

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 Martín *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-

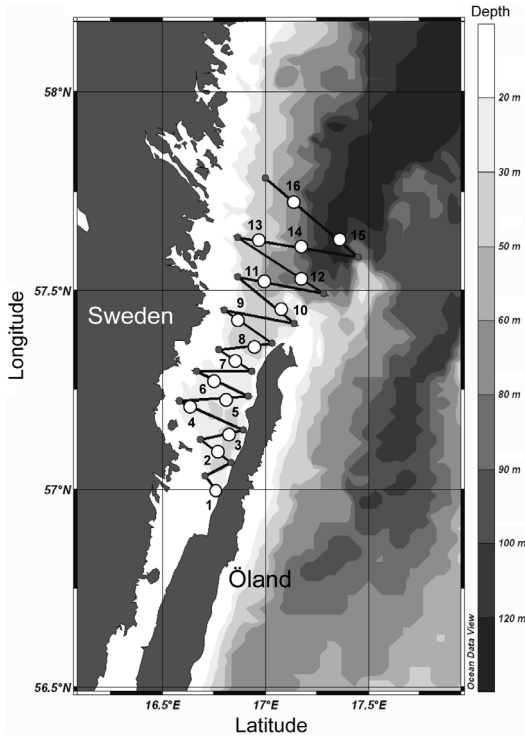


Fig. 1. Study area and sampling stations.

ables and nutrient concentrations regulating phytoplankton blooms (Hernroth 1981, Vuorinen *et al.* 1998, Möllmann *et al.* 2008, Hansson *et al.* 1990, 2010) or with global climate phenomena (e.g. North Atlantic Oscillation; Alheit *et al.* 2005, Möllmann *et al.* 2008). Top-down effects of planktivorous fish on zooplankton have also been reported in the Baltic Sea (Casini *et al.* 2008, 2009).

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.

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 ($> 200 \mu\text{m}$) and the larger fraction of microzooplankton (20–200 μm); for the sake of simplicity both fractions are henceforth referred to as “zooplankton”.

The zooplankton net was towed at a speed of 1.5 m s^{-1} . At the shallow stations (depth $< 50 \text{ m}$; 1–10 in Fig. 1) only one sample was collected from the sea bottom to the surface. At the deep stations (depth $> 50 \text{ m}$; 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 Mysidacea 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, Dvoretzky and Dvoretzky 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 $\geq 1\%$ 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

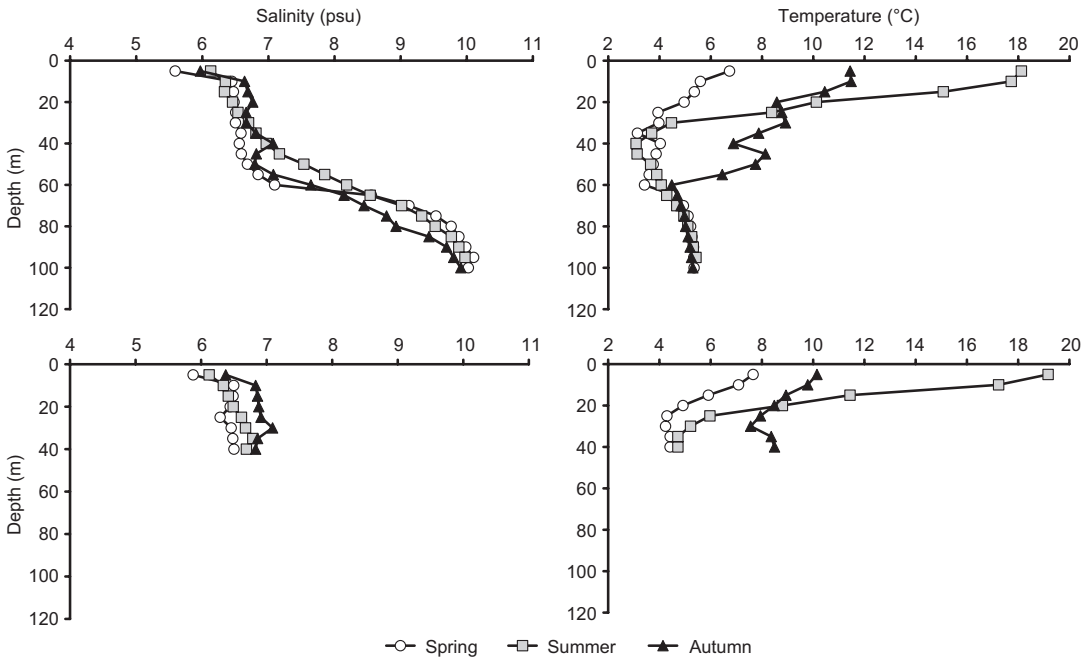


Fig. 2. Salinity and temperature profiles in open (top) and coastal (bottom) waters.

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

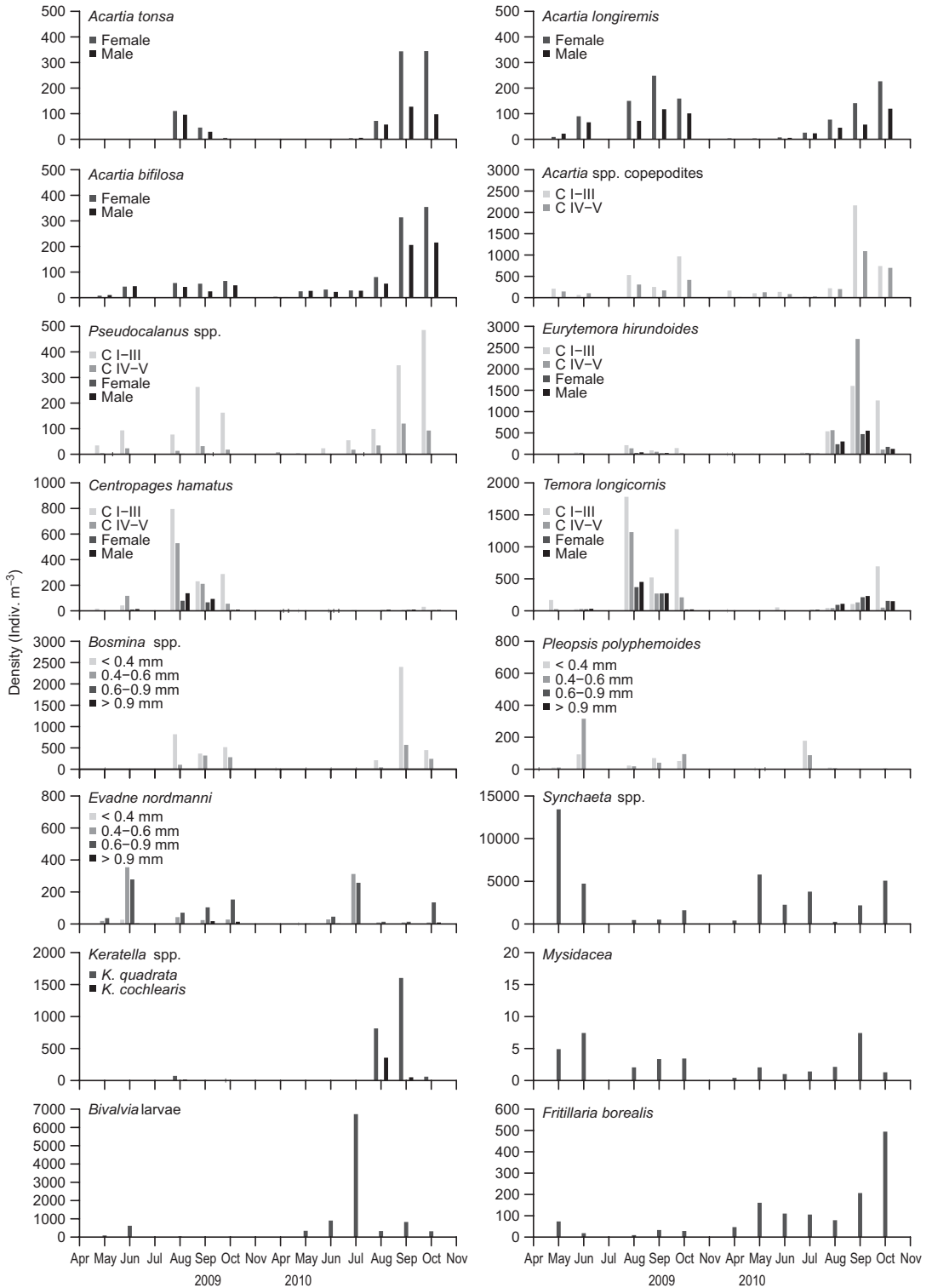


Fig. 3. Densities of the major zooplankton taxa (abundance $\geq 1\%$ of the total abundance). Although Mysidacea are not a major taxon, they are also presented because of their importance in the diet of large herring (Casini *et al.* 2004), and hence are ecologically important in the area.

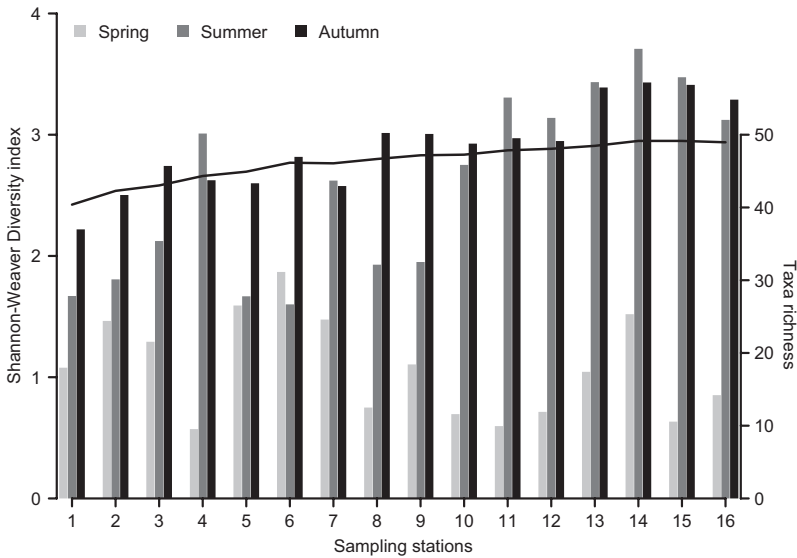


Fig. 4. Shannon-Weaver Diversity index calculated for each station and season (bars) and taxa richness at each station for the entire sampling period (line).

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. hirundooides* 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).

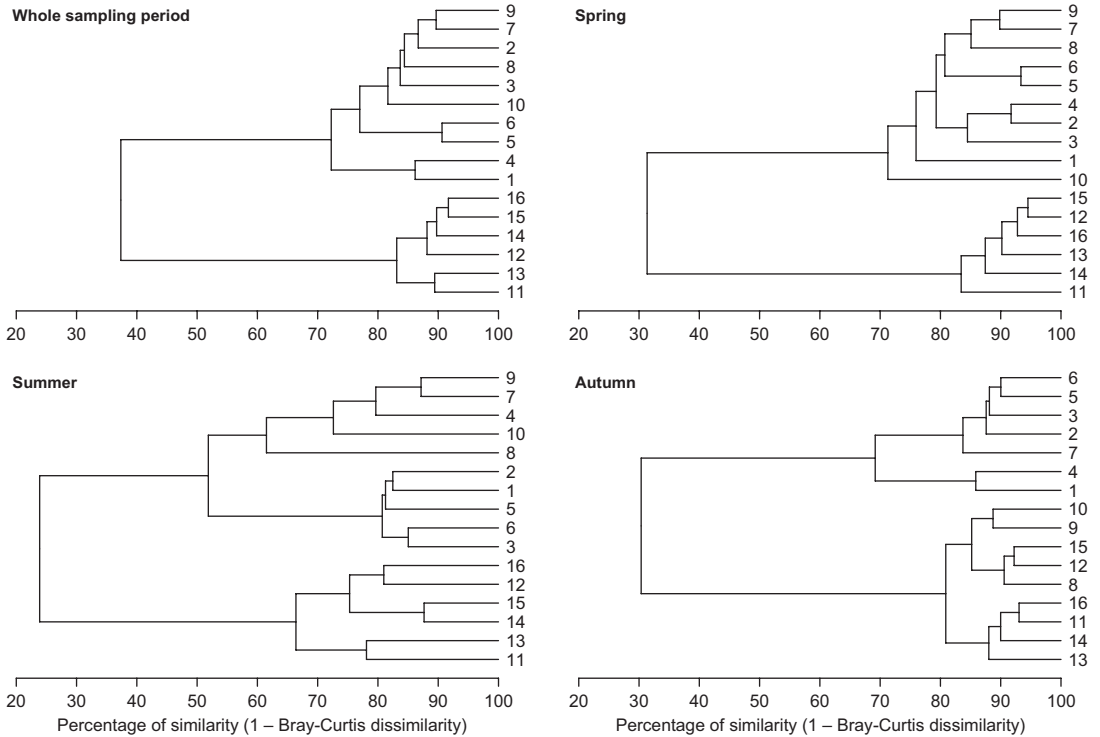


Fig. 5. Results of the cluster analysis.

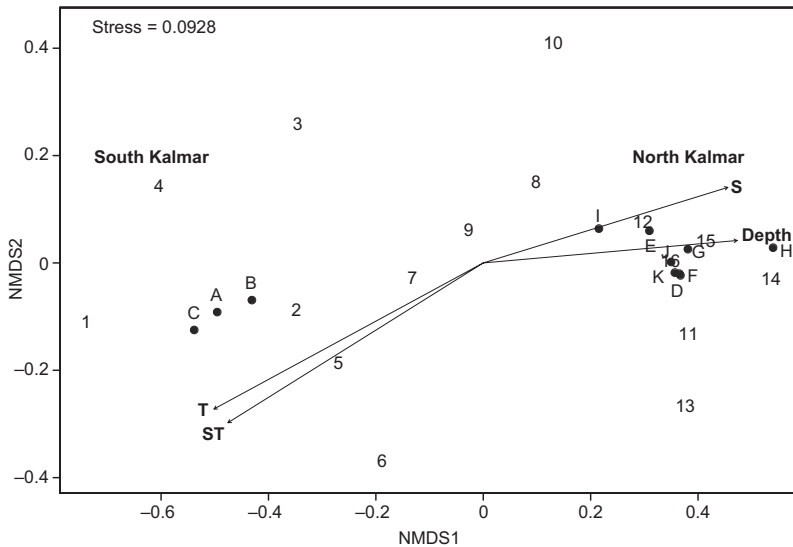


Fig. 6. NMDS analysis. The numbers (1 to 16) correspond to the stations and the letters to the indicator taxa (see Table 1). The arrows represent the fitted vectors of depth and hydrological variables: salinity of the entire water column (S), surface temperature (ST), and temperature of the entire water column (T).

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 (Paffenhöfer 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_{*ij*} 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.

Species	Code letter*	All samples		Spring		Summer		Autumn	
		IndVal _{<i>ij</i>}	<i>p</i>	IndVal _{<i>ij</i>}	<i>p</i>	IndVal _{<i>ij</i>}	<i>p</i>	IndVal _{<i>ij</i>}	<i>p</i>
SOUTH									
Acartia spp.	A	0.927	0.001	0.826	0.002	0.807	0.039	0.887	0.001
<i>A. tonsa</i>		0.858	0.004	–	–	–	–	0.857	0.007
Bivalvia	B	0.902	0.001	0.917	0.001	0.854	0.001	–	–
<i>Bosmina</i> spp.		–	–	0.898	0.008	–	–	–	–
Cyclopoida		0.809	0.001	–	–	–	–	–	–
Gastropoda	C	0.909	0.001	0.824	0.048	0.932	0.003	0.844	0.001
Harpacticoida		0.879	0.001	0.81	0.008	–	–	–	–
<i>Keratella cochlearis</i>		–	–	–	–	–	–	0.876	0.019
<i>K. cruciformis</i>		0.834	0.026	–	–	0.826	0.022	–	–
<i>K. quadrata</i>		0.840	0.009	–	–	–	–	0.868	0.001
Ostracoda		0.858	0.012	0.727	0.049	–	–	–	–
<i>Pleopsis polyphemoides</i>		0.833	0.026	–	–	–	–	–	–
Polychaeta		0.831	0.021	–	–	–	–	–	–
<i>Synchaeta</i> spp.		–	–	–	–	–	–	0.811	0.004
NORTH									
A. longiremis	D	0.822	0.006	–	–	0.822	0.009	0.881	0.001
Bosmina spp.	E	0.793	0.036	–	–	0.877	0.025	0.824	0.001
Centropages hamatus	F	0.830	0.003	–	–	0.842	0.004	0.859	0.001
Ctenophora		0.842	0.009	0.831	0.013	–	–	–	–
<i>Eurytemora hirundoides</i>		–	–	–	–	0.862	0.047	0.791	0.044
<i>Evadne anonyx</i>		0.816	0.007	–	–	–	–	0.752	0.034
<i>E. nordmanni</i>		–	–	–	–	–	–	0.901	0.001
Fritillaria borealis	G	0.824	0.010	0.840	0.006	0.819	0.018	0.907	0.001
Limnocalanus spp.	H	0.894	0.001	0.964	0.001	0.913	0.006	0.889	0.006
Medusae		0.834	0.014	–	–	–	–	0.847	0.021
<i>Podon intermedius</i>		–	–	–	–	0.825	0.001	0.806	0.012
P. leuckarti	I	0.819	0.016	0.813	0.037	0.818	0.030	–	–
Polychaeta		–	–	–	–	0.820	0.011	–	–
Pseudocalanus spp.	J	0.824	0.004	0.931	0.002	0.889	0.003	0.837	0.003
Temora longicornis	K	0.831	0.004	–	–	0.814	0.011	0.838	0.002

* see Fig. 6.

feeding conditions of zooplankton (Bondsdorff *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 Copepoda *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 (Parmanne *et al.* 1994).

Myxidacea 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 *Cerco-pagis 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.

	<i>F</i> -statistic	Partial <i>r</i> ²	<i>p</i>
All samples			
Salinity*	5.0602	0.17252	0.0028
Surface temperature	4.6946	0.16006	0.0067
Temperature*	2.7484	0.09371	0.0377
Residuals		0.37504	
Spring			
Salinity*	3.7632	0.151	0.0086
Surface temperature	1.5852	0.06361	0.1790
Temperature*	5.1385	0.20618	0.0011
Residuals		0.44138	
Summer			
Salinity*	2.8150	0.12767	0.0127
Surface temperature	2.3123	0.10487	0.0401
Temperature*	3.1547	0.14307	0.0056
Residuals		0.49889	
Autumn			
Salinity*	5.7576	0.20522	0.0026
Surface temperature	6.5927	0.23499	0.0020
Temperature*	1.1874	0.04232	0.2918
Residuals		0.39208	

* Temperature and salinity of the entire water column.

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

Arthropoda

Class Maxillopoda

Acartia bifilosa^a

Acartia longiremis^a

Acartia spp.^a

Acartia tonsa^a

Centropages hamatus^b

Pseudocalanus spp.^c

Temora longicornis^a

Eurytemora hirundoides^a

Calanoida

Cyclopoida

Harpacticoida

Limnocalanus macrurus

Limnocalanus spp.

Infraclass Cirripedia

Cirripedia

Balanus

Class Branchiopoda

Bosmina spp.^a

Evadne nordmanni^a

Evadne anonyx

Pleopsis polyphemoides^a

Cercopagis pengoi

Chydorus sphaericus

Chydorus spp.

Podon intermedius

Podon leuckarti

Class Malacostraca

Mysis mixta

Neomysis integer

Tanaidacea

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 eurotatoria

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
