Spatio-temporal composition and dynamics of zooplankton in the Kalmar Sound (western Baltic Sea) in 2009–2010

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In pelagic food webs, zooplankton is the link between lower and higher trophic levels. It is thus essential to know how the zooplankton community structure varies with its environment. We investigated the seasonal and spatial variation in the zooplankton diversity and community structure during two consecutive years in the Kalmar Sound, along the Swedish east coast, an area with a strong bathymetric gradient and of high ecological importance for e.g. commercial fish species. Two zooplankton communities were identified in the area: a coastal/estuarine community in the south and an open-water community in the north. They were separated mainly by differing salinity and temperature conditions. Biodiversity increased from spring to autumn and was higher in the open waters.

Introduction

Zooplankton plays a key role in the transfer of energy from the primary producers to the higher trophic levels (e.g., Dahmen 1999, Möllmann et al. 2000, San Martin et al. 2006, Holmborn 2009). Consequently, knowledge of zooplankton dynamics is essential to the understanding of the pelagic ecosystem. For instance, availability of suitable zooplankton affects growth and survival of fish that feed on it as well as variations in zooplankton abundance and community composition may affect recruitment of important commercial fish species, in both open and coastal waters (Cushing 1996, Nilsson et al. 2004, Möllmann et al. 2008, Casini et al. 2009, 2010). Zooplankton communities are also of great interest as potential indicators of climate change in the marine environment (Hays et al. 2005).

In the Baltic Sea, several studies have correlated the overall abundance and relative composition of zooplankton with hydrological vari-
This area also hosts populations of freshwater fish species, such as the northern pike (*Esox lucius*) and the Eurasian perch (*Perca fluviatilis*) (Nilsson et al. 2004). Therefore, studying the zooplankton community in this area would contribute to our understanding of the local ecosystem dynamics.

The objective of this study was to describe the seasonal and spatial variation in zooplankton diversity and community composition in the Kalmar Sound in 2009–2010. We hypothesized that the community composition would change along a coastal–open sea gradient following the spatial gradient of hydrological factors.

**Material and methods**

**Sampling and zooplankton density estimation**

A total of 288 zooplankton samples were collected from the Kalmar Sound (Fig. 1) during the vegetative period, once a month between April and October in 2009 and 2010 (except in April and July 2009). The samples were collected by vertical tows using a WP2 net (57 cm diameter opening, 260 cm total length and 90 µm mesh size) equipped with a flow meter (General Oceanics mechanical flow meter with standard rotor) to estimate the volume of water filtered. The zooplankton sampled by this net included the mesozooplankton (> 200 µm) and the larger fraction of microzooplankton (20–200 µm); for the sake of simplicity both fractions are henceforth referred to as “zooplankton”.

Although zooplankton dynamics in the Baltic Sea have been widely studied (e.g. Ackefors 1969, Hernroth 1981), the zooplankton in the Kalmar Sound, between the island of Öland and the Swedish mainland, have not been investigated in detail. This narrow and semi-enclosed area includes both shallow areas and deeper waters and thus offers an opportunity to study similarities and differences between coastal and open-water ecosystems.

The Kalmar Sound is a habitat for marine fish species, such as herring (*Clupea harengus*), sprat (*Sprattus sprattus*) and cod (*Gadus morhua*), and has been described as an important spawning area for herring (Parmanne et al. 1994, Eriksson et al. 2011). This area also hosts populations of freshwater fish species, such as the northern pike (*Esox lucius*) and the Eurasian perch (*Perca fluviatilis*) (Nilsson et al. 2004). Therefore, studying the zooplankton community in this area would contribute to our understanding of the local ecosystem dynamics.

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The zooplankton net was towed at a speed of 1.5 m s⁻¹. At the shallow stations (depth < 50 m; 1–10 in Fig. 1) only one sample was collected from the sea bottom to the surface. At the deep stations (depth > 50 m; 11–16 in Fig. 1), two samples were taken: from 50 m depth to the surface, and from 100 m depth to the surface (or from the sea bottom to the surface, at stations shallower than 100 m). Samples were preserved in 4% formalin in saltwater. Typically all 16 stations were sampled each month. At each station, at least one CTD profile was collected. The calibrated CTD probe (SAIV A/S, model SD204) was typically towed at a speed of 1.5 m s⁻¹ and...
one measurement of temperature and salinity per second was taken.

The volume of water filtered by the net during the zooplankton sampling was estimated (1) using the flow meter, or (2) using the depth of the tows in cases when the flow meter did not work properly. The correlation between the two estimates was very high ($r^2 = 0.94$).

Zooplankton identification was carried out according to the HELCOM COMBINE Manual (HELCOM 2001). Samples were divided into subsamples using a Motoda box splitter (Motoda 1959), and all subsamples were examined using a Bogorov counting chamber (Chojnacki et al. 2007, Aleksandrov et al. 2009). Specimens were identified to the lowest possible taxonomic level. Cyclopoida and Harpacticoida were not differentiated further, whereas Calanoida were identified to the species level with the exception of Pseudocalanus (which was identified to genus level). The developmental stages of Calanoida and Cyclopoida (divided into nauplii, copepodite stages CI–III and CIV–V, males and females) were determined (Hernroth and Viljama 1979). Nauplii and copepodite stages of Acartia longiremis, A. bifilosa and A. tonsa were identified to the genus level (Acartia spp.) (Mudrak and Żmijewska 2007). Cladocera were determined to the species level with the exception of Bosmina (which was identified to genus level). The taxa, and all the developmental stages were counted up to 50 individuals separately. If this number was not reached in one subsample, an additional subsample was analysed. If a component of a taxonomic group reached 50 individuals in a subsample, it was not considered in the following subsamples. Zooplankton densities (indiv. m$^{-3}$) were calculated for each sample.

Copepoda nauplii that were found in the samples were not considered in further analyses because the mesh size of the net was not adequate for their quantitative estimation. Due to their swimming ability, fish larvae and Mysidae could not be effectively sampled, hence they were also excluded from the analyses.

**Statistical analyses**

The densities of the major zooplankton taxa in 2009 and 2010 were compared using a $t$-test. The annual taxa richness was calculated for each station as a proxy for biodiversity. The Shannon-Weaver diversity index ($H'$) (Shannon 1948), integrating the number of taxa present and their density, was calculated for each station and season to investigate potential spatial differences in biodiversity in the different seasons. The seasons considered were spring (April–June), summer (July–August) and autumn (September–October).

To further explore the potential occurrence of different zooplankton communities in the study area, matrices of “station × density of taxa” (sampling stations as rows and density of taxa at each station as columns) were analysed for each season and for the whole sampling period using three multivariate techniques. (1) A hierarchical cluster analysis was performed using Ward’s linkage (Ward 1963, Singh 2008) with the Bray-Curtis dissimilarity measure (Bray and Curtis 1957). The data were fourth-root-transformed to handle zero-inflation and the few large values typical for density data sets, and standardized by range, which is one of the possible standardizations for the Bray-Curtis dissimilarity coefficient (Quinn and Keough 2002). (2) A non-metric multidimensional scaling (NMDS) (Kruskal and Wish 1978) was used to examine the relationships between the taxa and the stations, using Bray-Curtis dissimilarity as a distance measure. This technique has been widely used in marine ecosystem analyses (Field et al. 1982, Clarke and Warwick 1994) and has been particularly employed in the investigation of zooplankton communities (Keister and Peterson 2003, Isari et al. 2005, Dvoretsky and Dvoretsky 2009). The goodness of the NMDS was evaluated according to the stress value, which for 16 stations is considered acceptable if smaller than 0.242 (Sturrock and Rocha 2000). (3) An indicator species analysis (ISA) (Dufrêne and Legendre 1997, De Cáceres and Legendre 2009) was used to identify the indicator taxa responsible for the differences among the zooplankton groups found with the cluster analyses.

Zooplankton communities were related to hydrological data from the CTD casts. The hydrological variables were: average salinity over the entire water column (0–100 m or 0–sea
bottom for the stations shallower than 100 m depth), average surface temperature (0–50 m or 0–sea bottom for the stations shallower than 50 m depth) and average temperature over the entire water column (0–100 m or 0–sea bottom for the stations shallower than 100 m depth). Firstly, the hydrological variables were fitted as linear vectors onto the NMDS ordination, based on the squared linear correlation coefficient between the hydrological variables and the NMDS scores for the stations and zooplankton taxa. Fitted vectors are represented as arrows that point in the direction of the most rapid change in the hydrological variable and the length of the arrow is proportional to $r^2$ obtained (gradient) (Oksanen et al. 2011). Secondly, a permutational multivariate analysis of variance (PERMANOVA) was carried out to account for the potential linear relationship between the different hydrological variables, and presents only their direct influence on the variability in the zooplankton density matrix. PERMANOVA is based on the $F$-statistic, which is a multivariate equivalent of the Fisher’s $F$-ratio, and the $p$ values were calculated based on data permutations (Anderson 2001).

All the statistical analyses were carried out using the packages vegan (Oksanen et al. 2011) and indicspecies (De Cáceres and Legendre 2009) in R (www.r-project.org).

Results

Hydrological conditions

The halocline in the open waters of the Kalmar Sound was between 50 and 80 m depth, whereas no halocline was found in the coastal waters shallower than 40 m (Fig. 2). Salinity ranged between 6 to 7 psu from the surface down to a depth of 50 m, both in the coastal and the open waters; whereas below the halocline, salinity reached 10 psu at 100 m depth. Salinity did not show large seasonal changes. Above the halocline, temperature was higher in the coastal waters, both in spring and in summer, whereas in autumn higher temperatures were measured in the uppermost layers of the open waters. Below the halocline in the open waters, the temperature ranged from 4 to 5 °C (Fig. 2).

Zooplankton density, composition and biodiversity

A total of 49 zooplankton taxa were found in the Kalmar Sound in 2009–2010 (Appendix). The densities (Fig. 3) of the major taxa (abundance ≥ 1% of the total abundance) did not differ significantly between the years ($t$-test: $p > 0.05$), even when the analysis was performed seasonally.

The Shannon-Weaver Diversity Index ($H'$) varied between 0.57 and 3.70, being at its maximum in the open waters in summer and autumn (Fig. 4). $H'$ generally increased from spring to summer/autumn. In summer/autumn, $H'$ was lower in the coastal waters than in the open waters, whereas no clear difference was found in spring. The annual taxa richness (number of taxa) increased from the coastal (minimum of 37 taxa at station 1) to the open waters (maximum of 47 taxa at stations 15 and 16).

Spatial characterization of the zooplankton communities

Hierarchical cluster analysis determined two distinct zooplankton groups, one in the open waters (northern Kalmar Sound, stations 11–16) and one in the coastal waters (southern Kalmar Sound, stations 1–7) (Fig. 5). The zooplankton communities at stations 8, 9 and 10 clustered within the northern or southern parts of the Kalmar Sound depending on the season.

When NMDS was carried out for the whole sampling period the stress value equalled 0.0928 (Fig. 6), which is considered acceptable for 16 stations (Sturrock and Rocha 2000). When it was performed by season, the separation between the two groups remained unchanged with stress values of 0.0960 (spring), 0.1340 (summer), and 0.0616 (autumn).

The indicator taxa (ISA) for the open and coastal waters are presented in Table 1. The taxa identified as indicator taxa for the entire study period as well as those for at least two of the three seasons analysed were also included in the NMDS (Fig. 6). The open waters were characterized by Copepoda — A. longiremis, C. hamatus, Pseudocalanus spp., T. longicornis and Limnocalanus spp. (the last taxon present
in the samples in small quantities) — as well as by Cladocera (*Bosmina* spp. and *Podon* spp.) and the Appendicularia (*Fritillaria borealis*). The coastal waters were characterized by the copepodite stages of *Acartia* spp., the adults of *A. tonsa*, Mollusca larvae (Bivalvia and Gastropoda) and Rotatoria (*Keratella* spp. and *Synchaeta* spp.).

When the analyses (clustering, NMDS and ISA) were performed using only the surface samples (0–50 m for the stations > 50 m depth and 0–bottom for the stations < 50 m depth) the results did not change significantly.

Zooplankton communities and hydrological variables

The fitted vector analysis of the hydrological variables showed that salinity increased towards the open water, while temperature increased towards the coastal waters (Fig. 6). During the entire sampling period, the separation between the two zooplankton communities was related to salinity, whereas temperature had a greater effect in spring and summer (PERMANOVA; see Table 2).

**Discussion**

**Zooplankton diversity patterns**

In the current study, we found that the annual taxa richness in the Kalmar Sound increased steadily from the coastal to the open waters. Moreover, higher biodiversity was found in summer/autumn in the open waters which are also characterized by a higher number of indicator taxa. A wider vertical range of salinity in the open waters, may explain higher biodiversity in this area. Postel (2012) showed a decrease in biodiversity from the western towards the central Baltic which was also related to the salinity gradient.

The higher biodiversity in summer/autumn found in our study could be related to hatching of the resting stages deposited on the sea bottom, which need higher temperatures to develop. Warming of the bottom layer induces hatching of resting eggs of some Copepoda species, such as *A. bifilosa* and *Eurytemora hirundoides*. Other species (e.g. *A. tonsa* and *Bosmina* spp.) need even higher temperatures so their resting eggs hatch in late summer/autumn (Katajisto *et al.* 1998, Viitasalo and Viitasalo 2004). In spring, on
Fig. 3. Densities of the major zooplankton taxa (abundance ≥ 1% of the total abundance). Although Mysidacea are not a major taxon, they are also presented because of their importance in the diet of large herring (Casini et al. 2004), and hence are ecologically important in the area.
the other hand, biodiversity did not clearly vary in space, which is potentially attributable to the fact that the water in the shallower southern area warms up faster after winter than do the deeper waters in the northern area, compensating for the lower salinity. The difference in seasonal diversity could also be related to the different reproduction modes of zooplankton species (Postel 2012). For example, Cladocera, which produce temporarily large blooms, were nearly absent in spring but abundant in summer and autumn, explaining the increase in diversity during these seasons in the open waters where they characterized the zooplankton community. However, Postel (2012) showed a decrease in zooplankton diversity in the western Baltic in summer due to mass occurrence of Cladocera. These apparently contrasting results could have arisen because in our study the densities reached by Cladocera in summer were similar to the densities of the other species.

**Spatial characterization of the zooplankton communities**

We found two zooplankton communities the Kalmar Sound, one typical to open waters (the northern Kalmar Sound) and one to coastal waters (the southern Kalmar Sound). These areas differ in salinity, and during some seasons (spring and summer) in temperature. Although correlation does not necessarily mean causal relationship, our results suggest that hydrological conditions may be responsible for zooplankton dynamics in the Kalmar Sound. In several long-term studies in the Baltic Sea, salinity and temperature were found to affect zooplankton abundance or species composition (e.g. Viitasalo et al. 1995, Vuorinen et al. 1998, Dippner et al. 2000, Möllmann et al. 2000). The taxa characteristic for each of the two zooplankton communities identified in our study did not change throughout the sampling period, despite the changes in their densities.

Larger Copepoda were found in the open waters. Higher salinities below the halocline may explain the occurrence of some taxa: e.g., *Pseudocalanus* spp. which needs high salinities and low temperature for reproduction (Möllmann et al. 2000, Möllmann and Köster 2002) and has been found to inhabit the halocline zone of the Baltic Sea (Möllmann and Köster 2002, Hansen et al. 2005). Abundances of *Temora longicornis* and *C. hamatus* have also been shown to positively correlate with salinity (Vuorinen et al. 1998, Hänninen et al. 2003), which explains their occurrence in the open waters of the Kalmar Sound. Other Copepoda of considerable significance in the open waters of our study area were, despite their freshwater origin, *E. hirundoides* and *Limnocalanus* spp. The presence of *F. borealis* in the northern area is in line with its preference for cooler waters under the thermocline (Ackerfors 1969).
In the coastal waters of the Kalmar Sound, the zooplankton community was generally dominated by smaller-sized taxa and taxa of brackish-water origin. Copepoda were represented in this area by the early stages of *Acartia* spp. and adults of *A. tonsa*, the latter species being described as preferring lower salinities and estuarine conditions (Paffenholzer and Searns 1988, Cervetto et al. 1999, Vuorinen et al. 1998). *Acartia* spp. has been shown to prefer higher temperatures (Möll-
mann et al. 2000, Dippner et al. 2001) typical of the coastal waters of the Kalmar Sound. Rotatoria are species of freshwater origin and this likely explains why in our study Keratella spp. was found the coastal waters. Keratella spp. has been indicated before as a taxon representative for the low-saline Gulf of Bothnia (Ojaveer et al. 2010). High densities of Rotatoria, especially Synchaeta spp., in the coastal waters of the Kalmar Sound have also been reported in a previous study (Nilsson et al. 2004). The high density of meroplankton (Bivalvia and Gastropoda larvae) in the coastal waters indicates a strong linkage between the pelagic and benthic habitats in this shallow area. These species occur in benthic habitats, and their distribution and density in the north Kalmar Sound could be currently constrained by the large extent of anoxic bottoms in deeper regions (Hansson et al. 2010b).

Beside hydrological conditions, other factors that could potentially affect the spatio-temporal dynamics of zooplankton are abundance of zooplanktivorous fish (top-down forcing on zooplankton) and phytoplankton density (bottom-up force on zooplankton). The separation between coastal and open waters found in our study could also be potentially explained by eutrophication gradients affecting primary production and thus

Table 1. Indicator species analysis (ISA) results. IndVal$_i$ is the indicator value for the species in parts per unit. $P$ values are based on 999 permutations. Indicator taxa for the whole sampling period and at least two of the three seasons are in boldface.

<table>
<thead>
<tr>
<th>Species</th>
<th>Code letter</th>
<th>All samples</th>
<th>Spring</th>
<th>Summer</th>
<th>Autumn</th>
</tr>
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<tr>
<td></td>
<td></td>
<td>IndVal$_i$</td>
<td>$p$</td>
<td>IndVal$_i$</td>
<td>$p$</td>
</tr>
<tr>
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<td>0.001</td>
<td>0.826</td>
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<tr>
<td><em>A. tonsa</em></td>
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<td>0.004</td>
<td>–</td>
<td>–</td>
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<tr>
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<td>–</td>
<td>–</td>
<td>–</td>
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</tr>
<tr>
<td><strong>NORTH</strong></td>
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<td></td>
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<tr>
<td><em>A. longiremis</em></td>
<td>D</td>
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<td>–</td>
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<td>0.007</td>
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<td>–</td>
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<td>–</td>
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<td><em>Fritillaria borealis</em></td>
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<td>0.010</td>
<td>0.840</td>
<td>0.006</td>
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<td>0.004</td>
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<tr>
<td><em>Temora longicornis</em></td>
<td>K</td>
<td>0.831</td>
<td>0.004</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

* see Fig. 6.
feeding conditions of zooplankton (Bonds dorff et al. 1997, Wasmund et al. 2001). For example, the presence of Rotatoria, which in our study were typical to the coastal waters, has been related in the Baltic Sea to high levels of eutrophication (Johansson 1983).

**Zooplankton and fish stocks**

The zooplankton community from the open waters of our study area matches the feeding preferences of adult clupeid fish (Kornilovs et al. 2001, Möllmann and Köster 2002, Casini et al. 2004, 2006). This suggests that the northern Kalmar Sound is an adequate feeding area for adults of both herring and sprat, as also indicated by the high commercial catches of these clupeid species in this area (data from the Swedish Agency for Marine and Water Management). The early pelagic stages of cod (length < 50 mm) also prefer to feed on the zooplankton species found in this area, particularly the copepod *Pseudocalanus* spp., *Temora longicornis* as well as the cladocera *Bosmina* spp. and *Evadne nordmanni* (Hüssy et al. 1997, Hinrichsen et al. 2002). However, the cod in the Baltic Sea is currently restricted to the southernmost Baltic Sea (ICES 2011a), and therefore its current abundance in the Kalmar Sound is very low (ICES 2011b).

Smaller zooplankton present in the coastal waters is a suitable diet for larger larvae and young-of-the-year of clupeids (Voss et al. 2003, Arrhenius 1996), making this area ideal for the recruitment of herring and sprat. Herring migrate to coastal areas to spawn in spring (Aro 1989) and the Kalmar Sound has been described as one of the main spawning area for herring (Parmann et al. 1994).

Mysidacea present in the Kalmar Sound may also be important food items for adult herring and cod juveniles (length > 70 mm) (Hüssy et al. 1997).

The density of the invasive cladocera *Cercopagis pengoi* was low in our samples (on average 0.8 indiv. m$^{-3}$ over the whole period). This predatory cladocera feeds on other zooplankton species, competing directly with sprat and herring adults and cod larvae (Holmborn 2009, Kotta et al. 2004), even though it may also constitute a valuable food item for clupeids (Gorokhova et al. 2004). At the densities found in our study, *C. pengoi* should not be considered an important factor affecting the Kalmar Sound food web.

**Table 2.** The PERMANOVA results. *P* values are based on 10 000 permutations.

<table>
<thead>
<tr>
<th></th>
<th>F-statistic</th>
<th>Partial $r^2$</th>
<th>$p$</th>
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<tr>
<td><strong>All samples</strong></td>
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<td>Surface temp.</td>
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<td>Surface temp.</td>
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</table>

* Temperature and salinity of the entire water column.

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**References**


Alheit J., Möllmann C., Dutz J., Kornilovs G., Loewe P.,...


Appendix. All taxa found in the samples from the Kalmar Sound in 2009–2010. a major taxa (abundance ≥ 1%); b abundance ≥ 1% only in spring; c abundance ≥ 1% only in autumn.

**Arthropoda**

Class Maxillopoda  
Acartia bifilosa a  
Acartia longiremis a  
Acartia spp. a  
Acartia tons a  
Centropages hamatus b  
Pseudocalanus spp. c  
Temora longicornis a  
Eurytemora hirundoides a  
Calanoidea  
Cyclopoidea  
Harpacticoida  
Limnocalanus macrurus  
Limnocalanus spp.  

Infraclasse Cirripedia  
Cirripedia  
Balanus  

Class Branchiopoda  
Bosmina spp. a  
Euvalea nordmanni a  
Euvalea anonyx  
Pleopsis polyphemoides a  
Cercopagis pengoi  
Chydorus sphaericus  
Chydorus spp.  
Podon intermedius  
Podon leuckarti  

Class Malacostraca  
Mysis mixta  
Neomysis integer  
Tanaisidae  
Gammarus spp.  
Isopoda  

Class Ostracoda  
Ostracoda  

Class Arachnida  
Acarina  
Hydracarina  
Class Insecta  
Insecta  

**Chordata**

Class Actinopterygii  
Fish larvae  
Class Appendicularia  
Fritillaria borealis a  

**Rotifera**

Class euröstera  
Keratella cruciformis  
Keratella cochlearis typica a  
Keratella quadrata a  
Synchaeta spp. a  
Notholca spp.  

**Mollusca**

Class Bivalvia  
Bivalvia larvae a  
Class Gastropoda  
Gastropoda larvae  

**Cephalorhyncha**

Class Kinorhyncha  
Kinorhyncha  

**Annelida**

Class Polychaeta  
Marenzelleria neglecta  
Polychaeta  

**Nematoda**

Nematoda  

**Platyhelminthes**

Class Turbellaria  
Turbellaria  

**Ctenophora**

Ctenophora  

**Cnidaria**

Medusa