorporated into ecosystem models to enhance habitat overlap calculation between sprat and its prey and its main predator cod.

6.2. Introduction

The investigation and modelling of fish distribution is an important topic in ecosystem research, since fish is a main fraction of upper trophic levels in many marine ecosystems. Fish has a significant influence on lower trophic levels (Rudstam *et al.* 1994, Parmanne *et al.* 1994, Kornilovs *et al.* 2001, Möllmann *et al.* 2004), or can be controlled by fish or other predators of higher trophic levels than itself (Sparholt 1994).

Anyhow, ecosystem models often truncate the food web at the trophic level of zooplankton (e.g. Fennel 2001, Denman 2003, Woods 2005, Neumann and Fennel 2006, Tian 2006) or assume fish as uniform distributed predator-group (e.g. Dzierzbicka-Glowacka 2005). The latter results in problems for determining predation rates caused by higher trophic levels (Fennel and Neumann 2004); whereas other reasons for zooplankton mortality, for example environmental

conditions and food availability, are often included. On the other hand, Baltic multispecies stock models (like Multi-species-virtual population analysis – MSVPA) do not take into account the vertical distribution of the modelled fish species. Until now, a constant suitability factor is used in the Baltic MSVPA to parameterize the interspecific interaction.

The abundance of species in the food web is not the exclusive driving factor for trophic interactions. Other major factors are heterogeneity and patchiness along temporal and spatial scales, which are common for all ecological systems (Haury *et al.* 1978, Mason and Brandt 1999). This heterogeneity partly defines the spatial overlap of species and hence their possibility of interaction.

Spatial models of fish distribution often deal with horizontal migration, depending on horizontal patterns of factors governing the migration (such as temperature, salinity) or physiological reasons (such as feeding and spawning). Such a horizontal spatial model of Baltic sprat was described by Aps *et al.* (1987). Contrariwise, the vertical patterns of the environment and a resulting vertical distribution of fish is mostly not taken into account (e.g. Magnússon *et al.* 2004). Only few models of vertical distribution are published (Rudstam and Magnuson 1985, Bigelow *et al.* 2002).

The migration of fishes can be modelled in a variety of ways (Magnússon *et al.* 2004). At one hand, physiological fitness functions could be optimized (Fiksen *et al.* 1995), alternatively as dynamical system for individuals or as continuous density models. Both approaches are typically implemented with difference equations or differential equations (e.g. Okubo and Levin 2001). In this study, an approach similar to a transition matrix was used, whereas the elements $a(i,j,t)$ are the fraction of fish in cell i_j at time step t , which migrate to cells $i_{t+1}j_{t+1}$ at the next time step (Tjelmeland and Bogstad 1998). The transition-matrix is calculated as response of environmental parameters.

The predation pressure by visual oriented predators, calculated as response to environmental light conditions, is a common approach to quantify a predator dependent mortality. This approach neglects the vertical distribution of predators (e.g. Neumann and Kremp 2005). This approach usually fails in the central Baltic Sea, because high predation is calculated in the upper surface layers, whereas fish often occupy exclusively deeper water layers (see chapter 4 and 5).

Other authors took into account the vertical inhomogeneous distribution of predators. Andersen and Möllmann (2004) modelled the process oriented egg mortality for central Baltic Sea cod (*Gadus morhua callarias* L.). For sprat, they assumed a distribution over a restricted depth range, right above the oxygen depletion zone. While for some purposes and seasons, this will give a good approximation (and is therefore acceptable, the more so as it is easy to implement), this approach neglect several important factors, determining the vertical distribution of sprat.

Especially in the Baltic Sea, the vertical distribution is not homogeneous, due to pronounced vertical gradients of environmental parameters. Some of the hydrographical factors, influencing the vertical distribution of sprat in the central Baltic Sea, are described and discussed in chapter 4 and 5. Nevertheless, the influence of light was not discussed until now. With regard to the model approach, used in this paper, the possible influence of light on the vertical distribution of sprat has to be discussed, especially in the case of the diel vertical migration (DVM).

Often it is believed, that DVM of aquatic animals is an example for circadian rhythms, a kind of endogenous rhythm with a period of approximate 24h. External triggers synchronize most endogenous rhythms (Aschoff 1965, Takahashi and Zatz 1982). Potential triggers in marine environment are natural cyclic phenomena, like light, tides, and annual temperature changes. Several triggers are discussed for DVM (review by Neilson and Perry 1990), whereas light has attracted the greatest attention. Nevertheless, there is some experimental evidence, that there is no endogenous rhythm in the DVM of marine fish, but light acts upon the diel rhythm in a direct fashion (Blaxter 1975, Neilson and Perry 1990).

Two hypotheses are discussed for the question 'how light acts on the vertical distribution of fish' (Fig. 6.1). On the one hand several authors report that fish follow an optimum light level, which results in vertical migration (e.g. Woodhead 1966, Nilsson *et al.* 2003). This theory is illustrated in Fig. 6.1 (left column). The light-profile in the water column (Fig. 6.1 left, mid panel) induces behaviour of fish to move to a preferred light level or light range (Fig. 6.1 left, lower panel). This illustration is based on an idealized diel cycle of global radiation without noise in light level, e.g. induced by variations of cloud coverage. Other authors did not support this theory, but supposed that changes in brightness or sunrise and sunset itself induce migration behaviour (Blaxter 1975). In Fig. 6.1 (right column), this behaviour is shown for sunrise and sunset.

For the present study, the hypothesis of an optimal light range was applied. This was chosen following Neumann and Fennel (2006), who introduced this type of model for the vertical migration of zooplankton. Additionally in a quite recent study (Nilsson *et al.* 2003) it was concluded that clupeids in the Bornholm Basin followed an isolume during their upward migration at dusk.

At present, there is no model for the vertical distribution of sprat in the Baltic Sea, which goes beyond the concept presented by Andersen and Möllmann (2004). Consequently, the model was implemented to 1) test findings of previous chapters about the factors, determining the vertical distribution of sprat and 2) to go one-step onward to incorporate the vertical distribution of sprat into 3D ecosystem models of the Baltic Sea. This would (e.g.) enhance the precision of modelled mortality rates of copepods as caused by sprat predation.

In this paper, a model for the calculation of the vertical distribution of sprat, is presented. For test purposes, the model was applied to a specific dataset, collected in May 2001.

6.3. *Material and Methods*

General description of the method

The used model is adapted from Neumann and Fennel (2006). The aim of the model is to represent behaviour of sprat in the central Baltic Sea, which will influence the vertical distribution and hence the diurnal vertical migration of sprat. The model is a process model in which a simple population of free-swimming sprat is considered. Growth and mortality rates are neglected.

In contrast to zooplankton, where this kind of model was introduced (Neumann and Fennel 2006), several aspects has not to be taken into account while modelling the behaviour of adult fish. For instance, the migration of adult fish is usually not significant influenced by advection and turbulence. Additionally, at least for vertical migration, no different migration speeds have to be used for different size-classes (as should for stage resolving copepod models), although a wide range of vertical migration speeds of clupeids is given literature (Tab. 6.1).

In this model, oxygen, temperature, vertical temperature gradient and light were used as stimuli for the vertical migration of sprat. Since temperature gradient is a relative measure, the estimation procedure has to be described. The sign of the calculated value indicate the direction of the gradient. The vertical temperature gradient was calculated at depth z ($tempgrad_z$) as [$^{\circ}\text{C}/5\text{m}$]

$$1) \quad tempgrad_z = (temp_{z-1} - temp_{z+1}) * 5 / |z_{z-1} - z_{z+1}|$$

The modelled vertical distribution of sprat, as described in chapter 5, is a result of the combination of probabilities of occurrence. In contrast, the model, presented in this chapter, is stimulus induced and hence a 'real' reaction. The definition of functional relationship between stimulus and reaction are adjusted after plausible arguments and/or observations. For instance, oxygen depletion is a phenomenon of the bottom layer in the Baltic, therefore the only possible way to reach better oxygen condition is to move upward. Alternatively, due to increasing light intensities with decreasing depth, sprat has to swim upward when the surrounding light level falls below the acceptable range.

Tab. 6.1. Collection of references and data about the vertical migration speed of clupeids. Early references are extracted from Blaxter and Holliday (1963).

reference	species	stage	Area	type	direction	speed
Runnström 1941	herring	adult	atlanto-scandian	field	upward	100m/h=1.7m/min
Kreffth and Schüler 1951	herring	adult	North Sea	field	upward downward	75m/h=1.25m/min 200m/h=3.3m/min
Blaxter and Parrish 1958	herring	adult (15-25cm)		field/experim.	upward	13.5m/min
	herring	adult (15-25cm)		field/experim.	downward	36m/min
	sprat	5-15cm		field/experim.	upward	30m/min
Dragesund 1958	sprat?	adult		field/experim.	upward	15m/45min=0.3m/min
Stepputtis 2001; see chapter 10	sprat and herring	adult	Baltic	field	downward	4m/min

The final vertical migration speed (w_{fin}) of sprat at each model grid cell will be represented by the result of a maximum speed (w_{max}), which was set to 1 vertical grid cell/model-time-step which was modulated by a behavioural component (w_{behav}) within the range of -1 to 1. As a result the maximal range of w_{fin} is (of course) -1 to 1 grid cell per time-step, too. Hence, it is not possible for modelled sprat to overjump a grid cell, therefore model integrity is guaranteed. The necessary restriction of the migration speed requires a high temporal resolution of the model to resolve short-term events, such diel vertical migration in an adequate manner.

$$2) \quad w_{fin} = w_{max} w_{behav}$$

The behavioural component depends on the physical factors temperature, temperature gradient, oxygen and light (Tab. 6.2, Fig. 6.2). It incorporates 'real decisions' made by the fish, such 'if the oxygen level is lower than a specific level, move upward'. Decisions in natural populations are seldom switch function with sharp edge and no transition zone. Therefore, the knife-edge function was replaced by a function with transition along the parameter axis. The transition was chosen as linear change between a lower limit (LL) and an upper limit (UL). Below the lower limit and above the upper limit, the decision is fixed (Tab. 6.2, Fig. 6.2). Rules for all relevant factors were formulated as factor functions (f_i) (Tab. 6.2, Fig. 6.2), whereby a positive result for that specific parameter will indicate a proposed upward movement, while a negative value indicate a downward directed response (after Fennel and Neumann 2006).

Tab. 6.2. Parameters used for factor functions (f_i) and evaluation function (E). Note: When summing all g_i , light has to be considered only ones, so the sum is 1.

f_i	lower-limit (LL)	upper-limit (UL)	behaviour induced, if parameter...	direction of behaviour	g_i
oxygen	0.2ml/l	0.7ml/l	...falls below limits	upward	0.52
temperature	3°C	5°C	...falls below limits	downward	0.14
temperature gradient	-4°C/5m	-1.5°C/5m	...falls below limits	downward	0.14
light (1)	0.005 lx	0.1 lx	...falls below limits	upward	0.20
light (2)	10 lx	200 lx	...exceeds limits	downward	0.20

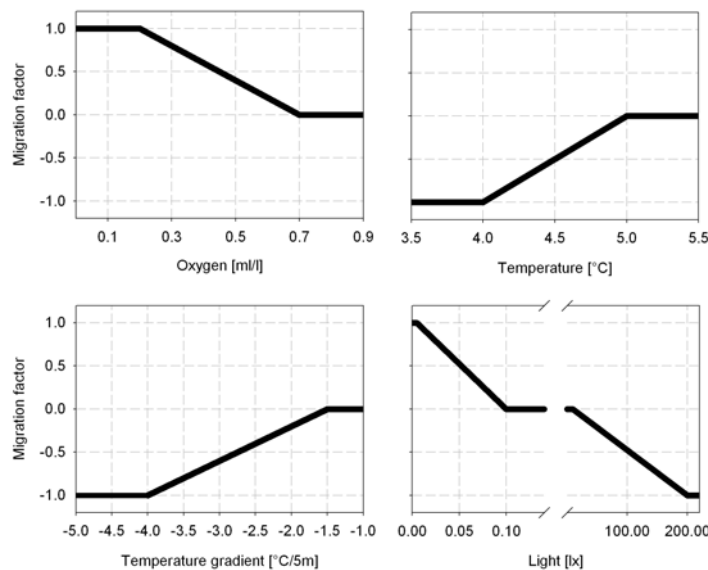


Fig. 6.2. Illustration of the factor functions (f_i) for all parameters, taken into account for the modelling the vertical distribution of sprat in the central Baltic Sea.

It is assumed, that the temperature gradient has no effect on the migration behaviour of adult, when water temperature is higher than 5°C (see chapter 4), hence $f_{tempgrad}$ was set to 0 if ambient temperature was higher than 5°C.

It is possible to get conflicting responses from factor functions (f_i) calculated for different parameters. Consequently, the next step is to calculate a resulting 'decision'. To handle conflicting situations, all parameters were weighted by their relative importance (g_i) combined in an evaluation function (E).

$$3) \quad E = g_1 f_1 + g_2 f_2 + \dots + g_n f_n$$

A list of weights for all factors is summarized in Tab. 6.2

To include some demographic noise or random behaviour of sprat and to smooth the induced behaviour, w_{behav} is calculated as limiting function. The stochastic element is necessary to enforce the modelled sprat to occupy the suitable habitat (compare Fig. 6.7 left and right).

$$4) \quad w_{behav} = \frac{(\xi_d + E)|\xi_d + E|}{h + (\xi_d + E)^2}$$

E is the output from the evaluation function and h is a 'half saturation'-parameter ($h=0.1$). A random number (ξ_d) induces the noise. Neumann and Fennel (2006) have chosen a random number in the range from -1 to 1 with a uniform distribution, resulting in very strong fluctuations. Here a random number taken out of a normal distribution with mean=0 and standard deviation=0.1 was used (Fig. 6.3 left). A Comparison of randomizations with uniform and normal distributed random numbers (Fig. 6.3 mid panel) and resulting transitions from E to w_{behav} (Fig. 6.3 right) are shown.

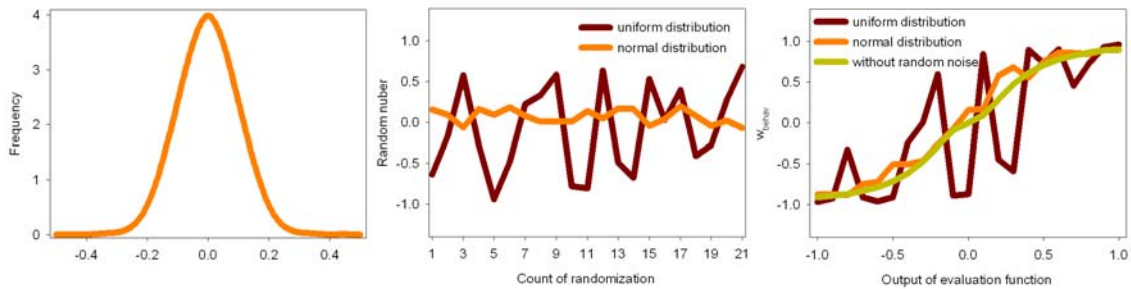


Fig. 6.3. Introduction of noise into the modelled behaviour of sprat. Left: Chosen normal distribution for randomization. Mid: Example for a series of randomizations were random numbers are uniformly distributed between -1 and 1 (as supposed by Fennel and Neumann 2006) and normal distributed around 0 (as used in this work). Right: Examples for calculation w_{behav} with randomization numbers as shown in the mid panel and without randomization.

The calculated behaviour was applied in a straightforward manner to the modelled sprat population. The model was initiated with a uniform distribution of sprat over all depth layers, i.e. each depth in the profile as the initial value $fish_{toz} = 1$. After the calculation of w_{fin} for every depth layer, the migration of sprat was calculated as relative change of 'abundance' between time steps and depth layers.

As mentioned above, the direction (dir) of migration is given by the sign of the calculated migration speed (w_{fin}).

$$5) \quad dir = sign(w_{fin})$$

For an easy implementation, the value of w_{fin} was treated as percentage of sprat, which will move to another depth in the next time step. Assuming $w_{fin} = 0.8$, 80% of all sprat at depth z at time (t) will move to the next deeper depth-layer in the next time step ($t+1$). The arriving sprat were, of course, added to the other sprat at this grid cell.

$$6) \quad fish_{(t+1)(z-dir)} = fish_{(t+1)(z-dir)} + fish_{tz} * |w_{fin}|$$

The non migrating part (in our example 20%) were moved to the same depth of the next model time step.

$$7) \quad fish_{(t+1)z} = fish_{(t+1)z} + fish_{tz} * (1 - |w_{fin}|)$$

The presented formulation of the behaviour response has the advantage of simple incorporation into computer languages. The response has to be calculated only once per model-step (time-or space-step) for every depth of the profile. The presented implementation was done in MATLAB (MATrix LABoratory) (The Mathworks 2005), which offers a further simplification by the possibility to run calculation for complete vectors and matrices.

Preparation of field data

For demonstration and testing purposes, the vertical distribution and the diel vertical migration of sprat was modelled for a hydrographic situation with known responding behaviour of sprat, as indicated by sprat distribution. While a detailed description is given in chapter 10, a short summary of the sampling and the preparation of data will be given here. The field data are collect during an intensive field study in June 2001 in the northern Bornholm Basin.

Hydrography

For modelling purposes the CTD-O₂ profile, shown in Fig. 10.4c (on page 137) was used for the simulation as constant profile over time. The profile was set to 2m vertical resolution. In addition to measured parameters (temperature, salinity and oxygen), the temperature gradient at each depth was calculated as difference between both surrounding cells and then standardized to temperature gradient per 5m [°C/5m] (see model description). The gradient of the top and the most lower depth was set to 0°C/5m.

Light

The vertical migration of clupeids is light induced, hence light profiles for every time step were needed. Since underwater light measurements during 48 hour sampling in June 2001 were not conducted with a sufficient equipment and temporal resolution, profiles have to be calculated. The vertical profiles of light were calculated depending on the surface light and a depth dependent attenuation (Fig. 6.5). Differences in the albedo of the water surface due a changing angle of incidence of solar

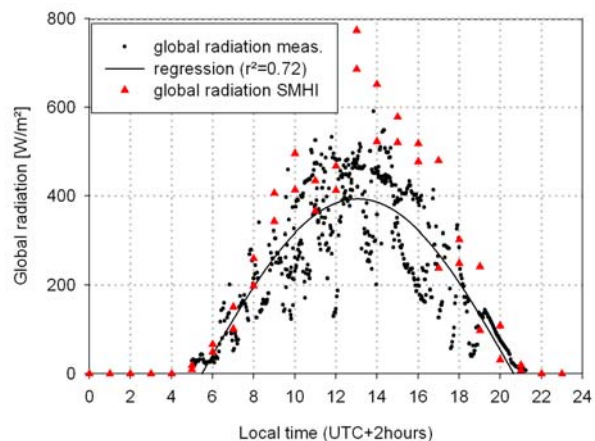


Fig. 6.4. Measured global radiation during field sampling in June 2001 in the central Baltic Sea (black dots), Calculated regression for measured data (line) and modelled global irradiance (SMHI 2006).

radiation were not taken into account for reasons of simplicity.

During field sampling, global radiation was measured by a radiometer onboard of RV 'Alkor' (Fig. 6.4). These data were used to calculate the light at the surface for each model time step. A regression was conducted, based on measured radiation during daytime, whereby values lower than 5W/m^2 were not taken into account and a 3-parameter sine-function was assumed. The time of day (t) is local time. The fit of the regression was acceptable with $r^2=0.72$ (Fig. 6.4).

$$8) \quad \text{Light}_{\text{surface}} = 393.1985 * \sin(2\pi t / 30.3702 + 5.1513)$$

Calculated surface radiation was converted to lux [lx], whereby values lower 2lx (during night) measurements were set to 2lx, which refers to moonlight.

The attenuation of light in the water column was taken from Nilsson *et al.* (2003). The attenuation was derived from field measurements in the northern Bornholm Basin in March 2002. The used light profiles were measured with a Seabird PAR-sensor (photosynthetic active radiation 400-700nm). A linear regression of the logarithm of light intensity at depth ($I(z)$), depending on light intensity at the surface $I(0)$ and the attenuation coefficient k was calculated.

$$9) \quad \ln I(z) = \ln(I(0)) - k * z$$

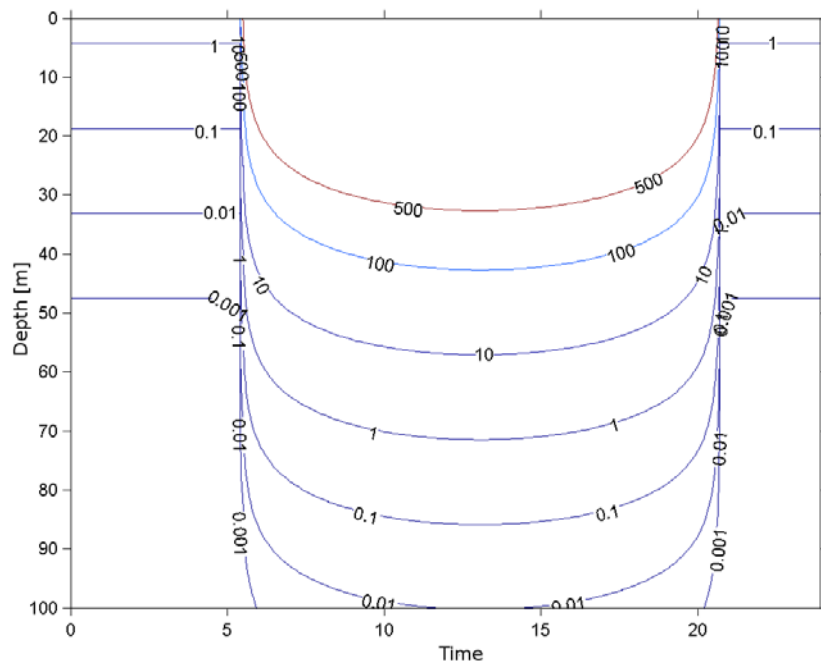


Fig. 6.5. Calculated light regime, as used for the modelling of the diel vertical migration of adult Baltic sprat. Light levels are given in lux [lx].

The attenuation coefficient k varied between 0.131 and 0.167m^{-1} . The higher level was used for our model calculations, because it is possible that attenuation in May was higher.

A conversion between PAR [$\mu\text{E s}^{-1} \text{m}^{-2}$], measured global radiation [W / m^{-2}] and radiation given in lux [lx] was described in detail by Brock (1981) and summarized below. A standard daylight spectral distribution has to be assumed.

$$10) \quad 1 \text{ Wm}^{-2} = 4.6 \mu\text{Es}^{-1} \text{m}^{-2}$$

$$11) \quad 1 \text{ lx} = 0.01953 \mu\text{Es}^{-1} \text{m}^{-2}$$

To reflect the relative fast changes of the (light-) environment during the diel cycle, a time increment of the model of 1/1000hours was chosen.

6.4. Results

The calculated light-regime during the diel cycle is shown in Fig. 6.5. A rapid change of light over depth can be found during the sunrise and the sunset, whereas during daytime, changes are not that pronounced.

As stated above, the first step when modelling the vertical distribution of adult sprat is to calculate the behaviour response for every environmental parameter. Fig. 6.6 shows profiles of behaviour responses caused by temperature, oxygen and light, which were calculated for noon (12:00h). This demonstrates the principle of calculating behaviour in the model.

The orange line indicates the result of the evaluation function (Equat. 3). Down to 64m, cold temperature and high light levels stimulate a downward movement, i.e. the evaluation function gives negative values. Below 80m, the insufficient oxygen content of the water induces an upward movement. Between 64m and 80m sprat has no stimulus for migration. Therefore, without an application of 'demographic noise', sprat would not occupy the whole depth range with sufficient hydrography (Fig. 6.7 right).

The simulated vertical distribution of adult sprat during the diel cycle (Fig. 6.7 left) shows a pronounced diel vertical migration.

The modelled migration pattern is in good accordance with hydroacoustical observations made between the 04th and the 6th June 2001 in the central Bornholm Basin (Fig. 6.8). Two differences between the modelled and the observed distribution has to be noted:

The model gives a broader night time distribution in the upper water layer (ranging from 0 to approx. 20m depth, Fig. 6.7), compared to integrated observed data (ranging from 10-20m, Fig. 6.8). Additionally, the modelled downward migration of adult sprat started later, than observations suggest.

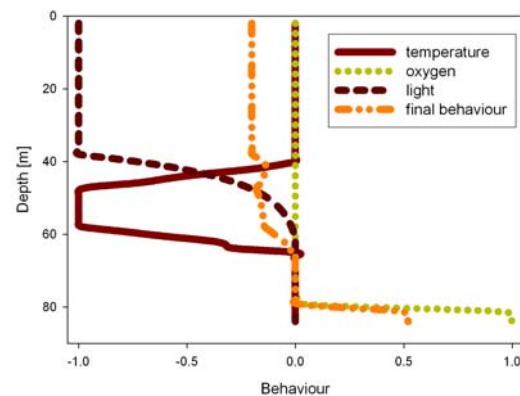


Fig. 6.6. Example for calculated behaviour responses for several parameters (temperature, oxygen and light) and the corresponding final behaviour (output of the evaluation function, before randomization) at noon. Negative values indicate a stimulus for downward and positive values indicate a stimulus for upward migration.

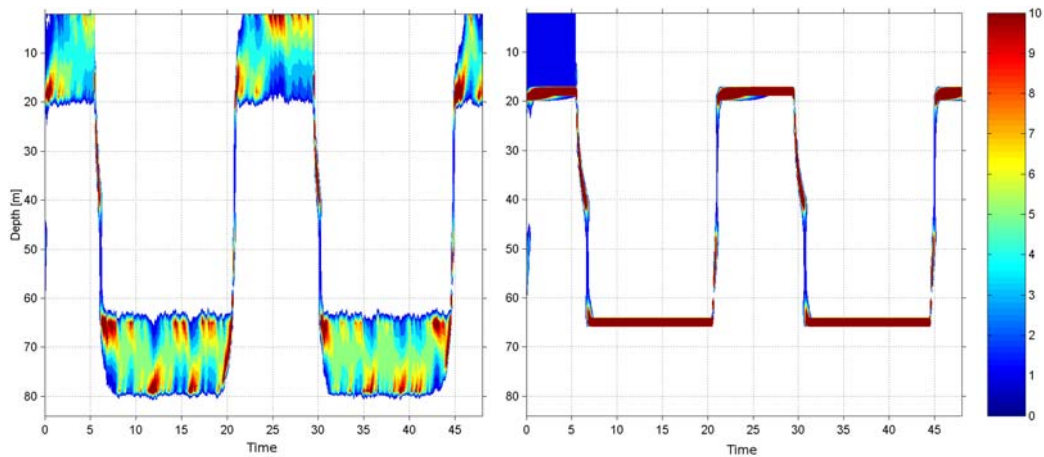


Fig. 6.7. Modelled diel vertical migration of adult sprat in the central Baltic Sea over a 48h-period in June 2001 (0, 24 and 48h refers to midnight). The first hours of model output reflect the way from initial uniform distribution to distribution caused by external stimuli. Left: Model output with demographic noise. Right: Model output without demographic noise.

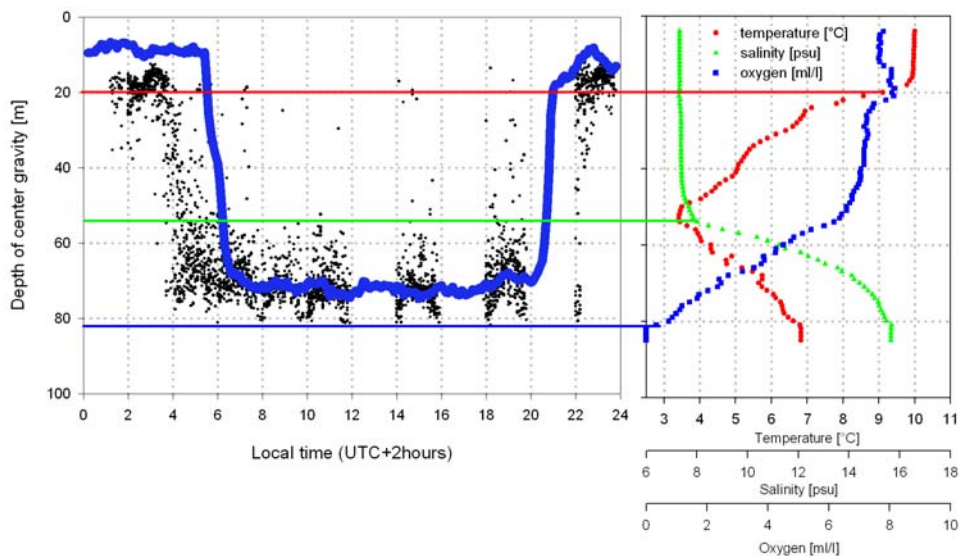


Fig. 6.8. Comparison of modelled and observed diel vertical migration of adult sprat. Right: Profiles of hydrography at sampling site in June 2001. Left: Scatter plot of weighted mean depths of echo-profiles during the run of the day (horizontal dimension of each profile is 0.1nm). Thick blue line indicates the calculated mean depth of the modelled vertical distribution of adult sprat. Straight horizontal lines represent important hydrographic features: the beginning of the thermocline, the halocline and the beginning of the anoxic layer.

6.5. Discussion

In this study, it was shown, that behaviour related to vertical migration of sprat can be adequately described and therefore modelled by dependencies of physical parameters, such as oxygen, temperature, vertical temperature gradient and light. Hence, the relevant parameters for the vertical distribution of sprat and their range, as found and described in previous chapters, were successfully confirmed.

Most papers, where new modelling approaches or their applications were presented, miss a real comparison with corresponding field observations. To avoid this, the presented model of the vertical migration of sprat was calculated for a data set with measured hydrography and fish distribution. Unfortunately, it was not possible to measure vertical profiles of light during the diel cycle, so these were calculated using an attenuation coefficient taken from Nilsson *et al.* (2003).

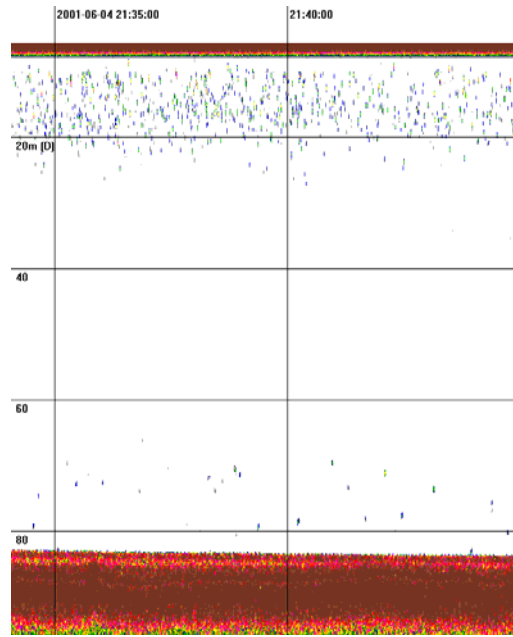


Fig. 6.9. Echogram from the night between the 4th to the 5th June 2001. Note the night time distribution of clupeids in the upper water layer.

The discrepancies between the modelled and the observed distribution, namely a broader modelled night time distribution and a delayed downward movement during dawn, are explainable. The observed, integrated night distribution is biased by lacking observations above the keel-depth of the vessel, the negligence of the upper 10m during the integration procedure and possibly an avoidance reaction of clupeids. Nevertheless, raw echo data (as shown in Fig. 6.9) give a more realistic picture of the distribution during night time than the integrated values. The observed (Fig. 6.9) distribution, as seen in the echogram, supports the broader night time distribution of sprat. The temporal mismatch between the observed and modelled downward migration in the morning could be an indicator for an incorrect described and modelled causal relationship between the light/diel cycle and the vertical migration of sprat, i.e. how light acts on vertical migration of sprat remained unclear. To introduce light (and as result diel cycle) into the model, the hypothesis of a preferred light level was chosen (Fig. 6.1 left column, Woodhead 1966, Nilsson *et al.* 2003), nevertheless it is not clear whether this is the underlying mechanism behind vertical migration of sprat, or not. Future versions of the model should evaluate the possibility of an influence of variations in brightness or sunrise and sunset as suggested by Blaxter (1975). A migration stimulated by sunrise (Fig. 6.1 right, lower panel), could overcome the delay in modelled downward migration (see above). Probably, both hypotheses could be combined.

Complementary, an incorrect simulated light regime could be the reason for the late downward movement of sprat in the morning. The calculation of the light regime, based on the regression of measured surface radiation is probably not an adequate way to capture the light environment, especially during the break of dawn. Nilsson *et al.* (2003) measured the surface radiation with a comparable light meter, but noted an insufficient sensitivity of the equipment to measure light

intensities at dawn and dusk. Therefore, they decided to model the light intensities using a model presented by Janiczek and De Young (1987).

Until now, the model was calculated for short time periods. Nevertheless, it is possible to calculate the vertical distribution of sprat during the seasonal cycle, based e.g. on the output of a 3D-hydrodynamic models. A theoretical surface light could be calculated for every geographical point and time, depending on cloud coverage of the sky (Janiczek and De Young (1987, Nilsson *et al.* 2003). An excellent alternative is delivered by the Swedish Meteorological and Hydrological Institute (Landelius *et al.* 2001, SMHI 2006). They provide modelled hourly global radiation for Scandinavia, the Baltic Sea and the North Sea since 1999 as time series for single positions or spatial data fields.

In addition to external factors, Fennel and Neumann (2006) used an internal factor to describe the vertical migration of zooplankton. They incorporated a parameter φ , which quantifies the status of nutrition. Therefore, in periods of low nutritional fitness (i.e. hunger) the search for food will overcome the induced stimuli as derived from other environmental parameter, e.g. the avoidance of cold water. The application of the presented model of sprat vertical distribution was possible without such nutritional factor. In contrast to modelled herbivore zooplankton with usually higher prey densities in the upper water column, sprat will find prey items in different layers of the water column, such as *Pseudocalanus* sp. below the halocline during spring (Köster and Schnack 1994). This is the layer where *Pseudocalanus* sp. reproduce (Möllmann *et al.* 2000, Schmidt *et al.* 2002). A shift in the diet composition can be found when sprat migrate into other depth layers (Casini *et al.* 2004, Möllmann *et al.* 2004, Möllmann *et al.* in prep. , chapter 7). During summertime the diet of sprat contains mainly the copepod *Temora longicornis* L., caught in higher water layers (Möllmann and Köster 2002).

Nevertheless, the incorporation of internal factors, such as hunger or temperature dependent fecundity would include an optimization of their physiological rates to get a higher reproduction success at the end (Giske *et al.* 1998). If future calculations of the model show misfits, such physiological factors could be needed to reduce the variance.

The modelling of the vertical distribution of sprat is the first step towards an incorporation of 'realistic' predation into ecosystem models and multispecies stock models of Baltic fish. The chosen implementation was relative straightforward and should allow an easy incorporation into existing models. Now it is possible to calculate potential vertical overlap of predator and prey, which could improve the estimation of predation on copepods or other prey items, such as cod eggs, as well as the understanding of the vulnerability of sprat toward predation by cod.

Previous approaches of modelling the predation pressure caused by sprat were quite rough estimates and hence very restricted in their predictive power. The light-dependent approach (Neumann and Kremp 2005) assumes an increase of foraging success (and as result of predation, too) with increasing light-intensity. One pitfall of this method is the assumption of a homogeneous vertical distribution of foraging specimen. Due to the light-dependence of mortality rate, the theoretical chance for zooplankton to die by predation is higher in the upper water column. This is not plausible in the investigated ecosystem, where the predator distribution is highly inhomogeneous in vertical scale and often concentrated in deeper parts of the water column. Additionally the possibility of non-visual orientated foraging is neglected. Batty *et al.* (1986) reported about a possible switch of herring from selective feeding toward filter

feeding when the light intensity falls below a certain limit. More plausible is the approach of assuming a vertical distribution of sprat based on a probability of occurrence, as given by Andersen and Möllmann (2004). They assumed a constant width over depth, limited below by low oxygen conditions. The model presented in chapter 5 is a combination of probability distribution depending on oxygen and temperature. Nevertheless, the use of probability functions is very restricted. Often this approach is only valid in a unique hydrographic situation. However, due to very few hydrographic parameters, taken into account, this procedure is very easy to implement and optimization is straightforward. For a more detailed discussion, please refer to chapter 5.

The modelled vertical distribution of sprat is needed for the estimation of physiological rates, too. Temming (1996) included the ambient temperature into the general model of gastric evacuation (Tyler 1970, Jones 1974), as a tool for the estimation of individual daily feeding rations of fishes. However, direct measurements of vertical distribution and hence ambient temperatures are not available quite often. These missing data are easy to extract from the model results, e.g. as weighted mean temperature.

Moreover, the knowledge of the vertical distribution is a needed module for the next step, the modelling of spatial pattern in horizontal scale, i.e. horizontal migration. For example, as described in chapter 5 (Fig. 5.11 on page 68 and Fig. 5.12 on page 68) unfavourable conditions such as cold water in upper water layers can prevent horizontal migration into shallower areas. As a result sprat was captured in the deep Basins below the halocline.

Even though the benchmark test was successful, hydrographic situations are possible where the model in its present configuration could fail. Therefore, additional model versus reality tests should be conducted to detect possible pitfalls. Additionally the sensitivity of parameterizations of the model has to be evaluated. A proper calibration and testing of the model remains a task for the future.

6.6. Acknowledgements

STRÅNG – light data used here, are from the Swedish Meteorological and Hydrological Institute (SMHI); these data have been produced with support from the Swedish Radiation Protection Authority and the Swedish Environmental Agency. Eberhard Götze and Uwe Böttcher delivered acoustic data for the DVM of sprat.

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

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7.1. **Abstract**

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

7.2. Introduction

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

The pelagic ecosystem of the Central Baltic Sea provides an example for an upper trophic level cascade due to the joint effect of overfishing and climate change (Köster *et al.* 2003). During the early-1990s the stock of the top-predator cod (*Gadus morhua*) collapsed due to climate-induced recruitment failure and high fishing pressure (Köster *et al.* 2005). The main food item of cod, i.e. sprat (*Sprattus sprattus*), increased subsequently to record levels due to recruitment success and lowered predation pressure (Köster *et al.* 2003; MacKenzie and Köster 2004). Sprat and herring (*Clupea harengus*) are the main planktivores in the system preying mainly on calanoid copepods (Möllmann *et al.* 2004). Despite the drastic increase in sprat stock size, not all mesozooplankton species declined. Rather the dominant calanoid copepods showed differential developments with *Acartia* spp. and *Temora longicornis* increasing and only *Pseudocalanus acuspes*¹ decreasing (Möllmann *et al.* 2000, 2003). Using time-series data from the neighbouring Gotland Basin, Möllmann and Köster (2002) showed that the increased sprat stock had a significant influence on *P. acuspes* and to a lesser degree on the *T. longicornis* population, but not on *Acartia* spp. This differential vulnerability of the copepods to predation was hypothesised to be due to differing vertical distributions (Möllmann and Köster 2002).

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

The deep basins of the Central Baltic Sea represent an example of a highly stratified physical environment. In addition to the development of a thermocline in spring, the positive freshwater balance of this semi-enclosed sea leads to a freshening of surface waters and the development of a permanent halocline. The water column is thus in spring and summer divided into a warm

¹ formerly called *P. elongatus*, but see Renz and Hirche (2006)

surface, a cold intermediate and a saline deep water body (Voipio 1981), providing local species with different habitats to choose with pronounced consequences for trophic interactions.

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

7.3. Material and methods

Sampling and laboratory analyses - We conducted systematic hydrography and zooplankton grid surveys during May, June and July 2002 in the Bornholm Basin, Central Baltic Sea with German research vessels RV 'Alkor' and 'Heincke'. Vertical profiles of salinity, temperature and oxygen concentration (CTD-O2) were collected on a grid of 45 stations. Zooplankton sampling was performed on a 9-station subset of the station grid (Fig. 7.1). We used a Bongo sampler (150 μ m mesh-size) for double-oblique hauls to in maximum 5m above the seafloor to record the zooplankton community integrated over the whole water column. Additionally we applied a 50 μ m Multinet resolving the water column in 10m depth intervals, providing vertical distribution patterns of zooplankton species. Samples were preserved in a 4%-formaldehyde/seawater solution. In the laboratory copepods were identified to species and developmental stage, i.e. nauplii, copepodites 1-5 (C1-5) as well as adults (C6).

We used hydroacoustic recording in combination with pelagic trawling on four transects in the Bornholm Basin with German research vessels RV 'Alkor' and 'Walther Herwig III' to estimate the spatio-temporal occurrence of planktivorous fish (Fig. 7.1). Acoustic measurements were conducted during the daytime feeding period of Baltic sprat and herring (Köster and Schnack 1994; Cardinale *et al.* 2003). A SIMRAD EK 500 echosounder was used on RV 'Walther Herwig III', while on RV 'Alkor' a SIMRAD EK 60 echosounder was deployed. Calibration of the gears was performed using the standard copper-sphere method (Foote *et al.* 1986, ICES 2001)). The procedure and the settings of the acoustic measurements as well as the data processing were conducted according to the 'Manual for the Baltic International Acoustic Survey' (ICES 2001). Digitized echograms were corrected for bottom topography and thin-echo-scattering-layers and other unwanted echoes, such as air-bubbles below the ship. Echo-data were integrated as 'nautical area backscattering coefficient' (NASC; [m^2/nm^2]) from 10m below the surface to 0.5m above bottom. We performed pelagic trawling with a Kombitrawl (Fa. Engel trawls) on the hydroacoustic transects targeting observed schools of pelagic fish. After each haul the total catch and the length-distribution of sprat and herring was recorded. Stock sizes of herring and sprat were computed for quarterly ICES (International Council for the Exploration of the Sea) rectangles (further on called rectangles, Fig. 7.1).

We collected stomachs of the clupeids for feeding analyses according to a length-stratified sampling scheme using 1cm length-classes for sprat, and 2 cm length-classes for herring. If available, contents of 3 stomachs per length-class were analysed per trawl station, summing up to in total 711 herring and 871 sprat stomachs. The total stomach content (in g wet weight) was measured as the difference between the full and the empty gut. Food items were identified to

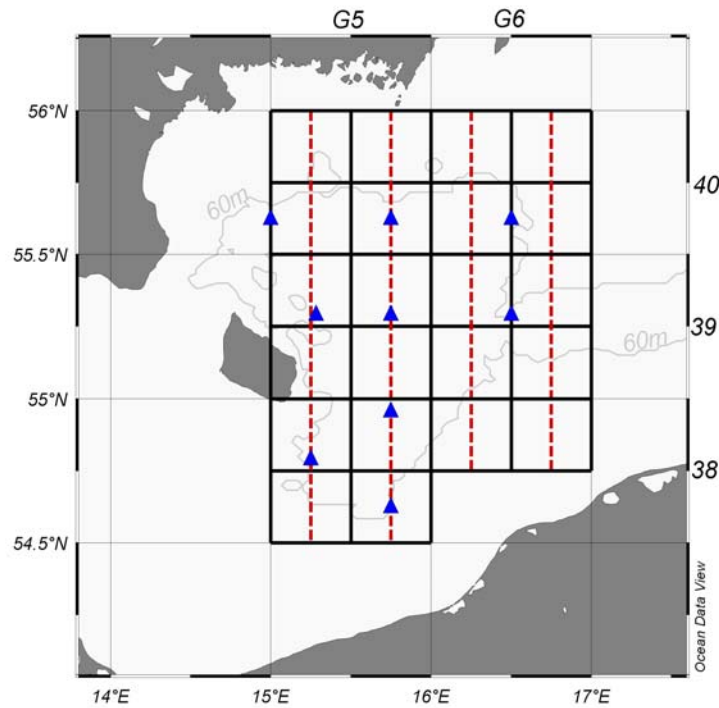


Fig. 7.1. Study area (Bornholm Basin) with plankton sampling stations (blue triangles) and hydroacoustic transects (red dashed lines).

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

Predator consumption - The average stomach fullness of herring and sprat in g wet weight was calculated per month and weighted according to the observed length-frequency distribution. We estimated individual daily rations (F_T) of herring and sprat per trawl station using an exponential form of the general model of gastric evacuation (Tyler 1970; Jones 1974) which incorporates the ambient temperature as a variable (Temming 1996):

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

with R' a food type constant (0.108 for sprat and 0.084 for herring), S the average stomach content, D the duration of the feeding period, A a temperature coefficient (0.073 for sprat and 0.129 for herring), T the ambient temperature, and S_t the average stomach content at the end as well as S_0 the average stomach content at the beginning of the feeding period. Values for S_t (44 and 10% for sprat and herring respectively) and S_0 (43 and 52% for sprat and herring

respectively) were estimated from 24-h fisheries representing mean relative deviations from the average stomach content during daytime, 2 hours before and after the food ingestion stopped and commenced, i.e. sunset and sunrise (Köster 1994). Baltic herring and sprat form schools during daylight feeding in deeper water layers, while during night the fish disperse in surface layers showing no feeding activity (Köster and Schnack 1994; Stepputtis 2001; Cardinale *et al.* 2003). We thus used ambient temperatures in the observed depth of the centre of mass of herring and sprat (Fig. 7.2) during the daytime feeding period in consumption estimations. A detailed description of the evacuation model and the estimation of the parameter values is given in Möllmann and Köster (1999). Eventually we computed population consumption rates by multiplication of individual daily rations with population sizes. Consumption values per m² were derived using the size of the area (Möllmann and Köster 2002). Consumed mass was converted to carbon assuming the carbon content to be 5% of the wet weight (Mullin 1969).

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

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

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

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

with *BW* the body weight (mg) from Hernroth (1985), as well as *a*=0.0111, *b*=-0.2917 and *c*=-0.6447.

Growth rates of broadcast spawning adults were only dependent on body weight:

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

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

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

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

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

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

Vertical overlap between predator and prey and weighted prey density - We assessed the vertical overlap (O_i) between the pelagic fish and the copepods using the Williamson overlap index (Williamson *et al.* 1989, Williamson and Stoeckel 1990):

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

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

The choice of a prey species by a predator may dependent on the relative abundances of the prey species. We thus calculated the density of each prey species available to the predators, the weighted density (WD_i):

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

Interaction strength - We calculated consumption to production ratios (C/P) as an index of the interaction strength between the different life-stages of the target copepod species and planktivorous fish. We assigned trawl and plankton stations to individual rectangles to yield spatially-resolved C/P-values (Fig. 7.1).

7.4. Results

Predator diet, stock size and consumption - We found the diet of herring and sprat to be very similar, being dominated by the three target copepod species (Fig. 7.4). We further observed a clear diet change between May and the later months. In May, both fish species preyed mainly upon older copepodites and adults of *P. acuspes*, while only smaller fractions of *T. longicornis* and *Acartia* spp. were found in the stomachs. Contrary, in June and July C4-6 of *T. longicornis* constituted the largest proportion of the herring and sprat diet.

Tab. 7.1. Consumption and stock size of herring and sprat: D – daily feeding period (hours), T – ambient temperature (°C), S – mean stomach content (g wet weight) ± s.e., F_T – individual daily ration (g wet weight) ± s.e., and N – stock size (millions).

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

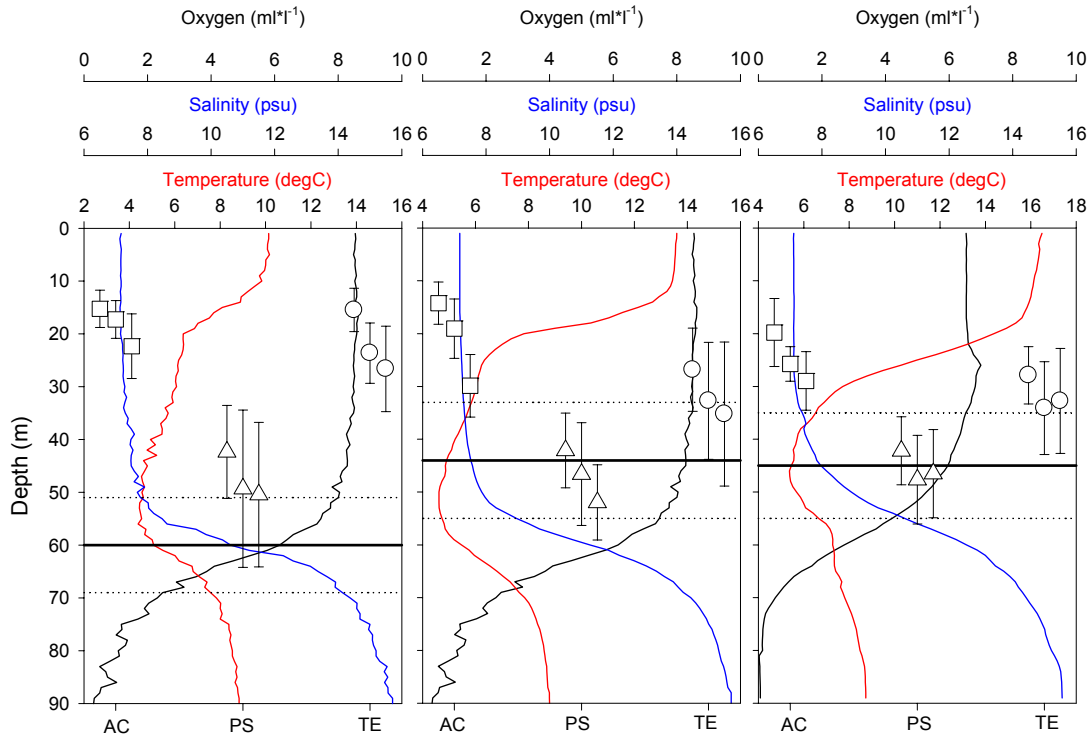


Fig. 7.2. Hydrographic situation and distribution of predator and prey in May (left), June (middle) and July (right); AC – *Acartia* spp., PS – *Pseudocalanus acuspes*, TE – *Temora longicornis*, C – copepodites; groups of symbols from left to right – copepodites 1-3, copepodites 4-5 and adults; error bars represent \pm s.d. of the mean, solid horizontal line – weighted mean depth of herring and sprat, dotted horizontal lines - \pm s.d. of the mean.

We found highest average stomach contents and individual daily rations of herring in June, with the latter being twice the rations in May and July (Tab. 7.1). For sprat, the mean stomach content as well as the daily individual consumption increased steadily during the observed period.

The stocks of herring and sprat showed a pronounced in- and out basin migration (Tab. 7.1). We observed the highest sprat abundance in May, decreasing during June and July. In contrast, herring stock size increased over the period. In all month, the pelagic fish community was numerically dominated by the sprat stock.

Combining individual rations with stock sizes, we yielded daily estimates of the fish population consumption (Tab. 7.2). We found the peak sprat population consumption in May on C4-5 and C6 of *P. acuspes*. Larger consumption rates were additionally observed for the later stages of *T. longicornis* in June and *Acartia* spp. in May. Herring population consumption peaked in June and July on C4-5 and C6 of *T. longicornis*.

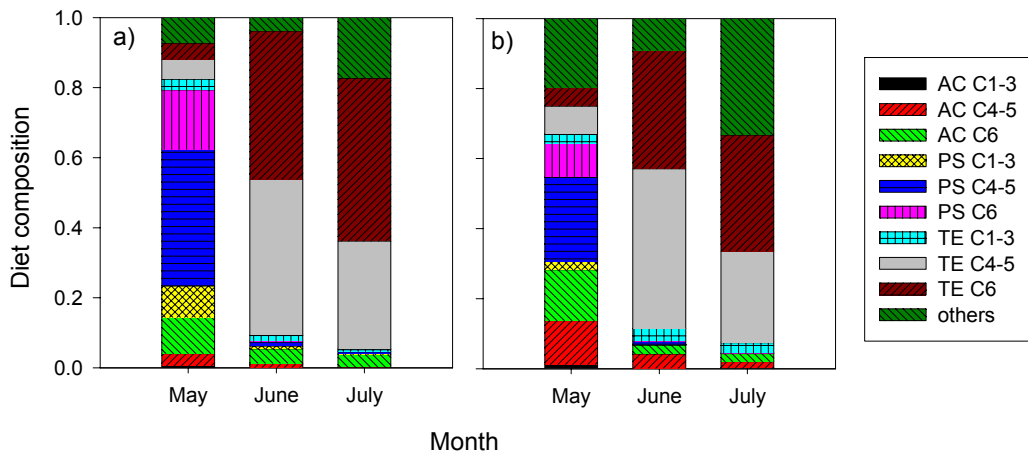


Fig. 7.4. Diet composition of herring (left) and sprat (right); AC – *Acartia* spp., PS – *Pseudocalanus acuspes*, TE – *Temora longicornis*, C – copepodites.

Prey production - We found considerable differences in stage-specific production between the 3 copepod species (Tab. 7.2). *T. longicornis* was the most productive copepod, followed by *Acartia* spp., and *P. acuspes* being the least productive. We found the same stage-specific production pattern in *Acartia* spp. in all months, with C6 having the highest production and C1-3 the lowest. In contrast, production patterns of *P. acuspes* and *T. longicornis* changed between months. *P. acuspes* C4-5 displayed the highest production in May and June, while C1-3 production was highest in July. In *T. longicornis* C1-3 production peaked in May, while in June and July C4-5 and especially C6 production was highest.

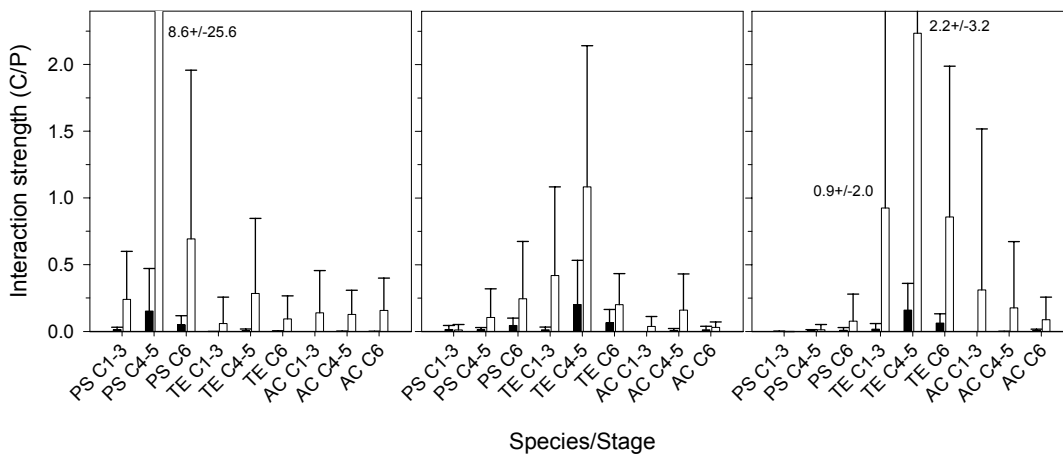


Fig. 7.3. Interaction strength (consumption/production) between herring (black bars) and sprat (white bars), and the different copepod species/stages in May (left), June (middle) and July (right); AC – *Acartia* spp., PS – *Pseudocalanus acuspes*, TE – *Temora longicornis*, C – copepodites, error bars represent s.d. of the mean.

Tab. 7.2. Production of copepod species/stages and consumption by herring and sprat. WMD – weighted mean depth [m], T – temperature in WMD [°C] ± s.e., g – daily growth rate, B – biomass [mg C*m⁻²] ± s.e., P – daily production [mg C*m⁻²] ± s.e., and population consumption by sprat – C_s, and herring – C_H [mg C*m⁻²] ± s.e. PS – *Pseudocalanus* sp., TE – *Temora longicornis*, AC – *Acartia* spp.; 1-3 and 4-5 – copepodites; 6 – adults.

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

Interaction strength - The strongest predation pressure was generally exerted by the sprat stock (Fig. 7.3). In May highest C/P were computed for C4-5 and C6 of *P. acuspes*, while in June and July the highest predation pressure occurred on *T. longicornis*, especially on C4-5. We estimated the sprat population to frequently consume more than the full copepod production of these copepods. Predation pressure by herring was in general very low.

Hydrographic structure and vertical distribution of predator and prey - We observed mean vertical hydrographic profiles from May, June and July to match the 'typical' spring/summer-stratification of the water column in a Central Baltic basin (Fig. 7.2). A thermocline separated the warm surface water from the cold intermediate water. The typical permanent halocline was observed below 60m and separated low saline surface waters from the saline bottom-water, which has low oxygen concentrations near the bottom.

We found the habitats of the three dominant copepods to be vertically segregated (Fig. 7.2). *Acartia* spp. was the most surface-orientated copepod with the copepodites dwelling directly in

the thermocline, while the adults are always found below the thermocline in colder water. The deepest distribution is displayed by *P. acuspes*, which dwell in the lowest part of the intermediate cold water down to the upper part of the permanent halocline. *T. longicornis* occurred always in the intermediate cold water.

Differences in the vertical distribution were supported by ANOVAs showing significant differences between the WMDs of the copepods (May: $F=25.0$, $p<0.01$; June: $F=19.2$, $p<0.01$; July: $F=16.1$; $p<0.01$). Post-hoc tests revealed no significant differences between the stages of single copepods, indicating similar habitats within a species. No significant differences in WMDs were found between all *Acartia* spp. stages and *T. longicornis* C1-3, between *Acartia* spp. C6 and *T. longicornis* C4-6 as well as between *P. acuspes* C1-3 and *T. longicornis* C4-6, indicating overlaps in vertical distribution.

We found differences in vertical orientation of copepods between May and June/July (Fig. 7.2). While the vertical position of *P. acuspes* remained stable, *Acartia* spp. and especially *T. longicornis* were found deeper in June and July, following the deepening of the thermocline. A change in vertical orientation between May and June/July was also found for herring and sprat. The planktivores occurred in May directly in the permanent halocline, while in June and July most fish were observed above the halocline in the cold intermediate water.

Tab. 7.3. Vertical overlap indices between fish and the different copepods species/stages (O_i), and weighted density of prey species (WD_i). * indicate $p<0.05$; p values are the proportions of randomized overlap indices which have a greater deviation from 1 than the observed value.

Species/stage	O_i			WD_i		
	May	June	July	May	June	July
PS 1-3	1.94*	1.44	1.71	2.46	5.03	9.40
PS 4-5	2.44*	2.02*	1.82	0.53	2.24	2.61
PS 6	2.32*	2.38*	1.82*	0.40	0.22	0.37
TE 1-3	0.12	0.86	1.45	0.01	0.33	0.16
TE 4-5	0.44	1.05	1.53	0.00	2.95	2.80
TE 6	0.33	1.43	1.43	0.01	8.85	9.28
AC 1-3	0.10*	0.68	1.19	0.00	0.01	0.00
AC 4-5	0.12*	0.74	1.42	0.00	0.08	0.23
AC 6	0.49	1.09	1.28	0.08	4.34	3.42

Mean temperature and salinity of predator and prey habitat - We recorded considerable differences in the average salinity and temperature preferences of the different copepod species. (Fig. 7.5). The average salinity values for *Acartia* spp. and *T. longicornis* were close to 7 in all months, irrespective of developmental stage. In contrast, *P. acuspes* had consistently higher average salinities with maximal values in May and lower values in June/July.

The experienced temperature range of *Acartia* spp. and *T. longicornis* was similar and relatively narrow in May, while in June and July the range was narrow for *T. longicornis*, but wide for *Acartia* spp. For the latter species, a pronounced ontogenetic trend in average temperature values was found, with decreasing values for older stages. Experienced temperatures for *P. acuspes* were generally the lowest, although for later copepodites and adults as high as for the two other species

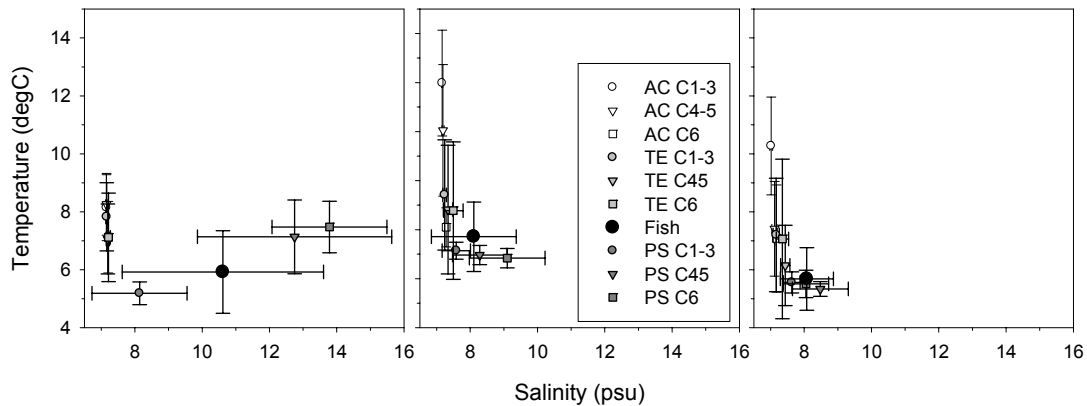


Fig. 7.5. Mean temperature and salinity values experienced by the different copepod species/stages and the predators; AC – *Acartia* spp., PS – *Pseudocalanus acuspes*, TE – *Temora longicornis*, C – copepodites, error bars represent \pm s.d. of the mean.

We observed the highest average salinities experienced by herring and sprat in May, while the average temperature was relatively stable, although highest in June. Mean hydrographic parameters for pelagic fish were generally similar to those of *P. acuspes*, especially in May.

Vertical overlap between predator and prey and weighted prey density - We found highest vertical overlap indices between planktivorous fish and copepods in all months for *P. acuspes*, indicating a strong spatial association (Tab. 7.3). Overlap indices were significantly different from random expectation for all *P. acuspes* stages in May, for later copepodites and adults in June, and only adults in July. Overlap indices < 1 indicating negative spatial association were calculated for *T. longicornis* and *Acartia* spp. in May, however being significant for copepodites of the latter species only. Vertical overlap indices for *T. longicornis* and *Acartia* spp. changed to values > 1 in June and July, being however not significantly different from random expectation.

Weighted densities encountered by the predators were highest for *P. acuspes* in May, while insignificant for the other copepod species (Tab. 7.3). In June and July, weighted densities for all species were higher compared to May. In these months we observed early copepodite weighted densities to be highest for *P. acuspes*, while late copepodite and adult densities were highest for *T. longicornis*. Considerable weighted densities of *Acartia* spp. were only observed for adults.

7.5. Discussion

We performed an in-situ process-study on the role of habitat heterogeneity for the vulnerability of calanoid copepods to predation by planktivorous fish in the Bornholm Basin, Central Baltic Sea. We first quantified the fish predation impact on dominating zooplankton species. Our estimates of predator consumption in relation to prey production show that, due to its presently small size, the herring population was not able to control any of the copepod populations. In contrast, we found the presently abundant sprat population to exert a strong predation pressure on later stages of *P. acuspes* in May and *T. longicornis* in June/July, a result which confirms a time-series study from a neighbouring Baltic basin (Möllmann and Köster 2002). The observed

pattern of predation impact was mainly determined by the diet of the clupeids, to a large degree composed of *P. acuspes* in May and *T. longicornis* in June/July. The observed diet composition of herring and sprat confirmed earlier investigations of their feeding ecology (e.g. Möllmann *et al.* 2004 and references therein).

We estimated the ratio of consumption to production as an index of interaction strength between planktivorous fish and the copepods. For the calculation of the daily food intake by individual herring and sprat we used a gastric evacuation model approach, which has been shown to yield in low estimates when compared to alternative bioenergetic modelling (Hansson *et al.* 1996; Möllmann and Köster 1999). Consequently, we consider our estimates as rather conservative and potentially underestimate of the true consumption by clupeid fish (Möllmann and Köster 2002). For the estimation of species- and stage-specific copepod production, we computed weight-specific growth rates using global models for broadcast spawning (*Acartia* spp. and *T. longicornis*) and egg-carrying species (*P. acuspes*) (Hirst and Lampitt 1998). Another common practice in the estimation of secondary production is to measure female egg production, and assume that somatic growth of the following developmental stages can be closely approximated by the weight-specific egg production (Berggreen *et al.* 1988; McLaren and Leonard 1995). Comparing our growth rates with rates derived from egg production experiments (EPR) in the same area (Hansen *et al.* 2006), showed both to be in good agreement for adults of *T. longicornis* and *Acartia* spp., but considerably higher for earlier stages of these species. EPR-derived growth rates for *P. acuspes* were slightly higher than our global model estimates for May, which is explainable by the seasonal peak egg production of this species at this time of the year (Hansen *et al.* 2006). Later in the season EPR-derived growth rates are lower than our global model estimates. The comparison of growth rates indicated that using EPR-derived growth rates would result on average in lower secondary production estimates than those computed with global models. A reason for the potential overestimation of copepod growth rates by the global models is that these are mainly based on data derived from true marine areas (Hirst and Lampitt 1998), being potentially of limited use for the brackish condition of the Baltic Sea. Indeed, copepod egg production rates of all species in the Bornholm Basin appear to be low compared to fully marine areas, which may indicate a salinity limitation (Hansen *et al.* 2006). Further, copepod egg production may be food-limited, which is not considered in the global models. Consequently our estimates of copepod production rates seem to be overestimates, while our fish consumption rates seem to be underestimates of the true values, supporting the conclusion of significant fish predation effects on Baltic copepods.

Our second aim in the present study was to test the hypothesis that a differential vertical overlap due to strong hydrographic preferences of predators and prey caused the differential vulnerability to predation in the heterogeneous environment of the Baltic Sea. Highest overlap indices for later copepodites and adults of *P. acuspes* explained the dominance of this copepod in the diet of the predators in May, and thus the strong predation pressure exerted on them. The strong vertical overlap in May was caused by the preference of both predator and prey species to high salinity, resulting in a similarly deep vertical distribution. The preference of *P. acuspes* to higher salinities and thus a deep distribution in the Central Baltic basins confirms results from other studies in the Bornholm Basin (Hansen *et al.* 2006; Renz and Hirche 2006). Similarly, the distribution of herring and sprat in the halocline during their daily feeding period has been reported before (e.g. Köster and Schnack 1994; Cardinale *et al.* 2003; Nilsson *et al.* 2003).

Vertical overlap indices increased for *T. longicornis* in June/July as a result of a deepening distribution of the copepod and a shallower distribution of pelagic fish. *T. longicornis* avoided

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

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

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

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

We show that the vertical distribution of copepods in the Baltic Sea is largely steered by hydrographic preferences, which supports earlier findings (Hansen *et al.* 2006; Renz and Hirche 2006). However, other factors might have contributed to the observed spatial patterns. We found Baltic copepods to be associated to hydrographic discontinuities, i.e. the thermo- and the halocline. It is well known that in these areas of changing density phyto- and microzooplankton food accumulates (e.g. Harris 1988; Munk *et al.* 1989; Roman *et al.* 2005). We thus cannot exclude that the observed association to hydrography is a response to a favourable feeding environment. Further, predator avoidance has been suggested to play a major role in vertical distribution/migration of copepods (Bollens and Frost 1989). However, as no significant diurnal vertical migration has been observed for the copepods in the area (Hansen *et al.* 2006; Renz and Hirche 2006) and our results show a strong vertical overlap with the predators, we exclude predation as a driving force for vertical distribution.

We recorded the vertical distribution of planktivorous herring and sprat using hydroacoustic measurements. It should be noted that hydroacoustic recording cannot distinguish between

these two similar fish species. However, as presently the sprat population is strongly dominating the pelagic fish community in the Baltic (Köster *et al.* 2003), we consider the observed vertical distribution to be mainly representative for sprat. Another flaw in our analysis may be the horizontal integration of all fish and plankton measurements to a single vertical overlap pattern. This procedure ignores variability in vertical distribution and thus overlap, an issue that needs further exploration.

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

7.6. Acknowledgements

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8. General Conclusion

The present thesis investigated the distribution of sprat (*Sprattus sprattus* L.) in the central Baltic Sea by combining field studies and model exercises. These results were applied in combination with stomach data of herring and sprat, as well as zooplankton distribution and production.

With these investigations, the given tasks for this thesis were successfully solved. These tasks were:

1. the identification of abiotic parameters that influence the distribution of adult sprat in the central Baltic Sea at several scales,
2. the investigation of possible implications for the (e.g. feeding) ecology of sprat and
3. the development of a habitat model for Baltic sprat.

Sprat distribution at different scales

It was shown that the distribution of sprat was strongly influenced by hydrographical conditions, which act on all investigated scales:

The *large-scale* distribution of sprat was studied in chapter 1, whereby climatic processes caused a modulation of the seasonal migration pattern. Prior to the major Baltic inflow (MBI) in January 2003, the seasonal development of sprat distribution within the Bornholm Sea indicated a 'typical' migration pattern. This includes a migration into the deeper areas of the Baltic Sea in winter and a coastward movement after spawning during spring/early summer, resulting in a coastal and an open sea type of distribution (Aro 1989, Hoziosky 1989 *et al.*). As hypothesised by Hoziosky *et al.* (1989), unfavourable local conditions can lead to redistribution within one type of distribution (e.g. from one deep basin to another). After the MBI, very cold water was found over the whole water column in the Bornholm Basin, whereas warmer water below the halocline was observed in the Gotland Basin. The data of the international spring hydroacoustic survey and the XSA-model output suggested a shift of sprat into the Gotland Basin, probably caused by the cold water in the Bornholm Basin. The observed example for interannual variability of sprat abundance in parts of the Baltic Sea indicates the importance of climate forcing on the large scale distribution patterns of sprat. The resulting changes of abundances could have implications for the biology of sprat (food web interactions, recruitment, physiology etc.).

Since seasonal abundance estimations from survey cruises are quite laborious, the presented investigation delivers a unique dataset for the seasonal abundance development of the main fish species (sprat, herring and cod) in the Bornholm Sea. This dataset is the basis for further analyses regarding the ecology of Baltic sprat, especially during the Baltic field campaign of the German GLOBEC-project. An example is given in chapter 7.

The influence of *meso-scale* processes on the distribution of sprat was studied in May 2002 (chapter 4). High-resolution CTD measurements were combined with hydroacoustics. The resulting dataset revealed insights into the behaviour of Baltic sprat and allowed an identification of relevant parameters that determine the vertical distribution of sprat. A hydrodynamic model was used to illustrate the development of the observed meso-scale pattern. Strong and steady winds induced water transport, which resulted in a partial replacement of the cold intermediate water in the northern Bornholm Basin. This resulted in different types of vertical distribution of sprat along the investigated transect. In those areas, where the cold intermediate water was present, sprat was captured between the cold mid water and the oxygen depletion zone above the bottom. This refers to a typical winter/spring distribution. In other parts of the transect, the vertical extent of sprat distribution was not limited by cold water, hence sprat occupied a wider depth range, as typical for summer and autumn. The found pattern supports temperature as the main driving factor for the vertical distribution of adult sprats.

The investigated *small-scale* patterns included the vertical distribution during daytime (chapter 5) and the diel vertical migration (DVM; chapter 10). The investigation of the vertical distribution during daytime was focused on the spawning time in April 2002, because the percentage of other species in the area was very low during this season. Therefore, the echoes measured during the survey were almost exclusively sprat-echoes. The relevant limits for sprat were identified with different methods. It was known that oxygen depletion in the deep Baltic Basins influence the distribution of sprat (Rechlin 1975, Hoziosky *et al.* 1989). The relevant limit was estimated as 1ml/l oxygen. This was relative constant during all investigated cruises. Additionally, it was shown that sprat do not occupy temperatures lower than 5°C during daytime. The diel vertical migration of sprat, herring and cod was described in detail. The timing of the sprat downward migration in the morning was in good accordance with sunset. During DVM sprat passed water layers with a minimum temperature of 3.4°C, whereby the found temperature gradients were relatively low in the water column.

Environmental parameters and their influence on sprat distribution

The ecological niche of Baltic sprat was described with regard to the physical environment. The ecological niche was formally described as n-dimensional space, whereby every dimension describes the activity range along an environmental factor (Hutchinson 1958). The results from the investigations, as previously described, can be summarized for each investigated parameter (dimension of the ecological niche):

Oxygen – The influence of the bottom-near oxygen depletion zone on the distribution of sprat in the deep Basins was shown. The 1ml/l oxygen isoline was found to be the relevant lower limit for the sprat distribution, regardless of the used method (cumulative plots, quotient plots, model optimization).

Salinity – The present study does not support salinity as the main driving factor for the distribution of sprat, as discussed earlier (Rechlin 1975). Since temperature and salinity are often correlated below the halocline, the investigation of the vertical distribution in April 2002 (chapter 5) did not answer the question, whether temperature or salinity restrict the sprat distribution in spring. However, several indicators were found which eliminate salinity as the relevant factor: In contrast to spring, sprat usually occupies a wider depth range including water layers above the halocline during summer time. It was not clear whether this difference is

caused by seasonal changes in environmental needs or not. It was possible to exclude seasonal effects, since both types of distribution (narrow distribution range between halocline and oxygen depletion zone, and broader distribution as typical for summer) were observed simultaneously in May 2002 (chapter 4), whereas no indications for a salinity-effect were found. Nevertheless, salinity could achieve some importance when the leading factor - temperature is out of acceptable limits (see next paragraph)

Temperature – Sprat usually do not occupy water layers colder than 5°C (chapters 4, 5 and 10). Two exceptions were described in this thesis. Firstly, during short-term migrations (i.e. diel vertical migration) cold water layers were passed if the vertical temperature gradient was low (chapter 10). Secondly, after the major Baltic inflow event in 2003 the temperature range observed in the Bornholm Basin in April 2003 was 2.6 to 3.6°C. A substantial part of the sprat population moved to the Gotland Basin, probably to avoid the cold temperatures in the Bornholm Basin. The remaining part of the population was confronted with the cold water and had no chance to move vertically into water layers warmer than 5°C. In this situation, sprat was found in the bottom near water layer (see Fig. 5.16 on page 73). Quotient plots (Fig. 5.17 on page 74) indicated a change from temperature induced vertical distribution to a pattern influenced by depth or salinity. This phenomenon was found only in April 2003.

Vertical temperature gradient – The vertical temperature gradient (VTG) is not relevant for the daytime distributions of sprat. In contrast, short term migrations, such as diel vertical migration are hampered by strong VTGs, whereby the minimum temperature of the water layers passed during migration has to be taken into account. If the temperature is higher than 5°C, even strong gradients do not have an influence on the migration. This was shown during the investigation of meso-scale hydrographical patterns in May 2002 (chapter 4). Along the sampled transect, relative high VTGs were found. However only in the southern parts of the transects with cold (lower than 5°C) intermediate water, the DVM was hampered. In contrast DVM was not interfered in May 1999 (chapter 10) by very cold temperatures in midwater (down to 3.4°C), because the VTG was fairly low. The reasons for the influence of VTG are not clear. An interesting hypothesis concerning the movement through sharp clines was given by Banse (1959). He assumed that an inhibition of short-term vertical movements (of copepods) by haline stratification is not a physiological, but a psychological problem.

Light – The importance of light for the vertical distribution and especially for the diel vertical migration was shown indirectly only. The description of the diel vertical migration (chapter 10) revealed a relation between the vertical migration of sprat and sunset. Nevertheless, the driving processes remained unclear (see chapter 6 for a detailed discussion). Pure endogenous rhythms, the migration to the depth of an optimal light level or behaviour that is induced by changes of brightness have to be considered.

Depth – In this thesis, it was not possible to extract the relevance of depth for the vertical distribution, because depth was always correlated with other important environmental parameters (e.g. temperature, light, salinity). In April 2003, after the major Baltic inflow 2003, a vertical distribution of sprat was found that was possibly determined by a depth preference of sprat (see the *temperature* – paragraph for more information). A reason for a possible depth selection of sprat could be an optimization to minimize the energetic costs for depth regulation, since the buoyancy of sprat is depth-dependent caused by pressure induced swimbladder compression.

Predator/prey – The influence of the abundance and the distribution of predators (e.g. cod) or prey (e.g. *Pseudocalanus* sp.) was not addressed in this thesis. However, the modelled vertical

distributions (see below and chapter 6) were in good accordance with observed distributions. This could indicate that the importance of predator and prey distributions is not significant for the vertical distribution of sprat.

Modelling the vertical distribution of adult sprat

The findings of previously described investigations were used to develop two models of the vertical distribution of Baltic sprat. A very simple model was used in chapter 5, whereas only temperature and oxygen were taken into account. This model approach was successfully applied to daytime data of spawning time in April 2002, but revealed discrepancies between modelled and observed vertical distribution for other seasons.

A more complex model was developed and described in chapter 6. The used behaviour based approach was introduced by Fennel and Neumann (2006) for the vertical distribution of zooplankton. The modelled migration behaviour of sprat depends on temperature, temperature gradient, light and oxygen. The model was successfully tested with the data set of diel vertical migration in May 2001, as described in chapter 10. The model was able to reflect the observed DVM-pattern very well. Further model runs for other scenarios (e.g. other seasons, stagnation period, post-inflow, seasonal development etc.) are needed to verify the generality of the actual model implementation. If future investigations reveal other factors to be relevant for the vertical distribution of sprat, these should be included to enhance the predictive power of the model.

Consequences

As an example for possible applications of the investigated distribution patterns of Baltic sprat, a study was presented that addresses the vulnerability of key zooplankton species to predation by herring and sprat (chapter 7). The results showed a strong impact of the sprat population on zooplankton species in the Bornholm Basin. This effect was modulated by preferences for different habitats and therefore by a differential vertical predator-prey overlap. Especially *Pseudocalanus acuspes* (in spring) and *Temora longicornis* (in summer) were affected by the predation of sprat.

Outlook

All assigned tasks were successfully solved, and consequently this study delivers an important contribution to the understanding of the biology of Baltic sprat. This knowledge can be used for further investigations, which could be focused on

- (i) the verification of found limits for the sprat distribution
- (ii) the improvement of the understanding of causal relationships between relevant parameters and sprat distribution (e.g. how the light influences the vertical migration).
- (iii) the further development of the behaviour based model and its usage as powerful tool.
- (iiii) the use of found distribution patterns to investigate a variety of questions, related to the Baltic ecosystem.

Further applications of the findings, presented in this thesis are in progress. For instance, the prey selectivity of herring and sprat was investigated including the vertical overlap of predator and prey (Bernreuther *et al.* in prep.). Until this study, calculations of feeding selectivity for sprat in the Baltic Sea neglected different vertical distributions of predator and prey.

Another application of the knowledge about distribution patterns of Baltic sprat, is the analysis of historical distribution data. A task of the German GLOBEC project is the archival storage and

analysis of historical survey data. The GDR and other Baltic countries conducted hydroacoustic surveys in the late 1970s and 1980s (an example echogram from May 1986 is shown in Fig. 8.1). This refers to the period prior to the dramatic regime shift in the Baltic Sea upper trophic food web (Köster *et al.* 2003). With this dataset, it is possible to compare acoustic sprat abundances and distribution patterns during two contrasting ecosystem regimes in the Baltic Sea, i.e. a cold, cod dominated phase and a warm, sprat dominated phase. This investigation will answer question, such as 'is there a change in the vertical distribution pattern, caused by high predator (i.e. cod) abundance?'. These analyses support focus 1 of the GLOBEC-Implementation Plan (IGBP 1999).

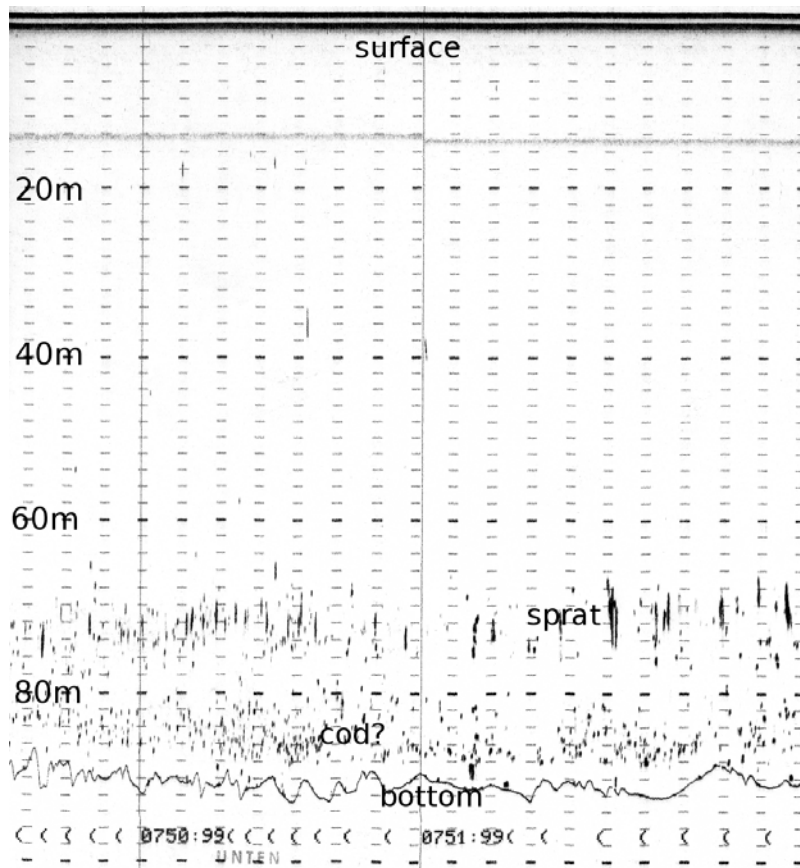


Fig. 8.1. Example echogram from May 1986 in the Bornholm Basin.

9. References

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10. Annex: Diel vertical migration of sprat, herring and cod in the central Baltic Sea

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10.1. **Abstract**

Hydroacoustics were used regularly for the investigation of diel vertical migration (DVM) patterns of pelagic fishes in the Baltic Sea. Until now, fish-echoes were used to describe a combined pattern for all pelagic fishes. This paper investigates the vertical migration of herring, sprat and cod at species level in relation to hydrography. Investigations were carried out in the central Baltic Sea (Bornholm Basin) in June 2001. Cod was found exclusively below the permanent halocline and therefore no significant DVM was found. In contrast to cod, herring and sprat showed pronounced vertical migrations within diel cycle, whereas the timing and schooling behaviour differed between both species.

Keywords: Baltic fish, sprat, herring, cod, diel vertical migration, behaviour, acoustic measurements

10.2. **Introduction**

The Baltic Sea is the largest brackish, semi-enclosed area in the world and consists of different deep basins, which are separated by sills. The hydrography is characterized by a strong thermo-haline stratification with less saline water in the upper layer and higher salinity below the halocline, which is usually found around 50-70m depth in the basins. Due to huge density differences, this stratification is very stable and vertical mixing between water layers is restricted. Therefore lateral transport of inflowing saline and oxygen-rich water from the North-Sea is very important for the renewal and the ventilation of the water below the halocline, but often hampered by the basin like bottom topography with different sills (e.g. Matthäus and Franck 1992). The salinity, the temperature, the oxygen-content and the vertical dimension of the deep water depend on inflow events. Only strong inflow-events will result in a renewal of the deep-water in the Bornholm Basin, Gdansk Deep and Gotland Basin (Börngen *et al.* 1990, Matthäus and Franck 1992, Matthäus and Schinke 1994). Due to a period of positive North Atlantic Oscillation (NAO), weather conditions have not supported strong inflows (Fonselius and

Valderamma 2003, Hänninen *et al.* 2000, Matthäus and Schinke 1999). Anoxic zones can be found in the bottom layer of the basins caused by an absence of sufficient inflows. The upper water layer is more influenced by river freshwater run-off and air temperature. During summertime an additional thermal stratification appears near the surface (around 20m), due to an warming of the upper water layer (Møller and Hansen 1994).

Sprat (*Sprattus sprattus* L.), herring (*Clupea harengus* L.) and cod (*Gadus morhua callarias* L.) presently dominate the fish community of the Baltic Sea. These species contribute 95% to the commercial fish catches in the Baltic (Sparholt 1994). Clupeids represent the main fraction of fish biomass in the Baltic Sea and are caught and consumed in large numbers by cod, salmon, marine mammals and humans. Additionally, clupeids are important predators on zooplankton (Rudstam *et al.* 1994, Parmanne *et al.* 1994, Kornilovs *et al.* 2001, Möllmann *et al.* 2004) and early life stages of fish, especially cod eggs (Köster and Schnack 1994, Köster and Möllmann 2000a), but are also cannibalistic (Köster and Möllmann 2000b).

The feeding of clupeids shows a clear diel pattern. Sprat feed exclusively during daytime (Köster and Schnack 1994, Cardinale *et al.* 2003). Cardinale (2003) found feeding-peaks for herring at dawn and dusk, whereby Köster and Schnack (1994) suppose that feeding will occur exclusively during daytime.

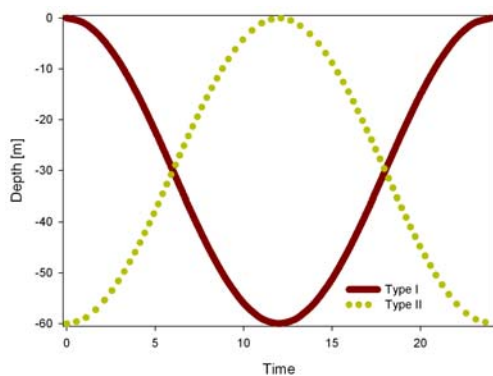


Fig. 10.1. Schematic representation of the two basic types of diel vertical migration (redrawn after Neilson and Perry 1990).

Diel vertical migration (DVM) is well-known for many aquatic species and documented in the literature (e.g. Lampert 1989, Levy 1990; Thomson and Allen 2000; Cardinale *et al.* 2003; Hays 2003). DVM patterns are usually triggered by light, but range and speed of these migrations are often limited by other factors, such as temperature, oxygen content of the water and prey availability. For pelagic fish, the general pattern seems to be a dispersed distribution during night and an aggregation during daytime (Blaxter and Holiday 1963, Woodhead 1966, Blaxter and Batty 1990, Giannoulaki 1999, Nilsson *et al.*

2003), which is often connected to DVM. These patterns are described for many areas, being especially pronounced for clupeids (Blaxter and Hunter 1982 as review). A comprehensive review of the diel vertical migration of marine fishes is given by Neilson and Perry (1990).

Many hypotheses have been developed to explain the selective advantages of such behaviour. The main hypotheses, discussed for diel vertical migration, are foraging, bioenergetic advantages and predator avoidance (e.g. Clark and Levy 1988, Bollens and Frost 1989). However, every theory, taken by its own, will usually not explain the complete migration pattern (e.g. Clark and Levy 1988).

Investigation of DVM with hydroacoustics gives the opportunity to get consecutive samples over the whole water layer at a high temporal and vertical resolution. Therefore, hydroacoustics play a major role for clarifying the relationship between DVM and the environment (MacLennan and Simmonds 1992, Nilsson *et al.* 2003, Massé and Gerlotto 2003).

The DVM of fishes in the Baltic Sea was mainly studied as an integration of all fish-echoes (Szczycka 2000, Orłowski 2001, Cardinale *et al.* 2003, Nilsson *et al.* 2003 etc.). A dispersion and upward migration at dusk and an aggregation and downward migration at dawn for the main bulk of pelagic fish was described. In the deep basins, fish-echoes were mostly found between halocline and oxygen-depletion zone during spring/early summer.

To link e.g. the feeding patterns, the spawning behaviour or different preferences of individuals to hydrography on species level, it is necessary to understand the species-specific migration patterns. For multispecies investigations, knowledge of the migration patterns for single species is essential to calculate the temporal and spatial overlap of predator and prey.

In this paper, investigations on the diel vertical migration of the three main fish-species in the Baltic pelagic ecosystem are presented. The focus will be (i) timing of vertical migration on species-level and (ii) its relation to hydrography.

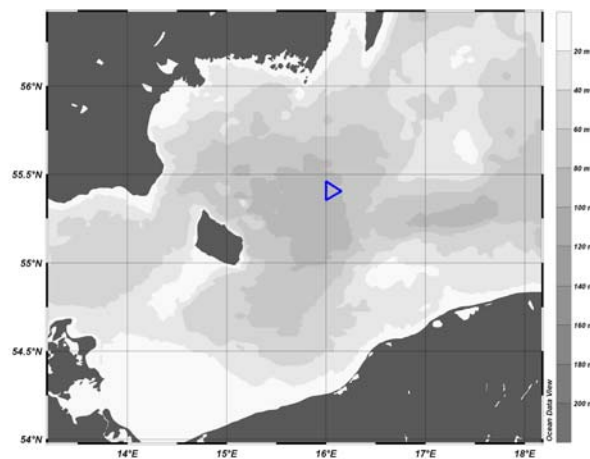


Fig. 10.2. Map of the sampling site in the central Baltic Sea (Bornholm Basin). The triangle marks the sampled transect. Starting point of hydroacoustic measurements was the most southern point and sampling was done anti-clockwise.

10.3. *Material and Methods*

Sampling

The study was carried out from the 4th to the 6th June 2001 in the Bornholm Basin (central Baltic Sea). Over a period of 48 hours a transect in triangle form (Fig. 10.2) with a side-length of approximately 6nm and starting point at 55°21'N 16°00'E was sampled by the German research vessels 'Walther Herwig III' and 'Alkor'. Water depth varied between 81 and 87 metres. During daytime the transect was regularly sampled with hydroacoustics by RV 'Walther Herwig III' at

least every 4 hours at a cruising speed of 10 knots, which resulted in a complete coverage after 2 hours. At the same intervals, plankton stations at the transect starting point were sampled by RV 'Alkor'. Between consecutive samplings of the transect/plankton station, fishery hauls were carried out by both vessels to cover the diel cycle of fish migration and feeding. In total 15 hauls were conducted, whereby it was distinguished between deep tows (9 during daytime, 1 during night time), covering the water layer below the halocline and shallow tows (5 during night time), covering the water layer above the summer thermocline in the surface layer.

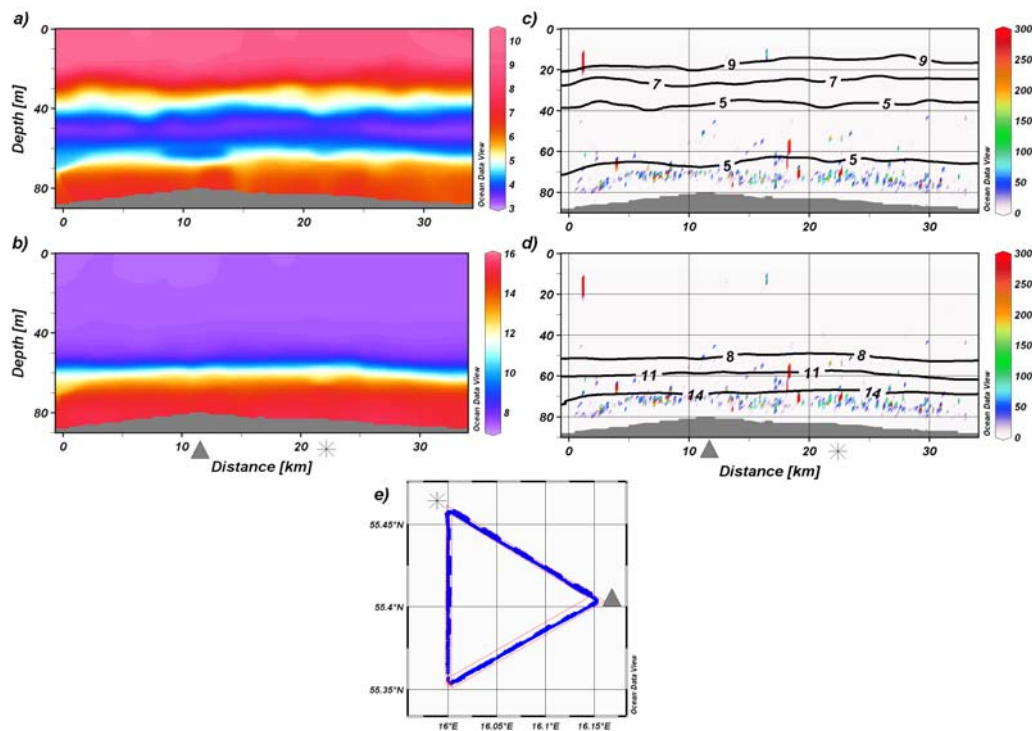


Fig. 10.3. Topography, hydrography and echo-distribution along the triangle transect sampled in June 2001 in the Bornholm Basin. Values are plotted over the distance from the starting point (southern edge) of the transect as sampled anti-clockwise. Edges of the triangle are indicated by triangle (eastern edge) and star (northern edge). a) Temperature [°C]. b) Salinity. c) and d) Integrated echo-values for one coverage of the transect at the 5th June 2001 from 16:00h to 18:00h (resolution: 1m vertical, 0.1nm horizontal). Echoes are given as NASC [m²/nm²] and were overlaid with iso-lines from c) temperature and d) salinity. e) Station map.

Additionally onboard RV 'Alkor' high-resolution measurements of hydrography with a towed and undulating CTD were conducted.

All given time data, unless otherwise noted, are local-time in 24 hours notation, which was Central European Summer Time (CEST; CEST=UTC+2h).

Hydrographic data

To determine the hydrographic factors influencing the distribution of fishes, vertical profiles of salinity, temperature and oxygen content were obtained regularly utilizing an ADM-CTD, equipped with an oxygen probe. Samples for salinity and oxygen calibration were taken regularly. For the investigation of meso-scale structures of hydrography along the transect, the CTD was mounted on a Gulf III sampler frame (without oxygen-sensor), which was deployed in U-tows from 10m below the surface to 6m above the bottom at a cruising speed of 5knots. Only slack-profiles were used for analysis and were plotted with the free software package 'Ocean Data View' (ODV, Schlitzer 2004).

Light-intensity and elevation of the sun

Global radiation was measured onboard RV 'Alkor' and recorded at 5 minutes intervals. Additionally elevation of sun was calculated for the location and the time of this study, using an algorithm for use with spread sheet programs (Giesen 2001). The measured global radiation was in accordance with the calculated elevation of the sun (Fig. 10.4a). Sunrise was at 04:27h and sunset at 21:23h local time.

Hydroacoustic measurements

Acoustic measurements were done onboard RV 'Walther Herwig III' with a SIMRAD echosounder EK500 and a hull mounted split beam transducer ES38B, working at a frequency of 38kHz. The echo data were recorded with the 'Bergen Integrator' (BI500) and later processed with 'Sonardata Echoview' (Sonardata 2005). The calibration of the acoustic equipment was conducted with the standard copper-sphere method (Foote *et al.* 1986), at the beginning of the cruise. The basic-settings and the procedure of acoustic measurements, fishery- and data-processing are described in detail in the 'Manual for the Baltic international acoustic survey' (ICES 2001). Digitized echograms were processed to correct bottom topography and to exclude thin-echo-scattering-layers and other unwanted echoes, such as air-bubbles below the ship. The echo-data were integrated as 'nautical area backscattering coefficient' (NASC; [m^2/nm^2]; MacLennan *et al.* 2002) from 10m below the surface to 0.5m above the bottom. The chosen vertical resolution was 1m, whereas the horizontal resolution was 0.1nm. For the calculation of an average fish-density at study site, only those echo-recordings, which were measured during daytime (6 to 20 o'clock), were used.

Weighted mean depth of echo-profiles

To illustrate the vertical migration, weighted mean depth (Bollens and Frost 1989) of measured echoes was calculated for every integrated echo-profile with a horizontal dimension of 0.1nm:

$$1) \quad z_c = \frac{\sum_{j=10}^n NASC_j \cdot z_j}{\sum_{j=10}^n NASC_j}$$

where $NASC_j$ is the 'nautical area backscattering coefficient' in each depth stratum j with the midpoint z_j .

Fishery data

To identify echoes, pelagic trawl hauls were carried out. The species composition and the length-distribution were estimated from these trawl hauls. Fishery hauls were grouped into three categories, depending on depth and time of the day (day-50m to bottom; night-50m to bottom; night-surface down to 30m). The headrope depth of the trawl was adjusted to get a representative sampling for one of the above mentioned groups. Day hauls were not carried out in the surface layer (surface down to 30m), because fish-echoes were very sparse in that layer during daytime. Trawl hauls were carried out at a mean speed of 3.5knots for 30minutes. The pelagic trawl net PSN205 (manufacturer: ROFIA Rostock, codend-meshsize: 10mm; vertical opening 12m) was used onboard RV 'Walther Herwig III', whereas a Kombitrawl (manufacturer: Engel-Netze Bremerhaven; codend-meshsize: 10mm; vertical opening 10m) was used onboard RV 'Alkor'. Processing of the fish samples followed normal procedures as described in ICES (2001), whereas herring was measured at centimetre below onboard RV 'Alkor', instead of half cm below.

10.4. Results

Hydrography

The hydrographic situation (Fig. 10.4c) was characterized by a strong vertical stratification of temperature, salinity and oxygen. Salinity was relatively constant with values around 7 from the surface to around 55m, i.e. start of the halocline. Below that depth the salinity increased sharply up to 16. The thermal stratification was characterized by a typical early-summer situation. Temperatures in the upper water layer were around 10°C. Below 20m depth, the temperature decreased rapidly. In the intermediate water layer minimum temperatures of 3.4°C were observed. Below the halocline, temperature slightly increased again up to 7°C. The oxygen content of the water varied above the halocline between 7 and 8ml/l. Below the halocline the oxygen content decreased rapidly to 0ml/l at around 80m. In the water column, relatively low gradients of temperature were found. The vertical temperature gradient ranged between -1.83°C/5m to 2.74°C/5m, whereas negative values indicate increasing temperatures with depth and is assumed to be more relevant for diel vertical migration.

The hydrography as sampled with a towed, vertical undulating CTD showed variation along the transect in temperature, as well as in salinity (Fig. 10.3). The depth of the 7°C-isotherme in the upper thermocline varied between 23 and 29m. The beginning of the halocline as marked by 8-isohaline varied between 49 and 55m. The bottom depth varied between 87m at the southern edge (start and end of triangle-course) and 81m at the most eastern point of the triangle transect. A correlation between variation in salinity and temperature with bottom topography was not found.

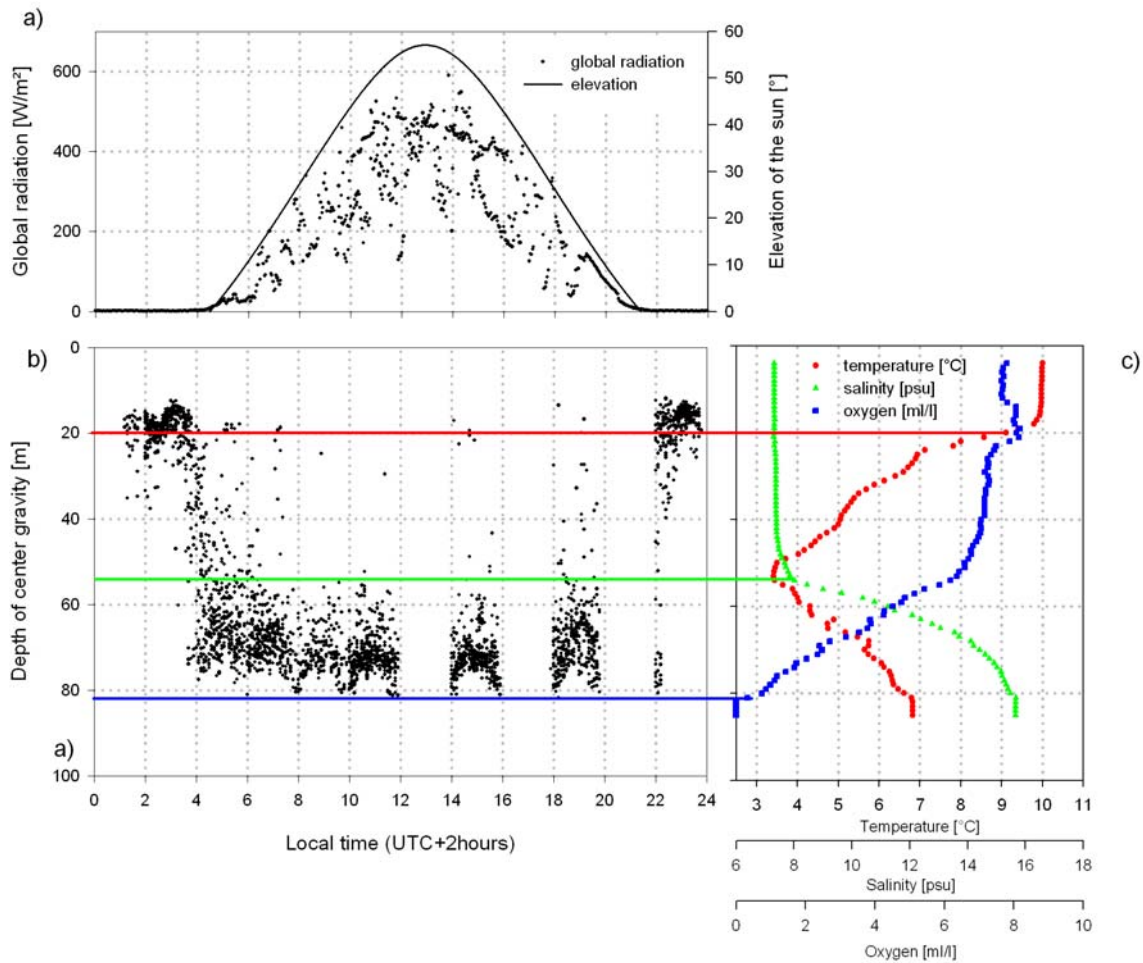


Fig. 10.4. Diel rhythm during 48h-sampling in June 2001. Shown are the distribution of echoes in relation to the elevation of the sun and hydrography. a) Measured global radiation and calculated elevation of the sun at the 4th June 2001 at sampling location. b) Weighted mean depth of all echo-profiles (horizontal dimension of 0.1nm). Time periods with no data are not covered with echo-recordings. c) Vertical temperature- salinity- and oxygen-profile. Drawn are lines, representing important hydrographic features: beginning of the thermocline, the halocline and the beginning of the anoxic layer.

Fish

During day, most of the fish was found below the halocline and a representative sampling of all fishes was assumed in deep hauls. On average 91.8% of all caught fishes were sprat. The fraction of herring and cod was at maximum 20% per haul per species, but on average only 4.5% for herring and 3.5% for cod (Fig. 10.5a). A mean density of fish 1.74 million [N/nm²] was estimated from hydroacoustics, with 1.6million sprat/nm², 0.08million herring/nm² and 0.06million cod/nm².

During night, similar fractions of fish-species were caught in hauls conducted deeper than 50m, but in extraordinary small numbers (868 individuals per half hour), whereas the mean value for daytime-hauls in that layer was 19300 individuals per half hour.

Tab. 10.1. Catch composition of near-surface fishery hauls, carried out during night in the framework of a 48-hour-sampling in the Bornholm Basin (central Baltic Sea) in June 2001. Given are numbers per 30min catch duration.

Haul	WH 162	WH 166	AL 19	AL 14	AL 17
start-time catch	22:10h	22:20h	00:42h	03:55h	04:25h
cod	0	1	0	0	0
herring	231	871	228	33	13
sprat	0	533	6198	15759	47538

The catch-compositions as derived from the near-surface night-hauls are not homogeneous (Fig. 10.5b). The fraction of herring caught in these hauls decreased strongly with time from 100% at 22:20h to 3.5% after midnight. Almost no herring was caught in the upper water layer around dawn. Only one cod was caught in these near-surface night-hauls. Mean length-distributions for sprat and herring is shown in Fig. 10.6. For cod a cumulative length distribution of all hauls is shown. There were no significant differences between combinations of daytime and depth.

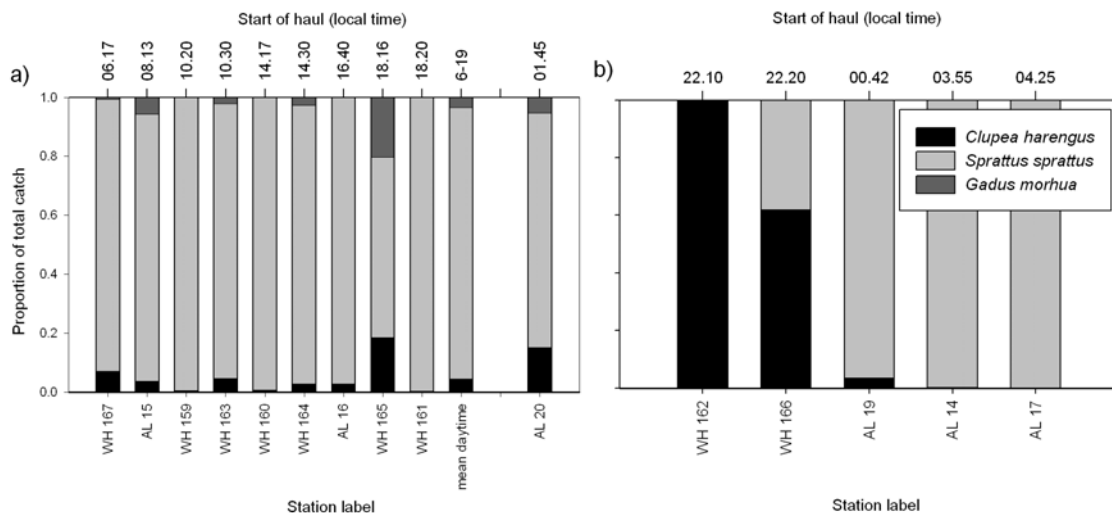


Fig. 10.5. Catch-composition in two depth strata at different times of the day during the 48h-sampling in Bornholm Basin in June 2001. Given is the start-time of the haul (in local time) at the top of each diagram and the station label at the bottom of the diagram (WH='Walther Herwig III'; AL='Alkor'). Caught species are herring, sprat and cod. a) Catch-composition of individual fishery-hauls, which were carried out during daytime below halocline, mean catch-composition during daytime and catch-composition of a haul which was conducted below the halocline during night. b) Catch-composition of night-hauls near the surface.

The acoustic measurements supported the results derived from catch data. During the dark-period, between 23h and 3:30h, almost all clupeids were found above the thermocline. Sprat and herring were distributed in a diffuse layer at this time. No schooling behaviour was observed in the echograms (Fig. 10.7 top). Below the thermocline and above the halocline no

fishes were observed at this time. The detected single-targets below the halocline during night suggest that almost no clupeids were present there, but only cod.

Already at 3:30h, one our before sunset, single echoes in the near-surface-layer unhinged and began to migrate downwards (Fig. 10.7 mid), so that single-echoes were found in the mid-water. Catch data (Fig. 10.5b; Tab. 10.1) suggest, that these echoes were herring. Due to the beginning downward migration of clupeids, the number of echoes below the halocline increased slightly. Simultaneously, the remaining sprat formed small schools above the thermocline (Fig. 10.7 mid). These schools began a relative fast downward migration directly before the sunset (Fig. 10.7 lower panel). Immediately after the sunset, most echoes were found below the halocline, whereas most small clupeid-schools dissolved again below the halocline (Fig. 10.8 top). Schools were formed again around 08:00h, as they can be found during daytime (Fig. 10.8 mid).

During daytime (between 5h and 20h), the weighted mean depth of echo-profiles was found in a water layer between the halocline and the oxygen-depletion zone (Fig. 10.4b). Usually the depth range occupied by echoes was quite narrow. Intense echoes of clupeid schools above the halocline were only measured sporadically. Most of these schools were observed above the summer thermocline. The weighted mean depth for the corresponding echo-profiles was calculated at shallower depth in these cases. After 19h clupeid-schools dissolved again and occupied a wider depth-range compared to day-time (Fig. 10.8 lower panel). The upward migration of clupeids in the evening was finished at 22:30h, i.e. 1 hour after sundown (Fig. 10.4a and b).

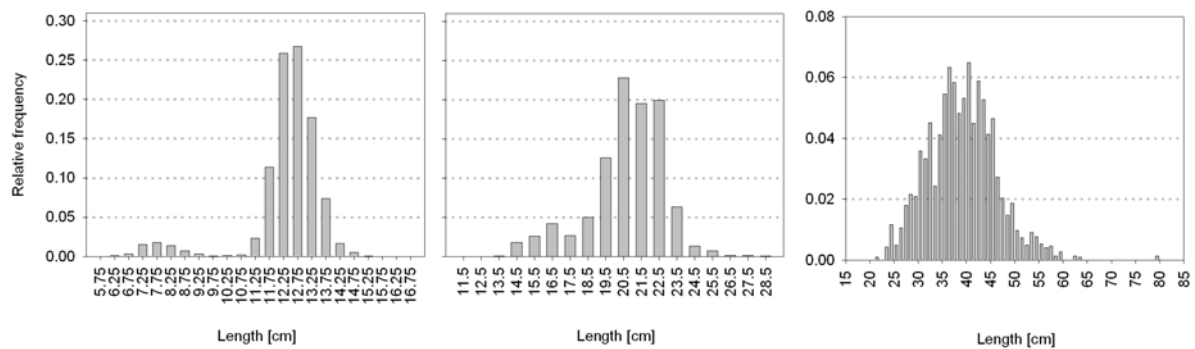


Fig. 10.6. Mean length-distributions of fishes in June 2001 at the sampling site in the Bornholm Basin (central Baltic Sea). Left: Sprat. Mid: Herring. Right) Cod.

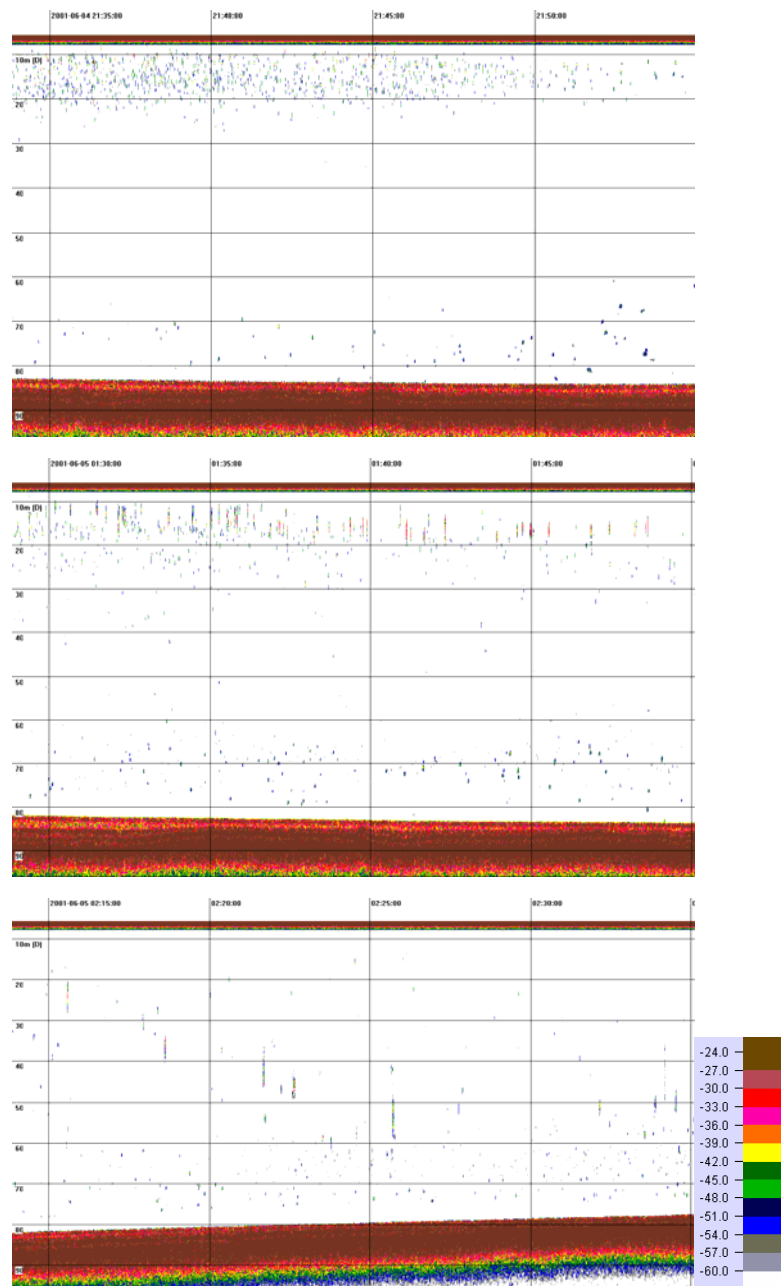


Fig. 10.7. Diel rhythm of fish echoes during 48h sampling in June 2001; shown are echogram recordings from the 04th to the 5th June 2001. Colours represent Sv-echo values in dB (see legend); the line in the top of each echogram indicates the transducer-depth, whereas the lower intense red area represents the bottom. Top) 23:30h. Mid) 03:30h. Lower) 04:15h. Times stated in the echograms are UTC-times (local time – 2h).

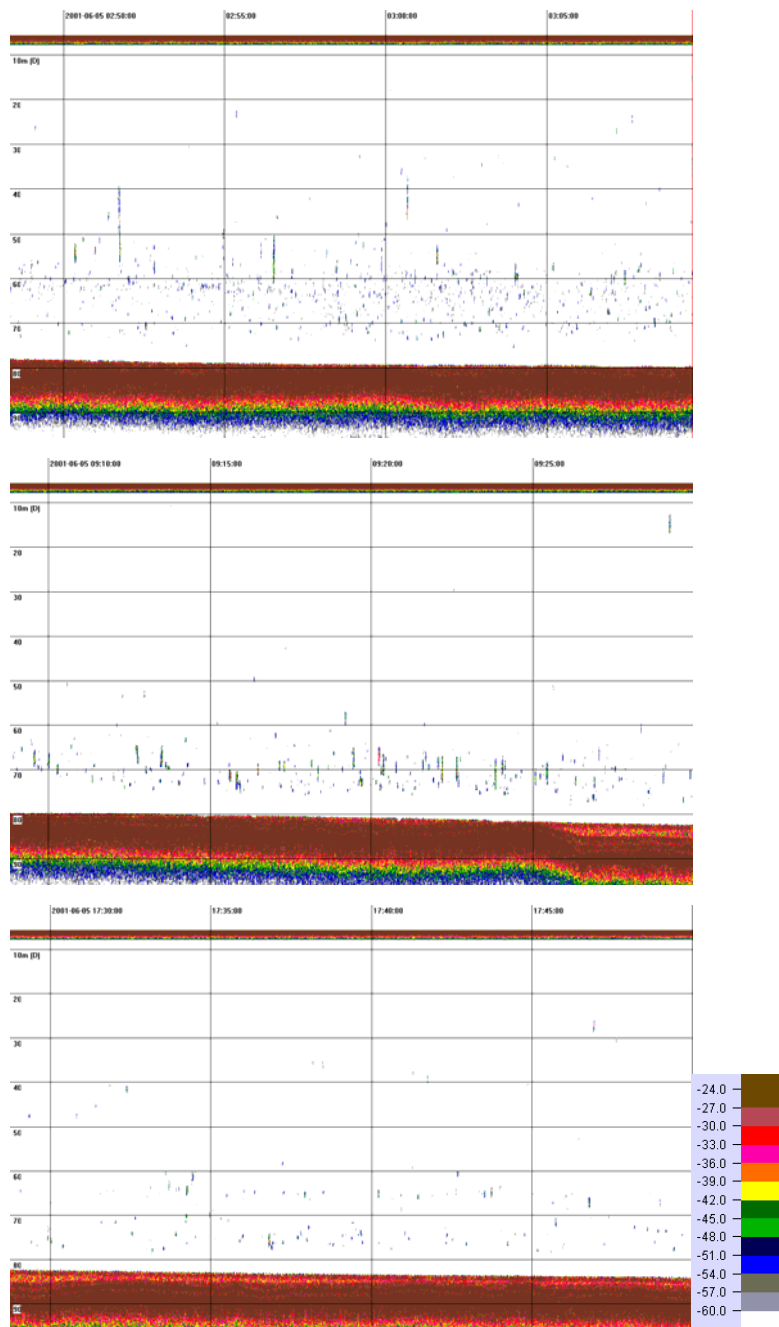


Fig. 10.8. Diel rhythm of fish echoes during 48h sampling in June 2001; shown are echogram recordings from the 04th to the 5th June 2001. Colours represent Sv-echo values in dB (see legend). The line in the top of each echogram indicates the transducer-depth, whereas the lower intense red area represents the bottom. Top) 04:50h. Mid) 11:10h. Lower) 19:30h. Times stated in the echograms are UTC-times (local time – 2h).

10.5. Discussion

The aim of the present study was to investigate the diel vertical migration of pelagic fishes in the central Baltic Sea. For that purpose, trawl catches were combined with hydroacoustic measurements, which allow a high resolution of these migration patterns. Diel vertical migration patterns of herring, sprat and cod were described at species level.

The overall hydrographic situation observed during the investigation was typical for the Bornholm Basin during stagnation periods, with a clear halocline and decreasing oxygen levels with depth, resulting often in an oxygen-depleted layer above bottom (e.g. Matthäus and Franck 1992). The temperature-profile was also consistent with previous observations of thermal mixing, due to cooling of surface waters in winter followed by a re-establishing of thermal stratification during spring and summer (Møller and Hansen 1994, Tomkiewicz *et al.* 1998, Gröhslers *et al.* 2000).

As known from previous investigations (e.g. Orłowski 1991, Gröhslers *et al.* 2000, Szczucka 2000) in spring and early summer, clupeids usually stay below the halocline during day and near the surface during night. The daytime distribution of all fishes was limited at depth by low oxygen-levels. According to the restriction of the fish distribution at low oxygen levels, there are hints for an up-doming of the oxygen-depletion-zone where the water-depth became shallower. In Fig. 10.3 one can see, that the lower border of echo-distribution is doming up at shallower areas in the middle of each 2hour sampling interval, which correspond with the part of the transect, where the water is most shallow.

It was not possible to target single clupeid schools in shallower waters during day-time with net-sampling, due to their rareness. Therefore it is not possible to assign these schools directly to either herring or sprat. Nevertheless, catch data suggest (Fig. 10.5; Tab. 10.1), that almost all herring migrated downward before sunrise, but sprat aggregate for the first time above thermocline shortly before sunrise. Taken this into account, it could be possible that some of these aggregated schools do not migrate downward at sunrise and stay during day in upper water layers.

The upward movement of clupeids at dusk was intensively described by Nilsson *et al.* (2003) for a sampling during March 2002. A large fraction of pelagic schools dispersed in deeper water layers, whereas the other part migrated as non-dispersed schools into surface layers following defined light levels. The upward movement of dispersed fishes began later and was much slower. This resulted in a widening of depth distribution of fish-echo signals. Catch data from the present study showed clearly, that herring dominated catch composition from early night hauls in the upper water layer. This indicates that herring move upward as school, whereas sprat probably migrates upward after dissolving of schools.

Below the halocline at dark hours only single targets were detected with a range of target strength, which indicate cod as echo-source. This was in agreement with previous investigations (Tomkiewicz *et al.* 1998) from May 1995 where analyses of single-targets suggested no clupeids in deep water during night. With these findings, clupeids caught during deep night-hauls seem to be an artefact, caused by slacking and heaving the net through near-surface-layers with high density of clupeids. The extraordinary small numbers of clupeids in that haul confirms this hypothesis. However, Cardinale *et al.* (2003) reported on a deep-haul in October 1997, where clupeids were caught during night, but no comparison of day-night differences in fish numbers, caught in deeper water layers was given.

In addition to a time-shift between herring and sprat during upward migration at dusk, a time-shift during downward migration at dawn was found. The downward movement of herring started earlier in the morning without a prior aggregation into Schools. In contrast sprat aggregated around sunset after schooling. It is not clear, why most of the schools dissolve again after reaching their day-time habitat. A possible explanation could be a light level below schooling threshold, which will be sufficient in deep water layers later in the morning.

It should be noted, that herring and sprat showed vertical migration while the intermediate water was relatively cold (3.4°C in minimum). Beside this absolute value, relative gradients of temperature seem to be important for inhibiting vertical migration of clupeids. During other survey-periods in Bornholm Basin with stronger temperature gradients a vertical migration into shallower depth at dusk did not occur, while the absolute temperature was much higher (Stepputtis pers.comm.). This is in accordance with previous studies about gradient-dependent inhibition of vertical migration of clupeids (Blaxter and Holliday 1963).

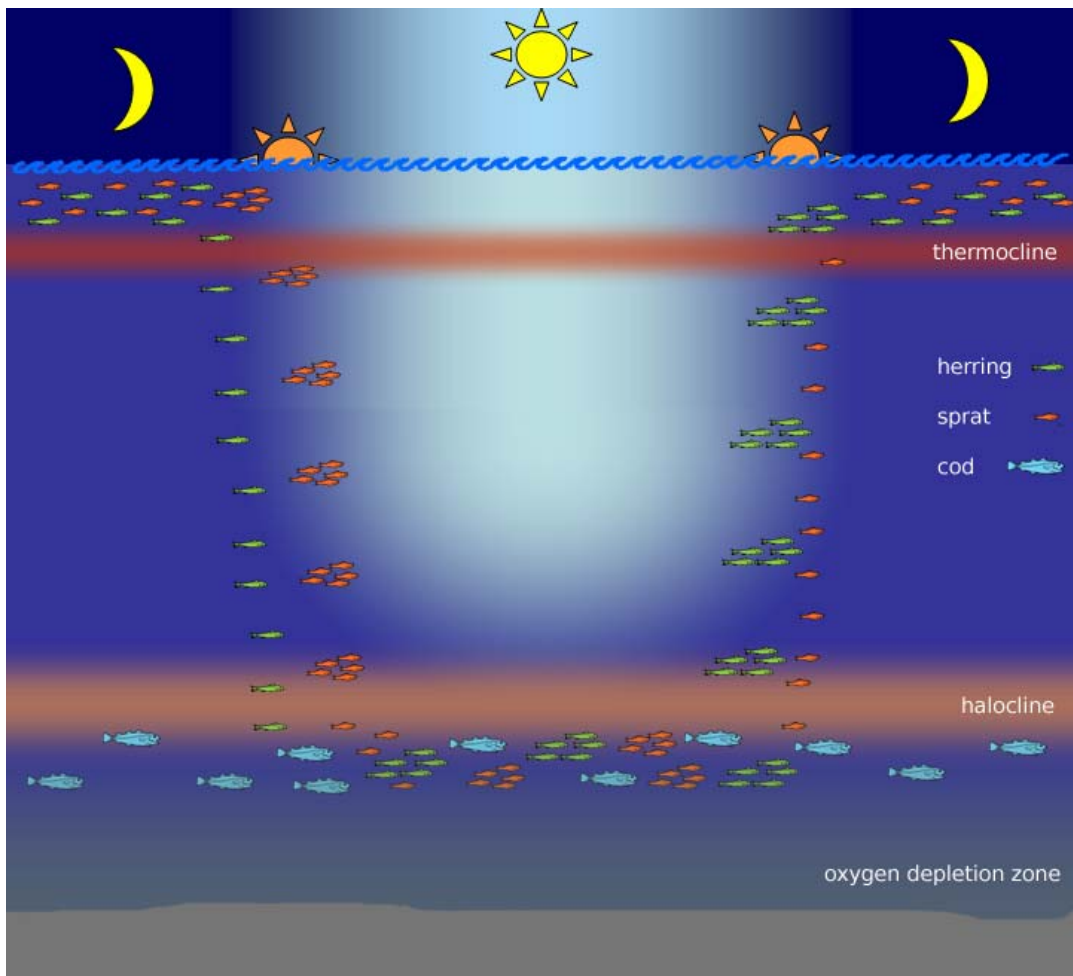


Fig. 10.9. Schematic presentation of the diel vertical migration of herring, sprat and cod in the central Baltic Sea during summer.

Hydroacoustic methods were used occasionally for describing diel rhythm in the Baltic, whereas acoustic backscatter usually being used as proxy for non species-resolving fish density (e.g. Orłowski 2000, Orłowski 2001, Cardinale *et al.* 2003, Nilsson *et al.* 2003, Orłowski 2005) or even as proxy for a combined fish and zooplankton pattern (Szczycka 2000). Due to high abundances of clupeids during the last decade, the overall pattern of diel characteristic of acoustic backscatter is highly influenced by the combined vertical migration pattern of herring and sprat. As seen in the present study, there are differences between the three most important fish-species in the central Baltic Sea (herring, sprat and cod). These results show that vertical migration-behaviour of fish is not homogeneous in the Baltic, and should therefore taken into account, when investigating e.g. temporal predator-prey overlap, timing of spawning, diurnal changes in acoustic characteristics of scatters in the Baltic etc.

The presented data suggest, that

- Herring, sprat and cod occupy almost the same water layer below halocline during daytime
- Herring and sprat undertake diel vertical migration
- Herring migrate upward earlier in the evening than sprat (as school)
- Sprat schools dissolve before rising up
- Herring migrating downward earlier in the morning than sprat (as individual fish)
- Sprat aggregate in surface layer before beginning their downward movement
- Cod don't migrate into shallower depth during night

The reasons for diel migration pattern of sprat, herring and cod were not directly investigated in the present study and have to be investigated in additional investigations.

10.6. *Acknowledgements*

We like to thank cruise participants and crew of RV 'Alkor' and RV 'Walther Herwig III'. Without their hard work, field sampling in May 2001 would not be possible.

Description of the individual scientific contributions to the multiple-author papers

The chapters of this thesis were written as manuscripts, with multiple authorship. This list identifies the contribution of the authors.

Manuscript 1 (chapter 1 on page 27): *Seasonal variation in fish abundance and distribution patterns in the central Baltic Sea under the influence of major Baltic Inflows 2002 and 2003*

Daniel Stepputtis did text writing, graphical presentation and most analyses. Dr. Uwe Böttcher and Eberhard Götze provided abundance data for May surveys. Dr. Gerd Kraus provided helpful comments to improve earlier versions of the manuscript. Cruise participants were instrumental during field sampling.

Manuscript 2 (chapter 4 on page 39): *Meso-scale hydrographic features in the central Baltic Sea and their influence on the distribution and vertical migration of sprat*

Daniel Stepputtis did all analyses, the text writing and graphical presentation. Hans-Harald Hinrichsen provided the modelled hydrography. The field sampling onboard RV 'Walther Herwig III' was planned and conducted by Daniel Stepputtis, Dr. Uwe Böttcher, Eberhard Götze and Hans-Harald Hinrichsen. Volker Mohrholz delivered valuable support while writing the manuscript.

Manuscript 3 (chapter 5 on page 53): *Observed and modelled vertical distribution of Baltic sprat*

Daniel Stepputtis did all analyses, the text writing and graphical presentation. Dr. Uwe Böttcher and Eberhard Götze provided data of RV 'Walther Herwig III'-cruises. Daniel Stepputtis and Ken Haste Andersen developed the presented model of vertical distribution. Dr. Jörn Schmidt and Dr. Gerd Kraus, were instrumental during field sampling and provided helpful comments to improve the manuscript.

Manuscript 4 (chapter 6 on page 77): *Modelling the vertical distribution of adult sprat in the central Baltic Sea*

Daniel Stepputtis did all analyses, the text writing and graphical presentation. Dr. Thomas Neumann provided helpful support during the early phase of model-development. Dr. Jörn Schmidt provided helpful comments to optimize the model and early versions of the manuscript.

Manuscript 5 (chapter 7 on page 93): *The role of habitat heterogeneity for the vulnerability of marine zooplankton to predation: implications for trophic cascades*

Dr. Christian Möllmann did all analyses, the text writing and graphical presentation in close cooperation with Daniel Stepputtis, Prof. Dr. Axel Temming, Matthias Bernreuther and Dr. Friedrich W. Köster. Daniel Stepputtis provided biological background data for adult sprat. Zooplankton and stomach samples were analysed by a sorting centre in Poland.

Manuscript 6 (chapter 10 – Annex on page 131): *Diel vertical migration of sprat, herring and cod in the central Baltic Sea*

This manuscript is derived from the Diploma thesis of Daniel Stepputtis (Stepputtis 2001) and is included to supplement the description of vertical distribution of sprat in general and to give a detailed description of the dataset, which was used in chapter 6.

Daniel Stepputtis did all analyses, text writing and graphical presentation. Dr. Uwe Böttcher, Eberhard Götze and Dr. Christian Möllmann provided help during planning and conducting the field sampling in May 2001. Authors provided helpful comments to improve the manuscript.

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Curriculum vitae

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1994-1995	Zivildienst in Behinderten- und Altenheimen
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Erklärung

Hiermit erkläre ich, dass die vorliegende Dissertation selbständig von mir angefertigt wurde. Die Dissertation ist nach Form und Inhalt meine eigene Arbeit und es wurden keine anderen als die angegebenen Hilfsmittel verwendet. Diese Arbeit wurde weder ganz noch zum Teil einer anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegt. Dies ist mein einziges und bisher erstes Promotionsverfahren. Die Promotion soll im Fach Fischereibiologie erfolgen. Des Weiteren erkläre ich, dass ich Zuhörer bei der Disputation zulasse.

Kiel, den 30.05. 2006

Daniel Stepputtis