JOURNAL OF PLANKTON RESEARCH | VOLUME 34 | NUMBER 4 | PAGES 298–307 | 2012

Ontogenetic and seasonal changes in diel vertical migration amplitude of the calanoid copepods *Eurytemora affinis* and *Acartia* spp. in a coastal area of the northern Baltic proper

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Received June 23, 2011; accepted in principle January 9, 2012; accepted for publication January 10, 2012

Corresponding editor: Mark J. Gibbons

We studied diel vertical migration (DVM) of the six copepodite stages of two of the most abundant crustacean zooplankton in the Baltic Sea, the calanoid copepods *Eurytemora affinis* and *Acartia* spp. The study was conducted monthly from May through October in a bay in the northwestern Baltic proper. Fish biomass, phytoplankton abundance and temperature were obtained in conjunction with the zooplankton sampling. Both copepod species performed DVM. With the exception of females, all *E. affinis* copepodite stages performed migrations of over 10 m with only a slight increase with the copepodite stage. Adult female *E. affinis* remained at depth with only slight upward movement at night. In *Acartia* spp., DVM amplitude increased with stage and size, suggesting an ontogenetic shift in behaviour; although they had a less pronounced DVM than *E. affinis.* Although DVM amplitude increased with size, indicative of visual predation, fish biomass did not correlate with the amplitude of DVM. However, fish were present throughout the study period. We surmise that these ontogenetic shifts in behaviour are due to size increase and therefore visibility to predators and that the difference in DVM between the species may well be a result of physiological differences and reproductive strategy.

KEYWORDS: weighted mean depth; Baltic Sea; zooplankton; thermocline; depth distribution

INTRODUCTION

Diel vertical migration (DVM) is a behaviour common in zooplankton and an ecological phenomenon affected by many environmental factors. An ultimate reason for DVM is diminishing mortality through predator avoidance (Zaret and Suffern, 1976; Kerfoot, 1985; Gliwicz, 1986; Lampert, 1993; Hays, 2003). Several proximate factors affect the development and expression of DVM, including changes in light, presence of predators, food and temperature (Ringelberg and van Gool, 2003). These factors can vary seasonally, especially at high latitudes, e.g. short summer nights reduce the dark period

doi:10.1093/plankt/fbs001, available online at www.plankt.oxfordjournals.org. Advance Access publication February 8, 2012

to such an extent that zooplankton might risk extensive predation by visually hunting predators during the long light period (Hays *et al.*, 1995). In systems where most fish are spring spawners, mortality through predation increases in summer when the young-of-year (YOY) become abundant. The greater biomass of fish increases the concentration of kairomones in the water, sensitizing zooplankton to relative changes in light intensity resulting in a stronger photobehaviour, thus initiating DVM in phenotypically plastic zooplankton (Ringelberg *et al.*, 1991). Predation can also lead to short-term genetic selection, shifting a partially migrating zooplankton population towards a migrating population (Haney, 1988). Variation in feeding conditions (availability of phytoplankton, Ricklefs, 2007) may determine whether zooplankton can perform DVM without compromising growth or reproduction rates. In poikilotherms, such as crustacean zooplankton, physiological temperature dictates production rates. Thus, zooplankton should limit the time spent in cooler water, possibly limiting the amplitude of DVM to avoid low temperatures (Calaban and Makarewicz, 1982). In the autumn when temperature drops and the water column mixes, becoming isothermic, there are no bioenergetic gains from DVM and, towards winter, many zooplankton go into diapause (Jarnagin *et al.*, 2004).

If vertical migration reflects individual needs and trade-offs, and not a schooling/flock behaviour (Neill, 1990), we could expect to find ontogenetic differences, as many zooplankton have discrete life stages, usually increasing in size with each stage. In copepods, there are six naupliar and five copepodite stages before reaching adulthood (Mauchline, 1998). With DVM often being attributed to avoiding predation from visual predators, size becomes important, as prey detection depends upon prey visibility, which increases with size (Brooks and Dodson, 1965). Therefore, it is expected that larger individuals have a more pronounced pattern of migration with shorter periods at the surface (Hays, 1995; De Robertis *et al.*, 2000).

In the coastal waters of the north western Baltic proper, the calanoid copepods *Eurytemora affinis* and *Acartia* spp. dominate the zooplankton community (Johansson, 1992). Although of similar size, there are species-specific physiological and ecological differences; *E. affinis* is an egg-sac spawner and predominantly a filter feeder (Gyllenberg, 1980), *Acartia* spp., on the other hand, are broadcast spawners capable of both raptoral and filter feeding (Tiselius, 1990; Engström *et al.*, 2000) and capable of consuming a broader size range of food particles (Adrian *et al.*, 1999). *Eurytemora affinis* has been found to have a stronger migration than *Acartia* spp. (Hansson *et al.*, 1990). Previous studies of Baltic copepod DVM have had a limited ontogenetic resolution (Hansson *et al.*, 1990; Hansen *et al.*, 2006). Our objectives are to study seasonal changes in DVM with a higher ontogenetic resolution than is common in the literature, including those studies performed in the Baltic Sea (Hansson *et al.*, 1990; Hansen *et al.*, 2006). While the species we compare are of similar size, they differ in other respects (see above) and we explore different aspects of DVM and relate these to their different traits.

METHOD

Study site and sampling

Himmerfjärden Bay is situated in the southern archipelago of Stockholm, northern Baltic proper. It is ~30 km long, has a mean salinity of 6 (PSU) and an average depth of 17 m. The sampling site is halfway up the bay at (N59°00.572, E17°44.943) with a water depth of close to 35 m (Fig. 1). The zooplankton community is dominated by rotifers, cladocerans and the calanoid copepods *E. affinis*, *Acartia bifilosa* and *Acartia longiremis* (Johansson, 1992). Dominating planktivores in the area are clupeids (herring, *Clupea harengus*, and sprat, *Sprattus sprattus*) and mysid shrimps (*Mysis mixta*) (Hansson *et al.*, 1990; Rudstam *et al.*, 1992). Since these clupeids spawn predominantly in spring and early summer, the fish abundance increases rapidly in July and peaks in August, with high densities of YOY herring exerting high predation pressure on the zooplankton (Axenrot and Hansson, 2004). The zooplankton decrease in autumn is possibly because of this (Johansson, 1992; Rudstam *et al.*, 1992). All of the planktivores have been documented as preferring copepods over other zooplankton (Hansson *et al.*, 1990; Rudstam and Hansson, 1990; Arrhenius, 1996).

Monthly sampling was carried out by day and night and as close to a waning quarter moon as practically possible to minimize the possible effect of variation in moon illumination. The study period covers May, when zooplankton start to become abundant (Johansson, 1992), through October 2009 (Table I). Samples were collected with a transparent acrylic glass tube sampler (25 L, 1.5 m long, 14.5 cm inner diameter), deployed while moored at an anchored buoy, lowered open to the selected depth then closed with a messenger and winched to the surface. Sampling started at the surface and was repeated every 2.5 m down the water column to 32.5 m (13 samples). The collected water was filtered through a 20 μm sieve and preserved with 4% borax buffered formalin. On each sampling occasion, a

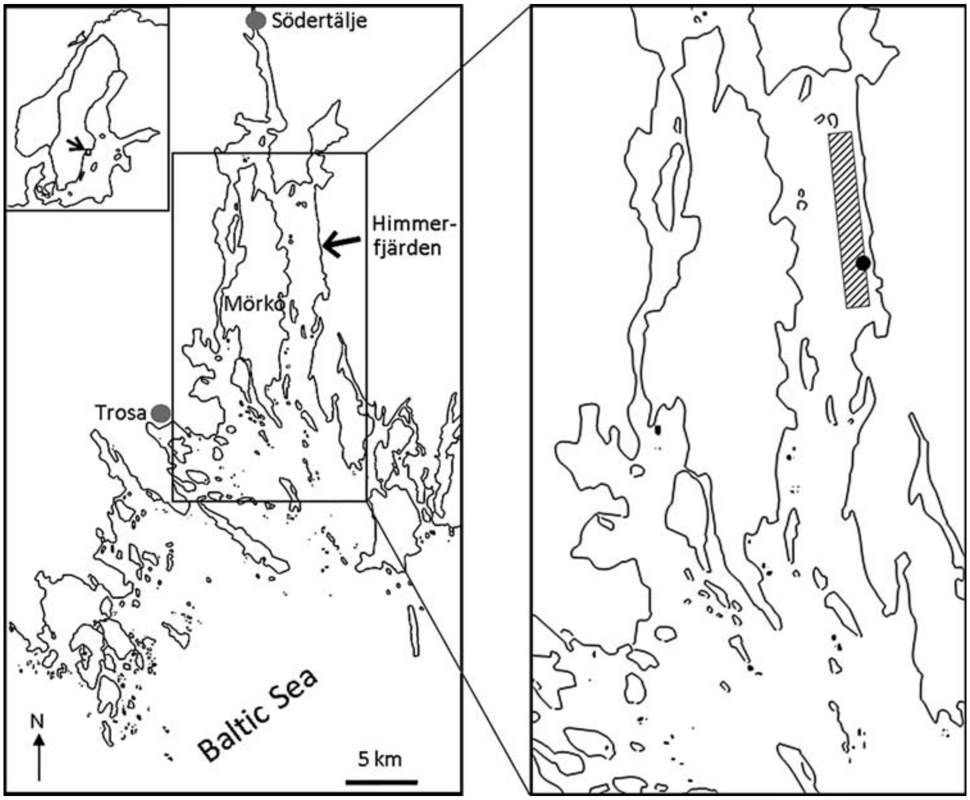

Fig. 1. Himmerfjärden. The hashed area denotes the sonar transect and the filled circle the site of zooplankton sampling at N 59°00.572 E 17°44.943.

Table I: Sampling dates 2009, duration of sampling and time of sunset

Sampling dates	Sunset	Sampling times Day	Night
19–20 May	21:20	14:30–17:00	22:40–00:00
16–17 June	22:05	14:15–16:30	23:35–01:00
14–15 July	21:48	15:15–16:45	23:30–00:30
12 August	20:45	14:30–16:30	22:15–23:50
14 September	19:12	14:00–15:40	20:30–22:15
12 October	17:51	13:30–15:30	19:30–21:05

vertical temperature profile was obtained with a CTD, while phytoplankton were collected in depth-integrated samples (0–14 m) preserved in acidic Lugol's solution and counted in sedimentation chambers using an inverted microscope (Leica DM IRB) following the standard protocol of HELCOM (HELCOM, 2009) (data provided by Dr S. Hajdu, address as the authors).

Each zooplankton sample was counted using a dissection microscope (Olympus SZH, GWH10X-D) at ×50 magnification. Species identified were the calanoid copepods *E. affinis* and *Acartia* spp. and their copepodite stages (I–VI). Older stages of *Acartia* were identified to species, all belonging to *A. bifilosa*; copepods younger than stage IV could not be identified to species and are referred to as *Acartia* spp. The weighted mean depth (WMD) was calculated for each copepodite stage separately and separately for day and night, and each sampling occasion:

$$\mathrm{WMD} = \frac{\sum (n_i d_i)}{\sum n_i}$$

where n_i is the abundance of individuals in depth interval i and d_i the midpoint depth interval i (Bollens and Frost, 1989b; Hansen *et al.*, 2006). To compare the difference in migration between the two species, the differences in WMD between equivalent stages of *E. affinis* and *Acartia* spp. were tested for with a *t*-test (Table II). Ontogenetic differences were tested for with Spearman's rank, to avoid the effect of variation in absolute values between months. In an attempt to explain variation in depth distributions of the copepods, generalized additive models (GAMs, applying identity link and Gaussian distribution in the *mgcv* module of the BRODGAR statistical package for R, Highland Statistics Ltd) were fitted to the data, with WMD as the

Table II: Summary of results from t*-tests on differences in WMD between equivalent copepodite stages of* E. affinis *and* Acartia *spp.*

	Difference in day depth		Difference in night depth	
Life stage	*t*-value	*P*-value	*t*-value	*P*-value
I	2.16	<0.09	−0.31	<0.8
II	3.09	<0.03	−0.56	<0.6
III	2.98	<0.04	−0.13	<0.9
IV	2.77	<0.04	0.41	<0.8
V	2.65	<0.05	0.03	<0.98
♂	1.73	<0.2	−0.72	<0.6
♀	2.12	<0.09	2.97	<0.04

Day and night depths are compared separately. One datum is derived for each month, resulting in $n = 6$ for both *E. affinis* and *Acartia* spp. in each test.

Table III: Prosome lengths (mm) of copepodites used in GAM analyses, derived from measurements by T. Holmborn, Department of Systems Ecology, Stockholm University

	Life Stage						
	I	II	III	IV	V	♂	♀
Acartia spp.							
May	0.43	0.51	0.57	0.65	0.75	0.8	0.8
Jun.	0.43	0.51	0.57	0.65	0.75	0.8	0.8
Jul.	0.33	0.41	0.47	0.55	0.65	0.7	0.7
Aug.	0.33	0.41	0.47	0.55	0.65	0.7	0.7
Sept.	0.33	0.41	0.47	0.55	0.65	0.7	0.7
Oct.	0.33	0.41	0.47	0.55	0.65	0.7	0.7
Eurytemora affinis							
May	0.43	0.51	0.58	0.64	0.71	0.73	0.73
Jun.	0.43	0.51	0.58	0.64	0.71	0.73	0.73
Jul.	0.33	0.41	0.48	0.54	0.61	0.63	0.63
Aug.	0.33	0.41	0.48	0.54	0.61	0.63	0.63
Sept.	0.33	0.41	0.48	0.54	0.61	0.63	0.63
Oct.	0.33	0.41	0.48	0.54	0.61	0.63	0.63

response variable and prosome lengths (Table III) of different copepodite stages as the explanatory variable. This was done for the two species and day and night separately. The residuals from these models indicate if the copepods occurred deeper or closer to the surface than expected from their size. These residuals were then correlated to independent variables that were expected to potentially influence the depth distribution.

Fish: sonar

Sonar surveys were conducted on the consecutive night to the zooplankton sampling, with a 70-kHz split beam transducer (Simrad ES70-7C) and a Simrad EK60 scientific echo sounder along a transect that passed close to the zooplankton sampling site (Fig. 1). Calibrations were performed with a standard copper sphere, as recommended by the manufacturer. In all surveys, pulse duration 0.5 ms, bandwidth 4.96 kHz and pulse rate 0.5 ping s^{-1} were applied. A 5-m boat was used in May, June and July and a 9-m boat in August, September and October. The transducer was mounted on a tow body, pulled at 5 knots, midships at 1 m depth and 1.5 m from the boat. With this arrangement, the acoustic axis was perpendicular to the sea surface and there were no problems with echoes from side-lobes hitting the hull of the boat or air bubbles from the hull/propeller. Data were analysed with the Sonar5-Pro software (version 5.9.8; Balk and Lindem, 2010). Fish density was analysed in 2 m layers. Fish biomass was derived from echo integration data (s_A), assuming a fish size distribution as described by the single fish echoes (echo length 0.8–1.3 pulse duration) with the minimum target strength set to −60 dB and an upper threshold of −42 dB. The Amp-threshold was set to −80 dB. Sizes expressed in TS were transformed to fish weight using the relationship found by Didrikas and Hansson (Didrikas and Hansson, 2004) and our own unpublished data on the length to weight relationship for herring:

$$\text{weight} = 6.27 \times 10^{-3} \times \left(10^{(\mathrm{TS}+73.6)/25.5}\right)^{3.014}$$

RESULTS

General description

Generally, both *Acartia* spp. and *E. affinis* performed DVM, migrating from depth up to the thermocline at night. In August, *Acartia* spp. stages I and II performed reverse DVM. *Eurytemora affinis* females only showed slight tendencies towards migration, remaining at depth both during the day and night, with the exception of August (Fig. 2C and D). In October, migration ceased and all stages of both species remained at depth. Younger copepodite stages tended to have a weaker migration than that of their older (larger) conspecifics (Fig. 2). *Acartia* spp. was generally distributed over a greater part of the water column (shown by higher standard deviations in depth, Fig. 2i–iv) during the day and more concentrated at night with little variation across the sampling season. *Eurytemora affinis* also showed a greater dispersal during the day than at night, although to a lesser extent than *Acartia* spp., but

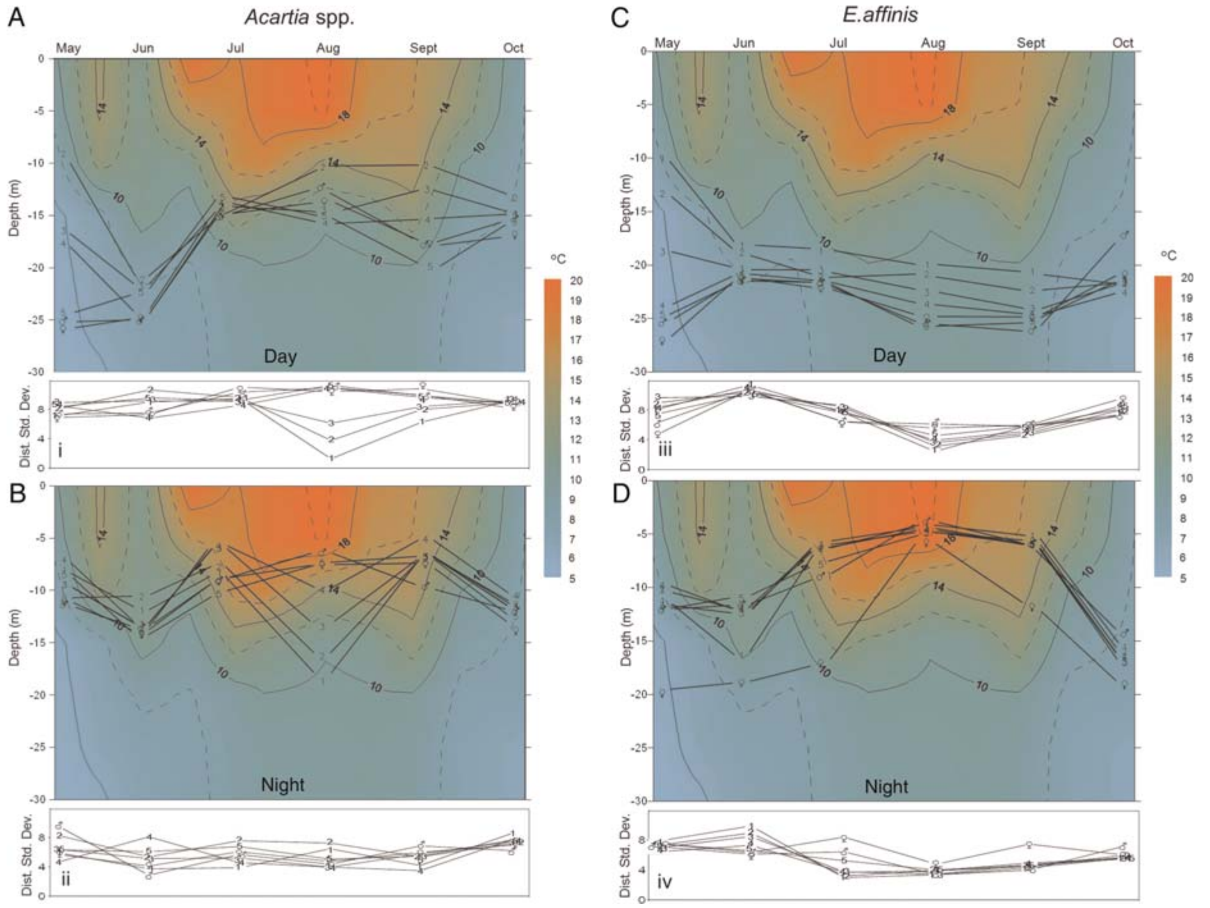

Fig. 2. WMD of day and night for all copepodite stages of *Acartia* spp. (**A**, *Acartia* day WMD; **B**, *Acartia* night WMD) and *E. affinis* (**C**, *Eurytemora* day WMD; **D**, *Eurytemora* night WMD). Isobars showing temperature (Celcius) of the water column. The panel below (i, ii, iii and iv) each shows the distribution standard deviation of the copepods from the WMD.

decreasingly so from June to September (Fig. 2i–iv). With the water column mixing in October, they again became more dispersed.

Intraspecific comparisons

For each sampling occasion, species and stage, we calculated the difference in WMD between day and night. The resulting differences were tested for deviation from zero (i.e. that they performed a DVM) using *t*-tests. All groups, except for copepodites I and II of *Acartia* spp., conduct significant migrations, although with notably weak significance for *E. affinis* I and females (Table IV). In all cases, the copepodites were closer to the surface at night.

These results indicate ontogenetic differences in DVM. To explore this further, the WMD and different stages were ranked separately for each month (rank 1 to the stage closest to the surface and 7 to the deepest occurring stage). This procedure was taken to remove effects of absolute depth values since these varied between months. The depth ranks were then correlated to the copepodite stage using Spearman's rank correlation. For both species, the depth increases significantly

Table IV: Summary of results from t*-tests on differences in WMD between day and night*

	Acartia spp.		*E. affinis*	
Life stage	*t*-value	*P*-value	*t*-value	*P*-value
I	0.75	<0.5	2.71	<0.05
II	0.92	<0.4	3.98	<0.02
III	4.42	<0.006	4.38	<0.01
IV	6.29	<0.002	5.75	<0.003
V	3.46	<0.02	4.93	<0.005
♂	4.79	<0.005	4.23	<0.01
♀	4.30	<0.008	2.72	<0.05

The hypothesis tested was that this difference is zero. One datum is derived for each month, resulting in $n = 6$ for each taxonomic group. *P*-values of <0.05 indicate differences in day and night distribution, in all cases with a deeper distribution in daytime (i.e. they perform DVM).

with stage and this is true both day and night (*E. affinis* day correlation 0.64, $P < 0.0001$, night: 0.45 and $P < 0.003$. *Acartia* spp. day: 0.54, $P < 0.0001$, night: 0.02 and $P < 0.05$).

Interspecific comparisons

Eurytemora affinis has a deeper distribution during the day than *Acartia* spp. (Fig. 2A and C) and for copepodite stages II–V, this difference is statistically significant (Table II). The night-time depth distribution of the two species is generally similar; with one exception, the deeper distribution of *E. affinis* females. Even if *E. affinis* has a deeper daytime distribution than *Acartia* spp. (Fig. 2A and C), the extent of the DVM range (day–night difference in WMD within each species stage) does not differ significantly between equivalent stages of the species (Table V). However, *E. affinis* shows a consistent tendency (except for females) to have a greater amplitude of migration (Fig. 2A–C). If all the 42 (stage × month) DVM ranges were tested simultaneously, the difference between species DVM becomes strongly significant ($t = 4.07$, $P < 0.0003$) and a similar result ($t = 5.24$, $P < 0.002$) is obtained if the input data are the seasonal averages of the DVM ranges for each life stage. If data for females are excluded from the analysis, the differences become even clearer (all DVM ranges: $t = 4.59$, $P < 0.00006$; seasonal averages of DVM ranges for each copepodite stage: $t = 13.49$, $P < 0.00004$). The conclusion is that *E. affinis* has a stronger DVM than *Acartia* spp., with the exception for females.

A final step in the comparison of the species was to explore whether the DVM range differed with copepodite stage (=size). To avoid problems with differences in absolute values between dates, the DVM range differences were ranked within each date; with the highest rank going to the copepodite stage with the highest value for the difference between *Eurytemora* DVM range minus *Acartia* DVM range. These ranges were then correlated with the copepodite stage (Spearman's rank); this yielded a negative correlation (−0.506 and $P < 0.00001$). The difference in DVM between the species hence decreases with size as suggested by the varying day depths in Table II.

Table V: Summary of t*-test results, comparing the range of DVM that* E. affinis *and* Acartia *spp. conducted.*

Life stage	DVM ranges *t*-value	*P*-value
I	1.32	<0.2
II	2.13	<0.09
III	1.91	<0.1
IV	2.23	<0.08
V	1.86	<0.1
♂	1.64	<0.2
♀	−0.09	<0.9

Each month produced one datum per taxonomic group, resulting in $n = 6$ for both *E. affinis* and *Acartia* spp. in each test. No statistical difference in DVM range was found between equivalent copepodite stages of *E. affinis* and *Acartia* spp.

Extrinsic factors that cause variation in DVM

The residuals derived from GAM models were correlated to biomass of pelagic fish and total phytoplankton densities (Fig. 3B and C) and the duration of night (sunset to sunrise, Fig. 4). Correlations would imply that deviations in the WMD were affected by one or more of these variables. No statistically significant or clear trends were seen in these tests. However, in August, *E. affinis* females, for the first time, performed a migration similar in amplitude to that of their conspecifics. This coincides with increased relative changes in light intensity at dawn and dusk, as it is first in August that twilight does not persist throughout the night (Fig. 4), also phytoplankton abundance is at its lowest, excluding October (Fig. 3C). This could indicate that changes in these factors cause *E. affinis* females to alter strategy.

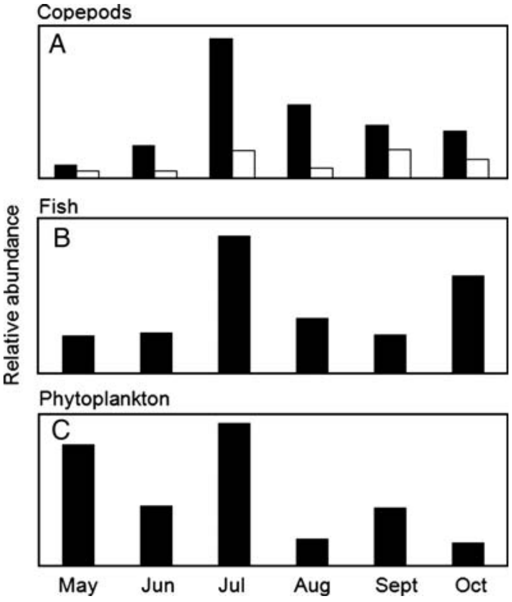

Fig. 3. Relative abundance of copepods, fish and phytoplankton in May–October. *Eurytemora affinis* is represented by the black bars and *Acartia* spp. the white. All groups had a peak in abundance in July. Phytoplankton data, analysed according to the standard protocol of Helcom courtesy of Hajdu (Hajdu, unpublished data).

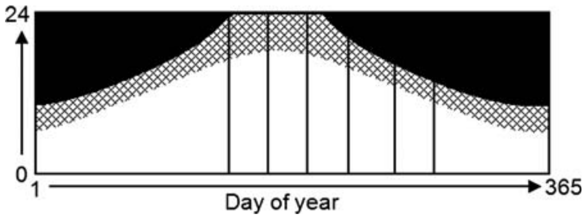

Fig. 4. Length of daylight, civilian twilight and night through the year as derived from Astronomy lab for the sampling site. Daylight in white, twighlight hashed and night black. The vertical lines represent the sampling occasions May–October.

Temperature may have an influence on the extent of DVM. Both copepod species migrate from below up to the thermocline having significantly different depth from the thermocline during the day but not at night (*t*-tests; *Eurytemora*, night WMD $P < 0.7$, *Eurytemora*, day WMD, $P < 0.00001$; *Acartia*, night WMD $P < 0.8$, *Acartia*, day WMD $P < 0.00001$).

Degree-hours

The female copepods reside at different depths for most of the season, *E. affinis* females remain at depth in cooler water while *Acartia* spp. females migrate and remain higher in the water column in warmer water (Fig. 2A–D). To explore possible bioenergetic differences resulting from this, we estimated the number of degree-hours (DH, summed products between temperature and the number of hours at that temperature) to see whether this could explain the higher population densities of *E. affinis* compared with *Acartia* spp. DH was derived by linear interpolation of the temperature data and female copepod depths between sampling occasions. *Eurytemora affinis* females had ~12% less DH (32.6×10^3 DH) compared with *Acartia* spp. females (37.09×10^3 DH). If only temperature is taken into consideration, one would expect *Acartia* spp. to dominate, as temperature regulates growth rate and development, both of eggs and adults (Vuorinen, 1987). This was however not the case, as *E. affinis* was the more abundant species throughout the season (Fig. 3A). Other factors must explain this, such as a food spectrum more suitable for *E. affinis* or that their more pronounced DVM, with egg-carrying females remaining at depth, gives a more successful protection from predation.

DISCUSSION

One ultimate reason for DVM is diminishing mortality through predation prevention. In the case of visually hunting predators, prey detection depends upon prey visibility, which increases with size (Brooks and Dodson, 1965). Hence, larger zooplankton should perform a more pronounced DVM than smaller zooplankters as they are more visible (cf. Hays *et al.*, 1994, 1995). Our results are consistent with this on an intraspecific level for both species. On the interspecific level, given their similar size, one would conjecture that *E. affinis* and *Acartia* spp. would have similar diel vertical migrations. This was however not the case, *E. affinis* has a stronger DVM than *Acartia* spp., with the notable exception of adult female *E. affinis* which most frequently remained at depth (further discussed below), suggesting that *E. affinis* is preferred by zooplanktivorous fish. However, studies on the selectivity of zooplanktivorous fish for these two copepods species are inconsistent (Arrhenius, 1996; Viitasalo *et al.*, 2001; Casini *et al.*, 2004). Other factors are likely to be involved in governing the different DVM strategies, e.g. life-history traits or physiological differences.

Marine copepods react to mechanical stimuli from predatory fish (Bollens and Frost, 1989a; Bollens *et al.*, 1994) and *Acartia* spp. have been shown to be very alert to hydrodynamic signals demonstrating early escape responses from such stimuli (Checkley, 1982; Viitasalo, 2001). This sensitivity is explained by the large setae on their antennae (Viitasalo, 2001) allowing for early detection of approaching predators, although earlier attributed to hydrodynamic detection of ciliates and rotifers (Stoecker and Egloff, 1987; Jonsson and Tiselius, 1990). These setae can allow *Acartia* spp. to perform evasive action instead of seeking safety in deeper and colder water. As *E. affinis* lacks these large setae, they may be less sensitive to hydrodynamic stimuli and so migrate to avoid predation.

On a population level, fecundity can affect susceptibility to predation, with more fecund species being able to tolerate higher levels of mortality and maintain population levels. Broadcast spawners have a greater weight specific fecundity than sac spawners (Kiørboe and Sabatini, 1995) and *Acartia* has an order of magnitude higher fecundity than that of *E. affinis* (Hirche, 1992). This may offset the need for *Acartia* to migrate to the same extent as the less fecund *Eurytemora*, although the higher abundance of *Eurytemora* implies that they have a more successful strategy at our study site where zooplanktivorous fish are abundant. Based on 12 years of data (1977–1988), Johansson (Johansson, 1992) found that the abundance relationships between *Acartia* and *Eurytemora* were the opposite in a nearby area with lower primary production and more exposed to open sea conditions. This implies that the relative benefit from a more pronounced DVM varies between locations and is determined by a complex matrix of environmental conditions.

While *Eurytemora* in general performed a pronounced DVM, we found that the females had only a weak migration, remaining at depth by both night and day. This is consistent with the strategy that Vuorinen (Vuorinen, 1987) proposed as the best possible for egg-carrying species if feeding conditions are adequate. Egg sacs increase copepod susceptibility to predation by slowing escape manoeuvres and rendering the copepod more obvious to predators (Devrekker *et al*., 2008). Bollens and Frost (Bollens and Frost, 1991) showed that females of another egg-sac-carrying calanoid copepod, *Euchaeta elongata*, remain at depth throughout the diel cycle and that a reduced adult mortality of 26% should be enough to offset the demographic cost of slowed egg development. This could be a relevant trade-off at our study site, as Flinkman *et al.* (Flinkman *et al*., 1992) found that herring in the Baltic Sea actively selected for ovigerous *Eurytemora*. As an exception in our data, *E. affinis* females exhibited a strong DVM in August when they approached the surface to the same extent at their younger conspecifics (Fig. 2C and D). This migration is similar to that reported for ovigerous *Eurytemora* by Vuorinen (Vuorinen, 1987). This change in DVM behaviour of *E. affinis* females coincides with two factors, first, the increased relative change in light intensity which could be the stimulus triggering this upward movement (Ringelberg, 2010), when twilight no longer persists throughout the night (Fig. 4). The second that phytoplankton reached the lowest biovolume of the sampling period (Fig. 3C). The DVM of copepods is known to be influenced by feeding conditions (Huntley and Brooks, 1982) and *E. affinis* may have responded to the low abundance of food, migrating upward to avoid starvation, despite the increased risk of predation.

Of particular relevance is a study by Bollens *et al.* (Bollens *et al*., 1993). They also found different predation prevention strategies when comparing the vertical distribution and DVM of two similar-sized copepods: *Metridia lucens* and *Calanus pacificus*. While both are broadcast spawners, their DVM differs significantly; *M. lucens* consistently migrates while *C. pacificus* displays variable migration behaviour. This despite the fact that *C. pacificus* is found to be selected for over *M. lucens* by zooplanktivorous fish. Thus, the authors sought to explain the difference with other traits including *C. pacificus* higher fecundity over *M. lucens*, so being able to afford weaker predator avoidance; or that *M. lucens* is more active. Ringelberg (Ringelberg, 2010, pp. 229) suggests that predator detection and greater escape capability is the most likely reason for the differing strategies; supported by the fact that *C. pacificus*, unlike *M. lucens*, has myelenated axons allowing for faster reaction times and so a faster escape response. When comparing the four species, there are striking similarities, with *Acartia* spp. and *C. pacificus* with higher fecundity and faster detection or response times with a less pronounced predation prevention strategy than the migrations of *E. affinis* and *M. lucens*. This suggests that physiological traits that give a more sensitive predator detection and fecundity can influence the susceptibility to predation of both population and individual to such an extent that an energetically costly migration is unnecessary. These strategies can be described as preventive and responsive; with *E. affinis* performing a preventative strategy against predation, performing DVM; using light as a proximal cue (Ringelberg and van Gool, 2003), and *Acartia* spp. relying more on a responsive strategy; reacting in real time to stimuli, such as approaching fish.

With no clear correlation between depth distribution and the factors of day length, fish biomass or phytoplankton biomass, it is not obvious which factors are causing the variation of DVM in this system. The lack of response to fish density is surprising. This could be that there is a constant presence of fish throughout the period (Fig. 3B) creating a permanent threat of predation. As predator detection is an important proximate causal stimulus for DVM and with increased stimulation, e.g. concentration of kairomones, the greater the phototactic response leading to greater amplitude of DVM (Ringelberg, 2010, pp. 64). With the migration amplitude of our two copepods seemingly unrelated to the changing biomass of fish suggests that the kairomone concentration surpasses the maximum possible photobehaviour response realizing a migration. In previous field studies where DVM has been linked to the presence of fish, extremes have commonly been compared, i.e. absence vs. presence of fish (Gliwicz, 1986; Horppila, 1997). In our system, there is no period free from fish, possibly making their influence difficult to detect. Temperature, however, may well play a part in the night distribution as both species appear to migrate to the thermocline layer, only remaining at depth in October when mixing has occurred and the water column was isothermal.

Our conclusion is that ontogeny, and therefore size, structures the amplitude of DVM on an intraspecific level due to higher risk of detection by visual predators, this being especially true for *Acartia*. *Eurytemora*, however, perform a greater migration than *Acartia*, with the two species employing different predation prevention strategies. This, we suggest, is related to differences in hydrodynamic sensitivity, fecundity and reproductive strategy; sac carrying or broadcast spawning. With these results concerning ontogeny, we would caution against the analysis of DVM for species with aggregated samples of mixed stages, when it is clear that ontogeny has an important role in governing this trait. In the future, traits important to DVM such as ontogenetic development of photobehaviour must be analysed. Experimental studies are likely to be of vital importance for this.

ACKNOWLEDGEMENTS

Susanna Hajdu provided data on phytoplankton, collected within research supported by the owner of the sewage treatment plant located at Himmerfjärden (Sydvästra stockholmsregionens va-verksaktiebolag SYVAB). Towe Holmborn and Börje Larsson gave us invaluable aid with zooplankton identification and field sampling, respectively.

FUNDING

This study was financed by the foundation Baltic Sea 2020.

REFERENCES

Adrian, R., Hansson, S., Sandin, B. *et al*. (1999) Effects of food availability and predation on a marine zooplankton community: a study on copepods in the Baltic Sea. *Int. Rev. Hydrobiol.*, **6**, 609–626.

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

Axenrot, T. and Hansson, S. (2004) Seasonal dynamics in pelagic fish abundance in a Baltic Sea coastal area. *Est. Coast. Shelf Sci.*, **60**, 541–547.

Balk, H. and Lindem, T. (2010) Sonar4 and sonar5-pro, post processing systems, operator manual. Lindem Data Acquisition, Oslo, Norway.

Bollens, S. M. and Frost, B. W. (1989a) Predator-induced diel vertical migration in a planktonic copepod. *J. Plankton Res.*, **11**, 1047–1065.

Bollens, S. M. and Frost, B. W. (1989b) Zooplanktivorous fish and variable diel vertical migration in the marine copepod *Calanus pacificus*. *Limnol. Oceangr.*, **34**, 1072–1083.

Bollens, S. M. and Frost, B. W. (1991) Ovigerity, selective predation, and variable diel vertical migration in *Euchaeta elongata* (Copepoda: Calanoida). *Oecologica*, **87**, 155–161.

Bollens, S. M., Frost, B. W. and Cordell, J. R. (1994) Chemical, mechanical and visual cues in the vertical migration behavior of the marine planktonic copepod *Acartia hudsonica*. *J. Plankton Res.*, **16**, 555–564.

Bollens, S. M., Osgood, K. E., Frost, B. W. *et al*. (1993) Vertical distributions and susceptibilities to vertebrate predation of marine copepods *Metrida lucens* and *Calanus pacificus*. *Limnol. Oceanogr.*, **38**, 1827–1837.

Brooks, J. L. and Dodson, S. I. (1965) Predation, body size, and composition of the plankton. *Science*, **150**, 28–35.

Calaban, M. J. and Makarewicz, J. C. (1982) The effect of temperature and density on the amplitude of vertical migration of *Daphnia magna*. *Limnol. Oceanogr.*, **27**, 262–271.

Casini, M., Cardinale, M. and Arrhenius, F. (2004) Feeding preferences of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the southern Baltic Sea. *ICES J. Mar. Sci.*, **61**, 1267–1277.

Checkley, D. M. (1982) Selective feeding by Atlantic herring (*Clupea harengus*) larvae on zooplankton in natural assemblages. *Mar. Ecol. Prog. Ser.*, **9**, 245–253.

De Robertis, A., Jaffe, J. S. and Ohman, M. D. (2000) Size-dependent predation risk and the timing of vertical migration in zooplankton. *Limnol. Oceanogr.*, **45**, 1838–1844.

Devrekker, D., Souissi, S., Molinero, J. K. *et al*. (2008) Trade-offs of the copepod *Eurytemora affinis* in mega-tidal estuaries: insights from high frequency sampling in the Seine estuary. *J. Plankton Res.*, **30**, 1329–1342.

Didrikas, T. and Hansson, S. (2004) In situ target strength of the Baltic Sea herring and sprat. *ICES J. Mar. Sci.*, **61**, 378–382.

Engström, J., Koski, M., Viitasalo, M. *et al*. (2000) Feeding interactions of the copepods *Eurytemora affinis* and *Acartia bifilosa* with the cyanobacteria *Nodularia* sp. *J. Plankton Res.*, **22**, 1403–1409.

Flinkman, J., Vuorinen, I. and Aro, E. (1992) Planktivorous Baltic herring (*Clupea harengus*) prey selectively on reproducing copepods and cladocerans. *Can. J. Fish. Aquat. Sci.*, **49**, 73–77.

Gliwicz, M. Z. (1986) Predation and the evolution of vertical migration in zooplankton. *Nature*, **320**, 746–748.

Gyllenberg, G. (1980) Feeding of the copepod *Eurytemora hirundoides* (Crustacea) on different algal cultures. *Ann. Zool. Fenn.*, **17**, 181–184.

Haney, J. F. (1988) Diel patterns of zooplankton behavior. *Bull. Mar. Sci.*, **43**, 583–603.

Hansen, F. C., Möllmann, C., Schultz, U. *et al*. (2006) Spatio-temporal distribution and production of calanoid copepods in the central Baltic Sea. *J. Plankton Res.*, **28**, 39–54.

Hansson, S., Larsson, U. and Johansson, S. (1990) Selective predation by herring and mysids, and zooplankton community structure in a Baltic Sea coastal area. *J. Plankton Res.*, **12**, 1099–1116.

Hays, G. C. (1995) Ontogenetic and seasonal variation in diel vertical migrationof the copepods *Metridia lucens* and *Metridia longa*. *Limnol. Oceangr.*, **40**, 1461–1465.

Hays, G. C. (2003) A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiology*, **503**, 163–170.

Hays, G. C., Proctor, C. A., John, A. W. G. *et al*. (1994) Interspecific differences in the diel vertical migration of marine copepods: the implications of size, color, and morphology. *Limnol. Oceanogr.*, **39**, 1621–1629.

HELCOM (2009) Guidelines concerning phytoplankton species composition, abundance and biomass. http://www.helcom.fi/groups/monas/CombineManual/AnnexesC/en_GB/annex6/

Hirche, H. J. (1992) Egg production of Eurytemora affinis –effect of k-strategy. *Estuar Coast Shelf Sci.*, **35**:395–407.

Horppila, J. (1997) Diurnal changes in the vertical distribution of cladocerans in a biomanipulated lake. *Hydrobiology*, **345**, 215–220.

Huntley, M. and Brooks, E. R. (1982) Effects of age and food availability on diel vertical migration of *Calanus pacificus*. *Mar. Biol.*, **71**, 23–31.

Jarnagin, T S., Kerfoot, C. W. and Swan, B. K. (2004) Life cycles: direct documentation of pelagic births and deaths relative to diapausing egg production. *Limnol. Oceanogr.*, **49**, 1317–1332.

Johansson, S. (1992) Regulating factors for coastal zooplankton community structure in the northern Baltic proper. PhD Thesis. Department of Zoology, Stockholm University, Stockholm.

Jonsson, P. R. and Tiselius, P. (1990) Feeding behaviour, prey detection and capture efficiency of the copepod *Acartia tonsa* feeding on planktonic ciliates. *Mar. Ecol. Prog. Ser.*, **60**, 35–44.

Kerfoot, W. C. (1985) Adaptive value of vertical migration: comments on the predation hypothesis and some alternatives. In Rankin, M. A. (ed.), *Migration: Mechanisms and Adaptive Significance*. Contributions in Marine Science 27. University of Texas, Port Aransas, pp. 91–113.

Kiørboe, T. and Sabatini, M. (1995) Scaling fecundity, growth and development in marine planktonic copepods. *Mar. Ecol. Prog. Ser.*, **120**, 285–298.

Lampert, W. (1993) Ultimate causes of diel vertical migration of zooplankton: new evidence for the predator avoidance hypothesis. *Arch. Hydrobiol. Beih. Ergebn. Limnol.*, **39**, 79–88.

Mauchline, J. (1998) The biology of calanoid copepods. *Adv. Mar. Biol.*, **33**, 1–710.

Neill, W. E. (1990) Induced vertical migration in copepods as a defence against invertebrate predation. *Nature*, **345**, 524–526.

Ricklefs, R. E. (2007) The Economy of Nature, *5th edn*. W.H. Freeman and Company, New York, USA. pp. 172.

Ringelberg, J. (2010) *Diel Migration of Zooplankton in Lakes and Oceans: Causes Explanations and Adaptive Significance*. Springer, London, UK.

Ringelberg, J., Flik, B. L. G., Lindenaar, D. *et al*. (1991) Diel vertical migration of *Daphnia hyalina* (sensu latiori) in Lake Maarsseveen: part: 1. Aspects of seasonal and daily timing. *Arch. Hydrobiol.*, **121**, 129–145.

Ringelberg, J. and van Gool, E. V. (2003) On the combined analysis of proximate and ultimate aspects in diel vertical migration (DVM) research. *Hydrobiology*, **491**, 85–90.

Rudstam, L. G. and Hansson, S. (1990) On the ecology of *Mysis-mixta* (Crustacean, Mysidacea) in a coastal area of the northern Baltic proper. *Ann. Zool. Fenn.*, **27**, 259–263.

Rudstam, L. G., Hansson, S., Johansson, S. *et al*. (1992) Dynamics of planktivory in a coastal area of the northern Baltic Sea. *Mar. Ecol. Prog. Ser.*, **80**, 159–173.

Stoecker, D. K. and Egloff, D. A. (1987) Predation by *Acartia tonsa*, Dana on planktonic ciliates and rotifers. *J. Exp. Mar. Biol. Ecol.*, **110**, 53–68.

Tiselius, P. (1990) Foraging behaviour and grazing pattern of calanoid copepods. PhD Thesis, University of Gothenburg, Gothenburg.

Viitasalo, M., Flinkman, J. and Viherluoto, M. (2001) Zooplanktivory in the Baltic Sea: a comparison of prey selectivity by *Clupea harengus* and *Mysis mixta*, with reference to prey escape reactions. *Mar. Ecol. Prog. Ser.*, **216**, 191–200.

Vuorinen, I. (1987) Vertical migration of *Eurytemora* (Crustacea, Copepoda)—a compromise between the risks of predation and fecundity. *J. Plankton Res.*, **9**, 1037–1046.

Zaret, T. M. and Suffern, J. S. (1976) Vertical migration in zooplankton as a predator avoidance mechanism. *Limnol. Oceanogr.*, **21**, 804–813.