

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

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*The Baltic Sea is the largest brackish water area of the world. On the basis of the data from 16 cruises, we show the seasonal and vertical distribution patterns of the appendicularians *Fritillaria borealis*, *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. The cold-water species *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 specimens outlast higher temperatures below the halocline. Distribution and strategy suggest that *F. borealis* might be a glacial relict species in the Baltic Sea. Although *Oikopleura dioica* is only abundant during summer, *O. similis* is present all year round. Both species have in common that their vertical distribution is restricted to the waters below the halocline, most likely due to their requirements of higher salinities. We argue that the observed strategies are determined by ecophysiological constraints and life history traits. These species share an omnivorous feeding behaviour and the capability to utilise a spectra of small particles as 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 in the Baltic Sea represent a habitat providing shelter from predation and food supply for adapted species that allows them to gather sufficient resources and to maintain populations.*

INTRODUCTION

The distribution patterns of zooplankton species in the water column often coincide with discriminable conditions of temperature, salinity and oxygen (e.g. Fager and McGowan, 1963; Owen, 1989; Geller *et al.*, 1992; Roemmich and 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 decreased vertical exchange between different water masses (Denman and Gargett, 1988) impacts both primary and

secondary production in as yet not completely understood ways (Owen, 1989; Cowles *et al.*, 1998).

There is an ongoing discussion on how zooplankton preferences for different layers are affected by hydrography. Ecophysiological demands (Saito and Hattori, 1997), the availability of food resources (Hattori and Saito, 1997) and predator avoidance (Bollens and Frost, 1989; Titelman and Fiksen, 2004) are significant factors for habitat selection. Ontogenetic migrations (Renz and Hirche, 2006), histo-geographic traits (Ojaveer *et al.*, 1998; Renz and 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 20–30 m. A permanent halocline separates the low saline surface water from a denser layer with higher salinity in ~60 m depth (Fonselius, 1970; Hernroth and Ackefors, 1979). Shallower areas lack these high saline bottom waters, whereas sills constrain water exchange between the deep basins. Degradation processes result in low oxygen concentrations below the halocline, whereas ventilation depends on inflows from the North Sea (Vallin and 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 and Ackefors, 1979). This results in the typical low diversity of brackish systems (Remane and Schlieper, 1971) and unoccupied ecological niches (Elmgren, 1984). Newly inserted species, arriving with inflow waters from the North Sea, 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). This results in characteristic assemblage patterns in certain depths and impacts 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, 2002), 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). On the basis of three stations with different depths and hence differently developed stratifications, we present a high-resolution dataset obtained during 16 cruises. The behaviour of these three marine species in relation to the changing physical parameters temperature, salinity and oxygen was investigated. Although the annual abundance of *Oikopleura dioica* contributes with only 0.02% to the community composition, *F. borealis* shows a proportion of ~8.2% and *O.*

similis of 4.6% (Schulz, 2006). Little is known about their life strategies, although these species represent an important contribution to the total biomass of zooplankton at certain times of the year (Hernroth and Ackefors, 1979; Hansen *et al.*, 2004). Investigations by Ackefors (Ackefors, 1969) and Hernroth and Ackefors (Hernroth and 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. The three species 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 in the Baltic Sea, *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. We discuss strategies how the three species cope with the challenging conditions of this highly stratified basin and trophodynamic implications for the food web.

METHODS

Hydrography

Data come from 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 Seabird CTD probe (Fig. 1). The stations were located on a west to east transect, perpendicular to 55.292°N, 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) using kriging as the 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).

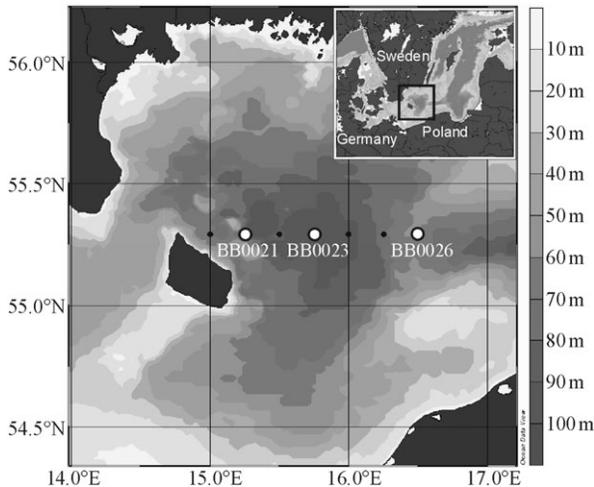


Fig. 1. Sampling site in the Bornholm Basin (central Baltic Sea) with the three stations at which zooplankton samples and CTD casts were obtained (white circles). Additional CTD casts were performed on four further stations along a transect through the Bornholm Basin (black dots).

Zooplankton data

Zooplankton sampling was performed with a multinet (50 μm mesh size, 0.25 m² mouth opening, HydroBios, Kiel, Germany) 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 2 days (Table I). Samples were taken regardless of daytime and preserved immediately aboard in a borax-buffered 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 *F. borealis*, *Oikopleura dioica* and *O. similis* were used for the analysis. Copepod stages were assigned to three groups: the binned copepodite stages C1–C5, female and male individuals. Nauplii data were not used for the analysis.

As an index of the vertical orientation of the standing stocks, the weighted mean depths (WMDs) were calculated. 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):

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

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

where d is the mid-depth of the range covered by the respective net, i the index of the species or stage, j the station, 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 r the depth range of the k^{th} 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.

Statistical investigations were performed to identify whether the surface temperature impacts the vertical orientation and whether the vertical orientation below the halocline is significant. For the tests, abundances of the deepest site BB0023 (55.292°N, 15.750°E) were used. The averaged temperature of the uppermost 10 m was calculated from the CTD values. To achieve comparable values, abundances of the stacked multinet samples were converted to mean abundance per cubic meter in the water column above and below the halocline. A net was defined to be below the halocline, when the mean salinity value of the respective sampling range r was >8 . From the two values, a new, non-dimensional numerical ratio index of the vertical orientation (VOR) was derived. It gives the ratio of individuals above the halocline to those below (Table II):

$$f_{VOR}(i, j) = \frac{m_{aj}}{m_{aj} + m_{bj}}$$

where m_a is the mean abundance of species in the water column above the halocline, m_b the respective value below the halocline, i the species or stage and j the samplings at the deepest site.

To investigate the impact of the surface temperature, a Spearman’s rank order test was performed. For this test, the averaged temperature value and the index of the vertical orientation were used. To investigate the significance whether a population dwells below the halocline, a Mann–Whitney U -test was performed on the values m_a and m_b for every i (Table II). Statistical tests were run under Statistica (Statsoft, Version 6.1, 2003).

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 less than 8 and

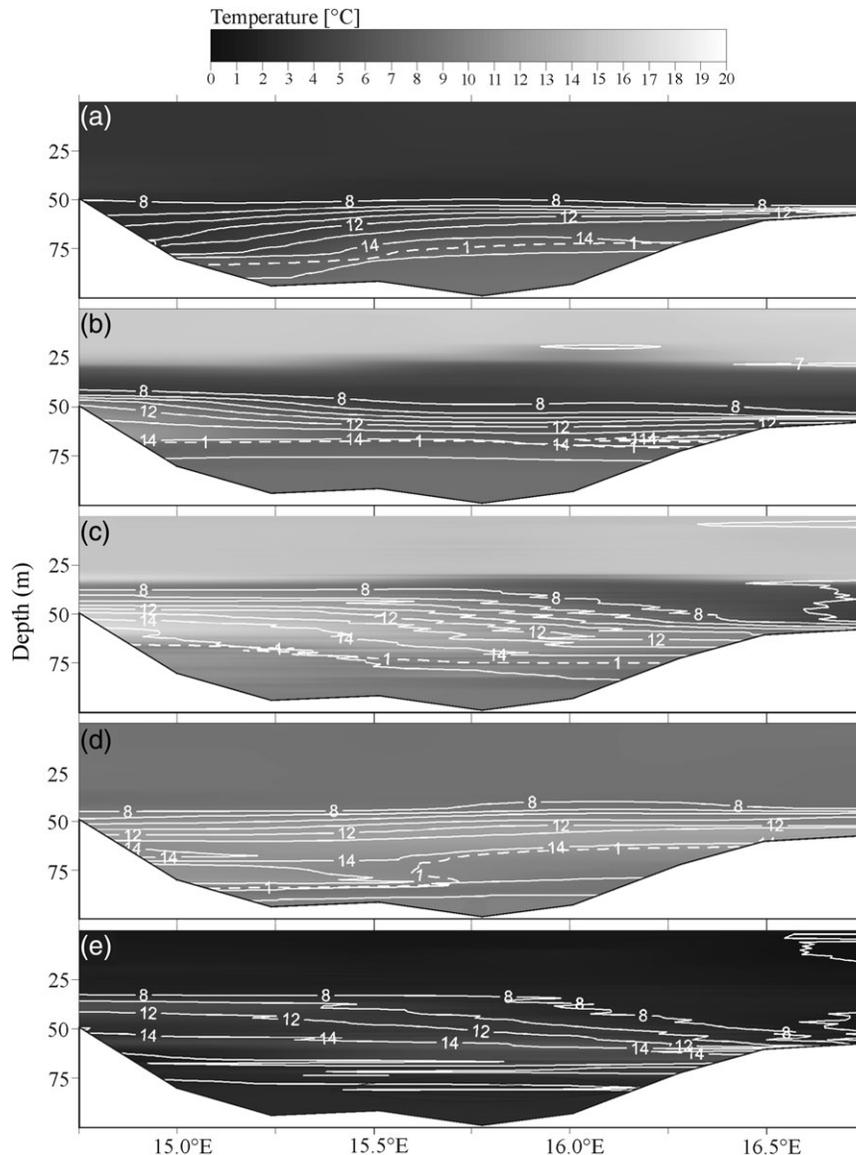


Fig. 2. Hydrographic transects through the Bornholm Basin covering the sampled stations. (a) April 2002, (b) July 2002, (c) October 2002, (d) November 2002 and (e) February 2003. Temperature is shown by grey scale background and salinity by solid isolines. The 1 mL L^{-1} oxycline is displayed by the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

temperatures of 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 and a decreased thickness of the winter water above the halocline. In July 2002, the warm surface waters reached down to 30 m depth (Fig. 2b). Highest surface temperatures $>20^\circ\text{C}$ were observed in August where calm weather conditions allowed the adjustment of a steep thermocline in ~ 20 m depth. Towards the end of summer, surface temperatures decreased to $\sim 15^\circ\text{C}$ in early October, and 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 northwestern end of the Bornholm Basin. In September/October 2002, the warm water masses were also found on station BB0023 (Fig. 2c). They stratified into ~ 60 m depth due to a lower density caused by higher temperatures than the resident haline water below and are hereafter referenced as BB60.

Table I: 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			
March 2002	18	18	–
April 2002	05	05	06
April 2002	21	21	19
May 2002	08	08	08
May 2002	25	26	26
June 2002	14	14	16
July 2002	25	25	27
August 2002	16	16	14
September 2002	06	07	07
October 2002	06	06	05
November 2002	16	16	14
January 2003	16	19	18
February 2003	13	14	16
March 2003	12	13	11
April 2003	20	18	23
May 2003	–	28	29

These waters caused unusually high temperatures of $>13^{\circ}\text{C}$ in the halocline at 60 m and decreased the thickness of the winter water layer from below. The BB60 water flowed out into the Gdansk Deep via the Slupsk Sill until December 2002. In November 2002, a second inflow entered the Bornholm Basin and replaced the stagnant water masses below 90 m ($\sim 9.5^{\circ}\text{C}$ and a salinity of 15 at BB0023, Fig. 2d). These waters are hereafter named BB90, according to Feistel *et al.* (Feistel *et al.*, 2004). After January 2003, a further inflow, which 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 salinities, low temperatures and high oxygen concentrations (Fig. 2e). It was followed by further inflow events enhancing the effect of the MBI. Before January 2003, the temperature of the water above the halocline was cooler than below. Because of the mixing along the transition zones, the inflow events caused a weaker salinity gradient. Although 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.* (Feistel *et al.*, 2003a, b, 2004).

Seasonal distribution of zooplankton

In 2002, *F. borealis* was most abundant between April and May with up to $445 \text{ n m}^{-2} 10^3$ (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 $1.7 \text{ n m}^{-2} 10^3$ in June. Although 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 $3496 \text{ n m}^{-2} 10^3$, 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 $0.9 \text{ n m}^{-2} 10^3$ were found at BB0023 and BB0021, respectively, and $13.9 \text{ n m}^{-2} 10^3$ in the following month on BB0021. During winter, *Oikopleura dioica* was completely absent. Small numbers were only recorded in April 2003 at the deepest station BB0023. *Oikopleura dioica* was never observed at the shallow station BB0026.

All stages of *O. 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, whereas female abundance was generally higher than male abundance. On the shallower station BB0021, copepodite and female abundances were in general lower than that on BB0023. 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, whereas females and copepodite stages appeared in April and May 2002 and together with the inflow events.

Vertical distribution

During winter, *F. 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 MBIs.

Table II: Test for the statistical significance of the vertical distribution patterns of *F. borealis*, *Oikopleura dioica* and *O. similis* derived from the WMD data

Dates	T _{0–10m} (°C)	Halocline Category	<i>Fritillaria borealis</i>		<i>Oikopleura dioica</i>		<i>Oithona similis</i>					
							C1–C5		AF		AM	
			n m ⁻³	VOR	n m ⁻³	VOR	n m ⁻³	VOR	n m ⁻³	VOR	n m ⁻³	VOR
March 2002	3.35	Above	643.20	0.92	0.00	–	4.00	0.02	0.72	0.01	0.00	0.00
		Below	53.45		0.00		211.95		81.03		11.68	
April 2002	3.59	Above	4583.76	0.89	0.00	–	1.92	0.00	0.00	0.00	0.00	0.00
		Below	571.40		0.00		531.30		106.20		7.30	
April 2002	4.41	Above	8668.16	0.97	0.00	–	12.80	0.00	0.32	0.00	0.00	0.00
		Below	308.80		0.00		2807.80		177.60		17.70	
May 2002	5.49	Above	2734.08	0.89	0.00	–	18.24	0.01	4.00	0.02	2.56	0.03
		Below	354.00		0.00		1838.40		256.60		78.00	
May 2002	9.84	Above	995.84	0.11	0.00	–	22.40	0.00	3.84	0.00	1.28	0.00
		Below	7970.13		0.00		5734.40		981.33		708.27	
June 2002	13.05	Above	7.68	0.19	0.00	–	7.68	0.00	10.24	0.03	2.56	0.02
		Below	33.60		0.00		2454.60		293.10		119.80	
July 2002	16.12	Above	0.00	0.00	0.00	–	0.00	0.00	0.00	0.00	0.00	0.00
		Below	4.80		0.00		1313.60		345.45		21.70	
August 2002	19.79	Above	0.00	0.00	0.00	0.00	7.40	0.00	1.50	0.00	0.00	0.00
		Below	37.60		0.32		1696.40		564.24		11.52	
September 2002	20.19	Above	0.00	0.00	0.00	0.00	46.40	0.04	24.00	0.06	2.40	0.03
		Below	28.88		0.14		1105.92		425.70		68.14	
October 2002	14.95	Above	6.40	0.22	0.00	0.00	12.80	0.02	6.40	0.03	6.40	0.23
		Below	23.20		12.16		787.52		248.64		20.88	
November 2002	8.93	Above	145.60	0.85	0.00	–	0.00	0.00	1.60	0.01	0.00	0.00
		Below	25.50		0.00		290.90		207.70		4.70	
January 2003	3.84	Above	604.16	0.78	0.00	–	2.88	0.01	0.96	0.00	0.00	0.00
		Below	174.40		0.00		283.07		195.73		122.53	
February 2003	1.85	Above	432.00	0.67	0.00	–	17.87	0.03	12.67	0.04	1.60	0.11
		Below	213.12		0.00		529.84		323.20		12.40	
March 2003	1.78	Above	2579.20	0.87	0.00	–	10.00	0.01	6.40	0.01	0.40	0.02
		Below	402.08		0.00		1172.80		741.12		24.48	
April 2003	3.31	Above	39 669.76	0.95	0.00	0.00	0.00	0.00	0.00	0.00	81.92	0.62
		Below	2162.04		0.15		915.78		444.36		49.16	
May 2003	11.06	Above	129.60	0.45	0.00	–	60.80	0.03	13.60	0.05	0.00	0.00
		Below	159.20		0.00		2169.20		293.60		14.80	
# Values			16/16	16	16/16	4	16/16	16	16/16	16	16/16	16
Spearman's rank order R				–0.785		–		–0.020		0.186		–0.093
P-value				<0.001		–		0.939		0.491		0.733
Mann–Whitney U-test			108		96		0		0		0	
P-value			0.451		0.035		<0.001		<0.001		<0.001	

To investigate the impact of surface temperature, the mean temperature of the upper 10 m (T_{0–10m}) was tested against the index of the vertical orientation (VOR) of each species or stage with a Spearman's rank order test. The mean abundance of a species in the water column above the halocline was tested against the abundance below the halocline with a Mann–Whitney U-test. Data of the deepest station were used.

Oikopleura dioica was always located in salinities >11 (Fig. 4a–c). In October 2002, the distribution centre of *Oikopleura 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 that *Oikopleura dioica* can invade deep into the oxygen depletion zone (Fig. 4a). Although salinities >11 were at least temporarily observed on station BB0026, no individuals were found (Fig. 4c).

All stages of *O. 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

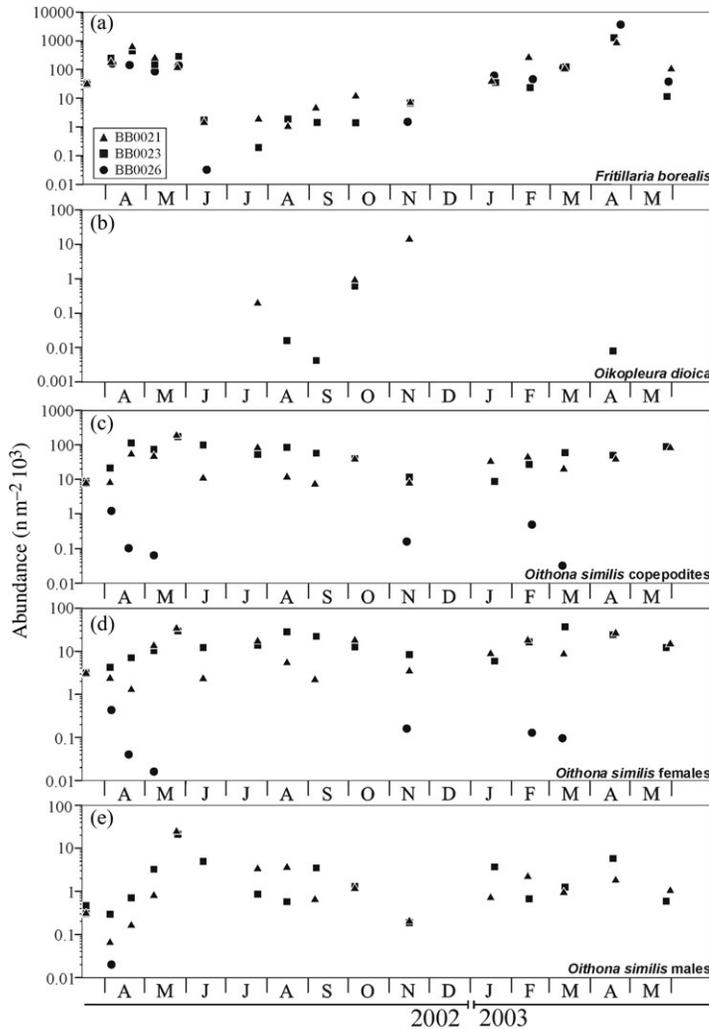


Fig. 3. Seasonal abundance of (a) *F. borealis*, (b) *Oikopleura dioica* and (c–e) *O. similis* at the stations BB0021, BB0023 and BB0026 in the Bornholm Basin. Note the logarithmic scaling.

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.

Statistical investigations were carried out to verify the results derived from the WMD analyses. Whereas we expected a significant relationship between surface temperature and vertical orientation for *F. borealis*, this relationship should be absent for the other species. On the other hand, we expected that the test, whether a species or stage is dwelling mainly below the halocline, is not significant for *F. borealis*, but for the others.

In the first approach, the mean surface temperature was tested with a non-parametric Spearman’s rank order correlation against a ratio of every investigated species or stage (Table II), which expressed the relative abundance above the halocline. The Spearman’s rank correlation showed a high significance, indicating that the vertical orientation of *F. borealis* is triggered by the surface temperature. Not enough abundance values were available for *Oikopleura dioica* to perform the statistics. The results for *O. similis* show that the preferred hydrographic stratum below the halocline is independent from surface temperatures.

The second approach tested for the significance, whether a species or stage mainly inhabits the layer below the halocline. The mean values of individuals per cubic meter above and below the halocline were tested by a Mann–Whitney *U*-test (Table II). The test showed

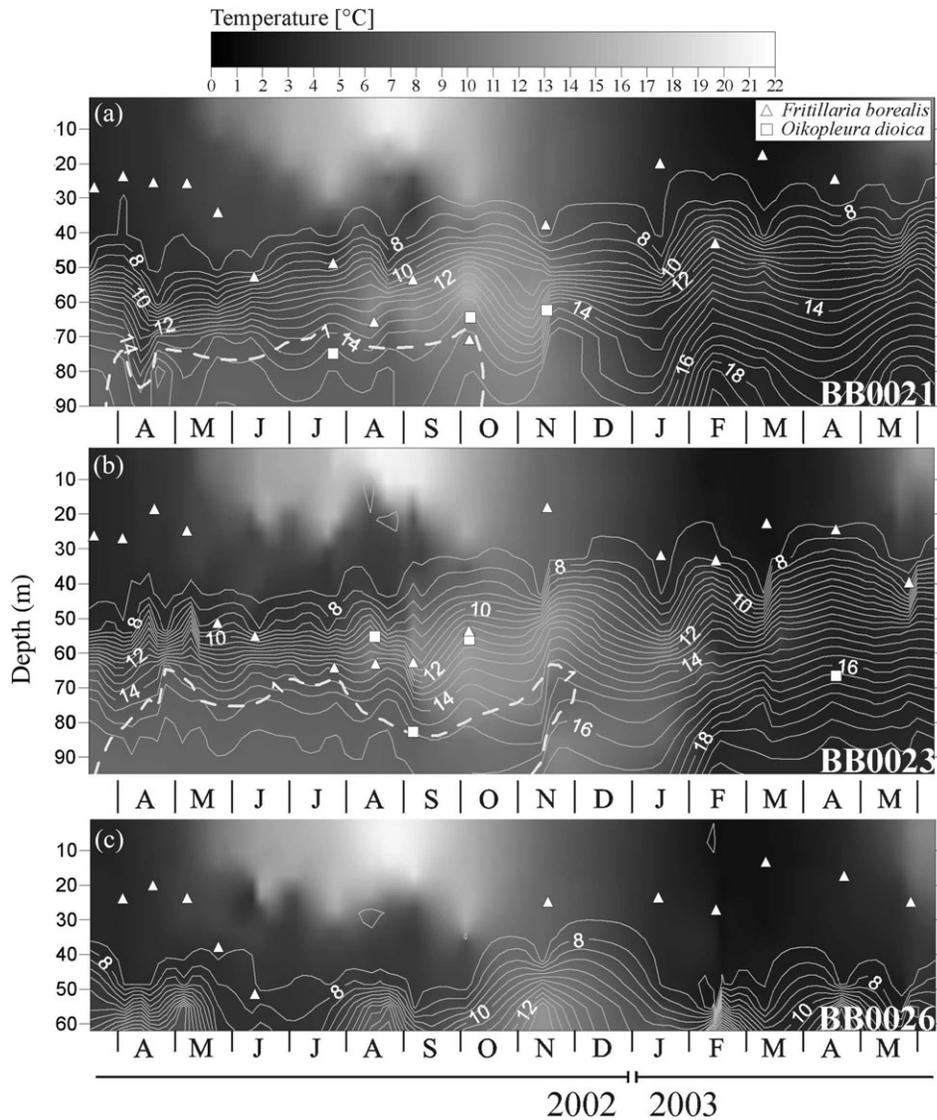


Fig. 4. WMD distribution of *F. borealis* and *Oikopleura dioica* at three stations (a) BB0021, (b) BB0023 and (c) BB0026 in the Bornholm Basin. Image map background shows the seasonal temperature development in the respective depth, solid lines represent isohaline levels and the dashed line indicates the 1 mL L⁻¹ oxygen concentration.

that the vertical orientation of *O. similis* below the halocline is significant. This result is also valid for *Oikopleura dioica*, whereas the test failed for *F. borealis*.

DISCUSSION

Distribution patterns

Inhomogeneous vertical distribution of zooplankton is a response to several parameters and the interplay between them (Titelman and Fiksen, 2004). The low salinity in the brackish Baltic Sea exerts osmotic stress on marine species. Consequently, the observed

distribution patterns are subjected to their physiological capabilities. With increasing temperatures, respiration and general metabolic demands increase disproportionately and lower the physiological tolerance to dilution (Lehman, 1988). In brackish waters, the expenditure for osmoregulatory energy is lowest below the halocline for marine species (Remane and Schlieper, 1971; Viitasalo, 1992). The observed distribution patterns of *F. borealis*, *Oikopleura dioica* and *O. similis* in the central Baltic Sea indicate that these species use different strategies to cope with the prevailing hydrographic conditions. They are conditioned by ecophysiological capabilities, this being also reflected in their zoogeographic distributions.

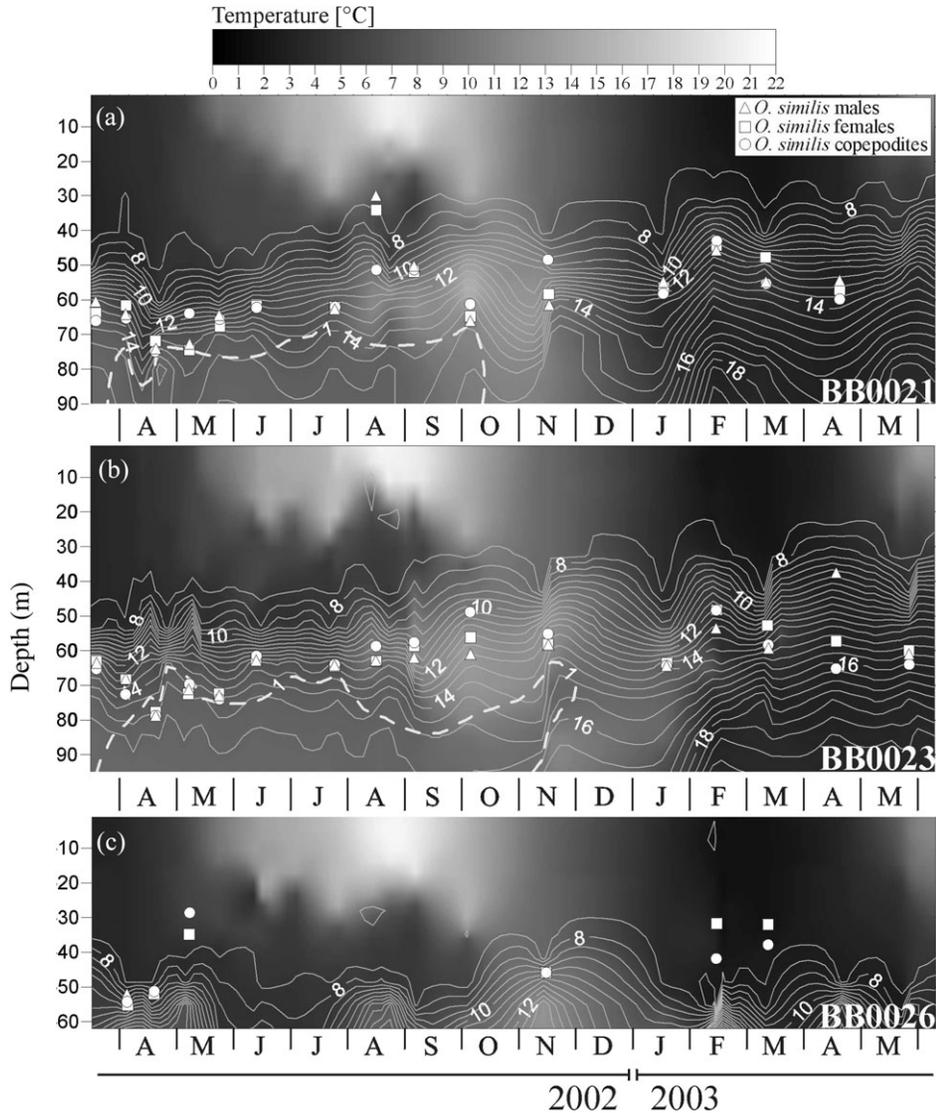


Fig. 5. WMD distribution of copepodites, females and males of *O. similis* at three stations (a) BB0021, (b) BB0023 and (c) BB0026 in the Bornholm Basin. Image map background shows the seasonal temperature development in the respective depth, solid lines represent isohaline levels and the dashed line indicates the 1 mL L⁻¹ oxygen concentration.

Although all three species are found in temperate waters, the zoogeographic distribution of *F. borealis* extends to both Polar regions (Fenaux *et al.*, 1998). The investigation of the WMD as well as the statistical investigations showed that *F. borealis* performs a seasonal migration, whereas the other two species are restricted to the layer below the halocline. *Fritillaria 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 stenothermic and euryhaline species prefers temperatures below 10°C (Berrill, 1950; 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, but 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 *F. borealis*, the seasonal appearance of *Oikopleura dioica* is exclusively restricted to summer in accordance with its zoogeographic distribution. It is also found in cool waters (Deibel, 1998), but appears in higher abundances from temperate waters to the warm Indian Ocean, the Red and Mediterranean Sea

(Lohmann, 1896; Fenaux *et al.*, 1998; Tomita *et al.*, 2003). It is also found in warm estuaries like the Amazon (Lohmann, 1896) or the North Inlet of South Carolina (Costello and Stancyk, 1983). This eurythermic species is abundant in near shore waters and requires salinities >11 (Lohmann, 1896). Behrends (Behrends, 1996) related the appearance of *Oikopleura dioica* in the Bornholm Basin to increasing temperatures. During our study, this species appeared only in summer, although the temperatures below the halocline did not increase. As *Oikopleura dioica* was already present in July 2002, prior to the inflows, the population does not seem to depend on advection. *Oikopleura dioica* finds the required salinity only below the halocline and accepts oxygen concentrations $<1 \text{ mL L}^{-1}$. During summer, it shares the habitat with the remaining *F. borealis* population.

Although the two appendicularian populations showed distinct seasonal abundance peaks, all developmental stages of the cosmopolitan (Paffenhöfer, 1993) cyclopid copepod *O. similis* were found in high numbers throughout the year below the halocline. The egg-carrying strategy of *O. similis* decreases the threat of loosing off-spring to the sediment (Nielsen and Sabatini, 1996) in noxious anoxic zones. This is advantageous compared with broadcast spawners, where recruitment from sediments is a critical stage in Baltic copepods (Dutz *et al.*, 2004). Hansen *et al.* (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 specimens were also recorded in deeper layers, suggesting 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 MBI. Similar to the ontogenetic vertical distribution of *Pseudocalanus acuspes*, also found below the halocline in the Bornholm Basin (Renz and Hirche, 2006), males of *O. similis* were often found deepest.

The seasonal submergence of *F. borealis* is a consequence of its requirement of low temperatures; it might be a member of the Baltic glacial relict fauna that retraces the heritage of its histogeographic origin (Ojaveer *et al.*, 1998). 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, like the copepod *Pseudocalanus acuspes* (Renz and Hirche, 2006).

At station BB0026, abundance of the investigated taxa was generally lower than that at the deeper stations

BB0021 and BB0023. At shallow sites, apparently the lack of favourable conditions of the deep layers restricts horizontal distribution. Although *Oikopleura 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. Obviously abundance of deep living species is a function of the available space between halocline and seafloor and the environmental conditions within this volume. Consequently, *Oikopleura dioica* and *O. similis* are expelled from shallow stations, because of the lack of adequate salinity. *Fritillaria borealis* is only expelled during the warm seasons (Schulz *et al.*, 2006), when the temperature in the whole water column is too high.

Inflows did not occur for several years prior to 2002. As the investigated species were already observed before the first inflow, they obviously maintain populations in the Bornholm Basin. However, 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, 2006). During propagation of inflow waters, mixing processes along their transition zones alter the original physical parameters (Feistel *et al.*, 2004). Consequently, conditions for entrained species change with propagation distance. Advectioned 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 do not survive or cannot reproduce under these conditions (Purasjoki, 1945; Mankowski, 1962; Schneider, 1987; Postel, 1996). Although the environmental conditions of the Bornholm Basin are within the tolerance ranges of *F. borealis* and *O. similis*, it seems that *Oikopleura dioica* finds only sub-optimum conditions, concluding from its decreased 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 BB60 summer inflow in 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 and Odum, 1996). The ensuing inflows ventilated the waters below the halocline and improved the conditions that had previously deteriorated during periods of stagnation (Fonselius, 1970). Thus available space increased for species sensitive to deteriorating salinity and oxygen conditions (Hansen *et al.*, 2004; Hansen *et al.*, 2006; Renz and Hirche, 2006). The raised halocline allowed species from below the halocline to access even shallower areas with the horizontally spreading saline bottom waters.

The time lag of a few days (Table I) between sampling the three stations might have biased the observed inter-station response of the species to hydrography due to internal waves (Banse, 1964), which often accompany inflow events. By this, the transport of *Oikopleura 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 appeared on a longer time scale than our monthly observations.

Diel vertical migration

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 decreased in the Baltic Sea (Titelman and Fiksen, 2004; Schmidt, 2006). It has recently been reported to occur only in *Acartia longiremis* and *Temora longicornis*, although they remain in the layer above the halocline (Schmidt, 2006). It is suggested that in the central Baltic Sea, few zooplankton species perform DVM through the halo- and thermocline into different hydrographic horizons (Schulz, 2006). The results obtained during this study period corroborate the assumption that *F. borealis*, *Oikopleura dioica* and *O. similis* did not perform DVM in the Bornholm Basin.

Feeding and predation

Fritillaria borealis, *Oikopleura dioica* and *O. 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 (van Beusekom *et al.*, 2007). 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 in the same period (Peters *et al.*, 2006). Such resources

accumulate in density gradients like the permanent halocline (Lande and Wood, 1987; MacIntyre *et al.*, 1995; Vallin and 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 *Oikopleura dioica* retains particles down to lesser micrometer and include colloidal fractions (Flood *et al.*, 1992; Gorsky *et al.*, 1999; López-Urrutia *et al.*, 2003b) and thus allows feeding in deep, detritus-based ecosystems (Gorsky and Fenaux, 1998). Grazing on such material is probably more important than on autotrophic organisms (López-Urrutia *et al.*, 2003a), and utilisation of small size classes decreases competition with other zooplankton species (Alldredge, 1972; Paffenhöfer, 1983; Gorsky and Fenaux, 1998). Availability of food might explain why *F. borealis* migrates into the saline waters and does not outlast the higher surface 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 (van Beusekom *et al.*, 2007), which coincided with the period of high abundances. In other times, due to their residence in deeper layers, a contribution of appendicularians to the vertical flux, especially by their abandoned houses (Alldredge, 1972), is less important in the Bornholm Basin than in areas, where they graze mostly in the upper layers. Nevertheless, the houses can be utilised by microbial and planktonic organisms, prior to sinking to the seafloor (Paffenhöfer, 1983; Steinberg, 1995; Gorsky and Fenaux, 1998; Maar *et al.*, 2006).

Oithona similis is also well known to utilise resources of different size spectra from vertical fluxes (González and Smetacek, 1994; Nielsen and Sabatini, 1996; Castellani *et al.*, 2005b; Hansen *et al.*, 2006; Reigstad *et al.*, 2005). The utilisation of faecal pellets is controversially discussed (Reigstad *et al.*, 2005; Poulsen and Kiørboe, 2006), as Reigstad *et al.* (Reigstad *et al.*, 2005) did not find *O. similis* to feed on this resource. The low inter-stage variations in the WMD values 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) seem to allow sustainable production even under extreme conditions (Fransz and Gonzales, 1995) as found in the Baltic.

As a spin-off the utilisation of the waters below the halocline represents a refuge against predation. The most abundant calanoid copepods of the Baltic Sea, *Acartia* spp., *Temora longicornis* and *Centropages hamatus*, feed on a spectrum of size classes that includes appendicularian eggs and juveniles (Sommer *et al.*, 2003), but they are most abundant above the halocline (Schulz *et al.*, 2006). Scyphomedusae are also most prominent in the upper layers (Barz and Hirche, 2005) and therefore excluded as predators. The occurrence of chaetognaths in the central Baltic Sea is restricted to advection with inflow events. Probably they do not grow and reproduce here (Maciejewska and Margonski, 2001); during stagnation periods, they are very rare. During our study period, the impact of chaetognaths on zooplankton communities was negligible (Barz, 2006). 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 adults feed in mid- and deep waters (Voss *et al.*, 2003). As *F. borealis* is the only species that utilises the upper layers, the remaining individuals benefit most from their summer submergence.

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