Alfred Wegener Institute
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Spatial and temporal distribution patterns of zooplankton in the central Baltic Sea and methods to detect them

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These laws, taken in the largest sense, being Growth with Reproduction; Inheritance which is almost implied by reproduction; Variability from the indirect and direct action of the external conditions of life, and from use and disuse; a Ratio of Increase so high as to lead to a Struggle for Life, and as a consequence to Natural Selection, entailing Divergence of Character and the Extinction of less-improved forms. Thus, from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows.

There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.

Charles Darwin, 1859
The origin of species - Chapter XIV

Abstract

English abstract

The Baltic Sea is the largest semi-enclosed brackish sea in the world and consists of several consecutive deep basins. Due to fresh water input, physical processes and topographic structures pronounced hydrographic stratifications persist. These stratifications are created from water masses of incompatible densities due to different temperatures and salinities. In the Bornholm Sea, a central basin of the southern Baltic Sea, a permanent density gradient is found in a depth of approximately 60 m (halocline) that demarcates less from more saline waters below. During summer another discontinuity layer is found in the upper 20-30 m (thermocline). This thermocline separates the warm surface water from the cooler winter water.

In this thesis the utilisation of the hydrographic layers by the dominant zooplankton species of the Bornholm Basin was investigated. A total of 832 multinet samples from different sites and depths were analysed for zooplankton composition and the relation to ambient environmental parameters by means of multivariate methods, weighted depth centroids and individual analyses of the vertical distribution. It was found that certain species and developmental stages are bound to distinct layers and partially migrate between them during the season. The aquatic layers put different demands on the physiology of the individual species and can therefore be conceived as habitats, determining the vertical distribution. A total of five different utilisation modes of the water column were identified. These utilisation modes are closely correlated to hydrographical volumes and represent characteristic zooplankton assemblages. Differences between the utilisation modes are partially subjected to seasonal variability. Potential effects of the segregation of the zooplankton community on the trophic system of the Bornholm Sea are discussed on the basis of the identified utilisation modes. Correlations between the heterogeneous habitat utilisation, climatic changes and an observed regime shift since the 1980s were revealed. Furthermore, to facilitate the analysis of such data, a software tool was compiled that imports, creates and displays the various data formats and also performs initial calculations.

When assessing the vertical distribution of plankton using nets the depth integration is a limiting factor intrinsic to the method, making a precise assessment of zooplankton species in different horizons more difficult. To solve this problem a new concept for optical *in-situ* detection of minute plankton species is introduced. A central aspect in the development of

such a high magnification photographic detection system was the design of suitable illumination devices, as the amount of light, i.e. the luminous flux, has to be increased exponentially with increasing magnification. The technical solutions presented create a suitable image illumination using high resolution digital cameras while allowing for simultaneous estimation of the photographed water volume. The constructed prototype was able to acquire images of plankton and particles in the water and stores them together with their simultaneously measured ambient environmental parameters. This system thus allows for a more efficient data acquisition as compared to net catches.

Deutsche Zusammenfassung

Die Ostsee ist das größte brackige Binnenmeer der Erde und besteht aus einer Abfolge mehrerer tiefer Becken. Aus Süßwassereintrag, physikalischen Prozessen und topographischen Strukturen resultieren ausgeprägte hydrographische Schichtungen. Diese Schichtungen rühren von Wassermassen her, welche sich in der Kombination der Parameter Temperatur und Salzgehalt unterscheiden und in der Folge unterschiedliche Dichten aufweisen. Im Bornholmbecken, einem zentralen Becken der südlichen Ostsee, findet sich in etwa 60 m Tiefe eine kontinuierliche Dichtesprungschicht (Halokline), die geringer saline Wassermassen von höher salinen, und dadurch schwereren, darunter abgrenzt. In den obersten 20-30 m findet sich eine weitere, saisonal ausgebildete Sprungschicht (Thermokline), die warmes Sommerwasser an der Oberfläche vom kühleren Winterwasser über der Haloklinen trennt.

In dieser Arbeit wurde die Nutzung der hydrographischen Schichten durch die dominanten Zooplanktonvertreter des Bornholmbeckens untersucht. Mit Hilfe multivariater Methoden, gewichteten Dichteschwerpunkten der Tiefenverteilung und individueller Analyse der Vertikalverteilung wurden insgesamt 832 Multinetzproben von unterschiedlichen Stationen und Tiefen bezüglich ihrer Zooplanktonzusammensetzung untersucht und in Relation zu den jeweiligen Umgebungsparametern gesetzt. Dabei stellte sich heraus, dass Arten und Entwicklungsstadien jeweils an einzelne hydrographische Schichten gebunden sind und teilweise saisonal zwischen diesen wechseln. Diese Schichten stellen unterschiedliche Anforderungen an die Physiologie der Plankter und können als Habitate aufgefasst werden, welche die Vertikalverteilung von Arten beeinflussen. Insgesamt wurden fünf verschiede Nutzungsmodi der Wassersäule identifiziert. Diese Nutzungsmuster sind eng an hydrographische Bereiche gekoppelt und zeigen charakteristische Zusammensetzungen der Zoo-

planktongemeinschaft. Die Unterscheidung zwischen den Nutzungsmustern ergibt sich teilweise aus der saisonalen Veränderungen der Hydrographie. Anhand der identifizierten Nutzungsmodi werden mögliche Auswirkungen der Separierung der Zooplanktongemeinschaft auf das trophische System des Bornholmbeckens diskutiert. Mögliche Zusammenhänge zwischen der heterogenen Habitatnutzung, klimatisch bedingten Änderungen der Hydrographie und einem beobachteten Regime Shift seit Beginn der 1980er Jahre werden aufgezeigt. Für die Datenverarbeitung wurde ein Softwarewerkzeug erstellt, welches die für die verwendeten Analysen benötigten Datenformate liest, erzeugt, darstellt und grundlegende Berechnungen durchführt.

Für die Untersuchung vertikaler Verteilungsmuster von Zooplanktern stellt die methodisch bedingte Tiefenintegration von Planktonnetzen einen limitierenden Faktor dar, der die Genauigkeit der Zuordnung einzelner Zooplankter zu unterschiedlichen Horizonten verringert. Um diesem Problem zu begegnen, wurden im Rahmen dieser Arbeit Konzepte zur optischen *in-situ* Detektion von kleinen Planktern vorgestellt. Da die Beleuchtungsstärke mit zunehmender Vergrößerung ansteigen muss, war ein zentraler Aspekt die Entwicklung von geeigneten Belichtungsinstrumenten. Die hier vorgestellten Optionen ermöglichen eine ausreichende Belichtung für die Bilderfassung mit gleichzeitiger Volumenabschätzung durch hochauflösende Digitalkameras. Diese Konzepte sind in einem Prototyp umgesetzt worden. Dieser soll es ermöglichen, photographisch erfasste Organismen und Partikel in Bezug zu gleichzeitig gemessenen physikalischen Umgebungsparametern zu setzen. Damit wird eine sinnvolle Ergänzung zu Netzfängen geboten.

Index

1. Introduction

1.1. Vertical distribution of zooplankton

1.1.1. Biological oceanography

The presence of discontinuity layers is a ubiquitous and recurrent feature in the world oceans. Of eminent biological importance are inhomogeneities in temperature, salinity and oxygen. These environmental parameters have a profound impact on the physiological conditions of zooplankton communities. Differences in zooplankton distribution often coincide with different water masses characterised by these three physical parameters (e.g. Fager & McGowan 1963, Owen 1989, Geller et al. 1992, Roemmich & McGowan 1995). In contrast to changes in oxygen levels, alterations in temperature or salinity influence the density of a body of water. Surface layers, heated by solar radiation, become lower in density and stratify over cooler and denser water layers. A thermocline marks the transition zone between layers of different temperatures and the stratification becomes more stable when the thermal gradient increases (e.g. Lalli & Parsons 1997). Removal or addition of fresh water changes the salinity and in turn also the density of seawater (e.g. Brown et al. 1998). As evaporation and freezing remove fresh water, the increasing concentration of dissolved salt in the remaining water volume increases its density. Conversely, precipitation, melting and river run-off decrease the salinity and cause lower densities. An area in which salinity changes rapidly with depth is termed halocline and separates waters of different densities vertically (e.g. Lalli & Parsons 1997). Stable clines generally separate water masses of different temperature and salinity combinations and can form stacked volumes of diverse ecological conditions on scales from centimetres to several hundreds of metres. Such clines often restrict mixing of adjacent layers and impact vertical processes of physical and biological exchange (Brainerd & Gregg 1995) and interrupt exchange processes between the euphotic zone and the mesopelagic (e.g. Humboldt Current: Escribano et al. 2004; California Current: Alldredge et al. 1984, Roemmich & McGowan 1995; Black Sea: Vinogradov 1993). Also in estuaries strong stratifications can reduce vertical exchange (Denman & Gargett 1988) and impact both primary and secondary production in of yet not completely understood ways (Owen 1989, Cowles et al. 1998). When water masses with a higher density are layered over ones of lower density, the stratification becomes

unstable and the above layer sinks down or admixes with the underlying one. In this case inherent species may be dislocated or face changing environmental conditions.

As many zooplankton species are poikilothermal and have a limited osmoregulatory capability, their distribution patterns are determined by the physiological tolerance for ambient parameters. In addition to physiological demands (Saito & Hattori 1997), the availability of food resources (Hattori & Saito 1997) and ontogenetic migrations (Renz & Hirche 2006) are often important factors for habitat selection. The influence of small scale turbulence on feeding strategies (Maar et al. 2006), histo-geographic traits (Ojaveer et al. 1998, Renz & Hirche 2006) and predator avoidance (Bollens & Frost 1989, Titelman & Fiksen 2004) further affect vertical distribution (Ohman 1988) and can constrain distribution to fringed layers (Gallager et al. 2004). Species adapted to cool waters show submergence towards greater depth at lower latitudes because of higher surface temperatures (Jespersen 1940). As light attenuation restricts primary production to a shallow layer, expelled species need to adapt to alternative food resources to prevent starvation. Small scale zooplankton patchiness and aggregation are effects of the physico-chemical structure of the water column and important features of the environment of planktivorous predators that impact both bottom-up and top-down processes (Owen 1989). As trophodynamic relationships in pelagic systems depend on temporal as well as spatial overlap, the understanding of mechanisms that lead to different vertical distributions is essential (Banse 1964). However, regarding zooplankton ecology, variability in the vertical plane is probably more important than in the horizontal plane (e.g. Dagg 1977, Longhurst & Harrison 1989). The match-mismatch theory (Cushing 1975, Cushing 1990) and most successors dealing with food requirement of fish larvae just consider temporal aspects and neglect heterogeneities in vertical distribution.

1.1.2. The Baltic Sea

The semi-enclosed Baltic Sea (Figure 1.1) is characterised by a strong fresh water influence. It covers an area of approximately 412.560 km^2 and is the largest brackish water system of the world (Fonselius 1970). Freshwater supply from river run-off and precipitation from the riparian states dilute the surface layer (Brogmus 1952, Fonselius 1970). Water exchange with the North Sea takes place via the connection of Skagerrak and Kattegatt, the only gateway for saline waters to enter this marginal sea. Dense saline waters are captured in the troughs and replaced during inflow events from the North Sea with highly saline and
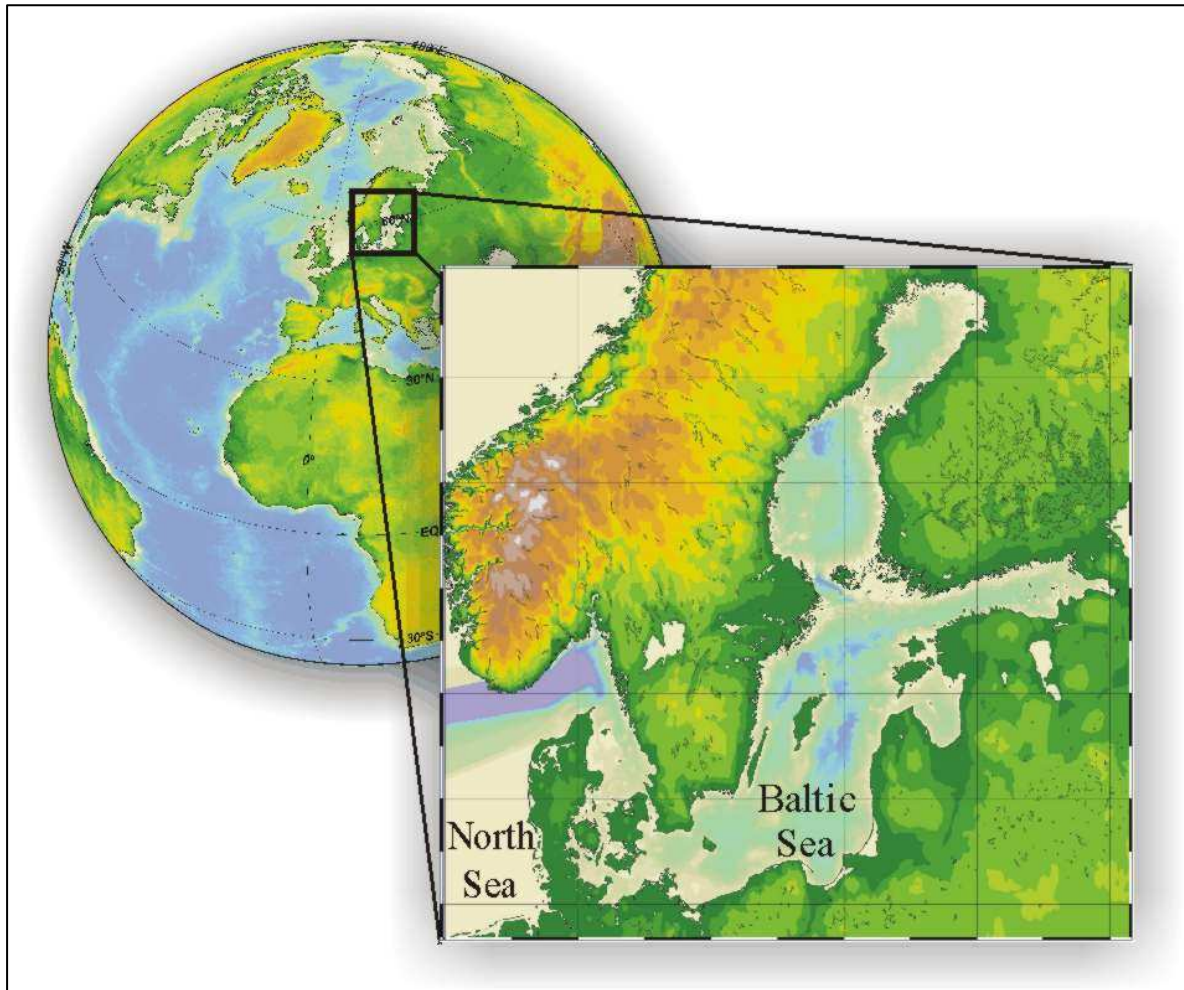
Figure 1.1: The Baltic Sea.

oxygenised waters (Matthäus & Schinke 1994). Sills separate several consecutive deep basins and constrain the exchange of high saline waters in the deep (Matthäus 1995). They also restrict propagation of haline waters from the North Sea towards the innermost basins. Inflow events are related to atmospheric circulation patterns and often separated by long stagnation periods (Matthäus & Franck 1992, Matthäus & Schinke 1994, Matthäus 1995, Lehmann et al. 2002). During these periods conditions below the halocline deteriorate due to decomposition processes of organic matter and lead to hypoxic or anoxic conditions in the deep, and only a narrow zone of oxygenated water remains below the halocline (Fonselius 1970). The decrease in salinity from the Skagerrak towards the eastern end is accompanied by distinct floral and faunal alterations (Bonsdorff 2006). In addition to a halocline, a seasonal thermocline establishes in spring and persists until fall. It separates the warm surface layer from the intermediate winter-water and forms a three-storeyed ecosystem of water masses with different thermal and haline combinations (Figure 1.2). The steep vertical gradients between the different layers make the Baltic Sea a unique study site
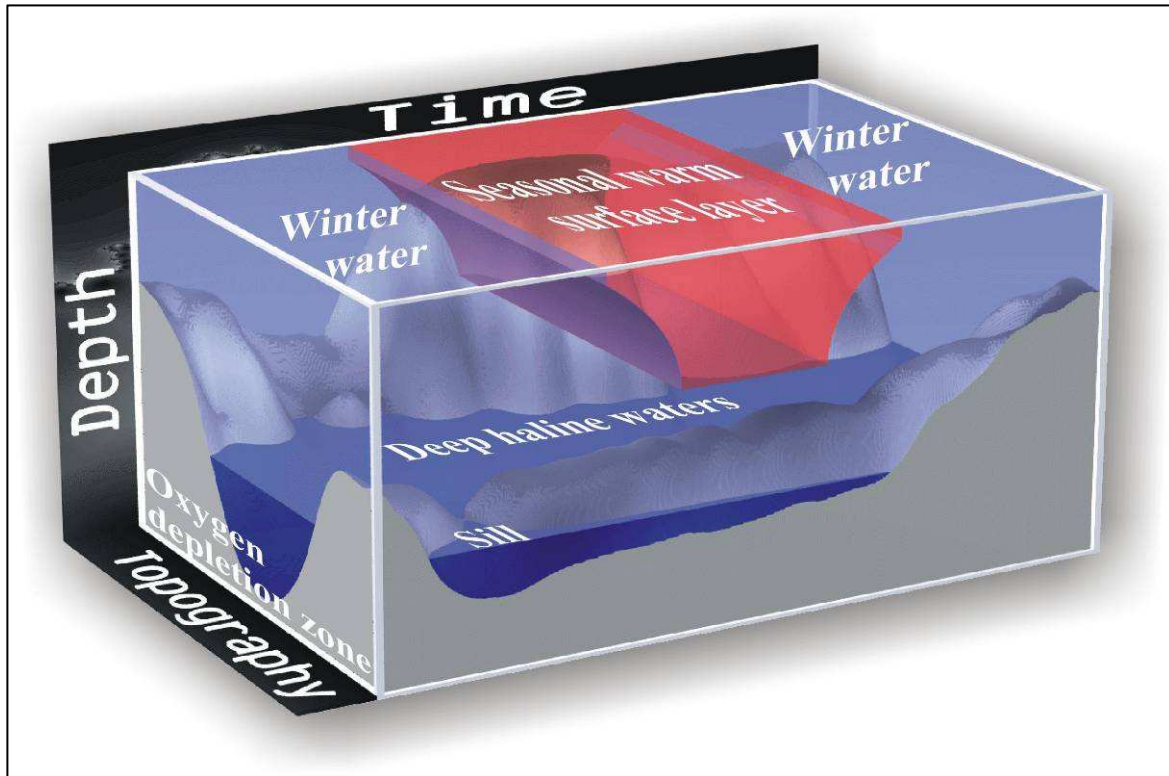
Figure 1.2: Schematic overview of the seasonal hydrographic situations in the Baltic Sea. During summer the seasonal thermocline compresses the continuously present winter water to a narrow layer between the thermo- and halocline. Due to its higher density the deep haline waters are restricted to troughs defined by local topography. The local topography that different layers interact with is independent from the time scale.

to investigate the relationship between hydrographic structures and the zonation of zooplankton. From a geological view the Baltic is a young sea, with biotic colonisation closely related to events after the last glacial period (Voipio 1981, Andrén et al. 2000, Andrén et al. 2002, Bonsdorff 2006). Consequently, few endemic species are found in this brackish environment (Ackefors 1969) and the characteristic low diversity of brackish systems (Remane & Schlieper 1971) results in unoccupied ecological niches (Elmgren 1984). The zooplankton community in the Baltic Sea consists of freshwater, brackish and marine species (e.g. Ackefors 1969, Remane & Schlieper 1971, Hernroth & Ackefors 1979, Ojaveer et al. 1998). Both horizontal and vertical distribution of zooplankton species is influenced by temperature and salinity gradients (Ackefors 1969, Hernroth & Ackefors 1979, Hansen et al. 2004) which also affect population dynamics (Viitasalo et al. 1995a, Viitasalo et al. 1995b, Vuorinen et al. 1998, Ojaveer et al. 1998, Dippner et al. 2000, Möllmann et al. 2000). While stenoecious species are expected to inhabit a distinct layer with certain hydrographic characteristics, euryoecious species may reside in different strata. Zooplankton investigations by Ackefors (1969) and Hernroth & Ackefors (1979) give a general over-

view on the vertical distribution of different species in the central Baltic Sea, but their low spatial and temporal sampling resolution is not sufficient to determine the main residence layers and life strategies. As several zooplankton species live at the lower limit of their physiological tolerances, small hydrographic changes can alter the structure of the pelagic community significantly (Hernroth & Ackefors 1979). Time series analyses have shown that zooplankton species are strongly affected by episodic inflow events from the North Sea. The decreasing frequency of inflows since the 1980's is responsible for observed shifts in the ecosystem structure due to changes in the hydrographic regime (e.g. Ojaveer et al. 1998, Möllmann et al. 2000, Möllmann et al. 2002).

1.1.3. Trophodynamic interactions

In the Baltic Sea a few key-species dominate the zooplankton community. These are major contributors structuring the ecosystem and hence crucial for the successful recruitment of higher trophic levels (Alheit et al. 2005). The commercially important fish species sprat (*Sprattus sprattus* L.), herring (*Clupea harengus* L.) and cod (*Gadus morhua* L.) are at least in early life stages planktivorous (e.g. Last 1980). The vertical distribution of their larvae and juveniles is subjected to hydrographic and environmental parameters and therefore their feeding sites are located at different depths (Voss et al. 2002, Voss et al. 2003). As many zooplankton species have potentially a similar role in the food web, inhomogeneous aggregation patterns would result in different prey fields among the layers. The feeding behaviour of fish is often triggered by parameters such as size, visibility, pigmentation, encounter rate or detectionable hydrodynamic cues created by the prey (e.g. Flinkman et al. 1993, Viitasalo et al. 2001 and references therein). In the case of different vertical zooplankton distributions an inhomogeneous access to this resource needs also to be considered. To investigate vertical distribution patterns requires a parallel evaluation of the abundance of dominant zooplankton species in different depths. Distinguishable groups and alterations between layers may impact eminent structures of the food web in terms of regime shift scenarios. Thus, a hydrographic segregation of different types of prey would create functional groups of accessibility.

1.2. Investigative approaches

1.2.1. Numerical ecology

As most traditional investigations regarding the vertical distribution of zooplankton focus on the distribution pattern of single species (e.g. Fager & McGowan 1963) the knowledge about the influence of physical parameters on the community scale is limited. Unequal catch-efficiencies for different species by various net types (e.g. Colton et al. 1980, Nichols & Thompson 1991) further bias abundance estimations. While fine mesh sizes cause retention by impact pressure, coarser mesh sizes do not catch smaller but yet important individuals adequately. Gelatinous zooplankton and other fragile taxa are often completely destroyed after contact with net gauze. To analyse the influence of stratification on the vertical distribution of zooplankton with numerical approaches requires a pool of stratified, small scale zooplankton data assigned to hydrographic measurements. Numerical methods can integrate all available information in a single analysis. While physical readings represent punctual measurements, zooplankton samples obtained by net catches integrate over a distinct range in the water column (e.g. Wiebe & Benfield 2003 and references therein). To find the parameters that explain most of the observed variances one is mainly faced with these problems. The assignment of two parameters, measured on different scales, with each other requires the conversion of one parameter. Thus, data with higher resolution are normally integrated to avoid initial extrapolation errors. Simplification can be achieved by using means and indices, representing complex characteristics as single values or matrices. However, one has to take into consideration that information content is rejected and artificial dependencies may be created. Multivariate approaches have proven to be powerful tools to extract meaningful results from highly variable data. They consider variables equally important at the start of the analysis to distinguish responses on given parameters (Manly 1994), but are susceptible for a violation of initial assumptions. Absence of factors like multivariate normality or independence of two or more variables to a given parameter reduces the power of a model. Such artificial dependencies can evolve from the integration of values over a certain range and require the exclusion of variables from complex analyses. Thus, relationships can be resolved by the variables included, but anticipate investigations on the full range of available data. More sophisticated methods and tools are capable to consider and partially compensate these facts. Nevertheless, it is desirable to substitute integrative measurements by ones on single specimens. Subsequently the need for new

methods has been discussed for decades (e.g. Banse 1964, Bergeron et al. 1988, Kils 1989, Tang et al. 1998, Tiselius 1998).

1.2.2. Optical methods for remote sensing of zooplankton

Since the 1950s several optical systems have been developed that provide a number of advantages over net-based systems (e.g. Foote 2000). Today the use of digital in-situ imaging techniques in combination with sensors for environmental parameters may allow achieving the goal of small-scale investigations over large horizontal and vertical distances. The image forming system takes pictures of randomly distributed species and objects in waters with a relative movement, passing the observation area of the camera. Sensors record the ambient environmental parameters and store them in a way that they can be assigned properly to the images. To ensure taxonomic identification, the submersible optical systems need to manage several problems. High magnification and short distances result in a small depth of field and high proportions of out-of-focus objects (e.g. Strickler 1977). Moreover, object blurring is a function of camera-object distance and water clarity (e.g. Pollio et al. 1979). Furthermore, short shutter times are required to avoid motion blurring (Mustard et al. 2003). To quantify abundances various approaches have been developed to gauge the volume that is imaged per frame.

Through-flow chambers constrain the volume physically to the camera's depth-of-field and provide easily manageable and reproducible illumination, although fine-scale patterns and fragile species are affected by the concentrating process for the chamber (e.g. Wieland et al. 1992). The volumes of images taken within a certain distance of the device are often calculated using software packages and adjusted to the depth of field by the sharpness of imaged particles (e.g. Davis et al. 1996). These techniques include a variety of uncertainties. The use of highly collimated light over short distances reduces scatter and high background noise from stray light. It also allows quantifying the recorded volume optically. High quality shadow images can be captured by using line scan cameras that image a line light across a flow-through channel (Samson et al. 2001). Based on measured flow values, the line data are assembled by software to a detailed 2D shadow image of the object. To display surface or internal structures of small organisms, a dark field illumination is required, which is even sufficient for transparent taxa (Kils 1989). Several systems (e.g. Benfield et al. 2000, Gorsky et al. 2000, Lunven et al. 2003) profile plankton and marine snow in volumes between 500 to 6500 ml, but cannot image minute species sufficiently for taxo-

nomic identification. These systems use cameras that aim at 90° relative to the illuminated scene. With decreasing volumes and higher magnifications, the required light flux for dark field illumination increases to sufficiently capture small-scale features. While the recording of various physical parameters can be achieved fairly easily, the sufficient imaging of size classes on scales of a few millimetres with a high depth of field is close to the feasible border of optical laws.

In this thesis a new approach of an in-situ imaging system for zooplankton is presented. It allows gauging the volume that is imaged per frame by an optical system. The in-situ imaging system projects a light-frame of known thickness into the water column which is photographed by a digital camera mounted perpendicular to the projected light-frame. With the dimensions of the camera picture the volume can be calculated, while only objects within the light-frame are illuminated.

2. Thesis objective

This thesis was conducted within the frame of the German GLOBEC (Global Ocean Ecosystem Dynamics) project[1], which investigates trophodynamic interactions between zooplankton and fish in relation to reproductive success under the impact of physical forcing. The aim of this thesis was to evaluate the structuring effect of the physico-chemical environment on the zooplankton community. A stratified zooplankton distribution would result in different prey fields for higher trophic levels depending on the hydrography. A central hypothesis on the way to clarifying the question was to determine whether the vertical zooplankton assemblages are different in the hydrographic strata of the Baltic Sea. Samples from different depths had to be distinguishable by variations in the abundance of the species present. Therefore, data from stratified zooplankton samples were evaluated by using three approaches to distinguish compositional patterns. Each approach is summarised in a scientific paper.

1. A Multivariate Discriminant Function Analysis (MDFA, Fisher 1936) was performed for one station in the deepest part of the Bornholm Sea to address the question of whether two or more groups of samples with given measurements can be distinguished based on these variables. Furthermore the influences of hydrographic changes were investigated.

2. As an example for the role of the continuously present halocline, different life strategies of three zooplankton species that survive under these diverse hydrographic conditions were analysed. Weighted means were used to investigate variations in the depth centroid of different zooplankton stocks and allowed to compare seasonal changes.

3. A third analysis was performed at basin scale on the Bornholm Sea. MDFA and traditional methods were used to investigate the vertical distribution of individual taxa and developmental stages in relation to the hydrography.

In preparation for the different analyses a software package was developed as an interface between native data and a range of different data processing tools. It allowed semi-

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[1] www.globec-germany.de

automated calculation of several of the required tables, indices and matrices, as well as charting algorithms. It also aids to create the required output formats for additional investigations and processing steps with other software packages.

As net samples cannot resolve small scale distributions across clines two new and non-invasive approaches for in-situ zooplankton imaging systems have been developed. The approaches allow the quantification of the volume that is observed per image by a combination of illuminating and optical components. In this thesis the concepts are presented that enable a more precise locating of species in relation to the environmental parameters.

1. The first approach projects a frame of light into the water column at which a camera is directed at a 90° angle. The respective illuminating device is mounted autonomously from the camera and uses a unidirectional projection. This approach is introduced by a pending patent application and a technical paper. Additionally, a utility model application and a second technical paper describe improvements in reflector techniques that can be used for this method.

2. The second illumination approach creates a frame of light as a circular device, surrounding the observation volume. The advantage is the reduction of casting shadows by particles in the water column. High power Light Emitting Diodes (LEDs) were used as a light source. As in the previous approach the camera points at the created light frame at an angle of 90°. The approach is introduced with a pending patent application, depicting the underlying thoughts.

In the synopsis chapter the results are summarised and discussed. It emphasises the importance of considering ambient environmental parameters in the evaluation of trophodynamic interactions and furthermore, gives an outlook of how additional remote sensing systems can improve the investigation of zooplankton ecology.

3. Material and methods

3.1. Study area

The study sites for the zooplankton investigations were located in the Bornholm Sea. It is one of the largest basins in the central Baltic Sea (Figure 3.1) with a maximum depth of approximately 100 m. At the western end it is bordered by the Arkona Sea and the isle of Bornholm. At the eastern side the Słupsk Sill marks the entrance to the Stolp Channel and the transition to the Gdansk Deep. The northern and southern ridges are flanked by the land masses of Sweden and Poland, respectively. Inflows of haline waters from the North Sea enter the Bornholm Sea from the north-western side along the deepest connections after traversing the Arkona Sea. The volume of the Bornholm Sea below the halocline, defined by the deepest point of the sill, is approximately 60 m deep, separating the deepest part of the Bornholm Sea from the Gdansk Deep via the Stolp Channel. Haline waters above this level flow over the sill into the next basin and result in a lowering of the halocline down to the level of the sill. Arriving inflows that do not fill the trough of the Bornholm Basin normally stop at Słupsk Sill. For a complete introduction to the hydrographic events of 2002/2003 refer to Feistel et al. 2003a, Feistel et al. 2003b and Feistel et al. 2004.
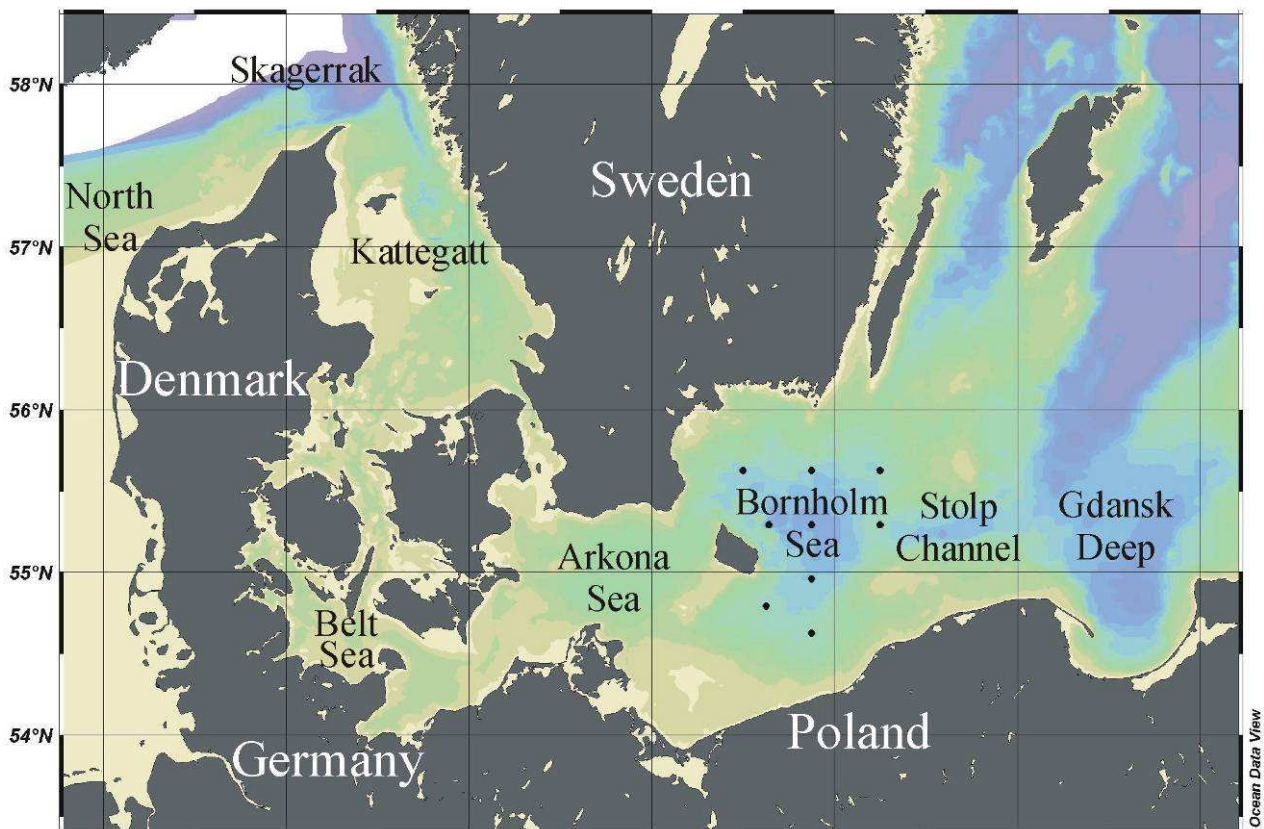
Figure 3.1: The central Baltic Sea. Sampling sites in the Bornholm Sea are marked as black dots.

3.2. Sampling

Zooplankton was sampled at nine stations in the Bornholm Sea (Figure 3.1, Table 3.1) between March 2002 and May 2003 with an almost monthly coverage (Table 3.2). Vertical sampling was performed with a multinet (Hydro-Bios, Kiel; 50 µm mesh size, 0.25 m^2 opening, 0.2 m s^{-1} towing speed) in stacked 10 m intervals from bottom to surface regardless of daytime. Samples were preserved immediately aboard with a borax-buffered 4% formalin-seawater solution. In addition to zooplankton sampling, vertical profiles of temperature, salinity and oxygen were determined by CTD casts.

Table 3.1: Positions of the nine focus stations where zooplankton sampling was performed.

Station name	Latitude (°N) [dec.]	Longitude (°E) [dec.]	Bottom depth [m]
BB0003	55.625	15.000	75
BB0006	55.625	15.750	70
BB0012	55.625	16.500	65
BB0021	55.292	15.283	85
BB0023	55.292	15.750	95
BB0026	55.292	16.500	65
BB0035	54.958	15.750	85
BB0041	54.792	15.250	70
BB0045	54.625	15.750	60

Table 3.2: Schedule of the zooplankton sampling campaigns in the Bornholm Sea obtained during GLOBEC-Germany with the research vessels Alexander von Humboldt (AvH), Alkor (AL) and Heincke (HE).

Cruise	Cruise start [dd.mm.yyyy]	Cruise end [dd.mm.yyyy]
AvH 44/02/08	12.03.2002	22.03.2002
AL 200	02.04.2002	30.04.2002
HE 168	05.05.2002	24.05.2002
AvH 44/02/03	15.05.2002	30.05.2002
AL 205	11.06.2002	23.06.2002
AL 207/208	22.07.2002	07.08.2002
HE 174	12.08.2002	21.08.2002
AL 210	03.09.2002	13.09.2002
AvH 44/02/11	30.09.2002	10.10.2002
HE 181	11.11.2002	29.11.2002
HE 182	13.01.2003	24.01.2003
AvH 44/03/01	10.02.2003	21.02.2003
AL 217	03.03.2003	22.03.2003
AL 219	17.04.2003	28.04.2003
AL 220	15.05.2003	03.06.2003

3.3. Data processing

3.3.1. Enumeration

Multinet sub-samples were analysed by the Sea Fisheries Institute, Gdynia, Poland, for abundance and composition of zooplankton species and developmental stages. At least 500 individuals were counted and analyses were continued until at least 150 individuals of each of the dominant copepod species *Acartia* spp., *Temora longicornis* and *Pseudocalanus acuspes* were found.

3.3.2. Multivariate discriminant function analysis

To investigate whether the zooplankton composition shows distinct differences in relation to different depths and hydrographic conditions a Multivariate Discriminant Function Analysis (MDFA) was performed on the multinet data. The MDFA allows one to investigate whether two or more naturally existing categories can be separated by measured parameters, although these factors do not differ clearly when investigated individually (Fisher 1936). It computes a new variable, the discriminant score, from the discriminant function as sum of the weighted measurements (Equation 3.1). In the application performed in this thesis the abundances of the zooplankton species in each sampling depth represent the measured variables. Each sample needs to be a member of exactly one category. As the aim was to investigate the relationship between the vertical zooplankton abundance and the ambient hydrography, the categories were determined by the parameters salinity and temperature. Three major categories (deep haline waters, intermediate winter water and warm summer surface water) were distinguished. Two more categories were included to account for different types of inflow water. In the preparation for the analysis every sample was algorithmically defined to belong to one of these categories. The MDFA model calculated the probability of a sample to belong to one of the given categories, based on the species composition. This expectation is then compared with the *a priori* defined classification to determine discrimination success. A computerised model was applied to calculate the discriminant classification score *DS* for each case in each category according to equation 3.1.

$$\boxed{DS_c = k_c + \sum_{s=1}^{n} w_{cs} * x_s}$$ **Equation 3.1**

The subscript c denotes the *a-priori* defined hydrographic category, n the number of variables and s the index of each taxon or stage, x_s is the respective abundance of s. The coefficients for the weighing of a variable w_{cs}, the category constant k_c and probabilities are calculated through stepwise regressions (for a complete description of the method refer to Jennrich 1977a, Jennrich 1977b). The automatically computed DS_c shows the probability of a sample to belong to the predefined category c. From the ratio between observed categories and predicted ones the significance of the model can be calculated. Variables have to be on continuous scale with no complete collinearity between two sets, due to the calculation of covariance matrices. For the hypothesis tests normality is required, but not for the method itself (Hair et al. 1998). If normality can not be achieved, alternative measures, like Wilk's Lambda, are available to interpret the significance of the MDFA model (e.g. Rao 1951). The variables that best discriminate between the categories and describe relationships between them can be determined by a subsequent Canonical Analysis (Manly 1994).

3.3.3. Weighted mean depth

As an index of the vertical orientation of the standing stocks the weighted mean depths (WMD) were calculated from abundances and depth information of the stacked samples. The WMD indicates the depth centroid of a stock as a single value. The method itself can be conceived as a weight function, frequently used in statistics and numerics. Elements of higher importance receive a higher loading in the calculation and consequently achieve a more prominent influence on the final result. In terms of species distribution a depth layer with a higher abundance attracts the calculated depth centroid towards its mid range according to equation 3.2.

$$f_{WMD}(i,j) = \frac{\sum_{k=0}^{l_j-1}(m_{ik}d_k)}{\sum_{k=0}^{l_j-1}m_{ik}}$$ **Equation 3.2**

Applied on the multinet data d is the mid-depth of one net's range covered in a haul, i the index of a species or stage, j the station (haul), k the index of the net on the jth station, l the total number of nets on a station and m gives the number of individuals per cubic meter. The representation of a stock as depth centroid requires careful interpretation as specimens can also be present above and below this point. In the case of a homogeneous depth distribution between bottom and surface the range is half of the bottom depth and not necessar-

ily an ultimate measure of the absolute residence layer. If all weights are equal and different from zero the output of the WMD is identical to the calculation of the arithmetic mean. However, the WMD still remains a valuable tool to investigate vertical abundance variations and is most reasonable to use when the sampling depth interval is smaller than the scale on which changes are expected. The WMD was first used for zooplankton investigations by Bollens & Frost (1989).

3.3.4. Conversion of volumetric to area abundance

To investigate horizontal distribution patterns and to determine the total abundance, multinet data were converted to abundances per square metre (*SQM*). With respect to the range covered by a single net in a haul (normally 10 m) the volumetric data were transformed using equation 3.3.

$$f_{SQM}(i,j) = \sum_{k=0}^{l_j-1}(m_{ik}\,n_k)$$

Equation 3.3

Applied to the multinet data, *i* is the index of the species or stage, *j* the station (haul), *k* the index of the net on the *j*th station, *l* the total number of nets on a station, *m* the number of individuals per cubic meter, and *n* represents the depth range of the *k*th net.

3.4. Software development

3.4.1. Ocean Sneaker's Tool

During the investigations various data file formats had to be analysed and processed. The number of different specifications reflects the various research topics as well as the number of different analytic tools used in the GLOBEC Germany studies. To facilitate access and comparison of different file formats a common platform with all-purpose import filters was designed. It allows displaying these data in a unified spreadsheet format. Conversion algorithms to unify or standardise different geographic formats were developed. They create a geo-referenced output used by several software packages for mapping purposes. Additional algorithms were implemented to cover specific processing tasks for marine data. Semi-automatic calculation of weighted mean depths and volumetric conversions is possible. Also basic statistical investigations and multivariate data ordination can be performed and

visualised. These modules were combined and now operate under the name Ocean Sneaker's Tool (OST). Although a wide range of software packages can convert, transform, rearrange and perform data, OST focuses on specific problems relevant to marine biologists. Intermediate steps are kept co-resident and can be accessed. OST was completely written in the Integrated Development Environment (IDE) Delphi 7 Studio from Borland[2]. The TChart® charting components from Steema[3] were additionally installed in the IDE. The project is freely accessible[4] together with the source code and allows users to modify the program for their own purposes.

3.5. Technical developments

3.5.1. Light management

Using in situ imaging of tiny objects, like zooplankton species, for taxonomic identification one is faced with several problems. At first it requires high magnifications, whereas available light decreases approximately by the factor four when magnification is doubled (Figure 3.2). Consequently, the luminous flux provided by the used light source is an important factor. As a second point the distance between the camera lens and the imaged volume needs to be short, as
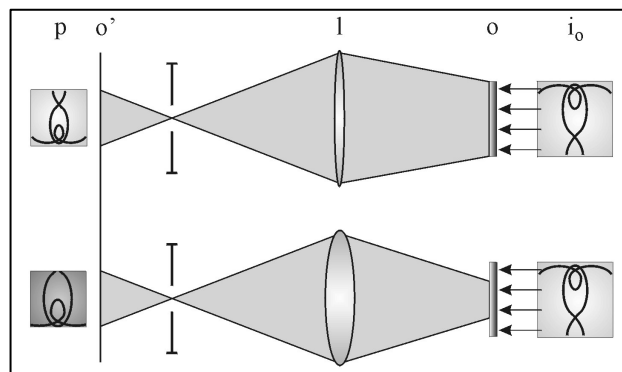
Figure 3.2: Items (i_o) in the object plane are projected by lens systems (l) onto the photosensitive area (p) in o'. At higher magnifications a smaller display window is imaged in o'. Therefore, less photons from the object excite the sensor and an image appears darker at higher magnifications.

particles and dissolved matter can detract image quality. High magnifications at short distances also result in a small depth-of-field (DOF). Points that lie in the object plane are correctly imaged as a point on a photosensitive sensor. With greater distance from the object plane the so called circles of confusion get larger. The DOF is defined as the range within the circles of confusion that remains small enough that a point in the object plane appears to the human eye as a single point (Figure 3.3). In digital imaging it is desirable to

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[2] www.borland.com
[3] www.steema.com
[4] www.awi.de/Software/OST (case sensitive URL)
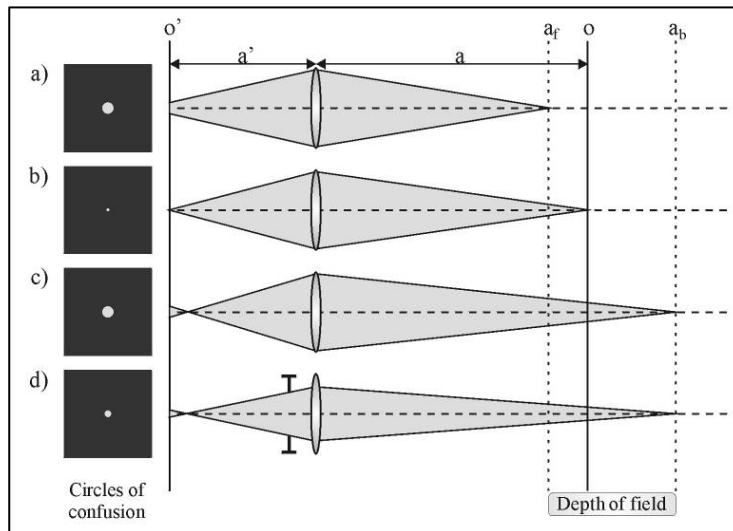
**Figure 3.3: Circles of confusion on the photosensitive area (o')
for a point a) at the near end (a_f) of the depth of field, b) in
the object plane (o) and c) at the rear end (a_b) of the depth of
field. d) The use of a diaphragm improves the image quality,
enlarges the depth of field but less light reaches the photosensitive area.**

keep the diameter small enough to reduce the number of pixels excited simultaneously by the same point. Thus taxonomic features, important for the identification of species, can only be obtained within a narrow depth of field at high magnifications. High f-values (small aperture opening) enlarge the DOF by minimising the circles of confusion, but reduce the utilised light (Figure 3.3d). To quantify the volume scanned per frame requires the knowledge of the width, height and depth of the observed volume. While the first two are physically defined by the size of the photosensitive sensor, the principal axis is infinite and needs to be constrained. As the depth of field is narrow, illumination is only necessary within this range. The approach introduced here is based on an illumination technique that projects a light frame of high luminous flux into the water. The camera aims with an angle of 90° at this light frame, whose depth is in the range of the DOF (Figure 3.4). Particles within this frame are illuminated, while not directly illuminated ones are nearly invisible. Thus, the required clipping along the principal axis is obtained for the depth axis. Consequently, the development of illumination devices with a high light flux and precise targeting is a pivotal precondition for in situ imaging of small planktonic species.

For this, two different approaches were developed (Chapter 4.3). The first was designed as a combination of a linear light source and three cylindrical lenses of different focal lengths (Patent T1, Paper T2). It creates a light frame constrained in one dimension that is used for depth limitation. In the other directions the light beam fans out and intensity decreases with distance from the source. To improve efficiency for the use of rod like high voltage discharge lamps a special reflector was designed (Paper T3, Paper T4). Although it resulted in an intense light beam the system was prone to cast shadows from objects due to the unidirectional illumination. As a further advancement of this device a second one was designed to illuminate a scene from all sides simultaneously. It was manufactured as a circular de-
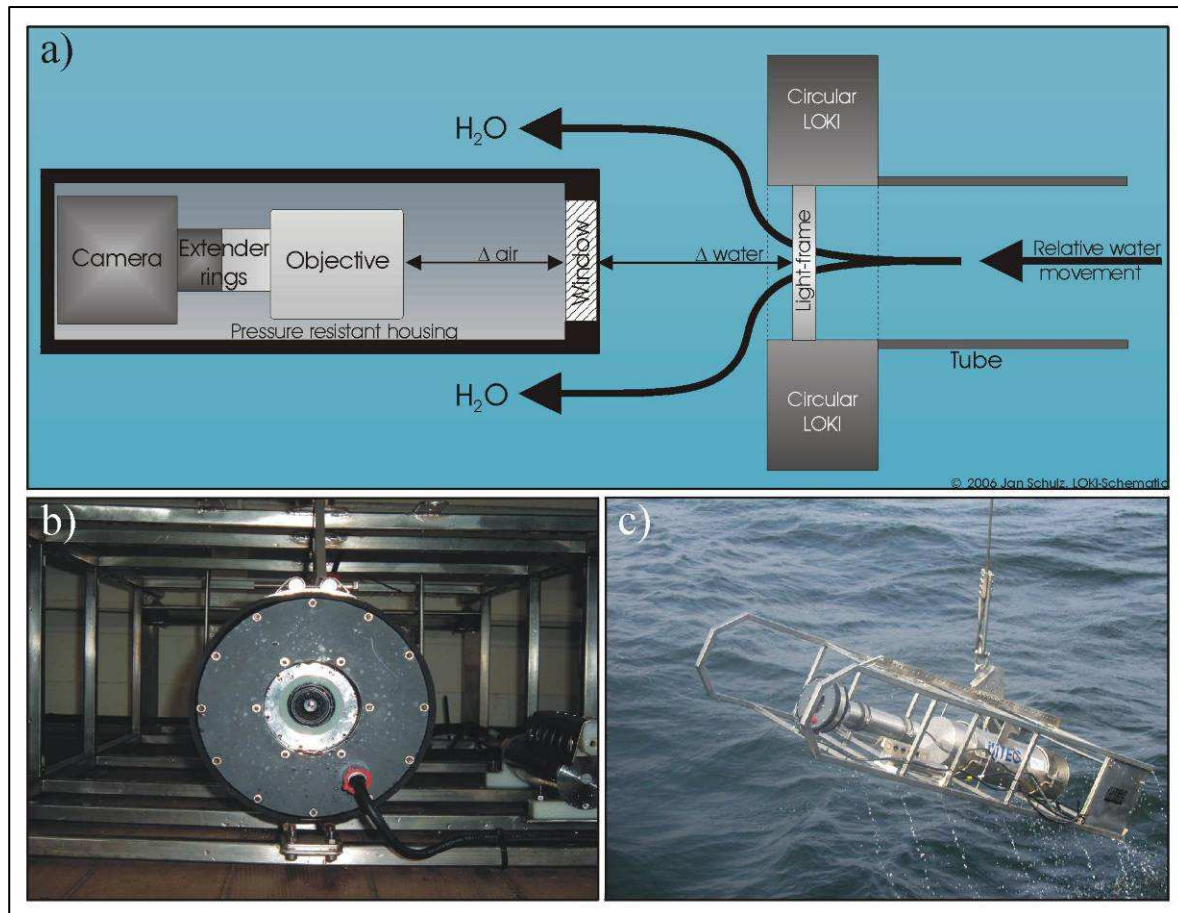
Figure 3.4: a) Schematic overview of the LOKI application. b) View from the front through the circular LOKI illumination and into the lens of the camera. c) The prototype during an initial test in the North Sea, showing the different components. From left to right the circular illumination device, the camera housing and the main housing, bearing the embedded PC can be seen.

vice, surrounding the observation volume (Paper T5). With high efficiency Light Emitting Diodes (LED) and cylindrical Fresnel-lenses a homogeneous illumination was achieved without casting shadows. As the observed volume is rather small, low abundant species have a higher probability to remain undetected. Thus the developed system was named Light-frame On-sight Key species Illumination (LOKI).

3.5.2. System specifications

Based on the circular illumination device a prototype was designed, where a camera looks over a short distance into the light frame. With a frequency of 15 frames per second a digital camera with four million pixels (JAI Pulnix® TM4000) takes images of objects within the light frame with shutter times below 1 ms. The illumination device creates a light frame with an extension in the depth of field range and is operated in flash mode. In towed operation mode a relative water movement replaces the water and entrained objects between two

Figure 3.5: Initial test of the prototype at Helgoland Roads in Summer 2006. Photo by courtesy of Carsten Wanke, Helgoland.

frames. Thus, objects or species appear just once and allow quantifying the abundance of different objects. The minimum object size for detection can be manually adjusted and reduces required data storage space. Every Area-Of-Interest (AOI) can be assigned to sensor readings of the ambient environmental parameters within a time frame of one second. Initial problems with the transmission of HF (high frequency) signals between camera housing and the main underwater unit were due to interactions with ambient sea water. Additional insulation techniques were used to avoid interferences. To date the initial laboratory phase is completed and field tests are in progress (Figure 3.5). The work for the evaluation of the hydrodynamic design has been completed. The camera is connected via CameraLink® interface with a PCI-X frame grabber board (Matrox® Helios® XCL) that processes the data stream of approximately 60 MB s^{-1}. Image frames are pre-processed in real time in the underwater unit and only parts that contain objects are stored as AOI. AOI extraction is executed by an Intel® Dual Xeon® board (clock rate 3.8 GHz, 2 GB central memory), that communicates with several microcontroller subunits by an internal Ethernet network. These subunits gather environmental information from various sensors, perform preliminary calculations and assist in the communication with the surface. The communication between surface and the underwater unit is achieved by an internet protocol signal (TCP/IP) modulated onto the power supply. This enables the use on ships with hawsers bearing just two-conductor cables for connection. A multi frequency modem allows communication between the underwater unit and the surface over more than 8 km of copper coax cable with a maximum speed of 1.5 MBit. The use of the TCP/IP also allows remote operation and data acquisition via the inter- or an intranet. Thus the gear can be operated on unmanned stations, while configuration and data access is accomplished by a remote operator.

4. Publications and manuscripts

The following chapter lists nine papers, manuscripts, patents and utility application written for this dissertation. Every document is introduced with a short overview on the actual status, authorship, contribution of each author and the content. The documents are grouped in the three chapters, zooplankton (Z), software (S) and technical development (T). As several copyright statements prohibit the use of documents in the layout of the respective journal or publishing boards, the latest versions prior to submission were included in this thesis. Differences in the used style sheets are a result of the guidelines of the respective journal or authority.

The zooplankton section incorporates three papers (Z1-Z3), dealing with the vertical distribution of dominant zooplankton species in the Bornholm Basin (central Baltic Sea) and possible implications for the ecosystem. The software section gives an overview on the software tool developed during the data analysis for a fast access to different data formats and simplified data processing. The software section includes one document (S1). The technical section includes five documents (T1-T5) about the construction and design of optical remote zooplankton sensing systems. As T1, T3 and T5 have been submitted to the German Patent Office these papers are in German.

4.1. Zooplankton of the Bornholm Sea

Z1: Vertical zonation of the zooplankton community in the central Baltic Sea in relation to hydrographic stratification as revealed by Multivariate Discriminant Function- and Canonical Analysis

Authors: Jan Schulz, Christian Möllmann, Hans-Jürgen Hirche

The paper describes the vertical community assemblage patterns of dominant zooplankton species at one station in the Bornholm Basin. By means of multivariate discriminant function analysis and canonical analysis three main habitats of different hydrographic parameters are demonstrated. These habitats were heterogeneously inhabited by examined species and indicate a distinct relation between hydrography and vertical appearance of zooplankton species. The initial idea for the design of the analysis was proposed by the first author. The manuscript was improved by the co-authors.

Vertical zonation of the zooplankton community in the Central Baltic Sea in relation to hydrographic stratification as revealed by Multivariate Discriminant Function- and Canonical Analysis

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Abstract

The vertical zonation of zooplankton in a deep central Baltic Sea Basin was studied in relation to hydrography based on vertically resolved sampling. The study period covered different seasonal hydrographic conditions as well as inflow events of water masses from the North Sea, important for the physical condition of this marginal sea. By means of multivariate discriminant function and canonical analysis we show a distinct vertical zonation of the zooplankton community in the water column. Three main habitats, which reflect the hydrographic situation, were identified with distinct differences in zooplankton composition: 1) The summer surface layer, bound by the thermocline at its lower rim. Species inhabiting this layer are only seasonally abundant or forced to adjust to the cooler winter water. 2) The intermediate winter water, bound by the halocline from below and the thermocline or surface as the upper boundary. Species dwelling in this layer face a reduced volume and are cut off from the high primary production when their habitat is limited from above by the summer thermocline. 3) The layer between the permanent halocline and the sea floor. The taxonomic composition in this layer shows no significant effect in relation to the observed inflows. The consequences of this zonation for trophodynamic interrelationships and advection processes are discussed.

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1. Introduction

In stratified waters different water masses are intercepted along their contact surfaces by changes in their physical parameters (clines). These clines are often characterised by steep gradients of temperature (thermocline) and salinity (halocline) and can put strong constraints on the distribution and dispersal of zooplankton species (e.g. Fager and McGowan, 1963; Banse, 1964; Ackefors, 1969; Hernroth and Ackefors, 1979; Owen, 1989; Gallager et al., 2004) may cause inhomogeneous biomass distribution in the water column and affect energy transfer within the food web (Roemmich and McGowan, 1995; Viitasalo et al., 1995; Vuorinen et al., 1998; Ojaveer et al., 1998; Dippner et al., 2000; Möllmann et al., 2000).

Steep vertical gradients make the deep basins of the Central Baltic Sea a unique study site to investigate the interrelationship between hydrographic structures and the zonation of zooplankton in the water column. A permanent halocline is present in approximately 60 m depth and separates deep waters with a salinity of often more than 12 captured in the deep troughs from less saline waters of approximately 7 (Fonselius, 1970). The upper layer is brackish, freshened by riverine input and precipitation. The deep saline waters are replaced during inflow events from the North Sea with highly saline and oxygenised waters (Matthäus and Schinke, 1994). In stagnant periods the conditions below the halocline deteriorate due to the decomposition processes of organic matter resulting in hypoxic or anoxic conditions at depth and only a narrow depth zone of oxygenated water and narrow the oxygenised space (Fonselius, 1970). During spring and summer a strong thermocline is established that separates the warm surface layer from an intermediate winter-water layer.

The zooplankton community in the Baltic Sea consists of freshwater, brackish and marine species (e.g. Ackefors, 1969; Remane and Schlieper, 1971; Hernroth and Ackefors, 1979; Ojaveer et al., 1998). While stenoecious species are expected to inhabit a distinct layer, euryoecious may access several strata. Consequently the vertical utilisation of different water masses depends on the ecophysiological tolerance and the availability of food resources. To investigate the physical processes that influence trophic interactions between zooplankton and higher trophic levels in the central Baltic Sea is one of the aims of GLOBEC-Germany. As trophodynamic relationships in pelagic systems depend on spatial overlap, the understanding of heterogeneities in the vertical distribution is important (Banse, 1964)

The working hypothesis of this paper is that if the zooplankton distribution is affected by the stratified environment distribution patterns must be diverse in accordance to hydrography. As most common investigation methods focus on distribution patterns of single species (e.g. Fager and McGowan, 1963) it is difficult to identify the influence of physical parameters on community assemblages. One parameter is often biased and heterodyned by a set of further variables and requires mathematical approaches to extract meaningful results from highly variable data. One way to identify compositional differences of stratified samples and the parameters that lead to the possible discrimination between samples is the use of multivariate discriminant function analysis (MDFA). The method addresses the problem how well it is possible to separates two or more groups of samples, given measurements for these on several variables, by a discriminant function calculated from the weighted variables (Manly, 1994). We used this method to investigate the relationship between abundant zooplankton species and hydrography in the Bornholm Basin. Samples are grouped in relation to the prevailing environmental conditions in the respective sampling depth. The abundance of the different zooplankton species in each sample represents the measured variables. The advantage of this approach in relation to similarity-matrix-based community analysis is the possibility of the *a posteriori* analysis of the separating parame-

ters and the quality of the classification. To our knowledge this work is the first application of a discriminant function analysis in the field of zooplankton ecology.

2. Material and methods

2.1. Sampling

Data were based on the analysis of samples collected on 15 cruises between March 2002 and May 2003 with an almost monthly coverage. Samples were taken at a station located in the deepest part of the Bornholm Basin (95 m depth; 55.292°N / 15.750°E; Fig. 1). Zooplankton was collected using a multinet (Hydrobios, Kiel, 0.25 m^2 mouth opening, 50 μm mesh size) in stacked, 10 m intervals from bottom to surface. As diel vertical migration is not pronounced in the Central Baltic Sea (e.g. Hansen et al., 2005; Hansen et al., 2006; Renz and Hirche, 2006) samples were taken regardless of the time of day. A total of 146 samples were preserved immediately after collection in borax-buffered 4% formalin-seawater solution.

2.2. Sample processing

Subsamples of the multinet samples were analysed for developmental stages of dominant zooplankton species until at least 500 individuals per sample were counted. Additional analyses were continued until at least 150 individuals of the three dominant copepod species *Acartia* spp., *Temora longicornis* and *Pseudocalanus acuspes* were counted. Data of the 16 most abundant species belonging to 5 taxa were used for the analysis (Table 1). To account for ontogenetic vertical distribution in copepods (e.g. Hernroth and Ackefors, 1979; Renz and Hirche 2006; Hansen et al., 2006) copepodite stages C1 to C3 and C4 to C6 were separated, resulting in a total number of 23 variables for the analysis (see 2.4.). Nauplii were not included in the analyses.

2.3. Hydrography

Profiles of temperature and salinity were obtained using a CTD probe (Fig. 2a and 2b). Measurements were vertically averaged for each 10 m multinet interval. The averaged layer salinity (ALS) and temperature (ALT) values were then assigned to the zooplankton counts in the respective depth. To establish categories for the hydrographic environment of a sample, an algorithm was developed by defining thresholds for ALS and ALT (Fig. 2c). An ALS below 9 characterises the waters above the halocline. Category *SUMMER* defined samples above the thermocline, with ALT > 8°C. This ALT was first found in May 2002 when the thermocline had been established (Fig. 2b). *WINTER* represented the samples between thermo- and halocline as well as the upper part of the water column during the unstratified winter situation. All other categories had an ALS > 9 in common. *HALINE* defined the stagnant water below the permanent halocline. The data include the period of two inflow events from the North Sea. *BB60* denotes the waters of an exceptionally warm inflow event in September 2002, which stratified into approximately 60 m depth due to a lesser density than the *HALINE* water. It was characterised by an ALS > 16 and an ALT > 9°C. In November 2002 a second inflow entered the Bornholm Basin. It replaced the stagnant water masses below 90 m. After January 2003 a further inflow event was recorded. The inflow fulfilled the criteria of a Major Baltic Inflow (MBI, Matthäus and Frank, 1992) and renewed the deep waters in the basin completely. The waters of the latter two inflows,

which affected the deep parts of the trough, are marked as *BB90*, according to the name chosen by Feistel et al. (2004) for the MBI and had an ALS > 16 and an ALT < 9°C. For a complete discussion of the inflow events we refer to Feistel et al. (2003a, 2003b, 2004).

2.4. Multivariate discriminant function analysis

To determine whether samples from different hydrographic conditions can be discriminated by their species composition, a multivariate discriminant function analysis (MDFA) was performed for the *a priori* defined categories. MDFA is used to determine the variables that best discriminate between a set of naturally occurring groups (Fisher, 1936) and to describe the relationship between them (Manly, 1994). For each sample a discriminant function differentiates a new variable computed from the weighted measurements. Each sample needs to be a member of only one category, which can be defined *a priori*. Variables have to be on continuous scale with no complete collinearity between two of them due to the calculation of covariance matrices. The size of each *a priori* defined category should be weighed, if the number of samples in the smallest group is lower than the number of variables or if category sizes differ. For the hypothesis tests normality is required, but not for the method itself (Hair et al., 1998). MDFA calculates the probability score of a sample to belong to one of the five hydrographic categories (*SUMMER*, *WINTER*, *HALINE*, *BB60*, *BB90*) based on the species composition. This value is then compared with the *a priori* defined classification. A complete description of the method is given by Jennrich (1977a, 1977b). The computerised model

$$DS_c = k_c + \sum_{s=1}^{n} w_{cs} * x_s$$

was applied to calculate the discriminant classification score *DS* for each case in each category. The subscript *c* denotes the five hydrographic categories, *n* the number of variables (23 taxonomic groups) and *s* the index of each taxon or stage. x_s is the respective log_{10} (1+*x*) transformed abundance of *s* to equilibrate variances. The respective coefficients for the weighing of a variable w_{cs}, the category constant k_c and probabilities are given in Table 2. The automatically computed DS_c shows the probability of a sample to belong to the predefined category *c*. The probability was weighed by the number of cases in each *a priori* defined category. The results are summarised in a classification matrix (Table 3) and show the matching of the discriminant membership prediction with the *a priori* classification. Wilk's Lambda was computed as a standard statistic to denote the significance of the model's discriminatory power (Rao, 1957) that can be converted to a probability value via F-test.

2.5. Canonical analysis

A canonical analysis was performed to identify how the 23 variables discriminate between the five categories. Hereby the number of the orthogonal functions (roots) is equal to the minimum number of categories or variables minus one, whichever bears the smaller number. This number can be seen as a function, which describes points in a normal space (e.g. with three points in space two orthogonal functions are needed to define a plane the points lay on).

As each successive function contributes less to the overall discriminatory power, the significance was tested with a step-down Chi[2]-test (Table 4). The first row indicates the significance for all roots. Each further line reports the significance with the preceding ones

removed and indicates the number of functions to interpret. The cumulative proportion of explained variance by each root was computed from the Eigenvalues. To determine the discriminative nature of each root, the means of the canonical variables were calculated (Table 5). The canonical factor structure coefficients give the unique partial contribution of each taxon and stage within each discriminant function and were used to interpret the nature of the canonical roots.

2.6. Computational work

Maps and hydrographic charts were performed with Ocean Data View (Schlitzer, 2004). Statistics were calculated with STATISTICA (StatSoft, Version 6.1). Ocean Sneaker's Tool (Schulz et al., 2005) was used to transform and convert raw data tables and to create additional charts.

3. Results

3.1. Multivariate discriminant function analysis

The multivariate discriminant function analysis (MDFA) model distinguished with high precision between samples derived from *SUMMER*, *WINTER* and the deep water samples of higher salinity (*HALINE*, *BB60*, *BB90*). More than 87% of the samples were correctly classified to their hydrographic origin by the MDFA (Table 3). Wilk's Lambda denoted a high significance of the model and a compositional difference in relation to hydrography. The calculated F-value also indicates significance (p <0.0001).

All samples of the category *SUMMER* were correctly classified. Misclassification increased with each further category. Within *WINTER*, two samples out of 56 showed a higher probability to belong to *HALINE* by the distance from the classification mean. A high discrimination rate between *HALINE*, *BB60* and *BB90* was not obtained (shaded area, Table 3). Misclassification was not observed between the samples from the two inflow events but with the stagnant haline waters. Therefore we include *BB60* and *BB90* to the *HALINE* category.

3.2. Canonical analysis

The Chi^2-test showed a significant discriminatory power only for the first two roots (Table 4). The Eigenvalues of these two roots showed them to explain most of the variance in composition. The first root on its own accounted for more than 60% of the explained variance and more than 93.5% together with the second.

The 2D canonical plot (Fig. 3) displays the distribution of the samples spanned by the first two roots. Samples of the category *SUMMER* and *WINTER* were well separated from each other and from waters of high salinity. No clear separation was obvious between the *HALINE*, *BB60* and *BB90* samples, but samples of the same category showed always a clustering tendency. The discriminating nature of the canonical roots was derived from their means for the individual categories (Table 5). It can be seen that the first root discriminated the samples below the halocline from the lower saline categories *SUMMER* and *WINTER*. The second root discriminated the two categories above the halocline and indicated a temperature driven characteristic. Among the categories of high salinity, the warm *BB60* inflow showed a closer mean to summer. The mean of *BB90* was closer to the *WINTER* water.

3.3. Species distribution in relation to hydrography

The canonical factor structure coefficients (CFSC) represent the unique variable loadings in each root. The CFSC loadings for the two significant roots are shown in Fig. 4 and indicate how exclusively a variable contributes within the roots (Fig. 4). Consequently the quadrants I-IV of the CFSC loading chart (Fig. 4) represent water masses of different salinity and temperature combinations and their use by different species.

As derived from the mean values quadrant II represents water masses from below the halocline. Here *Oithona similis*, *Pseudocalanus acuspes* C4-C6 and *Oikopleura* sp. were found. The salient loadings of the two *Oithona similis* stages indicate this species to inhabit mainly the region below the halocline with an affinity to warm waters. The other species of this quadrant were a less reliable indicator for higher salinity, and the small values of *Oikopleura* sp. on the first root indicate that this species may partially migrate above or into the halocline.

The species of quadrant I contributed most to the *SUMMER* samples. The abundant summer species *Bosmina coregoni maritima*, *Eurytemora* sp. and *Podon intermedius* showed highest CFSC on the second root, indicating a close association with the water above the thermocline. *Evadne nordmanni* and *Podon leuckarti* have an intermediate position. While *Acartia bifilosa* C4-C6, *Centropages hamatus* C1-C3 and *Temora longicornis* C1-C3 showed highest distances from the saline waters. *Keratella* sp. indicated a low contribution to salinity discrimination. *Pseudocalanus acuspes* C1-C3 showed the lowest contribution of all species to discrimination. The CFSC for *A. bifilosa* C1-C3 indicated a preference for low salinity, but no direct contribution to distinguish between *SUMMER* and *WINTER*. This suggests that this copepod inhabits either layers assigned to these categories or the thermocline itself.

The species of quadrant IV contributed to *WINTER*. High abundances of *Acartia longiremis*, Bivalvia, *Centropages hamatus* C4-C6 and *Temora longicornis* C4-C6 indicated samples of the *WINTER* category.

Fritillaria sp. was the only species in quadrant III and showed a completely different distribution pattern. Apparently it avoids warm water, but is less particular about salinity.

4. Discussion

4.1. Data analysis

Multivariate discriminant function analysis (MDFA) turned out to be a valuable tool for the investigation of characteristic zooplankton compositions in regions of pronounced hydrographic structures. The high misclassification rate among the categories *HALINE*, *BB60* and *BB90* indicates a similarity in species composition. As the model cannot discriminate these categories by the applied parameters we include *BB60* and *BB90* in the *HALINE* category. Possible advection of North Sea species with the inflow events (Postel, 1996) cannot be evaluated with this approach. MDFA combined with canonical analysis is a powerful method to determine compositional heterogeneities in distinct layers. As salinity and temperature account for more than 93% of the variance, other environmental factors are heterodyned and of minor importance for a vertical separation. The results show a significant difference in zooplankton composition between the three hydrographic categories *SUMMER*, *WINTER* and haline waters. The canonical factor structure coefficients (CFSC), representing the loadings in the model, do not represent an exclusive inhabitation of a distinct layer. Rather it is an indicator for the degree of coupling between a species and a dis-

tinct water mass. Individual specimens may dwell to a certain extent also in adjacent strata, while the major part of the stock would be expected to be found in the respective stratum. With a higher CFSC distance from the separating axes, the residence probability in one of the identified layers is larger, although the clustering in each quadrant needs attention.

Quadrant I represents the area above the thermocline. Individuals who utilise this volume are only seasonally abundant or able to take advantage of this temporary habitat. Here the summer species *Bosmina coregoni maritima*, *Eurytemora* sp. and *Podon intermedius* (Hernroth and Ackefors, 1979) show salient loadings. While *B. coregoni maritima* is most dominant at temperatures above 15°C (Hernroth and Ackefors, 1979), *Eurytemora* sp. is eurytherm, but limited by too high temperatures (Ackefors, 1969). It is found in quadrant one as its life cycle starts when surface temperatures decrease (Eriksson, 1973). It utilises the space above the thermocline then, while it outlasts as resting eggs the residual time (Ban and Minoda, 1989). The loadings are close to that of *B. coregoni maritima* and *P. intermedius* in spite if seasonal partitioning of the habitat (Hirche, 1992). *Evadne nordmanni* and *Podon leuckarti* are less tolerant to high temperatures (Ackefors, 1969; Gieskes, 1971a, 1971b) and disappear from the plankton after the summer stratification breaks down (Hernroth and Ackefors, 1979). The thermophilic species *Acartia bifilosa* (Chojnacki et al., 1984) also inhabits the warm surface layer, where it can find favourable conditions for reproduction (Koski and Kuosa, 1999).

Quadrant II includes species dwelling mainly below the halocline. Although *Oithona similis* is described as a euryhaline, eurythermal and omnivorous species (Fransz et al., 1991) it is the most important indicator of haline water masses. In the Bornholm Basin it is trapped below the halocline and exposed to hydrographic conditions in the trough (Hansen et al., 2004). *Pseudocalanus acuspes* as the second marine species (Renz and Hirche, 2006) shows lower CFSC loadings, while the C1-C3 copepodites are found in quadrant I. This may relate to different ontogenetic distributions of the copepodites as described by Renz and Hirche, 2006 and Hansen et al., 2006.

Fritillaria sp. is the only species represented in quadrant III. It is tolerant to a wide range of salinities, but restricted to cool water (Ackefors, 1969). This allows it to obtain a unique distribution pattern of both categories below the thermocline.

Quadrant IV represents the *WINTER* water masses between halocline and thermocline as long as the latter persists. The mesotherm *Temora longicornis* (Hernroth and Ackefors, 1979) and oligotherm *Acartia longiremis* (Ackefors, 1969) were found here. *Centropages hamatus* and *Bivalvia* larvae are known to utilise the warm surface layer to a minor extent but show surface avoidance (Ackefors, 1969; Hernroth and Ackefors, 1979). This results in higher abundances out of the *SUMMER* volume and shifts loadings to the *WINTER* category. The detached CFSC values of *Synchaeta* sp. indicate a different life strategy. This oligotherm species is found early in the season above and below the developing thermocline and outlasts the high temperatures as resting eggs (Hernroth and Ackefors, 1979).

CFSC close to the separating planes may indicate an equal distribution in both habitats or an utilisation of the cline itself, whichever this axis separates. This is likely for *A. bifilosa* C1-C3 and even reported for *Pseudocalanus* spp. copepodites (Hansen et al., 2006). It is, to a minor extent, biased by the sampling intervals and the use of the mean temperature (ALT) and salinity (ALS) for every 10 m layer. Consequently samples are included that contain overlapping hydrographic categories while the *a priori* definition is determined by the higher proportion of the respective temperature and salinity. Assuming homogeneous species dispersal in each category the samples contain proportional compositions from both sides. Hence the respective lower share may impact the weighting of the variables in the model. Although this may weaken the strength of the MDFA model, clear discriminations were found. Instead of MDFA it would also be possible to apply N one-way

ANOVA's on each of the variables, but this is rather time consuming and would not take advantage of the multivariate nature of the data (Zuur et al., 2006).

As normality is not assured in ecological data, Wilk's Lambda should be used instead of the p-value of the F-test to interpret the explanatory power of the MDFA model. In combination with the classification success of more than 87% it indicates a distinct vertical zonation of the zooplankton community. This implies that the different water masses are characterised by the specific species compositions. As the analysis bases on the compositional patterns in distinct layers it is less sensitive to the effects of station, depth, or variations in the horizontal distribution. However, the vertical zonation might be a secondary effect, not directly driven by the principal parameters temperature and salinity.

4.2. Effect of zonation

While the species identified to dwell in the deeper layers are mainly found in the central part of the Bornholm Basin, species in shallower layers are also abundant in the marginal parts (Ackefors, 1969; Hernroth and Ackefors, 1979). These findings help to explain differences in the horizontal distribution. For example, we propose that *WINTER* species are expelled from shallow areas when the thermocline reaches the seafloor and displace their habitat downward. Similar mechanisms apply to *HALINE* species, when the level of the halocline is deeper than the bottom depth.

During stagnation periods following inflow events, species are trapped below the halocline in the trough of the basin. Here they are faced with deteriorating conditions by degradation processes (Fonselius, 1970), which narrow the size of this habitat for sensitive species (Hansen et al., 2004; Renz and Hirche, 2006; Hansen et al., 2006). During inflow events this water is renewed and enables species to reutilise this water mass down to the seafloor (Leppäkoski, 1971, 1975). Furthermore, individuals can be washed out with a shoaling halocline and carried over the sill to the next basin. Consequently, advection below the halocline depends on the trough and sill structure of the Baltic Sea and is mainly driven by the inflows. In the upper layers, local circulation patterns derived from wind shear and river run-off are the major controls of advection (Krauss and Bruegge, 1991).

Although the *WINTER* zone is present year round, its volume is reduced when the seasonal *SUMMER* zone is formed by the thermocline. High solar radiation causes a steep thermocline with high primary production in the uppermost layer and is reduced in the deep (Hansen et al., 2006). Calm weather conditions reduce deep mixing and cause a shallow thermocline, respective a thinner layer with higher temperatures. As species abundance in distinct layers correlates with their ecophysiological requirements (Ojaveer et al., 1998; Vuorinen et al., 1998), climatic variances may impact their horizontal distribution. Stenoecious species adapted to cooler waters, such as the species belonging to the *WINTER* class in this study, are separated from the surface as long as the thermocline above persists and cannot take advantage of the favourable feeding conditions above the thermocline (Hansen et al., 2006). Species with broader ecophysiological ranges cope with these environmental changes and occupy this layer.

4.3. Importance of zonation for predator-prey interactions

We found a pronounced zonation of zooplankton in the Central Baltic Sea indicating the existence of depth-specific prey fields. Thus, the spatial overlap of predator and prey populations determines prey access and hence predator diet. This specific prey composition explains partly the predator's diet and, thus determines differences in predation pressure on zooplankton species. It addresses a fundamental subject examined for decades by fish

ecologists (e.g. Cushing, 1975; Last, 1980; Legget and Deblois, 1994; Arrhenius, 1996), as the predators show distinct age-specific depth preferences (e.g. Wieland and Zuzarte, 1991; Rudstam et al., 1994; Bagge et al., 1994; Wieland et al., 1994). Our results explain some of the most important predator-prey interactions in the system. Herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.) are the dominant planktivorous in the Baltic Sea (Möllmann and Köster, 2002). Diet analyses indicate that both clupeid fish species feed in spring mainly on older stages of *Pseudocalanus acuspes* (Möllmann et al., 2004). According to our analysis, this species inhabits the deep haline waters coinciding to the water masses where also herring and sprat feed in spring (Köster and Schnack, 1994). In summer, older stages of *Temora longicornis* contribute most to the diet of sprat (Möllmann et al., 2004). According to our analysis these are found in the winter water, which is the main foraging arena of sprat during this season (Köster and Schnack, 1994). A consequence of these very specific interactions is the strong predation pressure of the large sprat stock on *P. acuspes* and *T. longicornis* since the 1990s (Möllmann and Köster, 2002).

A further example for the importance of the vertical zonation of zooplankton for predator-prey interactions is the interaction between the larval stages of sprat and cod (*Gadus morhua* L.) in the Baltic. Eggs of both fish species are spawned in the deeper layers of the Central Baltic basins. While sprat larvae migrate to the surface for feeding cod remains in the haline water (Voss et al., 2006). Our results indicate the reasons for their different feeding behaviour. While sprat larvae take advantage of *Acartia* sp., the deeper living cod larvae prey on *P. acuspes* (Voss et al. 2003).

Depth-dependent feeding can also explain the specific prey composition of gelatinous zooplankton. For example, the medusa *Aurelia aurita* appears in summer mainly in the upper 20 m and feeds to a large extend on *B. coregoni maritima* (Barz and Hirche, 2005). This cladoceran is identified in our analysis as occupant of the warm water above the thermocline.

Consequently, the potential prey fields are influenced by hydrography and spatial congruence, as well as by the local topography and physical features that need be considered in the design of ecological models. Furthermore, climate change scenarios and altered mean layer thickness may drive cascading effects by shifting environmental parameters (Owen, 1989) and impacts energy transfer between layers.

5. Summary

The vertical zooplankton composition in the Bornholm Basin (central Baltic Sea) was studied and related to the hydrography. The pronounced stratification leads to at least three different habitats, detected by using multivariate discriminant function analysis. These habitats are heterogeneously inhabited by different zooplankton communities. With canonical analysis it was possible to assign most species clearly with the main habitats. As the vertical zonation leads to inhomogeneous vertical distribution the vertical match of predator and prey must be considered to determine available prey fields.

Acknowledgements

References

Ackefors, H., 1969. Ecological zooplankton investigations in the Baltic Proper 1963-1965. Fish. Bd. Sweden, Inst. Mar. Res., Ser. Biol. Report No 18.

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

Bagge, O., Thurow, F., Steffensen, E., Bay, J., 1994. The Baltic Cod. Dana 10, 1-28.

Ban, S., Minoda, T., 1989. Seasonal distribution of *Eurytemora affinis* (Poppe, 1880) (Copepoda, Calanoida) in freshwater Lake Ohnuma, Hokkaido. Bull. Fac. Fish. Hokkaido Univ. 40, 147-153.

Banse, K., 1964. On the vertical distribution of zooplankton in the sea. Prog. Ocean. 2, 53-125.

Barz, K., Hirche, H.J., 2005. Seasonal development of scyphozoan medusae and the predatory impact of *Aurelia aurita* on the zooplankton community in the Bornholm Basin (central Baltic Sea). Mar. Biol. 147, 465-476.

Chojnacki, J., Drzycimski, I., Siudzinski, K., 1984. The ecological characteristics of the main species of Crustacea in Plankton of the southern Baltic. Articles on Biological Productivity of the Baltic Sea, Moscow, 2, 148-171.

Cushing D.H., 1975. Marine Ecology and Fisheries. Cambridge University press pp 1-292.

Dippner, J.W., Kornilovs, G., Sidrevics, L., 2000. Long-term variability of mesozooplankton in the Central Baltic Sea. J. Mar. Sys. 25, 23-31.

Eriksson, S., 1973. Preliminary Zooplankton investigations in the Öregrund Archipelago (Southwestern Bothnian Sea) during the summer 1970. Zoon 1, 95-111.

Fager, E.W., McGowan, J.A., 1963. Zooplankton species groups in the North Pacific. Science 140(3566), 453-460.

Feistel, R., Nausch, G., Mohrholz, V., Łysiak- Pastuszak, E., Seifert, T., Matthäus, W., Krüger, S., Hansen, I.S., 2003a. Warm Waters of Summer 2002 in the Deep Baltic. Oceanologia 45 (4), 571-592.

Feistel, R., Nausch, G., Matthäus, W., Hagen, E., 2003b. Temporal and spatial evolution of the Baltic deep water renewal in spring 2003. Oceanologia, 45 (4), 623-642.

Feistel, R., Nausch, G., Matthäus, W., Łysiak- Pastuszak, E., Seifert, T., Hansen, I.S., Mohrholz, V., Krüger, S., Buch, E., Hagen, E., 2004. Background data to the exceptionally warm inflow into the Baltic Sea in late summer of 2002. Meereswiss. Ber. / Mar. Sci. Rep. Institute for Baltic Research 58, 1-58.

Fisher, R.A., 1936. The utilization of multiple measurements in taxonomic problems. Ann. Eugen. 7, 179-188.

Fonselius, S.H., 1970. On the stagnation and recent turnover of the water in the Baltic. Tellus 22(5), 533-544.

Fransz, H.G., Colebrook, J.M., Gamble, J.C., Krause, M., 1991. The zooplankton of the North Sea. Neth. J. Sea Res. 28, 1-52.

Gallager, S.M., Yamazaki, H., Davis, C.S., 2004. Contribution of fine scale vertical structure and swimming behaviour to formation of plankton layers on Georges Bank. Mar. Ecol. Prog. Ser. 267, 27-43.

Gieskes, W.W.C., 1971a. Ecology of the Cladocera of the North Atlantic and the North Sea, 1960-67. Neth. J. Sea Res. 5, 342-376.

Gieskes, W.W.C., 1971b. The succession of two Podon-species in the North Sea. Neth. J. Sea Res. 5, 377-381.

Hair, J.F., Anderson, Tatham, Black, B., 1998. Multivariate data analysis. Prentice Hall Pearson Education, London, fifth edition.

Hansen, F.C., Möllmann, C., Schütz, U., Hinrichsen, H.H., 2004. Spatio temporal distribution of *Oithona similis* in the Bornholm Basin (Central Baltic Sea). J. Plankt. Res. 26(6), 659-668.

Hansen, F.C., Möllmann, C., Schütz, U.,Neumann, T., 2006. Spatio temporal distribution of calanoid copepods in the central Baltic Sea. J. Plankt. Res. 28(1), 39-54.

Hernroth, L., Ackefors, H., 1979. The zooplankton of the Baltic Proper - A long term investigation of the fauna, its biology and ecology. Fish. Bd. Sweden, Inst. Mar. Res., Report Vol. 2.

Hirche, H.-J., 1992. Egg production of *Eurytemora affinis* - Effect of k-strategy. Estuar. Coast. Shelf Sci. 35, 395-407.

Jennrich, R.I., 1977a. Stepwise regression. In K. Enslein, A. Ralston and H.S. Wilf (eds.), Statistical Methods for digital Computers, New York. Wiley.

Jennrich, R.I., 1977b. Stepwise discriminant analysis. In K. Enslein, A. Ralston and H.S. Wilf (eds.), Statistical Methods for digital Computers, New York. Wiley.

Krauss, W., Bruegge, B, 1991. Wind-produced water exchange between the deep basins of the Baltic Sea. J. Phys. Oceanogr. 11, 373-384.

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

Koski, M., Kuosa, H., 1999. The effect of temperature, food concentration and female size on the egg production of the planktonic copepod *Acartia bifilosa*. J. Plankt. Res. 21(9), 1779-1789.

Last, J.M., 1980. The food of twenty species of fish larvae in the west - central North Sea. In Fisheries research technical report, MAFF Directorate of Fisheries Research, Lowestoft, 60. pp 1-44.

Leggett, W.C., de Blois, E., 1994. Recruitment in marine fishes. Is it regulated by starvation and predation in the egg and larval stages?. Neth. J. Sea Res. 32(2), 119-134.

Leppäkoski, E., 1971. Benthic recolonization of the Bornholm Basin (Southern Baltic) in 1969-71. Thalassia Jugoslavica 7(1), 171-179.

Leppäkoski, E., 1975. Macrobentic fauna as indicator of ozeanization in the southern Baltic. Merentutkimuslait. Julk. Havsforskningsinst. Skr. No. 239, 280-288.

Manley, B.F.J., 1994. Multivariate statistical methods. A Primer. Chapman and Hall, London.

Matthäus, W., Frank, H., 1992. Characteristics of Major Baltic Inflows - a statistical analysis. Cont. Shelf. Res. 12(12), 1375-1400.

Matthäus, W., Schinke, H., 1994. Mean atmospheric circulation patterns associated with major Baltic inflows. Dt. Hydrogr. Z. 46, 321-338.

Möllmann, C., Kornilovs, G., Sidrevics, L., 2000. Long-term dynamics of main mesozooplankton species in the central Baltic Sea. J. Plankt. Res. 22(11), 2015-2038.

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

Ojaveer, E., Lumberg, A., Ojaveer, H., 1998. Highlights of zooplankton dynamics in Estonian waters (Baltic Sea). ICES J. Mar. Sci. 55, 748-755.

Owen, R.W., 1989. Microscale and finescale variations of small plankton in coastal and pelagic environments. J. Mar. Res. 47, 197-240.

Postel, L., 1996. Meereskunde der Ostsee. ed. Rheinheimer, Springer Verlag Berlin-Heidelberg-New York.

Rao, C.R., 1951. An asymptotic expansion of the distribution of Wilk's criterion. Bull. Int. Stat. Inst. 33, 177-181.

Remane, A., Schlieper, C., 1971. Biology of Brackish Water. Wiley Interscience Division, John Wiley&Sons, Inc. New York-Toronto-Sydney.

Renz, J., Hirche, H.-J., 2006. Life cycle of *Pseudocalanus acuspes* Giesbrecht (Copepoda, Calanoida) in the Central Baltic Sea. I. Seasonal and spatial distribution. Mar. Biol. 148, 567-580.

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

Schlitzer, R., 2004. Ocean DataView. http://www.awi.de/GEO/ODV .

Schulz, J., 2005. Ocean Sneaker's Tool- An open source software for marine data. http://www.awi.de/Software/OST [case sensitive URL].

StatSoft, Inc., 2003. STATISTICA for Windows [Software-System for data analysis]. Version 6, http://www.statsoft.com.

Viitasalo, M., Koski, M., Pellikka, K., Johansson, S., 1995. Seasonal and long-term variations in the body size of planktonic copepods in the northern Baltic Sea. Mar. Biol. 123, 241-250.

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

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

Vuorinen, I., Hänninen, J., Viitasalo, M., Helminen, U., Kuosa, H., 1998. Proportion of copepod biomass declines with decreasing salinity in the Baltic Sea. ICES J. Mar. Sci. 55, 767-774.

Wieland, K., Waller, U., Schnack, D., 1994. Development of Baltic cod eggs at different levels of temperature and oxygen content. Dana 10, 163-177.

Wieland, K., Zuzarte, F., 1991. Vertical distribution of cod and sprat eggs and larvae in the Bornholm Basin (Baltic Sea) 1987-1990. ICES CM1991/J.37.

Yamazaki, H., Mackas, D., Demnan, K., 2002. Coupling small scale physical processes with biology-towards a Lagrangian approach. In Robinson, A.R., McCarthy, J.J., Rothschild, B.J. (ed.) The sea, biological-physical interaction in the ocean, Vol. 12 John Wiley & Sons, New York, p 51-112.

Zuur, A.L., Ieno, E.N., Smith, G.M., 2006. Analysis of ecological data, Springer Verlag, in press.

Description of the figures

Figure 1: Sampling site in the Bornholm Basin (Central Baltic Sea).

Figure 2: a) Depth-profiles (m) of salinity and b) temperature (°C) at 55.292°N/15.750°E between March 2002 and May 2003; c) Algorithmic categorisation of a sample based on the average layer salinity (ALS) and –temperature (ALT) in the layer sampled by the multinet. Reading starts on the left with *SAMPLE*. At each bifurcation a decision leads closer to the final category. Category *SUMMER* includes the warm and temporary surface water above the thermocline; *WINTER* the unstratified winter water, as well as the intermediate water between the thermo- and halocline as long as the *SUMMER* water prevails. *HALINE* includes the waters of higher salinity below the halocline. Categories *BB60* and *BB90* refer to inflow events during the observation period.

Figure 3: Canonical plot of all samples for the first two roots based on multivariate discriminant function analysis of the log_{10} transformed abundances of the 23 taxa and stages. The categories refer to those algorithmically defined in Figure 2c.

Figure 4: The canonical factor structure coefficients (CFSC) of the first two roots show the loadings of the variables. Quadrant I represents the *SUMMER*, II the *HALINE* and IV the *WINTER* category. Higher absolute variable values on one axis indicate a greater importance in the discrimination on the respective axis. Variables in quadrant III indicate a distribution pattern different from the defined categories.
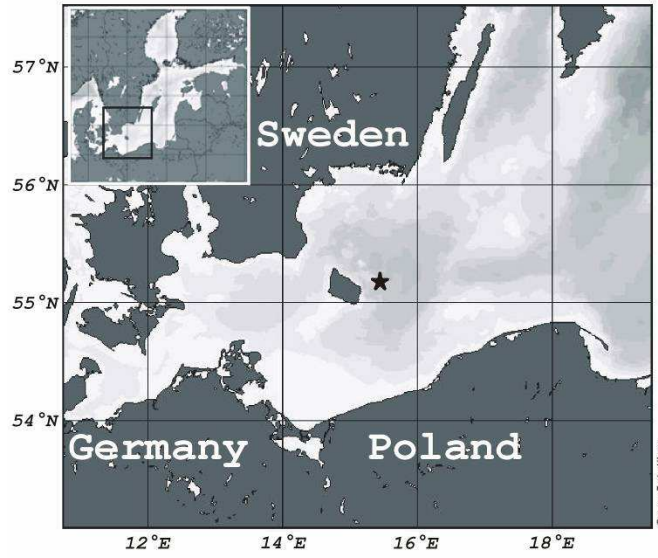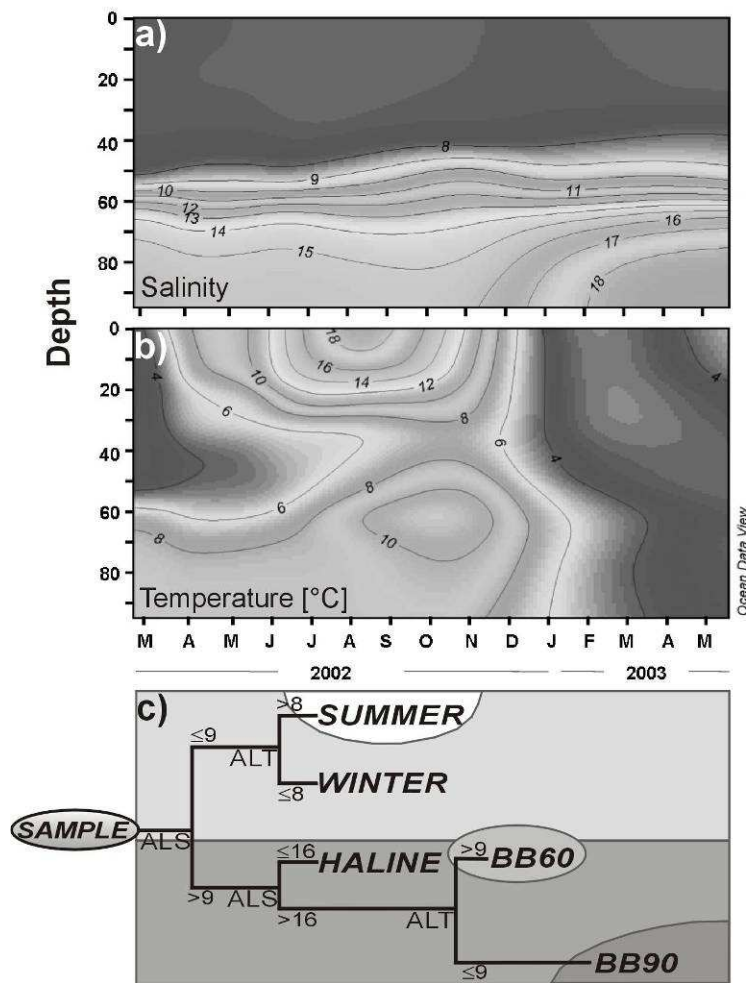
Fig. 1

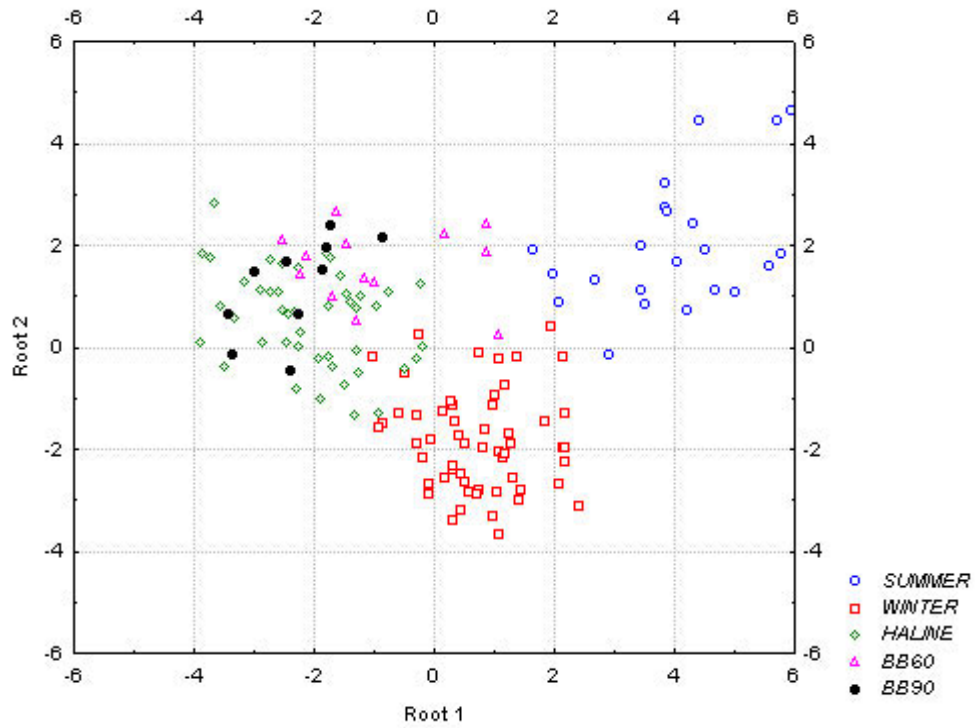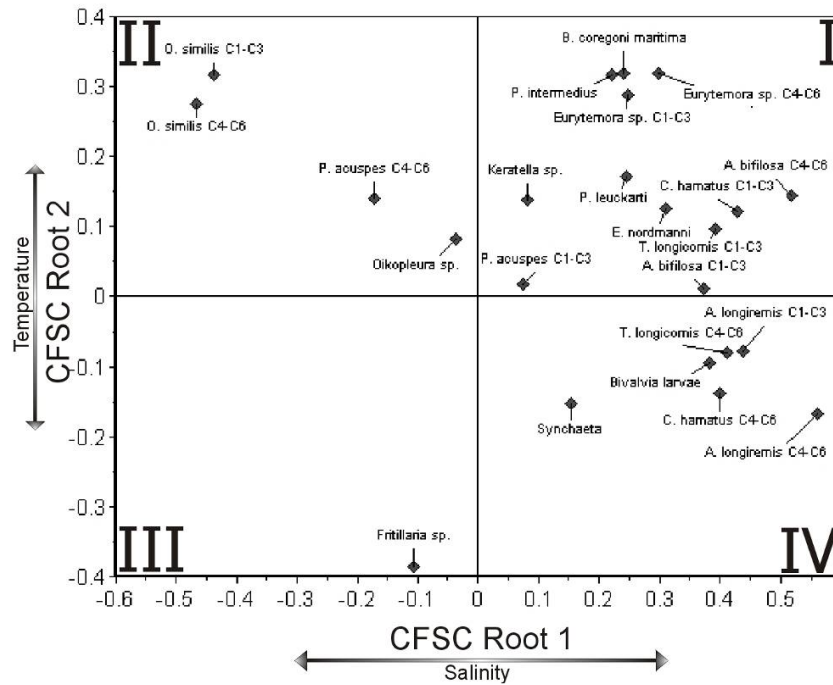
Fig. 2

Fig. 3

Fig. 4

Tables

Table 1: Zooplankton taxa and stages used for the analysis.

Appendicularia	*Fritillaria* sp.
	Oikopleura sp.
Bivalvia	*Bivalvia* larvae
Cladocera	*Bosmina coregoni maritima*
	Evadne nordmanni
	Podon intermedius
	Podon leuckarti
Copepoda	*Acartia bifilosa* C1-C3
	Acartia bifilosa C4-C6
	Acartia longiremis C1-C3
	Acartia longiremis C4-C6
	Centropages hamatus C1-C3
	Centropages hamatus C4-C6
	Eurytemora sp. C1-C3
	Eurytemora sp. C4-C6
	Oithona similis C1-C3
	Oithona similis C4-C6
	Pseudocalanus acuspes C1-C3
	Pseudocalanus acuspes C4-C6
	Temora longicornis C1-C3
	Temora longicornis C4-C6
Rotatoria	*Keratella* sp.
	Synchaeta sp.

Table 2: Coefficients for the set-up of the discriminant function analysis model.

	SUMMER	*WINTER*	*HALINE*	*BB60*	*BB90*
Probability	0.15068	0.38356	0.30822	0.08904	0.06849
A. bifilosa C1-C3	3.9611	2.9566	1.9103	2.0359	1.9038
A. bifilosa C4-C6	1.9371	0.1114	0.3880	1.1255	1.1201
A. longiremis C1-C3	4.9366	-0.1524	0.4955	1.3707	1.3322
A. longiremis C4-C6	2.3637	6.8350	1.6463	2.8151	0.1784
Bivalvia larvae	1.8459	1.0527	0.7009	1.0885	0.5680
B. coregoni maritima	5.6133	3.8996	2.5759	3.4962	2.1412
C. hamatus C1-C3	4.1528	2.0538	0.3440	1.4848	-0.3700
C. hamatus C4-C6	1.9033	-0.6910	0.8012	0.0063	0.9919
Eurytemora sp. C1-C3	-2.0486	-4.5543	-2.7879	-4.3357	-3.2377
Eurytemora sp. C4-C6	2.4650	1.4438	0.8940	3.8085	1.4834
E. nordmanni	-0.0423	-0.1476	-0.5830	-0.4323	0.4634
Fritillaria sp.	1.0929	5.0223	2.4710	2.0925	2.2962
Keratella sp.	-6.9410	-4.2724	-2.8239	-4.8141	-3.8527
Oikopleura sp.	-1.3094	-2.4064	-0.9327	6.7379	0.9643
O. similis C1-C3	2.1711	-0.3004	1.6350	0.8067	3.5874
O. similis C4-C6	-2.4265	-0.5961	1.3053	2.3284	-0.4262
P. intermedius	-0.6131	-1.4655	0.1793	0.2463	-0.2201
P. leuckarti	0.1174	-0.9954	-0.6825	-1.6678	0.0216
P. acuspes C1-C3	-0.0966	-0.8936	-0.2557	-0.1286	-1.2668
P. acuspes C4-C6	5.6785	3.6664	2.4787	3.1149	4.5518
Synchaeta sp.	0.7686	0.7458	0.5609	0.2043	-0.1208
T. longicornis C1-C3	-2.0670	-1.8969	-0.3590	-0.0810	-0.3368
T. longicornis C4-C6	0.6205	2.3738	1.8201	0.7561	2.3023
Constants	-39.9275	-24.6367	-13.8410	-21.8851	-18.3821

Table 3: Discriminant function analysis. Classification matrix of the observed and predicted categories. Deep and haline waters are shaded.

Observed	Cum. percent	Predicted category				
		SUMMER	WINTER	HALINE	BB60	BB90
SUMMER	100.0000	22	0	0	0	0
WINTER	96.4286	0	54	2	0	0
HALINE	88.8889	0	2	40	1	2
BB60	61.5385	0	0	5	8	0
BB90	40.0000	0	0	6	0	4
Total	87.6712	22	56	53	9	6
Wilk's Lambda	0.0351866					
F (92, 473)	6.842463					
p-Level	<0.0001					

Table 4: Chi^2-test for the significance of the roots in the canonical analysis.

Root	Eigenvalue	Wilk's Lambda	Chi^2	DF	Cum %	p-Level
1	4.487715	0.035187	438.4688	92	0.609233	< 0.0001
2	2.403534	0.193094	215.4397	66	0.935530	< 0.0001
3	0.336036	0.657202	54.9890	42	0.981144	0.086285
4	0.138893	0.878046	17.0374	20	1.000000	0.650542

Table 5: Means of the canonical variables in each root.

Category	Root 1	Root 2	Root 3	Root 4
SUMMER	3.96521	2.00518	-0.276406	0.07415
WINTER	0.73207	-1.83085	0.064898	-0.05956
HALINE	-2.06359	0.56459	-0.238311	0.35689
BB60	-0.93581	1.61962	1.660217	-0.23316
BB90	-2.32034	1.19518	-0.841222	-1.13251

Z2: Living below the halocline - Strategies of deep living species in the highly stratified and brackish Bornholm Sea (central Baltic Sea)

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Fritillaria borealis, *Oikopleura dioica* and *Oithona similis* were identified to reside in the area below the halocline at least temporarily. Based on these three species strategies of deep living zooplankton were exemplarily demonstrated. Data from three stations with different depths along a west to east transect in the Bornholm Sea were used. By means of a weighted mean depth index this paper shows vertical distribution patterns of different species in relation to the seasonally changing hydrography. We discuss strategies required to be present in this highly stratified and brackish sea within particular ecophysiological ranges. The initial idea of analysis was proposed by the first author. The manuscript was improved by the co-author.

Living below the halocline -
Strategies of deep-living species in the highly stratified brackish Bornholm Basin (central Baltic Basin)

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Abstract

The Baltic Basin is the largest brackish water area of the world. Based on data from 16 cruises we show the seasonal and vertical distribution patterns of the appendicularians *Fritillaria borealis* and *Oikopleura dioica* and the cyclopoid copepod *Oithona similis*, in the highly stratified Bornholm Basin. These species live at least temporarily below the permanent halocline and use different life strategies to cope with the brackish environment. *F. borealis* is abundant in the upper layers of the water column before the thermocline develops. With the formation of the thermocline abundance decreases and the remaining specimens outlast higher temperatures below the halocline. Distribution and strategy suggest that *F. borealis* might be a glacial relict species in the Baltic Sea. *O. dioica* is only abundant during summer and occurs exclusively in high saline waters below the halocline. *O. similis* is present all year round and dwells also below the halocline. We argue that the observed strategies are determined by ecophysiological constraints and life history traits. The three species share an omnivorous feeding behaviour and the capability to utilise small size spectra of food. As phytoplankton concentration is negligible below the halocline, we suggest that these species feed on organic material and heterotrophic organisms that accumulate in the density gradient of the halocline. Therefore the deep haline waters represent a habitat providing shelter from predation and food supply for adapted species that allows them to gather sufficient resources and to maintain populations.

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Introduction

The distribution patterns of zooplankton species in the water column often coincide with discriminable conditions of temperature, salinity and oxygen (e.g. Fager & McGowan 1963, Owen 1989, Geller et al. 1992, Roemmich & McGowan 1995). The physical layering can limit species dispersal and constrain appearance to fringed layers (Gallager et al. 2004). Especially in regions with strong fresh water influence the reduced vertical exchange between different water masses (Denman & Gargett 1988) impacts both primary and secondary production in as yet not completely understood ways (Owen 1989, Cowles et al. 1998). Several aspects are discussed how zooplankton preferences for different layers are affected by hydrography. Ecophysiological demands (Saito & Hattori 1997), the availability of food resources (Hattori & Saito 1997) and predator avoidance (Bollens & Frost 1989, Titelman & Fiksen 2004) are significant factors for habitat selection. Ontogenetic migrations (Renz & Hirche 2006), histo-geographic traits (Ojaveer et al. 1998, Renz & Hirche 2006) and the impact of turbulence on feeding (Maar et al. 2006) further impact the optimum depth (Ohman 1988).

The Baltic Sea is the largest brackish water area in the world and is characterised by strong thermal and saline stratifications (Fonselius 1970). During summer a thermocline forms a steep temperature gradient in the upper 20 to 30 m. A permanent halocline separates the low saline surface water from a denser layer with higher salinity in approximately 60 m depth (Fonselius 1970, Hernroth & Ackefors 1979). Shallower areas lack these high saline bottom waters and sills constrain water exchange between the deep basins. Degradation processes result in low oxygen concentrations below the halocline, while ventilation depends on inflows from the North Sea (Vallin & Nissling 2000), which communicates with the Baltic Sea via the Belt Sea and the Danish Sound (Brogmus 1952). From a geological view the Baltic is a young sea (Andrén et al. 2000, Andrén et al. 2002), with biotic immigration closely related to the events after the last glacial period. Consequently few endemic species are present in this brackish environment (Ackefors 1969) and many species live at the lower range of their osmotic tolerance limit (Hernroth & Ackefors 1979). This results in the typical low diversity of brackish systems (Remane & Schlieper 1971) and unoccupied ecological niches (Elmgren 1984). Newly inserted species have the possibility to establish in this evolutionary proving ground and are frequently observed with varying success (cf. Postel 1996). Although the role of the thermo- and halocline is not completely understood in this system, the physical layering separates the water column into different habitats and impacts vertical zooplankton community assemblages (Schulz et al. 2006). Thus habitat selection is constrained by the physical parameters and assemblage patterns in certain depths impact the interactions with different trophic levels. Successful species either require a euryoecious capacity or are forced to develop a suitable niche and survival strategy.

In the Bornholm Basin, one of the target areas of GLOBEC-Germany, the appendicularians *Fritillaria borealis*, *Oikopleura dioica* and the cyclopoid copepod *Oithona similis* are members of the zooplankton community below the halocline (Hansen et al. 2004, Schulz et al. 2006). Little is known about their life strategies, although these species represent an important contribution to the total biomass at certain times of the year (Hernroth & Ackefors 1979, Hansen et al. 2004). While the seasonal abundance of *Oikopleura dioica* contributes with only 0.02% to the community composition, *Fritillaria borealis* shows a proportion of approximately 8.2% and *Oithona similis* of 4.6% (Schulz, in preparation). Investigations by Ackefors (1969) and Hernroth & Ackefors (1979) give a general overview on the vertical distribution of different zooplankton species in the Baltic Sea, but low vertical and temporal sampling resolution does not allow determining the main residence layers

and life cycles. They are good examples for successful immigration and allow studying the effect of hydrography on the vertical distribution. The overall knowledge of appendicularian vertical distribution, as well as their diet is quite limited (Fenaux 1968, Bone 1998, Calbet 2001) and little information is available for the Baltic. Although *O. similis* is widely distributed its vertical abundance pattern and role in the food web is not fully understood (Turner 2004). Recent investigations have shown that *O. similis* dwells mainly in the halocline (Hansen et al. 2004).

This study contributes to the understanding of the halocline as an environmental characteristic of the Bornholm Basin that impacts vertical zooplankton community assemblages. Based on three stations with different depths and hence differently developed stratifications we present a high resolution data set obtained during 16 cruises. The behaviour of the three marine species in relation to the changing physical parameters temperature, salinity and oxygen was investigated. We discuss the strategies how they cope with the challenging conditions of this highly stratified basin and trophodynamic implications for the food web.

Material and Methods

Hydrography

Data are based on 16 cruises between March 2002 and May 2003 with an almost monthly coverage. On seven stations in the Bornholm Basin vertical profiles of temperature, salinity and oxygen were obtained by using a CTD probe (Fig. 1). The stations were located on a west to east transect, representing a section through the Basin, the communicating water masses from the North Sea successively pass (Fig 2). Spatial and seasonal charts were created with Surfer (Golden Software Inc., Surfer version 8) and krigging as gridding method. Temperature was visualised as greyscale background with a contour plot overlay rendered from salinity data. The 1 ml l^{-1} oxygen isopleth was additionally included. Bathymetric maps were generated with Ocean Data View (Schlitzer 2004).

Zooplankton data

Zooplankton sampling was performed with a multinet (50 µm mesh size, 0.25 m^2 mouth opening, HydroBios, Kiel) on three of the seven stations (Fig. 1). Samples were taken from bottom to surface in stacked 10 m intervals. The time lag between sampling the three stations on each cruise was normally less than two days (Table 1). Samples were taken regardless of day time and preserved immediately aboard in 4% formalin-seawater solution. Subsamples of at least 500 individuals were enumerated and the number of individuals extrapolated to individuals per cubic meter (n m^{-3}) in each depth stratum. Data of *Fritillaria borealis*, *Oikopleura dioica* and *Oithona similis* were used for the analysis. As an index of the vertical orientation of the standing stocks the weighted mean depths (WMD) were calculated according to Bollens & Frost (1989). With respect to the covered depth range of a single net in a haul the abundance data were also used to compute the number of individuals per square meter (SQM, n m^{-2}):

$$f_{WMD}(i,j) = \frac{\sum_{k=0}^{l_j-1}(m_{ik}d_k)}{\sum_{k=0}^{l_j-1}m_{ik}}$$

$$f_{SQM}(i,j) = \sum_{k=0}^{l_j-1}(m_{ik}\,n_k)$$

where d is the mid-depth of one net's range covered in each haul, i the index of the species or stage, j the station, k the index of the net on the jth station, l the total number of nets on a station, m the number of individuals per cubic meter and n the depth range of the kth net. For semi-automated processing the formulas were coded as algorithms, implemented into Ocean Sneaker's Tool (Schulz 2005) and thereafter used for the conversions. Charts were created with Sigma Plot (Version 6, SPSS Inc.). The WMD results were plotted onto the hydrographic charts.

Results

Hydrography

In March and April 2002 the water column was separated by the permanent halocline into two layers (Fig. 2a). The continuously present winter water of the upper 60 m was characterised by a salinity <8 and temperatures less than 5°C. After May 2002 the increasing surface temperature formed a thermocline in the Bornholm Basin between 10 and 20 m depth. It resulted in a three-storeyed water column accompanied with a reduced thickness of the winter water. In July 2002 the warm surface waters reached down to 30 m depth (Fig. 2b). Highest surface temperatures >20°C were observed in August and calm weather conditions allowed the adjustment of a steep thermocline in ~20 m depth. Towards the end of summer surface temperatures decreased to approximately 15°C in early October, while the surface layer showed a thickness of 30 m, before the thermocline disappeared after October. In 2003 the formation of a thermocline was again observed in May.

In August 2002 the first signatures of an exceptionally warm inflow event of North Sea waters were observed at station BB0021. In September 2002 the intrusion water propagated eastward from the Arkona Basin at the north western end of the Bornholm Basin. In September/October 2002 the warm water masses were also found on station BB0023 (Fig. 2c). They stratified into approximately 60 m depth due to a lesser density caused by higher temperatures than the resident haline water below and are referenced hereafter as BB60. These waters caused unusually high temperatures of > 13°C in the halocline at 60 m and compressed the layer of the winter water from below. The BB60 water flew out into the Gdansk Deep via Slupsk Sill until December 2002. In November 2002 a second inflow entered the Bornholm Basin and replaced the stagnant water masses below 90 m (approx. 9.5°C and a salinity of 15 at BB0023, Fig. 2d). These waters are named hereafter BB90, according to Feistel et al. (2004). After January 2003 a further inflow, that fulfilled the criteria of a Major Baltic Inflow (MBI, Matthäus and Frank 1992), renewed the waters below the halocline completely. The MBI was characterised by high salinity, low temperatures and high oxygen concentrations (Fig. 2e). It was followed by further inflow events enhancing the effect of the MBI. Prior to January 2003 the temperature of the water above the halocline was cooler than below. Due to mixing along the transition zones the inflow events caused a weaker salinity slope. While the temperature development at station BB0026 followed that of the deeper stations it showed only temporarily higher salinities at the bottom. For a complete discussion of the inflow events we refer to Feistel et al. (2003a, 2003b, 2004).

Seasonal distribution

In 2002 *Fritillaria borealis* was most abundant between April and May with up to 445 n m^{-2} 10^3 (Fig. 3a). After the formation of a thermocline in May 2002 the population decreased rapidly by more than two orders of magnitude to values below 1.7 n m^{-2} 10^3 in June. While abundance remained on a comparably low level at BB0021 and BB0023 no individuals were observed on station BB0026 between July and November. With the appearance of the BB60 waters after August 2002 abundance increased successively from west to east. In January 2003 abundances partially exceeded those of March 2002. The population peak was again observed in April, with values of up to 3496 n m^{-2} 10^3, which is one order of magnitude higher than in the previous year.

Oikopleura dioica was recorded between July and November 2002 with the highest abundances after the BB60 event (Fig. 3b). In October 2002 values of 0.6 and 0.9 n m^{-2} 10^3 were found on BB0023 and BB0021 respectively and 13.9 n m^{-2} 10^3 in the following month on BB0021. During winter *O. dioica* was completely absent. Small numbers were only recorded in April 2003 at the deepest station BB0023. *O. dioica* was never observed at the shallow station BB0026.

All stages of *Oithona similis* were permanently present at the stations BB0021 and BB0023 (Fig. 3c-e). Copepodite abundance increased from April 2002 onwards and lowest abundances were recorded during winter. Abundance patterns of adult stages followed that of the younger, while female abundance was generally higher than male abundance. On the shallower station BB0021 copepodite and female abundances were in general lower than on BB0023. In opposite to the stations BB0021 and BB0023 all stages of *O. similis* were seldom observed at the easternmost station BB0026. Males were only found in April 2002, while females and copepodite stages appeared in April and May 2002 and together with the inflow events.

Vertical distribution

During winter *Fritillaria borealis* dwelled in the cool waters above the halocline in a salinity <7.5 (Fig. 4a-c). With the onset of thermal stratification the individuals invaded the deeper waters below the halocline on all stations. Between June and October individuals were located in salinities >9. With the BB60 waters the main distribution was still in the haline water, but *F. borealis* avoided the warm core of the inflow. It remained below the halocline until the surface water cooled down again. It was not observed at the shallow station BB0026 during summer (Fig. 4c). With the cooling of the surface after November 2002 individuals were found in shallower depths and again observed on the shallow station BB0026. From January 2003 onwards the stock maximum was found above the halocline, as well as in the upper part of the haline waters, where cool temperatures were available after the MBI's.

Oikopleura dioica was always located in salinities >11 (Fig. 4a-c). In October 2002 the distribution centre of *O. dioica* was closer to the warm core of the BB60 inflow water than that of *F. borealis*. The shallowest distribution centre was in 55 m depth. The vertical orientation shows *O. dioica* to deeply invade the oxygen depletion zone (Fig. 4a). Although salinities >11 were at least temporarily observed on station BB0026 no individuals were found here (Fig. 4c).

All stages of *Oithona similis* were centred between a salinity of 12.5 and 14 prior to the inflow events at the deeper stations BB0021 and BB0023 (Fig. 5a-b). Between March and May 2002 distributions down to 80 m depth were observed. The stock maximum was located closely to the 1 ml l^{-1} oxygen isocline. With the first BB60 inflow waters in August

2002 adults on BB0021 dwelled mainly in the uppermost part of the haline layer and out of the exceptional warm water in this depth (Fig. 5a-b). Decreasing strengths of the salinity gradient coincided with a broader WMD range between the different stages. With steeper salinity gradients all stages were observed closely below these gradients and inter-stage variation was low. The depth centre was found to be 5-10 m above those from March to May 2002 with higher salinity and oxygen concentrations. Males were often located deeper than females and except for April 2002 no males were observed on BB0026 (Fig. 5c). In contrast to the deeper stations the vertical orientation on BB0026 was found to be above the halocline in May 2002 and after the major inflow in January 2003. In November females and copepodites were mainly distributed in the upper part of the haline waters on station BB0026 with a salinity of 9.5.

Discussion

Distribution patterns

Inhomogeneous vertical distribution of zooplankton is a response to several parameters and the interplay between them (Titelman & Fiksen 2004). The observed distribution patterns of *Fritillaria borealis*, *Oikopleura dioica* and *Oithona similis* indicate that the species use different strategies to cope with the prevailing hydrographic conditions. These strategies are adapted to the stratified situation of the Baltic Sea. They are conditioned by ecophysiological capabilities, also reflected in the zoogeographic distributions. While all three species are found in temperate waters, the zoogeographic distribution of *F. borealis* extends to both Polar regions (Fenaux et al. 1998). *F. borealis* is most abundant when surface temperatures are low (Fenaux et al. 1998) and is considered as an indicator for Arctic waters on the northern hemisphere (Lohman 1895, Grainger 1965). This stenotherm and euryhaline species prefers temperatures below 10°C (Berrill 1959, Ackefors 1969) and salinities of at least 6-7 (Purasjoki 1945, Ackefors 1969). This physiological window allows it to inhabit the Bornholm Basin year round. During its abundance maximum in spring it utilises the upper layers before the thermocline develops. In the Bornholm Basin it is expelled from the surface layer in the warm season and uses the waters below the halocline as retreat to outlast unfavourable conditions.

In contrast to *Fritillaria borealis*, the appearance of *Oikopleura dioica* is exclusively restricted to summer and reflects the zoogeographic distribution from temperate waters to the warm Indian Ocean, the Red and Mediterranean Sea (Lohmann 1896, Fenaux et al. 1998, Tomita et al. 2003). This eurytherm species is abundant in near shore waters and requires salinities >11 (Lohmann 1896). It is also found in warm estuaries, like the Amazon (Lohmann 1896) or the North Inlet of South Carolina (Costello & Stancyk 1983). In the Bornholm Basin the appearance of *O. dioica* is correlated with increasing temperatures (Behrends 1996). We found this species during summer confirming these observations, although the temperatures below the halocline did not increase. As *O. dioica* was already present in July 2002, prior to the inflows, the initial appearance is not likely to originate from advection with North Sea waters. It remains unclear where these individuals came from. *O. dioica* finds the required salinity only below the halocline and accepts oxygen concentrations <1 ml l^{-1}. During summer it shares the habitat with the remaining *F. borealis* population.

While the two appendicularian populations showed distinct seasonal abundance peaks all developmental stages of the cosmopolitan cyclopoid copepod *Oithona similis* (Paffenhöfer 1993) were found in high numbers throughout the year. Due to few pretensions and a eu-

ryoecious physiological window *O. similis* inhabits this volume below the halocline permanently. The egg-carrying strategy of *O. similis* reduces the threat of loosing off-spring to the sediment (Nielsen & Sabatini 1996) in noxious anoxic zones. This is advantageous compared to broadcast spanners, where recruitment from sediments is a critical stage in Baltic copepods (Dutz et al. 2004). Hansen et al. (2004) report that *O. similis* utilises the layer between the 2 ml l^{-1} oxygen isopleth and the halocline. We found *O. similis* mainly close to the halocline on the higher saline side, but the vertical distribution indicates an oxygen tolerance down to 1 ml l^{-1}. This would increase the available space with favourable salinity and oxygen conditions for the population, as the lower fringe of the inhabitable volume is deeper. Anyhow, the depth centroids of the different stages were located close to the halocline after the Major Baltic Inflow (MBI). Similar to the ontogenetic vertical distribution of *Pseudocalanus acuspes* in the Bornholm Basin (Renz & Hirche 2006) males of *O. similis* were often found deepest.

With the lower salinity in the brackish Baltic Sea these three marine species are exposed to osmotic stress. Consequently the observed distribution patterns are subjected to their physiological capabilities. With increasing temperatures respiration and general metabolic demands increase disproportionally and lower the physiological tolerance to dilution (e.g. Lehman 1988). Below the halocline the expenditure for osmoregulatory energy is lowest in brackish waters (Remane & Schlieper 1971, Viitasalo 1992). Thus the annual submergence of *F. borealis* can be interpreted as an adaptation to the environmental conditions of the Baltic Sea reducing osmotic stress. By this *F. borealis* might be seen as one of the Baltic glacial relict species (Ojaveer et al. 1998) that retraces the heritage of its histogeographic origin. A complete avoidance of warm surface waters and presence in the deep layers is also reported for other members of the glacial relict fauna in the Baltic (Renz & Hirche 2006).

At the shallow station BB0026 abundance of the investigated taxa was generally lower than at the deeper stations BB0021 and BB0023. The lack of favourable conditions of the deep layers at shallow sites restricts horizontal distribution. While *O. dioica* was completely absent at the shallow site, the appearance of *O. similis* was coupled to prominent salinity increases at the bottom. Comparable abundances between the deep stations and BB0026 were only found for *F. borealis* during winter and spring, as long as it used the upper part of the water column. Consequently abundance of deep living species is a function of the available space between halocline and seafloor and the respective environmental conditions within this volume. Consequently *O. dioica* and *O. similis* are expelled from shallow stations, as well as *F. borealis* during the warm seasons (Schulz et al. 2006), although underlying mechanisms differ.

Inflows did not occur for several years prior to 2002. As the investigated species were already observed before the first inflow they obviously abide sustainable populations in the Bornholm Basin. Although total abundances did not increase after inflows, advection is likely as all species were more or less abundant in the North Sea during the respective events (BSH-MURSYS database). During propagation of inflow waters mixing processes along their transition zones alter the primordial physical parameters (Feistel et al. 2004). Consequently conditions for entrained species change with propagation distance. Advected species that can cope with the environmental conditions at the arrival or exit point find a habitat constrained by the characteristic Baltic layers. It is a common way by which new species are injected into the Baltic (cf. Postel 1996), although many species fade away or cannot abide a population (Purasjoki 1945, Mankowski 1962, Schneider 1987, Postel 1996). While the environmental conditions of the Bornholm Basin are within tolerance ranges of *F. borealis* and *O. similis*, it seems that *O. dioica* finds sub-optimum conditions,

concluding from the reduced abundance compared to warmer and more haline waters (Lohman 1895).

In the Bornholm Basin the BB60 event caused the highest temperatures on record in the depth of the halocline (Mohrholz et al. 2006). In contrast to the MBI event the salinity remained low and the volume below the halocline was still delimited by the deep oxygen minimum zone. The distribution of the three species at the fringes of the inflow core suggests that these waters are less invaded and act as a horizontal hydrographic disturbance in these depths. Although the summer inflow 2002 was exceptionally strong, the frequency of these anomalies increased since 1990 (Mohrholz et al. 2006). This may disrupt conventional life history strategies, as these events bias vertical exchange processes and pivotal requirements (Rhodes & Odum 1996). The following inflows ventilated the waters below the halocline and improved the conditions deteriorated by degradation processes during periods of stagnation (Fonselius 1970). Thus claimable space increased for species sensitive for deteriorating salinity and oxygen conditions (Hansen et al. 2004, Renz & Hirche 2006, Hansen et al. 2006). The raised halocline allowed species from below the halocline to access even shallower areas with the horizontally spreading haline bottom waters.

The time lag of a few days (Table 1) between sampling the three stations might have biased the observed inter-station response of the species to hydrography due to internal waves (Banse 1964). By this the transport of *O. dioica* with inflow waters over Slupsk Sill and consequently a temporary appearance on the shallow station BB0026 might have been missed. This might also apply for the other two species. Anyhow the major changes between the sites appear on a longer time scale than our monthly observations.

Feeding and predation

Fritillaria borealis, *Oikopleura dioica* and *Oithona similis* are often associated with chlorophyll peaks in the euphotic zone (Lohmann 1895, López-Urrutia et al. 2003a, Tomita et al. 2003). In the deep layers of the Bornholm Basin chlorophyll concentration was low in 2002 (Beusekom et al. submitted). Consequently species below the halocline depend on alternative resources, like organic matter from vertical fluxes, ciliates or heterotrophic flagellates, which were found in these depths by Peters et al. (Peters et al. 2006). Such resources accumulate in density gradients like the permanent halocline (e.g. Lande & Wood 1987, MacIntyre et al. 1995, Vallin & Nissling 2000) and result in organic-rich layers important for species that feed on the respective size spectra (Cowles et al. 1998, Maar et al. 2006). As appendicularians, due to low metabolic reserves, survive only short starvation periods (Deibel 1998), the presence of a population indicates that their residence layers provide sufficient food (Gorsky et al. 1990, Gorsky et al. 1991). The specialised filter apparatus of *F. borealis* and *O. dioica* retains particles down to the submicronic and colloidal fraction (Flood et al. 1992, Gorsky et al. 1999, López-Urrutia et al. 2003b) and thus allows feeding in deep, detritus-based ecosystems (Gorsky & Fenaux 1998). Grazing on such material is probably more important than on autotrophic organisms (López-Urrutia et al. 2003a) and utilisation of small size spectra reduces competition with other zooplankton species (Alldredge 1972, Paffenhöfer 1983, Gorsky & Fenaux 1998). These aspects might explain why *F. borealis* migrates into the haline waters and does not outlast the higher temperatures in the winter water between the halo- and thermocline. Additionally to these resources its physiological window allowed *F. borealis* to access the surface spring bloom in April/May 2002 (Beusekom et al. submitted), which coincided with the high abundances.

Appendicularians affect the vertical flux in two ways: they transform sinking matter and their abandoned houses add organic material of nutritional value (Alldredge 1972). Al-

though the houses have a high settling velocity, they can be utilised by microbial and planktonic organisms (Paffenhöfer 1983, Steinberg 1995, Gorsky & Fenaux 1998, Maar et al. 2006).

Oithona similis is also well known to utilise resources of different size spectra from vertical fluxes (Gonzàlez & Smetacek 1994, Nielsen & Sabatini 1996, Castellani et al. 2005b, Reigstad et al. 2005, Hansen et al. 2006). The utilisation of faecal pellets seems likely in this depth, but is controversially discussed (e.g. Reigstad et al. 2005, Poulsen & Kiørboe 2006). The low inter-stage WMD variations under steep gradients and the affinity to the halocline suggest the utilisation of the density gradient by all stages. Low specialisation (Paffenhöfer 1993) together with an omnivorous feeding behaviour (Castellani et al. 2005b) and low metabolic rates (Castellani et al. 2005a) allow sustainable production even under extreme conditions (Fransz & Gonzales 1995) as found in the Baltic.

As a spin-off the utilisation of the waters below the halocline also represents a refuge against predation. The calanoid copepods of the Baltic Sea *Acartia* spp., *Temora longicornis* and *Centropages hamatus* feed on a size spectrum that includes appendicularian eggs and juveniles (Sommer et al. 2003), but are most abundant above the halocline (Schulz et al. 2006). Scyphomedusae are most prominent in the upper layers (Barz & Hirche 2005) and therefore also excluded as predators. Planktivorous larvae of the dominant fish species sprat (*Sprattus sprattus* L.) and herring (*Clupea harengus* L.) are abundant between April and July and prey close to the surface (Dickmann 2005, Dickmann et al. in press). Only the adult stages feed in mid- and deep waters (Voss et al. 2003). As *F. borealis* is the only species that utilises upper layers, the remaining individuals benefit most from their summer submergence.

Acknowledgement

References

Ackefors H (1969) Ecological zooplankton investigations in the Baltic Proper 1963-1965. Fish. Bd. Sweden, Inst Mar Res, Ser Biol Rep 18

Alldredge AL (1972) Abandoned larvacean houses: A unique food source in the pelagic environment. Science 177:885-887

Andrén E, Andrén T, Sohlenius G (2000) The Holocene history of the southwestern Baltic Sea as reflected in a sediment core from the Bornholm Basin. Boreas 29:233-2 50

Andrén T, Lindeberg G, Andrén E (2002): Evidence of the final drainage of the Baltic Ice Lake and the brackish phase of the Yoldia Sea in glacial varves from the Baltic Sea. Boreas 31:226-238

Barz K, Hirche HJ (2005) Seasonal development of scyphozoan medusae and the predatory impact of *Aurelia aurita* on the zooplankton community in the Bornholm Basin (central Baltic Sea). Mar Biol 147:465-476

Behrends G (1996) Long-term investigation of seasonal mesozooplankton dynamics in Kiel-Bight, Germany. Proceed 13th Symp Balt Mar Biol 93-98

Berrill NJ (1950) The Tunicata, with an account of the British Species. The Ray Society, London, pp 354

Bollens SM, Frost BW (1989) Diel vertical migration in zooplankton: Rapid individual response to predators. J Plank Res 13(6):1359-1365

Bone Q (1998) The biology of pelagic tunicates. Oxford University Press, Oxford

Brogmus W (1952) Eine Revision des Wasserhaushalts der Ostsee. Kieler Meeresforschungen 9(1):15-42

BSH (2006) MURSYS database: http://www.bsh.de/de/Meeresdaten/Beobachtungen/MURSYS-Umweltreportsystem/index.jsp

Calbet A (2001) Mesozooplankton grazing effect on primary production: a global comparative analysis in marine ecosystems. Limnol Oceanogr 46:1824-1830

Castellani C, Robinson C, Smith T, Lampitt RS (2005a) Temperature affects respiration rate of *Oithona similis*. Mar Ecol Prog Ser 285:129-135

Castellani C, Irigoyen X, Harris RP, Lampitt RS (2005b) Feeding and egg production of *Oithona similis* in the North Atlantic. Mar Ecol Prog Ser 288:173-182

Costello J, Stanzyk SE (1983) Tidal influence upon appendicularian abundance in North Inlet estuary, South Carolina. J Plankt Res 5:263-277

Cowles TJ, Desiderio RA, Carr ME (1998) Small scale planktonic structure: persistence and trophic consequences. Oceanography 11:4-9

Deibel D (1998) Feeding and metabolism of Appendicularia. The Biology of Pelagic Tunicates (ed. Q. Bone) Oxford University Press London, 139-149

Denman KL, Gargett AE (1988) Multiple thermoclines are barriers to vertical exchange in the subarctic Pacific during SUPER, May 1984. J Mar Res 46:77-103

Dickmann M (2005) Feeding ecology of sprat (*Sprattus sprattus* L.) and sardine (*Sardina pilchardus* W.) larvae in the Baltic Sea and in the North Sea. PhD thesis, University of Rostock, Germany

Dickmann M, Möllmann C, Voss R (submitted) Feeding ecology of central Baltic sprat (*Sprattus sprattus* L.) larvae in relation to zooplankton dynamics – Implications for survival. Mar Ecol Prog Ser

Dutz J, Mohrholz V, Peters J, Renz J, Alheit J (2004) A strong impact of winter temperature on spring recruitment of a key copepod species in the Bornholm Basin: potential linkages to climate variability. GLOBEC Int Newsletter 10(1):13-14

Elmgren R, Rosenberg R, Andersin AB, Evans S, Kangas P, Lassig J, Leppaekoski E, Varmo R (1984) Benthic macro- and meiofauna in the Gulf of Bothnia (northern Baltic). Finn Mar Res, Helsinki. No. 250:3-18

Fager E, McGowan J (1963) Zooplankton species groups in the North Pacific. Science 140(3566): 453-460

Feistel R, Nausch G, Mohrholz V, Łysiak-Pastuszak E, Seifert T, Matthäus W, Krüger S, Hansen IS (2003a) Warm Waters of Summer 2002 in the Deep Baltic. Oceanologia 45 (4), 571-592.

Feistel R, Nausch G, Matthäus W, Hagen E (2003b) Temporal and spatial evolution of the Baltic deep water renewal in spring 2003. Oceanologia 45 (4), 623-642

Feistel R, Nausch G, Matthäus W, Łysiak-Pastuszak E, Seifert T, Hansen IS, Mohrholz V, Krüger S, Buch E, Hagen E (2004) Background data to the exceptionally warm inflow into the Baltic Sea in late summer of 2002. Meereswiss Ber / Mar Sci Rep, Institute for Baltic Research 58, pp 1-58

Fenaux R (1968) Some appendicularians from the coast of Peru. Bol Inst Mar Peru 1(9):536-552

Fenaux R, Bone Q, Deibel D (1998) Appendicularian distribution and zoogeography. The Biology of Pelagic Tunicates (ed. Q. Bone) Oxford University Press London, 252-264

Flood PR, Deibel D, Morris C (1992) Filtration of colloidal melanin from seawater by planktonic tunicates. Nature 355:630-632

Fonselius SH (1970) On the stagnation and recent turnover of the water in the Baltic. Tellus 22(5):533-544

Fransz HG, Gonzalez SR (1995) The production of *Oithona similis* (Copepoda: Cylclopoida) in the Southern Ocean. ICES J Mar Sci 52:549-555

Gallager SM, Yamazaki H, Davis CS (2004) Contribution of fine-scale vertical structure and swimming behavior to formation of plankton layers on Georges Bank. Mar Ecol Prog Ser 267:27-43

Geller W, Pinto-Coelho R, Pauli HR (1992) The vertical distribution of zooplankton (Crustacea, Rotatoria, Ciliata) and their grazing over the diurnal and seasonal cycles in Lake Constance. Arch Hydrobiol Beih 35:79-85

GLOBEC-Germany (2002) Clarification of trophodynamic interactions between zooplankton and planktivorous fish in relation to reproductive success under the impact of physical forcing. www.globec-germany.de

Gorsky G, Laval P, Youngbluth MJ, Palazzoli I (1990) Appendiculaires mésopélagiques, indicateurs potentials des couches riches en matiére organique. Rapports et Procèsverbaux des Rèunions-Comission Internationale pour l'Exploration Scientifique de la Méditerranée 32(1) :200

Gorsky G, Lins da Silva N, Dallot S, Laval P, Braconnot JC, Prieur L (1991) Midwater tunicates: Are they related to the permanent front of the Ligurian Sea (NW-Mediterranean)? Mar Ecol Prog Ser 74:195-204

Gorsky G, Fenaux R (1998) The role of Appendicularia in marine food webs. In: The Biology of Pelagic Tunicates (ed. Q. Bone) Oxford University Press London pp:161-169

Gorsky G, Chrétiennot-Dinnet MJ, Blanchot J, Palazzoli I (1999) Picoplankton and nanoplankton aggregation by appendicularians: fecal pellet contents of *Megalocercus huxleyi* in equatorial Pacific. J Geophys Res C 104:3381-3390

Grainger EH (1965) Zooplankton from the Arctic Ocean and adjacent Canadian waters. J Fish Res Bd Canada 22:543-564

Hansen FC, Möllmann C, Schütz U, Hinrichsen HH (2004). Spatio temporal distribution of *Oithona similis* in the Bornholm Basin (Central Baltic Sea). J Plankt Res 26(6), 659-668

Hansen FC, Möllmann C, Schütz U, Neumann T (2006). Spatio temporal distribution of calanoid copepods in the central Baltic Sea. J. Plankt. Res. 28(1), 39-54

Hattori H, Saito H (1997) Diel changes in vertical distribution and feeding activity of copepods in ice-covered Resolute Passage, Canadian Arctic, in spring 1992. J Mar Sys 11(1-2):205-219

Hernroth L, Ackefors H (1979) The zooplankton of the Baltic Proper. Report Fish Bd Sweden, Inst Mar Res 2:1-60

Krause M, Dippner JW, Beil J (1995) A review of hydrographic controls on the distribution of zooplankton biomass and species in the North Sea with particular reference to a survey conducted in January-March 1987. Prog Oceanogr 35:81-152

Lande R, Wood M (1987). Suspension times of particles in the upper ocean. Deep Sea Res 34:61-72

Lehman JT (1988) Ecological principles affecting community structure and secondary production by zooplankton in marine and freshwater environments. Limnol Oceanogr 33:931-945

Lohmann H (1895) Ueber die Verbreitung der Appendicularien im Atlantischen Oceane. Verhandlungen der Gesellschaft deutscher Naturforscher und Ärzte; Zweite Gruppe der naturwissenschaftlichen Abtheilungen-Vereinigte Abteilungen für Zoologie und Entomologie 67:113-120

Lohmann H (1896) Die Appendicularien der Plankton-Expedition. Ergebnisse der in dem Atlantischen Ocean von Mitte Juli bis Anfang November 1889 ausgeführten Plankton-Expedition der Humboldt-Stiftung, Hensen V (ed) 2(Ec):1-148

López-Urrutia A, Irigoien X, Acuna JL, Harris R (2003a) In situ feeding physiology and grazing impact of the appendicularian community in temperate waters. Mar Ecol Prog Ser 252:125-141

López-Urrutia A, Acuna JL, Irigoien X, Harris R (2003b) Food limitation and growth in temperate epipelagic appendicularians (Tunicata). Mar Ecol Prog Ser 252:143-157

Maar M, Visser AW, Nielsen TG, Stips A, Saito H (2006) Turbulence and feeding behaviour affect the vertical distributions of *Oithona similis* and *Microsetella norwegica*. Mar Ecol Prog Ser 313:157-172

Mankowski W (1962) Biological macroplankton indicators of the inflow of salt water from the North Sea into the Baltic Sea. Przeglad Zool 6(1):38-42

MacIntyre S, Alldredge AL, Gotschalk CC (1995). Accumulation of marine snow at density discontinuities in the water column. Limol Oceanogr 40:449-468

Matthäus W, Frank H (1992) Characteristics of Major Baltic Inflows - a statistical analysis. Cont. Shelf. Res. 12(12), 1375-1400

Mohrholz V, Dutz J, Kraus G (2006) The impact of exceptionally warm summer inflow events on the environmental conditions in the Bornholm Basin. J Mar Sys 60:285-301

Nishida S (1985) Taxonomy and distribution of the family Oithonidae (Copepoda, Cyclopoida) in the Pacific and Indian Oceans. Bull Ocean Res Inst Univ Tokyo 20:1-167

Nielsen TG, Sabatini M (1996) Role of cyclopoid copepods *Oithona* spp. in the North Sea plankton communities. Mar Ecol Prog Ser 139:79-93

Ohman MD (1988) Behavioural response of zooplankton to predation. Bull Mar Sci 43:530-550

Ojaveer E, Lumberg A, Ojaveer H (1998) Highlights of zooplankton dynamics in Estonian waters (Baltic Sea). ICES J. Mar. Sci. 55, 748-755

Owen RW (1989) Microscale and finescale variations of small plankton in coastal and pelagic environments. J Mar Res 47:197-240

Paffenhöfer GA (1983) Vertical zooplankton distribution on the northeastern Florida shelf. J Plankt Res 5(1):15-33

Paffenhöfer GA (1993) On the ecology of marine cyclopoid copepods (Crustacea, Copepoda). J Plankt Res 15(1):37-55

Peters J, Renz J, van Beusekom J, Boersma M, Hagen W (2006) Trophodynamics and seasonal cycle of the copepod *Pseudocalanus acuspes* in the central Baltic Sea (Bornholm Basin): evidence from lipid composition. Mar Biol doi:10.1007/s00227-006-0290-8

Postel L (1996) Zooplankton. In: Rheinheimer G (Eds.), Meereskunde der Ostsee. Springer Verlag, Berlin – Heidelberg - New York, pp. 150-160

Poulsen LK, Kiørboe T (2006) Vertical flux and degradation rates of copepod faecal pellets in a zooplankton community dominated by small copepods. Mar Ecol Prog Ser 323:195-204

Purasjoki KJ (1945) Über das Vorkommen von *Fritillaria borealis* Lohm. (Appendicularia) im nördlichen Teil der Ostsee an den Küstengewässern Finnlands. Soc Scient Fenn Comm Biol 9(1):1-8

Reigstad M, Wexels Riser C, Svensen C (2005) Fate of copepod faecal pellets and the role of *Oithona* spp. Mar Ecol Prog Ser 304:265-270

Remane A, Schlieper C (1971) Biology of brackish water. Wiley Interscience Division John Wiles & Sons, Inc. New York-Toronto-Sydney

Renz J, Hirche HJ (2006) Life cycle of *Pseudocalanus acuspes* Giesbrecht (Copepoda, Calanoida) in the Central Baltic Sea: Seasonal and spatial distribution. Mar Biol 148:567-580

Rhodes OE jr, Odum EP (1996) Spatiotemporal approaches in ecology and genetics: the road less travelled. In: Rhodes OE jr, Chesser RK, Smith MH (eds) Population dynamics in ecological space and time. University of Chicago press, Chicago, 1-8

Roemmich D, McGowan J (1995) Climatic warming and the decline of zooplankton in the California Current. Science 267:1324-1326

Saito H, Hattori H (1997) Diel vertical migration and feeding rhythm of copepods in a shallow food-abundant embayment. Plankt Biol Ecol 44(1-2):13-29

Schlitzer R (2004) Ocean Data View. http://www.awi-bremerhaven.de/GEO/ODV

Schneider G (1987) Role of advection in the distribution and abundance of *Pleurobrachia pileus* in Kiel Bight. Mar Ecol Prog Ser 41(1):99-102

Schulz J (2005) Ocean Sneaker's Tool. www.awi-bremerhaven.de/Software/OST

Schulz J, Möllmann C, Hirche HJ (2006) Vertical zonation of the zooplankton community in the Central Baltic Sea in relation to hydrographic stratification as revealed by Multivariate Discriminant Function- and Canonical Analysis. J Mar Sys doi:10.1016/j.jmarsys.2006.09.004

Sommer F, Hansen T, Fechtmayr H, Santer B, Tokle N, Sommer U (2003) Do calanoid copepods suppress appendicularians in the coastal oceans? J Plankt Res 25(7):869-871

Steinberg DK (1995) Diet of copepods (Scopalatum vorax) associated with mesopelagic detritus (giant larvacean houses) in Monterey Bay, California. Mar Biol 122(4):571-584

Titelman J, Fiksen Ø (2004) Ontogenetic vertical distribution patterns in small copepods: field observations and model predictions. Mar Ecol Prog Ser 284:49-63

Tomita M, Shiga N, Ikeda T (2003) Seasonal occurrence and vertical distribution of appendicularians in Toyama Bay, southern Japan Sea.J Plankt Res 25(6):579-589

Turner JT (2004) The importance of small planktonic copepods and their roles in pelagic marine food webs. Zool Stud 43:255-266

van Beusekom JEE, Mengedoht D, Augustin CB, Mario Schilling M, Boersma M (submitted) Phytoplankton and nutrient dynamics in the Bornholm Basin 2002-2003 during the German GLOBEC Project. Int J Earth Sci

Vallin L, Nissling A (2000) Maternal effects on egg size and egg buoyancy of Baltic cod, *Gadus morhua*-Implications for stock structure effects on recruitment. Fish Res 49:21-37

Viitasalo M (1992) Mesozooplankton of the Gulf of Finland and northern Baltic Proper-A review of monitoring data. Ophelia 35(2):147-168

Description of the figures

Figure 1: Sampling site in the Bornholm Basin (Central Baltic Sea) with the three stations at which zooplankton samples and CTD casts were obtained (white circles). Additional CTD casts were performed on four further stations along a transect through the Bornholm Basin (black dots).

Figure 2: Hydrographic transects through the Bornholm Basin covering the sampled stations. a) April 2002, b) July 2002, c) October 2002, d) November 2002 and e) February 2003. Temperature is shown by grey scale background and salinity by solid isolines. The 1 ml l^{-1} oxycline is displayed by the dashed line. In February 2003 oxygen concentration was never found to be below 3 ml l^{-1}.

Figure 3: Seasonal abundance of a) *Fritillaria borealis*, b) *Oikopleura dioica* and c-e) *Oithona similis* at the stations BB0021, BB0023 and BB0026 in the Bornholm Basin. Note the logarithmic scaling.

Figure 4: Weighted mean depth distribution of *Fritillaria borealis* and *Oikopleura dioica* at three stations a) BB0021, b) BB0023 and c) BB0026 in the Bornholm Basin. Image map background shows the seasonal temperature development in the respective depth, solid lines represent isohaline levels and the dashed line indicates the 1 ml l^{-1} oxygen concentration.

Figure 5: Weighted mean depth distribution of copepodites, females and males of *Oithona similis* at three stations a) BB0021, b) BB0023 and c) BB0026 in the Bornholm Basin. Image map background shows the seasonal temperature development in the respective depth, solid lines represent isohaline levels and the dashed line indicates the 1 ml l^{-1} oxygen concentration.

Fig. 1

Temperature [°C]
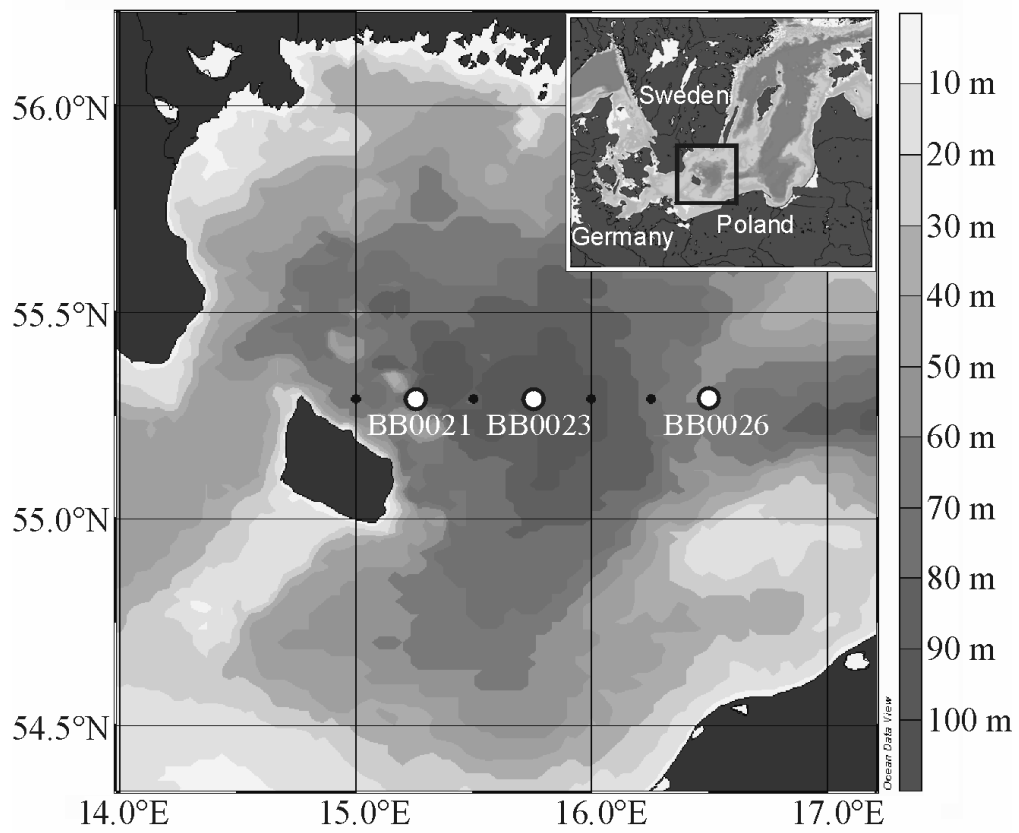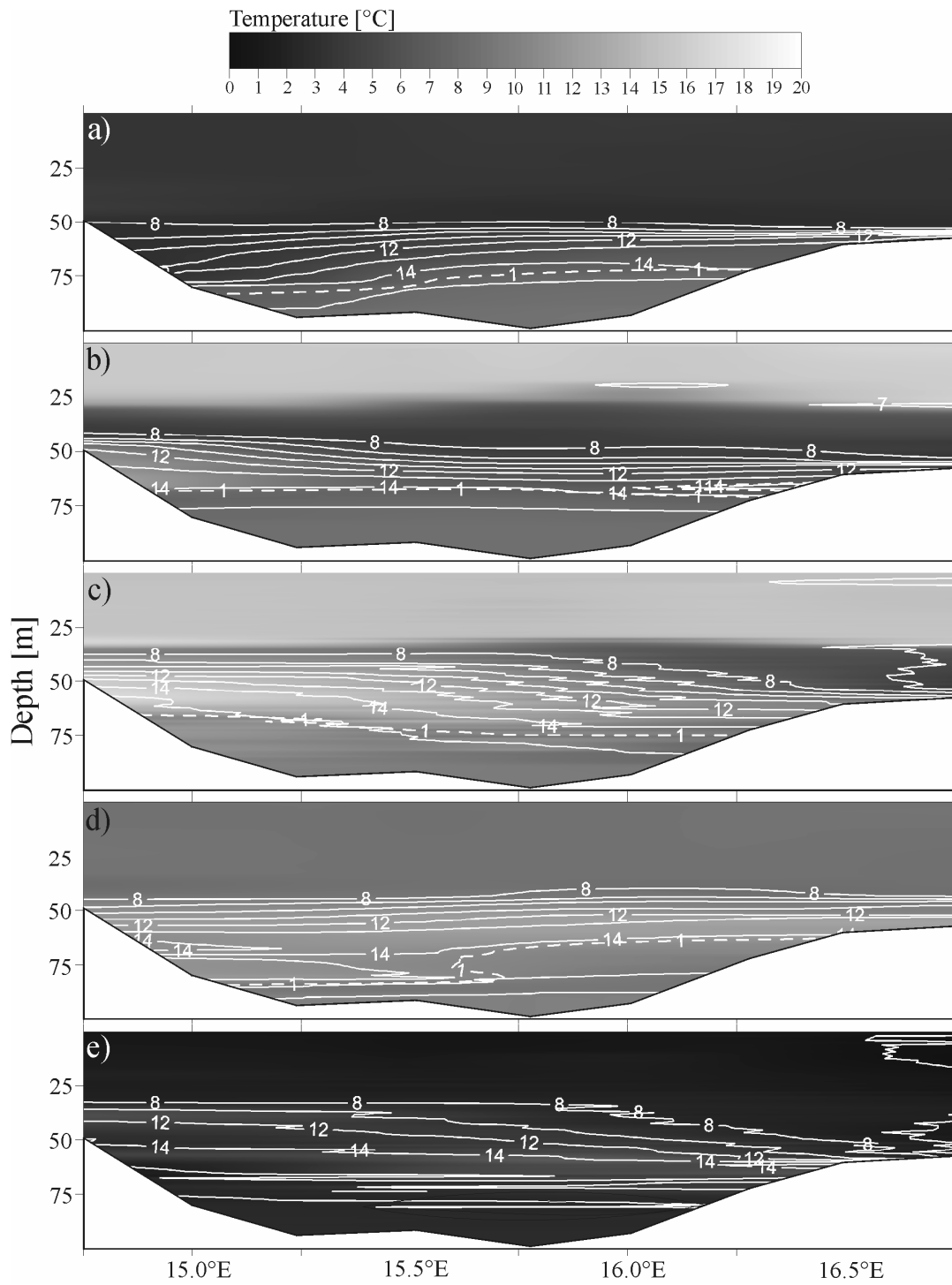
Fig. 2
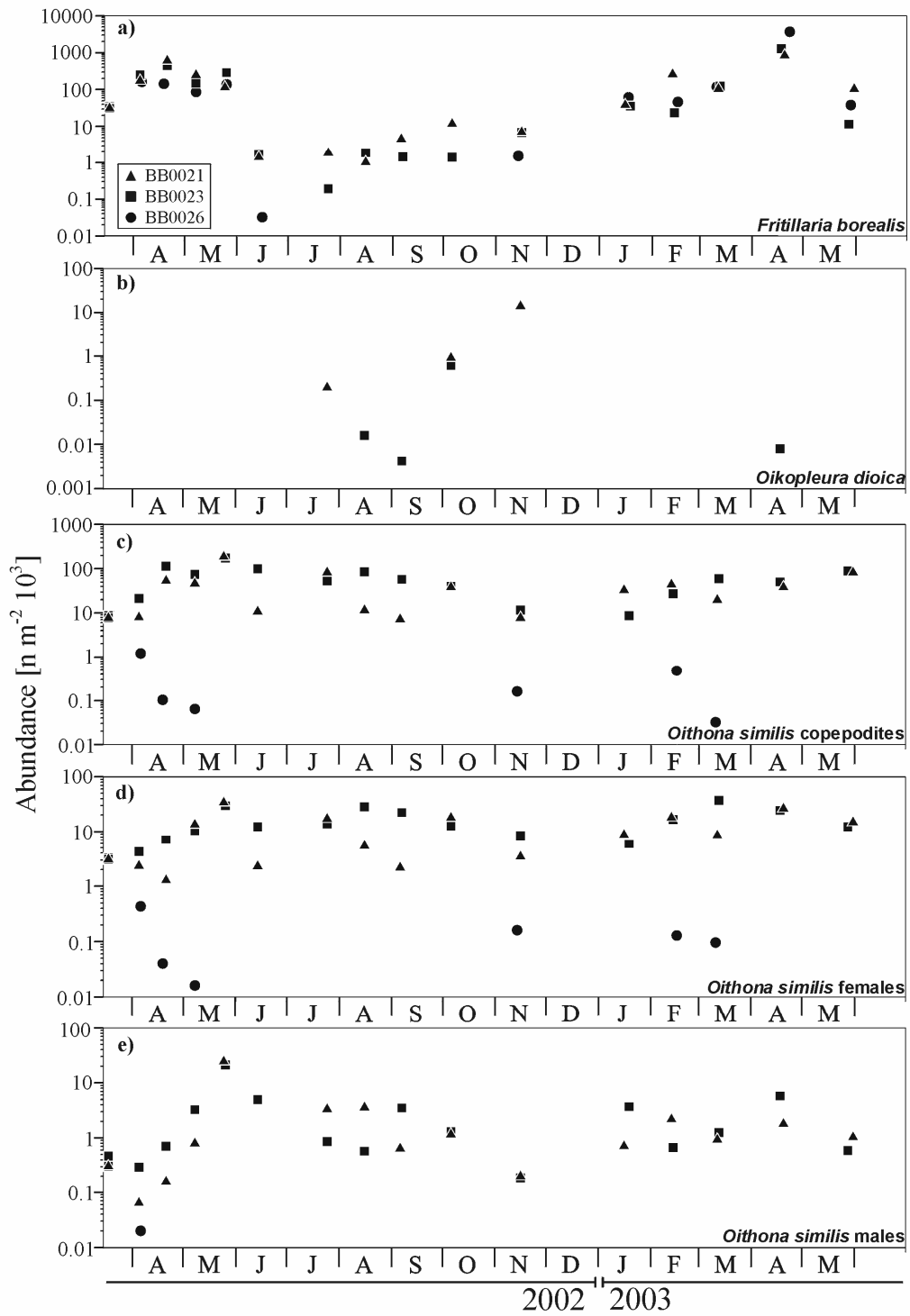
Fig. 3
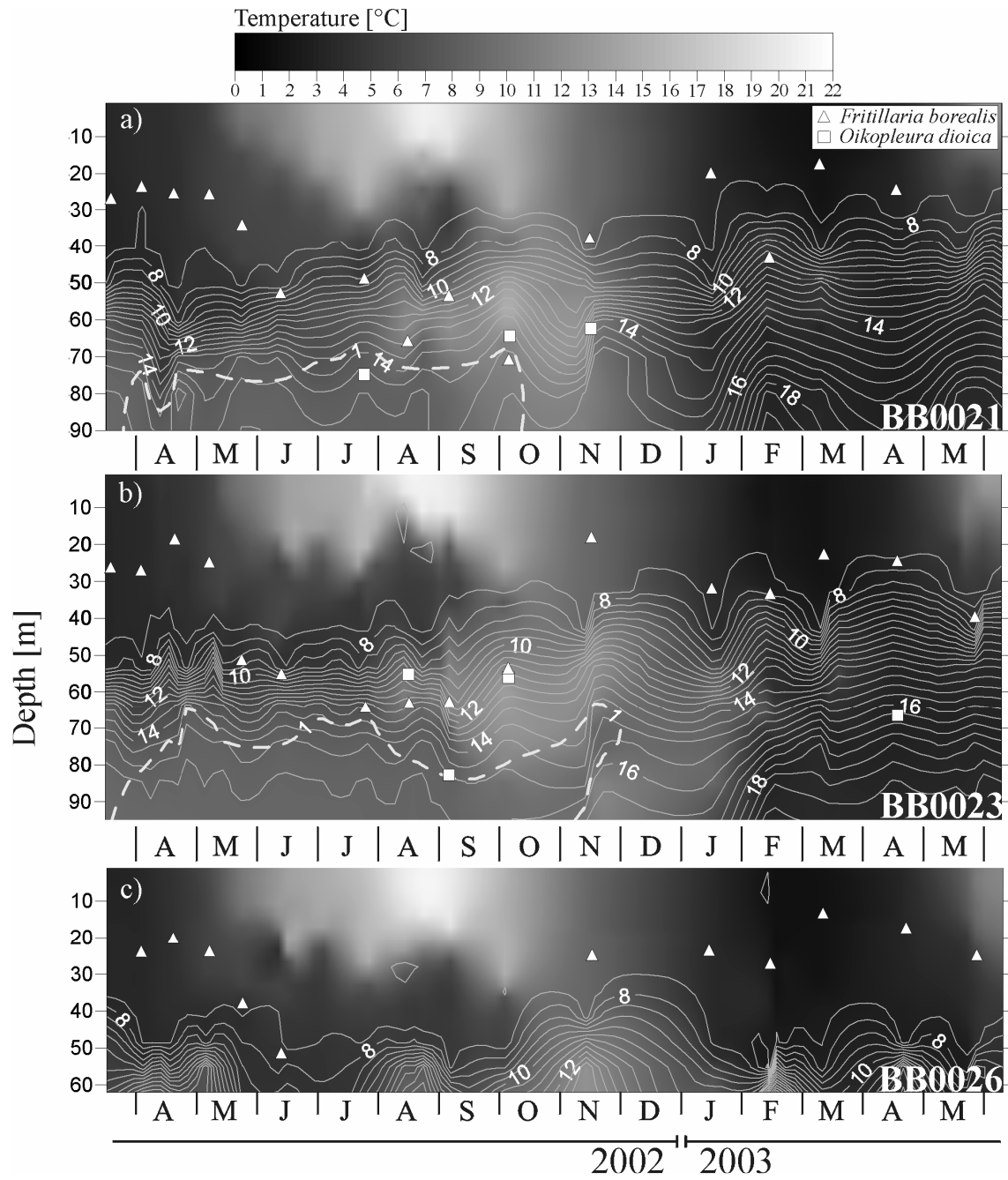
Fig. 4
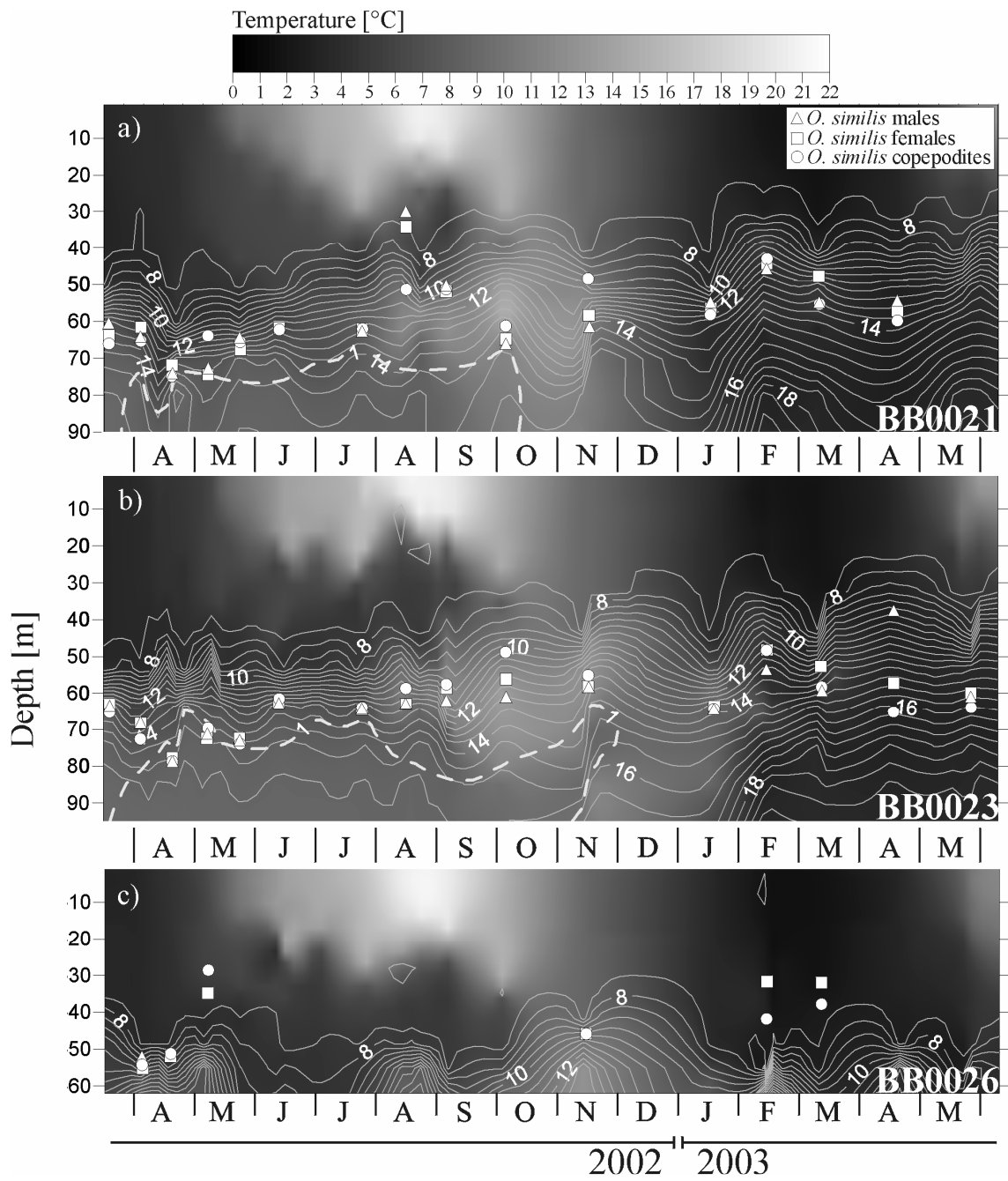
Fig. 5

Tables

Table 1: Sampling sites and dates in the Bornholm Basin (central Baltic Sea).

Station	BB0021	BB0023	BB0026
Latitude [deg, dec]	55.292	55.292	55.292
Longitude [deg, dec]	15.283	15.750	16.500
Bottom depth [m]	90	95	62
Sampling dates			
Mar 2002	18.	18.	-
Apr 2002	05.	05.	06.
Apr 2002	21.	21.	19.
May 2002	08.	08.	08.
May 2002	25.	26.	26.
Jun 2002	14.	14.	16.
Jul 2002	25.	25.	27.
Aug 2002	16.	16.	14.
Sep 2002	06.	07.	07.
Oct 2002	06.	06.	05.
Nov 2002	16.	16.	14.
Jan 2003	16.	19.	18.
Feb 2003	13.	14.	16.
Mar 2003	12.	13.	11.
Apr 2003	20.	18.	23.
May 2003	-	28.	29.

Z3: Spatial and temporal segregation of zooplankton in the Bornholm Sea

Authors: Jan Schulz, Hans-Jürgen Hirche
Status: Manuscript

This manuscript sketches an overview of zooplankton species in the Bornholm Sea. The underlying data represent one of the largest high resolution data sets on record for the respective area, obtained by GLOBEC-Germany. The seasonal cycles of dominant species are shown and the spatial distribution was investigated on the basin scale. Possible implications for the trophic interactions with the commercially important fish species cod (*Gadus morhua* L.), sprat (*Sprattus sprattus* L.) and herring (*Clupea harengus* L.) are discussed. The initial idea of analysis was proposed by the first author. The manuscript was improved by the co-author.

Spatial and temporal segregation of Zooplankton in the Bornholm Sea (central Baltic Sea)

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Abstract

Water bodies of different combinations in temperature and salinity structure the water column into regions of heterogeneous ecological conditions. The ecophysiological tolerance of zooplankton species can result in an inhomogeneous vertical and horizontal utilisation of these regions. Thus in highly stratified systems the spatial overlap is a key for predator-prey interactions in addition to the temporal overlap. Between March 2002 and May 2003 the zooplankton composition at nine stations of the Bornholm Sea was investigated. With an almost monthly coverage a total of 832 vertically stacked samples were taken with a multinet in 10 m intervals and correlated with the ambient hydrography. Five taxa (*Bosmina coregoni maritima*, *Acartia* spp., *Pseudocalanus* sp., *Temora longicornis*, *Synchaeta* spp.) contributed with more than 10% each to the zooplankton community. The successive appearance of cladocerans was mainly correlated with the seasonal increase in temperature and the development of a thermocline. *B. coregoni maritima*, dominating during the warm periods, preferred the upper, warm stratified water column. Copepods showed distinct distribution patterns with seasonal and ontogenetic variations. The rotifer *Synchaeta* sp. dominated the zooplankton during a peak in May. Based on a multivariate approach and the evaluation of vertical distribution patterns five major strategies for the utilisation of the water column were identified. Our data implicate that the characteristic thermal and haline stratification of the Baltic Sea is a key factor for the vertical distribution of zooplankton. As fish and gelatinous plankton often feed in distinct layers or show feeding migrations, the inhomogeneous distribution of potential prey can result in a spatial mismatch. Based on the five patterns we discuss how trophic interactions may be driven by hydrographic and climate influence.

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Introduction

Variability in the vertical plane is probably more important in the ecology of zooplankton than variability in the horizontal plane (e.g. Dagg 1977, Longhurst & Harrison 1989). However, the well-known match-mismatch theory (Cushing 1975, Cushing 1990) and most followers-up dealing with the overlap of fish and prey just consider temporal aspects. The small scale physico-chemical structure of the water column controls both bottom-up and top-down processes. Clines may act as physiological barriers, which hinder accessibility of phytoplankton for herbivorous zooplankton, but also may prevent zooplankton from predation. Discontinuity zones are known to interrupt exchange processes between the euphotic zone and the mesopelagic (e.g. Humboldt Current: Escribano et al. 2004; California Current: Alldredge et al. 1984, Roemmich & McGowan 1995, Black Sea: Vinogradov 1985). Thus in highly stratified systems the spatial overlap is also important.

The hydrographic conditions of the Baltic Sea are characterised by a summer thermocline and a permanent halocline (Fonselius 1970), which restricts the water exchange between bottom and surface layers (Launiainen et al. 1987). This sea represents the largest semienclosed, brackish water area of the world (Fonselius 1970), where submarine sills separate a cascade of several deep basins (Matthäus 1995). Within the basins decomposition processes often deplete oxygen and cause an anoxic zone at the seafloor (Fonselius 1970, Laine et al. 1997). Both horizontal and vertical distribution of marine and limnic zooplankton species is determined by the physical gradients (Ackefors 1969, Hernroth & Ackefors 1979, Hansen et al. 2004). Small hydrographical changes can alter the structure of the pelagic community significantly. As several zooplankton species live at the edge of their physiological capabilities (Hernroth & Ackefors 1979), recent changes in hydrographic patterns also affected population dynamics (Viitasalo et al. 1995, Vuorinen et al. 1998, Ojaveer et al. 1998, Dippner et al. 2000, Möllmann et al. 2000). Therefore the Baltic Sea is an ideal location to study the influence of hydrography on community separating processes. Time series analyses have shown that zooplankton composition is strongly affected by episodic inflow events from the North Sea (e.g. Ojaveer et al. 1998, Möllmann et al. 2000, Möllmann et al. 2002) renewing and ventilating deep waters of higher salinity. These events are related to atmospheric circulation patterns and often followed by long stagnation periods (Matthäus & Franck 1992, Matthäus & Schinke 1994, Matthäus 1995, Lehmann et al. 2002). During the last decades the frequency of inflow events decreased and affected trophic interactions in the water column (Alheit et al. 2005). Despite the economically important fishery for herring, sprat and cod, knowledge about interactions between hydrography, zooplankton and fish is still fragmentary. Although earlier investigations provided overviews of the zooplankton distribution in relation to the stratified water column (e.g. Ackefors 1969, Hernroth & Ackefors 1979) a low spatial, temporal and vertical resolution prevented detailed investigations. In this study we present a high resolution zooplankton data set from the Bornholm Sea (central Baltic Sea) collected during the German Global Ocean Ecosystem Dynamics project (GLOBEC-Germany, www.globec-germany.de). This data set provides detailed information on the zooplankton distribution and their dependence on hydrography. Our aim was to identify distinct seasonal and vertical distribution patterns of important zooplankton species and to investigate the composition of the zooplankton community in relation to the hydrographic layers of the Bornholm Sea. Therefore we performed a multivariate data analysis, investigated vertical abundances and give a review of the known appearance under different environmental conditions. Furthermore we discuss potentially available prey fields in different depths and the impact of hydrography on trophodynamic relationships between zooplankton species and their predators.

Material and methods

Zooplankton samples were taken on 15 cruises from March 2002 to May 2003 (Table 1) with almost monthly coverage. Sampling was performed in stacked 10 meter intervals from bottom to surface with a multinet (Hydro-Bios, Kiel, 50 µm mesh size, 0.25 m^2 mouth opening, 0.2 m s^{-1} towing speed) on 9 focus stations in the Bornholm Basin (Figure 1, Table 2). Samples were taken regardless of day time and preserved with a buffered 4% formalin-seawater solution. At least 500 individuals of a sub-sample were enumerated and the number of individuals in the sub-sample extrapolated to individuals per cubic meter (n m^{-3}) in each depth stratum. A total of 832 samples from different depth were used for the analyses. Assignment of night- and day-haul was done by comparing start time and sunrise/sunset of the referring month. The abundances were used for the investigation of the vertical zooplankton distribution.

Vertical profiles of salinity, temperature and oxygen were determined by an additional CTD cast. The CTD measurements were averaged in 10 meter steps to assign an averaged layer temperature (ALT) –salinity (ALS) and –oxygen concentration (ALO) to each stacked zooplankton sample.

With respect to the range of a single net in a haul the n m^{-3} values were further used to compute the number of individuals per square meter (n m^{-2}):

$$f_{IM2}(i,j) = \sum_{k=0}^{l_j-1}(m_{ij}\,n_k)$$

with i as the index of the species or taxon, j the station, k the index of the net on a station, l is the total number of nets on a station, m is the number of individuals per cubic meter and n represents the depth range of the kth net. For semi-automated processing these formulas were coded as algorithms and integrated into Ocean Sneaker's Tool (Schulz et al. 2005). For the preparation of maps Ocean Data View (Schlitzer 2004) was used.

To determine the relative importance of the taxa the mean n m^{-2} abundance of each taxon from the nine stations was calculated. To display abundance cycles these data were normalised to one and displayed as relative seasonal charts (Figures 6-8). The proportion of summed n m^{-2} abundances from each cruise was determined for every taxon (Table 3).

To identify whether samples from different depth strata can be discriminated by species composition in relation to the prevailing hydrography a Multivariate Discriminant Function Analysis was performed (MDFA, Fisher 1936). The 23 dominant planktonic species and taxa were included in this analysis (Table 3). Prior to the analysis n m^{-3} multinet abundances were *log (1+x)* transformed. Every sample was assigned to a hydrographic category that represents distinguishable conditions of the respective stratum. The categories of high saline bottom and inflow waters were characterised by an ALS>9. An ALS>16 showed that a water mass belonged to one of the deep inflows between November 2002 and March 2003. As these waters affected the Bornholm Sea down to the seafloor in more than 90 m depth the category was named *BB90* in the analysis. Saline waters with 9<ALS<16 were further discriminated by temperature. An ALT>9°C indicated waters of the summer inflow that stratified into approximately 60 m depth and were named *BB60*. Haline waters with an ALT<9 were characteristic for the normal stagnant haline waters below the halocline and named *HALINE*. Our use of the name *BB90* for a category in the Multivariate Discriminant Function Analysis differs from the name used by Feistel (Feistel et al. 2003a). As we were interested in the impact of ecologically discriminable conditions on the zooplankton community we included all deep inflows to this group. Samples with an ALS<9 indicated waters above the halocline and were further distinguished by temperature. Values of ALT>9°C characterised the warm surface layer during summer and defined as *SUMMER*.

Values of ALT<9°C were an indicator for the low saline and cool winter waters and therefore named *WINTER* in the analysis. Each of the 832 samples was assigned to one of the categories *SUMMER*, *WINTER*, *HALINE*, *BB60* or *BB90*. With the MDFA model the different multinet samples were investigated for characteristic differences between the 23 included variables (species and taxonomic groups) in relation to the five hydrographic categories. With a subsequent Canonical Analysis the influence of the 23 variables in the differentiation was determined and the affinity of the variables to different physical conditions. The application of the MDFA approach is described in detail in Schulz et al. (2006).

Results

Hydrography

The hydrographic situation of the central Baltic Sea during the study period was continuously characterised by strong gradients. In April 2002 the halocline was located in 50-60 m and elevated to 40-50 m in November 2002 (Figure 2). During this period a salinity of 7 above the halocline and 15 below the halocline was observed. In March 2002 the sea surface temperature (SST) in the mixed layer was ~2°C. SST increased from 4°C in the middle of April to 10°C at the end of May 2002. In May 2002 a thermocline developed with a steep gradient in 20 m depth. The temperature in the surface layer increased from ~13°C in June to more than 17°C in July affecting the upper 30 m. In August the temperature exceeded 20°C and affected just the upper 20 m, maybe due to calm weather conditions (Feistel, personal communication). Thereafter cooling started and in November the thermocline was resolved.

In late summer a series of inflow events started, which terminated a long stagnation period in the Baltic Sea. For a detailed description confer to Feistel et al. (2003a, 2003b, 2004) and Mohrholz & Schuffenhauer (2004). The summer inflow between August and October 2002 showed a lower density and stratified into a layer at 60 m depth (BB60), where it caused the highest annual temperature (13.79°C) on record in this depths of the Bornholm Basin (Feistel et al. 2004). The water of the second inflow was more saline and elevated the old water, which gradually flew out over the level of Słupsk Sill into the Gdansk Deep until December. The oxygen concentration at the bottom increased to more than 2 ml l⁻¹. In January 2003 the first Major Baltic Inflow (MBI) of cold, saline North Sea water after seven years took place (Feistel et al. 2004) and caused a steep increase of salinity to more than 18 at the bottom. It completely replaced the deep waters of the previous events. Thereafter the water cooled down to around 2.5°C above the halocline and 4°C below the halocline and stayed low until May. Consequently, temperature was 1.5°C lower in the mixed layer and 4°C lower in the rest of the water column than during spring of the previous year (Figure 2).

Oxygen concentration above the halocline was always >6 ml l⁻¹. Between April and October 2002, deep waters in the centre of the basin were characterised by oxygen concentrations <1 ml l⁻¹. The MBI ventilated the deeper part of the Bornholm Basin; oxygen concentrations increased up to 6 ml l⁻¹ between the halocline and the bottom and remained high until April 2003.

Zooplankton composition

Copepods were by far the most abundant group (Table 3), followed by rotatoria, Cladocerans, appendicularians and Bivalvia. The relevance of the major groups was characterised

by one or few species within. The five most abundant species, with more than 10% each, were *Synchaeta* spp. (23.4%), *Temora longicornis* (14.2%), *Acartia* spp. (13.4%), *Bosmina coregoni maritima* (10.8%), and *Pseudocalanus* sp. (10.2%). Of minor importance were *Fritillaria borealis*, Bivalvia larvae, *Oithona similis, Centropages hamatus* and *Evadne nordmanni* (descending order). The stocks of *Oikopleura dioica*, *Podon* spp., *Eurytemora* sp., *Pleurobrachia pileus*, polychaets and *Keratella* spp. contributed less than 1%.

Seasonal cycles

The seasonal abundance cycle of the large taxonomic groups and their relative contribution to the zooplankton community is shown in Figure 3. The annual cycles of all taxa investigated are presented in Figures 6-8. While the dominant copepods are abundant throughout the year, other taxa mark their importance within a short period. The total number of organisms showed a modal distribution with low numbers in winter, a rapid increase in April and a pronounced maximum at the end of May 2002, which was higher by a factor of >20 than winter abundance. It consisted to a large degree of rotifers (59.4%), which hatched from resting eggs at that time, and copepods (24.7%). Cladocerans were most prominent between July and October with a maximum of 69.9% in August, mainly represented by *Bosmina coregoni maritima*. This species was the most important cladoceran and dominated the community during summer. It started late in the year and its abundance reflects the evolution of the temperature in the surface layer. An even more pronounced temporal appearance was observed for *Synchaeta* spp. The rest of the time the community was dominated by copepods with more than 90% during winter 2002/2003. Other taxa had pronounced peaks in winter/spring and were more or less absent for long periods during the year. Appendicularians made up 28.8% of the zooplankton individuals in early April 2002 and 50.3% in April 2003. Meroplanktic larvae of Bivalvia contributed 28.5% at their maximum occurrence in March 2002. Table 7 summarises the averaged temperature-, salinity- and oxygen ranges of the layers a taxon was most prominent in. Corresponding values from the literature are also listed.

Discriminant and canonical analysis

The results of the Multivariate Discriminant Function Analysis (MDFA) show that samples from different depth strata can be distinguished by their species composition (Figure 4). The classification accuracy of the model shows that 84% of the samples were correctly classified by differences in species composition (Table 4). As normality can not be fully achieved with these ecological data, Wilk's Lambda should be interpreted instead of the p-Level from the F-Test. Anyhow both show a significant discrimination and imply that species compositions vary among the hydrographic categories. Discrimination is most proper for the low saline waters *SUMMER* and *WINTER*. Discrimination success is lowest among the haline waters *HALINE, BB60* and *BB90*. Subsequently a Canonical Analysis (CA) was performed. A step down χ^2 test on the roots of the CA shows that the first two roots explain more than 95% of the variance, although the first three roots are significant (Table 5). The mean values of the hydrographic categories (Table 6) show that the first root separates the *SUMMER* and *WINTER* category form the waters of higher salinity. The value for the *WINTER* category is very close to this separating plane. Thus the first root appears as the main discrimination between the high and low saline waters. The second root indicates a further discrimination within the two groups of the previously separated low and high saline waters. The separation among the haline waters is less obvious, but indicates differences. Thus the second root obviously indicates a separation by temperature. As the most

important parameters in the analysis are salinity and temperature, the third root is neglected. Though it indicates further differences among the haline waters, but explains less than 4% of the variance. From the hydrographic results is obvious that these differences are based on temperature.

The Canonical Factor Structure Coefficients (CFSC) of the CA represent the loadings of the variables in the analysis. These allow the interpretation of species behaviour in relation to the hydrography (Figure 5). Based on the knowledge of the roots the different quadrants can be assigned to different hydrographic conditions. The first root separates the high from the low saline waters. The algebraic sign indicates that objects with values above zero on the first root are mainly associated with the low saline waters (Table 6). Respectively values below zero indicate a higher contribution to the waters below the halocline. Accordingly the objects with values above zero on the second root show an association with low temperatures, and below zero with higher temperatures. Thus, the quadrants I-IV (Figure 5) separate species with different strategies in the utilisation of the prevailing hydrographic conditions. Quadrant I mainly includes species that prefer the cool waters of the *WINTER* category above the halocline. In quadrant II the species show a lower loading on the first root, than species in quadrant III. This indicates a lower affinity to the saline waters, but obviously an avoidance of higher temperatures. The species in quadrant III mainly live below the halocline in the *HALINE* category. Finally quadrant IV includes all species that utilise the *SUMMER* category above the thermocline. Species being present when the thermocline is absent have to cope with the waters of the *WINTER* category. To confine the results obtained from the MDFA and CA we attach an overview of the seasonal appearance and vertical distribution at selected stations.

Vertical distribution patterns

Appendicularia

Fritillaria borealis LOHMANN

Synopsis: *Fritillaria borealis* is considered oligotherm with a preference for temperatures<10°C (Berrill 1950, Ackefors 1969) and a salinity range of 6-35 (Ackefors 1969). In the Baltic it is abundant in May with up to 350.000 n m^{-2}, almost missing between August and October and avoids warm surface waters during summer (Hernroth & Ackefors 1979). In the Mediterranean near Villefranche-Sur-Mer and in the Bay of Biscay *F. borealis* appears between December and January (Fenaux et al. 1998).

GLOBEC data: *Fritillaria borealis* was by far the most important appendicularian and was, at least in small numbers, present the whole year around (Figure 6). Abundance increased in both years at the end of March, reached a peak in the second half of April and declined thereafter till the end of May. In April 2002 approximately 320.000 and in April 2003 nearly one million n m^{-2} were found. During summer they were absent at shallower stations. Prior to the formation of the thermocline highest abundances were found above the halocline in the *WINTER* water (Figure 9). The decline of the population coincided with the development of the thermocline, when the individuals withdrew to cooler strata below the halocline. This is also reflected in the CFSC values, which indicate avoidance of warm and the utilisation of haline waters (Figure 5). In September 2002 it was found in the signature of the warm *BB60* inflow waters at the entrance of the Bornholm Sea.

Oikopleura dioica, FOL

Synopsis: In the Baltic Sea *Oikopleura dioica* is the most common appendicularian (Hernroth & Ackefors 1979). It stays mainly in the deeper waters below the halocline (Ackefors 1969). Reproduction depends on higher salinity 16.5. In autumn this species is often very abundant in Kiel Bight (Lohmann 1899). Jespersen (1949) noted that *O. dioica* did not occur regularly from year to year in the Danish Isefjord and is mainly found from July to October with highest numbers in July. The abundance was not related to hydrographic conditions. Rasmussen (1973) found it in the Outer Broad of the Danish Isefjord from August on, reaching highest values in August and October. Blanner (1982) noted rather large numbers in the Danish Limfjord in July, September and October. In the North Sea it can be found almost everywhere, and resembles a distribution pattern similar to that of the copepod *Paracalanus parvus* (Krause 1995).

GLOBEC data: *Oikopleura dioica* was always less abundant than *Fritillaria borealis* and occurred in summer with peaks at the end of July and in the middle of November (Figure 4), when *F. borealis* abundance was low. The latter peak coincided with the BB90 inflow that renewed the deep waters in the trough of the basin. A reverse situation was found after the MBI when stock size decreased despite improved oxygen and salinity conditions below the halocline. In the CFSC analysis this species shows an affinity to the haline waters and moderate temperatures (Figure 5). The individuals were mainly found below the halocline, with highest abundances in strata with higher temperatures (Figure 9).

Bivalvia

Synopsis: Common bivalves of the Baltic Proper are *Macoma baltica* L., *Cardium glaucum* BRUGUIERE, *C. hauniense* PETERSEN & RUSSEL, *Mya arenaria* L. and *Mytilus edulis* L. (Hernroth & Ackefors 1979). The greatest spawning density of *M. edulis* in the Baltic Proper is between August and October, with low densities in November. The other species appear between May and August, with low densities from September to April, with decreasing densities from north-west to south-east (Hernroth & Ackefors 1979). In Danish waters the spawning of *M. edulis* starts in May and continues until July (Rassmussen 1973). In the North Sea and the Danish Limfjord the maximum spawning time of most bivalve larvae is reported from July to October (Rees 1954, Rasmussen 1973, Blanner 1982).

GLOBEC data: Larvae were not determined to species level. Lowest abundance (321 n m^{-2}) was observed in early May 2002. A single peak was recorded three weeks later (Figure 3, Figure 6), before abundance decreased again. The spring increase in March/April 2003 did not reach the same numbers as in 2002. The larvae showed a preference for the upper layers. With SST >11°C the highest densities were observed closer to the thermocline (Figure 9). This result is also found in the CFSC. It shows the utilisation of the low haline waters, but just a minor impact in the temperature differentiation of the Canonical Analysis.

Cladocera

Bosmina coregoni maritima P. E. MÜLLER
Synopsis: *Bosmina coregoni maritima* is an endemic subspecies in the Baltic Proper, the only brackish water form and more prominent in shallower areas (Purasjoki 1958). This polytherm and oligohaline species appears first in April, at SST of 2°C in the Baltic Proper. The stock remains small until the temperature reaches 15°C. During the warmer months this species can become dominant (Hernroth & Ackefors 1979). After September the stock decreases rapidly and is absent from January to March. Stratified sampling shows

the greatest proportion of the population above the thermocline, but up to 20% of the population are also found below (Hernroth & Ackefors 1979). It appears later in the year than *Evadne nordmanni* (Eriksson 1973b).

GLOBEC data: *Bosmina coregoni maritima* was found in small numbers all year round, with minimum numbers in March of both years. Stock size spanned a range of seven orders of magnitude between March and August. It became more abundant at SST >16°C and reached maximum numbers when temperatures exceeded 20°C, the extreme temperature reported by Ackefors (1969). Some of the highest abundances on record (more than 297.000 n m^{-3} in the upper 10 m at station BB0006 and more than 267.000 n m^{-3} at BB0023) were found in August after a continuous increase of more than three orders of magnitude during the last eight weeks (Figure 10). This maximum was followed by a sharp decline in early September 2002. The main part of the population was always found above the thermocline. The CFSC show a prominent impact in the warm surface layers (Figure 5). The sparse individuals between January and May were mainly distributed in the mixed layer above the halocline.

Evadne nordmanni LOVÉN

Synopsis: *Evadne nordmanni* appears in the Baltic Proper regularly in April and May and is important from the end of May to November, while few individuals can be found the whole year round (Hernroth & Ackefors 1979). Largest proportions of the stock dwell in surface waters, but up to 25% may be present in cooler waters below 25 m in the Baltic Proper (Hernroth & Ackefors 1979). Hence it is the only cladoceran in the Baltic tolerating higher salinities (Chojnacki et al. 1984). In the Baltic Proper the abundance decreases from south to north (Hernroth & Ackefors 1979). In the Danish Limfjord it is recorded from April to October (Blanner 1982), similar to the Kattegatt and the North Sea (Gieskes 1970, Gieskes 1971a), where it is more abundant in the northern part (Hay et al. 1991).

GLOBEC data: First individuals were already found in March 2002 at the beginning of our observations. In April 2002 the individuals were mainly found below the halocline with a peak within the halocline. The temperature was higher in these layers than in the unstratified water column. With a further increase of the temperature the stock ascended to the surface waters and from SST >4.5°C increased by four orders of magnitude from March until the end of May 2002. From the end of May to August 2002 the population decreased steadily. At the beginning of September, after the *BB60* inflow, a second peak developed and reached highest values in the middle of October 2002. Thereafter the population decreased and few individuals were found until March 2003 when the onset of the next generation was observed. At the time of its first appearance it was found above the halocline. With the formation of the thermocline the main abundance was in the warm layers above and in the thermocline. With temperatures exceeding ~15°C in the upper 10 m the vertical abundance maximum shifted to the layer of the thermocline (Figure 10). The CFSC indicate that the behaviour of this species is not clearly associated with a hydrographic category (Figure 5), although the highest values are found above the halocline. Depending on the hydrographic conditions highest vertical abundances were seen in the depth where temperatures were around 15°C.

Podon spp.

Synopsis: The two most common *Podon* species in the Baltic Proper are *Podon intermedius* and *Podon leuckarti* (Hernroth & Ackefors 1979). *P. intermedius* is larger by a factor of 1.2-1.4 (Gieskes 1971b). Juvenile *Podon* were not determined to species level and data were pooled. Two consecutive peaks were observed at the end of May and July 2002 (Figure 7). After these main abundances a slight increase was observed at the beginning of Oc-

tober 2002. Between January and April 2003 no juveniles were found. The next juveniles were recorded in May 2003.

Podon intermedius LILLJEBORG

Synopsis: The population density of *Podon intermedius* is low all over the Baltic Proper and appears in June (Hernroth & Ackefors 1979). In Danish waters the first individuals usually appear in July in the Kattegatt, reaching the maximum one month later (Eriksson 1974, Gieskes 1971b), while they are few in August in the Öregrund Archipelago (Eriksson 1973b). In the North Sea it does not appear prior to June, reaching peaks in August and September and is more abundant in the eastern parts (Gieskes 1971a). *P. intermedius* requires higher temperatures than *P. leuckarti* and starts to propagate at a temperature of 9.5°C, being most abundant around 15°C in the North-Sea.

GLOBEC data: *Podon intermedius* appeared first in April 2002, but the main peak was found in July/August 2002, followed by a second and smaller one in September/October 2002 (Figure 7). Few individuals were recorded until November 2002 From November to April 2003 it was absent from the water column. In 2003 the first appearance was recognized in May, one month later than in the previous year, and with lower numbers than in May 2002. The highest proportion of the stock was found above the thermocline, although few individuals were observed below. The CFSC show an affinity to the warm surface layer (Figure 5). With the *BB60* inflow the sparse individuals remaining were also found in and below the inflow waters, which had a higher salinity and temperature.

Podon leuckarti G. O. SARS

Synopsis: *Podon leuckarti* is a neritic cladoceran, characterised as stenohaline and stenothermal (Ackefors 1969). In the North Sea it is scarce in areas with oceanic saltwater inflows (Gieskes 1971b). First appearances in the North Sea are at SST of 6.5°C and highest abundances between 12-13°C (Gieskes 1971a). It is dominant there up to the end of June, when egg-carrying females appear.

GLOBEC data: Few individuals of *Podon intermedius* were found in March and early April 2002. The first population peak was found approximately two months earlier (Figure 7) and nearly twice as high than that of *P. intermedius*. The duration of this first peak was much shorter than that of *P. intermedius*. Two further, but much smaller peaks were observed in August and October 2002. Between November 2002 and February 2003 it was not observed. Few individuals were found between March and April 2003 and the stock restarted to increase in May 2003. More than 95% of the stock was found above the thermocline between May and June (Figure 10). During the BB60 inflow the stock showed a slight increase. The CFSC show *P. leuckarti* as species of the low saline surface waters.

Copepoda

Acartia spp.

Synopsis: The copepods *Acartia bifilosa* and *Acartia longiremis* are the only common species of this genus in the Baltic (Ackefors 1969). They seem to breed all the year round in the Baltic Proper, with maximum nauplii abundances in February-March and in November (Hernroth & Ackefors 1979). Both species are widespread over the Baltic Proper and the nauplii are often not separated (Hernroth & Ackefors 1979).

GLOBEC data: *Acartia* nauplii were not separated to species level. Most likely they belonged to *A. bifilosa* and *A. longiremis.* They were already abundant at the beginning of the observation period and declined until the beginning of May 2002 (Figure 8). However, at

the end of May their abundance reached highest values. Thereafter the abundance decreased until August and reached a second maximum in the middle of November 2002.

Acartia bifilosa GIESBRECHT

Synopsis: *Acartia bifilosa* prefers lower salinities and thus is common in the Baltic Sea (Ackefors 1969). Experiments have shown that vertical distribution depends to a lesser extend on salinity (Lance 1962). In the Bothnian Sea it reaches considerable population numbers in August and the nauplii are proportionally important in June (Eriksson 1973b).

GLOBEC data: In our study *Acartia bifilosa* showed three peaks (Figure 8). The first peak for the CI-CIII was found at the end of May 2002, the second in October 2002. After low abundances in winter the onset of the new generation was again in April 2003. The peaks of the CIV-CVI succeeded that of the younger stages with a delay of nearly half a month. During summer *A. bifilosa* was mainly found above the thermocline (Figure 11). In winter it stayed in the upper 30 m, preferably the upper 10 m (Figure 11). The younger and the older copepodites were both characterised by the CFSC as individuals who migrate into the warm surface layer (Figure 5).

Acartia longiremis LILLJEBORG

Synopsis: *Acartia longiremis* is more abundant than *Acartia bifilosa* in the southern Baltic Proper (Hernroth & Ackefors 1979). It is a euryhaline and oligothermal species (Ackefors 1969), but is rare in the North Sea. In the Atlantic this species is found in deeper water layers in more southern latitudes (Jespersen 1940).

GLOBEC data: The onset of the CI-CIII stages of *A. longiremis* was observed at the end of April, one month earlier than *A. bifilosa* and maintained higher abundances during the formation of the thermocline. With increasing temperatures and strengthening of the thermocline the older *A. longiremis* species preferred the intermediate waters of the *WINTER* category between thermo- and halocline (Figure 11). This is reflected by the CFSC values for the CIV-CVI stages. The nauplii and younger copepodites were also found above and in the depth stratum of the thermocline, reflected in lower CFSC values on temperature. During night CIV-CVI stages were also found above the thermocline. In winter they shared the mixed layer above the halocline.

Centropages hamatus LILLJEBORG

Synopsis: *Centropages hamatus* is abundant in temperate-boreal waters (Eriksson 1973c) and accepts a wide range of salinity (Blanner 1982). Its main distribution area is the northern Atlantic and adjacent seas (Jespersen 1940). It can dynamically shift its thermal tolerance range to the temperature window of a specific environment (Halsband-Lenk et al. 2002) and is a euryhaline and mesotherm species. In the Baltic it most abundant between 15 and 50 m, living at its uttermost salinity (Ackefors 1969) where it is common from Gotland (Ackefors 1969) to the Kattegatt and in the North Sea (Eriksson 1973a, Eriksson 1973c). There it disappears from the water column in October (Hay et al. 1991) and overwinters as resting eggs (Engel & Hirche 2004). In contrast, *C. hamatus* is found all year round in the Danish Limfjord with highest abundances in June (Blanner 1982). In the southern Baltic Proper it is abundant above the thermocline, but not in the northern Baltic.

GLOBEC data: *Centropages hamatus* was only important between April and June. The stock of nauplii started to develop at the end of April, reaching a maximum in late May when CI-CIII stages dominated (Figure 8). The highest abundances of the CIV-CVI stages were found in the middle of June 2002. Species were mainly found above the halocline (Figure 11). During summer the CI-CIII stages were mainly located in and above the thermocline, while the remaining CIV-CVI were found in and below the thermocline. These

observations are also confirmed by the results of the CFSC. When the thermocline untied they dwelled in the upper mixed waters. In March 2003 small numbers were recorded in slightly warmer waters above the halocline.

Eurytemora sp.

Synopsis: The taxonomy of the genus *Eurytemora* is not clarified as yet. While some authors report *E. affinis*, *E. hirundoides* and *E. hirundo* from the Baltic Sea (Lindquist 1959), Gurney (1931) considers *E. hirundoides* to be a form of *E. affinis*. It is often the dominant species in the estuaries of rivers and fjords in the Baltic (Arndt 1973, Hirche 1992). In the Öregrund Archipelago *E. affinis* is the most important species, with low abundances in June/July and an increase in August (Eriksson 1973b). It is described as eurytherm and oligohaline (Ackefors 1969) and produces resting eggs (Ban & Minoda 1989).

GLOBEC data: *Eurytemora* spec. showed one distinct peak in a short period between September and November 2002 and was rare during the rest of the year. The nauplii, CI-CIII and CIV-CVI showed a simultaneous high abundance in early October 2002 after a strong increase during the last 4 weeks (Figure 8). The presence of CI-CIII lasted several weeks and the maximum was found in November 2002. During its short presence in the plankton this species was found above the thermocline and in the upper unstratified waters in winter (Figure 11). This is also reflected by the CFSC.

Oithona similis CLAUS

Synopsis: The cyclopoid *Oithona similis* is a boreal, euryhaline and eurythermal species and common in both neritic and oceanic regimes (Nielsen & Sabatini 1996). It is well known for the Baltic (Ackefors 1969) North Sea, Skagerrak and Kattegatt (Blanner 1982). In the Baltic it lives under sub-optimal conditions and its horizontal distribution is closely related to the circulation regime in the dwelling depth during stagnant inflow periods (Hansen et al. 2004). These authors could not detect diurnal vertical migration. Its lower tolerance limit for salinity is at about 7 (Ackefors 1969). In the Bornholm Basin it is found at the bottom where salinity is 14.5 (Ackefors 1969). In the Danish Limfjord it prefers more saline waters (Blanner 1982). Due to its small size the stock is often underestimated when inappropriate mesh-sizes are used (Rae & Fraser 1941, Colebrook et al. 1961, Krause et al. 1995).

GLOBEC data: *Oithona similis* was found the whole year round, with highest abundances between April and September 2002 (Figure 8). The horizontal distribution showed always higher abundances at stations deeper than 60m. It was absent in depth strata with an ALO< 0.5 ml l^{-1}. The CIV-CVI inhabited often even deeper layers than the nauplii and CI-CIII. They were often found close to the halocline (Figure 11). During the *BB60* and *BB90* inflows the species was also found in the upper range of the halocline. In March 2003 the individuals were to a large extend found in slightly warmer waters around the halocline. The CFSC values show clearly, that it inhabits the layer below the halocline.

Pseudocalanus group (*Pseudocalanus acuspes* BOECK / *Paracalanus parvus* CLAUS)

Synopsis: Because of the difficulties in differentiating *Pseudocalanus* sp. and *Paracalanus parvus* Gran et al. (1936) recommended the combination of these two to one group. Rae & Rees (1947) even included *Microcalanus pusillus*. Recent findings have shown that *P. acuspes, P. elongatus* and *P. parvus* are found within the same sample (Renz & Hirche 2005, Grabbert personal communication). According to Renz & Hirche (2005) individuals of this group consisted mainly of *Pseudocalanus acuspes*. These authors give a detailed description of the abundance and vertical distribution based on German GLOBEC data. We pooled these individuals to the *Pseudocalanus* group. *Pseudocalanus* sp. is a well

known euryhaline and oligotherm species in the Baltic (Ackefors 1969), with importance for the diet of cod, herring and sprat (Voss et al. 2003). In the North Sea it appears usually in the southern parts and is common in autumn and winter (Rae & Rees 1947). In open oceans it occurs near the coasts and is hardly present in the central part of the northern Atlantic, where it dwells in deeper waters in more southern latitudes (Jespersen 1940).

GLOBEC data: Highest abundances were found between April and June 2002 (nauplii) and from May to October 2002 (copepodites) although individuals were recorded the whole time (Figure 8). After the MBI's at the beginning of 2003 the nauplii abundance was higher than 2002 and the elder stages showed a strong increase towards May/June 2003. The population showed a distinct ontogenetically vertical distribution. Adult stages showed highest abundances below the halocline (Figure 11). Between May and October 2002 CIV-CVI stages were found below the halocline in cool strata. After the thermocline resolved in November 2002 these stages inhabited even layers up to the surface. Nauplii and CI-CIII stages were found the whole year round from surface to deepest layers, but mainly above the CIV-CVI stages. The CFSC values show that older copepodites live mainly below the halocline, while the younger ones also appear in higher strata, with low temperatures.

Temora longicornis P. MÜLLER

Synopsis: In the southern Baltic Proper *Temora longicornis* is an euryhaline and mesotherm species, abundant between April and September with maximum values from July to September (Ackefors 1969, Hernroth & Ackefors 1979). In summer individuals are only found during night above the thermocline, while they are more evenly distributed during the rest of the year (Hernroth & Ackefors 1979). It is often found in temperate and coastal seas (Jespersen 1940).

GLOBEC data: The nauplii showed a multimodal appearance between April and October 2002. During winter a minimum of nauplii abundance was recorded (Figure 8). The peak in April 2003 exceeded that of 2002. The CI-CIII stages were most abundant at the end of May 2002. The CIV-CVI peak was found in June with high values until the end of July 2002. In May 2003 an increase in copepodite abundance was observed. After the formation of the thermocline the CIV-CVI stages were mainly found below. In night hauls these stages they also appeared above the thermocline. Nauplii were also found above the thermocline during day. During winter the stock was found above the halocline in the unstratified water. In March 2003 the low numbers of CIV-CVI stages were to a large extend found in slightly warmer waters above the halocline. Anyhow the CFSC values indicate that the copepodites are mainly associated with the winter water below the thermocline.

Ctenophora

Pleurobrachia pileus O. F. MÜLLER

Synopsis: This species is euryhaline and oligotherm in the Baltic (Ackefors 1969). The maximum larvae abundance in the Baltic Proper can be found from February to May in cold waters and mainly in a salinity range of 6-8 (Hernroth & Ackefors 1979). In another stratified sea, the Black Sea, this species is found in deeper layers and in the suboxic zone down to the upper boundary of the H_2S zone (Mutlu & Bingel 1999, Kideys & Romanova 2001).

GLOBEC data: In 2002 juvenile *Pleurobrachia pileus* were mainly found between March and April, with highest abundances in April, declining till the end of July (Figure 6). Thereafter no individuals were recorded until October 2002. The abundance was low until February 2003 and exceeded the values of April 2002 more than 1.7 times. In April 2003 abundance was lower than in the previous year, but increased again at the end of our ob-

servation time. The main proportion of the stock was found above the halocline with low abundances in layers with ALS >11.5 (Figure 9). Above the halocline highest abundance was mainly observed in layers with lowest temperatures. With the development of a thermocline *P. pileus* was mainly found in cooler waters below and stock size decreased.

Polychaeta (Subadults and trochophora)

Synopsis: Polychaeta larvae are abundant in the Baltic Proper, more numerous in greater depths and avoid warm surface waters in summer (Hernroth & Ackefors 1979). The trochophora larvae develop into polychaeta larvae before switching to benthic life. Deeper parts can be re-colonised if oxygen is not depleted, thus depending on mechanisms of water exchange processes (Leppäkoski 1971, Leppäkoski 1975).
GLOBEC data: Subadult polychaeta were found during the whole year 2002 with small peaks between the end of July and November (Figure 6). Trochophora larvae became most abundant after the MBI in 2003. The abundance of both stages was higher in 2003. An isochronous increase in abundance of subadults and trochophora was mainly observed in the timeframes of the inflow events. While the subadults showed an avoidance of the layers above the thermocline, they were found all over the water column during the rest of the year (Figure 9). The trochophora larvae were mainly recorded in deeper layers with higher salinity.

Rotatoria

Keratella spp.
Synopsis: According to Ackefors (1969) and Hernroth & Ackefors (1979) the genus *Keratella* is represented by four species (*K. eichwaldi, K. platei, K. quadrata, K. recurvispina*) in the Baltic Sea. They are found in the warm surface layers and are abundant from July-November and most frequent in September (Hernroth & Ackefors 1979).
GLOBEC data: *Keratella* spp. were abundant between June and October 2002 with two prominent peaks (Figure 6). At this time the highest abundances were found at stations BB0021 and BB0041 closest to Bornholm Island. A temporary minimum in August preceded a more intense peak in early September. In stratified waters individuals were mainly found above the thermocline (Figure 9) and along the shallower borders of the examination area. They showed avoidance for layers below the halocline. This distribution pattern can also be seen in the CFSC values.

Synchaeta spp.
Synopsis: In the Baltic the genus Synchaeta is represented by 6 species (*S. baltica, S. curvata, S. fennica, S. gyrina, S. monopus, S. triophthalma*), with *S. baltica* and *S. monopus* being the most common (Ackefors 1969, Hernroth & Ackefors 1979). They are abundant all over the Baltic Proper and important between May and July with values of about 1.000.000 $n\,m^{-2}$ in June/July (Hernroth & Ackefors 1979), where they can make up 20-80% of all individuals in a net haul. Start of population growth is coupled to the development of resting eggs (Hernroth & Ackefors 1979). They are located both above and below the thermocline in a temperature range of 8-16°C (Ackefors 1969, Hernroth & Ackefors 1979).
GLOBEC data: *Synchaeta* spp. first appeared in April at the deepest stations (BB0003, BB0021 and BB0023) and showed one distinct peak from May to June 2002 (Figure 6). Thereafter abundance decreased rapidly. In May 2003 the stock started to increase again, but did not reach the numbers of 2002. During the rest of the year individuals were sparse.

The abundance in 2002 was much higher than the values reported by Hernroth & Ackefors (1979) for the Baltic Proper, but the time of appearance coincided with our observations. During the time of their prominent appearance most individuals were found below the developing thermocline (Figure 9). During the decrease of the stock high abundances were also locally found above the thermocline. Eggs were mainly observed in the same layers as the adults. As highest abundances were found prior to the development of the thermocline the CFSC values are mostly assigned with the *WINTER* category. Between September and November 2002 no eggs were recorded.

Discussion

Vertical distribution

To identify whether the characteristic stratification of the Baltic Sea separates the zooplankton community a Multivariate Discriminant Function Analysis (MDFA) was performed and verified by individual observations. The results indicate that the depth distribution of zooplankton species in the Bornholm Basin is subjected to the hydrographic stratification. The species dwell in distinct layers, set up by combinations of different hydrographic conditions and are subjected to seasonal and atmospheric forcing. The observed interspecific differences confirm earlier studies (e.g. Ackefors 1969, Hernroth & Ackefors 1979, Ojaveer et al. 1998, Schulz et al. 2006) and are within physiological ranges that can be found in the literature (Table 7). The higher spatial and vertical resolution of our data set allows a more precise description and classification of zooplankton behaviour. As we were not able to clearly distinguish waters of the categories *HALINE*, *BB60* and *BB90* by MDFA we combine these waters to *HALINE*. The distribution of the zooplankton species can be grouped to different patterns conditioned by the different layers. Thus the volumes of different combinations of temperature and salinity can be conceived as habitats, separated by the clines. The physiological capability affects the range of habitats a species can utilise. Our observations imply five different modes to utilise the available habitats (Figure 12, Table 8). The first three modes are determined by the position of the halocline and just have to be distinguished during summer. The differences among these three were set by the thermocline between May and October 2002:

Mode I is characterised by species being mainly present during the warm season in waters of the category *SUMMER*. All stages of *Eurytemora* sp., *Bosmina coregoni maritima* and *Podon intermedius* were found to be abundant in the surface layer, when temperatures increased. The rest of the year these species were more or less completely absent. Cladocerans outlive the deteriorating conditions in winter as resting eggs. They restart their life cycle in spring, fostered by improving conditions and the increasing temperature. The most important species of this mode was *B. coregoni maritima*, although the stock broke down in early September 2002, when temperatures were still high.

Mode II includes the species which are also present when the thermocline is absent, but with a preference for higher temperatures above the thermocline when established. This refers to an utilisation of the categories *WINTER* and *SUMMER*. All stages of Acartia bifilosa and the CI-CIII stages of Centropages hamatus and Temora longicornis showed this behaviour. Also *Bivalvia* larvae, *Evadne nordmanni*, *Podon leuckarti* and *Keratella* spp. were assigned to this mode. The decreasing *E. nordmanni* stock seems to invade strata closer to and in the thermocline from July on, maybe as a response to the high surface temperature. While *E. nordmanni* and *P. leuckarti* were mainly abundant around the time the thermocline developed or disappeared, the period of high *Keratella* spp. abundance was

found in a period that started a few weeks prior and lasted a few weeks longer than the persistence of our algorithmic defined *SUMMER* category. Thus it can be suggested, that *Keratella* spp. can be seen as a summer species, that should be included in mode I.

In contrast, mode III includes the species, which are also present most of the year, but do not utilise the warm surface layer. Thus their vertical distribution is restricted to the category *WINTER*. All stages of *Acartia longiremis*, *Centropages hamatus* CIV-CVI, *Temora longicornis* CIV-CVI and *Synchaeta* spp. were found to utilise the *WINTER* waters. Less thermal affection (Jespersen 1940, Halsband-Lenk et al. 2002) and the evasion of predation seem likely in summer, when young clupeids prey in the upper layers during daytime (e.g. Voss et al. 2003, Dickmann & Voss 2005).

Mode IV includes the species that utilise both low and high saline waters, avoid the warm surface layer and are only present in the waters of the categories *WINTER* and *HALINE*. *Fritillaria borealis*, *Pseudocalanus* sp. CI-CIII and subadult polychaeta showed this behaviour, with highest abundances during the cold months.

Mode V includes species that utilise the volume below the halocline, respectively the *HALINE* category, which is only available at the deeper stations. We identified *Oikopleura dioica*, all stages of *Oithona similis* and *Pseudocalanus* sp. CIV-CVI as well as trochophora larvae in these waters. While the latter two showed highest abundances in strata with low temperatures, *O. dioica* was often found in saline and warm waters. Below the halocline *O. similis* benefits from its low respiration rates in combination with low temperatures (Castellani et al. 2005) during stagnant inflow periods. The CIV-CVI stages of the *Pseudocalanus* group were mainly found below the halocline, while the CI-CIII copepodites were also found above the halocline. This confirms earlier studies on *Pseudocalanus* sp. in the Bornholm Basin that describe an ontogenetic vertical distribution (Renz & Hirche 2005).

Although our results show species specific depth preferences, still higher sampling resolution is required to understand the fine structure of vertical segregation in the vicinity of discontinuity layers. The problem of different comprehensible scales has been noted earlier by Steele (Steele 1989) and appears here in the conversion of punctual CTD measurements to averaged values for assignment with the plankton hauls. Furthermore, the method-borne integration of plankton nets over the used sampling range of 10 m may be influenced by the internal waves, which are common in stratified waters (Banse 1964). Net clogging in certain layers, caused by blooms, bears another power to bias sampling efficiency.

Noticeable is the observation that the stocks of most copepods living above the halocline showed temporary peaks between September and November 2002 with the *BB60* and *BB90* waters. The *BB60* waters caused the highest temperature on record in the layer of the halocline. Due to a lower salinity than the deep waters the *BB60* waters stratified into the corresponding depth and caused a new temporary layer. Waters with higher densities remained captured in the trough of the Bornholm Basin until November 2002. Here the topography of Słupsk Sill inhibited a further propagation of the inflow. Beside advection with North Sea waters (Postel 1996) a hatching of resting eggs from shallower sediments due to a temperature induced termination of dormancy is possible in *Centropages hamatus*, *Temora longicornis* (Engel & Hirche 2004) and *Acartia* spp. (Dutz et al 2004). In the *BB60* and *BB90* water masses some species showed a distribution different from the rest of the year and indicates a link between deep and surface processes. During periods of stagnant inflows the deep water conditions deteriorate and degradation processes form an anoxic layer close to the seafloor. Furthermore, the inhabitable volume below the halocline is smaller at shallower stations when the transition zone between low and higher saline water is close to the bottom or absent (e.g. Hansen et al. 2004, Schmidt et al. 2004). The decreasing *Pseudocalanus* sp. stocks in the Baltic are related to reduced Major Baltic Inflows (MBI), at-

mospheric forcing and a freshening of the Baltic Sea by increasing rainfalls (Möllmann et al. 2003). During MBI's the halocline elevates and increases the space below and species assigned to mode V find an enlarged inhabitable environment with improving conditions. Thus inflows improve the conditions for *Oithona similis* (Hansen et al. 2004) and *Pseudocalanus* sp. (Renz & Hirche 2005). It allows benthic re-colonisation of deserted areas (Leppäkoski 1971, Leppäkoski 1975, Laine et al. 1997) and improves conditions for organisms close to the seafloor and their offspring. The advection of polychaeta seems possible but would not explain the time shift between subadults and trochophora in January/February 2003. Thus higher abundances of polychaeta/trochophora abundances may be an indicator for temporary improved deep water conditions. Oxygen depletion and decomposition processes decrease this volume again and narrow the vertical space continuously. Due to vertical mixing salinity in upper layers increases after inflows and provides renewed nutrients (Fonselius 1970).

Significant alterations in trophic structure of this ecosystem are suggested to be influenced by climatic changes. The observed temperature increase since the 1980s also influenced the zooplankton community (Möllmann et al. 2000, Lehman et al. 2002, Möllmann et al. 2003) and fostered *Acartia* sp. stocks (Möllmann & Köster 2002). Hydrography in the Baltic Sea is related to local wind fields and sea level pressure, coupled to the North Atlantic Oscillation (Lehman et al. 2002). Water mass exchange with the North Sea decreased within the last decades as a consequence of the prevailing atmospheric conditions. This in turn reduced the renewal of saline waters, increased river run-off and freshened the Baltic (Matthäus & Franck 1992, Matthäus & Schinke 1994). The decrease in salinity also induced a shift towards oligohaline species, as the endemic *Bosmina coregoni maritima*. During summer the high temperature allows this cladoceran to outgrow competitors and predators by parthenogenetic reproduction (Viitasalo et al. 2001) and becomes the most abundant species of the upper layers. Up to 87% of the diet of *Aurelia aurita* consisted of this copepod, although jelly abundance was to low to affect the stock (Barz & Hirche 2005).

For a surface wind stress the upwelling displacement of the thermocline is inversely proportional to stratification and increases with temperature (Gill 1982). This led to a shallow and strong thermocline during the calm summer 2002, but is likely for years with similar conditions. A shallow thermocline narrows the size of the habitat and insulates the deeper nutrient rich layers by a steep thermo-gradient, what can even reduce primary production (Roemmich & McGowan 1995). Limited resources increase niche competition and higher densities foster predators by narrowing the predator-prey distance. In August 2002 a steep and shallow thermocline, a reduction of copepod stocks and lower phytoplankton fluorescence in the warm surface waters than directly below (Mengedoht personal communication) was observed.

Trophic interactions

In the Bornholm Basin the diet composition of fish larvae can to a large extend be explained by seasonal trends (Voss et al. 2003) which show marked changes since the 1980s, the time since when cod stock size decreases, while sprat increases. In addition to fisheries pressure (Bagge et al. 1994) interactions between the identified utilisation modes of the zooplankton species and physical forcing seems important. By this calculated selection-preference of a predator does not necessarily indicate active behaviour. It can rather reflect spatial heterogeneity of prey distribution in relation to the predators preferred depth, when calculated from depth-integrated samples. The separation of zooplankton by hydrography concentrates potential prey unequally in the water column and creates heterogeneous prey

fields. As larvae and Young-of-Year take up high proportions of the zooplankton production (Arrhenius & Hansson 1993) the accumulation of prey in hydrographic strata impacts predators, too. Thus recruitment success is at least partially driven by the availability of prey in a layer. The main planktivorous fish in the Baltic are cod larvae, all age classes of herring (*Clupea harengus*, L.) and sprat (*Sprattus sprattus*, L.). Adult cod (*Gadus morhua*, L.) is the most piscivorous, while the two former species are the dominant fish prey in the Baltic Proper (Rudstam et al. 1994, Bagge 1989). Young and larval sprat concentrate in upper layers (Wieland & Zuzarte 1991, Makarchouk & Hinrichsen 1998, Dickmann et al. submitted) and feed during daytime with a preference for *Acartia* sp. (Voss et al. 2003). In gut contents higher proportions of adult *Acartia* sp., lower of *Temora longicornis* and the absence of *Pseudocalanus* sp. (Dickmann et al. submitted) indicate that the feeding site of larval sprat is mainly above the thermocline in summer, where they prey on zooplankton species of the modes I and II. Thus factors affecting the availability of *Acartia* sp. are important for larval growth, survival and correlate with year class strength (Dickmann 2005). The high abundance of *Bosmina coregoni maritima* makes it a valuable prey item in July/August for the growing sprat larvae, which are then large enough to ingest them (Dickmann et al. submitted). This cladoceran can contribute up to 40% of the diet of sprat (Dickmann 2005). While adult sprat has a shallow vertical distribution during summer, it concentrates in layers deeper than 50 m the rest of the year (Köster & Schnack 1994). This represents a spatial match with zooplankton species of the modes III-V. In these depth sprat preys on *Pseudocalanus* sp. and *Temora* sp. and competes with herring (Möllmann & Köster 2002). The summer shift from a copepod towards a cladoceran dominated zooplankton community decreases the food gain for the deeper living herring (Flinkman et al. 1998, Viitasalo et al. 2001). In the respective months we found an at least slight decrease in abundance of *T. longicornis* and *Pseudocalanus* sp., while *B. coregoni maritima* peaked. We assume this phenomenon to create a further spatial mismatch. As cod needs higher salinities for development, its main habitat is in deeper layers than sprat, where the decreasing *Pseudocalanus* sp. stock is the most important food item (Voss et al. 2003). After spawning cod eggs float in a narrow layer with a salinity of approximately 11 and oxygen values of at least 2.3 ml l^{-1} (Wieland & Zuzarte 1991, Bagge et al. 1994, Wieland et al. 1994). In this layer adult herring and sprat feed on cod eggs during day with rates in the range of 20 to 100%, depressing the recruitment success (Schnack & Köster 1994). Thus an increase in clupeids depresses the probability of strong year classes of cod and vice versa (Rudstam et al. 1994). Especially the recruitment of sprat may capitalise from the changes in the surface layers.

Outlook

To understand the inhomogeneous distribution of species in stratified systems and the constraints set up by the clines improves our appreciation how physical forcing and climate can affect food web structures. Interactions between different trophic levels can be triggered by the segregation of the zooplankton community and have profound impact on the ecosystem functioning. It can be expected that the properties, which have been identified for the central Baltic Sea, are also present in other seas and areas, although the ultimate characteristic depends on the strength of the formed gradient between two strata. It has been noted for different parts of the world that climatic changes appear synchronously with alterations in hydrography and the zooplankton compositions in distinct layers (e.g. Barents Sea: Orlova et al. 2002; California Current: Roemmich & McGowan 1995; Fjords: Gorsky et al. 2000). Especially climatic influence that prolongs the period of a warm surface layers can drive cascading ecological effects throughout stratified marine systems that

are elusive. The complex interactions that are induced by temperature are often less obvious and just allow to consider that changes appear (e.g. Roemmich & McGowan 1995). In the adjacent North Sea profound changes in the fish community have been observed too, but can not directly be related to temperature (Beare et al. 2004). Also in frontal systems horizontal and vertical gradients determine the distribution of different taxa (e.g. Neuenfeldt 2002, Escribano et al. 2004). Thus the identification of functional groups, like the five utilisation modes in the Bornholm Basin, may improve our understanding of food-web structures.

Acknowledgements

References:

Ackefors, H. (1969). Ecological zooplankton investigations in the Baltic Proper 1963-65. Institute of Marine Research Lysekil, Ser Biol Rep 18, 1-139.

Alheit, J., Möllmann, C., Dutz, J., Kornilovs, G., Loewe, P., Mohrholz, V., Wasmund, N. (2005). Synchronous ecological regime shifts in the Central Baltic and North Sea in the late 1980s. ICES Journal of Marine Science, doi:10.1016/j.icesjms.2005.04.024.

Alldredge, A.L., Robinson, B.H., Fleminger, A., Torres, J.J., King, J.M., Hamner, W.M. (1984) Direct sampling and in situ observation of a persistent copepod aggregation in the mesopelagic zone of the Santa Barbara Basin. Marine Biology, 80(1), 75-81.

Arndt, E.A., Heidecke, D. (1973). Zooplanktonuntersuchungen im Küstenbereich der Mecklenburger Bucht. Wissenschaftliche Zeitschrift der Universität Rostock, Mathematisch Naturwissenschaftliche Reihe, 22(6-7), 599-616.

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

Bagge, O., Thurow, F., Steffensen, E., Bay, J. (1994). The Baltic Cod. Dana, 10, 1-28.

Bagge, O. (1989). A review of investigations of the predation by cod in the Baltic. Rapport P.V. Réun. CIEM, 190, 51-56.

Ban, S., Minoda, T. (1989). Seasonal distribution of *Eurytemora affinis* (Poppe, 1880) (Copepoda, Calanoida) in freshwater Lake Ohnuma. Hokkaido Bulletin Fac. Fish. Hokkaido University, 40, 147-153.

Banse, K. (1964). On the vertical distributionof zooplankton in the sea. Progress in Oceanography, 2, 53-125.

Barz, K., Hirche, H.J. (2005). Seasonal development of Scyphozoan medusae and the predatory impact of *Aurelia aurita* on the zooplankton community in the Bornholm Basin (Central Baltic Sea). Marine Biology, DOI 10.1007/s00227-005-1572-2.

Beare, D.J., Burns, F., Greig, A., Jones, E.G., Peach, K., Kienzle, M., McKenzie, E., Reid, D.G. (2004). Long-term increases in prevalence of North Sea fishes having southern biogeographic affinities.; Marine Ecology Progress Series, 284, 269-278.

Berrill, N.J. (1950). The tunicate with an account of the British species. The ray society, London, pp 354.

Blanner, P. (1982). Composition and seasonal variation of the Zooplankton in the Limfjord (Denmark) during 1973-1974. Ophelia, 21(1), 1-40.

Castellani, C., Robinson, C., Smith, T., Lampitt, R.S. (2005). Temperature affects respiration rate of *Oithona similis*. Marine Ecology Progress Series, 285, 129-135.

Chojnacki, J., Drzycimski, I., Siudzinski, K. (1984). The ecological characteristics of the main species of Crustacea in Plankton of the southern Baltic. Articles on Biological Productivity of the Baltic Sea, Moscow, 2, 148-171.

Colebrook, J.M., John, D.E., Brown, W.W. (1961). Contributions towards a plankton atlas of the northeastern Atlantic and the North Sea. Part II, Copepoda. Bulletin Maraine Ecology, 5, 90-97.

Cushing D.H. (1975). Marine Ecology and Fisheries. Cambridge University Press, pp 1-292.

Cushing, D. H. (1990). Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. Advances in Marine Biology, 26, 249-294.

Dagg, M. (1977). Some effects of patchy food environments on copepods. Limnology and Oceanography, 22, 99-107.

Dickmann, M. (2005). Feeding ecology of sprat (*Sprattus sprattus* L.) and sardine (*Sardina pilchardus* W.) larvae in the Baltic Sea and North Sea. PhD thesis, University of Rostock, Germany, pp 95.

Dickmann, M., Möllmann, C., Voss, R. (submitted). Feeding ecology of central Baltic sprat (*Sprattus sprattus* L.) larvae in relation to zooplankton dynamics – Implications for survival. Marine Ecology Progress Series.

Dippner, J.W., Kornilovs, G., Sidrevics, L. (2000). Long-term variability of mesozooplankton in the Central Baltic Sea. Journal of Marine Systems, 25, 23-31.

Dutz, J., Mohrholz, V., Peters, J., Renz, J., Alheit, J. (2004). A strong impact of winter temperature on spring recruitment of a key copepod species in the Bornholm Basin: potential linkages to climate variability. GLOBEC International Newsletter, 10(1), 13-14.

Engel, M., Hirche, H.J. (2004). Seasonal variability and inter-specific differences in hatching of calanoid copepod resting eggs from sediments of the German Bight (North Sea). Journal of Plankton Research, 26(9), 1083-1093.

Eriksson, S. (1973a). Abundance and composition of zooplanktonon the west coast of Sweden. Zoon, 1, 113-123.

Eriksson, S. (1973b). Preliminary Zooplankton investigations in the Öregrund Archipelago (Southwestern Bothnian Sea) during the Summer 1970. Zoon, 1, 95-111.

Eriksson, S. (1973c). The biology of marine planktonic copepods on the west coast of Sweden. Zoon, 1, 37-68.

Eriksson, S. (1974). The occurrence of marine Cladocera on the west coast of Sweden. Marine Biology, 26, 319-327.

Escribano, R., Daneri, G., Farías, L., Gallardo, V.A., González, H.E., Gutiérrez, D., Lange, C.B., Morales, C.E., Pizarro, O., Ulloa, O., Braun, M. (2004). Biological and chemical consequences of the 1997-1998 El Nino in the Chilean coastal upwelling system: a synthesis. Deep Sea Research II, 51, 2389-2411.

Feistel, R., Nausch, G., Mohrholz, V. Łysiak-Pastuszak, E., Seifert, T., Matthäus, W., Krüger, S., Hansen, I.S. (2003a). Warm Waters of Summer 2002 in the Deep Baltic. Oceanologia, 45(4), 571-592.

Feistel, R., Nausch, G., Matthäus, W., Hagen, E. (2003b). Temporal and spatial evolution of the Baltic deep water renewal in spring 2003. Oceanologia, 45(4), 623-642.

Feistel, R., Nausch, G., Matthäus, W., Łysiak-Pastuszak, E., Seifert, T., Hansen, I., S., Mohrholz, V., Krüger, S., Buch, E., Hagen, E. (2004). Background data to the exceptionally warm inflow into the Baltic Sea in late summer of 2002. Meereswissenscahftliche Berichte / Marine Science Repoprt, Institute for Baltic Research, Rostock, Germany, 58, 1-58.

Fenaux, R., Bone, Q., Deibel, D. (1998). Appendicularian distribution and zoogeography. The Biology of Pelagic Tunicates, Bone, Q. (ed.), Oxford University Press, p 251-264.

Fisher, R.A. (1936). The utilization of multiple measurements in taxonomic problems. Annals Eugenics, 7, 179-188.

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

Fonselius, F.S. (1970). On the stagnation and recent turnover of the water in the Baltic. Tellus, 22(5), 533-544.

Gieskes, W.W.C. (1970). The cladocera of the North Atlantic and the North Sea: Biological and ecological studies. Ph.D. thesis, Mc Gill University Montreal, Canada.

Gieskes, W.W.C. (1971a). Ecology of the Cladocera of the North Atlantic and the North Sea, 1960-67. Netherland Journal of Sea Research, 5, 342-376.

Gieskes, W.W.C. (1971b). The succession of two Podon-species in the North Sea. Netherland Journal of Sea Research, 5, 377-381.

Gill, A.E. (1982). Atmosphere-ocean dynamics. Academic Press, New York, pp 662.

Gorsky, G., Flood, P.R., Youngbluth, M., Picheral, M., Grisoni, J.M. (2000). Zooplankton distribution in four western Norwegian fjords. Estuarine, Coastal and Shelf Science, 50, 129-135.

Gran, H.H., Hentschel, E., Russell, F.S., (1936). Handliste zur Bestimmung nordischen Planktons; Rapports et Proces-Verbaux des reunions, C(III), 15-20.

Gurney, R. (1931). British fresh water copepoda I. General Part and Calanoida. The Ray Society, London, p 1-238.

Halsband-Lenk, C., Hirche, H-J., Carlotti, F. (2002). Temperature impact on reproduction and development of congener copepod populations, Journal of Experimental Marine Biology and Ecology, 271, 121-153.

Hansen, F.C., Möllmann, C., Schütz, U., Hinrichsen, H.H. (2004). Spatio-temporal distribution of *Oithona similis* in the Bornholm Basin (Central Baltic Sea). Journal of Plankton Research, 26(6), 659-668.

Hay, S.J., Kiørboe, T., Matthews, A. (1991). Zooplankton biomass and production in the North Sea during the Autumn Circulation Experiment, October 1987-March 1988. Continental Shelf Research 11(12), 1453-1476.

Hernroth, L., Ackefors, H. (1979). The Zooplankton of the Baltic Proper. Report, Fishery Bdoard of Sweden, Institute Marine Research, 2, 1-60.

Hirche, H.J. (1992). Egg production of *Eurytemora affinis* - Effect of k-strategy. Estuarine, Coastal and Shelf Science, 35, 395-407.

Jespersen, P. (1940). Non-parasitic copepoda. Zoology of Iceland, III(33), 1-116.

Jespersen, P. (1949). Investigations on the occurrence and quantity of holoplankton animals in the Isefjord, 1940-45. Meddr Kommn Danm. Fisk.- og Harvunders, Plankton, 5(3), 1-18.

Kideys, A.E., Romanova, Z. (2001). Distribution of gelatinous macrozooplankton in the southern Black Sea during 1996-1999. Marine Biology, 139, 535-547.

Köster, F.W., Möllmann, C. (1997). Predation by sprat and herring on early life stages of cod and sprat in the Central Baltic. American Fisheries Society, Lowell Wakefield Fish Symposium Series, 14, 41-69.

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

Krause, M., Dippner, J.W., Beil, J. (1995) A review of hydrographic controls on the distribution of zooplankton biomass and species in the North Sea with particular reference to a survey conducted in January-March 1987. Progress in Oceanography, 35, 81-152.

Laine, A.O., Sandler, H., Andersin, A.B., Stigzelius, J. (1997). Long term changes of macrozoobenthos in the Eastern Gotland Basin and the Gulf of Finland (Baltic Sea) in relation to the hydrographical regime. Journal of Sea Research, 38, 135-159.

Lance, J. (1962). Effects of water of reduced salinity on the vertical migration of zooplankton. Journal of the Marine Biological Association U.K., 42, 131-154.

Launiainen, J., Matthaeus, W., Fonselius, S., Francke, E. (1987). Hydrography (Baltic Sea). Lassig J (ed) University Helsinki, Department Geophys, Helsinki, Finland.

Lehmann, A., Krauss, W., Hinrichsen, H.H. (2002). Effects of remote and local forcing on circulation and upwelling in the Baltic Sea. Tellus, 54A, 299-316.

Leppäkoski, E. (1971). Benthic recolonization of the Bornholm Basin (Southern Baltic) in 1969-71. Thalassia Jugoslavica, 7(1), 171-179.

Leppäkoski, E. (1975). Macrobentic fauna as indicator of ozeanization in the southern Baltic. Merentutkimuslait Julk Havsforskningsinstitut Skr, No. 239, 280-288.

Lindquist, A. (1959). Studien über das Zooplankton der Bottensee. II Zur Verbreitung und Zusammensetzung des Zooplanktons. Institute Marine Research, Lysekil, Series Biology, 11, 1-136.

Lohmann, H. (1899). Das Gehäuse der Appendicularien, sein Bau, seine Funktion und seine Entstehung. Schriften des Naturwissenschaftlichen Vereins für Schleswig Holstein, 11(2), 347-407.

Longhurst, A.R., Harrison, W.G. (1989). The biological pump: Profiles of plankton production and consumption in the upper ocean. Progress in Oceanography, 22, 47-123.

Makarchouk, A., Hinrichsen, H.H. (1998). The vertical distribution of ichtyoplankton in relation to the hydrographic conditions in the Eastern Baltic. ICES, CM 1998/R:11.

Matthäus, W. (1995). Natural variability and human impacts reflected in long-Term changes in the Baltic deep water conditions – A brief review. Deutsche Hydrographische Zeitschrift, 47(1), 47-65.

Matthäus, W., Frank, H. (1992). Characteristics of major baltic inflows – a statistical analysis. Continental Shelf Research, 12(12), 1375-1400.

Matthäus, W., Schinke, H. (1994). Mean atmospheric circulation patterns associated with major Baltic inflows. Deutsche Hydrographische Zeitschrift, 46, 321-338.

Möllmann, C., Kornilovs, G., Fetter, M., Köster, F.W., Hinrichsen, H-H. (2003). The marine copepod, Pseudocalanus elongatus, as a mediator between climate variability and fisheries in the Central Baltic Sea. Fisheries Oceanography, 12(4/5), 360-368.

Möllmann, C., Köster, F.W. (2002). Population dynamics of calanoid copepods and the implications of their predation by clupeid fish in the Central Baltic Sea. Journal of Plankton Research, 24(10), 959-977.

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

Mohrholz, V., Schuffenhauer, I. (2004). The exceptional inflow 2002: climatological aspects. http://www.ifm.zmaw.de/globec/pub/gg_Poster2004_VMohrholz.pdf.

Mutlu, E., Bingel, F. (1999). Distribution and abundance of ctenophores and their zooplankton food in the Black Sea. Marine Biology, 135, 589-601.

Neuenfeldt, S. (2002). The influence of oxygen saturation on the distributional overlap of predator (cod, *Gadus morhua*) and prey (herring, *Clupea harengus*) in the Bornholm Basin of the Baltic Sea; Fish. Oceanography 11(1), 11-17.

Nielsen, T.G., Sabatini, M. (1996). Role of cyclopoid copepods *Oithona* spp. in the North Sea plankton communities. Marine Ecology Progress Series, 139, 79-93.

Ojaveer, E., Lumberg, A., Ojeveer, H. (1998). Highlights of zooplankton dynamics in Estonian waters (Baltic Sea). ICES Journal of Marine Science, 55, 748-755.

Orlova, E.L., Boitsov, V.D., Nesterova, V. N., Ushakov, N.G. (2002). Composition and distribution of copepods, a major prey of capelin in the central Barents Sea, in moderate and warm years. ICES Journal of Marine Science, 59, 1053-1061.

Postel, L. (1996). Meereskunde der Ostsee. Rheinheimer (ed.), Springer Verlag Berlin Heidelberg New York.

Purasjoki, K.J. (1958). Zur Biologie der Brackwasserkladozere *Bosmina coregoni maritima.* Ann Zool Soc Vanamo, 19(2), 1-117.

Rae, K.M., Fraser, J. H. (1941). Continuous Plankton Records. The copepods of the southern North Sea, 1932-37. Hull Bulletin Marine Ecology, 1, 171-238.

Rae, K.M., Rees, C.B. (1947). Continuous plankton records: the Copepoda in the North Sea, 1938–1939. Hull Bulletin Marine Ecology, 2(11), 95-132.

Ramner, W. (1930). Crustacea, Phyllopoda. Tierwelt in Nord und Ostsee, X, pp 32.

Rasmussen, E. (1973). Systematics and ecology of the Isefjord marine fauna (Denmark). Ophelia, 11, 1-507.

Rees, C.B. (1954). Continuous plankton records: The distribution of Lamellibranch larvae in the North Sea, 1950-51. Hull Bulletin Marine Ecology, 4(27), 21-46.

Renz, J., Hirche, H.J. (2006). Life cycle of *Pseudocalanus acuspes* Giesbrecht (Copepoda, Calanoida) in the Central Baltic Sea: Seasonal and spatial distribution. Marine Biology, 148, 567-580.

Roemmich, D., McGowan, J. (1995). Climatic warming and the decline of zooplankton in the California Current. Science, 267, 1324-1326.

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

Schmidt, J.O., Möllmann, C., Temming, A., Herrmann, J.P., Flöter, J., Sell, A., St. John, M. (2003). Unusual water mass advection affected Central Baltic key species 2: *Pseudocalanus* and the winter inflow. International GLOBEC Newsletter, 9(2), 28-29.

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

Schlitzer, R. (2004). Ocean Data View. http://www.awi.de/GEO/ODV.

Schulz, J. (2005). Ocean Sneaker's Tool. http://www.awi.de/Software/OST (case sensitive URL).

Schulz, J., Möllmann, C., Hirche, H.J. (2006). Vertical zonation of the zooplankton community in the Central Baltic Sea in relation to hydrographic stratification as revealed by Multivariate Discriminant Function- and Canonical Analysis. Journal of Marine Systems doi:10.1016/j.jmarsys.2006.09.004.

Steele, J. H. (1989). The ocean landscape. Landscape ecology, 3, 185-192.

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

Viitasalo, M., Koski, M., Pellikka, K., Johansson, S. (1995). Seasonal and long-term variations in the body size of planktonic copepods in the northern Baltic Sea. Marine Biology, 123, 241-250.

Vinogradov, M.E., Flint, M.V., Shushkina, E.A. (1985). Vertical distribution of mesoplankton in the open area of the Black Sea. Marine Biology, 89, 95-107.

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

Vuorinen, I., Haenninen, J., Viitasalo, M., Helminen, U., Kuosa, H. (1998). Proportion of copepod biomass declines with decreasing salinity in the Baltic Sea. ICES Journal of Marine Science, 55, 767-774.

Wieland, K., Waller, U., Schnack, D. (1994). Development of Baltic cod eggs at different levels of temperature and oxygen content. Dana, 10, 163-177.

Wieland, K., Zuzarte, F. (1991). Vertical distribution of cod and sprat eggs and larvae in the Bornholm Basin (Baltic Sea) 1987-1990. ICES CM1991/J:37.

Description of the figures:

Figure 1: The positions of the nine focus-stations in the Bornholm Basin.

Figure 2: Vertical profiles of temperature, salinity and oxygen in the central Bornholm Basin at position 55.3016°N/15.7966°E. Graphic by courtesy of Rainer Feistel (Baltic Sea Research Institute).

Figure 3: Seasonal composition und structure of the zooplankton community in the Bornholm Basin.

Figure 4: Results of the Multivariate Discriminant Function Analysis as canonical plot for the first two canonical roots.

Figure 5: The canonical factor structure coefficients show the loadings of the species and developmental stages in the analysis. The quadrants can be assigned to different hydrographic conditions.

Figure 6: Seasonal appearance of taxa other than cladocerans and copepods. Scaling is normalised to one. Vertical lines indicate sampling dates.

Figure 7: Seasonal appearance of cladocerans. Scaling is normalised to one. Vertical lines indicate sampling dates.

Figure 8: Seasonal appearance copepods. Scaling is normalised to one. Vertical lines indicate sampling dates.

Figure 9: Vertical distribution of taxa other than cladocerans and copepods. Note the different scaling. Day hauls are indicated by an open circle, night hauls by asterisk.

Figure 10: Vertical distribution of Cladocerans. Note the different scaling. Day hauls are indicated by an open circle, night hauls by asterisk.

Figure 11: Vertical distribution of copepods on station BB0023. White bars: nauplii; grey bars: CI-CIII; black bars: CIV-CVI; Note the different scaling. Day hauls are indicated by an open circle, night hauls by asterisk. *Acartia* nauplii are pooled and are the same for both species.

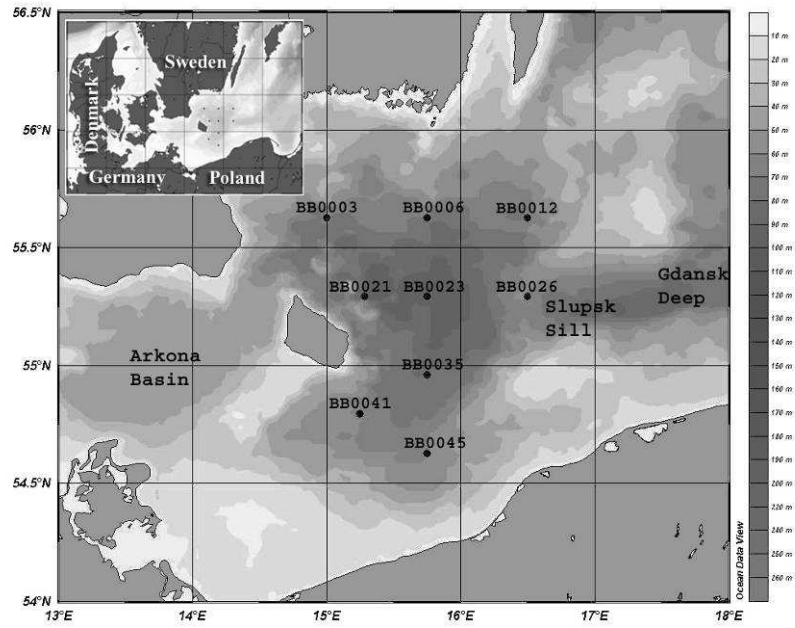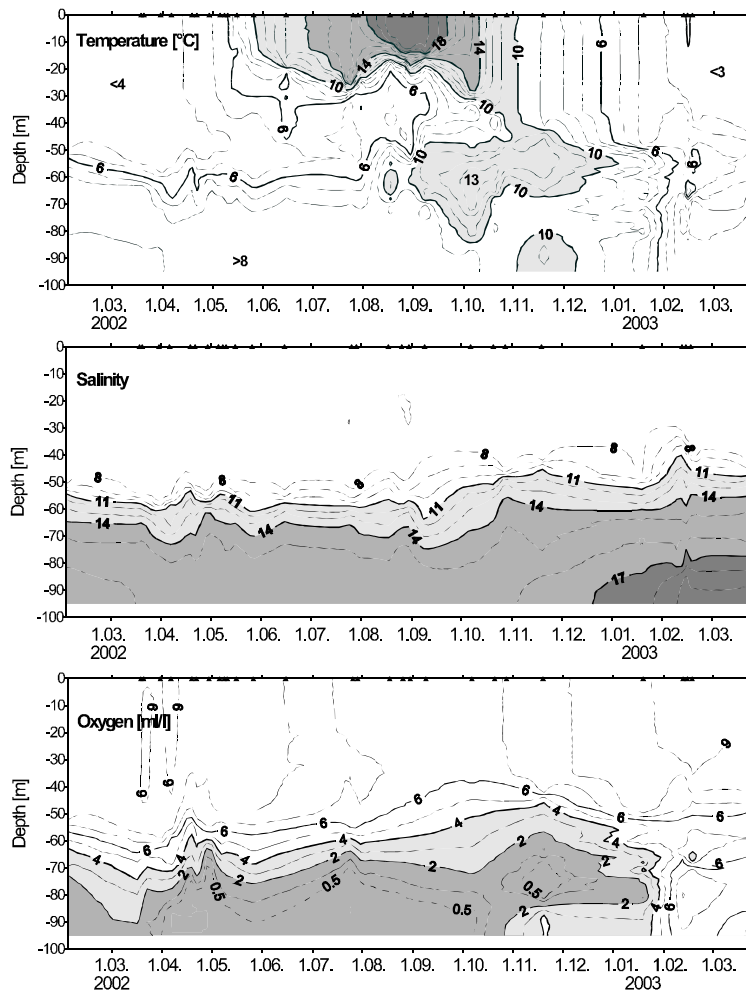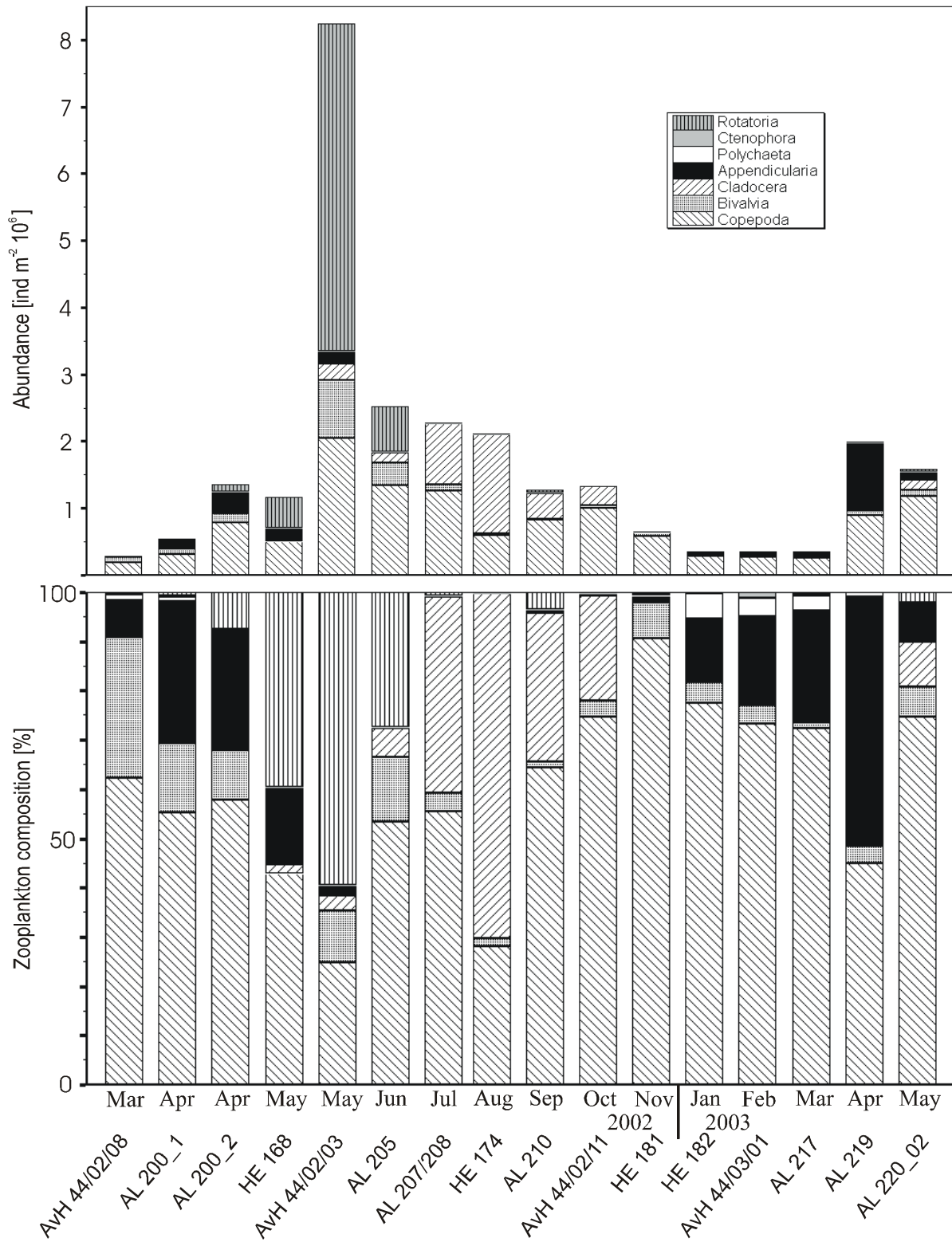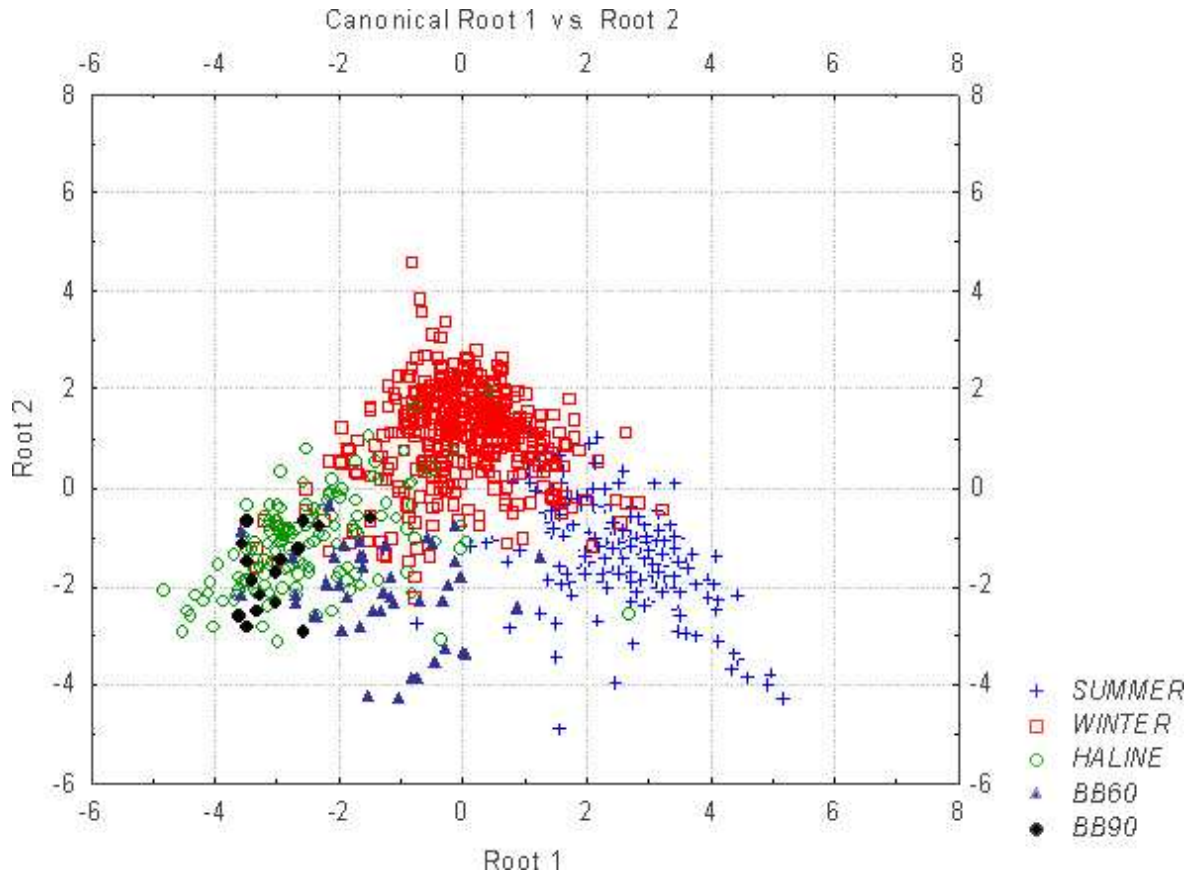Figure 12: The different utilisation modes which species are assigned to.

Fig. 1

Fig. 2

Fig. 3

Fig. 4
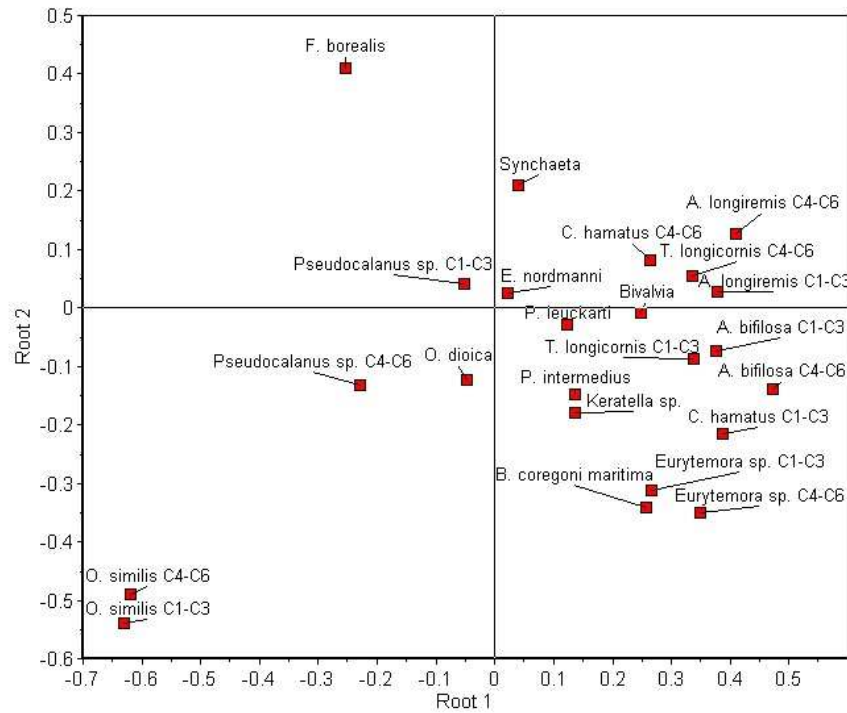
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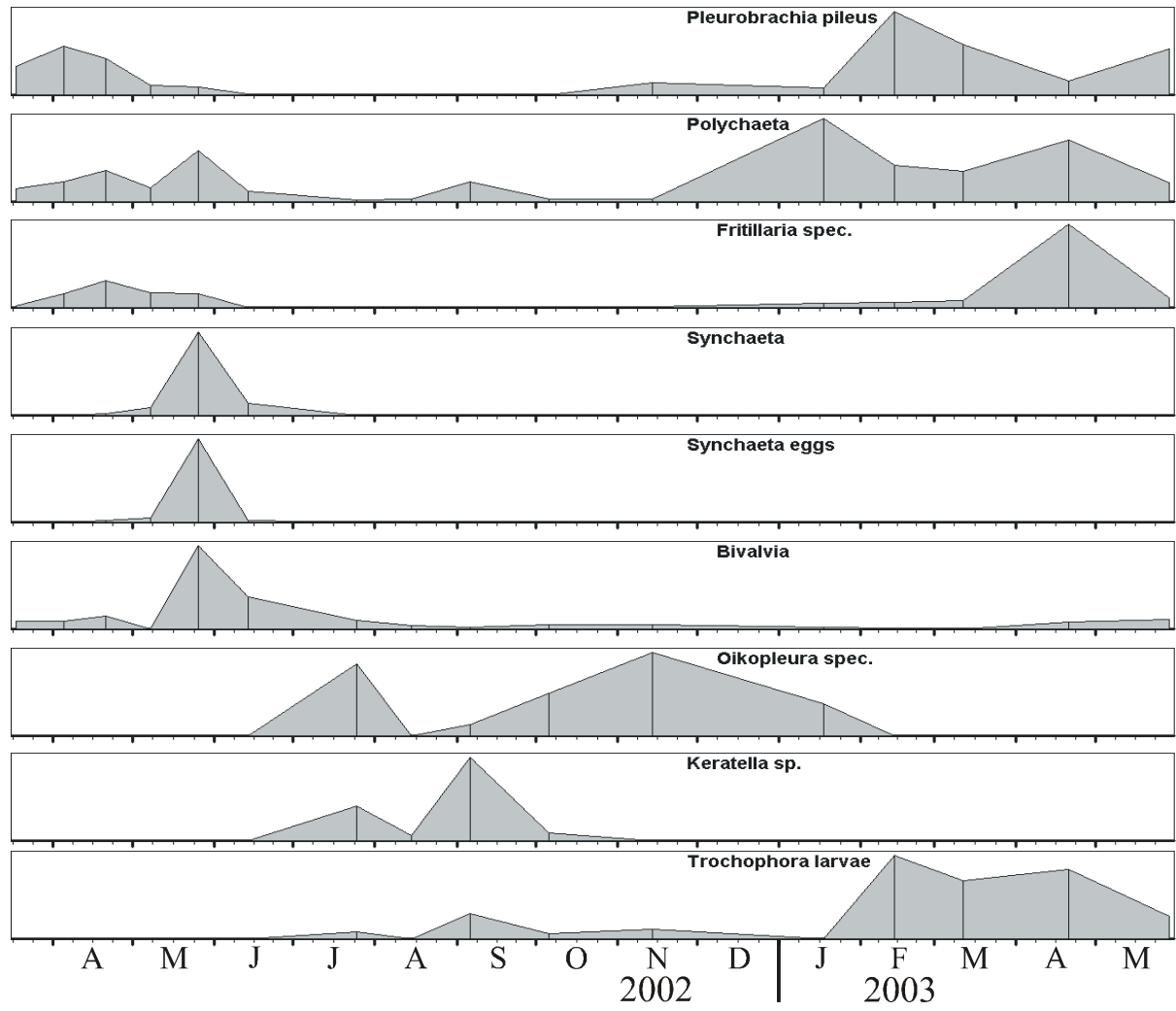
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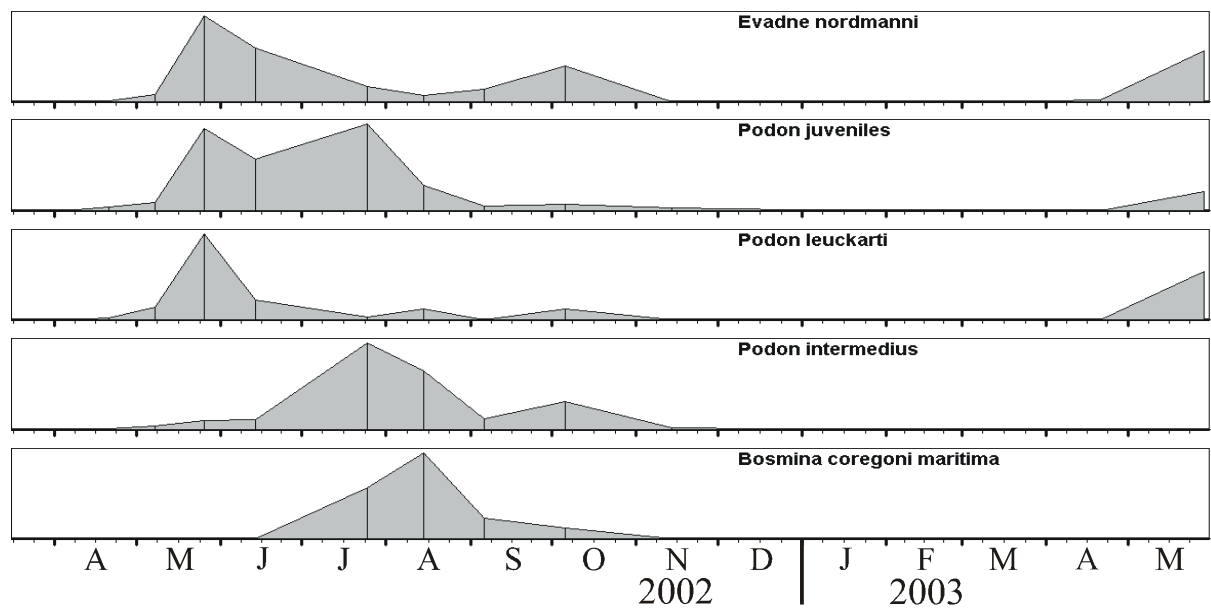
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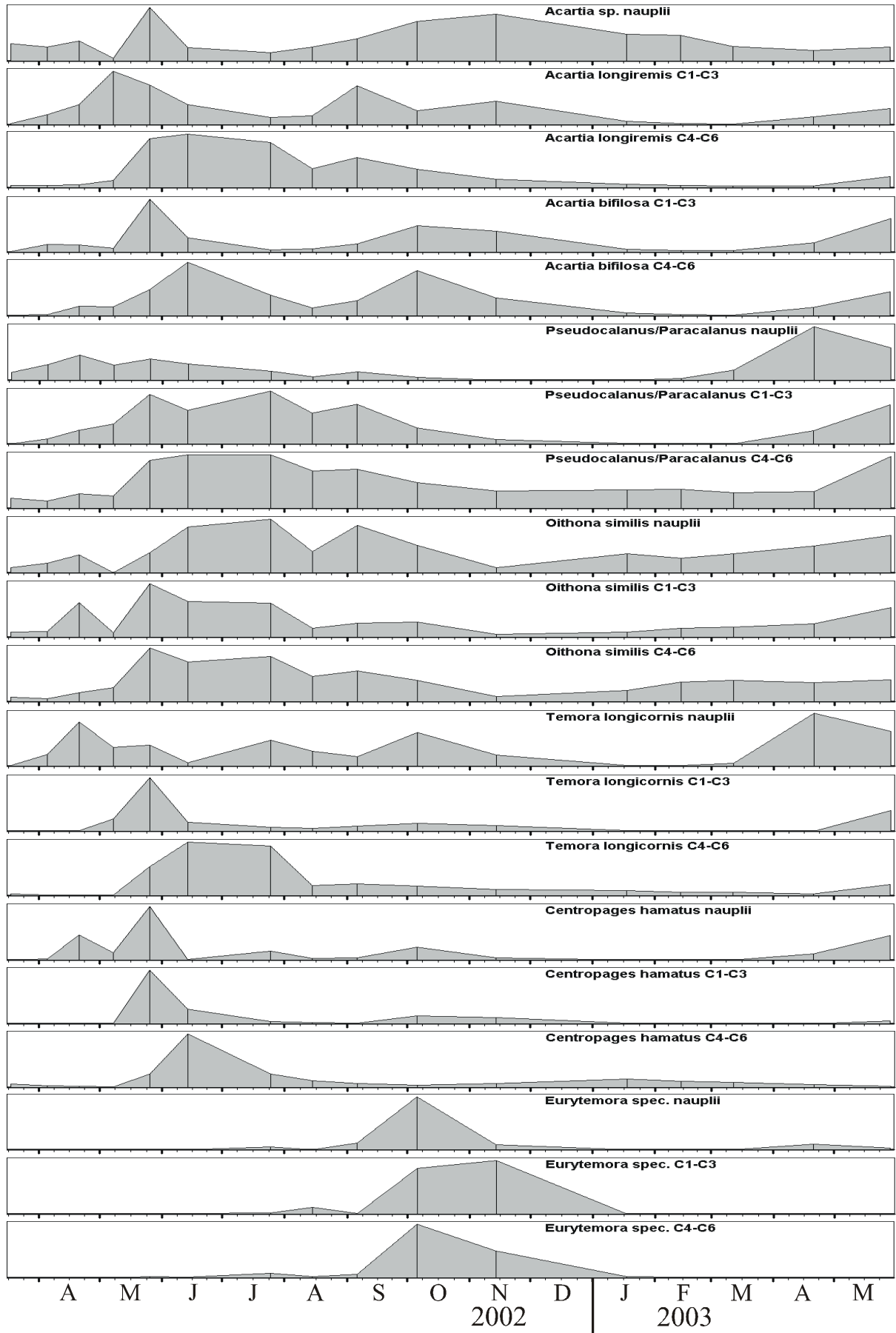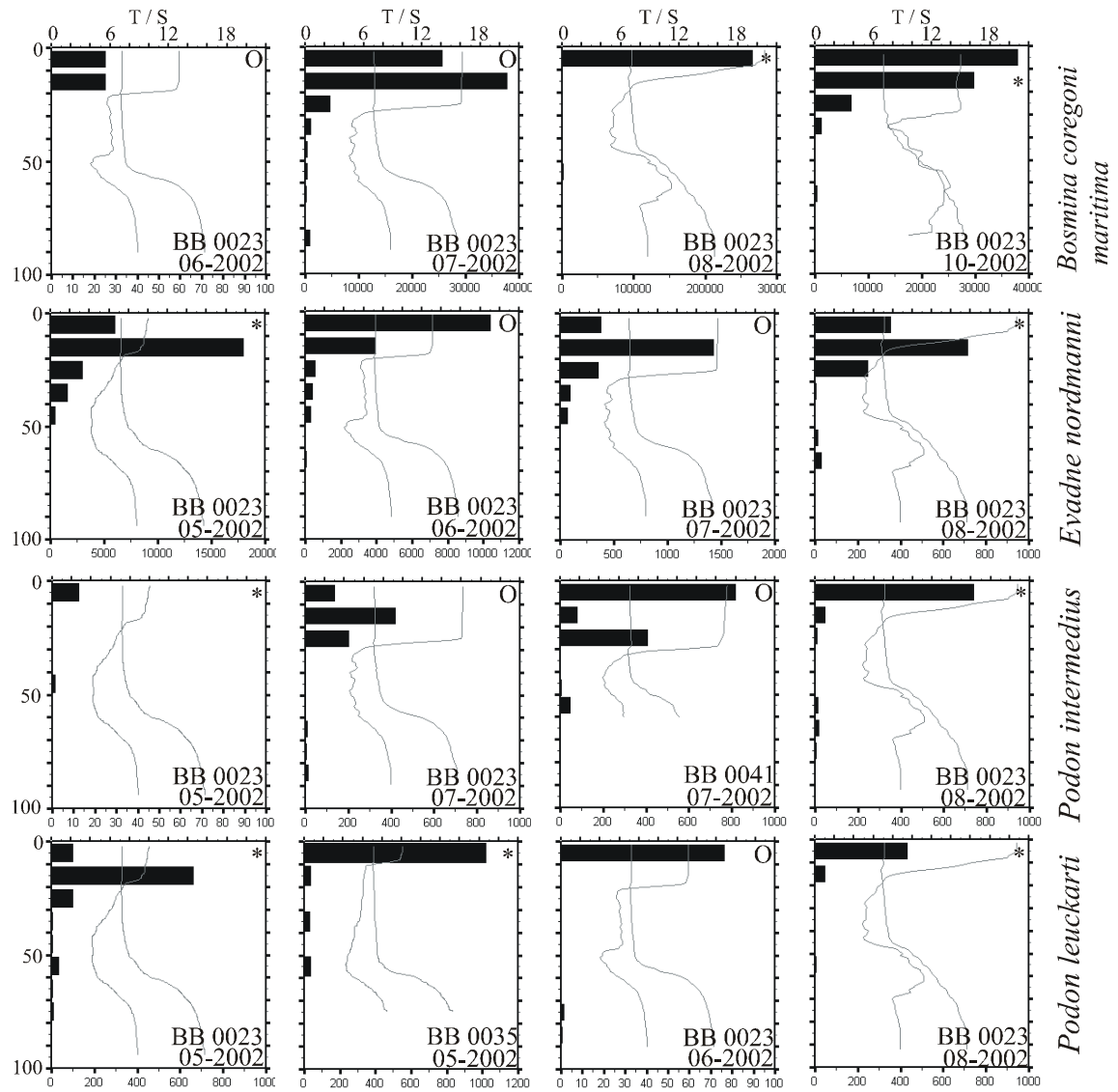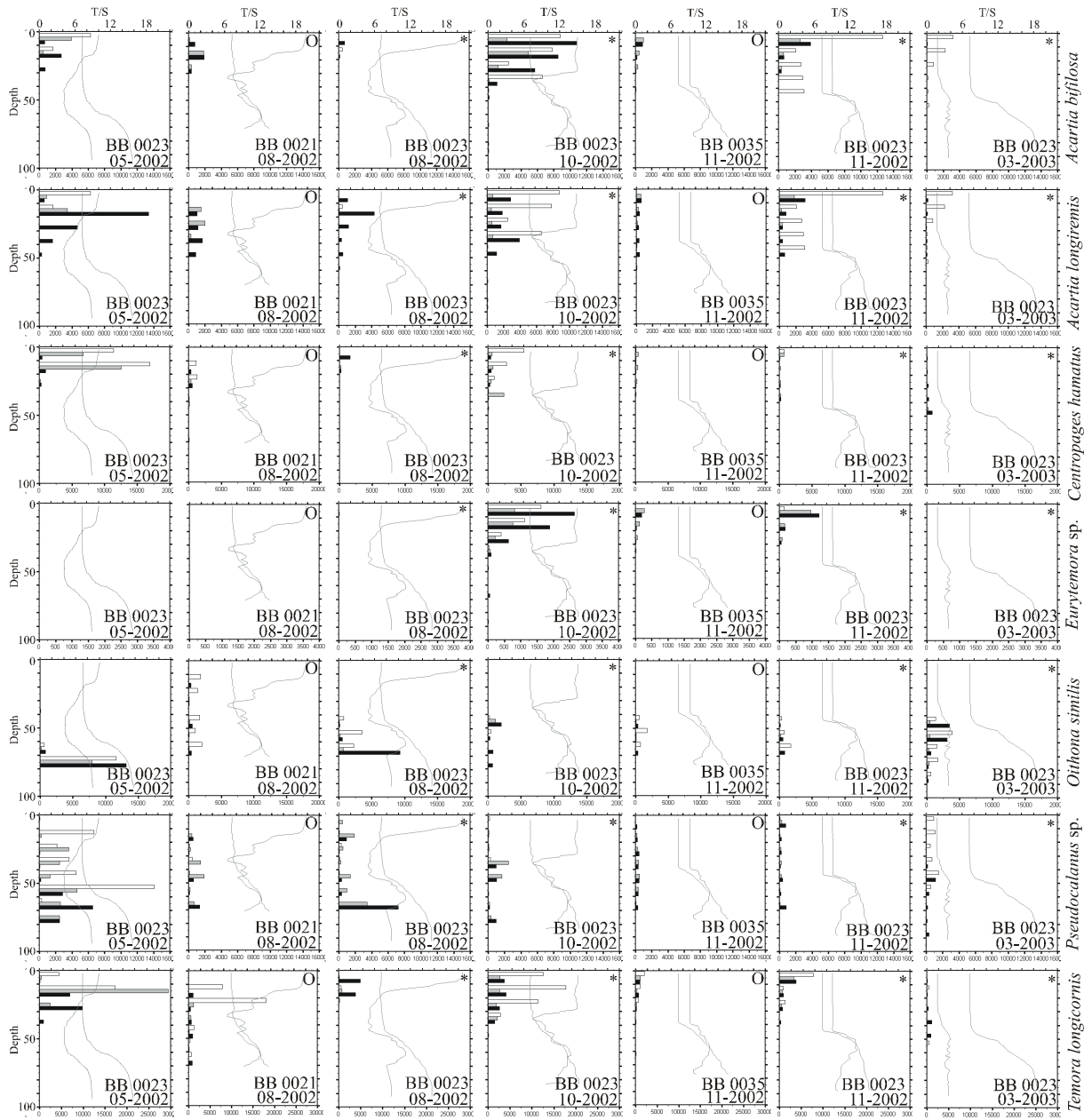
Fig. 8
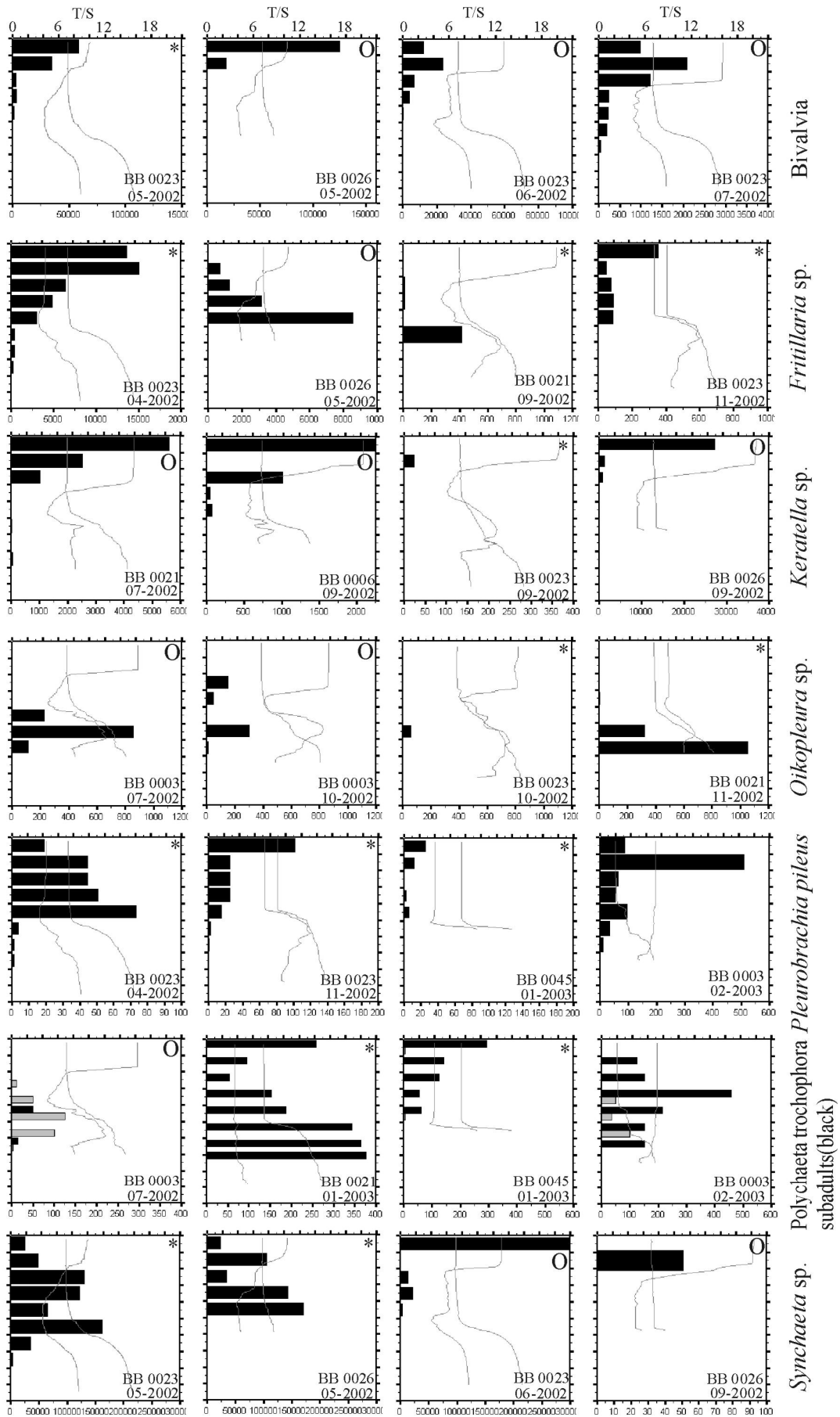
Fig. 9

Fig. 10

Fig. 11

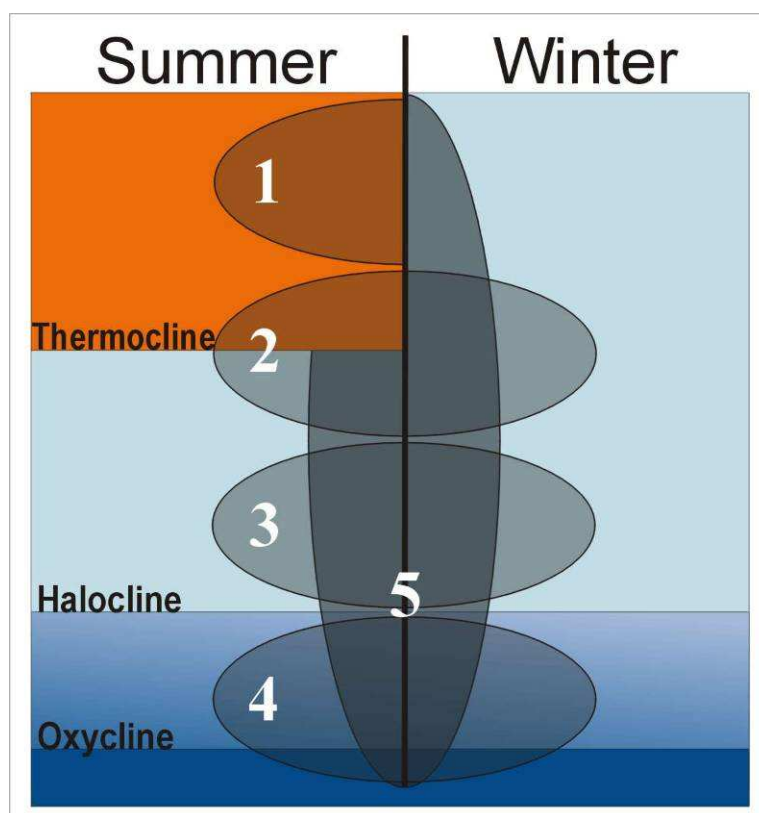**Fig. 12**

Table 1: Schedule of the sampling campaigns.

Cruise	Cruise start [dd.mm.yyyy]	Cruise end [dd.mm.yyyy]
AvH 44/02/08	12.03.2002	22.03.2002
AL 200	02.04.2002	30.04.2002
HE 168	05.05.2002	24.05.2002
AvH 44/02/03	15.05.2002	30.05.2002
AL 205	11.06.2002	23.06.2002
AL 207/208	22.07.2002	07.08.2002
HE 174	12.08.2002	21.08.2002
AL 210	03.09.2002	13.09.2002
AvH 44/02/11	30.09.2002	10.10.2002
HE 181	11.11.2002	29.11.2002
HE 182	13.01.2003	24.01.2003
AvH 44/03/01	10.02.2003	21.02.2003
AL 217	03.03.2003	22.03.2003
AL 219	17.04.2003	28.04.2003
AL 220_02	15.05.2003	03.06.2003

Table 2: The positions of the nine focus stations in the Bornholm Basin.

Station name	Latitude (°N) [dec.]	Longitude (°E) [dec.]	Bottom depth [m]
BB0003	55.625	15.000	75
BB0006	55.625	15.750	70
BB0012	55.625	16.500	65
BB0021	55.292	15.283	85
BB0023	55.292	15.750	95
BB0026	55.292	16.500	65
BB0035	54.958	15.750	85
BB0041	54.792	15.250	70
BB0045	54.625	15.750	60

Table 3: Mean abundance ($n\ m^{-2}$) of zooplankton taxa in the Bornholm Basin for all cruises.

Taxon	Individuals [(Ø $n\ m^{-2}$)]	[%]	Included in MDFA
Appendicularia	**2190744**	**8.28**	
Fritillaria borealis	2186267	8.26	Yes
Oikopleura dioica	4476	0.02	Yes
Bivalvia	**1936222**	**7.32**	
Larvae and subadults	1936222	7.32	Yes
Cladocera	**3619520**	**13.67**	
Bosmina coregoni maritima	2858967	10.80	Yes
Evadne nordmanni	737565	2.79	Yes
Podon juveniles	2781	0.01	No
Podon intermedius	7530	0.03	Yes
Podon leuckarti	12676	0.05	Yes
Copepoda	**12330371**	**46.59**	
Acartia spp. nauplii	1705903	6.45	No
Acartia bifilosa C1-C6	678700	2.57	Yes
Acartia longiremis C1-C6	1159052	4.38	Yes
Centropages hamatus	1024915	3.87	Yes
Eurytemora sp.	64563	0.24	Yes
Oithona similis	1225831	4.63	Yes
Pseudocalanus spp.	2702873	10.21	Yes
Temora longicornis	3768530	14.24	Yes
Ctenophora	**17374**	**0.07**	
Pleurobrachia pileus	17374	0.07	No
Polychaeta	**110314**	**0.42**	
Subadults	93945	0.36	No
Trochophora larvae	16368	0.06	No
Rotatoria	**6258531**	**23.65**	
Keratella sp.	68313	0.26	Yes
Synchaeta sp.	6190218	23.39	Yes

Table 4: Classification matrix of the Multivariate Discriminant Function Analysis (MDFA).

Observed	Cum.%	Predicted				
		SUMMER	*WINTER*	*HALINE*	*BB60*	*BB90*
SUMMER	84.74577	150	22	1	4	0
WINTER	91.70306	13	420	23	2	0
HALINE	77.37226	1	19	106	4	7
BB60	50.00000	2	3	17	22	0
BB90	12.50000	0	0	14	0	2
Total	84.13461	166	464	161	32	9
Wilk's Lambda	0.09327					
F(92, 3188)	28.45346					
p-Level	< 0.001					

Table 5: Test for significance of the roots in the canonical analysis.

Root	Eigenvalue	Wilk's λ	χ^2	DF	Cum.%	p-Level
1	2.58397	0.09327	1938.13108	92	0.60080	< 0.001
2	1.54454	0.33428	895.25392	66	0.95991	< 0.001
3	0.15087	0.85058	132.21776	42	0.99499	< 0.001
4	0.02154	0.97891	17.41191	20	1.00000	0.62609

Table 6: Means of the canonical variables in each root.

	Root 1	Root 2	Root 3	Root 4
SUMMER	2.48890	-1.30846	-0.15752	-0.013182
WINTER	-0.00010	1.10336	0.04928	0.012621
HALINE	-2.44682	-1.11559	-0.30134	-0.168490
BB60	-1.29020	-2.14061	1.43089	0.115564
BB90	-3.03152	-1.66979	-1.02288	0.909449

Table 7: Physiological ranges of the investigated species and developmental stages. The given values indicate the ranges, within abundances of more than 10% of the maximum value were observed. Respective values highest abundances were observed are given in brackets. In the reference columns values from previous investigations are given.

Species	Salinity ALS	Reference	Temperature [°C] ALT	Reference	Oxygen [ml l^{-1}] ALO
Appendicularia					
Fritillaria sp.	7.0-12.0 (7.0)	6-35 [1]	2.0-10.0 (4.0)	< 10 [1,2]	5.5-9.5 (9.0)
Oikopleura sp.	7.5-15.0 (13.0)	>16.5 [1]	4.0-16.0 (11.0)		2.0-10.0 (4.5)
Bivalvia					
Larvae and subadults	7.0-8.5 (7.5)		2.5-17.0 (9.0)		5.5-10.0 (8.5)
Cladocera					
B. coregoni maritima	7.0-14.0 (7.0)	2.5-6 [1] 0.1-10.7[1]	7.0-21.0 (19.0)	13-18 [1] 5-20 [1]	4.5-7.5 (6.5)
E. nordmanni	7.0-14.5 (7.0)	2-35 [1,9] 1.33-35.4 [1]	2.5-20.5 (9.5)	4-18 [4,5,6] 1-22.6 [1]	1.5-9.0 (8.5)
P. juveniles	7.0-14.0 (7.0)		4.0-20.0 (13.0)		2.5-9.0 (7.0)
P. intermedius	7.0-15.0 (7.0)	3.5-35.3 [1] 2.4-35.3 [1] 3.6-35 [4]	5.0-20.0 (17.0)	9-18 [1] 4.8-20.59 [1] 8-17 [4] 13-16 [7]	2.5-9.0 (6.5)
P. leuckarti	7.0-16.5 (7.0)	23-35 [1] 6.2-35.5 [1]	3.0-17.0 (10.0)	10-17 [1] 0-17.4 [1] 8-17 [4]	4.0-9.0 (8.5)
Copepoda					
Acartia sp. nauplii	7.0-9.50 (7.0)		2.0-19.0 (10.0)		4.5-10.0 (8.5)
A. bifilosa C1-C3	7.0-7.50 (7.0)		3.5-18.0 (10.5)		4.5-10.0 (8.5)
A. bifilosa C4-C6	7.0-15.2 (7.0)		3.5-20.0 (12.0)		4.5-9.5 (8.0)
A. longiremis C1-C3	7.0-8.50 (7.0)		3.0-20.0 (9.0)		4.5-9.0 (8.0)
A. longiremis C4-C6	7.0-15.0 (7.0)		4.0-20.0 (6.0)		4.0-9.0 (8.0)
C. hamatus nauplii	7.0-12.5 (7.0)		2.5-20.0 (10.0)		3.5-9.0 (8.0)
C. hamatus C1-C3	7.0-10.0 (7.0)		5.0-16.0 (10.0)		4.5-9.0 (8.5)
C. hamatus C4-C6	7.0-12.0 (7.0)	>7 [1]	4.0-20.0 (8.5)		4.5-9.0 (8.5)
Eurytemora sp. nauplii	7.0-13.2 (7.0)		2.5-20.0 (15.0)		4.5-9.0 (6.5)
Eurytemora sp. C1-C3	7.0-14.0 (7.0)		7.5-16.0 (9.5)		4.5-8.0 (8.0)
Eurytemora sp. C4-C6	7.0-14.0 (7.0)		8.0-20.0 (15.0)		4.5-8.0 (6.5)
O. similis nauplii	8.0-16.5 (12.0)	>7 [1]	2.5-14.5 (6.0)		0.5-7.5 (3.5)
O. similis C1-C3	8.0-18.5 (14.0)	>14.5 [1]	3.0-13.5 (7.0)		0.5-8.0 (3.5)
O. similis C4-C6	7.0-18.5 (13.5)		3.0-15.0 (6.5)		0.5-8.5 (3.5)
Pseudocalanus sp. nauplii	7.0-19.0 (9.0)		2.0-20.0 (3.5)		3.5-10.0 (7.5)
Pseudocalanus sp. C1-C3	7.0-17.0 (8.5)		3.0-19.5 (5.5)		0.5-9.5 (7.5)
Pseudocalanus sp. C4-C6	7.0-19.0 (12.0)		2.0-18.0 (5.0)		0.5-9.0 (7.0)
T. longicornis nauplii	7.0-16.0 (7.0)		2.5-20.0 (9.5)		4.5-10.5 (7.5)
T. longicornis C1-C3	7.0-10.0 (7.0)		5.0-20.0 (9.5)		4.5-9.0 (8.5)
T. longicornis C4-C6	7.0-13.5 (7.0)		2.0-20.0 (9.0)		4.5-9.5 (7.5)
Ctenophora					
P. pileus	7.0-13.0 (7.50)	6-8 [8]	1.5-11.5 (4.0)	< 8 [10]	3.5-10.0 (7.0)
Polychaeta					
Subadults	7.0-16.0 (7.50)		2.0-10.5 (3.0)		3.5-9.0 (8.5)
Trochphora	7.0-16.0 (7.50)		2.0-20.0 (3.5)		3.5-9.5 (9.0)
Rotatoria					
Keratella sp.	7.0-12.5 (7.25)		10.0-20.0 (17.0)		6.0-7.0 (6.5)
Synchaeta sp.	7.0-13.0 (7.50)		4.0-13.0 (6.0)	8-16 [1,8]	4.5-9.0 (8.5)

1) Ackefors 1969, 2) Blanner 1982, 3) Berill 1950, 4) Erikson 1974, 5) Gieskes 1970, 6) Gieskes 1971a, 7) Gieskes 1971b, 8) Hernroth & Ackefors 1979, 9) Ramner 1930, 10) Mutlu & Bingel 1999.

Table 8: The different utilisation modes as revealed by MDFA.

Pattern	Distribution range	Species
1	Species being mainly abundant during summer in waters of the *SUMMER* category	**Cladocera** *Bosmina coregoni maritima* *Podon intermedius* **Copepoda** *Eurytemora* CI-CIII *Eurytemora* CIV-CVI
2	Species being abundant for long times of the year in the categories *SUMMER* and *WINTER*	**Bivalvia** *Bivalvia* larvae **Cladocera** *Evade nordmanni* *Podon leuckarti* **Copepoda** *Acartia bifilosa* CI-CIII *Acartia bifilosa* CIV-CVI *Centropages hamatus* CI-CIII *Temora longicornis* CI-CIII **Rotatoria** *Keratella* spp.
3	Species being abundant for long times of the year, but restricted to the category *WINTER*	**Copepoda** *Acartia longiremis* CI-CIII *Acartia longiremis* CIV-CVI *Centropages hamatus* CIV-CVI *Temora longicornis* CIV-CVI **Rotatoria** *Synchaeta* spp.
4	Species being present in the category *WINTER* and *HALINE*	**Appendicularia** *Fritillaria borealis* **Copepoda** *Pseudocalanus* sp. CI-CIII
5	Species being mainly present in the category *HALINE*	**Appendicularia** *Oikopleura dioica* **Copepoda** *Oithona similis* CI-CIII *Oithona similis* CIV-CVI *Pseudocalanus* sp. CIV-CVI

4.2. Software development

S1: Ocean Sneaker's Tool - An open code software tool for fast processing, exploring and visualising marine and aquatic data

Authors: Jan Schulz, Michael Potthoff, Miriam Dickmann
Status: Published in GLOBEC International Newsletter 12(1):84-85

This paper briefly sketches the extent of the software project. It highlights several applications and options for processing marine data sets. It was written by the first author and improved by the co-authors, who were also partially involved in the source code development.

Ocean Sneaker's Tool –
An open code software tool for fast processing, exploring and visualising marine and aquatic data

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[*]Institute for Baltic Research, Warnemünde

Aquatic data often require various processing steps from collection to analysis. This might include the adding of metadata to measured values for mapping software, the conversion of stacked net data to area related or other complex transformations. Although these steps can be accomplished quickly for single parameters it is a time consuming process with increasing numbers. As a spin-off of GLOBEC-Germany the software package 'Ocean Sneaker's Tool' (OST) was developed (Fig. 1). Its focus is to aid biological researchers with their daily work and to facilitate initial exploring of datasets. OST includes a basic spreadsheet analysis, provides a universal import filter for ASCII plaintext formats and supports several specific file types generated by different oceanographic gears. Three major modules cover a wide range of processing, converting, exploring and visualising of selected data subsets.

The data mining module can create reports for statistics, calculate percentile proportions, perform various transformations and conversions and provides iterative data scaling. Statistical analysis includes basic descriptive statistics as e.g. *mean*, *median*, *sum*, *range*, *variance*, *SD*, *SE*, and *VC*. For similarity and dissimilarity based investigations (Clarke and Warwick 1994) matrices according to *Bray-Curtis*, *Canberra*, *Manhattan-* or *Euclidean distance* can be computed. The Sammon mapping option provides an easy multidimensional scaling technique (Sammon, 1969) that reveals inherent structures in order to explore data sets, like finding possible clusters, correlations or underlying distributions and can be run with raw data. Prior to analyses data can be automatically *log*, *ln*, *sqrt* or *arcsin* transformed. For the conversion of $n*m^{-3}$ from stacked nets, to $n*m^{-2}$ functions are available, and can also calculate the weighted mean depth (Bollens and Frost, 1989) for several species simultaneously.

The geo-coded export module includes metadata like cruise, station, date, time longitude, latitude and bottom depth to measured values. The output format can be imported directly to Ocean Data View (Schlitzer, 2004) or other mapping programs for further investigation. The various formats latitude and longitude values can be given in are auto converted to decimal degree notation as required for computer assisted work.

The visualising module allows for the display of data sets in various graph forms, e.g. as line, bar, area, polar, scatter, stacked and surface plots (examples in Fig. 1). All properties can be customised to modify the appearance in 2D or 3D mode. Additional algorithms can create interpolated isolines, allow labelling of charts and to adjust the desired perspective. Charts can be saved in different formats (e.g. emf, eps, gif, jpg, pdf, wmf and several others) and displayed data can be exported as excel, HTML or native ASCII format.

At present OST is in the beta phase of version 2.0 after pervasive modifications during the last year. The project now consists of more than 23.000 lines of source code distributed over 25 units and is written in easy understandable object pascal (Borland Delphi). The source code can be downloaded from the website (Schulz, 2005, www.awi.de/Software/OST) and allows users to inspect algorithms, modify functions as desired and developers to implement new features.

Since the reorganisation of the web site in October 2005 the tool has drawn international attention beyond Germany (Fig. 2). It is now referenced by other institutes and projects like CENSOR, IOC Ocean-Teacher and Pangaea. OST runs under Windows 95/98/2k/XP and no problems have been reported so far when used with emulators under Linux and Mac environments. The use of efficient code and the waiving of specific code linked to an operating system results in stand-alone software of just 2.5 MB. As neither additional libraries nor an installation is required OST can even be run directly out of a zip-archive from an USB stick on machines with different regional preferences.

References

Bollens, S.M.; Frost, B.W.; 1989: Predator induced diel vertical migration in a planktonic copepod; J. Plankt. Res. 11(5):1047-1065

Borland Delphi; 2006: http://www.borland.com/de/products/delphi

Globec-Germany: www.Globec-Germany.de

Sammon, J.W.; 1969: A Nonlinear Mapping Algorithm for Data Structure Analysis, *IEEE Trans. Comput.*, Vol. C-18:401-409

Schulz, J.; 2005: Ocean Sneaker's Tool; http://www.awi.de/Software/OST

Clarke, K.R.; Warwick R.M.; 1994: Change in Marine Communities: an approach to statistical analysis and interpretation; Plymouth: Plymouth Marine Laboratory, 144 pp

Schlitzer, R.; 2004: Ocean Data View; http://www.awi.de/GEO/ODV

Description of the Figures:

Figure 1: Screen shot of the current Ocean Sneaker's Tool version. The application navigator (lower left) makes it simple to access the different chart- (right) and data-windows (upper left). Windows are resizable and can be arbitrarily positioned.

Figure 2: Website usage by country between December 2005 and February 2006 generated from the web logs.
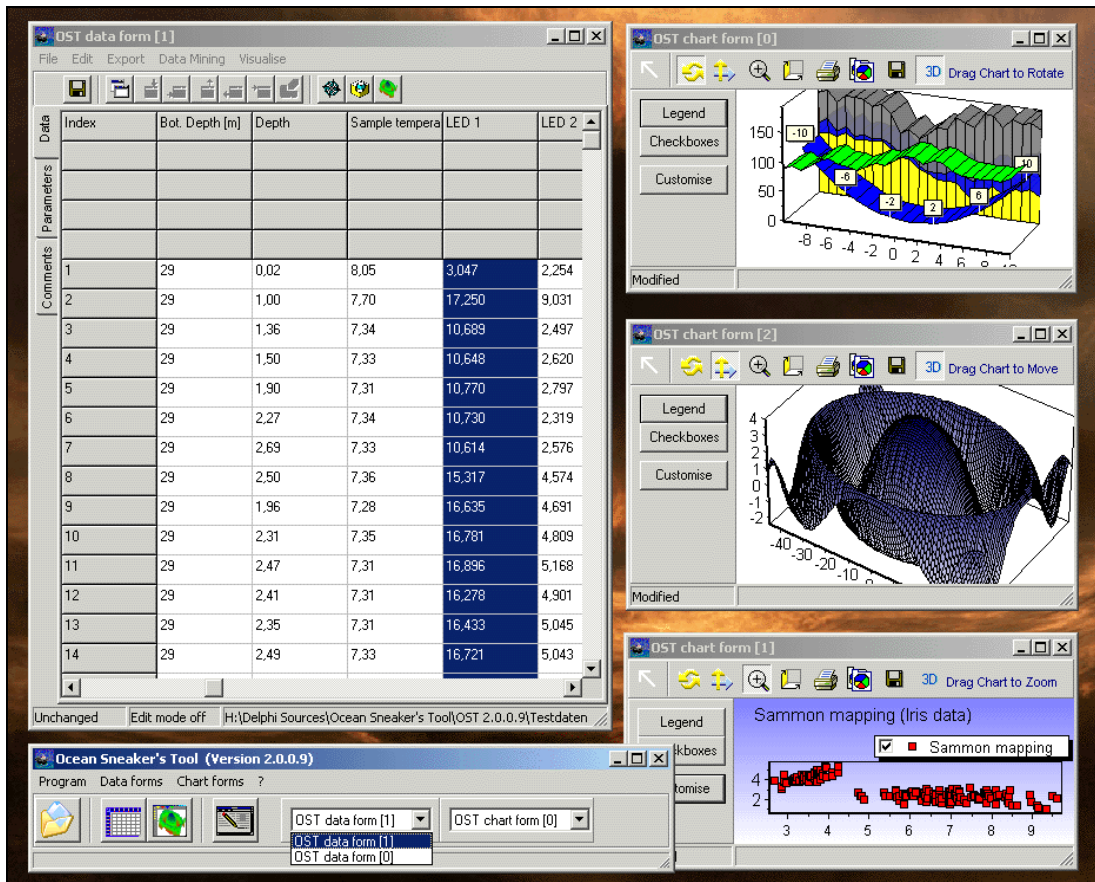
Fig. 1
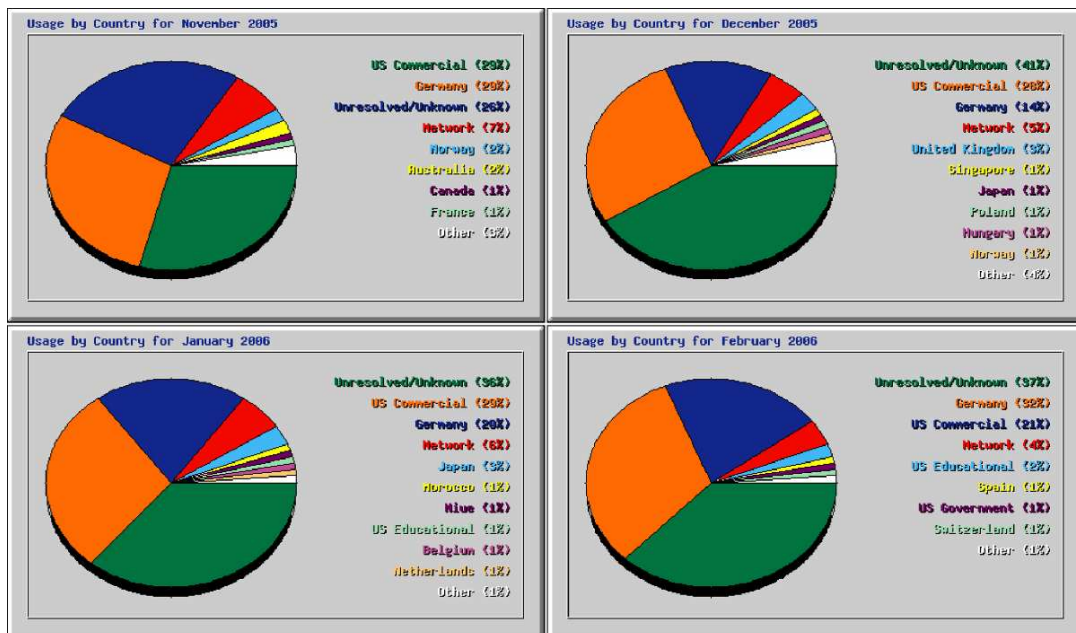
Fig. 2

4.3. New methods for zooplankton detection

T1: Vorrichtung zur Partikeldetektion in einer tiefenbegrenzten Lichtscheibe

Inventor: Jan Schulz
Status: Pending patent application in Germany (DE 10 2005 028 893.6)

The text of this patent application includes the basic functional principle of the developed zooplankton detection method. With a combination of different cylindrical lenses and a linear light source a frame of light is created and projected into the water. Particles and organisms that enter this light frame are illuminated and scatter light. Only light scattered in this light-frame is detected by the camera. The basic text and figures were provided by the inventor and edited by the patent agents N. Cochu and J. Cochu, Berlin, to comply with the legal formalities of the German Patent Office (Deutsches Patent- und Markenamt[5]).

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[5] www.dpma.de

Vorrichtung zur Partikeldetektion in einer tiefenbegrenzten Lichtscheibe

Beschreibung

Die Erfindung bezieht sich auf eine Vorrichtung zur Partikeldetektion in einem strömenden Fluid in einem optisch begrenzten Messvolumen mit einer Beleuchtungseinrichtung aus einer Lichtquelle, einem Blendensystem und einem fokussierenden Linsensystem sowie mit einer optischen Auswerteeinheit mit weiteren Blenden und Linsen und einem auf das Messvolumen ausgerichteten Aufnahmesystem.

Ein zentrales Ziel der Meeresökologie ist das Verständnis der Verteilung von planktischen Organismen im Meer und deren regulierende Prozesse. Besonders von Interesse sind hierbei Abundanz und Diversität kleiner Plankter, die auf Grund ihrer Individuenanzahlen eine der größten Quellen tierischen Eiweißes im Meer darstellen. Ihnen kommt dadurch eine wichtige Bedeutung im biologischen Stoffkreislaufsystem zu. Der ungeklärte Einfluss von anthropogenen und klimatischen Veränderungen auf marine Ökosysteme ist dabei in den letzten Jahren und Jahrzehnten in den Blickpunkt der Wissenschaft geraten. Es wird heute allgemein anerkannt, dass Abundanz und Diversität verschiedener planktischer Organismen unter anderem mit den physikalischen Parametern der Umgebung korreliert sind. Die hydrodynamischen Prozesse im Wasserkörper können dabei sowohl zu einer Dispersion der Plankter als auch zu gehäuftem Auftreten führen. Diese regulierenden Prozesse der Verteilung von Zooplankton in Zeit und Raum sind von zentraler Bedeutung, um auf Zusammenhänge mit biotischen und abiotischen Veränderungen zu schließen und Aussagen über das Ökosystem zu treffen. Dazu werden Methoden benötigt, um diese Verteilungen großflächig auf räumlich und zeitlich kleinen Skalen aufzulösen. Die traditionelle Methode der Beprobung mit Netzen ist sehr zeitintensiv und ermöglicht nur eine begrenzte Auflösung im kleinskaligen Bereich. Aus diesem Grund sind in der Vergangenheit eine Reihe neuer Methoden und Ansätze entwickelt worden, um das Verständnis der systemischen Ökologie zu erweitern. Neben den akustischen ist besonders der Bereich der bildgebenden Verfahren von Interesse. Die hier eingesetzten Geräte werden als „Video-Plankton-Rekorder" VPR bezeichnet. Sie bieten zudem den Vorteil, dass fragile Arten, wie z.B. gelatinöses Plankton, in situ untersucht werden können und Informationen über die Biologie dieser Vertreter erhalten werden, die mit klassischen Methoden während der Beprobung zerstört würden. Bilder dieser Arten im natürlichen Habitat lassen Rückschlüsse auf Verhalten, Verbreitung und Interaktionen zu.

Stand der Technik

Aus dem Stand der Technik sind verschiedene VPR für einen mobilen Schleppbetrieb bekannt. Der VPR von der Firma SEASCAN, Inc. Falmouth, MA, USA ist beispielsweise aus der **Veröffentlichung I** „Autonomous Vertically Profiling Plankton Observatory" (Coastal Ocean Institute WHOI, abrufbar aus dem Internet unter der Webadresse http://4dgeo.whoi.edu/vpr/_vpr_overview.html, Stand 08.06.2005), der **Veröffentlichung II** „Video Plankton Recorder on CTD" (NOAA Arctic Research Office, abrufbar im Internet unter der Webadresse http://www.arctic.noaa.gov/aro/russian-american/cruise10-ctd-rosette.htm, Stand 08.06.2005) oder aus dem Globec-Newsletter Vol.8, No. 2, October 2002, pp 20-21 unter der **Veröffentlichung III** „Video Plankton Recorder reveals envi-

ronmental problems of marine copepod" von C. Möllmann et al. bekannt. Dieses Gerät wird hinter einem Schiff geschleppt und dient der profilierenden Planktondetektion mit einem Videokamerasystem. Einzelheiten zum eingesetzten Blenden- und Linsensystem sowie zur Ausgestaltung der Lichtquelle sind nicht bekannt. Der relativ aufwändige und Platz einnehmende Aufbau fördert jedoch Störungen im Betrieb und bei der Handhabung sowie Probleme bei der Auswertung. Außerdem kann das Gerät nicht, ohne größeren Aufwand/Modifikationen, stationär autark arbeiten. Bei einem ähnlichen Gerät aus Kanada handelt es sich um einen Optical-Plankton-Counter. Dieses Gerät liefert jedoch keine Bilder, sondern misst nur Partikelgrößenverteilungen, welche nur mit einer gewissen Unsicherheit einzelnen Arten zugewiesen werden können. Neuere Modelle nutzen eine Laserlichtquelle zur verbesserten Größenauflösung.

Alle bekannten VPR nutzen punktförmige Lichtquellen und einzelne sphärische Linsen zur Kollimation. Im großskaligen Bereich kommen auch starke Halogensysteme und Fresnellinsen zum Einsatz. Die bekannten Vorrichtungen haben aber zum Problem, dass keine scharfe optische Begrenzung des Messvolumens erzeugt werden kann und die Tiefenschärfe im Messvolumen softwaretechnisch justiert wird, was im kleinskaligen Bereich der Planktonbeobachtung zu hohen Ungenauigkeiten der Volumeneinschätzung führt.

Auf dem allgemeinen Gebiet der Partikeldetektion sind weitere verschiedene Vorrichtungen bekannt. Aus der **DD 232 552 A1** ist eine Einrichtung zur Zählung und Klassifizierung von dispergierten Teilchen in Flüssigkeiten, z.B. Farben, mit einem von einer Messzelle räumlich begrenzten Messvolumen bekannt. Zur Ausleuchtung des Messvolumens dient ein Laserstrahl, wobei der Strahlfokus in der Mitte des Messvolumens liegt, sodass das detektierte Messvolumen auf einen Punkt reduziert wird. Zur Detektion wird die Streulichtintensität jedes Teilchens gemessen. Dabei wird angenommen, dass die Intensität des Streulichts unter kleinen Winkeln eine Funktion des Partikelvolumens ist. Das Messvolumen ist durch die Ausbildung der Messzelle so eingeengt, dass sich immer nur ein Teilchen im Lichtfokus befindet, dessen Streuung im Laserlicht gemessen wird. Die Flüssigkeiten werden mit einer Injektionsspritze in die Messkammer eingespritzt, eine Erfassung und Bestimmung von Partikeln in einem frei strömenden Fluid ist mit der bekannten Einrichtung nicht möglich. Weiterhin können nur relativ große Partikel detektiert werden, die sich in der Messzelle vereinzeln lassen. Die **DD 221 861 A1** beschreibt eine Beleuchtungseinrichtung zur Erzeugung eines zweidimensionalen Lichtstreifens zur Mustererkennung und Identifizierung von Werkstücken in industrieller Umgebung. Dazu wird eine lineare Lichtquelle verwendet, deren Strahlen durch eine Lamellenblende gerichtet und durch eine Zylinderlinse auf das zu erkennende Objekt gebündelt werden. In dem Aufnahmesystem wird durch Kontrasteinstellung ein scharfes Schwarzweißbild des jeweils beleuchteten Streifens erzeugt und analysiert. Ein Reflektor kann für eine höhere Lichtausbeute hinter der Lichtquelle angebracht werden. Die Objekte werden unter spitzem Winkel beleuchtet und die Kamera befindet sich senkrecht darüber. Menge und Art von Teilen können je nach Auflösungsvermögen der Kamera bestimmt werden. Zur Begrenzung des Betrachtungsraums ist ein fester Hintergrund erforderlich. Weiterhin ist aus der **DE 298 13 109 U1** eine Beleuchtungsvorrichtung zur Erzeugung eines langen, schmalen Lichtbandes mit zweidimensionaler Ausprägung bekannt, bei der das Licht einer Anzahl von Lampen in einem engen Gehäuse mit einer ersten jeweils eigenen und einer zweiten gemeinsamen Linse zu einem schmalen Strahl mit Fokus auf einer Linie wählbarer Entfernung erzeugt wird. Die Lichtausbeute entspricht etwa dem Abstrahlwinkel und ist damit sehr gering. In der **DE 197 36 172 B4** wird eine Vorrichtung zur Analyse von in einem strömenden Fluid dispergierten Teilchen beschrieben, die mit Blenden arbeitet, deren Kanten hyperbelartig gekrümmt sind und damit ein dreidimensionales Messvolumen mit einem bekannten

Schärfentiefenbereich definieren, das kegelstumpfartig mit gebogenen Kanten ausgebildet ist. Im zugehörigen Verfahren werden Teilchen mit definierter Laufzeit im Messvolumen ausgewertet. Die Form des optisch abgegrenzten Messvolumens erlaubt es, Teilchen unterschiedlicher Geschwindigkeit bei konstant vorgegebener Laufzeit im Messvolumen zu berücksichtigen, wobei durch die definierte Tiefenschärfe ein dreidimensionales Messvolumen vom Detektor erfasst wird. Es werden bevorzugt Teilchen mit Größen im Bereich von Mikrometern betrachtet. Die Beleuchtungseinrichtung ist parallel zum Detektor angeordnet, das Detektionssignal wird über ein Prisma aus dem Messvolumen umgelenkt.

Die **Veröffentlichung IV** „Particle size distribution analysis by scattered light measurements using optically defined measuring volume" (H. Umhauer, J.Aerosol.Sci. Vol.14, No.6, 1983, pp 765-770), von der die vorliegende Erfindung als nächstliegendem Stand der Technik ausgeht, beschreibt einen Partikelzähler für strömende Fluide nach dem Prinzip der Streulichtmessung an den Partikeln, wobei insbesondere das Randzonenproblem gelöst werden soll, das durch Teilchen entsteht, die nur teilweise am Rand des Messvolumens erfasst und demzufolge durch das reduzierte Streulicht als zu klein gemessen werden. Es sollen Teilchenverteilungen von Feststoffen in Gasen oder Flüssigkeiten, aber auch von Flüssigkeitströpfchen in Gasen und anderen Flüssigkeiten bei sehr kleinen Abmessungen im Mikrometerbereich durch Partikelvereinzelung und deren serielle Erfassung festgestellt werden. Dazu weist der Partikelzähler eine Beleuchtungseinrichtung aus einer punktförmigen Lichtquelle, ein Blenden- und Linsensystem zur optischen Definition eines dreidimensionalen Messvolumens mit würfelförmigen Abmessungen in einem Strömungskanal auf. Dabei liegt der Fokus der Lichtquelle in der Mitte des Messvolumens, Ziel dieser Fokuslage ist die erforderliche Vereinzelung der Partikel zur besseren Streulichtdetektion, was aber insbesondere bei kleinsten Partikeln nicht sicher gewährleistet ist. Die Detektion erfolgt in einer optischen Auswerteeinheit mit weiteren Blenden und Linsen und einem Aufnahmesystem, wobei die Auswerteeinheit in Form eines Photomultikanalverstärkers parallel zur Beleuchtungseinrichtung ausgerichtet ist, sodass sich eine räumlich kompakte Bauform ergibt, und das optische Detektionssignal durch eine 90°-Strahlumlenkung aus dem Messvolumen erfasst wird.

Aufgabenstellung und erfindungsgemäße Lösung

Ausgehend von der nächstliegenden Veröffentlichung ist die **Aufgabe** für die vorliegende Erfindung darin zu sehen, eine Vorrichtung der eingangs erläuterten gattungsgemäßen Art zur Verfügung zu stellen, die in einem strömenden Fluid in Echtzeit alle in einem vorgegebenen Messvolumen auftretenden Partikel zuverlässig und genau detektiert. Dabei soll die Vorrichtung einfach und robust im Aufbau und in der Handhabung auch unter widrigen Umweltbedingungen gestaltet sein und einen flexiblen Einsatz ermöglichen. Die erfindungsgemäße **Lösung** für diese Aufgabe ist dem Hauptanspruch zu entnehmen. Vorteilhafte Weiterbildungen der erfindungsgemäßen Vorrichtung sind in den Unteransprüchen aufgezeigt und werden im Folgenden im Zusammenhang mit der Erfindung näher erläutert.

Die erfindungsgemäße Vorrichtung ist dadurch gekennzeichnet, dass das optisch festgelegte Messvolumen auch in der Tiefe eng begrenzt ist und als dreidimensionale, von einer linearen Lichtquelle tiefenbegrenzten Lichtscheibe ausgebildet ist, deren Dicke durch rechteckige Aperturblenden und plankonvexe oder asphärische Stablinsen festgelegt ist. Diese sind achsenkongruent zu der linearen Reflektorleuchte angeordnet, sodass ihre Längsachsen parallel verlaufen. Die Fokuslinie der Stablinsen liegt vor dem Messvolumen.

Die Fokussierung erfolgt gezielt außerhalb des Messvolumens, wodurch eine gleichmäßige Ausleuchtung des Messvolumens ohne Lichtkonvergenz oder –divergenz erreicht wird. Wenn die Fokuslinie beispielsweise ca. 30 cm vom Objektiv einer Videokamera als Aufnahmesystem eingestellt ist, sollte ein Streifen von ca. 0,5 cm vor und hinter der vom Aufnahmesystem am schärfsten erfassten Ebene der Lichtscheibe ausgeleuchtet sein, sodass die Lichtscheibe insgesamt eine Dicke von ca. 1 cm aufweisen. Scheibendicken zwischen 0,5 cm und 3 cm sind denkbar. die Dickenwahl hängt dabei auch von der Art der zu detektierenden Partikel ab. Die Aufweitung des Strahlengangs nach vorne ist dabei nahezu vernachlässigbar bzw. kann rechnerisch gut erfasst werden. Die Bestimmung des aufgenommenen Messvolumens ist von essenzieller Bedeutung, um eine Konzentrationsangabe auf den gemessenen Wasserkörper bezüglich der Abundanz und Diversität der Plankter im entsprechenden Gebiet zu liefern.

Bei dem Aufnahmesystem der Vorrichtung nach der Erfindung handelt es sich um eine orthogonal zur Lichtscheibe angeordnete Videokamera, der ein Mustererkennungssystem nachgeschaltet sein kann. Die Vorrichtung arbeitet also mit einem bildgebenden Aufnahmesystem und verwendet nicht das Prinzip der Streulichtmessung zur Partikeldetektion. Bei der Verwendung einer Videokamera als Aufnahmesystem können über deren Auflösung nur die zwei Dimensionen der orthogonal zur Videokamera ausgerichteten Fläche des Messvolumens beschrieben werden. Das Bild besitzt bei einer gleichmäßigen Ausleuchtung und entsprechenden Lichtverhältnissen somit eine theoretisch unendliche Tiefendimension. Durch die Vorgabe der Lichtscheibe mit einer definierten Tiefenbegrenzung bei der erfindungsgemäßen Vorrichtung wird nunmehr auch die Tiefendimension genau festgelegt. Die Tiefe des Fokusbereichs für das Aufnahmesystem wird damit durch eine direkte Beleuchtung aufgelöst. Dabei sind nur Partikel im beleuchteten Messvolumen zu sehen. Störungen von außerhalb des Messvolumens sind minimal und können toleriert werden. Dies stellt ein Verfahren in der Unterwassermessung dar, das in dieser Form bislang von keinem optischen Plankton-Recorder verwendet wird.

Somit wird mit der erfindungsgemäßen Vorrichtung ein Gerät zur Verfügung gestellt, das beispielsweise als Video-Plankton-Rekorder (VPR) Video- und Stillbilder von Planktern in natürlicher Umgebung in einem optisch eng begrenzten und genau definierten Messvolumen, beispielsweise von etwa 4 cm³ Größe, in relativ zum Gerät vorbeiströmendem Wasser aufnehmen kann, die dann von der Auswerteeinheit zuverlässig ausgewertet werden können. Es sind aber auch andere Einsatzfälle mit dem Erfordernis einer Partikeldetektion, beispielsweise in Klärbecken oder in chemischen Kolonnen, möglich. Die Einsatzpalette ist sehr breit gefasst. Dabei ist durch die schnelle, hochauflösende Bilderfassung und -speicherung mit Hilfe einer Auswertungssoftware sowohl eine Partikelzählung als auch eine Partikelidentifizierung, beispielsweise zum Erkennen wichtiger Planktonarten möglich. In Kombination mit relevanten Schiffsdaten wie Position, Geschwindigkeit und Zeit sowie weiteren vor Ort gemessenen, insbesondere hydrographischen Umweltparametern kann somit relativ schnell ein dreidimensionales Bild der Planktonverteilung ermittelt werden. Somit entsteht mit der erfindungsgemäßen Vorrichtung ein intelligentes wissenschaftliches System, das weltweit bei Forschungsinstituten, Umweltorganisationen und Umweltbehörden eingesetzt werden kann. Durch den kompakten Aufbau der Vorrichtung als VPR kann dieser sowohl als geschlepptes Gerät bei Schiffseinsätzen, aber auch als verankerbare bzw. fest montierbare Einheit für einen stationären Betrieb eingesetzt werden und von einem definierten Volumen der Wassersäule kontinuierlich Aufnahmen machen. Dabei ist der durch die verwendeten Komponenten bedingte geringe Stromverbrauch günstig, da dadurch ein autarker Einsatz des VPR bei stationärem Betrieb möglich ist. Die in der Was-

sersäule enthaltenen Plankter werden als interessierende Gebiete (Region of Interest, ROI) aus den Gesamtaufnahmen herausgeschnitten, mit den lokalen physikalischen Parametern verbunden und durch das Mustererkennungssystem als Teil der Auswerteeinheit klassifiziert. Entgegen der traditionellen Planktonbeprobung zeichnet sich die erfindungsgemäße Vorrichtung durch einen deutlich niedrigeren Bearbeitungsaufwand der gewonnenen Daten aus und ermöglicht einfach zu gewinnende, hochauflösende und großräumige Zeitserienstudien. Durch die Möglichkeit, Umweltsensoren wie Salinitäts-, Tiefen-, Temperatur-, Fluoreszenz- oder Sauerstoffsonden an die erfindungsgemäße Vorrichtung anzuschließen, werden mit jedem aufgenommenen Bild Umweltparameter verbunden. Dadurch werden auch jedem planktischen Vertreter die physikalischen Parameter seiner direkten Umgebung zugeordnet. Eine Untersuchung der Korrelation des Auftretens mit hydrographischen Phänomenen wie Fronten, Klinen etc., ist dadurch realisierbar. Die erfindungsgemäße Vorrichtung bietet damit die Möglichkeit, Abundanz und Diversität einzelner planktischer Organismengruppen kleinskalig zu ermitteln. Neben der hohen räumlichen Auflösung der Vertikalverteilung auf der Zentimeterskala, lassen sich auch Variabilitäten des Zooplanktons bei entsprechender Probennahmefrequenz auf kleinen Zeitskalen schnell quantifizieren. Die entstehenden Daten sollen dazu beitragen, das Verständnis von biologisch-physikalischen Zusammenhängen zu vervollständigen, neue in-situ-Einblicke in die Ökologie einzelner Organismen geben und einen wichtigen Beitrag zu anderen Zeitserienstudien liefern.

Der VPR kann neue Möglichkeiten in der Planktonforschung eröffnen, die auf diese Weise von keinem anderen Plankton-Recordersystem bereitgestellt werden. Besonderer Wert wird auf die Modularität und Skalierbarkeit gelegt, damit einzelne Komponenten einfach zu modifizieren sind und auch nach dem Bau noch Verfeinerungen zulassen. Allgemein kann der VPR überall dort eingesetzt werden, wo die Bestimmung der Abundanz und Diversität von Planktern von Interesse ist. Dabei besteht keine Beschränkung, ob es sich um Einschätzungen für Nahrungskettenanalysen oder annuell bedingter Aufklärung der Variabilität, der tageszeitlichen Vertikalwanderung, der Besiedlungssukzession oder des Erscheinens von meroplanktischen Larven handelt. In allen Fällen lässt sich das Auftreten mit den physikalischen Parametern festhalten. Eine Erhöhung der Druckstabilität weit jenseits der 100 bar Grenze eröffnet zudem die Möglichkeit neben der neritischen auch weit in die Tiefen der ozeanischen Provinz vorzudringen, die bisher überwiegend durch klassische Methoden beprobt wurde und somit völliges Neuland für VPR-Systeme darstellt. Im Fall des Einsatzes in einer Verankerung lässt sich in nahezu Echtzeit eine kontinuierliche Beprobung durchführen, die ohne weiteren Aufwand möglich ist. Nach der Installation und der Sicherstellung der Energieversorgung, sowie der Datenübertragung ließen sich eine Vielzahl von Fragestellungen mit diesem VPR bearbeiten, ohne dass aufwändige Beprobungen mit Schiffen, Netzen und einer Vielzahl von Personen wetterabhängig durchgeführt werden müssen. Fragestellungen zu meroplanktischen Larven können durch die kleinskalige Planktonbetrachtung im Wasserkörper detaillierter bearbeitet werden.

Da jeweils auf ein sehr geringes Messvolumen fokussiert wird, ist es von entscheidender Bedeutung, eine hohe Anzahl von Videoaufnahmen in einem kurzen Zeitraum zu machen. Bei einem Messvolumen von z.B. 10x10x10 mm werden 1000 Bilder benötigt, bis ein Wasservolumen von einem Liter äquivalent beprobt ist. Bei einer hypothetischen Frequenz von 24 Bildern pro Sekunde vergehen dabei etwa 42 s. Zwischen zwei Bildern muss gewährleistet sein, dass das Messvolumen zu 100% ausgetauscht wird. Ist dies nicht der Fall, besteht die Möglichkeit, dass ein Plankter auf zwei Bildern erscheint und die Statistik verfälscht. Von höherer Bedeutung als im Schelfbereich kann dies im offenen Ozean sein, wo

die durchschnittliche Abundanz einzelner Arten äußerst gering ist. Dementsprechend muss die relative Wegstrecke zwischen zwei Bildern mindestens der Diagonale (Maximalwert bei Anströmung parallel zur Beleuchtung) des aufgenommenen Bildes der Kamera entsprechen. Im genannten Beispiel 14,1 mm. Bei 24 Bildern pro s entsprechend 339,4 mm/s = 0,3394 m/s = 1,222 km/h = 0,65 Kn. Die Geschwindigkeit von 0,65 Knoten lässt sich im Operationsmodus an Bord eines Schiffes relativ sicher bereitstellen. Für ortsfeste Verankerungen (Moorings) muss jedoch darauf geachtet werden, dass diese Anströmgeschwindigkeit auch gewährleistet ist.

Die einzelnen Plankter, die in die Lichtscheibe und gleichzeitig in das Sichtfeld der Videokamera eintreten, werden von einer CCD- Videokamera in einem normalen Aufnahmezyklus erfasst. Um Bewegungsartefakte klein zu halten, benötigt die Videokamera eine sehr kurze Belichtungszeit sowie eine Triggerung mit einem Shutter bei Stroboskopeinsatz. Vor die Videokamera wird mit Hilfe von Extenderringen ein Tele- bzw. Makroobjektiv gesetzt, welches eine Auflösung von etwa 10 µm pro Pixel gewährleistet. Die Qualität der Bilder wird von weiteren Parametern wie Schwebstoffen und ähnlichem beeinflusst. Um die Aussagequalität über den Bezug zur räumlichen Skala hoch zu halten, muss die Videokamera über eine hohe Auflösung (z.B. 2000 x 2000 Pixel entsprechend 20 x 20 mm) verfügen. Ein Plankter von 2 x 1,5 mm würde bei 8 Bit Farbtiefe entsprechend 200 x 150 x 8 ≈ 30 kByte reine Bildinformation unkomprimiert liefern. Die Vergrößerungsstufe soll möglichst konstant sein, um der Auswertung immer die gleichen Parameter zu bieten. Die Genauigkeit der Abundanzberechnungen steigt mit dem beprobten Volumen pro Zeit und damit auch durch eine höhere Auflösung, welche bei gleichem µm/Pixel-Wert das gescannte Volumen pro Bild erhöht.

Ein Auswertungsmodul stellt die ROI-Extraktion und die Verknüpfung mit den Parametern sicher und kann auf einem Rechner in der Unterwassereinheit stattfinden. Die Daten können dann z.B. online via Internet oder LAN an einen weiteren Rechner im Netz oder an Bord gesendet werden, der die Auswertung, möglichst in Echtzeit, vornimmt. Es wird erwartet, dass auf ca. jedem zweiten bis achten Bild Organismen und Partikel auftreten. Augenmerk muss auf die Tatsache gelegt werden, dass einzelne Strukturen nicht immer zusammenhängend erscheinen können (siehe unten). In einzelnen Bereichen kann sich die Anzahl der ROIs pro Aufnahme jedoch stark erhöhen. Die ROIs werden zusammen mit den Metadaten, wie Cruisename, Datum, Zeit, Breitengrad, Längengrad und den physikalischen Parametern, wie CTD Daten und Wasservolumen gespeichert. Für den Fall, dass die Energieversorgung unerwartet unterbrochen wird, muss sichergestellt sein, dass die bisher erhobenen Daten erhalten bleiben. Aus dem gleichen Grund ist in diesem, wie in allen anderen Folgemodulen, eine hohe Systemstabilität zu gewährleisten. Die Bilder müssen unverändert gespeichert werden, damit eine spätere Auswertung von weiteren Faktoren, wie Ausrichtung der Organismen (z.B. von Überwinterungsstadien an Klinen) und ähnlichem möglich ist.

In einer Ausführungsform der erfindungsgemäßen Vorrichtung, im Folgenden kurz VPR genannt, können zwei rechteckige Aperturblenden vorgesehen sein, wobei die zweite rechteckige Aperturblende schmaler ausgebildet ist als die erste rechteckige Aperturblende und die Fokuslinie zwischen beiden rechteckigen Aperturblenden liegt. Die rechteckigen Blenden sorgen zusammen mit den plankonvexen oder asphärischen Stablinsen für die rechteckige Ausprägung der Lichtscheibe. Durch die in Richtung auf das Messvolumen kleiner werdenden rechteckigen Aperturblenden wird eine Erhöhung der Beleuchtungsstärke in Richtung auf das Messvolumen im Sinne einer Aufkonzentrierung erreicht. Eine

im Bereich der Fokuslinie achsenkongruent dazu angeordnete rechteckige Gesichtsfeldblende sorgt für eine sichere Ausblendung von Streulicht im außerhalb des beleuchteten Messvolumens liegenden Teil des Wasserkörpers und damit für eine verbesserte Videodetektion der Partikel. Zur Erreichung einer besonderen Kompaktheit der VPR kann weiterhin das Aufnahmesystem parallel zur Beleuchtungseinrichtung ausgerichtet sein, wobei die Lichtscheibe dann über eine 90°-Strahlumlenkung rechtwinklig umgelenkt wird, um zu gewährleisten, dass die Aufnahmerichtung der Videokamera orthogonal auf der Lichtscheibe steht. Für andere Anwendungen können andere Umlenkwinkel, mehrere Umlenkungen oder auch eine Ausführung ohne Umlenkung in Betracht kommen. Wichtig dabei ist lediglich, dass die Aufnahmeachse senkrecht zur Lichtscheibe ausgerichtet ist.

Zur optimalen Ausleuchtung der Lichtscheibe ist es weiterhin vorteilhaft, wenn die lineare Lichtquelle einen Abstrahlwinkel von unter 70° und eine maximale Lichtleistung aufweist. Dies kann erreicht werden, wenn die lineare Lichtquelle als Reflektorleuchte ausgebildet ist, die einen kombinierten Reflektor aus einem elliptisch ausgedehnten und einem sphärisch ausgedehnten Spiegel mit einer zentralen Apertur und ein in der Brennlinie des Reflektors angeordnetes, lineares Leuchtmittel aufweist. Hierbei kann es sich beispielsweise um eine starke Blitz-/Halogen-/Xenonlampe oder ein High-Efficiency-LED-Feld, insbesondere in der Ausgestaltung als Reihe aus mehreren benachbarten Leuchtdioden handeln. Hierbei kann der Reflektor den einzelnen Leuchtdioden zugeordnete Reflektorbereiche aufweisen. Durch die Verwendung mehrerer in einer Linie stehender Leuchtdioden in der Fokuslinie der ersten plankonvexen oder asphärischen Stablinse wird eine höhere Gesamtlichtausbeute erreicht, weil nicht wie bei sphärischen Linsen aus beiden Raumrichtungen punktförmig auf einen Brennpunkt fokussiert wird, sondern nur aus einer Richtung. Dadurch wird jeder Punkt innerhalb der Lichtscheibe (bis auf die Randbereiche) von mehreren benachbarten Leuchtdioden angestrahlt. Vorteilhaft ist hierbei, dass Partikel, welche in der Lichtscheibe angestrahlt werden, nur einen verminderten Schattenwurf aufweisen und somit die Detektion nicht verfälschen.

Die Lichtstrahlen werden über den optischen Apertur- und Blendenaufbau zusammengefasst, gerichtet, umgelenkt und als Lichtband parallel zur Schlepp- bzw. Fierrichtung ins Wasser projiziert. Die erste Blende bestimmt dabei die Breite der Lichtscheibe. Ein Vorteil dieser Beleuchtungsmethode besteht darin, dass nicht der gesamte Wasserkörper angestrahlt und somit Hintergrundrauschen während der Aufnahme vermindert wird. Über die Einstellung der Blenden (0,5 – 3,0 cm) kann die Breite der Lichtscheibe variiert werden, auf die die Videokamera im rechten Winkel gerichtet ist. Über die Kontrast- und Blendeneinstellungen lassen sich somit Organismen, die vor oder hinter dem beleuchteten Messvolumen liegen, weitestgehend ausblenden. Über den horizontal und vertikal in der Fläche erfassten Ausschnitt der Videokamera und der Dicke der Lichtscheibe als Tiefenbegrenzung kann das dabei aufgenommene Wasservolumen bestimmt werden.

Eine andere Modifikation des VPR sieht vor, dass zumindest die Lichtquelle und die Videokamera in einem druckfesten und strömungsgünstig geformten Gehäuse angeordnet sind. Weiterhin können auch die rechteckigen Aperturblenden, die rechteckige Gesichtsfeldblende und die plankonvexen oder asphärischen Stablinsen in dem Gehäuse angeordnet sein, wobei dieses auf seiner Innenseite eine Verspiegelung aufweist. Eine angestrebte flache Bauform des VPR ermöglicht es dabei, das Gehäuse möglichst strömungsgünstig gestalten zu können. Bei dem VPR handelt es sich daher um ein Gerät, welches durch seine Gestaltung einen geringen Staudruck aufbaut. Dadurch wird verhindert, dass kleine Plankter um den Probennahmeort herumgeschwemmt werden und der Auswertung entgehen.

Auf der anderen Seite wird die Anzahl wenig abundanter Arten durch die Methode der Probennahme teilweise unterschätzt oder sie werden gar nicht erfasst. Um diesem vorzubeugen, muss eine hohe Beprobungsrate erreicht werden wie auch eine exakte Bestimmung des Messvolumens. Es muss im Moment der Aufnahme so ungestört wie möglich vorliegen. Der VPR muss in Schlepp- oder Fierrichtung so ausgerichtet werden, dass Verwirbelungen und Staudruck so niedrig wie möglich gehalten werden. Schließlich müssen die einzelnen Umweltsonden in der Nähe des Fokusbereichs der Videokamera liegen, bzw. auf der gleichen horizontalen Ebene. Durch die Verspiegelung auf der Gehäuseinnenseite kann auch Licht außerhalb der zentralen Achse durch Mehrfachreflexion eingefangen und auf das Messvolumen gerichtet werden, sodass sich eine Intensitätserhöhung des Lichts ergibt. Schließlich können in einer weiteren Modifikation die lineare Reflektorleuchte, die rechteckigen Aperturblenden, die rechteckige Gesichtsfeldblende und die plankonvexen oder asphärischen Stablinsen über die vier Seitenkanten eines Quaders bildende Gewindestangen miteinander verbunden und zueinander einstellbar angeordnet sein. Dadurch ergibt sich eine kompakte Bauform mit einer guten Stabilisierung durch die Gewindestangen, die gleichzeitig der parallelen Verstellung und Fixierung der einzelnen Blenden und Stablinsen dienen. Weitere konstruktive Einzelheiten der Vorrichtung nach der Erfindung sind dem nachfolgenden speziellen Beschreibungsteil zu entnehmen.

Ausführungsbeispiele

Ausführungsformen der Vorrichtung nach der Erfindung werden nachfolgend zu deren weiterem Verständnis anhand der schematischen Figuren näher erläutert. Dabei zeigt

Figur 1	eine Ausführungsform als VPR in der Seitenansicht im Längsschnitt,
Figur 2	eine Ausführungsform als VPR in der Aufsicht mit einer Verspiegelung,
Figur 3	eine Ausführungsform als VPR in der perspektivischen Seitenansicht ohne Gehäuse und
Figur 4	die Beleuchtungseinrichtung mit einer linearen Reflektorleuchte in der Draufsicht.

In **Figur 1** ist die Vorrichtung in der Ausführungsform eines Video-Plankton-Rekorders **VPR** dargestellt, bei dem eine Beleuchtungseinrichtung **BE** und eine Auswerteeinheit **AW** in einem druckfesten Gehäuse **DG** mit zwei druckdicht in die Gehäusewandung eingepassten Fenstern **FE1, FE2** angeordnet sind. Ein solcher Video-Plankton Rekorder kann auch englisch als „Light frame On-sight Key species Investigation" mit dem Akronym „LOKI" treffend bezeichnet werden. Die optische Beleuchtungseinrichtung **BE** hinter dem Fenster **FE1** umfasst eine lineare Lichtquelle **LQ** und zwei plankonvexe oder asphärische Stablinsen **SL1, SL2** eines fokussierenden Linsensystems **LN**. Zu der Auswerteeinheit **AW** hinter dem Fenster **FE2** gehört eine Videokamera **VK** als Aufnahmesystem **AS** und weitere Blenden und Linsen sowie Mittel zur Datenverarbeitung, beispielsweise ein Mustererkennungssystem, und –speicherung, die aber in **Figur 1** nicht weiter dargestellt sind. Bei den eingesetzten Stablinsen **SL1, SL2** handelt es sich um kommerziell erhältliche Komponenten. Die Brennweiten sind dabei mit 8 cm und 6 cm im Ausführungsbeispiel hoch gewählt, um flache Winkel gegenüber der optischen Achse des Video-Plankton-Rekorders **VPR** zu gewährleisten, was Abbildungsfehler reduziert. Geeignet sind Stablinsen aus Glas mit höherem Brechungsindex (Glassorte SF6). Die Option, die Stablinse **SL1** mit mehr als 3 cm Höhe zu verwenden, scheidet aus, da gleichzeitig die Fokuslinie **FL** weiter von der Stab-

linse **SL1** wegrückt, weil diese mit einer benötigten höheren Rundung der konvexen Seite physikalischen Begrenzungen gemäß der Formel: Zylinderradius = Brennweite x (Brechungsindex – 1) unterliegt. Zudem würde dadurch der Winkel zwischen der Senkrechten auf der planen Linsenseite und der Abweichung des Lichtstrahls **LT** von der optischen Achse im Randbereich zu groß, wodurch ebenfalls die Lichtintensität verringert werden würde.

Der Video-Plankton-Rekorder **VPR** erzeugt zur Partikeldetektion in einem strömenden Fluid ein optisch begrenztes Messvolumen **MV**, das als dünne, tiefenbegrenzte Lichtscheibe **LS** ausgebildet ist. Das Messvolumen **MV** wird vom Wasser frei durchströmt, die Strömungsrichtung verläuft senkrecht zur Zeichenebene, sodass sich das Messvolumen **MV** kontinuierlich füllt und entleert und immer neue Wasservolumina detektiert werden können. Das druckfeste Gehäuse **DG** kann in Strömungsrichtung strömungsgünstig geformt vorgesehen sein, sodass bei der Anströmung durch das Wasser keine die Detektionsergebnisse störenden Wirbel entstehen. Die Lichtscheibe **LS** wird von der Lichtquelle **LQ** erzeugt, deren Lichtstrahl **LT** mittels der ersten plankonvexen oder asphärischen Stablinse **SL1** parallelisiert und mittels der zweiten plankonvexen oder asphärischen Stablinse **SL2** auf eine Fokuslinie **FL** fokussiert wird. Dabei liegt die aufgrund der verwendeten linearen Lichtquelle **LQ** linear ausgeprägte Fokuslinie **FL** außerhalb des druckfesten Gehäuses **DG** und vor der Lichtscheibe **LS**. Die Breite **B1** des Lichtstrahls **LT** wird durch eine erste rechteckige Aperturblende **AB1** im druckfesten Gehäuse **DG** eingestellt, die zwischen den beiden Stablinsen **SL1**, **SL2** angeordnet ist. Hinter der Fokuslinie **FL** wird der fokussierte Lichtstrahl **LT** durch eine dritte plankonvexe oder asphärische Stablinse **SL3** außerhalb des druckfesten Gehäuses **DG** wieder parallelisiert. Gleichzeitig erfolgt durch eine zweite rechteckige Aperturblende **AB2** hinter der Fokuslinie **FL** außerhalb des druckfesten Gehäuses **DG**, die schmaler ist als die erste rechteckige Aperturblende **AB1**, eine Intensitätskonzentrierung des Lichtstrahls **LT** durch eine Verschmälerung des Lichtstrahls **LT** auf eine Breite **B2**, durch die dann die Dicke **d** der Lichtscheibe **LS** als Tiefenbegrenzung des Messvolumens **MV** festgelegt ist. Im Bereich der Fokuslinie **FL** ist achsenkongruent eine rechteckige Gesichtsfeldblende **GB** zur Verminderung von Streulicht angeordnet. Hinter der zweiten rechteckigen Aperturblende **AB2** ist ein Umlenkspiegel **US** angeordnet, der den aufkonzentrierten Lichtstrahl um rechtwinklig umlenkt. Damit gelangt der Lichtstrahl in den Aufnahmelichtstrahl **AF** der Videokamera **VK**, der durch eine weitere Blende **WB** begrenzt wird und senkrecht auf dem Lichtstrahl **LT** steht, sodass die Breite **B2** des Lichtstrahls **LT** nunmehr der Dicke d der Lichtscheibe **LS** entspricht. Alle genannten Komponenten sind auf Gewindestangen **GS** verschiebbar angeordnet. dadurch können sie in ihrem Abstand zueinander eingestellt und anschließend fixiert werden. Die beschriebene Anordnung und Ausstattung des dargestellten Video-Plankton-Rekorder **VPR** mit Linsen und Blenden ist nur beispielhaft und kann erforderlichenfalls auch anders aussehen.

Die **Figur 2** zeigt in der Draufsicht einen Video-Plankton-Rekorder **VPR**, bei dem alle Komponenten in einem druckfesten Gehäuse **DG** angeordnet sind (hier nicht erläuterte Bezugszeichen siehe **Figur 1**). Zur Erhöhung der Lichtausbeute ist in dieser Ausführungsvariante auf der Innenseite des druckfesten Gehäuses **DG** eine Verspiegelung **VS** vorgesehen. Eingezeichnet ist ein exemplarischer Strahlengang entlang der optischen Achse des Systems.

In der **Figur 3** ist eine perspektivische Seitenansicht des Video-Plankton-Rekorders **VPR** ohne druckfestes Gehäuse **DG** dargestellt. Die lineare Lichtquelle **LQ** besteht aus einer Reihe von einzelnen Leuchtdioden **LED**, die von einem gemeinsamen rechteckigen Re-

flektor **RF** umgeben sind. Leuchtdioden **LED** sind kommerziell am Markt einfach erhältlich – auch mit einem Abstrahlwinkel von 70° oder weniger – leuchtstark und langlebig (3 W - 5 W, 100.000 Betriebsstunden). Dabei weist der Reflektor **RF** den einzelnen Leuchtdioden **LED** zugeordnete Reflektorbereiche **RB** auf. Diese Reflektorbereiche **RB** können eine Ausprägung aufweisen, wie sie in **Figur 4** näher erläutert wird. An den vier Ecken des Reflektors **RF** ist jeweils eine Gewindestange **GS** vorgesehen. Zwischen den vier Gewindestangen **GS** werden die optischen Komponenten des Video-Plankton-Rekorders **VPR** gelagert und fixiert (hier nicht erläuterte Bezugszeichen siehe **Figur 1**). Dabei sind die Tragrahmen **TR** für die Komponenten mit einer Ausnahme alle gleich ausgeführt. Die Ausnahme bildet der Tragrahmen **TR** für den Umlenkspiegel **US**, dem ein Längsrahmenabschnitt fehlt. Der vorhandene Längsrahmenabschnitt **LA** weist eine 45°-Schräge auf, in die der Umlenkspiegel **US**, der größer als der Tragrahmen **TR** ist, einlegbar ist.

In der **Figur 4** ist eine lineare Lichtquelle **LQ** als lineare Reflektorleuchte **RL** mit einem kombinierten Reflektor **KR** mit zentraler Apertur **ZA** dargestellt. Der kombinierten Reflektor **KR** weist einen elliptischen Spiegel **SE** in Form eines ausgedehnten Rotationsellipsoids **RE** und einen sphärischen Spiegel **SS** in Form einer ausgedehnten Kugelschale **KS** auf. Die lineare Lichtquelle **LQ** ist in der ersten Brennlinie **BL1** des elliptischen Spiegels **SE** angeordnet. Der sphärische Spiegel **SS** ist mit seiner Mittellinie ebenfalls in der ersten Brennlinie **BL1** des elliptischen Spiegels **SE** angeordnet, seine zentrale Apertur **ZA** befindet sich genau in der zweiten Brennlinie **BL2** des elliptischen Spiegels **SE**. Die Lichtausbeute derartiger kombinierter Reflektoren **KR** ist besonders hoch, da alle Lichtstrahlen, die nicht direkt durch die zentrale Apertur **ZA** austreten, von dem sphärischen Spiegel **S2** auf den elliptischen Spiegel **SE** zurückgeworfen und von da aus zur zentralen Apertur **ZA** reflektiert werden. Lediglich in den Randbereichen eines linear ausgedehnten kombinierten Reflektors **KR** treten Verluste auf.

Bezugszeichenliste

AB	rechteckige Aperturblende
AF	Aufnahmelichtstrahl
AS	Aufnahmesystem
AW	Auswerteeinheit
B	Breite des Lichtstrahls
BE	Beleuchtungseinrichtung
BL	Brennlinie
d	Dicke der Lichtscheibe
DG	druckfestes Gehäuse
FE	Fenster
FL	Fokuslinie
GB	rechteckige Gesichtsfeldblende
GS	Gewindestange
KR	kombinierter Reflektor
KS	Kugelschale
LA	Längsrahmenabschnitt
LED	Leuchtdiode
LN	Linsensystem
LQ	lineare Lichtquelle
LS	Lichtscheibe
LT	Lichtstrahl
MV	optisch begrenztes Messvolumen
RB	Reflektorbereich
RE	Rotationsellipsoid
RF	rechteckiger Reflektor
RL	Reflektorleuchte
SE	elliptischer Spiegel
SL	plankonvexe oder asphärische Stablinse
SS	sphärischer Spiegel
TR	Tragrahmen
US	Umlenkspiegel
VK	Videokamera
VPR	Video-Plankton-Rekorder
VS	Verspiegelung
WB	weitere Blende
ZA	zentrale Apertur

Patentansprüche

1. Vorrichtung zur Partikeldetektion in einem strömenden Fluid in einem optisch begrenzten Messvolumen mit einer Beleuchtungseinrichtung aus einer Lichtquelle, einem Blendensystem und einem fokussierenden Linsensystem sowie mit einer optischen Auswerteinheit mit weiteren Blenden und Linsen und einem auf das Messvolumen ausgerichteten Aufnahmesystem,
dadurch gekennzeichnet, dass
das optisch begrenzte Messvolumen (MV) als dreidimensionale, von einer linearen Lichtquelle (LQ) tiefenbegrenzten Lichtscheibe (LS) ausgebildet ist, deren Dicke (d) durch rechteckige Aperturblenden (AB1, AB2) im Blendensystem und plankonvexe oder asphärische Stablinsen (SL1, SL2, SL3) im fokussierenden Linsensystem (LN) festgelegt ist, wobei die rechteckigen Aperturblenden (AB1, AB2) und Stablinsen (SL1, SL2, SL3) achsenkongruent zu der linearen Lichtquelle (LQ) angeordnet sind und die Fokuslinie (FL) der Stablinsen (SL1, SL2, SL3) vor dem Messvolumen (MV) liegt, und dass das Aufnahmesystem (AS) eine orthogonal zur Lichtscheibe (LS) angeordnete Videokamera (VK) ist.

2. Vorrichtung nach Anspruch 1,
dadurch gekennzeichnet, dass
das Aufnahmesystem (AS) ein Mustererkennungssystem aufweist.

3. Vorrichtung nach Anspruch 1 oder 2,
dadurch gekennzeichnet, dass
zwei rechteckige Aperturblenden (AB1, AB2) vorgesehen sind, wobei die zweite rechteckige Aperturblende (AB2) schmaler ausgebildet ist als die erste rechteckige Aperturblende (AB1) und die Fokuslinie (FL) zwischen beiden rechteckigen Aperturblenden (AB1, AB2) liegt.

4. Vorrichtung nach einem der Ansprüche 1 bis 3,
dadurch gekennzeichnet, dass
im Bereich der Fokuslinie (FL) achsenkongruent dazu eine rechteckige Gesichtsfeldblende (GB) angeordnet ist.

5. Vorrichtung nach einem der Ansprüche 1 bis 4,
dadurch gekennzeichnet, dass
das Aufnahmesystem (AS) parallel zur Beleuchtungseinrichtung (BE) ausgerichtet und die Lichtscheibe (LS) über eine 90°-Strahlumlenkung (US) rechtwinklig umgelenkt ist.

6. Vorrichtung nach einem der Ansprüche 1 bis 5,
dadurch gekennzeichnet, dass
die lineare Lichtquelle (LQ) einen Abstrahlwinkel von unter 70° und eine maximale Lichtleistung aufweist.

7. Vorrichtung nach Anspruch 6,
dadurch gekennzeichnet, dass
die lineare Lichtquelle (LQ) als Reflektorleuchte (RL) ausgebildet ist, die einen kombinierten Reflektor (KR) aus einem elliptischen Spiegel (SE) und einem sphärischen Spiegel (SS) mit einer zentralen Apertur (ZA), wobei die lineare Lichtquelle (LQ) in der Brennlinie (BL1) des elliptischen Spiegels (SE) angeordnet ist.

8. Vorrichtung nach Anspruch 7,
dadurch gekennzeichnet, dass
die lineare Lichtquelle (LQ) als Reihe aus mehreren benachbarten Leuchtdioden (LED) ausgebildet ist und der kombinierte Reflektor (KR) den einzelnen Leuchtdioden (LED) zugeordnete Reflektorbereiche (RB) aufweist.

9. Vorrichtung nach einem der Ansprüche 1 bis 8,
dadurch gekennzeichnet, dass
zumindest die lineare Lichtquelle (LQ) und die Videokamera (VK) in einem druckfesten und strömungsgünstig geformten Gehäuse (DG) angeordnet sind.

10. Vorrichtung nach einem der Ansprüche 1 bis 9,
dadurch gekennzeichnet, dass
auch die rechteckigen Aperturblenden (AB1, AB2), die rechteckige Gesichtsfeldblende (GB) und die plankonvexen Stablinsen (SL1, SL2, SL3) in dem druckfesten Gehäuse (DG) angeordnet sind, wobei dieses auf seiner Innenseite eine Verspiegelung (VS) aufweist.

11. Vorrichtung nach einem der Ansprüche 1 bis 10,
dadurch gekennzeichnet, dass
die lineare Lichtquelle (LQ), die rechteckigen Aperturblenden (AB1, AB2), die rechteckige Gesichtsfeldblende (GB) und die plankonvexen Stablinsen (SL1, SL2, SL3) über die vier Seitenkanten eines Quaders bildende Gewindestangen (GS) miteinander verbunden und zueinander einstellbar angeordnet sind.

Zusammenfassung

Vorrichtung zur Partikeldetektion in einer tiefenbegrenzten Lichtscheibe

Bekannte Vorrichtungen zur Detektion von Partikeln in einem optisch begrenzten Messvolumen arbeiten entweder nach dem Streulichtprinzip oder verwenden ein bildgebende Videokamera, die jedoch nur die zweidimensionale Fläche auflöst. Die Tiefendimension des Messvolumens bleibt unberücksichtigt. Bei der erfindungsgemäßen Vorrichtung, die bevorzugt bewegt oder stationär als Video-Plankton-Rekorder zur Zählung und Identifikation von Plankton in marinen Gewässern ausgebildet sein kann, ist daher das optisch begrenzte Messvolumen (MV) als dreidimensionale, von einer linearen Lichtquelle (LQ) tiefenbegrenzten Lichtscheibe (LS) ausgebildet, deren Dicke (d) durch rechteckige Aperturblenden (AB1, AB2) im Blendensystem und plankonvexe oder asphärische Stablinsen (SL1, SL2, SL3) im fokussierenden Linsensystem (LN) festgelegt ist, wobei die rechteckigen Aperturblenden (AB1, AB2) und Stablinsen (SL1, SL2, SL3) achsenkongruent zu der linearen Lichtquelle (LQ) angeordnet sind und die Fokuslinie (FL) der Stablinsen (SL1, SL2, SL3) vor dem Messvolumen (MV) liegt. Eine Videokamera (VK) als Aufnahmesystem (AS) ist orthogonal zur Lichtscheibe (LS) angeordnet. Die Tiefe des Fokusbereichs der Videokamera (VK) wird damit durch eine direkte Beleuchtung aufgelöst. Dabei sind die beleuchteten Partikel nur im beleuchteten Messvolumen zu sehen.

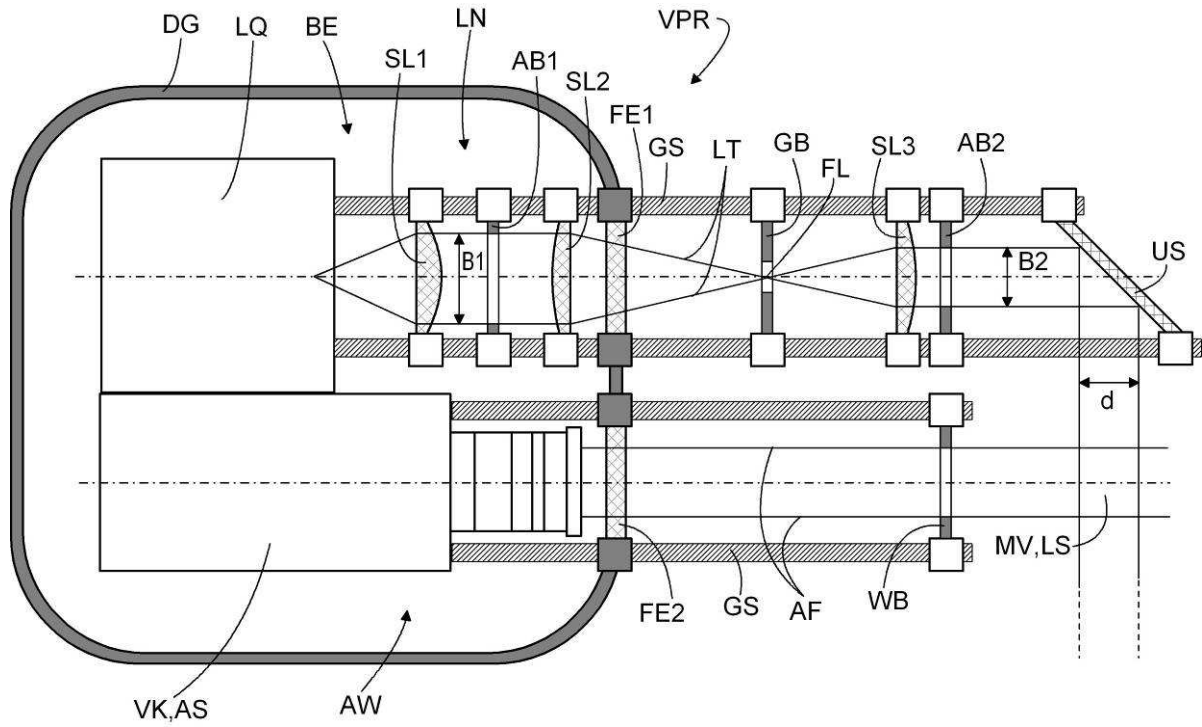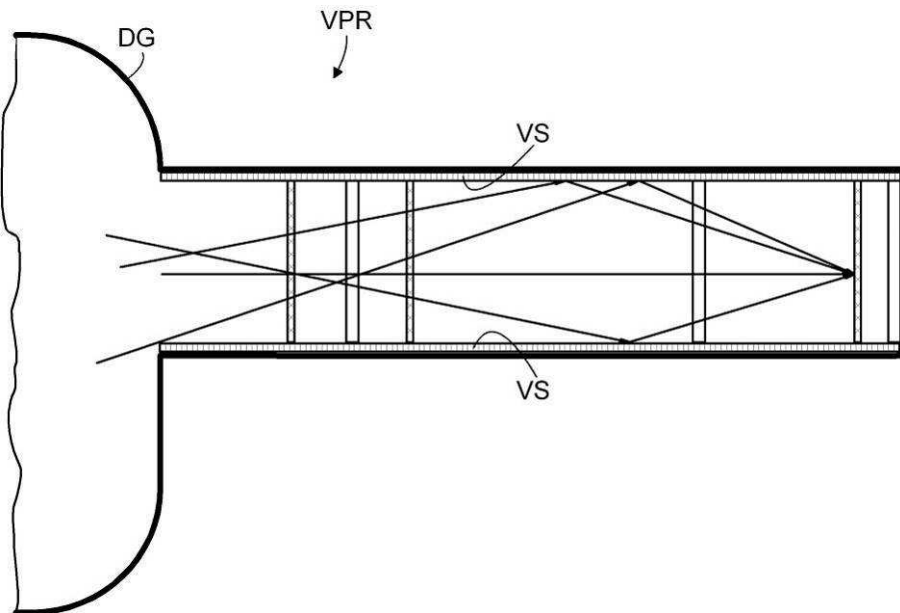Signifikante Figur für die Zusammenfassung : **Figur 1**

Fig. 1

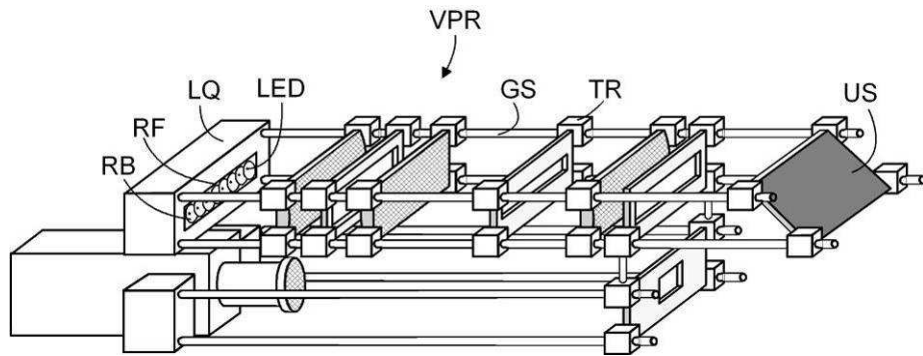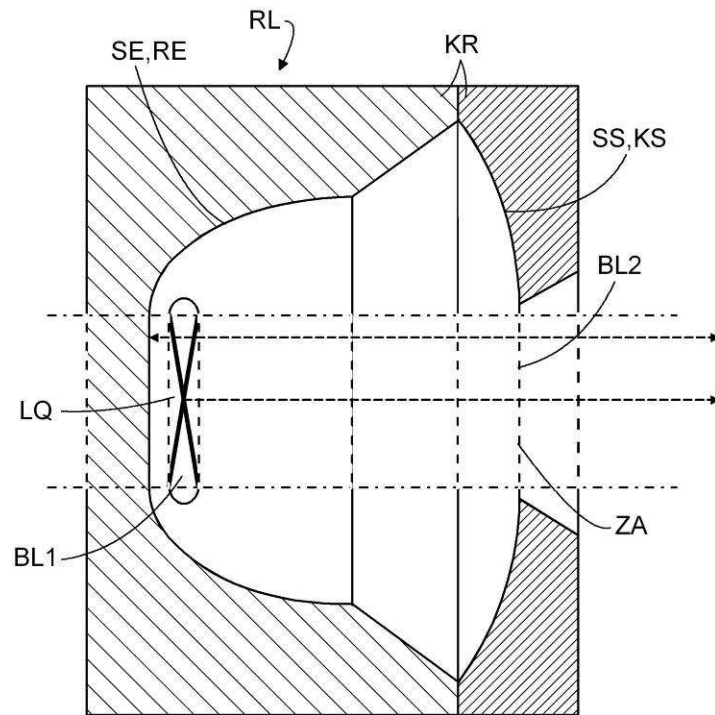
Fig. 2

Fig. 3

Fig. 4

T2: Imaging defined volumes - LOKI – Light frame On-sight Key species Investigation

Authors: Jan Schulz, Dirk Mengedoht, Hans-Jürgen Hirche
Status: Submitted to IEEE Journal of Oceanic Engineering

This paper shows the method to image particles and species in a defined water volume based on the invention described in the first patent application. It summarises the technical specification of the light frame and demonstrates an example. The manuscript was written by the first author and improved by the co-authors.

Imaging defined volumes
LOKI – Light frame On-sight Key species Investigation

Technical communication

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Abstract

In-situ imaging of plankton taxa is a helpful tool to identify species, ambient physical parameters and interrelationships among them. These data contribute to the understanding of small-scale effects in addition to integrating net samples. The available light is a limiting factor in imaging species of less than 2 mm in size at high magnifications and short shutter times in moving water masses. Here we demonstrate a concept for *in-situ* dark-field imaging on small scales in optically defined volumes. The method is introduced as 'Light frame On-sight Key species Investigation' (LOKI). Using a combination of cylindrical lenses and a linear light source a beam of high light flux is projected into the water. The beam is precisely constrained in one dimension and creates a light frame along the principal axis of the system. Particles within this frame scatter light by surface or internal refraction and are recorded by a camera that is positioned orthogonally to this beam. With a telecentric objective, the sampled volume is quantified by calculating the width and height of the image and the extension of the constrained light frame. It allows the assessment of detailed information on the structure of an imaged object. Otherwise interfering objects outside of the light frame are nearly invisible. This illumination technique allows sensitive cameras to be operated at shutter speeds below 1 ms and to image objects on scales down to 20 µm per pixel in a quality sufficient for taxonomic identification.

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Introduction

Zooplankton species < 2 mm are an important energy resource in the trophodynamic linkage of primary and tertiary levels of production within both limnic and marine ecosystems. The allocation of zooplanktonic organisms often displays distinct vertical distributions depending on hydrographic features [1]. This distribution impacts the availability of food for predators, thus influencing a crucial variety of recruitment processes. These heterogeneous composition patterns can be assessed with plankton nets and linked to environmental parameters like salinity, temperature or dissolved oxygen on scales of several meters. As zooplankton consuming predators often show depth preferences a fine-scale investigation of potentially available prey fields is limited by the method-borne integration of net catches. This option is further depressed by unequal catch-efficiency for several species by different net types [2, 3]. While fine meshes cause retention by impact pressure, wider mesh sizes do not catch smaller but important specimens. Gelatinous zooplankton and other fragile taxa are often completely destroyed on contact with any type of gauze. Subsequently the need for new methods has been discussed for decades [1, 4, 5, 6, 7].

At the present time, digital techniques allow imaging of species *in-situ* while the ambient environmental parameters can be recorded simultaneously by using a variety of different sensors. To ensure taxonomic identification the submersible optical systems are faced with a range of conceptual formulations. Using a high magnification at short distances results in a small depth of field and a high percentage of out-of-focus objects [8]. High shutter speeds are necessary to avoid motion blurring. Moreover, object blurring can also be depending on the distance from camera to object, as well as water clarity [9]. To quantify abundances requires the determination of the imaged volume per frame, for which various approaches have been developed.

Through-flow chambers constrain the volume physically to the cameras depth of field and provide easily manageable and reproducible illumination [10]. However, fine-scale patterns and fragile species are affected by the concentrating process for the chamber. The volumes of imaged spaces within a defined distance of the device are often determined by software and adjusted to the depth of field by the sharpness of the imaged particles [11]. These techniques include a variety of uncertainties, as well as stray light causes a high background noise. Images of individuals < 2 mm are often smeared and provide little taxonomic information for taxonomic determination. The use of highly collimated light beams over short distances reduces scatter and supports more precise quantification of the imaged volume. High quality shadow images can be captured using line scan cameras that image a line light across a flow-through channel [12]. Based on measured flow values the line data are assembled by software to a detailed 2D shadow image object. To display surface and internal features of small organisms dark field illumination is required. This is even sufficient to capture transparent objects [5]. Several systems [13, 14, 15] profile plankton and marine snow in sampling volumes between 500 and 6500 ml by using a camera that aims at 90° relative to a light frame. With decreasing volumes and higher magnifications the required light flux for dark field illumination increases to adequately depict small-scale features. Here, we demonstrate a method to create a light-frame of high intensity with an extension that can be adjusted to the depth of field of the light-sensing device.

Approach and results

An illumination device consisting of a combination of a linear light source and cylindrical lenses is used to take images of high magnification in the depth of field along a cameras

principal axis. For the desired application, the beam extension needs to have a boxlike shape which is accomplished by the cylindrical lenses. Using spherical lenses would focus rays rotationally into one, symmetrical focal point. Consequently this would result in conical light beams where potentially useable light rays would have to be gated out to create a constrained boxlike beam. In contrast to spherical lenses, cylindrical lenses have focal lines and refract rays differently in the horizontal and vertical plane (Figure 1a and 1b).

In the vertical plane the lens L_1 works as a collimator and the light source is set up in its focal line (Figure 1b). It can be seen that the opening angle (α in Figure 1b) between the light source and L_1 specifies the utilised light and can not be expanded beyond a certain point. The maximum width and focal distance of a cylindrical lens is determined by the refractive index (n_G) and the radius (r_G) of the glass cylinder from which it is cut (Figure 2):

$$r_G = f_L (n_G - 1)$$

Consequently, the diameter of the glass cylinder specifies the maximum width (b_L) of a cylindrical lens and the refractive index limits the maximum acceptance angle for light rays. The width of the first two lenses needs to be dimensioned to the flare angle of the light source, while light sources with small flare angles are most efficient. The collimated light behind L_1 is then focussed by L_2. The distance between L_1 and L_2 is of minor importance and can be kept small for a packed construction. An aperture diaphragm D_1 adjusts the height of the beam and gates out aberration effects at the rim of the lenses. Behind L_2 the rays converge and an image of the light source is projected in the distance of the focal length of L_2 where a correcting diaphragm is placed. Lens L_3 is put at a distance of its focal length and re-parallelises the diverging rays. By using a lens with a shorter focal distance than L_2, the height of the light beam is smaller and the flux is increased. This increase is approximately given by the ratio h_1:h_2 (Figure 1b), while the focal length ratio L_2:L_3 determines the vertical dimension h_2. A third diaphragm (D_3) is used to sharpen the light frame before it is targeted by a mirror (M_1) into the water. The axis of the focal point of the camera is orthogonal to this frame (Figure 1c). Using telecentric objectives the sampled volume can be calculated by width and height of the image and the depth of the light frame.

In the horizontal plane, rays are not refracted into the focal lines of the cylindrical lenses. Horizontal rays (Figure 1a) with high deviation from the principal axis are re-injected into the optical path by the mirrored walls (M_2 and M_3). Consequently even light emitted from beyond the extension of L_1 contributes to the total output. Reflected rays irradiate in oblique angles into the imaging area and reduce shading behind illuminated particles. Unaligned rays are gated out by the diaphragms to avoid soft transitions at the borders of the light frame. An array of high efficiency Light Emitting Diodes (LEDs) provides an energy efficient linear light source of dense packaging. LEDs provide a small and nearly punctual light source that fit the requirements of the cylindrical lenses in the vertical plane.

Through an exit window W_e the light frame is projected into the medium. The camera aims onto this plane at an angle of 90° and the focal point is adjusted to range within the frame (Figure 1c). The water current moves in the direction of the camera. Particles in the water enter the light frame for a short moment long enough to be detected prior to being flushed out of sight and around the camera housing. In the transition zone between in- and outside of the illuminated frame (Figure 3a) a relative difference of light intensity of more than one order of magnitude is obtained (Figure 3b). This is sufficient to only capture objects within the light frame and to blank out unwanted objects positioned outside of the light frame. With a vertical extension of the light frame of less than 1 cm, small volumes can be imaged

in high detail (Figure 4a). Characteristics down to at least 20 µm can be discriminated well *in-situ* (Figure 4b-d). The detection limit of taxonomic important properties on scales below 1 mm depends on the pre-selected f-value and the sensitivity of the camera system.

Discussion

The presented method allows correct imaging and identification of particles of at least 1 mm in size at high magnification and resolution in moving water masses. The alignment of the light frame reduces scatter and increases the signal-to-noise ratio. Only objects that are in focus are imaged. Objects outside the light frame are almost invisible but can contribute to the background noise [9, 16]. Funnelling the water at a 90° angle towards the camera decreases horizontal and vertical movement of the photographed objects and further reduces motion blurring.

An intrinsic problem of the system is the way the light is used. The application would work best with punctiformous line lights. However, these are hypothetical and each time the beam is parallelised (L_1 and L_3) aberration and loss occurs. This requires small light sources of high power and small flare angles. With adjusted reflectors, even high voltage discharge lamps, which provide output energies of up to 1 Joule, can be used next to LEDs [17]. With respect to the transmissivity of the optical components, LEDs with different spectra can be combined to emit specific spectral components into the observation volume, e.g. for fluorescent excitation. When operated in flash mode LEDs can emit a maximum output within few microseconds. This shortens shutter times, reduces blurring and helps to suppress phototaxis depending on flash frequency. If flash duration is shorter than 1 ms the maximally allowed forward current of most LED types can be increased up to tenfold before further gain is negligible (Schulz, unpublished observations). However, this reduces the life span of the LEDs to a few weeks under continuous operation. The use of expanded lasers might also be interesting for various other investigations. However, the sensitivity of the sensing device is often not sufficient for the use of monochromatic light in plankton sensing. Several planktonic species camouflage themselves by transparency, thus they do not scatter light equally in all parts of the spectrum [18, 19]. A broad light spectrum with more than one spectral component yields more detailed images.

Although the desired dimensions of a light frame can easily be created, the image quality is mostly determined by sensitivity of the camera. Light that induces a signal on the photosensitive sensor of a camera derives from reflection and refraction within an object or at its surface. Most of the light passes the imaged volume without hitting an object and is consequently not used in dark field applications. At low magnifications a high number of photons from one object illuminate a single pixel on the photosensor. At higher magnification the light is distributed over more pixels, therefore small features are subjected to aliasing effects by contiguous pixels [15]. With constant illumination a signal decreases approximately by factor four when magnification is doubled. Consequently, a high light flux and degree of utilisation improves the capability of the system to image small objects when irradiated from one side only. When light is not a limiting factor high f-numbers and short shutter times improve the signal-to-noise ratio. It also reduces scatter, enlarges the depth of field and facilitates software based detection of particles passing the light frame. Using shorter distances between light source and sampling volume, as well as between the sampling volume and camera always improves image quality [9].

Although high sampling frequencies can be used, rare taxa will continue to have a higher probability of being undetected due to the small volume scanned per frame [20] and a statistically lower estimation of their abundance may be obtained. However, the main dynam-

ics of plankton biomass are often driven by the spatio-temporal variability of few, but abundant taxa, which hence are important for trophodynamic investigations. The strength of the system described here is the ability to identify the small-scale distributions, e.g. in distinct strata, which are often characterised by specific community compositions [21]. The resolution of this method is suitable to detect these key species in a sufficient quantity and may act as an additional technique to investigate their fine-scale distribution. Due to this we call this method 'Light frame On-sight Key species Investigation' (LOKI). Alternatively it is possible to combine the device with a photomultiplier instead of a camera and to evaluate relative signal strength for qualitative detection tasks.

Acknowledgement

References

[1] K. Banse "On the vertical distribution of zooplankton in the sea" Prog. Ocean. 2, 53-125, 1964

[2] J.B. Colton, J.R. Green, R.R. Byron, Frisella "Bongo net retention rates as effected by towing speed and mesh size" Can. J. Fish. Aquat. Sci 37, 606-623, 1980

[3] J.H. Nichols, A.B. Thompson "Mesh selection of copepodite and nauplius stages of four calanoid copepod species", J. Plank. Res. 13(3), 661-671, 1991

[4] E. Bergeron, A.D. Bowen, W.J. Hersey, W. Lange, J.R. Strickler "Reaching the ultimate goal: Observing live zooplankton in situ", EOS 69(44), 1087, 1988

[5] U. Kils "On the micro-structure of micro layers, Results of an in-situ zooplankton-counter", ICES C.M. 1989/L:15, 1989

[6] X. Tang, W.K. Stewart, L. Vincent, H. Huang, M. Marra, S.M. Gallager, C.S. Davis "Automatic plankton image recognition", Art. Intell. Rev. 12, 177-199, 1998

[7] P. Tiselius "An in situ video camera for plankton studies: design and preliminary observations", Mar. Ecol. Prog. Ser. 164, 293-299, 1998

[8] J.R. Strickler "Observation of swimming performances of planktonic copepods", Limn. Oceano. 22, 165-170, 1977

[9] J. Pollio, R. Meyer, L.D. Sivak "Model analysis of underwater photographic and visibility systems from observed data", In: Proc. Soc. of Photo-Optical Instr. Engin. Volume 208: Ocean Optics 6, Publ. by: Soc. Photo-Optical Instrumentation Engineers; Bellingham, WA (USA), 1979, p. 232-241, Proc. Soc. Photo-Optical Instrum. Eng.

[10] K. Wieland, B. Hermann, J. Kreikemeier, J. Lenz, S. Mees, D. Schnack "Preliminary results of the small-scale distribution of herring larvae in the English Channel as obtained by means of a towed video recording system", Deep Sea Res. 30, 331–342, 1992

[11] C.S. Davis, S.M. Gallager, M. Marra, W.K. Stewart "Rapid visualization of plankton abundance and taxonomic composition using the video plankton recorder", Deep Sea. Res. 43, 1947-1970, 1996

[12] S. Samson, T. Hopkins, A. Remsen, L. Langebrake, T. Sutten, J. Patten "A system for high resolution zooplankton imaging", IEEE J. Ocean. Eng. 26, 671-676, 2001

[13] G. Gorsky, M. Picheral, L. Stemmann "Use of the underwater video profiler for the study of aggregate dynamics in the North Mediterranean", Estuar. Coast. Shelf Sci. 50, 121-128, 2000

[14] M.C. Benfield, R.F. Shaw, C. Schwehm "Development of a vertically profiling, high-resolution, digital still camera system", ONR Annual Report to Office of Naval Research, NR Grant No.: N00014-98-1-0563, 6 pp., 2000

[15] M. Lunven, P. Gentien, K. Kononen, E. Le Gall, M.M. Daniélou "In situ video and diffraction analysis of marine particles", Estuar. Coast. Shelf Sci. 57, 1127-1137, 2003

[16] P.J.S. Franks, J.S. Jaffe, "Microscale distribution of phytoplankton: initial results from a two-dimensional imaging fluorometer, OSST ", Mar. Ecol. Prog. Ser. 220, 59-72, 2001

[17] J. Schulz, D. Thum, D. Mengedoht, M. Potthoff, H. Lilienthal, H.J. Hirche, W. Riggers, M. Dickmann, T. Fleige "A new high gain reflector for rod-like high voltage discharge lamps in underwater imaging applications", IEEE J. Ocean. Eng. submitted

[18] S. Johnsen "Transparent animals", Scientific American February 2000, 80-89, 2000

[19] M.J. Weissburg, H.I. Browman "Sensory biology: linking the internal and external ecologies of marine organisms", Mar. Ecol. Prog. Ser. Theme Section 287, 263-307, 2005

[20] C.S. Davis, S.M. Gallager, M.S. Berman, L.R. Haury, J.R. Strickler "The video Plankton Recorder (VPR) Design and initial results", Arch. Hydrobiol. Beih. Ergebn. Limnol 36, 67-81, 1992

[21] J. Schulz, C. Möllmann, H.J. Hirche "Vertical zonation of the zooplankton community in the Central Baltic Sea in relation to hydrographic stratification as revealed by Multivariate Discriminant Function- and Canonical Analysis", J. Mar. Sys. DOI:10.1016/jmarsys.2006.09.004, 2006

Description of the figures

Figure 1: Example rays in the a) horizontal and b) vertical plane of the 'Light frame On-sight Key species Investigation' device. c) Schematic view of the camera and light frame positioning. The legend for used abbreviations can be found in Table 1.

Figure 2: Relations and limitations between a glass cylinder and a cut out cylindrical lens. The legend for used abbreviations can be found in Table 1.

Figure 3a) Experimental bench-top setup to show the operation mode of the LOKI illumination; mirrors M_2 and M_3 removed. b) Interpolated intensity distribution through the light-frame, based on measurements with a LiCor Li1000 Datalogger and sensor head equipped with a 0.6 mm pinhole diaphragm. The legend for used abbreviations can be found in Table 1.

Figure 4a) Image of dispersed North Sea plankton species (approx. 25*25*6 mm; 2048*2048 pixel, 8 bit greyscale). Magnified areas of interest of the framed objects show: b) *Acartia* sp., c) *Pseudocalanus* sp., d) *Temora* sp. and e) diatom algae.
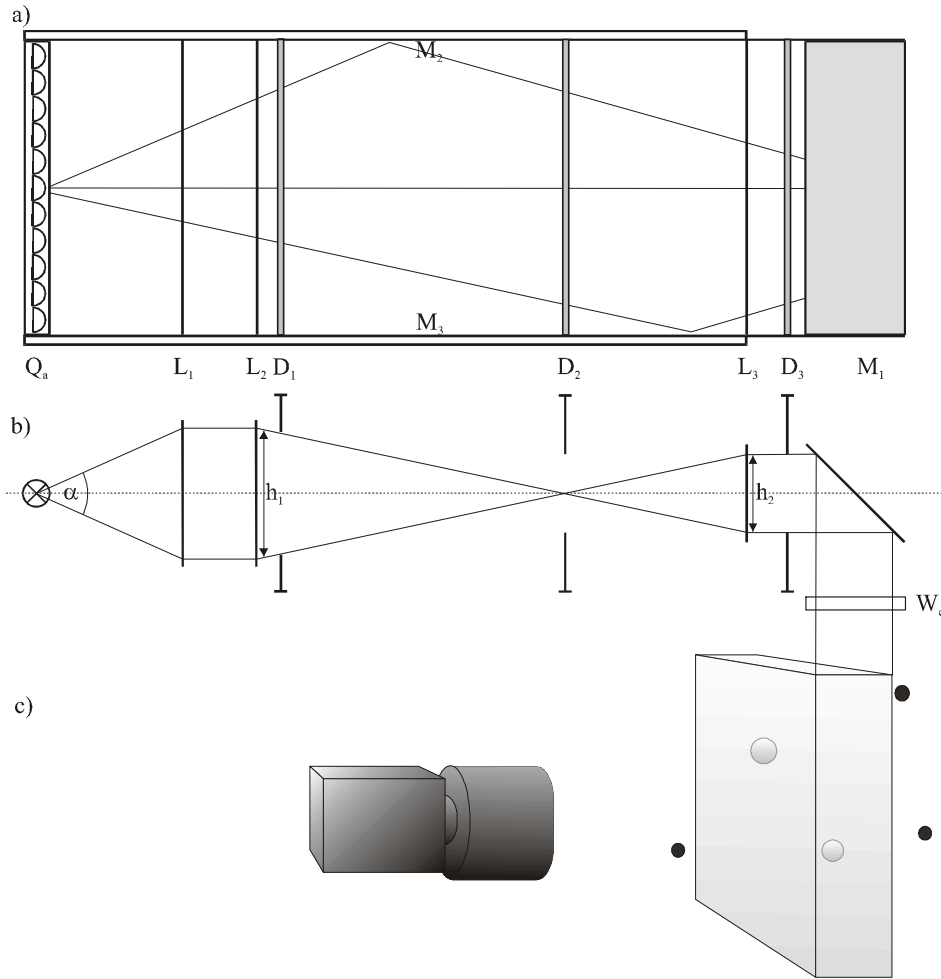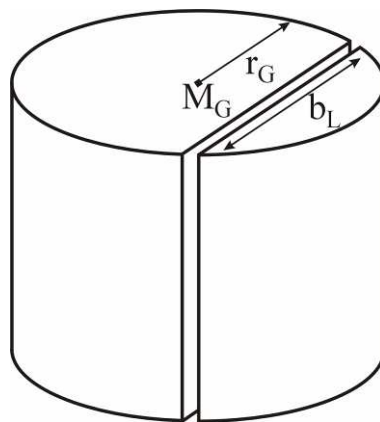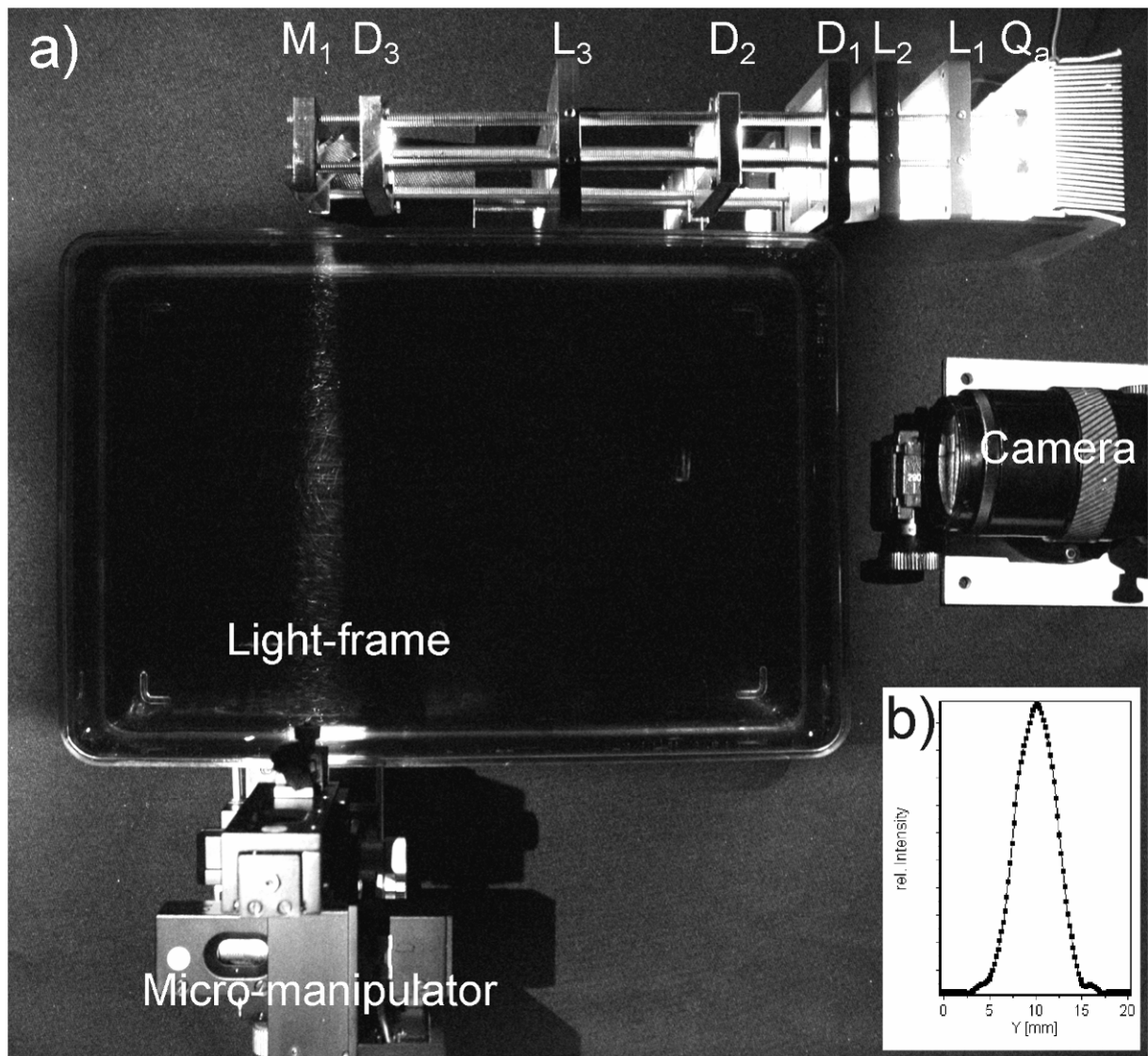
a)

b)

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Fig. 1

Fig. 2

Fig. 3
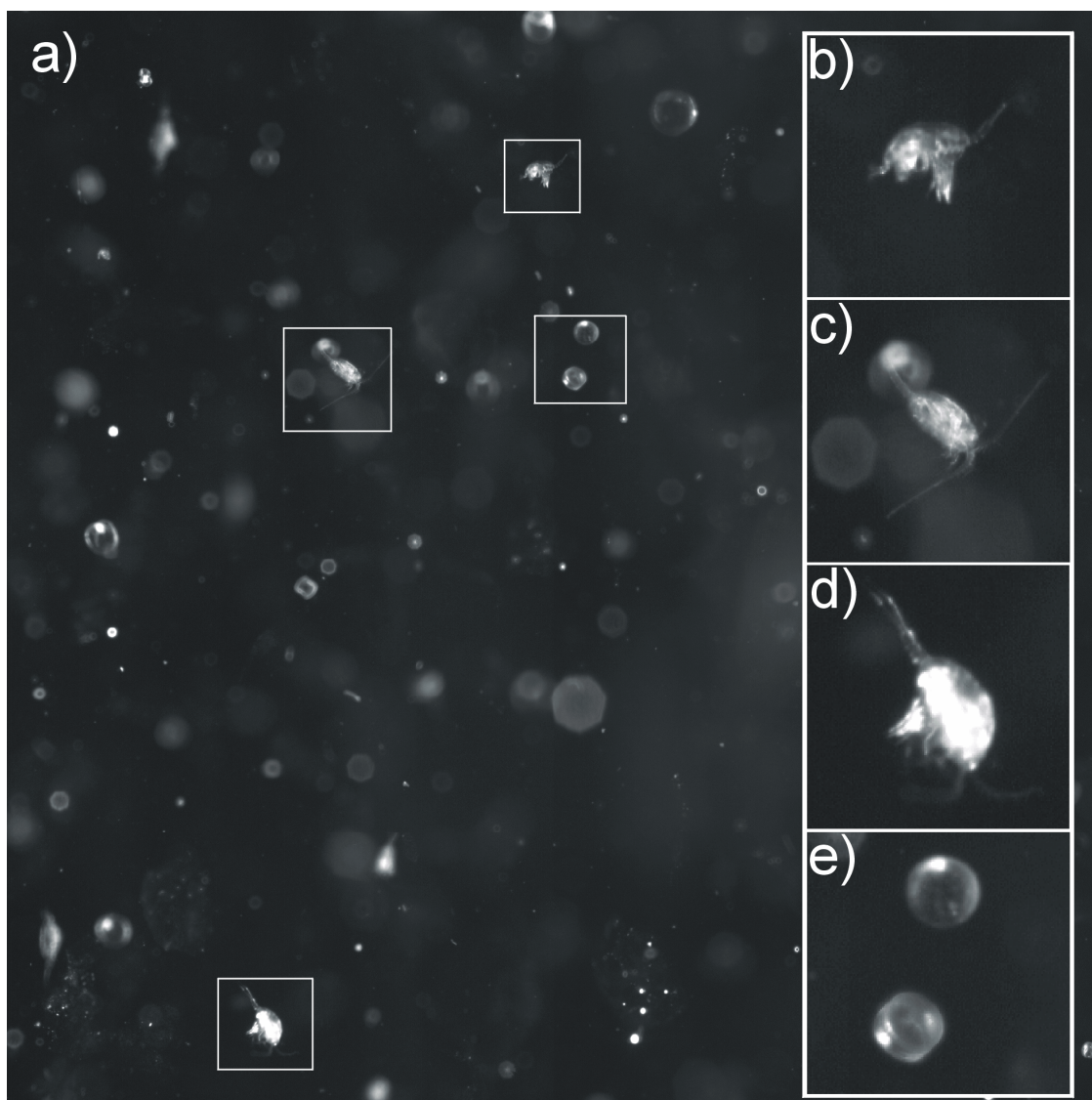
Fig. 4

Table 1: Key to the symbols and abbreviations used in the figures and equations.

Symbol	Key
D_1	Aperture diaphragm to adjust the height
D_2	Correcting diaphragm
D_3	Aperture diaphragm
f_L	Focal length of a cylindrical lens
h_1	Vertical extension of the collimated light-frame
h_2	Vertical extension of the targeting light-frame
L_1	Cylindrical lens
L_2	Cylindrical lens
L_3	Cylindrical lens
M_1	Targeting mirror
M_2	Mirrored side
M_3	Mirrored side
n_G	Refractive index of a glas cylinder
Q_a	Light source
r_G	Radius of a glas cylinder
W_e	Exit window

T3: Reflektorleuchte

Inventor: Jan Schulz
Status: Granted protection of utility patents in Germany (DE 20 2005 009 814.0)

The text of the granted utility model right describes a new type of reflector for rod like high voltage discharge lamps. This special design combines an elliptical and a spherical mirror to form and emit a diverging light beam. This beam originates from a focal line in the constructed reflector that is not identical to that of the discharge lamp. The basic text and figures were provided by the inventor and edited by the patent agents N. Cochu and J. Cochu, Berlin, to comply with the legal formalities of the German Patent Office (Deutsches Patent- und Markenamt[6]).

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[6] www.dpma.de

Reflektorleuchte

Beschreibung

Die Neuerung bezieht sich auf eine Reflektorleuchte mit einem kombinierten Reflektor aus einem ersten Spiegel in Form eines Rotationsellipsoidenabschnitts, der zu der Verbindungslinie zwischen den Brennpunkten des Rotationsellipsoiden als Rotationsachse symmetrisch ist, einem zweiten Spiegel in Form eines Kugelschalenabschnitts mit einem Radius, der dem Abstandsmaß zwischen den Brennpunkten des Rotationsellipsoiden entspricht, und einer zentralen Apertur, wobei der zweite Spiegel in Bezug auf den ersten Spiegel derart angeordnet ist, dass der Ursprung des Radius der Kugelschale mit dem ersten Brennpunkt des Rotationsellipsoiden und der Mittelpunkt der zentralen Apertur mit dem zweiten Brennpunkt des Rotationsellipsoiden zusammenfällt, und mit einer Lichtquelle im ersten Brennpunkt des Rotationsellipsoiden.

Derartige Reflektorleuchten weisen eine besonders hohe Lichtausbeute beziehungsweise geringe Verluste durch Streuung auf. Alle Lichtstrahlen, die von der Lichtquelle ausgehen und den ersten elliptischen Spiegel treffen, werden in den zweiten Brennpunkt des Rotationsellipsoiden reflektiert. Alle nach vorne zur Öffnung des ersten Spiegels hinausgehenden Strahlen, die nicht den ersten Spiegel treffen, werden von dem vor dem ersten Spiegel angeordneten zweiten sphärischen Spiegel wieder auf den ersten Spiegel reflektiert und von da aus ebenfalls auf den zweiten Brennpunkt geleitet. Der zweite Spiegel hat eine zentrale Aperturöffnung, die den gesamten Lichtaustritt ermöglicht. Derartige Anordnungen werden für Anwendungen eingesetzt, bei denen einen hohe Lichtausbeute von Vorteil ist, z.B. bei der Lichteinspeisung von Glasfasern oder als Fahrzeugscheinwerfer.

Stand der Technik

Aus der **FR 2 718 825 A1** ist eine Reflektorleuchte bekannt, die aus einem nicht geschlossenen System von zwei Spiegeln besteht, die einen bestimmten Lichtanteil in eine Glasfaser hinein bündelt. Die Anordnung der kleinen Teilspiegel lassen einen variablen Austrittswinkel aus der Leuchte zu, folgt aber nicht dem Prinzip, Ellipsenbrennpunkte einerseits und Kugelmittelpunkt sowie Apertur andererseits in Übereinstimmung zu bringen und ist daher nicht zuerst auf hohe Ausbeute ausgelegt. Die Lampe stellt eine weitgehend punkförmige Lichtquelle dar. Aus der **US 2005/0036314 A1** ist ein Projektor bekannt, dessen Beleuchtungseinrichtung eine Reflektorleuchte mit symmetrisch angeordneten Spiegeln ist. Der elliptische Spiegel sitzt hinter der Lampe, der sphärische Spiegel ist eine Kugelhalbschale mit kleinem Durchmesser, der unmittelbar an der kugelförmigen Lampe anliegt. Hier wird eine höhere Ausbeute angestrebt, indem der Mittelpunkt der Lampe und damit auch des Spiegels im ersten Brennpunkt der Ellipse liegt. Die Anordnung lässt außerdem keine Strahlen zu, die direkt außerhalb der beiden Spiegel fallen. Allerdings wird ein nicht unbedeutender Lichtanteil durch die beide Spiegel durchdringende Lampenfassung absorbiert. Aus der **JP 11064795** ist eine Reflektorleuchte bekannt, bei der die Lichtquelle punktförmig im ersten Brennpunkt des elliptischen Spiegels sitzt und durch einen spärischen Spiegel abgeschlossen wird, der eine sehr große Apertur aufweist, an die sofort eine optische Linse anschließt. Lichtverluste treten auch hier nur durch die Lampenfassung auf, die durch den elliptischen Spiegel dringt, aber auch Abstrahlung in direkter Richtung auf den zweiten Brennpunkt verhindert. Bei dieser Anordnung wird das Licht vor dem Errei-

chen des zweiten Brennpunkts durch die vorgesetzte Linse gestreut und ein Bündel paralleler Strahlen erzeugt. Die **GB 173,243**, von der die vorliegende Neuerung als nächstliegendem Stand der Technik ausgeht, offenbart in Figur 3 einen Autoscheinwerfer, der wieder aus zwei einander gegenüberliegenden Spiegeln besteht, wobei die Anordnung aus elliptischem und sphärischem Spiegel mit dem Mittelpunkt der Kugelschale und der Lampe im ersten Brennpunkt des Rotationsellipsoiden einen Lichtverlust weitgehend verhindert. Lediglich die hier nicht weiter angedeutete Lampenfassung sorgt für einen Verlust. Die Apertur ist derart ausgeformt, dass ein für Autoscheinwerfer besonders vorteilhafter Lichtkegel erzeugt wird, der eine Blendung entgegenkommender Fahrer verhindern soll. Allen bekannten Reflektorleuchten ist somit gemeinsam, dass sie einen rotationsymmetrischen Raum ausleuchten. Eine Ausleuchtung eines rechteckigen Raums nach Art eines Lichtbandes, wie sie beispielsweise für die Partikelbestimmung in Fluiden erforderlich ist, ist mit der bekannten reflektorleuchte nicht möglich.

Aufgabenstellung

Die **Aufgabe** für die vorliegende Neuerung ist daher darin zu sehen, dass ein weitestgehend ungestörter Lichtstrahl in Form eines in der Breite linear ausgedehnten Lichtbandes hoher Lichtausbeute erzeugt werden soll. Die Reflektorlampe soll einfach und preiswert herstellbar sein. Die neuerungsgemäße **Lösung** für diese Aufgabe ist dem Hauptanspruch zu entnehmen. Vorteilhafte Weiterbildungen der neuerungsgemäßen Reflektorleuchte sind in den Unteransprüchen aufgezeigt und werden im Folgenden im Zusammenhang mit der Neuerung näher erläutert.

Bei der neuerungsgemäßen Reflektorleuchte werden der kombinierte Reflektor und die Lichtquelle senkrecht zu einer die Verbindungslinie zwischen den Brennpunkten des Rotationsellipsoiden einschliessenden Symmetrieebene linear ausgedehnt. Als Hilfsvorstellung kann ein rotationssymmetrischer kombinierter Reflektor derart geschnitten gedacht sein, dass die Schnittebene auf einer die Verbindungslinie der Brennpunkte einschließenden Ebene liegt. Wenn die beiden Hälften des kombinierten Reflektors so auseinander gezogen sind, dass ein gleichmäßiger Abstand zwischen ihnen herrscht, kann eine der Schnittlinie folgend geformte, in der Richtung der Ausdehnung aber lineare Spiegelfläche die Lücke ausfüllend gedacht sein. Damit entsteht ein Reflektor, der einerseits die Charakteristika einer extrem verlustarmen Anordnung aufweist, aber andererseits eine linienförmige Lichtquelle im ersten Brennpunkt, oder quasi einer der linearen Ausdehnung entsprechenden Brennlinie, aufnehmen kann. Zur Erzeugung eines rechteckig begrenzen Lichtstrahls ist es von Vorteil, wenn die zentrale Apertur in dem zweiten, sphärischen Spiegel ein in gleicher Richtung und im gleichen Maß wie die Spiegel linear ausgedehnter Schlitz ist. Die Funktion des Reflektors ist damit sehr ähnlich der eines entsprechend rotationssymmetrischen Reflektors. Alle Lichtstrahlen, die senkrecht von der linienförmigen Lichtquelle abgegeben werden, treffen entweder auf den ausgezogenen Mittelteil des ersten, elliptischen, Spiegels und werden, immer noch senkrecht zur linienförmigen Lichtquelle, in Richtung auf die zweite Brennlinie refektiert, oder auf den ausgedehnten Mittelteil des zweiten, sphärischen, Spiegels und werden, auch hier immer senkrecht zur linienförmigen Lichtquelle, zunächst wieder auf den ersten, elliptischen, Spiegel und dann in Richtung auf die zweite Brennlinie refektiert. Hier treten sie durch die linienförmige Apertur nach außen. Alle schräg abgegeben Lichtstrahlen werden solange zwischen den Spiegeln hin und her geleitet, bis sie auf die abschließenden Halbschalen treffen und von dort ebenfalls durch die Apertur austreten. Im Randbereich des austretenden Lichtstrahls kommt es daher zu

Abweichungen von der linearen Lichtausbreitung in Form von seitlichen Streuungen. Für eine möglichst gleichmäßige Lichtverteilung in dem erzeugten Lichtstrahl ist es von Vorteil, wenn die linear ausgezogene Lichtquelle eine Entladungslampe ist. Ferner wird die geringstmögliche Störung der Lichtverteilung erreicht, wenn die elektrischen Anschlüsse der Entladungslampe an deren Enden angeordnet und außerhalb des ausgedehnten Bereichs des kombinierten Reflektors nach außen geführt sind. In dem ausgedehnten Bereich des Reflektors wird die Lichtausbreitung damit durch keine Elemente von Lampenfassungen gestört. Mit der Reflektorleuchte nach der neuerung ist es möglich, einen rechteckigen Raum gleichmäßig und ungestört auszuleuchten. Dies ist besonders vorteilhaft für Anordnungen, bei denen in einem definierten Wasserkörper, der durch die scharf begrenze Ausleuchtungszone beschrieben wird, die Anzahl der schwebenden Partikel gemessen werden soll. Derartige Anordnungen werden zur Gewässerforschung und im Umweltschutz eingesetzt.

Ausführungsbeispiele

Ausbildungsformen der Reflektorleuchte nach der Neuerung werden nachfolgend zum weiteren Verständnis der Neuerung anhand der schematischen Figuren näher erläutert. Dabei zeigt

Figur 1   eine Reflektorleuchte im Querschnitt und
Figur 2   eine Reflektorleuchte im Längsschnitt.

Figur 1 zeigt ein Beispiel für eine Reflektorleuchte **RL** aus einem kombiniertem Reflektor **KR** und einer Lichtquelle **LQ**, die zur Herstellung aus zwei Teilen zusammengesetzt ist. Im linken Teil ist ein erster Spiegel **S1** in Form eines Rotationsellipsoidenabschnitts **RE** ausgearbeitet, der zu einer Verbindungslinie **VL** zwischen einem ersten Brennpunkt **B1** und einem zweiten Brennpunkt **B2** symmetrisch ist. Im rechten Teil ist ein zweiter Spiegel **S2** in Form eines Kugelschalenabschnitts **KS** mit einem Radius **RB**, der dem Abstand der Brennpunkte **B1**, **B2** entspricht, ausgearbeitet. Der zweite Spiegel **S2** weist eine zentrale Apertur **ZA** auf. Der zweite Spiegel **S2** ist gegenüber dem ersten Spiegel **S1** derart angeordnet, dass der Ursprung des Radius **RB** mit dem ersten Brennpunkt **B1** und der Mittelpunkt der zentralen Apertur **ZA** mit dem zweiten Brennpunkt **B2** zusammenfällt. Im linken Teil ist zusätzlich zum ersten Spiegel **S1** noch eine Verbindungsfläche **VF** zwischen den Spiegeln **S1**, **S2** kegelstumpfartig ausgearbeitet, deren Berandungslinie einem Lichtstrahl **SL** folgt, der gerade eben eine Vorderkante **VK** des ersten Spiegels **S1** streift. Von einer Lichtquelle **LQ** im ersten Brennpunkt **B1** gehen beispielhaft die Lichtstrahlen **L1**, **L2** und **L3** aus. Lichtstrahl **L1** zeigt, wie alle Lichtstrahlen, die von der Lichtquelle **LQ** aus direkt den ersten Spiegel **S1** treffen, unmittelbar in den zweiten Brennpunkt **B2** reflektiert werden. Der Lichtstrahl **L2** fällt von der Lichtquelle **LQ** in den zweiten Spiegel **S2**, wird von dort in den ersten Brennpunkt **B1** und weiter in den ersten Spiegel **S1** reflektiert, von wo aus er, wie Lichtstrahl **L1**, auch in den zweiten Brennpunkt **B2** reflektiert wird. Lichtstrahl **L3** repräsentiert einen zentralen Lichtstrahl **ZL**, der in Verlängerung der Verbindungslinie **VL** der Brennpunkte **B1**, **B2** direkt durch die zentrale Apertur **ZA** austritt.

Figur 2 zeigt einen Längsschnitt durch die Reflektorleuchte entlang der Fläche A-A. Der kombinierte Reflektor **KR** und die Lichtquelle **LQ** weisen darin eine lineare Ausdehnung **LA** auf, die senkrecht zu einer Symmetrieebene **SE** verläuft, die die Verbindungslinie **VL** der Brennpunkte **B1**, **B2** des ursprünglichen Rotationsellipsoiden einschließt. Die Fläche

der linearen Ausdehnung **LA** besteht ebenfalls aus einer Spiegelfläche **SF**, die hier zwar der zentralen Kontur des kombinierten Reflektors **KR** durch zwei Raumrichtungen folgt, in der dritten Raumrichtung aber linear verläuft. Durch die lineare Ausdehnung **LA** werden die Brennpunkte **B1**, **B2** quasi zu Brennlinien **R1**, **R2**, die Lichtquelle **LQ** wird zur linearen Lichtquelle **LL** und die zentrale Apertur **ZA** zur linearen Apertur **LP**. Alle aus der linearen Lichtquelle **LL** rechtwicklig austretenden Lichtstrahlen, hier der zentrale Lichtstrahl **ZL** und ein parallel dazu verlaufender Lichtstrahl **PL**, können entweder unmittelbar durch die lineare Apertur **LP** in der zweiten Brennlinie **R2** verlaufen oder an der Spiegelfläche **SF** reflektiert werden und anschließend durch die lineare Apertur **LP** verlaufen. Seitlich aus der linearen Lichtquelle **LL** austretende Lichtstrahlen werden entweder durch die Spiegel **S1**, **S2** auch in die lineare Apertur **LP** reflektiert oder gehören zu dem geringen Verlustanteil der linear ausgedehnten Reflektorleuchte **RL**.

Bezugszeichenliste

B1	erster Brennpunkt
B2	zweiter Brennpunkt
EA	elektrische Anschlüsse
EL	Entladungslampe
KR	kombinierter Reflektor
KS	Kugelschalenabschnitt
L1, **L2**, **L3**	Lichtstrahl
LA	lineare Ausdehnung
LL	lineare Lichtquelle
LP	lineare Apertur
LQ	Lichtquelle
PL	paralleler Lichtstrahl
R1, **R2**	Brennlinie
RB	Radius
RE	Rotationsellipsoid
RL	Reflektorleuchte
S1	erster Spiegel
S2	zweiter Spiegel
SE	Symmetrieebene
SF	Spiegelfläche
SL	Lichtstrahl
VF	Verbindungsfläche
VK	Vorderkante
VL	Verbindungslinie
ZA	zentrale Apertur
ZL	zentraler Lichtstrahl

Schutzansprüche

1. Reflektorleuchte mit einem kombinierten Reflektor aus einem ersten Spiegel in Form eines Rotationsellipsoidenabschnitts, der zu der Verbindungslinie zwischen den Brennpunkten des Rotationsellipsoiden als Rotationsachse symmetrisch ist, einem zweiten Spiegel in Form eines Kugelschalenabschnitts mit einem Radius, der dem Abstandsmaß zwischen den Brennpunkten des Rotationsellipsoiden entspricht, und einer zentralen Apertur, wobei der zweite Spiegel in Bezug auf den ersten Spiegel derart angeordnet ist, dass der Ursprung des Radius der Kugelschale mit dem ersten Brennpunkt des Rotationsellipsoiden und der Mittelpunkt der zentralen Apertur mit dem zweiten Brennpunkt des Rotationsellipsoiden zusammenfällt, und mit einer Lichtquelle im ersten Brennpunkt des Rotationsellipsoiden,
dadurch gekennzeichnet, dass der kombinierte Reflektor (KR) und die Lichtquelle (LQ) senkrecht zu einer die Verbindungslinie zwischen den Brennpunkten (B1,B2) des Rotationsellipsoiden (RE) einschliessenden Symmetrieebene (SE) linear ausgedehnt sind.

2. Reflektorleuchte nach Anspruch 1,
dadurch gekennzeichnet, dass die linear ausgedehnte Lichtquelle (LL) eine Entladungslampe (EL) ist.

3. Reflektorleuchte nach Anspruch 2,
dadurch gekennzeichnet, dass die elektrischen Anschlüsse (EA) der Entladungslampe (EL) an deren Enden angeordnet und außerhalb des Bereichs der linearen Ausdehnung (LA) des kombinierten Reflektors (KR) nach außen geführt sind.
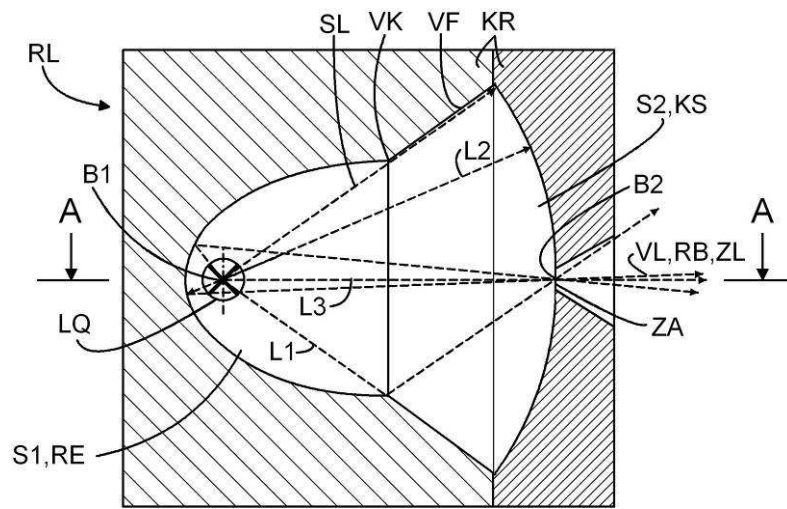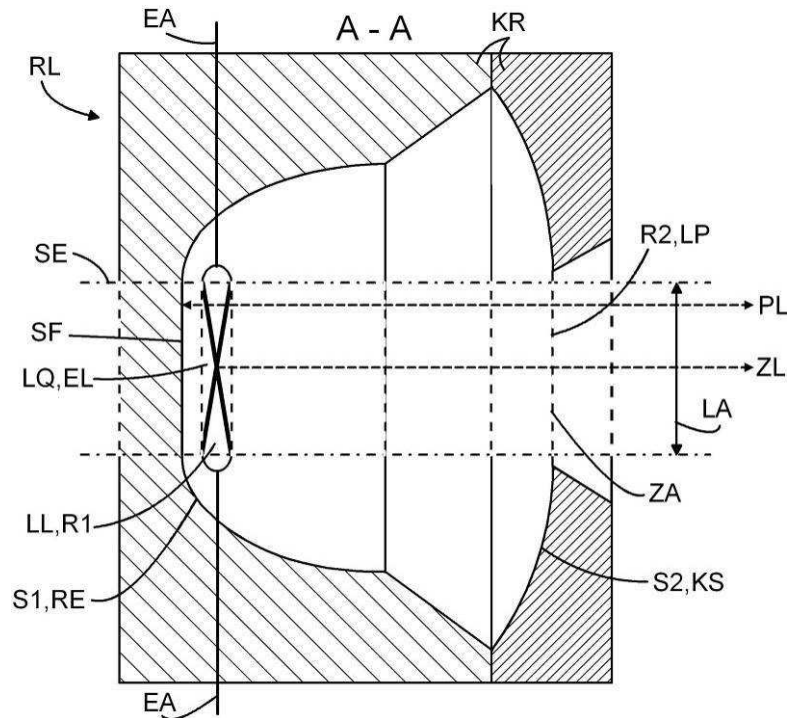
Fig. 1

Fig. 2

T4: A new high gain reflector for rod-like high voltage discharge lamps for underwater imaging applications

Authors: Jan Schulz, Dirk Thum, Dirk Mengedoht, Michael Potthoff, Heiko Lilienthal, Hans-Jürgen Hirche, Werner Riggers, Miriam Dickmann, Tobias Fleige
Status: Submitted to IEEE Journal of Oceanic Engineering

This paper summarises the text of the granted utility model protection for the new reflector type. The design and construction of the combined elliptical and spherical mirror is presented in a short and traceable way. Furthermore, the equations for locating the important points are derived from few initial parameters and allow the calculation of the outlines. The text was originally prepared by the first author. D. Thum constructed and manufactured the shown prototype of the reflector, M. Potthoff supported the development of the ray-tracing model and H. Lilienthal developed the circuits for the high voltage triggering. W. Riggers incorporated his knowledge on optical surface coatings. D. Mengedoht, H.-J. Hirche, M. Dickmann and T. Fleige improved the manuscript.

A new high gain reflector for rod-like high voltage discharge lamps for underwater imaging applications

Technical communication

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Abstract

Aquatic imaging applications often require light sources of high flux in evironments with limited energy conditions. High voltage discharge lamps provide short pulses of high intensity as required for photographic use. As lamps emit light in all directions the reflector type defines the illumination of targeted objects. Efficiency and precision of targeting determines the quality of the obtained images. Here a new reflector for rod-like high voltage discharge lamps is introduced. It combines an elliptical and a spherical mirror of defined specific dimensioning and distances. Almost all emitted light is reflected onto one focal line where the beam leaves the system through an aperture in the head of the reflector. The beam is constrained in height and provides a defined aperture angle. The created focal line can be used to inject light efficiently into lens systems and can be used for a variety of illumation tasks.

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Introduction

Imaging systems in marine science and related fields that require the quantification of the imaged volume by dark field illumination need high luminous fluxes [e.g. 1, 2, 3, 4]. Limits regarding package dimensions and energy consumption often do not allow substituting a given light source for a device of higher power or size to increase light flux. In lens applications the alignment of emitted rays is further crucial for efficiency of the illuminating device.

Having an output greater than one Joule per flash, high-voltage discharge lamps are an outstanding as powerful light sources for use under finite energy conditions. A variety of different shaped lights, ranging from round or helical to rod-like cover a wide field of applications. Most types are operated with an anode voltage of a few hundred volts. To initiate the flash, an external trigger pulse of several kV is applied by a wire onto the surface of the glass housing.

The task of reflectors is to focus the flash into one direction or at one focal point. Thereafter, the reflected light can be used to illuminate objects or to be injected into an optical unit. Although standard reflectors parallelise or align large amounts of rays in a manner suitable for lens systems, the unaligned rays cause stray light and aberration. As reflectors are open on one side a considerable number of such unaligned rays is emitted in conventional systems. To reduce these rays additional metallic reflectors on the surface of the lamp are commonly used. They reflect rays back into the system and force them to hit the main reflector, from where the leave the system aligned. However, this solution is problematic in high voltage discharge lamps as trigger energy from the supply wire could come to contact with the housing. This weakens ignition voltage, results in inhomogeneous flash operation and might even harm the operators. Due to the produced ozone inert metallic parts or coatings should be given preference to ensure durability in non-ventilated underwater housings. Here we describe a reflector for rod-like high voltage discharge strobes composed of a combination of elliptical and spherical reflective faces to bypass the forementioned limitations.

Approach and Results

Optical targeting or focussing units align large amounts of rays from a light source to share equal optical properties. The use of a collimating lens systems (Figure 1a) or spherical mirrors (Figure 1b) results in parallel alignments. A key to the abbreviations used in the equations and graphics is given in Table 1. Elliptical mirrors (Figure 1c and 1d) focus high numbers of rays into one focal point, where they can be injected, for example, into a fiber optic. For use in lens systems, the conditions shown in Figure 1a and 1c are similar for lenses set up in a pre-calculated distance from the focal point or light source itself. The angle α increases with decreasing distance and determines the angle of a ray to the surface normal vector at the rim of a lens. Higher values cause loss due to reflection on the surface and aberrations at the borders of a lens. Thus a small angle α is desired, but reduces yield without adequate reflectors. The reflectors shown in Figure 1a-1d are for ideal punctual light sources. For light sources that are not punctual, a larger relation of reflector to lamp size is needed. For practical reasons, halved elliptical and rotational solids are often used, where rays leave the system on the open side. Rays that originate in f_1 and do not hit the reflective face before M_E are only partially available in lens systems (Figure 2a, thin ray in the upper half of the ellipse). A spherical mirror close to the surface of the light source

(Figure 1d) forces light rays to leave the reflector via the face of the elliptical mirror. This reduces stray light and increases efficiency.

Technical applications often use elliptical mirrors that have two focal points (Figure 1c, 1d; Figure 2a: f_1 and f_2). Rays that originate in f_1 traverse f_2 and vice versa. These points are located where a circle, centred at M_C with radius a, intersects the principal axis of the ellipse. The distance e of the focal points f_1 and f_2 from the centre of the ellipse M_E is given by:

$$e = \sqrt{a^2 - b^2} \quad \text{[Equation 1]}$$

Another common reflector is based on a spherical mirror. Every ray that originates in the centre of the sphere (M_S) is reflected to its point of origin (Figure 2b).

For the present application, we combined an elliptical mirror with a modified spherical mirror. The elliptical mirror is cut in half at its centre (M_E), parallel to the plane given by b (Figure 3). In the first focal point f_1 the midpoint of a spherical mirror M_S is arranged. The radius of the spherical mirror is $2e$ and consequently intersects f_2. The discharge strobe is located in f_1 of the elliptical mirror. This setup reflects rays that hit the reflective face of the elliptical mirror into f_2. Rays that hit the spherical mirror are reflected back into the light source, pass the glass housing a second time, hit the elliptical mirror and behave as the latter ones.

In f_2 an image of the light source is produced and rays leave the system in this focal point through an aperture in the spherical mirror. The dimension of the aperture should be in the same range as the diameter of the light source and is symmetrically constructed in height of the principal axis. The diverging angle β depends on the $b{:}a$ ratio:

$$\beta = 2 \sin^{-1}\left(\frac{b}{a}\right) \quad \text{[Equation 2]}$$

To meet the requirements of the rod-like structure of the discharge lamp both the elliptical and the spherical mirror are cut in half along the principal axis. The distance between the two parts is linearly extended and mirrored. The dimension is chosen equal to the irradiating section of the discharge lamp. Subsequently the central section of the reflector refers to an extrusion body and the focal points f_1 and f_2 are extended to a focal line. Beyond this linear part the edges follow the elliptical or respective spherical curvature. The internal height h of the reflector can be calculated with the basic dimensions of the system:

$$h = 2\,r\,\sin\left(\frac{\beta}{2}\right) \quad \text{[Equation 3; } r = 2e \text{ from Equation 1; } \beta \text{ from Equation 2]}$$

To evaluate our theoretical approach, a model was designed in the Persistence of Vision raytracing environment [5] and rendered in radiosity and photon simulation mode. A scattering particle field was applied in the height range of the reflector to display internal reflections. The rhomboid area was created by the intersecting rays that span between f_1, f_2 and the outer borders of the elliptical reflector (Figure 4a). It demonstrates the high yield in f_2, where rays exit the system confined to a small angle β. Based on the results of the model a prototype was built for underwater applications. Figure 4b shows the disassembled prototype with the position of the discharge lamp. A protection of utility patent was granted for this device by the patent office of the Federal Republic of Germany [6].

Discussion

The reflector described here can be used in applications where it is desired to focus emitted light into one narrow band with high accuracy. In our application, the beam is precisely targeted and leaves the system under a defined flare angle. This allows an easy injection into optical applications, with reduced stray light. With this reflector it is possible to set up a headlight projecting to infinity with one or few lenses. It was originally designed as a light source for a LOKI dark field illumination application [4], but can cover a wide range of other applications. Stray light in *in-situ* dark field imaging applications can illuminates unintentional objects that are out of focus, reducing accuracy of the method. Consequently rays outside of the defined angle and path need to be gated out by diaphragms. For this setup, one has to take into consideration that the required precise adjustment makes the construction more complex and expensive as compared to standard devices. However, this is more than compensated by a highly increased efficiency and accuracy. Compared with reflector-free systems (Figure 1a) the utilise/loss ratio is almost inverted and thus much higher than in standard devices.

In practice the ratio of *lamp diameter* to h should be greater than 1:10. Smaller ratios may cause higher inaccuracy due to the non-punctiformity of the discharge lamp and deviation by parallel translation when passing the glass housing a second time. This results in a widening of the focal line, causing distortion in lens applications.

It has been observed that a halved ellipse combined with a sphere offers a good trade-off for most applications. Larger extensions of a result in larger β values smaller ones in larger h values. Even though the beam is sharply constrained when it exits, the beam intensity decreases from the centre towards the periphery. This results in increased distortion with increasing distance from the principle axis and is depending on the angle at which a ray hits the outer parts of the elliptical reflector [7]. Closer to the principal axis, the angle is lower and more rays per area unit are reflected (see Figure 4a). When necessary it can be improved by using a smaller ellipse and a larger sector of the circle.

As the life time of high-voltage discharge lamps can be longer than 10^9 flashes, they can often be employed for long-term applications. Here the produced ozone might corrode non-inert materials in un-ventilated housings. Consequently, metal is suitable for continuous operation. For internal heat dissipation, the connecting surface between the elliptical and spherical mirror can be used to set ventilation slits without loss of reflective surface. The given equations allow computing the dimensioning for appropriate devices.

Acknowledgement

References

[1] H. Umhauer "Particle size distribution analysis by scattered light measurements using an optically defined measuring volume", J. Aerosol. Sci 14(6), 765-770, 1983

[2] G. Gorsky, M. Picheral, L. Stemmann "Use of the underwater video profiler for the study of aggregate dynamics in the North Mediterranean", Estuar. Coast. Shelf Sci. 50, 121-128, 2000

[3] M.C. Benfield, R.F. Shaw, C. Schwehm "Development of a vertically profiling, high-resolution, digital still camera system", ONR Ann. Rep. to Office of Nav. Res., NR Grant No.: N00014-98-1-0563, 6 pp., 2000

[4] J. Schulz, D. Mengedoht, H.J. Hirche "Imaging defined volumes; LOKI – Light frame On-Sight Key species Investigation", IEEE J. Ocean. Eng. submitted

[5] PovRay Team "Persistance of Vision Raytracer Version 3.6", http://www.povray.org

[6] J. Schulz "Reflektorleuchte" German utility model DE 20 2005 009 814.0, 2005

[7] H. Rehn "Optical properties of elliptical reflectors", Optic. engineer. 43(7), 1480-1488, 2004

[8] G. Schröder, H. Treiber "Technische Optik", Kamprath, Würzburg, 2002

Description of the figures

Figure 1: Schematics of a light source in a) a collimating lens application, b) spherical mirror, c) elliptical mirror and d) elliptical mirror with a partial spherical reflective face around the light source. Bold rays are useable for the given application, while the thin ones are inappropriate for a range of optical systems (Examples modified after Schröder and Treiber [8]).

Figure 2: Important locations and distances in a) elliptical and b) spherical mirrors. Bold lines represent useable rays for the given application.

Figure 3: Scheme of the reflector as a combination of an elliptical and a spherical mirror. The light source is located at f_1 on the principal axis of the system. Bold lines represent usable rays for lens applications.

Figure 4: a) A model of the reflector in a simple lens and diaphragm application compiled and rendered under PovRay to visualise internal reflections. b) Photo of the disassembled device. For the use in round, pressure resistant housings it was given a spherical diameter.
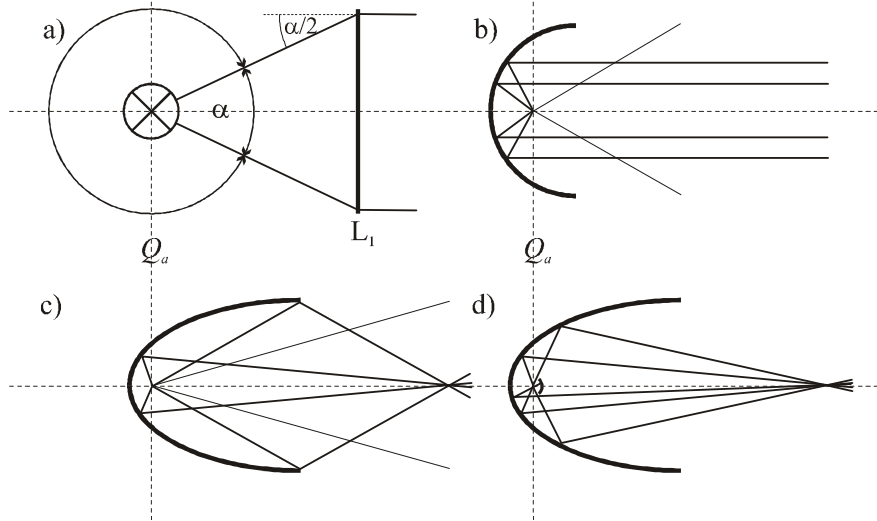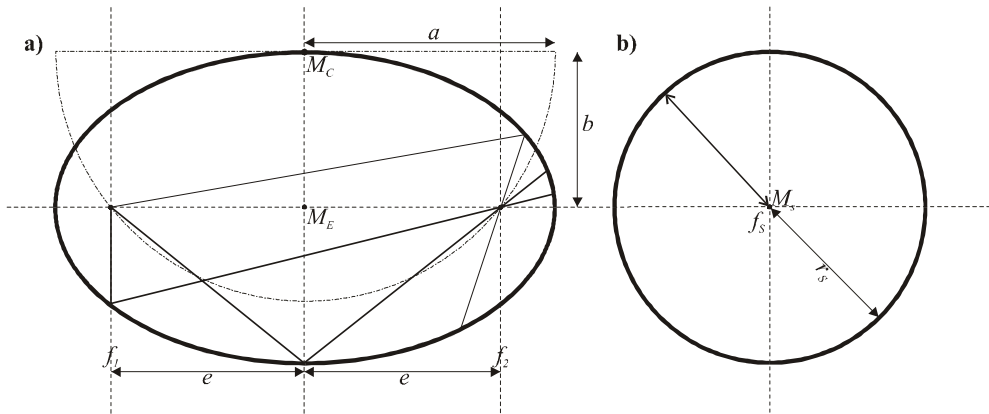
Fig. 1

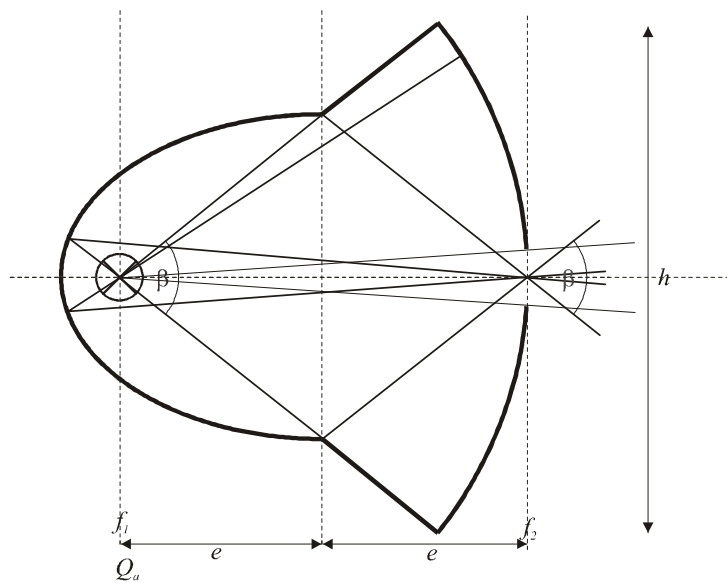
Fig. 2

Fig. 3

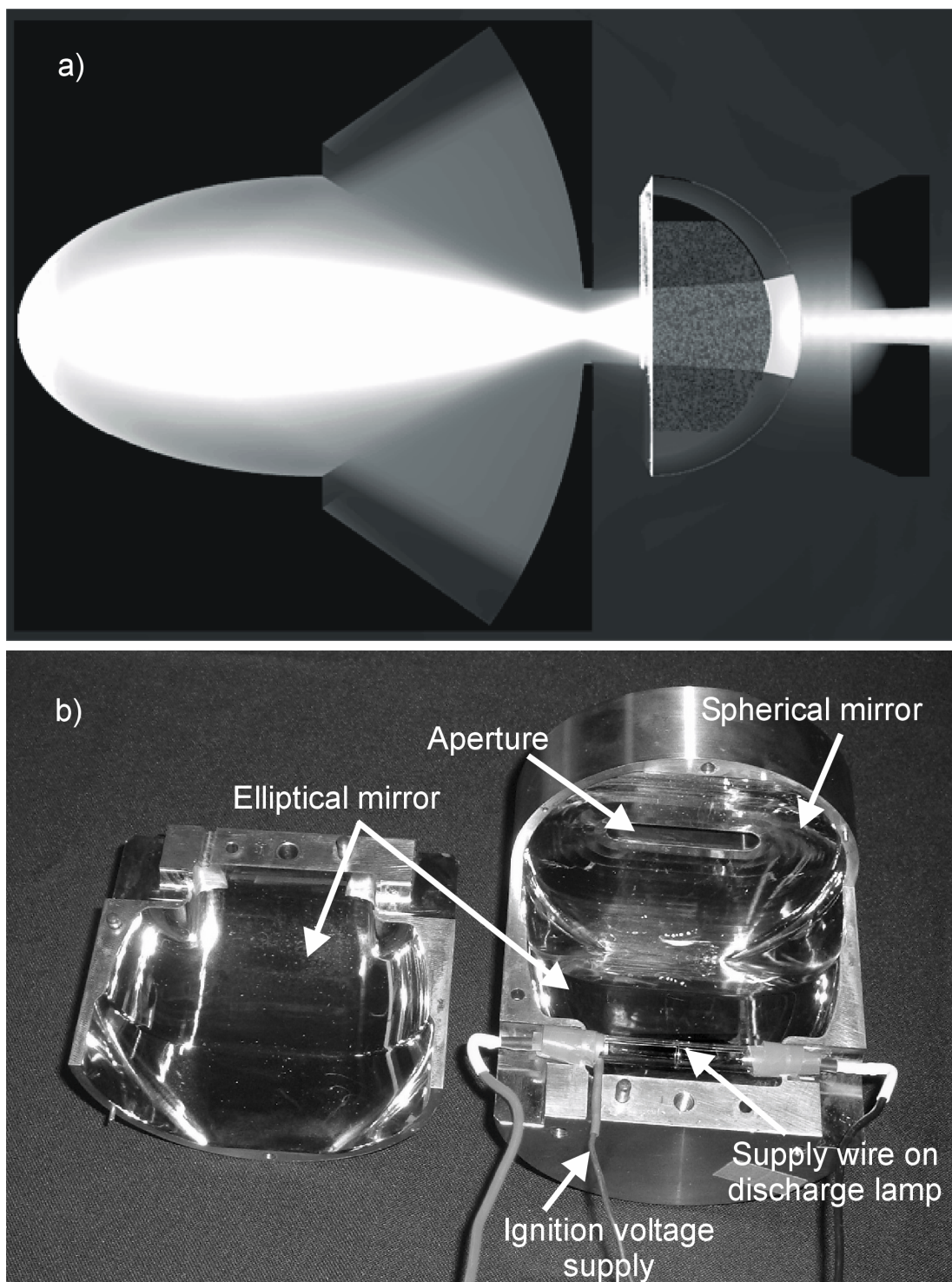**Fig. 4**

Table 1: Key to the symbols that are used in the equations and figures.

Symbol	Key
a	Long radius of the ellipse
α	Angle within light rays are used in a simple lens system
b	Short radius of the ellipse
b_L	Width of a cylindrical lens
β	Angle in which the rays leave the reflector through the exit window
e	Distance from ellipse's midpoint to it's focal point
f_1	First focal point of an ellipse, position of the light source
f_2	Second focal point of an ellipse
f_S	Focal point of an spherical mirror
h	Total inner height of the reflector
M_C	Midpoint of the construction circle to find f_1 and f_2
M_E	Midpoint of the ellipse
M_S	Midpoint of the spherical mirror
Q_a	Light source
r_S	Radius of the spherical mirror

T5: Ringleuchte zur Ausleuchtung eines begrenzten Volumens und deren Verwendung

Inventor: Jan Schulz
Status: Pending patent application in Germany (DE 10 2005 050 722.0)

As a further advancement of the first patent application a circular illumination was developed that allows unidirectional illumination of a defined volume with improved luminous flux. The basic text and figures were provided by the inventor and edited by the patent agents N. Cochu and J. Cochu, Berlin, to comply with the legal formalities of the German Patent Office (Deutsches Patent- und Markenamt[7]).

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[7] www.dpma.de

Ringleuchte

Beschreibung

Die Erfindung bezieht sich auf eine Ringleuchte mit einer als Hohlzylinder ausgebildeten Lichtquelle mit einer auf die Achse des Hohlzylinders weisenden Lichtabstrahlrichtung, mit Leuchtdioden für weißes Licht als Leuchtmittel und mit einer Einrichtung zur Lenkung der Lichtabstrahlung.

Derartige Ringleuchten sind z.B. um Kameraobjektive zur Makrofotografie, als Operationsfeldbeleuchtung in der Medizin oder auch zur Durchlicht- oder Auflichtbeleuchtung in der Lichtmikroskopie im Einsatz. Dabei ist eine solche Ringleuchte konzentrisch zur optischen Achse der abbildenden Optik angeordnet. Es wird damit im Gegensatz zur Spotbeleuchtung eine schattenfreie Beleuchtung des abzubildenden Objekts erzielt. Auch auf dem Gebiet der Partikeldetektion in Strömungen wird eine schattenfreie, gleichmäßige und intensive Beleuchtung benötigt, hier jedoch innerhalb eines begrenzten Volumens, wodurch nur die mit der Strömung jeweils in den beleuchten Bereich eintretenden Partikel betrachtet werden.

Stand der Technik

Auf dem Gebiet der Partikeldetektion sind verschiedene Beleuchtungsvorrichtungen bekannt. Aus der **DD 232 552 A1** ist eine Einrichtung zur Zählung und Klassifizierung von dispergierten Teilchen in Flüssigkeiten mit einem von einer Messzelle räumlich begrenzten Messvolumen bekannt, bei dem zur Ausleuchtung des Messvolumens ein Laserstrahl dient, wobei der Strahlfokus in der Mitte des Messvolumens liegt, sodass das detektierte Messvolumen auf einen Punkt reduziert wird. Das Messvolumen ist durch die Ausbildung der Messzelle so eingeengt, dass sich immer nur ein Teilchen im Lichtfokus befindet, dessen Streuung im Laserlicht gemessen wird. Die **DD 221 861 A1** beschreibt eine Beleuchtungseinrichtung zur Erzeugung eines zweidimensionalen Lichtstreifens zur Mustererkennung und Identifizierung von Werkstücken in industrieller Umgebung. Dazu wird eine lineare Lichtquelle verwendet, deren Strahlen durch eine Lamellenblende gerichtet und durch eine Zylinderlinse auf das zu erkennende Objekt gebündelt werden. In dem Aufnahmesystem wird durch Kontrasteinstellung ein scharfes Schwarzweißbild des jeweils beleuchteten Streifens erzeugt und analysiert. Ein Reflektor kann für eine höhere Lichtausbeute hinter der Lichtquelle angebracht werden. Weiterhin ist aus der **DE 298 13 109 U1** eine Beleuchtungsvorrichtung zur Erzeugung eines langen, schmalen Lichtbandes mit zweidimensionaler Ausprägung bekannt, bei der das Licht einer Anzahl von Lampen in einem engen Gehäuse mit einer ersten jeweils eigenen und einer zweiten gemeinsamen Linse zu einem schmalen Strahl mit Fokus auf einer Linie wählbarer Entfernung erzeugt wird. Die Lichtausbeute entspricht etwa dem Abstrahlwinkel und ist damit sehr gering. In der **DE 197 36 172 B4** wird eine Vorrichtung zur Analyse von in einem strömenden Fluid dispergierten Teilchen beschrieben, die mit Blenden arbeitet, deren Kanten hyperbelartig gekrümmt sind und damit bei Beleuchtung ein dreidimensionales Messvolumen mit einem bekannten Schärfentiefenbereich definieren, das kegelstumpfartig mit gebogenen Kanten ausgebildet ist. Im zugehörigen Verfahren werden Teilchen mit definierter Laufzeit im Messvolumen ausgewertet. Die Beleuchtungseinrichtung ist parallel zum Detektor angeordnet, das Detektionssignal wird über ein Prisma aus dem Messvolumen umgelenkt.

Bekannte Video-Plankton-Rekorder (VPR) nutzen punkt- oder linienförmige Lichtquellen und einzelne sphärische Linsen zur Kollimation. Im großskaligen Bereich kommen auch starke Halogensysteme zum Einsatz. Die bekannten Vorrichtungen haben aber zum Problem, dass keine scharfe optische Begrenzung des Messvolumens erzeugt werden kann und die Tiefenschärfe im Messvolumen aufwändig softwaretechnisch justiert wird, was im kleinskaligen Bereich der Planktonbeobachtung zu hohen Ungenauigkeiten der Volumeneinschätzung führt.

Als Kameraleuchte ist die Ringleuchte für schattenfreie Reprofotografie aus der **DE 299 21 150 U1** bekannt. Bei dieser, als technischer Hintergrund zu der vorliegenden Erfindung anzusehenden Druckschrift wird als Leuchtmittel eine handelsübliche Ring-Leuchtstofflampe eingesetzt. Sie strahlt ihr Licht gleichmäßig nach allen Seiten, also auch nach innen in Richtung auf die Achse der Lichtquelle ab. Eine Einrichtung zur Lenkung der Lichtabstrahlrichtung wird hier durch eine Vorrichtung gebildet, die hauptsächlich den Lichteinfall auf das zu beleuchtende Objekt verändert, indem das Leuchtmittel angehoben oder abgesenkt wird. Ferner ist eine Ringleuchte aus der **DE 102 11 768 A1** bekannt, von der die vorliegende Erfindung als nächstliegendem Stand der Technik ausgeht. Diese Druckschrift offenbart eine aus einem Ring von Leuchtdioden für weißes Licht bestehende, als flacher Hohlzylinder ausgebildete Lichtquelle, deren Abstrahlrichtung nach innen auf die Achse des Hohlzylinders weist. Durch eine zweigeteilte Konstruktion kann der die Leuchtdioden tragende erste Ring in Bezug auf einen feststehenden zweiten Ring im Durchmesser verändert werden. Dadurch, dass die die Dioden tragende, flexible, kreisförmig gebogene Platine mit ihrem unteren Ende im feststehenden zweiten Ring und mit ihrem oberen Ende im veränderbaren ersten Ring angeordnet ist, wird mit Veränderung des Durchmessers des ersten Rings der Winkel der Abstrahlung in Bezug auf die Achse der Ringleuchte verändert. Diese Vorrichtung dient der Optimierung einer schattenfreien Ausleuchtung verschiedener abzubildender, feststehender Objekte. Die beschriebene Einrichtung zur Lenkung der Lichtabstrahlung kann jedoch kein streng begrenztes Volumen ausleuchten. Das Licht wird, nur begrenzt durch die in ihren Abmessungen nicht weiter definierten Kanten der beiden gegeneinander verschiebbaren Ringe, frei abgestrahlt und spannt damit ein nach oben und unten nur unscharf begrenztes, doppelt kegelförmiges Volumen mit erheblich darüber hinaus gehenden Streuungsbereichen auf.

Aufgabenstellung

Ausgehend von der Ringleuchte der nächstliegenden Veröffentlichung besteht die **Aufgabe** für die hier vorliegende Erfindung darin, eine Ringleuchte der eingangs erläuterten gattungsgemäßen Art bereitzustellen, die ein in allen drei Raumdimensionen streng begrenztes Volumen besonders hell ausleuchtet. Dabei soll die Ringleuchte einfach, robust im Aufbau und in der Handhabung gestaltet und kostengünstig herstellbar sein.

Als erfindungsgemäße **Lösung** für diese Aufgabe ist die vorliegende Erfindung dadurch gekennzeichnet, dass die Einrichtung zur Lenkung der Lichtabstrahlung ein Linsensystem (LY) ist, das zumindest eine exakt in die orthogonal zur Achse des die Lichtquelle (LQ) bildenden Hohlzylinders (H1) orientierte Radialebene (RE) fokussierende Linse (LE), die als weiterer Hohlzylinder (H2) ausgebildet ist, und eine ringförmige, im Strahlengang hinter der einen fokussierenden Linse (LE) zentriert angeordnete Aperturblende (AB) aufweist, und dass die Lichtquelle (LQ) und das Linsensystem (LY) in der Länge identisch und sowohl achsen- als auch längenkongruent angeordnet sind, wobei die vom Innenradius (I3) des Linsensystems (LY) bestimmte Querschnittsfläche und die Länge des Linsensystems (LY) ein streng begrenztes Volumen (BV) aufspannen.

Zur Verwendung solcher Ringleuchten in Vorrichtungen zur Partikeldetektion, z.B. Video-Plankton-Rekordern (VPR), ist die erzeugte Lichtscheibe für die optische Auswertung von durch sie hindurchtretende Partikel in dunkler oder gering beleuchteter Umgebung dann besonders geeignet, wenn die erzeugte Lichtscheibe scharf begrenzt und nicht wesentlich dicker als das größte abzubildende Objekt ist sowie Lichtstreuung außerhalb der Licht-scheibe weitestgehend vermieden wird. Die erfindungsgemäße Ringleuchte weist Leucht-mittel auf, die auf einer als Hohlzylinder ausgebildeten Lichtquelle gleichmäßig verteilt angeordnet sind. Die Leuchtmittel sind dabei mit ihrer Abstrahlrichtung nach innen senk-recht zur Achse des Hohlzylinders und daher mit der orthogonal zur Achse des Hohlzylin-ders orientierten Radialebenen übereinstimmend ausgerichtet. Durch diese Anordnung wird erreicht, dass der Haupt-Lichtstrom unmittelbar das Innere des Hohlzylinders beleuchtet und nur ein sehr geringer Streuanteil diesen von dem Querschnitt und der Länge des Hohl-zylinders aufgespannten Raum verlässt. Es kann so ein streng begrenztes dreidimensionales Volumen betrachtet werden. Durch die Art der rundum angeordneten Leuchtmittel wird eine weitestgehend gleichmäßige und schattenfreie Beleuchtung von in dem Volumen be-findlichen Objekten erzielt.

Im Hinblick auf einen möglichen Einsatz der Ringleuchte nach der Erfindung in Video-Plankton-Rekordern kann die Länge des Hohlzylinders besonders gering gestaltet sein, so dass von einer dünnen, kreisförmigen Lichtscheibe gesprochen werden kann. Mit der Strö-mung hindurchtretende Plankter werden schlagartig sehr hell beleuchtet und können dabei mit einem in einer die Strömung nicht beeinträchtigenden Entfernung befindlichen Kame-rasystem registriert werden. Anschließend werden sie übergangslos wieder abgedunkelt und so undefinierte Randbereiche vermieden. Bei einem genauen Fokus auf die dünne Lichtscheibe werden zwischen Kamera und Lichtscheibe, aber auch hinter der Lichtscheibe befindliche, unbeleuchtete Plankter die Aufnahme nur gering dämpfen. Je dünner die Lichtscheibe ist, desto weniger Licht wird durch die hindurchtretenden Plankter nach außen gestreut und an noch oder schon wieder unbeleuchteten Planktern in die Aufnahme stören-der Weise reflektiert. Die minimale Dicke der Lichtscheibe richtet sich einerseits nach den möglichen konstruktiven Gegebenheiten und den zu erwartenden Strömungs-geschwindigkeiten sowie andererseits nach der Größe der abzubildenden Plankter, die zu-mindest kurzzeitig komplett im Licht sein sollen, wobei die notwendigen Belichtungs- und Prozesszeiten für die Kamera als weitere Parameter hinzu kommen.

Für den Einsatz unter Wasser, und gegebenenfalls in großen Tiefen ist eine hohe Lichtaus-beute bei hohem Wirkungsgrad gefordert, d.h. sowohl lange Batteriestandzeiten als auch geringe Wärmeentwicklung an der Lichtquelle. Es sind daher weiße Leuchtdioden als Leuchtmittel vorgesehen. Leuchtdioden haben einen hohen Wirkungsgrad und eine beson-ders hohe Lebenserwartung. Sie erzeugen somit nur eine geringe Verlustwärme und haben eine Standzeit, die regelmäßig die Nutzungsdauer der übrigen Bauteile übersteigt. Leucht-dioden sind klein und eine Vielzahl davon können eng beieinander angeordnet die Licht-quelle bilden. Durch ihren geringen Durchmesser lässt sich ein Hohlzylinder sehr geringer Höhe bilden, wie er z.B. für einen VPR für kleinere Plankter und geringere Strömungsge-schwindigkeiten oder auch für eine hochempfindliche Kamera gefordert werden kann. Erst seitdem die Industrie weiße Leuchtdioden großer Helligkeit anbietet, sind Anwendungen wie die hier beschriebene Ringleuchte überhaupt technisch und wirtschaftlich sinnvoll möglich geworden. Alle anderen Leuchtmittel liefern entweder einen zu geringen oder energetisch uneffektiven Lichtstrom (Entladungslicht, Glühlicht) oder eine ungenügende Ausleuchtung (Laserlicht).

Die kegelförmige Abstrahlung der Leuchtdiode oder auch einer anderen Lichtquelle muss für eine in der Länge des Hohlzylinders streng begrenzte Lichtscheibe zu einem waagerechten Strahlengang fokussiert werden. Dazu ist es vorteilhaft, wenn in einer Weiterbildung der Ringleuchte nach der Erfindung die eine fokussierende Linse eine Fresnellinse ist. Fresnellinsen oder genauer Fresnel'sche Stufenlinsen sind optische Linsen, die ursprünglich für Leuchttürme entwickelt wurden. Sie ermöglichen die Konstruktion großer Linsen mit kurzer Brennweite ohne das Gewicht und Volumen herkömmlicher Linsen. Die Verringerung des Volumens geschieht bei den Fresnellinsen durch eine Aufteilung in ringförmige Bereiche. In jedem dieser Bereiche wird die Dicke gegenüber der herkömmlichen Linse verringert, sodass die Fresnellinse eine Reihe ringförmiger Stufen erhält, die die gleiche Krümmung wie der jeweilige Abschnitt der ursprünglichen Linse aufweist. Da Licht nur an der Oberfläche einer Linse gebrochen wird, ist der Brechungswinkel nicht von der Dicke, sondern nur vom Winkel zwischen den beiden Oberflächen einer Linse abhängig. Deshalb behält die Fresnellinse ihre optischen Eigenschaften bei, obwohl die Bildqualität durch die Stufenstruktur etwas beeinträchtigt wird. Fresnellinsen werden dort eingesetzt, wo das Gewicht oder die Abmessungen ausschlaggebend und die Abbildungsqualität zweitrangig sind. Beispiele sind Schiffslaternen oder Leuchttürme. Fresnellinsen können auch aus Kunststoff gepresst werden und finden dann unter anderem in Tageslichtprojektoren und bei einfachen Handlupen Verwendung. Im Falle der Ringleuchte nach der hier vorliegenden Erfindung wird eine weitere, besonders vorteilhafte Weiterbildung dadurch erreicht, dass die Fresnellinse als eine höchstens 2 mm dicke transparente, biegsame Folie ausgebildet ist. Durch die geringe Dicke der als Folie gepressten Fresnellinse lässt sie sich biegen und dem Innenradius des die Lichtquelle bildenden Hohlzylinders anpassen. Wenn die Brennweite der Fresnellinse so ausgelegt ist, dass sie gleich dem Abstand zwischen den Leuchtdioden und der Fresnellinse ist, werden die Lichtstrahlen der Leuchtdioden aus der Fresnellinse genau in die Radialebene des Hohlzylinders abgelenkt und dadurch die Dicke der Lichtscheibe bei maximaler Ausnutzung des von den Leuchtdioden gelieferten Lichtstroms bestimmt.

Eine nächste vorteilhafte Weiterbildung der Ringleuchte nach der Erfindung ergibt sich, wenn eine weitere fokussierende Linse, die als dritter, glattwandiger, nicht weiter strukturierter Hohlzylinder ausgebildet und in der Länge mit der einen fokussierenden Linse identisch ist, mit dieser achsen- und längenkongruent angeordnet ist. Der Außenradius dieses dritten Hohlzylinders dient als Aufnahme für die Fresnellinse, deren biegsame Folie einen steifen Körper als formende Anlagefläche benötigt. Die durch den glattwandigen und nicht weiter strukturierten dritten Hohlzylinder gebildete Linse beugt die Lichtstrahlen der Leuchtdioden horizontal weiter auf die Achse der Lichtquelle zu und sorgt so für eine verbesserte Lichtausrichtung ins Innere der Ringleuchte.

Eine vorteilhafte Weiterbildung der Ringleuchte nach der Erfindung ergibt sich weiterhin, wenn die Lichtquelle und das Linsensystem in ein druckfestes Gehäuse aus einer äußeren und einer inneren zylinderförmigen Wandung und einem oberen und einem unteren ringförmigen Deckel mit je einer Öffnung derart eingeschlossen sind, dass der Innenraum der innersten, als dritter Hohlzylinder ausgebildeten weiteren Linse frei bleibt. Damit ist für den Einsatz unter Wasser die Voraussetzung geschaffen. Die empfindlichen elektrischen Teile sind vor dem Meerwasser wirksam geschützt und der Strömungskanal im Innenraum der Ringleuchte, in dem die Lichtscheibe erzeugt wird und sich die abzubildenden Objekte ungestört bewegen können, bleibt frei. Vorteilhaft ist weiterhin, wenn die äußere Wandung durch die als Hohlzylinder ausgebildete Lichtquelle und die innere Wandung durch die als Hohlzylinder ausgebildete weitere fokussierende Linse gebildet sind. Der die Lichtquelle

bildende Hohlzylinder wird in diesem Falle durch eine zylindrische, druckfeste Außenwand begrenzt, auf deren Innenseite die Leuchtdioden angeordnet sind. Der die Fresnellinse bildende weitere Hohlzylinder markiert mit seinem Außenradius den Innenradius der Lichtquelle. Der die weitere Linse bildende dritte Hohlzylinder, der auf seinem Außenradius die Fresnellinse aufnimmt, ist als druckfeste Innenwandung des Gehäuses ausgelegt und bezeichnet mit seinem Innenradius gleichzeitig den Innenradius des Gehäuses und damit der Ringleuchte. Je ein druckfester, als Ring mit Öffnung ausgelegter Deckel am oberen und unteren Ende der Hohlzylinder komplettiert das Gehäuse und definiert die Gesamtabmessungen der Ringleuchte. Die Außenradien der Deckel entsprechen dem Außenradius der Lichtquelle und die Innenradien der Deckel entsprechen dem Innenradius der weiteren Linse. Damit ist der Innenraum der Ringleuchte mit der Lichtscheibe zur Durchströmung offen und die Lichtquelle vor Einflüssen durch das strömende Medium geschützt.

Eine besonders vorteilhafte, spezielle Ausführung der Ringleuchte nach der Erfindung ergibt sich, wenn der Außenradius des druckfesten Gehäuses im Bereich zwischen 100 mm und 150 mm und sein Innenradius im Bereich zwischen 40 mm und 60 mm liegt und die Länge der die Lichtquelle und das Linsensystem bildenden Hohlzylinder nicht mehr als 10 mm und die Gesamtlänge der Ringleuchte nicht mehr als 40 mm beträgt.

Ausführungsbeispiele

Ausbildungsformen der Ringleuchte nach der Erfindung werden nachfolgend anhand der schematischen Figuren näher erläutert. Dabei zeigt:

Figur 1	eine Draufsicht einer Ringleuchte ohne oberen Deckel,
Figur 2	einen Schnitt entlang der Markierung X-X in Figur 1,
Figur 3	eine perspektivische Ansicht eines Ausschnitts der Ringleuchte gemäß Figur 1 und
Figur 4	den Strahlengang der Ringleuchte gemäß Figur 1.

Figur 1 zeigt eine Ringleuchte **RL** für den möglichen Einsatz in einem Video-Plankton-Rekorder in der Draufsicht ohne den oberen Deckel **DO**. Ganz außen ist die Lichtquelle **LQ** angeordnet, die als Hohlzylinder **H1** ausgebildet ist. Seine Außenkontur **A1** markiert gleichzeitig die äußere Berandung **AG** des die Ringleuchte **RL** umschließenden druckfesten Gehäuses **DG**. Seine Innenkontur **I1** ist gleichzeitig die Außenkontur **A2** des die eine fokussierende Linse **LE** bildenden weiteren Hohlzylinders **H2**. Die eine fokussierende Linse **LE** ist dabei als in eine weniger als 2 mm dicke biegsame Folie gepresste Fresnellinse **FL** ausgebildet. Die als Hohlzylinder **H2** ausgebildete Fresnellinse **FL** ist mit ihrer Innenkontur **I2** fest an die Außenkontur **A3** des die weitere fokussierende Linse **LW** bildenden Hohlzylinders **H3** angelegt. Die weitere fokussierende Linse **LW** ist ein einfacher, nicht weiter strukturierter Körper, der mit seiner Innenkontur **I3** gleichzeitig die innere Berandung **IG** des die Ringleuchte **RL** umschließenden druckfesten Gehäuses **DG** bildet. Die Fresnellinse **FL** und die weitere Linse **LW** bilden zusammen das Linsensystem **LY**. Die hier nicht weiter dargestellten oberen und unteren Deckel **DO, DU**, die jeweils eine Öffnung **OE** von der Größe des Innenradius **I3** des Gehäuses **DG** aufweisen, vervollständigen das druckfeste Gehäuse **DG**. Der Innenraum **IB** der Ringleuchte **RL**, der sich innerhalb der inneren Berandung **IG** des druckfesten Gehäuses **DG** befindet, bleibt an den Enden offen und stellt den von der Lichtquelle **LQ** beleuchteten Strömungskanal **SK** dar, der der Beobachtung und Abbildung hindurchtretender Objekte dient. Die Lichtquelle **LQ** weist

Leuchtdioden **LD** als Leuchtmittel **LM** auf. Die Leuchtdioden **LD** sind dabei an einem Zwischenradius **ZR** der als Hohlzylinder **H1** ausgebildeten Lichtquelle **LQ** gleichmäßig verteilt angeordnet, der gleichzeitig die innere Berandung der äußeren Wandung **WA** des die Ringleuchte **RL** umschließenden druckfesten Gehäuses **DG** bildet. Das von den Leuchtdioden **LD** abgestrahlte Licht **LL** durchquert den Luftraum **L1** in dem Hohlzylinder **H1**, wird von der Fresnellinse **FL** aufgenommen und auf das Zentrum **ZB** der Ringleuchte **RL** fokussiert. Durch die weitere Linse **LW**, die die innere Wandung **WI** des Gehäuses **DG** bildet und eine bikonvexe Form aufweist, wird das Licht **LL** weiter verdichtet. An der Innenkontur **I3** der weiteren Linse **LW** tritt das Licht **LL** schließlich in den Innenraum **IB** der Ringleuchte **RL** aus und verbreitet sich wegen vielfacher Reflexionen in der Radialebene **RE** an der gegenüberliegenden Wand der weiteren Linse **LW** gleichmäßig. Die Wandungen **WA, WI** des Gehäuses **DG** weisen Schraubenlöcher **SL** auf, durch die sie mit den Deckeln **DO, DU** verschraubt und zum Gehäuse **DG** komplettiert werden. Um die Leuchtdioden **LD** vor Feuchtigkeit und das Eindringen von Druckwasser zu schützen, sind zwischen den Wandungen **WA, WI** und den Deckeln **DO,DU** O-Ring-Dichtungen **OD** vorgesehen. Sie liegen in Nuten **ON**, die in die Wandungen **WA, WI** eingelassen sind. Die O-Ring-Dichtungen **OD** in der inneren Wandung **WI** dienen gleichzeitig als ringförmige, im Strahlengang hinter der einen fokussierenden Linse **LE** zentriert angeordnete Aperturblenden **AB** für das Licht **LL** zur Beleuchtung des begrenzten Volumen **BV** und vermindern so weiter die Lichtstreuung außerhalb der Lichtscheibe **LS**, für die die Zeichnungsebene gleichzeitig die Radialebene **RE** darstellt.

Figur 2 stellt einen Schnitt entlang der Linie X-X in Figur 1 dar. Es sind die oberen und unteren Deckel **DO, DU** mit ihren Öffnungen **OE** dargestellt, die mit Schrauben **SG** in den Schraubenlöchern **SL** das druckfeste Gehäuse **DG** zusammenspannen. Auch wird die Anordnung der O-Ring-Dichtungen **OD** deutlich, die in den Nuten **ON** der fokussierenden Linse **LW** des Linsensystems **LY** und der äußeren Wandung **WA** liegen und einerseits das Innere der Lichtquelle **LQ** vor eindringendem Wasser schützen und andererseits als Aperturblenden **AB** das Licht **LL** auf die Lichtscheibe **LS** und damit auf das begrenzte Volumen **BV** beschränken und die Streuung vermindern. Bei kurzen Hohlzylindern **H1, H2, H3** wird die Gesamtlänge **HG** der Ringleuchte **RL** und damit die Länge **HL** der Lichtscheibe **LS** gering. Als Zahlenbeispiel wird ein Außenradius **A1** von 100 bis 150 mm, ein Innenradius **I3** von 40 bis 60 mm, eine Gesamtlänge **HG** von kleiner oder gleich 40 mm und eine Länge **HL** der Lichtscheibe **LS** von kleiner oder gleich 10 mm genannt. Andere Abmessungen sind ebenfalls möglich.

Figur 3 zeigt eine perspektivische Ansicht eines Ausschnitts aus Figur 1. Sie dient der weiteren Veranschaulichung des Aufbaus der Ringleuchte **RL**, enthält aber keine darüber hinaus gehenden Einzelheiten. Im Wesentlichen werden die Nuten **ON** mit den als Aperturblenden **AB** wirkenden O-Ring-Dichtungen **OD** in den Wandungen **WA, WI** sowie die Anordnung der Schraubenlöcher **SL** außerhalb der O-Ring-Dichtungen **OD** in Bezug auf den Luftraum **L1** gezeigt.

Figur 4 zeigt schließlich den Strahlengang des Lichts **LL** von der Leuchtdiode **LD** auf der äußeren Wandung **WA** durch den Luftraum **L1**, durch das Linsensystem **LY** mit der einen fokussierende Linse **LE**, die als Fresnellinse **FL** ausgebildet ist, und der weiteren fokussierenden Linse **LW**, die als einfacher, nicht weiter strukturierter Körper ausgebildet ist, in den Innenraum **IB** der Ringleuchte **RL**. Auch hier wird der Einfluss der O-Ring-Dichtung **OD** in den Nuten **ON** als Aperturblende **AB** deutlich.

Bezugszeichenliste

A1	Außenradius Hohlzylinder
A2	Außenradius weiterer Hohlzylinder
A3	Außenradius dritter Hohlzylinder
AB	Aperturblende
AG	äußere Berandung
BV	begrenztes Volumen
DG	Gehäuse
DO	oberer Deckel
DU	unteren Deckel
FL	Fresnellinse
H1	Hohlzylinder
H2	weiterer Hohlzylinder
H3	dritter Hohlzylinder
HG	Gesamtlänge
HL	Länge der Lichtscheibe
I1	Innenradius Hohlzylinder
I2	Innenradius weiterer Hohlzylinder
I3	Innenradius dritter Hohlzylinder
IB	Innenraum
IG	innere Berandung
L1	Luftraum
LD	Leuchtdiode
LE	eine fokussierende Linse
LL	Licht
LM	Leuchtmittel
LQ	Lichtquelle
LS	Lichtscheibe
LW	weitere fokussierende Linse
LY	Linsensystem
OD	O-Ring-Dichtung
OE	Öffnung
ON	Nuten
RE	Radialebene
RL	Ringleuchte
SG	Schraube
SK	Strömungskanal
SL	Schraubenlöcher
WA	äußere Wandung
WI	innere Wandung
ZB	Zentrum
ZR	Zwischenradius

Schutzansprüche

1. Ringleuchte mit einer als Hohlzylinder ausgebildeten Lichtquelle mit einer auf die Achse des Hohlzylinders weisenden Lichtabstrahlrichtung, mit Leuchtdioden für weißes Licht als Leuchtmittel und mit einer Einrichtung zur Lenkung der Lichtabstrahlung,
dadaurch gekennzeichnet, dass
die Einrichtung zur Lenkung der Lichtabstrahlung ein Linsensystem (LY) ist, das zumindest eine exakt in die orthogonal zur Achse des die Lichtquelle (LQ) bildenden Hohlzylinders (H1) orientierte Radialebene (RE) fokussierende Linse (LE), die als weiterer Hohlzylinder (H2) ausgebildet ist, und eine ringförmige, im Strahlengang hinter der einen fokussierenden Linse (LE) zentriert angeordnete Aperturblende (AB) aufweist, und dass die Lichtquelle (LQ) und das Linsensystem (LY) in der Länge identisch und sowohl achsen- als auch längenkongruent angeordnet sind, wobei die vom Innenradius (I3) des Linsensystems (LY) bestimmte Querschnittsfläche und die Länge des Linsensystems (LY) ein streng begrenztes Volumen (BV) aufspannen.

2. Ringleuchte nach Anspruch 1,
dadurch gekennzeichnet, dass
die eine fokussierende Linse (LE) eine Fresnellinse (FL) ist.

3. Ringleuchte nach Anspruch 2,
dadurch gekennzeichnet, dass
die Fresnellinse (FL) als eine höchstens 2 mm dicke transparente, biegsame Folie ausgebildet ist.

4. Ringleuchte nach einem der Ansprüche 1 bis 3,
dadurch gekennzeichnet, dass
das Linsensystem (LY) eine weitere fokussierende Linse (LW) aufweist, die als dritter, glattwandiger, nicht weiter strukturierter Hohlzylinder (H3) ausgebildet ist, der in der Länge mit der einen fokussierenden Linse (LE) identisch und mit dieser achsen- und längenkongruent angeordnet ist.

5. Ringleuchte nach einem der Ansprüche 1 bis 4,
dadurch gekennzeichnet, dass
die Lichtquelle (LQ) und das Linsensystem (LY) in ein druckfestes Gehäuse (DG) aus einer äußeren und einer inneren zylinderförmigen Wandung (WA, WI) und einem oberen und einem unteren ringförmigen Deckel (DO, DU) mit je einer Öffnung (OE) eingeschlossen sind.

6. Ringleuchte nach Anspruch 5,
dadurch gekennzeichnet, dass
die äußere Wandung (WA) durch die als Hohlzylinder (H1) ausgebildete Lichtquelle (LQ) und die innere Wandung (WI) durch die als Hohlzylinder (H3) ausgebildete weitere fokussierende Linse (LW) gebildet sind.

7. Ringleuchte nach Anspruch 6,
dadurch gekennzeichnet, dass
die Aperturblende als an die Deckel (DO, DU) anschließende, in die Stirnseiten des die weitere fokussierende Linse (LW) bildenden Hohlzylinders (H3) als innerer Wandung (WI)

eingelassene und und damit im Strahlengang der Lichtquelle (LQ) und des Linsensystems (LY) angeordnete O-Ring-Dichtungen (OD) ausgebildet ist.

8. Ringleuchte nach einem der Ansprüche 5 bis 7,
dadurch gekennzeichnet, dass
der Außenradius (A1) des druckfesten Gehäuses (DG) im Bereich zwischen 100 mm und 150 mm und sein Innenradius (I3) im Bereich zwischen 40 mm und 60 mm liegt und die Länge der die Lichtquelle (LQ) und das Linsensystem (LY) bildenden Hohlzylinder (H1, H2, H3) nicht mehr als 10 mm und die Gesamtlänge der Ringleuchte (RL) nicht mehr als 40 mm beträgt.

9. Anwendung der Ringleuchte nach einem der Ansprüche 1 bis 8, **gekennzeichnet durch** eine Anordnung als Beleuchtungsvorrichtung in einem Video-Plankton-Rekorder.

Zusammenfassung

Ringleuchten werden als Objektbeleuchtung an Kameras, Mikroskopen usw. und bei Partikeldetektoren, z.B. Video-Plankton-Rekordern (VPR) eingesetzt. Ringleuchten mit nach innen abstrahlenden Lichtquellen als ringförmige Leuchtstofflampen und ringförmig angeordnete Leuchtdioden sind bekannt. Das Licht wird nachteilig bezüglich des Einsatzes in einem VPR nicht auf ein scharf begrenztes Volumen fokussiert. Die erfindungsgemäße Ringleuchte (RL) vermeidet diesen Nachteil, indem sie das Licht (LL) der Lichtquelle (LQ) mit Hilfe einer zylinderförmigen Fresnellinse (FL) gleicher Länge exakt in Richtung ihrer Radialebene (RE) fokussiert und so eine in allen drei Dimensionen scharf begrenzte Lichtscheibe (LS) erzeugt. Eine ringförmige Aperturblende (AB) im Strahlengang unterstützt diese Begrenzung. Die Lichtquelle (LQ) wird von einem druckfesten Gehäuse (DG) zum Unterwassereinsatz umgeben, das gleichzeitig Lichtstreuung in die Umgebung der Lichtscheibe (LS) vermeidet. Die Dicke der Lichtscheibe (LS) ist nur von der Länge der Lichtquelle (LQ) und der Fresnellinse (FL) abhängig und kann für die genaue Abbildung von Partikeln sehr dünn, d.h. im Bereich der Dicke der größten zu erwartenden Partikel gehalten werden.

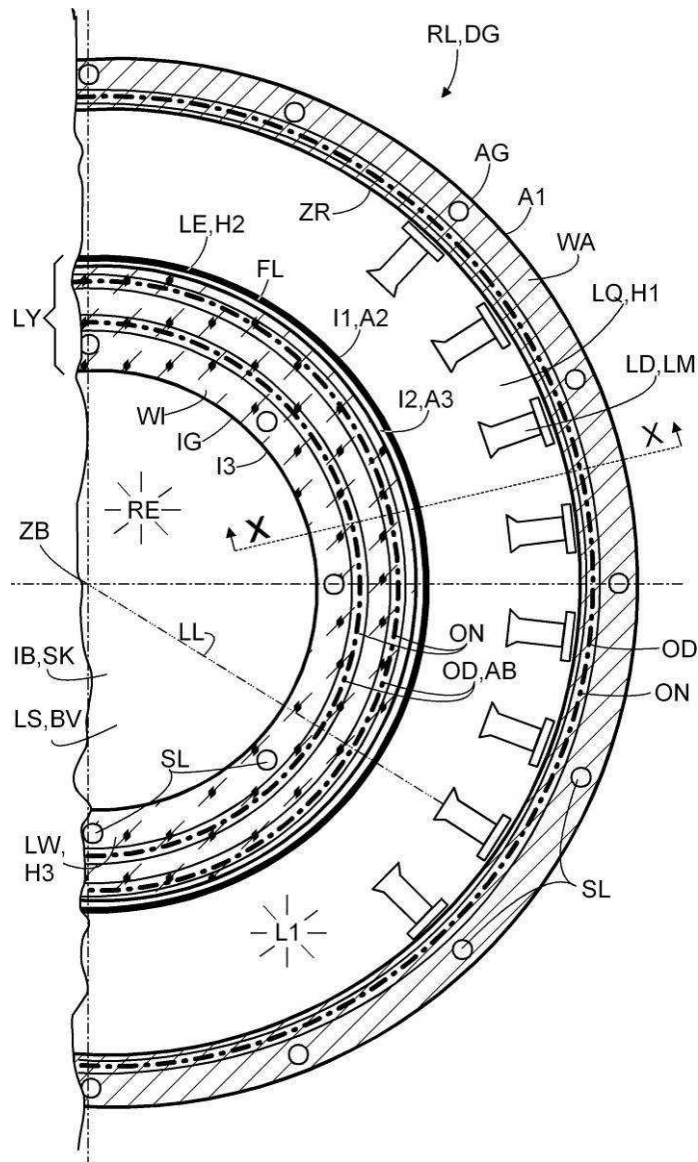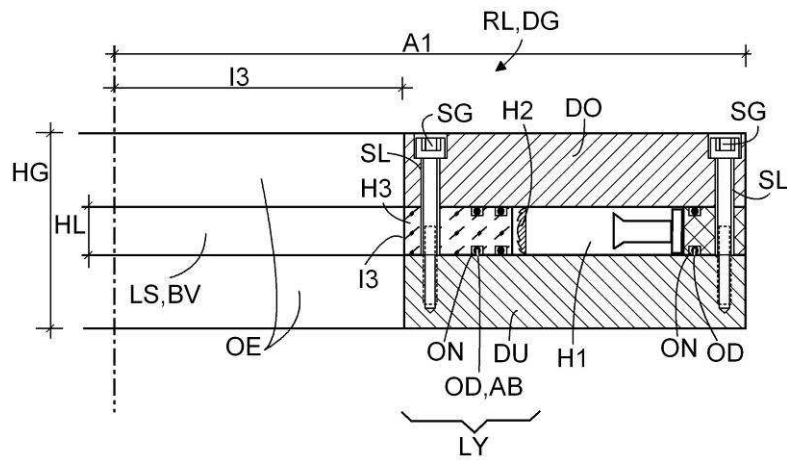Signifikante Figur für die Zusammenfassung: **Figur 1**

Fig. 1

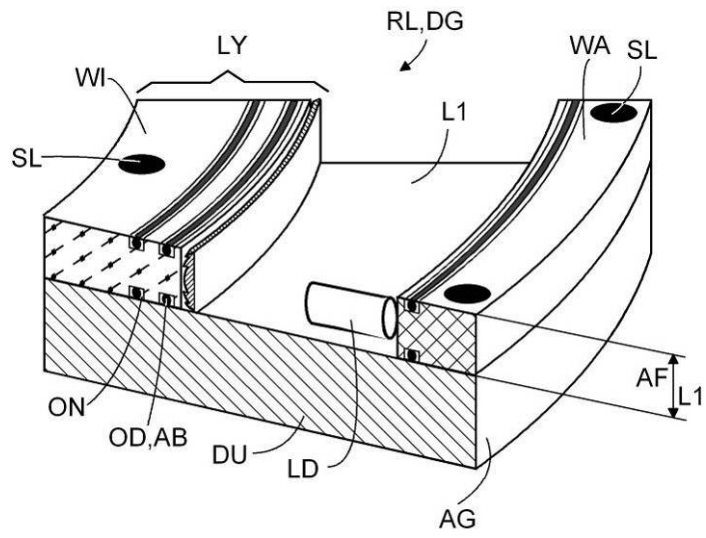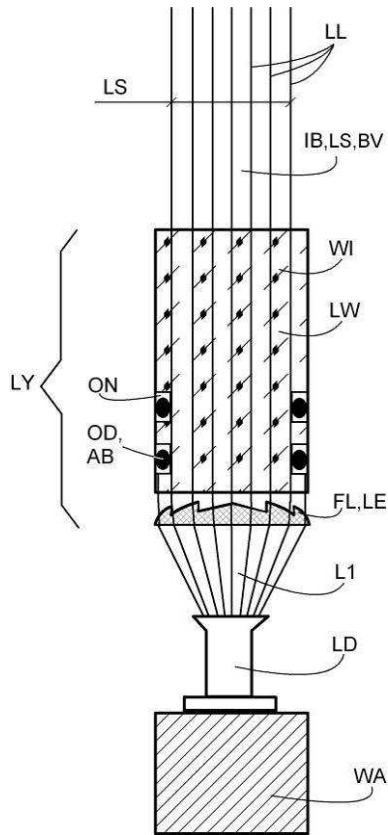

Fig. 2
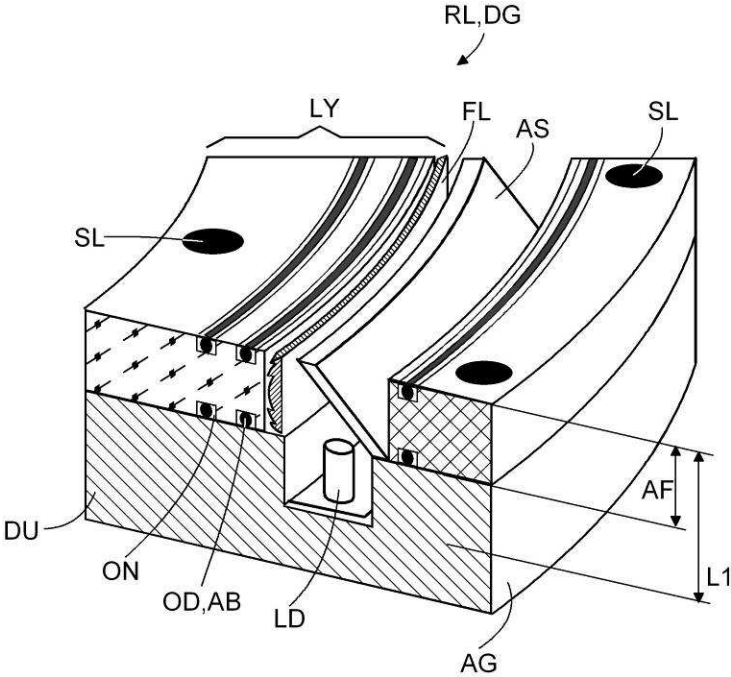
Fig. 3

Fig. 4

Fig. 5

5. Synopsis

5.1. Zooplankton of the Baltic Sea

5.1.1. Vertical distribution

To clarify the central hypothesis whether the vertical zooplankton composition in the Bornholm Sea changes with different hydrographic parameters, it was necessary to determine whether samples from different layers can be distinguished by their species composition. To achieve this goal multivariate statistical analyses and conventional techniques were used. The results show that the characteristic stratification of the Bornholm Sea divides the water column into zones, differently inhabited by zooplankton species. The physical outlines of these zones are defined by different combinations of temperature and salinity. Consequently, two zones are present during winter, when the halocline separates the high saline bottom water from the lower saline intermediate winter water above. Three zones are found after the formation of the thermocline during summer. The intermediate winter water is then compressed by the seasonal summer water. The inhomogeneous utilisation of the zones indicates that they are of heterogeneous ecological importance and can be conceived as distinct habitats. To survive under these hydrographic conditions species are impelled to utilise one or several of these habitats according to their ecophysiological tolerances (Paper Z1-Z3). None of the investigated zooplankton species and developmental stages utilised all available habitats. No direct evidence was found, that the inflow waters differed significantly from the stagnant haline waters in species composition. The limited number of habitats results in five categorical utilisation modes (Figure 5.1) that group similar strategies of utilisation. Every utilisation mode (mode I-V) is characterised by at least one dominant species:

I. The first mode includes species which are most abundant during the warm season and mainly restricted to the area above the thermocline (Figure 5.1a). Although they can become an eminent part of the zooplankton community they are only seasonally present. The endemic and due to parthenogenesis fast reproducing cladoceran *Bosmina coregoni maritima* is the dominant species of mode I. Furthermore, the cladoceran *Podon intermedius* and all developmental stages of *Eurytemora* sp. are most abun-

dant in the warm surface layer, but more or less completely absent during the rest of the year.

II. Species assigned to the second mode are abundant the whole year round and seasonally take advantage of the warm surface layer. They access the volume above the thermocline during summer and reside in the winter water for the rest of the year (Figure 5.1b). The copepod *Acartia bifilosa* is the dominant species of this mode. All developmental stages of *A. bifilosa* showed this behaviour. Also *Keratella* spp. and the C1-C3 stages of *Centropages hamatus* and *Temora longicornis* utilise the warm surface water when present.

III. The third mode includes species preferring the lower temperatures between the thermo- and halocline. They reside mainly in the intermediate winter water and are excluded from the surface during summer (Figure 5.1c). All developmental stages of the copepod *Acartia longiremis* are characteristic for this mode. *A. longiremis* is abundant throughout the year, but avoids the
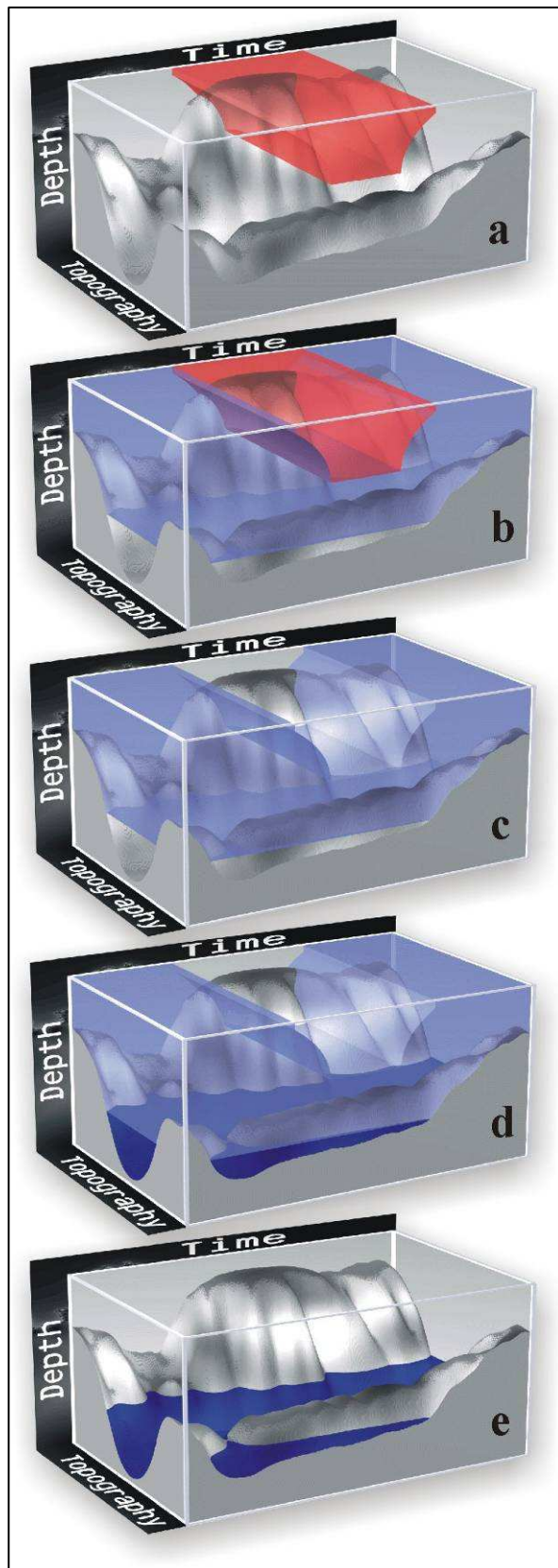
Figure 5.1: The five different utilisation modes of zooplankton in relation to hydrographic parameters as revealed by Multivariate Discriminant Function Analysis and traditional approaches. The modes include species a) that are only present when a warm surface layer is established and dwell mainly in this layer, b) that utilise the warm surface layer but are also present prior to and after the formation of this seasonally appearing habitat, c) that are present the whole year, but reside in the layer of the intermediate winter water between thermo- and halocline during summer, d) that utilise the complete water column except for the warm surface layer in summer and e) that are bound to the deep haline waters.

warm surface layer during summer. This was also found for *Synchaeta* spp. and the C4-C6 stages of *Centropages hamatus* and *Temora longicornis*.

IV. Mode four includes species that utilise the winter water and the deep haline waters. Characteristic for this mode is the appendicularian *Fritillaria borealis*. It mainly resides in the winter water before the thermocline develops. With the formation of the thermocline it migrates below the halocline. The water above the thermocline in summer is the only unused layer (Figure 5.1d).

V. Mode five includes the species living mainly below the halocline (Figure 5.1e). *Oithona similis* is a signature species of this utilisation mode. Also *Oikopleura dioica* and the C4-C6 stages of *Pseudocalanus* sp. were mainly found in the high saline waters.

Most of the investigated zooplankton taxa could be clearly assigned to one of these five modes. Different results between analyses of one station (Paper Z1) and the complete data set (nine stations covering the Bornholm Basin, Paper Z3) were obtained only for the taxa Bivalve larvae and *Pseudocalanus* sp. C1-C3 and the cladocerans *Evadne nordmanni* and *Podon leuckarti*. This might be explained by assignment problems of mean values for temperature and salinity across clines. Every net that samples through a cline contains species of two different habitats, while the algorithmic classification assigns the sample to the category where physical parameters had the greatest influence. Most of these four taxa belong to categories that usually inhabit the upper layers, but show an indifferent behaviour compared to the algorithmic definition of the layers. Bivalve larvae utilise the warm surface water, but seem to avoid the warmest and uppermost layers. *E. nordmanni* and *P. leuckarti* are most abundant when the thermocline develops or disappears. Therefore it seems appropriate to assign these taxa to mode II. Further the grouping of copepodids to only two different groups might impact the analysis, as several species show ontogenetic vertical distributions or sex differences. This applies at least to the C1-C3 stages of *Pseudocalanus* sp. (Renz & Hirche 2005). The data suggest that they have to be assigned to mode IV. As the samples used for the analyses were taken regardless of daytime a possible diel vertical migration (DVM) might also have influenced the results. However, the DVM is reduced in the Baltic Sea (e.g. Titelman & Fiksen 2004, Schmidt 2006) and has recently been reported to occur only in *Acartia longiremis* and *Temora longicornis* (Schmidt 2006). During summer the depth centroid of *T. longicornis* was found at approximately 20 m at night and 60 m during the day, while *A. longiremis* performed DVM in the depth range of the thermo-

cline (Schmidt 2006). Both species showed lower abundances in the uppermost layer, when temperatures were highest. Therefore the assignment to vertical distribution modes defined by the ambient temperature and salinity may be a simplification and not necessarily the primordial causal connection. This can be seen in *Fritillaria borealis*, a presumptive glacial relict species, which is capable of utilising the low saline surface layer. During summer *F. borealis* protrudes down into the haline waters, although a layer of the cool intermediate winter water is still present (Paper Z2). This may be due to the fact that in the density gradient of the halocline organisms and particles of size classes sufficient for its feeding can accumulate (Lande & Wood 1987, MacIntyre et al. 1995, Vallin & Nissling 2000). The period during which *Keratella* spp. showed high abundances was found in a time frame that started a few weeks prior and lasted a few weeks longer than the persistence of the algorithmic defined *SUMMER* category. The temperature threshold of 8°C for this category was chosen for proper identification of the thermal stratification. The beginning of this stratification was already observed below the chosen temperature threshold. Thus, it can be suggested that *Keratella* spp. should be seen as a summer species and assigned to mode I.

5.1.2. Ecological implications

The modes identified during this study can be conceived as functional groups representing major life strategies of the zooplankton species in the Bornholm Sea. Subsequently, species within the same group share equal environmental conditions and compete with each other for resources during times of synchronous appearance or intersection of their habitats. This results in a concept similar to the definition of guilds[8] and is of importance for a variety of different processes. Beside a direct impact on the food web structure it bears also implications for theoretical ecology and modelling aspects. The assignment of the dominant zooplankton species to vertically separated habitats helps to explain differences in zooplankton distribution between shallow and deep sites. Species sensitive to higher temperatures are expelled from shallow areas where the thermocline contacts the seafloor (Figure 5.1c-d). A stable stratification reduces vertical mixing and excludes species of the modes III and IV for a longer period from the surface. A similar mechanism is obvious for the species of mode V, captured below the halocline in the trough of the basin. In this case the inhabit-

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[8] "A guild is defined as a group of species that exploit the same class of environmental resources in a similar way. This term groups together species, without regard to taxonomic position, that overlap significantly in their niche requirements." (Root 1967).

able volume is lower at shallower sites when the halocline is close to the seabed or absent (e.g. Hansen et al. 2004, Schmidt et al. 2004). Therefore, the invasion of shallow areas is only possible when the halocline is elevated. During inflows haline waters often cascade over the sills, which separate the basins of the Baltic Sea. Thus, it is reported that species assigned to mode V are found in higher abundances in more eastern parts of the Baltic Sea after inflow events (e.g. Mankowski 1951). The environmental gradient from marine conditions in the Skagerrak towards an almost fresh water dominated system at the north eastern end that is found in the surface waters can also be seen in an alleviated form in the deep layers of the Baltic Sea (Bonsdorff 2006). The sills being higher than the halocline form natural barriers for the saline deep waters. The hindered exchange of these waters also avoids advection of zooplankton specimens assigned to mode V. Thus, the topographic separation of local populations in the troughs may enforce local differentiation of sub-populations that may subsequently constitute genetically independent lineages. A similar effect has recently been described for herring (*Clupea harengus* L.) in the Baltic Sea (Jørgensen et al. 2005). In this species the separation by the basins seems to induce barriers to gene flow. This may also apply to less mobile zooplankton species living in the troughs and being constricted in their horizontal dispersion.

Significant changes in the zooplankton structure since the 1980s (Möllmann et al. 2000, Lehman et al. 2002, Möllmann et al. 2003) are suggested to be influenced by climate changes (Alheit et al. 2005). Increasing temperatures prolonged the periods of warm surface layers (Alheit et al. 2005) and fostered stocks of *Acartia* sp. (Möllmann & Köster 2002). The large scale atmospheric conditions are influenced by the North Atlantic Oscillation (NAO, Lehmann et al. 2002). Years with high positive NAO indices are correlated with stronger than average westerly winds, as well as mild winters in Western Europe (Hurrell 1995). Mild winters prevent deep mixing and with the first signs of solar heating the water column stratifies again (Alheit et al. 2005). The summer 2002 was characterised by high temperatures and calm weather. As wind stress upwelling of the thermocline is inversely proportional to the strength of stratification (Gill 1982), the 2002 summer conditions led to a shallow and strong thermocline. Increasing rainfalls decreased salinity and induced a shift towards oligohaline species, such as the endemic cladoceran *Bosmina coregoni maritima*. It is the most abundant species in the upper layer during summer, where high temperatures foster its parthenogenetic reproduction and help to outgrow competitors and predators (Viitasalo et al. 2001). *B. coregoni maritima* abundances at levels of approximately 300.000 m^{-3} in the upper 10 m of the Bornholm Sea are some of the highest

values on record (Paper Z3). As this recording represents an integrated value from a haul, it can be expected that the abundance of this surface species showed a gradient with even higher values closer to the surface. The shallow thermocline narrowed the habitat for species assigned to mode I and II and consequently reduced the inter- and intra-species distance, which may have increased niche competition and predation pressure by fish. The hydrography in the deep layers is also related to wind and sea level pressure, which are coupled with the NAO (Matthäus & Schinke 1994, Schinke & Matthäus 1998, Lehmann et al. 2002). These atmospheric conditions drive to a large extend the inflows from the North Sea that renew the waters in the basins (Matthäus & Franck 1992, Matthäus & Schinke 1994). During periods of stagnation the deep water conditions deteriorate (Fonselius 1970) and narrow the volume of this habitat for sensitive species. The decreasing *Pseudocalanus* sp. stock in the Baltic was related to the decreasing salinity, as a consequence of the reduced frequency of inflow events since the 1980s (Möllmann et al. 2003). After inflows species assigned to mode V find an increased volume with favourable conditions, which foster *Oithona similis* (Hansen et al. 2004) and *Pseudocalanus* sp. (Renz & Hirche 2006).

The introduction of functional groups, which shape the zooplankton community vertically, fulfils the basic criteria of the *lex parsimoniae*[9] for modelling aspects. Based on this concept the estimation of available resources from abundance data can be assigned to different depths. As vertical distribution patterns differ, models concerning the availability of prey fields require the consideration of seasonal cycles as well as the inhabited strata. Therefore, 2D approaches should be treated with care in highly stratified systems. They may not be capable to differentiate resources in the depth where predators linger and need a careful interpretation respecting the spatial overlap of predators and prey.

5.1.3. Food web implications

Important consumers of the zooplankton production in the Baltic Sea are a minor number of fish species. Larvae and young-of-year of the main fish species cod (*Gadus morhua* L.), sprat (*Sprattus sprattus* L.) and herring (*Clupea harengus* L.) take up a large portion of the zooplankton production (Arrhenius & Hansson 1993) and their recruitment is related to the availability of these resources. Since the 1980s the diet composition of fish larvae showed distinct changes (Voss et al. 2003), while the stock size of cod decreased and sprat in-

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[9] "Entia non sunt multiplicanda praeter necessitatem." *Entities should not be multiplied beyond necessity.* (William of Ockham, 14th century).

creased. In addition to fisheries pressure (Bagge et al. 1994) interactions between the zoo-plankton composition in different strata of the Bornholm Sea and the depth preference of larval fish seems important, as they bias the availability of resources. Cod larvae need higher salinities for development and their main habitat is close to the halocline, where older stages of *Pseudocalanus* sp., assigned to zooplankton utilisation mode V, are the most important food items (Voss et al. 2003). Adult cod is the main piscivorous fish species in the central Baltic Sea, with sprat and herring as the dominant prey (Rudstam et al. 1994, Bagge 1989). Young and larval sprat concentrate in shallower layers (Wieland & Zuzarte 1991, Makarchouk & Hinrichsen 1998, Dickmann et al. submitted). Thus, the diet of larval sprat is dominated by the zooplankton species of the modes I and II, close to the surface. Analyses of larval sprat gut contents show high feeding rates on *Acartia* spp. and lower on *Temora longicornis*, while *Pseudocalanus* sp. is absent in the diet (Voss et al. 2003, Dickmann 2005). This may help to explain, why years with high *Acartia* spp. abundances are correlated with strong year classes of sprat (Dickmann 2005). Another surplus can be the temporal match of the *B. coregoni maritima* peak (Paper Z3) and the growth of sprat larvae in July, when the larvae become large enough to ingest this cladoceran (Dickmann 2005). Adult sprat has a shallow vertical distribution in summer, while they concentrate below 50 m the rest of the year (Köster & Schnack 1994). In these depths sprat competes with herring for *Pseudocalanus* sp. and *Temora* sp. (Möllmann & Köster 2002). Furthermore, both clupeids feed on cod eggs with rates of 20 to 100%, depressing the recruitment success of cod (Schnack & Köster 1994). Therefore, an increase in clupeids depresses the probability of strong year classes of cod and vice versa (Rudstam et al. 1994). The improved conditions for zooplankton species of the modes I and II, in concert with deteriorating conditions for species of mode V, bears obviously an at least partial explanation of the observed ecosystem shift from a gadoid towards a clupeid dominated system as a result of changes in hydrography. Furthermore, the idea of active selection (Viitasalo et al. 2001) appears as not sufficiently concise with the knowledge of the spatial predator-prey overlap. Thus, selection indices calculated from unstratified zooplankton samples not necessarily reflect active behaviour, but rather spatial heterogeneity of prey distribution in relation to the preferred depth of the predators. Preference for more active prey, due to hydrodynamic detection, is obvious (Viitasalo et al. 1998), but needs to consider the respective prey field in the vicinity of a predator.

5.2. Investigative approaches

5.2.1. Numerical ecology

The approach of a Multivariate Discriminant Function Analysis (MDFA) was successfully used in this thesis to differentiate between distinct zooplankton assemblage patterns. Today the application of this statistical approach to marine pelagic data is not common and the papers and manuscripts in this study are probably the first published applications in the field of zooplankton ecology. The MDFA turned out to be an adequate method to identify heterogeneities in the vertical distribution of the zooplankton community, in relation to the hydrography of the Bornholm Sea. In contrast to similarity based methods (Clarke & Warwick 1994) MDFA takes abundance variations into account and is less sensitive to joint absence or presence between two sites (Zuur et al. in press). The method allows determining the impact of a single variable and the examination of proportional differences. Abundance variations are retained and not reduced to binary flags during the identification of similarities (e.g. adjacency matrices and similar approaches, like Jaccard-Index, Sörensen-Index; confer Legendre & Legendre 1986). As most multivariate methods MDFA requires to satisfy initial assumptions and the power of the model is prone to a violation of these. Collinearities may be present when two or more variables respond equally to the same combination of parameters or may be artificially created when integrated or averaged values are linked. Artificial dependencies can result in ill-conditioned matrices and lower the statistical power of a model. Multivariate normality is also seldom achieved in ecological data and often seems to be ignored. The advantage of the MDFA is that normality is not required for the method itself (Hair et al. 1998). If normality is not achieved the significance of the model can be determined by other methods, like Wilk's Lambda (Rao 1951).

The modules included in the software package Ocean Sneaker's Tool (OST) reflect the requirements that arose during the analysis and visualisation of several parameters presented in this thesis (Paper S1). As the specific needs are not restricted to this thesis it was made available to the public[10]. Today OST is referenced by several international institutes, projects and data centres. Among these are the Alfred Wegener Institute[11], Censor[12], Pangaea[13] and the Ocean Teacher Program of the Intergovernmental Oceanographic Commis-

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[10] http://www.awi.de/Software/OST
[11] http://www.awi.de
[12] http://www.censor.name
[13] http://www.pangaea.de/

sion/UNESCO[14], where it is listed as one of the official tools to convert different formats of geographic positions (Paper S1). Further developments are in progress and include a numerical library. Emphasis is put on the multivariate investigation of data from the zooplankton imaging system under development (Chapter 4.3). This allows combining observations on single species with the ambient environmental conditions. An observation on n variables can be conceived as an object in an n-dimensional space. In terms of species it is able to correlate n ambient environmental parameters for every observation of an individual. Plotted in the multidimensional space observations with similar properties form clusters and groups. Significant differences between taxa result in discriminable clusters in such a space. Along the axes for which a species shows a stenoecious capability small scatter is expected, while scatter increases on axes on which species show euryoecious tolerances. The fringes of the cluster span the ecological range that a species tolerates on the observed n parameters. Distances between single observations and the centroid of a respective cluster can be expressed as the observations probability to belong to this cluster. Interactions between two or more species can only be expected when at least small intersections in the multivariate space exist and allow a more detailed insight than with broad integration intrinsic to sample sets collected by plankton nets.

5.2.2. Optical methods for the remote sensing of zooplankton

The developments conducted during this thesis have reached a status to image species and particles in relation to the ambient parameters. It should help to gather auxiliary information on the fine scale distribution of zooplankton species. With the introduced illumination devices (Document T1-T5) it is possible to capture sufficiently illuminated images of tiny zooplankton species. The aim to image volumes of two times two centimetres with a small depth range is close to the limit that can be achieved under the principal laws of optics (Paper T2). While laboratory conditions deliver remarkable results (Figure 5.2), under insitu conditions debris and suspended sediments blur images. Therefore, it seems impossible with current day technology to achieve the same taxonomic identification rate as with conventional enumeration under a microscope. The great advantages however, are small scale investigations over short periods of time in regions inaccessible with plankton nets. Images are digitally linked with the environmental parameters and can easily be sorted by individual parameters and investigated for characteristic species compositions.

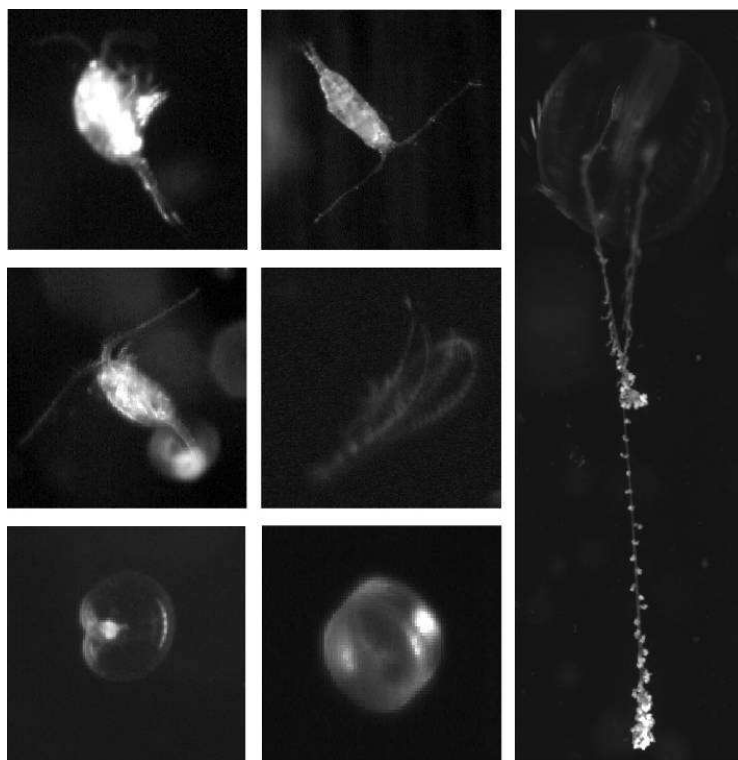[14] http://ioc.unesco.org/oceanteacher/oceanteacher2/TOC.htm

Figure 5.2: Examples of North Sea plankton including different species and size classes. Images were taken by a circular LOKI system and the developed prototype.

5.3. Outlook

To understand the inhomogeneous distribution of species in stratified systems and the constraints set up by the clines improves our idea of how physical forcing and climate can affect food web structures. Interactions between different trophic levels can be triggered by the segregation of the zooplankton community and have profound impact on the ecosystem functioning. It can be expected that the properties identified for the central Baltic Sea, might also be found in other seas and aquatic areas. However, the ultimate characteristic depends on the strength of the formed gradient between two strata. It has been noted for different parts of the world that climatic changes appear synchronously with alterations in hydrography and the zooplankton compositions in distinct layers (e.g. Barents Sea: Orlova et al. 2002; California Current: Roemmich & McGowan 1995; Fjords: Gorsky et al. 2000). Especially climatic influence that prolongs the period of a warm surface layer can drive elusive ecological effects cascading throughout stratified marine systems. The complex interactions that are induced by an increase in temperature are often less obvious and just allow to consider that changes appear (e.g. Roemmich & McGowan 1995). In the adjacent

North Sea profound changes in the fish community have been observed too, but can not directly be related to a change in temperature (Beare et al. 2004). Also in frontal systems horizontal and vertical gradients determine the distribution of different taxa (e.g. Neuenfeldt 2002, Escribano et al. 2004). Thus, the identification of functional groups like the five utilisation modes in the Bornholm Basin may improve the understanding of food-web structures.

To overcome the limitations of sampling zooplankton with nets, the introduced optical methods for remote sensing of zooplankton may emerge as a promising option. A universal interface allows the connection of a variety of different sensors for measuring environmental parameters. Due to the standardised communication protocol between the developed equipment and a remote control station it is possible to deploy the units continuously on unmanned platforms. The merging of data from different positions and the evaluation can then be performed by operators in a data centre, without time consuming and expensive cruises (Figure 5.3).
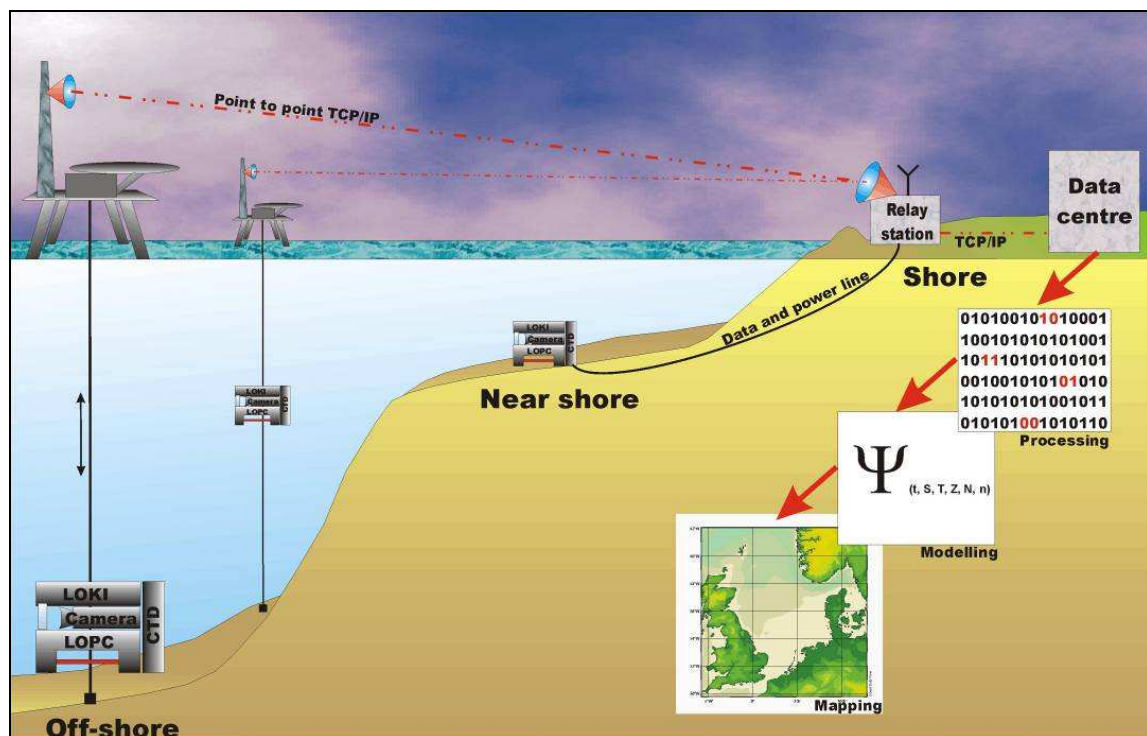

Figure 5.3: A possible zooplankton observing network to enhance traditional methods of zooplankton sampling.

6. Acknowledgements

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7. References cited

Ackefors H (1969) Ecological zooplankton investigations in the Baltic Proper 1963-1965. Fish Bd Sweden, Inst Mar Res, Ser Biol Rep No. 18

Alheit J, Möllmann C, Dutz J, Kornilovs G, Loewe P, Mohrholz V, Wasmund N (2005) Synchronous ecological regime shifts in the Central Baltic and North Sea in the late 1980s. ICES J Mar Sci doi 10.1016/j.icesjms.2005.04.024

Alldredge AL, Robinson BH, Fleminger A, Torres JJ, King JM, Hamner WM (1984) Direct sampling and in situ observation of a persistent copepod aggregation in the mesopelagic zone of the Santa Barbara Basin. Mar Biol 80:75-81

Andrén E, Andrén T, Sohlenius G (2000) The Holocene history of the southwestern Baltic Sea as reflected in a sediment core from the Bornholm Basin. Boreas 29:233-250

Andrén T, Lindeberg G, Andrén E (2002) Evidence of the final drainage of the Baltic Ice Lake and the brackish phase of the Yoldia Sea in glacial varves from the Baltic Sea. Boreas 31:226-238

Arrhenius F, Hansson S (1993) Food consumption of larval, young and adult herring and sprat in the Baltic Sea. Mar Ecol Prog Ser 96:125-137

Bagge O (1989) A review of investigations of the predation by cod in the Baltic. Rapp PV Réun CIEM 190:51-56

Bagge O, Thurow F, Steffensen E, Bay J (1994) The Baltic Cod. Dana 10:1-28

Banse K (1964) On the vertical distribution of zooplankton in the sea. Prog Oceanogr 2:53-125

Benfield MC, Shaw RF, Schwehm C (2000) Development of a vertically profiling, high-resolution, digital still camera system. ONR Ann Rep Office Nav Res, NR Grant No.: N00014-98-1-0563, pp 6

Bergeron E, Bowen AD, Hersey WJ, Lange W, Strickler JR (1988) Reaching the ultimate goal: Observing live zooplankton in situ. EOS 69(44):1087

Bollens SM, Frost BW (1989) Diel vertical migration in zooplankton: Rapid individual response to predators. J Plank Res 13(6):1359-1365

Bonsdorff E (2006) Zoobenthic diversity-gradients in the Baltic Sea: Continuous post-glacial succession in a stressed ecosystem. J Exp Mar Biol Ecol 330:383-391

Brogmus W (1952) Eine Revision des Wasserhaushalts der Ostsee. Kieler Meeresforschungen 9(1):15-42

Brown J, Colling A, Park D, Phillips J, Rothery D, Wright J (1998) Ocean circulation. Bearman G (ed), The Open University, Walton Hall, England, pp 238

Clarke KR, Warwick RM (1994) Change in marine communities: An approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth, United Kingdom, pp 144

Colton JB, Green JR, Byron R.R, Frisella (1980) Bongo net retention rates as effected by towing speed and mesh size. Can J Fish Aquat Sci 37:606-623

Cowles TJ, Desiderio RA, Carr ME (1998) Small scale planktonic structure: persistence and trophic consequences. Oceanography 11:4-9

Cushing DH (1975) Marine Ecology and Fisheries. Cambridge University press, pp 1-292

Cushing DH (1990) Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. Adv Mar Biol 26:249-294

Dagg M (1977) Some effects of patchy food environments on copepods. Limnol Oceanogr 22:99-107

Darwin C (1859) On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray publishing, Albemarle Street, London

Davis CS, Gallager SM, Marra M, Stwart WK (1996) Rapid visualization of plankton abundance and taxonomic composition using the video plankton recorder. Deep Sea Res 43:1947-1970

Denman KL, Gargett AE (1988) Multiple thermoclines are barriers to vertical exchange in the subarctic Pacific during SUPER, May 1984. J Mar Res 46:77-103

Dickmann M (2005) Feeding ecology of sprat (*Sprattus sprattus* L.) and sardine (*Sardina pilchardus* W.) larvae in the Baltic Sea and North Sea. PhD thesis, University of Rostock, Germany, pp 95

Dickmann M, Möllmann C, Voss R (submitted) Feeding ecology of central Baltic sprat (*Sprattus sprattus* L.) larvae in relation to zooplankton dynamics – Implications for survival. Mar Ecol Prog Ser

Dippner JW, Ornilovs G, Sidrevics L (2000) Long-term variability of mesozooplankton in the Central Baltic Sea. J Mar Sys 25:23-31.

Elmgren R, Rosenberg R, Andersin AB, Evans S, Kangas P, Lassig J, Leppaekoski E, Varmo R (1984) Benthic macro- and meiofauna in the Gulf of Bothnia (northern Baltic). Finn Mar Res, Helsinki. No. 250:3-18

Escribano R, Daneri G, Farías L, Gallardo VA, González HE, Gutiérrez D, Lange CB, Morales CE, Pizarro O, Ulloa O, Braun M (2004) Biological and chemical consequences of the 1997-1998 El Nino in the Chilean coastal upwelling system: a synthesis. Deep Sea Res II 51:2389-2411

Fager E, McGowan J (1963) Zooplankton species groups in the North Pacific. Science 140(3566):453-460

Feistel R, Nausch G, Mohrholz V, Łysiak-Pastuszak E, Seifert T, Matthäus W, Krüger S, Hansen IS (2003a) Warm Waters of Summer 2002 in the Deep Baltic. Oceanologia 45(4):571-592

Feistel R, Nausch G, Matthäus W, Hagen E (2003b) Temporal and spatial evolution of the Baltic deep water renewal in spring 2003. Oceanologia 45(4):623-642

Feistel R, Nausch G, Matthäus W, Łysiak-Pastuszak E, Seifert T, Hansen IS, Mohrholz V, Krüger S, Buch E, Hagen E (2004) Background data to the exceptionally warm inflow into the Baltic Sea in late summer of 2002. Meereswiss Ber/Mar Sci Rep Institute for Baltic Research 58:1-58

Fisher RA (1936) The utilization of multiple measurements in taxonomic problems. Ann Eugen 7:179-188

Flinkman J, Vuorinen I, Hakala I, Salemaa H, Vaelipakka P (1993) Herring predation avoidance in the Northern Baltic copepods and mysids. ICES CM 1993/J:20

Fonselius FS (1970) On the stagnation and recent turnover of the water in the Baltic. Tellus 22(5):533-544

Foote KG (2000) Optical methods. In Harris RP, Wiebe PH, Lenz J, Skjoldal HR, Huntley M (eds). ICES zooplankton methodology manual, pp 259-295

Gallager SM, Yamazaki H, Davis CS (2004) Contribution of fine-scale vertical structure and swimming behaviour to formation of plankton layers on Georges Bank. Mar Ecol Prog Ser 267:27-43

Geller W, Pinto-Coelho R, Pauli HR (1992) The vertical distribution of zooplankton (Crustacea, Rotatoria, Ciliata) and their grazing over the diurnal and seasonal cycles in Lake Constance. Arch Hydrobiol Beih 35:79-85

References cited.

Gill AE (1982) Atmosphere-ocean dynamics. Academic Press New York, pp 662

Gorsky G, Picheral M, Stemmann L (2000) Use of the underwater video profiler for the study of aggregate dynamics in the North Mediterranean. Estuar Coast Shelf Sci 50:121-128

Hair JF, Anderson, Tatham, Black B (1998) Multivariate data analysis. Prentice Hall Pearson Education, London, pp 768

Hansen FC, Möllmann C, Schütz U, Hinrichsen HH (2004) Spatio temporal distribution of *Oithona similis* in the Bornholm Basin (Central Baltic Sea). J Plankt Res 26(6):659-668

Hansen FC, Möllmann C, Schütz U, Neumann T (2006). Spatio temporal distribution of calanoid copepods in the central Baltic Sea. J Plankt Res 28(1):39-54

Hattori H, Saito H (1997) Diel changes in vertical distribution and feeding activity of copepods in ice-covered Resolute Passage, Canadian Arctic, in spring 1992. J Mar Sys 11(1-2):205-219

Hernroth L, Ackefors H (1979) The zooplankton of the Baltic Proper. Rep Fish Bd Sweden, Inst Mar Res (2):1-60

Hurrell JW (1995) Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. Science 269:676-679

Jennrich RI (1977a) Stepwise regression. In: Enslein K, Ralston A, Wilf HS (eds), Statistical Methods for digital Computers, Wiley, New York.

Jennrich RI (1977b) Stepwise discriminant analysis. In: Enslein K, Ralston A, Wilf HS (eds), Statistical Methods for digital Computers, Wiley, New York.

Jespersen P (1940) Non-parasitic copepoda. Zoology of Iceland III(33):1-116

Jørgensen HBH, Hansen MM, Bekkevold D, Ruzzante DE, Loeschcke V (2005) Marine landscapes and population genetic structure of herring (*Clupea harengus* L.) in the Baltic Sea. Mol Ecol 14:3219-3234

Kils U (1989) On the micro-structure of micro layers, Results of an in-situ zooplankton-counter. ICES CM 1989/L:15

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

Last JM (1980) The food of twenty species of fish larvae in the west-central North Sea. In: Fisheries research technical report, MAFF Directorate of Fisheries Research, Lowestoft, 60, pp 1-44

Lalli CM, Parsons TR (1997) Biological oceanography – An introduction. Lalli CM, Parsons TR (eds), Butterworth-Heinemann, Oxford, England, pp 314

Lande R, Wood M (1987) Suspension times of particles in the upper ocean. Deep Sea Res 34:61-72

Legendre P, Legendre L (1987) Developments in numerical ecology. Proceedings of the NATO Advanced Research Workshop on Numerical Ecology at Station Marine de Roscoff, Brittany, France, June 3-11 1986, NATO ASI Series, G: Ecological Sciences Vol 14, Springer Verlag Berlin Heidelberg, pp 587

Lehmann A, Krauss W, Hinrichsen HH (2002) Effects of remote and local forcing on circulation and upwelling in the Baltic Sea. Tellus 54A:299-316

Longhurst AR, Harrison WG (1989) The biological pump: Profiles of plankton production and consumption in the upper ocean. Prog Oceanogr 22:47-123

Lunven M, Gentien P, Kononen K, Le Gall E, Daniélou MM (2003) In situ video and diffraction analysis of marine particles. Estuar Coast Shelf Sci 57:1127-1137

MacIntyre S, Alldredge AL, Gotschalk CC (1995) Accumulation of marine snow at density discontinuities in the water column. Limol Oceanogr 40:449-468

Maar M, Visser AW, Nielsen TG, Stips A, Saito H (2006) Turbulence and feeding behaviour affect the vertical distributions of *Oithona similis* and *Microsetella norwegica*. Mar Ecol Prog Ser 313:157-172

Matthäus W (1995) Natural variability and human impacts reflected in long-Term changes in the Baltic deep water conditions – A brief review. Dtsch Hydrogr Z 47(1):47-65

Makarchouk A, Hinrichsen HH (1998) The vertical distribution of ichtyoplankton in relation to the hydrographic conditions in the Eastern Baltic. ICES CM 1998/R:11

Mankowski W (1951) Biological changes in the Baltic during the last fifty years. Prace MIR w Gdyni 6:96-118

Manly BFJ (1994) Multivariate statistical methods - A Primer. Chapman and Hall, London, pp 159

Matthäus W, Frank H (1992) Characteristics of major Baltic inflows – a statistical analysis. Cont Shelf Res 12(12):1375-1400

Matthäus W, Schinke H (1994) Mean atmospheric circulation patterns associated with major Baltic inflows. Dtsch Hydrogr Z 46:321-338

Möllmann C, Kornilovs G, Sidrevics L (2000) Long-term dynamics of main mesozooplankton species in the Central Baltic Sea. J Plankt Res 22(11):2015-2038

Möllmann C, Köster FW (2002) Population dynamics of calanoid copepods and the implications of their predation by clupeid fish in the Central Baltic Sea. J Plankt Res 24(10):959-977

Möllmann C, Kornilovs G, Fetter M, Köster F W, Hinrichsen HH (2003) The marine copepod, *Pseudocalanus elongatus*, as a mediator between climate variability and fisheries in the Central Baltic Sea. Fish Oceanogr 12(4/5):360-368

Mustard AT, Conquer MD, Allen JT (2003) Laboratory evaluation of a high specification digital CMOS camera for imaging zooplankton at high towing speeds. Southampton Oceanography Centre, Internal Document No. 89, pp 17

Neuenfeldt S (2002) The influence of oxygen saturation on the distributional overlap of predator (cod, *Gadus morhua*) and prey (herring, *Clupea harengus*) in the Bornholm Basin of the Baltic Sea. Fish Oceanog 11(1):11-17

Nichols JH, Thompson AB (1991) Mesh selection of copepodite and nauplius stages of four calanoid copepod species. J Plank Res 13(3):661-671

Ohman MD (1988) Behavioural response of zooplankton to predation. Bull Mar Sci 43:530-550

Ojaveer E, Lumberg A, Ojaveer H (1998) Highlights of zooplankton dynamics in Estonian waters (Baltic Sea). ICES J Mar Sci 55:748-755

Orlova EL, Boitsov VD, Nesterova VN, Ushakov NG (2002) Composition and distribution of copepods, a major prey of capelin in the central Barents Sea, in moderate and warm years. ICES J Mar Sci 59:1053-1061

Owen RW (1989) Microscale and finescale variations of small plankton in coastal and pelagic environments. J Mar Res 47:197-240

Pollio J, Meyer R, Sivak LD (1979) Model analysis of underwater photographic and visibility systems from observed data. In: Proc Soc Photo-Optic Instr Engin, Ocean Optics 6, 208: 232-241

Rao CR (1951) An asymptotic expansion of the distribution of Wilk's criterion. Bull Int Stat Inst 33:177-181

Remane A, Schlieper C (1971) Biology of brackish water. Wiley Interscience Division John Wiles & Sons, Inc. New York-Toronto-Sydney, pp 372

Renz J, Hirche HJ (2006) Life cycle of *Pseudocalanus acuspes* Giesbrecht (Copepoda, Calanoida) in the Central Baltic Sea: I. Seasonal and spatial distribution. Mar Biol 148:567-580

Roemmich D, McGowan J (1995) Climatic warming and the decline of zooplankton in the California Current. Science 267:1324-1326

Root R (1967) The niche exploitation pattern of the blue-grey gnatcatcher. Ecol Monogr 37:317-350

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

Saito H, Hattori H (1997) Diel vertical migration and feeding rhythm of copepods in a shallow food-abundant embayment. Plankt Biol Ecol 44(1-2):13-29

Samson S, Hopkins T, Remsen A, Langebrake L, Sutten T, Patten J (2001) A system for high-resolution zooplankton imaging. IEEE J Ocean Eng 26:671-676

Schinke H, Matthäus W (1998) On the causes of Major Baltic Inflows and analysis of long time series. Cont Shelf Res 18:67-97

Schmidt JO, Möllmann C, Temming A, Herrmann JP, Flöter J, Sell A, St. John MA (2003) Unusual water mass advection affected Central Baltic key species 2: *Pseudocalanus* and the winter inflow. GLOBEC Int Newsletter 9(2):28-29

Schmidt JO (2006) Small and meso-scale distribution patterns of key copepod species in the Central Baltic Sea and their relevance for larval fish survival. PhD thesis Christian-Albrechts-University Kiel, Germany, pp 89

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

Strickler JR (1977) Observation of swimming performances of planktonic copepods. Limnol Oceanogr 22:165-170

Tang X, Stewart WK, Vincent L, Huang H, Marra M, Gallager SM, Davis CS (1998) Automatic plankton image recognition. Art Intellig Rev 12:177-199

Tiselius P (1998) An in situ video camera for plankton studies: design and preliminary observations. Mar Ecol Prog Ser 164:293-299

Titelman J, Fiksen Ø (2004) Ontogenetic vertical distribution patterns in small copepods: field observations and model predictions. Mar Ecol Prog Ser 284:49-63

Vallin L, Nissling A (2000) Maternal effects on egg size and egg buoyancy of Baltic cod, *Gadus morhua*-Implications for stock structure effects on recruitment. Fish Res 49:21-37

Viitasalo M, Koski M, Pellikka K, Johansson S (1995a) Seasonal and long-term variations in the body size of planktonic copepods in the northern Baltic Sea. Mar Biol 123:241-250.

Viitasalo M, Vuorinen I, Saesmaa S (1995b) Mesozooplankton dynamics in the northern Baltic Sea: implications of variations in hydrography and climate. J Plankton Res 17:1857–1878

Viitasalo M, Kiørboe T, Flinkman J, Pedersen LW, Visser AW (1998) Predation vulnerability of planktonic copepods: Consequences of predator foraging strategies and prey sensory abilities. Mar Ecol Prog Ser 175:129-142

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

Vinogradov ME, Flint MV, Shushkina EA (1985) Vertical distribution of mesoplankton in the open area of the Black Sea. Mar Biol 89:95-107

Voipio A (1981) The Baltic Sea. Elsevier, Amsterdam, pp 418

Voss R (2002) Recruitment processes in the larval phase: the influence of varying transport on cod and sprat larval survival. PhD thesis, Christian-Albrechts-University Kiel, Germany, pp 138

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

Vuorinen I, Hänninen J, Viitasalo M, Helminen U, Kuosa H (1998) Proportion of copepod biomass declines with decreasing salinity in the Baltic Sea. ICES J Mar Sci 55:767-774

Wiebe PH, Benfield MC (2003) From the Hensen net toward four-dimensional biological oceanography. Prog Oceanogr 56:7-136

Wieland K, Hermann B, Kreikemeier J, Lenz J, Mees S, Schnack D (1992) Preliminary results of the small-scale distribution of herring larvae in the English Channel as obtained by means of a towed video recording system. Deep Sea Res 30:331-342

Wieland K, Zuzarte F (1991) Vertical distribution of cod and sprat eggs and larvae in the Bornholm Basin (Baltic Sea) 1987-1990. ICES CM 1991/J:37

Zuur AL, Ieno EN, Smith GM (in press) Analysis of ecological data. Springer Verlag Berlin Heidelberg New York

8. Appendix I

Erklärung gemäß §6(5) Nr. 1-3 Promotionsordnung der Universität Bremen

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Ich erkläre hiermit, dass ich

1. die vorliegende Arbeit ohne unerlaubte fremde Hilfe angefertigt habe,

2. keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe und

3. die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen als solche kenntlich gemacht habe.

Jan Schulz

Bremerhaven im Dezember 2006

;-)