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Status and vertical size-distributions of a pelagic mysid community in the northern Baltic proper

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We report on abundance, biomass, trophic position and vertical size distribution of pelagic mysids (*Mysis mixta*, *Mysis relicta*/*salemaai*, *Neomysis integer*) in a coastal Baltic Proper area. As compared with the situation in this area in the 1980s, the formerly dominating *M. mixta* has declined and the total mysid biomass decreased by 50%. *Neomysis integer* now constitutes the bulk of the mysids. Stable isotopes indicate that they feed on a lower trophic level than *Mysis* spp., and *M. relicta* appears more carnivorous than *M. mixta*. For *N. integer*, size increases with depth and decreases with *in situ* light. This was not found for *Mysis* spp., probably due to their narrow size span and smaller sample size than for *N. integer*. In *N. integer*, *in situ* light explained the size variation with depth better than temperature, indicating that this variation is a response to predation rather than size-related thermal preference.

Introduction

In the late 1980s, the Baltic Sea, like the North Sea, underwent a regime shift driven mainly by climatic changes (Alheit *et al*. 2005). Higher winter temperatures, lesser influxes of salt water through the Danish straights and decreased spring convections of the water column led to changes in species composition and abundances across trophic levels. At the time, the dominant top predator cod (*Gadus morhua*) decreased to extremely low levels, sprat (*Sprattus sprattus*) increased as a consequence of decreased predation by cod and increased food supply of warm-water thriving zooplankton species (Möllmann *et al*. 2000), and total annual phytoplankton biomass increased. The abundance of the third dominating fish species in the Baltic, herring (*Clupea harengus membras*), decreased substantially during the last decades of the 20th century, probably as a result of intensified fishing in combination with competition from sprat (Möllmann *et al*. 2005, Casini *et al*. 2006). The decline in abundance was followed by a decrease in herring condition (Möllmann *et al*. 2004), which is currently well below the pre-1986 levels (mean weight-at-age approx. 50% lower; *see* ICES 2010). This could be explained by competition for zooplankton with sprat (Casini *et al*. 2006) and/or a parallel decline in mysids, which herring can feed extensively on during late autumn and winter (Aneer 1975, Arrhenius and Hansson 1993, Möllmann and Köster 1999).

Mysid shrimps are common in many marine and deep-lacustrine systems across Eurasia and North America (Mauchline 1980). They contain high amounts of polyunsaturated fatty acids and are for that reason believed to be important for the overwintering survival of many fish species

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(Arts and Johannsson 2003). Simultaneously they compete with young fish for zooplankton and are known to be efficient zooplanktivores (Rudstam *et al*. 1992). Like many zooplankton species, mysids perform diel vertical migrations (DVM) and are thus important in benthic–pelagic coupling.

During the mid-1980s, before the regime shift, extensive efforts were made to map the distribution and investigate the role of mysid shrimps in the Baltic Sea ecosystem (Hansson *et al*. 1990b, Rudstam *et al*. 1989, Rudstam *et al*. 1986, Salemaa *et al*. 1986, Salemaa *et al*. 1990). Due to their patchy distribution, laborious and difficult sampling, very few surveys have been carried out in recent times. However, anecdotal information suggests that the abundance of *Mysis mixta*, the previously most abundant pelagic species, in fact has decreased considerably in many parts of the northern Baltic Sea (own observations and M. Lehtiniemi, FIMR, Helsinki, pers. comm.).

Observations of a mysid decline, in combination with general trophic changes linked to the regime shift proposed by Alheit *et al*. (2005) and the lack of modern data motivated a survey in a previously well studied coastal area of the northern Baltic Sea (Rudstam *et al*. 1986, 1989, Rudstam and Hansson 1990, Hansson *et al*. 1990b).

In the present study, first we compare the current abundances and biomasses of the most abundant pelagic mysids (*Mysis mixta*, *Mysis relicta*/*salemaai* and *Neomysis integer*) in this area with those of the mid-1980s. For ease of comparison with historical data, we did not distinguish between the cryptic *M. relicta* and *M. salemaai* which hereafter will be referred to as *M. relicta*. Additionally, we also investigated possible changes in the mysid trophic position which may have changed as a result of the "regime shift".

Second, we investigate the impacts of temperature and light on the vertical size-distribution of mysids in the water column, i.e. their relative importance and effect on the vertical size-distribution. This is consequential not only from an ecological point of view but also for sampling. Mysids have traditionally been collected with vertical hauls, but because of their often very patchy distribution, hydroacoustic techniques are becoming more common (MacLennan and Holliday 1996, Holbrook *et al*. 2006, Rudstam *et al*. 2008), since acoustics allow for extensive coverage at a reasonably low cost. Interpretation of hydroacoustic information is however not trivial and good knowledge of the behavior and position of the studied organisms is crucial for correct abundance and biomass estimations (Simmonds and MacLennan 2005). This is when models predicting the distribution of such organisms become important. A few studies have been able to successfully predict the distribution of mysids based on temperature and light preferences (Gal *et al*. 2004, Boscarino *et al*. 2007, Boscarino *et al*. 2009, Boscarino *et al*. 2010b) These models, however, pertained to the average size of individuals within the population. It is known that there are ontogenetic behavioral differences in mysids resulting in smaller individuals being usually found in shallower waters (Hessle and Vallin 1934, Grossnickle and Morgan 1979, Salemaa *et al*. 1986, Kotta and Kotta 1999). This is most prominent in juveniles *versus* adults but has also been observed within cohorts of subadult animals (Rudstam *et al*. 1989). The relative importance of light and temperature as cues driving vertical size-distributions are however not well understood (but *see* Boscarino *et al*. 2010a). Moreover, size, energy content and behavior becomes important when incorporated into bioenergetic and food-web models, since factors such as light and temperature are important drivers of energy flow in a system. Furthermore, since light is believed to be one of the major mechanistic factors governing vertical size-distributions in aquatic animals (Bekli oglu *et al*. 2008, Hansson and Hylander 2009) and that those distributions ultimately are driven by predation (Blaxter and Batty 1987, Batty *et al*. 1990, Flinkman *et al*. 1992, De Robertis *et al*. 2002), we wanted to examine the distribution of mysids in relation to the light needed for predation by clupeid fish; one of the most important planktivores in the Baltic Sea.

Material and methods

General sampling design

Mysids were collected in August–November

2008, at six sites in the Askö–Himmerfjärden area, northern Baltic proper (Fig. 1). Sampling was restricted to this time of year because light and short nights during summer at this latitude restrict DVM of *Mysis* spp. (Rudstam *et al*. 1989). Collection of mysids started at the earliest one hour after sunset with ship's lights off and ended before sunrise. We assumed that during this period the mysids were at their nighttime depth distribution (*see* De Robertis *et al*. 2002). We did not conduct any sampling in daylight, since overall low catches are expected during the day (Hansson *et al*. 1990a). All sites except one (site 10) had a fairly flat bottom at approximately 30–35 meters. At site 10, bottom depth varied considerably more and maximum depth in the vicinity of the sampled area exceeded 70 m. Salinity below the thermocline was stable at 6.5–7 psu throughout the sites without any clear halocline (maximum decrease of 0.8 psu from the surface to the bottom).

Mysids were collected from varying depths with a three-bag Tucker trawl (effective opening area 0.25 m^2, mesh size 500 μm). Each depth was trawled for about 20 minutes at a speed of approximately 1.5 knots covering a distance of ~1000 m). The trawling depth was logged with a standard diving depth meter (Sensus ultra, ReefNet Inc., West Seneca, USA) mounted in the trawl opening. Filtering efficiency was assumed to be high and close to that of the Bongo trawl used in the 1980s (Pepin and Shears 1997).

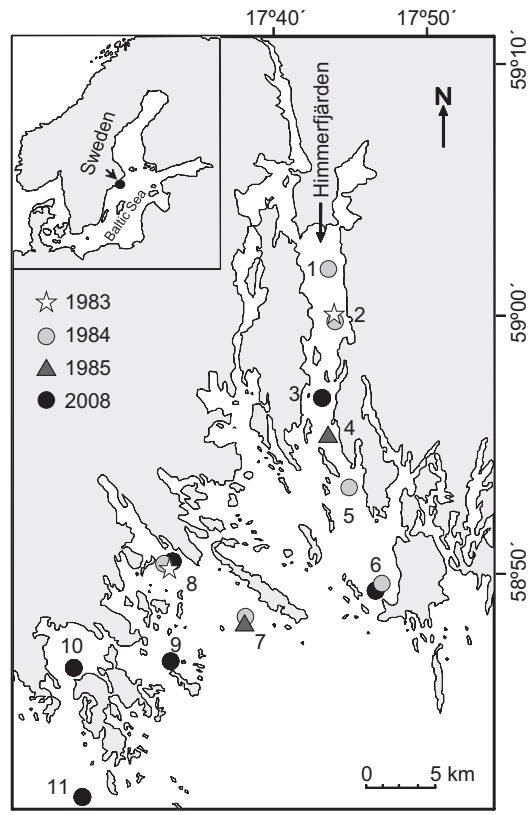

Fig. 1. Map of the study area with 11 sites sampled on different dates in 1983–1985 and 2008.

Abundance and biomass estimation

Our intention was to quantify mysids with hydroacoustics, but due to technical complications this was not possible. The Tucker trawl samples in our study were from discrete depths and did not include the entire water column as did the oblique Bongo tows taken in the 1980s (Rudstam and Hansson 1990). However, on most occasions we sampled many depths and consider the combined catches to represent the entire water column reasonably well. Moreover, most samples were collected below the thermocline and/or in light levels preferred by *Mysis* spp. (Rudstam and Hansson 1990, Gal *et al*. 2004, Boscarino *et al*. 2009). Therefore, at least for *Mysis* spp. the abundances should be reasonably accurate despite the shortcomings of this sampling technique. Consequently, this also means that *N. integer* abundances may be underestimated as they normally prefer higher temperatures (Kotta and Kotta 2001).

Samples were preserved in 70% ethanol (final concentration). When possible, at least 30 individuals per species were randomly selected from each depth and the carapace length was measured from the tip of the rostrum to the mediodorsal margin. For *Mysis* spp. this was done with a digital caliper (accuracy 0.01 mm), while the notably smaller *N. integer* were measured using a scale in a stereo microscope. Carapace length was used because alcohol preservation fixes animals in a bent position, making it difficult to measure body length accurately. For ease of comparison with other studies, we recalculated *M. mixta* and *M. relicta* carapace lengths (CL, mm) to their respective body lengths

(BL, mm) with the following formula: BL = (CL – 0.12)/0.42. Although this formula was developed for *M. mixta* (Gorokhova and Hansson 2000), we also used it for *M. relicta* assuming that in this species the relationship between these dimesions is the same as in *M. mixta*. CL of *Neomysis integer* was converted to as follows: BL = (CL – 0.15)/0.29 ($r^2 = 0.97$, $n = 9$).

For biomass calculations, total lengths (TL, mm) (from the tip of rostrum to the end of telson) of mysids from 1984 (Rudstam *et al*. 1986) were converted to dry weights (DW, mg) as described for *M. mixta*: $DW = 0.00126 \times TL^{3.07}$ (Rudstam 1989) assuming equal relationships for all species. Dry weights of all mysids from 2008 were derived from their body lengths (BL, mm) using the following formula for *M. mixta*: $DW = 0.0032 \times BL^{2.85}$ (Gorokhova and Hansson 2000). Integrated abundances (numbers per m^2) for 2008 were calculated from depth-specific densities using linear interpolation (*see* Beeton 1960); these results could then be compared with the values obtained in the 1980s for the same area.

All abundances and biomasses for 1983–1985 presented here were derived from original protocols (Rudstam *et al*. 1989, 1986, Rudstam and Hansson 1990, Hansson *et al*. 1990a).

Stable isotope analysis

On 9 September 2008, mysids for stable-carbon and nitrogen-isotope analyses were collected at site 8 from the depth of 25 m. Immediately after capture, all *M. mixta* and a sub-sample of *M. relicta* were frozen with dry ice, but because of practical constraints the remaining part of the *M. relicta* sample was preserved in 70% ethanol for approximately 3 months prior to drying. Since alcohol preservation may affect the isotope composition (Feuchtmayr and Grey 2003), $\delta^{15}N$ values from frozen samples were adjusted by using the equation:

$$\delta^{15}N_{\text{adjusted}} = \delta^{15}N_{\text{frozen}} + \left(\overline{x}_{\delta^{15}N_{\text{alcohol}}} - \overline{x}_{\delta^{15}N_{\text{frozen}}}\right) \quad (1)$$

where $\overline{x}_{\delta^{15}N_{\text{alcohol}}}$ and $\overline{x}_{\delta^{15}N_{\text{frozen}}}$ are the average nitrogen isotope signatures for *M. relicta* preserved in alcohol and frozen, respectively. Ultimately, only $\delta^{15}N$ values for frozen *M. mixta* were adjusted. In total, tail-muscle samples from 12, 18 and 23 specimens of *N. integer*, *M. relicta* and *M. mixta* (BL (mean ± SD), mm: 9.2 ± 1.2, 14.2 ± 1.0, and 14.1 ± 0.9), respectively, were analyzed for isotope composition. We tried to select mysids of similar size for the analysis but the largest *N. integer* were still considerably smaller than the smallest *Mysis* spp. Irrespective of the treatment, the $\delta^{13}C$ values were corrected for differences in lipid composition according to Post *et al*. (2007). Isotopic analyses were performed at the UC Davis Stable Isotope Facility, University of California, Davis with a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Two working standards (homogenized mysid tissue) were run for every 42 ± 2 samples ($n = 28$). The analytical precision for $\delta^{15}N$ and $\delta^{13}C$ was ±0.13‰. Analytical and method blanks were also included to control for possible analytical drift as well as contamination risk during laboratory work.

Vertical size distribution

Light and temperature

At each station, a temperature profile at 0.25-m intervals from the surface to the bottom was taken using a CTD water profiler unit (Sea & Sun Technology, Trappenkamp, Germany).

Surface light intensity at the time of sampling was measured every 10 seconds with a sensitive photometer (range = 0.001–50 lux, Skye SKL 2630L, Skye Industries Ltd., Powys, UK) mounted at a high location on land close to the sampling sites, where shadowing from trees was minimal. Subsequently, average intensity values were calculated for every one-minute interval. When light intensities fell below the lower sensitivity threshold of the light-meter (10^{-3} lux), we applied a fixed light intensity of 10^{-5} lux, equivalent to total starlight on an overcast night (Clark 1990). The sampling was carried out during new-and full-moon conditions as well as at variable cloudiness.

The *in-situ* light intensities for different depths were calculated from the surface

1-min averages using the Beer-Lambert equation (Hutchinson 1957): ln(*in situ* irradiance) = ln(surface irradiance) – $k \times$ depth (in m), with the light extinction coefficient (k) set to a universal average value of 1.7/secchi-depth (Poole and Atkins 1929, Gisselson *et al*. 2002). The Secchi-depth readings (U. Larsson, Systems Ecology, Stockholm University, unpubl. data) were from the sampling sites or sites located nearby, and the measurements were carried out no more than a few days apart from our sampling dates.

Statistical analyses

Abundance and biomass comparisons

For each species, possible changes in abundance and biomass over the years and decades were modeled with a mixed effects $ANCOVA_{LME/GLME}$ using the nlme (Pinheiro *et al*. 2011) and lme4 packages (Bates *et al*. 2011) in R ver. 2.13.0 (R Development Core Team 2011). "Year" and "Decade" were set as categorical variables and "Dyear" (day of the year) as a continuous covariate, since sampling was carried out during different times in the year. "Site" was entered as a random component with random intercept due to the hierarchical and unbalanced nature of the data (i.e. spatial and temporal heterogeneity and repeated measures per site (*see* Fig. 1 and Table 1 for details). Similar approaches are becoming common practice in analyses of fisheries data that often contain temporal/spatial correlations, nested structures and pseudoreplicates (Millar and Anderson 2004). We did not find any significant Site:Dyear interaction which is why it was excluded; models including this term produced a higher AIC (Akaike information criterion; a measure of goodness of fit). Abundances and biomasses were log(x + 1)-transformed because of zeros in the data except for *M. relicta* which was modeled using a Poisson distribution because of slight zero inflation. Due to the inherent nested and unbalanced structure in the data, we always included random effects even though they sometimes slightly increased AIC. In all cases, model residuals were checked for patterns and station coordinates were plotted in a variogram against model residuals to examine possible signs of spatial correlation. As the sites proved to be spatially independent, no spatial correlation structure was added to the models. Due to heterogeneity in variances between years we added a constant "varIdent" variance structure to the models (Pinheiro and Bates 2000) which allows for the observed heterogeneity. For *M. relicta*, heterogeneity was stabilized by the introduction of a random slope, since the "varIdent" variance structure could not easily be implemented using the lme4 package. Models containing the random slope were significantly

Table 1. Dates of sampling and number of samples per year and site for the years 1983–1985 and 2008.

Year	Site	Sample 1	Sample 2	Sample 3	Sample 4	Sample 5
1983	2	23 Jul	25 Aug			
1983	8	25 Jul	25 Aug			
1984	1	23 Jul	2 Oct	4 Dec		
1984	2	24 Jul	2 Oct	4 Dec		
1984	5	24 Jul	2 Oct	3 Dec		
1984	6	24 Jul	3 Oct	3 Dec		
1984	7	24 Jul	3 Oct	3 Dec		
1984	8	23 Jul	9 Oct	3 Dec		
1985	4	31 Jul	28 Aug	24 Sep	22 Oct	
1985	7	31 Jul	28 Aug	25 Sep	23 Oct	
2008	3	13 Nov				
2008	6	26 Aug	8 Sep	10 Sep	22 Sep	
2008	8	27 Aug	9 Sep	11 Sep	23 Sep	14 Nov
2008	9	25 Sep				
2008	10	20 Oct	22 Oct			
2008	11	24 Sep				

better in all cases (ΔAIC > 50).

As a precaution, sites 9–11 in 2008 were excluded from all biomass and abundance analyses because they were far outside the area that was sampled in the 1980s and were somewhat deeper, thus site-specific differences could not be ruled out. For the *Neomysis* models, we also excluded samples from site 8 on 9 September, and site 6 on 22 September 2008 because too few depths above the thermocline were sampled. These depths are avoided by *Mysis* spp. (avoidance of high temperatures) but may be inhabited by *N. integer*. Some sites were also sampled further up in Himmerfjärden during the 1980s as compared with 2008 (Fig. 1). These samples were, however, not excluded as we could not find any significant differences in abundances between the sites in 1984 (Kruskal-Wallis: $H_{5,18}$ = 3.1, p = 0.68; $H_{5,18}$ = 5.6, p = 0.35; and $H_{5,18}$ = 2.6, p = 0.76; for *M. mixta*, *M. relicta* and *N. integer* respectively) indicating that in this case site-specific differences were negligible.

Possible differences in abundance and biomass between year pairs were estimated using Tukey's HSD multiple comparisons.

Vertical size distribution

Possible trends in mysid size at different depths and the impact of light and temperature were explored with linear mixed-effects models using the lme4 package (Bates *et al*. 2011) in R ver. 2.13.0 (R Development Core Team 2011) after having been checked for linear relationships using generalized mixed effects (GAMM) mgcv package (Wood 2000). We constructed separate models for each of the species but because our data contained tows during isothermal conditions, giving less variation and weight to the effect of temperature relative to light, we further divided the analysis by subsetting data to include sampling occasions when the water was thermally stratified or isothermal. Comparing these data sets enabled us to check for any inconsistencies in the models. The full dataset, including both thermally stratified and isothermal profiles could, as stated before, be problematic. If however, the dataset containing only thermoclines produced similar results, we could be fairly confident that the models were adequately specified. Finally, the last control was to check that results obtained using the isothermal data did not produce significance for temperature, as it per definition has near-zero variance.

Correlations between the explanatory variables were checked using the variance infliction factor, VIF = $1/(1 - r^2)$; where r^2 is the coefficient of determination when a variable is regressed on all the other explanatory variables in the model. *In situ* light and temperature produced low VIF values (< 2) indicating a low and acceptable degree of collinearity as it has been shown that VIF values > 2 bias the results in multiple regressions (Graham 2003). In case of depth, however, substantially higher VIFs (4.5–9) were derived from all data subsets and for all species (*see* Graham 2003 for further discussion on multicollinearity).

To account for the nested structure of the data and potential effects of site and growth over the study period of 2.5 months, site/date was entered as a nominal, random component with random intercept and slope (*N. integer* models only). For *Mysis* spp., the data were insufficient to accurately estimate the variance of the random intercept which is why site/date was entered as a fixed factor with random slopes. Tows were nested within each site/date. Temperature and log-transformed *in-situ* light intensity were simultaneously entered as the continuous variables, while depth was analyzed separately due to its correlation with both temperature and *in-situ* light intensity. Mysid length was set as the response variable. Each tow contained length measurements of 5–40 individuals. Catches with less than five individuals were thus not analyzed. All model residuals were also regressed on the fixed effects to check for patterns.

Results

Species composition and distribution in 2008

In the 2008 survey, the three mysid species displayed different size distributions, with a narrower range for the *Mysis* species than for *N. integer* (Fig. 2). In *Mysis* spp., a single cohort

dominated, but there were also a few large individuals that most probably belonged to the previous year's cohort. For *M. relicta*, these individuals were all gravid females, whereas all large *M. mixta* were at the sub-adult stage. All these unusually large individuals were sampled close to the bottom.

The overall abundance of mysids in 2008 varied considerably among sampling occasions and sites, with *N. integer* being consistently and considerably more abundant than the other species (Figs. 3 and 4). The vertical distributions differed among the species. *Mysis* spp. aggregated primarily in or below the thermocline where estimated light intensities were well below those required for visual feeding by herring (i.e. $< 10^{-4}$ lux, *see* Batty *et al*. 1990). *Neomysis integer* was most abundant in the more illuminated and warmer, upper mixed layer (Fig. 3).

Species composition, abundance and biomass change over time

As compared with those in 1983–1985 (Rudstam *et al*. 1986, Rudstam and Hansson 1990), *M. mixta* abundances were significantly lower in 2008 but did not differ significantly within the 1980s (Tables 2–3 and Fig. 4A). Biomasses differed significantly between decades and all years except 1983 and 1985. The *Mysis mixta* biomass in 2008 was moreover lower than in any year during the 1980s (Tables 2–3 and Fig. 4B).

We did not find any consistent change in the *M. relicta* abundance over time, although abundances were significantly higher in 2008 as compared with those in 1985 when this species was almost absent (Tables 2–3 and Fig. 4C). *Mysis relicta* thus seems to have increased since the 1980s as it constituted only a small portion of the total mysid abundance and biomass at the time (< 5%). Now it is substantially more common in the study area (Fig. 5).

Neomysis integer did not show a consistent change over time although its abundance and biomass was higher in 2008 than in 1984 (Tables 2–3 and Fig. 4E–F). The biomass of this species was also especially high in 1984 (Tables 2–3 and Fig. 4F), which can be attributed to an unusually large average size.

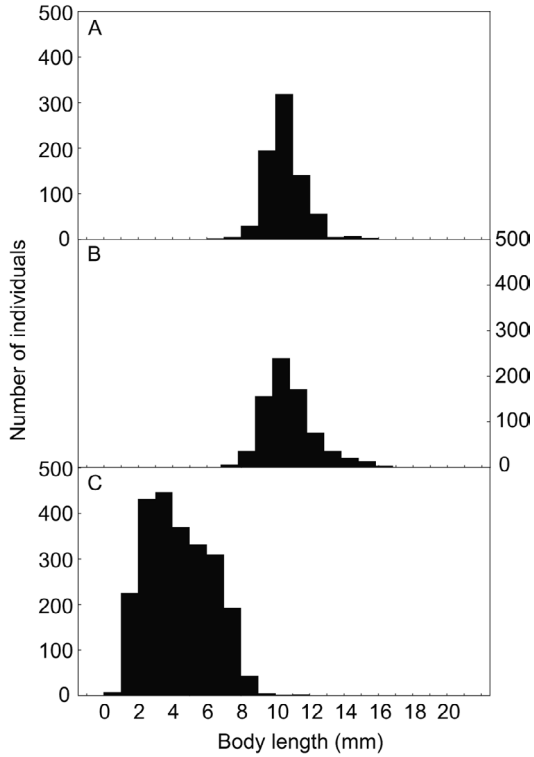

Fig. 2. Size distributions of (**A**) *M. mixta* (n = 760), (**B**) *M. relicta* (n = 759) and (**C**) *N. integer* (n = 2368), pooled over time (August–November) including all stations (modified from Ogonowski *et al.* 2010: fig. 2).

While the mean total mysid abundance did not show any signs of decadal change (Tables 2–3 and Fig. 4G), the total mysid biomass decreased considerably after 1983, and the bulk of the biomass now consists of juvenile *N. integer* as opposed to the 1980s when *M. mixta* was the dominating species (Tables 2–3 and Fig. 5).

Stable isotope analysis

The ethanol preservation increased δ^{15}N values by 0.38‰ ± 0.09‰ (95% bootstrapped confidence interval) as compared with samples that had been frozen prior to preparation for stable isotope analyses. This difference was significant (*t*-test: $n_1 = 18, n_2 = 20, t = -5.1, p < 0.0001$) and was compensated for according to Eq. 1 (one-way ANOVA (uncompensated *vs*. compensated *M. relicta*): $F_{1,36} = 0, p = 1$). For δ^{13}C values, no

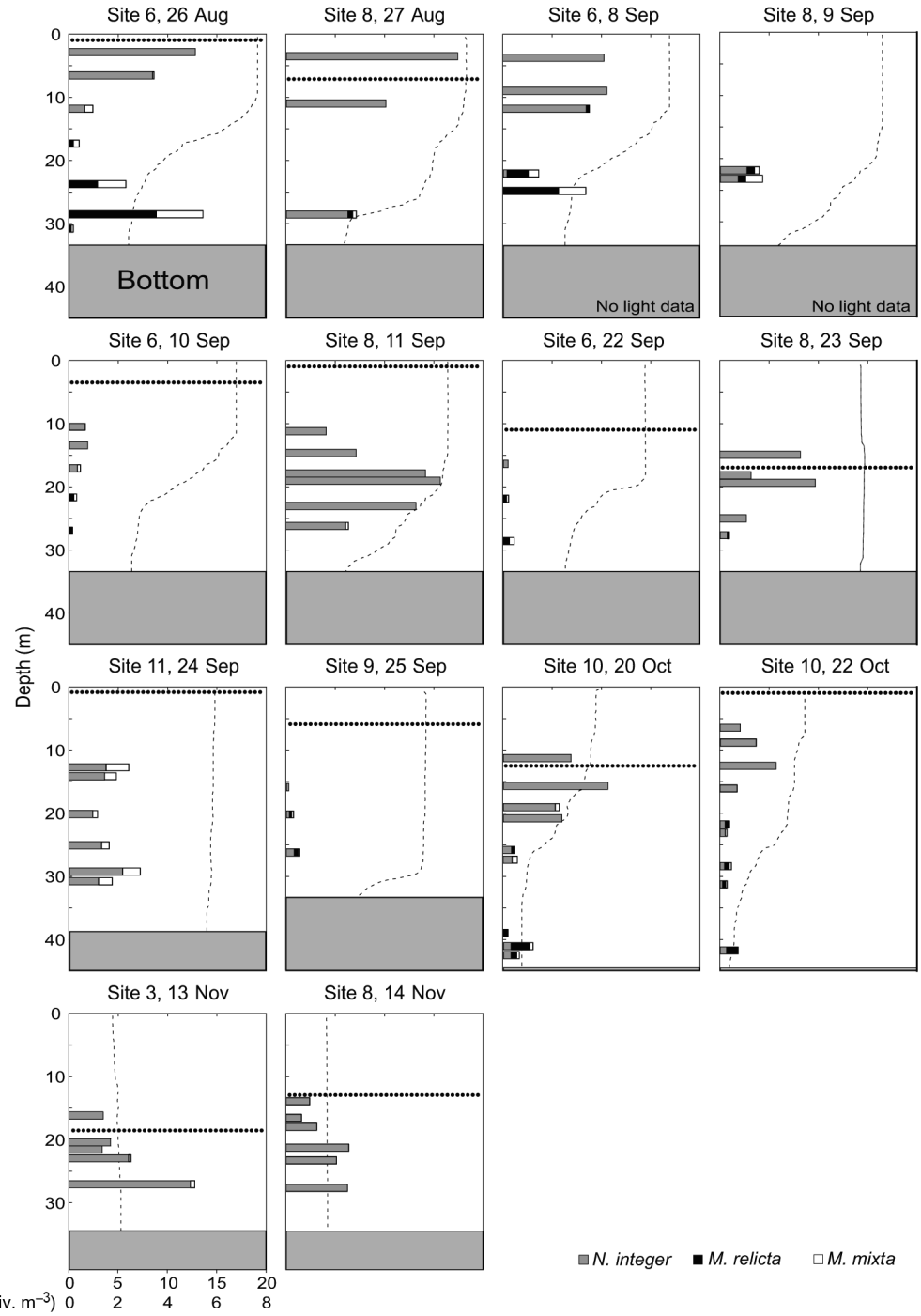

Fig. 3. Temperature profiles (dashed, vertical lines) and abundances (bars) of *N. integer* (grey), *M. relicta* (black) and *M. mixta* (white) for each of the sampling dates. The dotted, horizontal lines represent a light level of 10^{-4} lux (for the calculation method *see* chapter 'Light and temperature'. All tows contained mysids of some species (modified from Ogonowski *et al*. 2010: fig. 3).

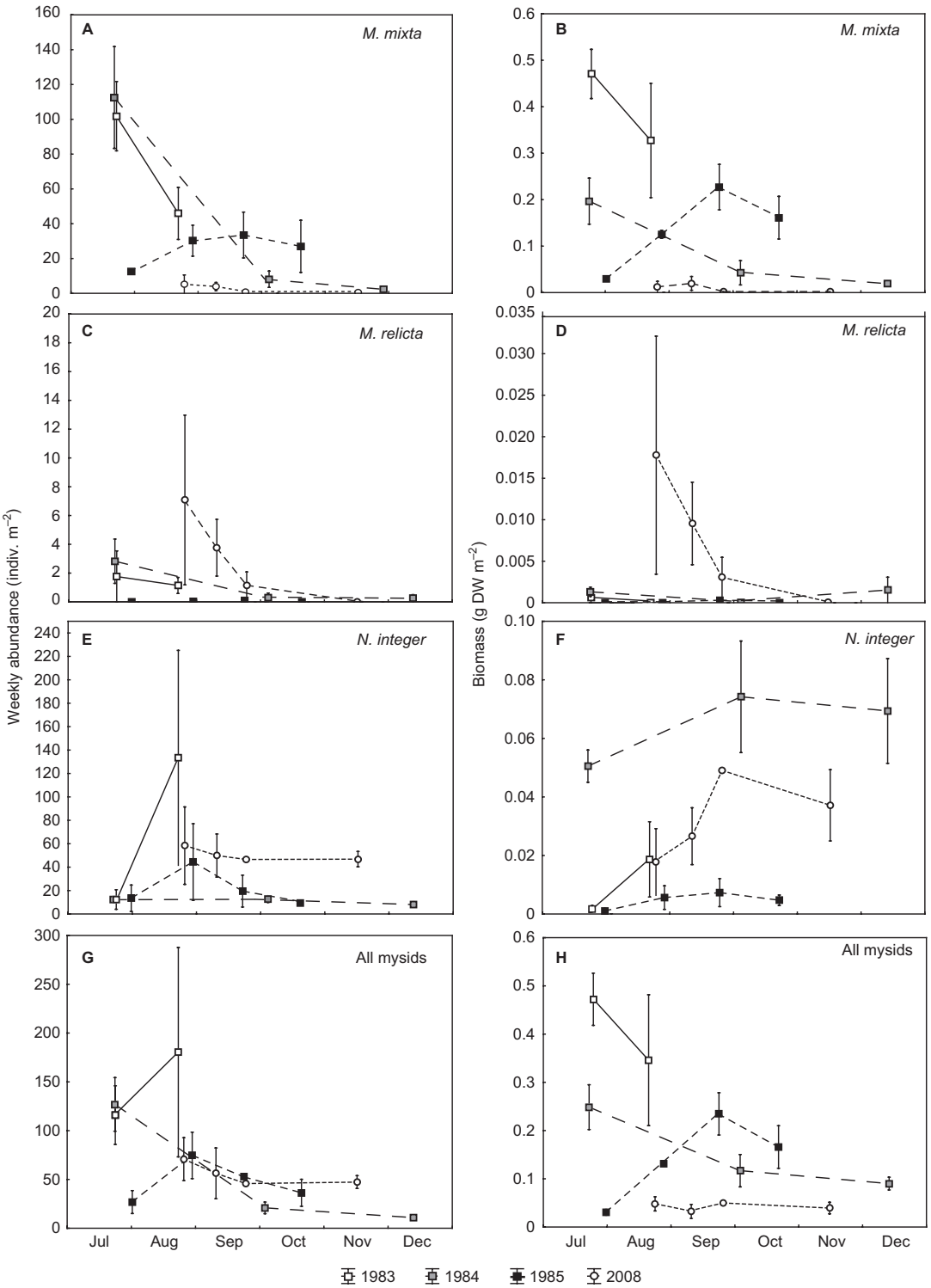

Fig. 4. Station-pooled, weekly abundance (indiv. m^{-2}, panels **A**, **C**, **E**, **G**) and biomass (g_{DW} m^{-2}, panels **B**, **D**, **F**, **H**) from July to December in the years 1983–1985 and 2008 of *M. mixta*, *M. relicta*, *N. integer* and all mysids. Shown are means ± 1 SEs.

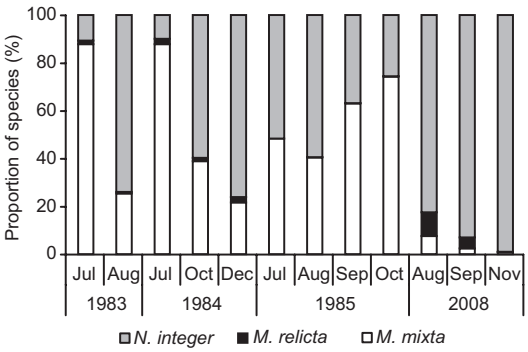

Fig. 5. Mean monthly abundance proportions of *M. mixta*, *M. relicta* and *N. integer* in the years 1983–1985 and 2008. Each bar consists of pooled samples from different sites.

Table 2. ANOVA results from the (G)LME models explaining abundance (indiv. m^{-2}) and biomass (g_{DW} m^{-2}) of *Mysis mixta*, *Mysis relicta*, *Neomysis integer* and their total abundance and biomass (Total). Explanatory variables were: day in the year (Dyear), Year and Decade. Significant results are set in boldface.

Species and dependent variable	Source of variation	*n*	*p*
Mysis mixta			
Abundance	Dyear	40	< **0.0001**
	Decade		< **0.0001**
	Year		**0.006**
Biomass	Dyear	40	**0.003**
	Decade		**0.032**
	Year		**0.003**
Mysis relicta			
Abundance	Dyear	40	0.92
	Decade		0.058
	Year		< **0.0001**
Biomass	Dyear	38	**0.029**
	Decade		**0.026**
	Year		< **0.0001**
Neomysis integer			
Abundance	Dyear	38	0.19
	Decade		**0.0093**
	Year		**0.0007**
Biomass	Dyear	38	0.073
	Decade		0.45
	Year		< **0.0001**
Total			
Abundance	Dyear	38	< **0.0001**
	Decade		0.37
	Year		0.28
Biomass	Dyear	38	**0.03**
	Decade		**0.002**
	Year		< **0.0001**

significant effect of preservation method was found (*t*-test: $n_1 = 18$, $n_2 = 20$, $t = 0.84$, $p = 0.4$) and thus no compensation was applied.

We found significant differences in average $\delta^{15}N$ and $\delta^{13}C$ among species (one-way ANOVA: $F_{2,49} = 343$, $p < 0.001$; $F_{2,49} = 11.41$, $p < 0.001$; $\delta^{15}N$ and $\delta^{13}C$, respectively; *see* Fig. 6 and Table 4). *Mysis relicta* showed a slightly but significantly higher $\delta^{15}N$ value than *M. mixta*; $\delta^{15}N$ of both *Mysis* species was positioned approximately 3‰ higher than that of *N. integer*. $\delta^{13}C$ differed less between species but *M. relicta* had significantly higher $\delta^{13}C$ values than both *N. integer* and *M. mixta* indicating a different food source. The $\delta^{13}C$ value for *N. integer* was significantly lower than that for *M. relicta* but not different from that of *M. mixta*.

The average effect of mysid size (BL) on the isotopic signatures was not significant (Table 4), and there was no significant interaction between species and BL for $\delta^{15}N$ (Table 4), however, a weak but significant interaction was found for $\delta^{13}C$ (Table 4). It was caused by a slight increase in $\delta^{13}C$ with size of *M. relicta* ($F_{1,16} = 6.2$, $p = 0.025$) but not of the other species.

Vertical size distribution

Neomysis integer showed a significant, positive linear relationship between size and depth and a negative relationship with temperature and *in situ* light when these explanatory variables were entered independently (models 1–3, Full and stratified data, Table 5). In model 4, that contained both temperature and *in situ* light, only light was significant, indicating that, in at least *N. integer*, light explains more of the variation in the vertical size distribution as compared with temperature. The best models however (lowest AIC) contained only light or depth showing that light alone, explained most of the variation in juvenile and subadult mysids. No significant size-related relationships could be found for *Mysis* spp. (Table 5). For the isothermal dataset (*N. integer*), we did not find any significance for temperature (which was expected), which indicates that the models performed satisfactory in all data subsets. Isothermal data could not be modeled for *Mysis* spp. due to lack of data (Table 6).

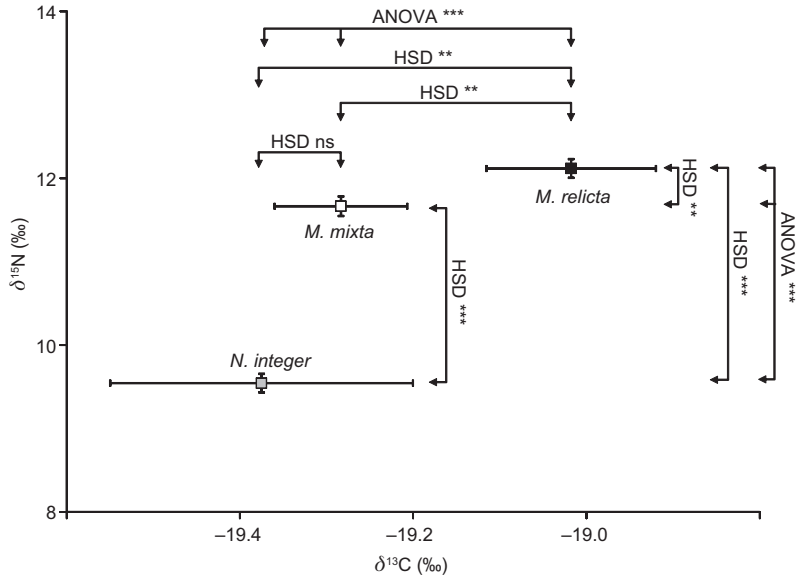

Fig. 6. δ^{15}N and δ^{13}C composition (mean ± 95%CI) in muscle tissue of *N. integer* (n = 11), *M. relicta* (n = 18) and *M. mixta* (n = 23) at station 3 (25 m depth). δ^{15}N and δ^{13}C values differed significantly among species (one-way ANOVA: $F_{2,49}$ = 343, $p < 0.001$, and $F_{2,49}$ = 11.41, $p < 0.001$; for δ^{15}N and δ^{13}C, respectively). Results of pairwise comparisons (Tukey's HSD post-hoc test) for unequal sample sizes are shown. ns = $p > 0.05$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$ ***. (modified from Ogonowski *et al.* 2010: fig. 7).

Discussion

The decline of *Mysis mixta*

In the 1980s, *M. mixta* was the dominant species throughout the summer, whereas juvenile *N. integer* dominated slightly in the autumn (Rudstam *et al.* 1986). The abundance of *M. relicta* was consistently low. In 2008, juvenile *N. integer* was by far the most abundant species in nearly all samples, and it is clear that the proportion of this species increased considerably in

Table 3. Tukey's HSD multiple-comparison results showing pairwise differences in abundance and biomass between years. ↑ and ↓ indicate significant increase or decrease over time, respectively. *p* values indicating significant differences are set in boldface.

Years	*Mysis mixta*		*Mysis relicta*		*Neomysis integer*		All mysids pooled	
	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass
1983/1984	0.48	< **0.001**	0.39	0.96	0.64	< **0.001** (↑)	0.31	**0.003** (↓)
1983/1985	0.96	0.06	**0.003** (↓)	< **0.001** (↓)	0.85	0.89	0.57	**0.003** (↓)
1983/2008	< **0.001** (↓)	< **0.001** (↓)	0.96	0.17	0.97	0.54	0.94	< **0.001** (↓)
1984/1985	0.95	< **0.001** (↓)	**0.04** (↓)	< **0.001** (↓)	0.90	< **0.001** (↓)	0.99	0.97
1984/2008	**0.002** (↓)	**0.01** (↓)	0.11	**0.02** (↑)	< **0.001** (↑)	**0.01** (↓)	0.62	< **0.001** (↓)
1985/2008	**0.006** (↓)	< **0.001** (↓)	< **0.001** (↑)	< **0.001** (↑)	0.09	0.07	0.88	**0.02** (↓)

Table 4. Effects of species, body length (BL) and Species × BL on δ^{15}N and δ^{13}C signatures as revealed by ANCOVA.

	δ^{15}N				δ^{13}C			
Variable	SS	df	*F*	*p*	SS	df	*F*	*p*
Species	0.50	2,46	3.10	0.054	0.20	2,46	3.20	0.052
BL	0.001	1,46	0.01	0.914	0.01	1,46	0.37	0.544
Species × BL	0.01	2,46	0.05	0.947	0.26	2,46	3.95	0.026

relation to *M. mixta* (Figs. 4 and 5). In fact, some of the 2008 abundances may even be underestimates since some samples did not cover the upper 10 meters; depths that may be favored by juvenile *N. integer* (Kotta and Kotta 2001). The total late-season biomass of mysids also seems to have decreased by at least 50%, and in 2008 it consisted primarily of *N. integer*.

Since there are no long-term monitoring data on mysid abundances and biomasses available from the Baltic, it is impossible to judge whether today's pelagic mysid community or that of the 1980s is the most "normal". Moreover, some precaution should be taken regarding the interpretation of our results, due to differences in sampling techniques used earlier and in 2008, and because only one year was sampled in the 2000s which could have been an unusual and extreme year. Nevertheless, our observations corroborate anecdotal evidence for a decline

Table. 5. Goodness of fit (AIC), parameter estimate (Est.) and *p* values for explanatory variables of species-specific, vertical size-distribution models. Models were run with three subsets of data: (1) samples during thermally-stratified and isothermal conditions (All data), (2) samples collected when a thermocline was present (Stratified data), and (3) samples collected during isothermal conditions (Isothermal data). The best-performing model is characterized by the lowest relative AIC value (set in boldface). All *N. integer* models contain random intercept and slope, whereas *Mysis* spp. models use site/date as a fixed factor with random slope. The effect of site/date was significant in all cases ($p < 0.05$). Due to lack of data, no model results are reported for *Mysis* spp. in the isothermal dataset.

		N. integer			*M. relicta*			*M. mixta*		
Model	Variables	AIC	Est.	*p*	AIC	Est.	*p*	AIC	Est.	*p*
All data										
1	Depth	**4230**	0.028	< **0.001**	1018	0.009	0.120	586	0.002	0.570
2	Light	4235	–0.060	< **0.001**	**1013**	–0.068	0.110	**582**	0.013	0.470
3	Temp	4246	–0.055	**0.003**	1016	–0.022	0.490	584	–0.014	0.580
4	Light	4248	–0.056	**0.002**	1022	–0.081	0.144	592	0.019	0.400
	Temp		–0.023	0.240		0.015	0.720		–0.006	0.640
Stratified data										
1	Depth	**2446**	0.017	< **0.001**	994	0.009	0.120	472	0.002	0.710
2	Light	**2446**	–0.043	**0.001**	**990**	–0.068	0.113	**470**	0.017	0.490
3	Temp	2449	–0.066	**0.004**	992	–0.022	0.490	471	0	0.980
4	Light	2460	–0.035	**0.030**	998	–0.081	0.147	480	0.027	0.395
	Temp		–0.016	0.450		0.015	0.722		–0.008	0.600
Isothermal data										
1	Depth	**1791**	0.042	**0.007**						
2	Light	1794	–0.116	< **0.001**						
3	Temp	1801	0.026	0.140						
4	Light	1804	–0.146	**0.001**						
	Temp		–0.073	0.090						

Table 6. Total numbers (*n*) of measured animals, sampling occasions and tows. 'All data' = samples collected during thermally-stratified and isothermal conditions. 'Stratified data' = samples collected when a thermocline was present. 'Isothermal data' = samples collected during isothermal conditions.

	Mysis relicta			*Mysis mixta*			*Neomysis integer*		
	Measured animals	Sampling occasions	Tows	Measured animals	Sampling occasions	Tows	Measured animals	Sampling occasions	Tows
All data	553	8	20	567	10	32	2154	12	60
Stratified data	536	6	18	359	7	23	1278	7	34
Isothermal data	17	2	2	208	3	9	876	5	26

in *M. mixta* and it could be argued that the changed mysid composition could be related to the "regime shift" described by Alheit *et al.* (2005) which took place in the late 1980s. Some support to this hypothesis is also given by Kotta *et al.* (2004) who observed a sharp increase in *N. integer* abundance after 1986 in the Gulf of Riga and coupled this to increased winter NAO (North Atlantic Oscillation). However, anecdotal observations (Mohammadian *et al.* 1997, Hamrén and Hansson 1999, Gorokhova and Hansson 2000) show that *M. mixta* was abundant and dominated the pelagic mysid community during 1993–1996, i.e. clearly after the supposed regime shift.

Although reasons for the observed changes in the mysid community are unclear, those changes could partly be attributed to a spillover effect from increased populations of littoral *N. integer*, which migrate into the pelagic zone to avoid warm waters in late summer (Arndt and Jansen 1986, Thiel 1992, Välipakka 1992). Perch (*Perca fluviatilis*) and northern pike (*Esox lucius*) have had recruitment problems in the outer archipelago of the Swedish east coast since the beginning of the 1990s. This has been explained by low abundances of zooplankton for the juvenile fish to feed on (Ljunggren *et al.* 2010). As *N. integer* is known to be an opportunistic and efficient littoral predator (Vilas *et al.* 2008), increased abundance of this species along the coastlines could have been a reason for the recruitment problems of perch and pike, and also a possible reason for the high abundances that are seen in the pelagic zone today. The constant supply of juveniles throughout the season also indicates a steady recruitment from the littoral as very few adults were found in the pelagic zone. Unfortunately, there are no abundance data for littoral *N. integer* available for testing the herein alleged littoral increase.

The 3‰ difference in δ^{15}N signature indicates that *N. integer* feeds one trophic level lower (Post 2002) than *Mysis* spp. With *Mysis* spp. being mainly zooplanktivorous (Rudstam 1989, Hansson *et al.* 1990a, Rudstam *et al.* 1992, Viherluoto *et al.* 2000), the diet of *N. integer* should thus consist primarily of phytoplankton. This trophic position difference could however be related to size (i.e. ontogenetical diet differences) and not necessarily to species-specific differences. Analyzed specimens of *N. integer* were smaller than those of *Mysis* spp., and even though all analyzed *N. integer* were > 8 mm — the proposed threshold size at which *Mysis* spp. switch to zooplanktivory (Rudstam and Hansson, 1990, Viherluoto *et al.* 2000) — the isotope composition of the muscle tissue may reflect feeding at a smaller size (Post *et al.* 2007). Interestingly, Lehtiniemi and Nordström (2008) observed that small, littoral *N. integer* (3.5–8 mm), were significantly more carnivorous than larger individuals; eating mostly microzooplankton. This is not supported by our results and may indicate that the diet of *N. integer* differs in the pelagic zone as compared with that in the littoral. The small but significant isotope differences between *M. relicta* and *M. mixta* indicate that the species have some differences in their diet. One possible explanation is that *M. mixta*, which seem to have a shallower, nocturnal depth distribution (this study and author's unpubl. data), consume more pelagic food, either ^{15}N-depleted nitrogen-fixing cyanobacteria (Gorokhova 2009) or food that is isotopically lighter because of nitrogen leakage from decaying cyanobacteria (Rolff *et al.* 2007, Ploug *et al.* 2010), while *M. relicta* may feed more on benthic detritus (Viherluoto *et al.* 2000).

In this context, it is also important to note that although different preservation methods were used for *M. relicta* and *M. mixta*, the effect of preservation was successfully compensated for and did not affect our conclusions on the interspecific diet differences. A comparison of frozen *M. relicta* and *M. mixta* produced similar results as the mix of treatment-compensated and -uncompensated samples that were used in our analyses (one-way ANOVA: $F_{(\text{frozen})1,41} = 34$, $p < 0.0001$, $F_{(\text{mix})1,39} = 90$, $p < 0.0001$ for δ^{15}N and $F_{(\text{frozen})1,41} = 25$, $p < 0.0001$, $F_{(\text{mix})1,39} = 18$, $p < 0.0001$ for δ^{13}C) indicating that any bias that may have been introduced was negligible.

Fish kairomones (fish scent) are known to be detected by *M. mixta* and may alter their behavior (Hamrén and Hansson 1999). Mysids in our study probably experienced higher levels of such chemical cues as compared with the studies in the 1980s (acoustic clupeid biomasses (mean ± SD) recorded with a 70 kHz echosounder in the study area were 885 ± 1030 kg ha^{-1}

and 120 ± 66 kg ha^{-1}, in 2008 and 1985, respectively; authors' unpubl. data) which could have restricted their DVM and thus the possibility to feed on high quality food. *Nota bene*, reported acoustic biomasses may differ by chance but they do reflect the overall increase in clupeid biomass observed throughout the Baltic Sea that followed the collapse of the cod stock (cf. Möllmann *et al*. 2005, Casini *et al*. 2006). The increased biomass of fish could also have increased predation pressure on *M. mixta*, diminishing the population. Pothoven *et al*. (2010) observed a recent decrease in *M. diluviana* abundance in Lake Michigan and proposed that it could be attributed to increased predation by alewifes (*Alosa pseudoharngus*) as a consequence of decreased *Diporeia* spp. abundance (an alternative food source). A similar decline has been observed throughout the Baltic Sea for the analogues *Pontoporeia femorata* and *Monoporeia affinis* (SHARK database, Swedish Meteorological and Hydrological Institute, and BEDA database, Department of Systems Ecology, Stockholm University) and could potentially have led to increased predation pressure on mysids. However, high abundances of *N. integer* in well-illuminated water and a low degree of niche overlap between *N. integer* and *Mysis* spp. suggest that *N. integer* may be a valuable resource for clupeids without competing much for food with other mysid species. Predation by clupeids is thus not the most probable explanation for the decline in *M. mixta*. It is more probable that *M. mixta* (i) feeding conditions have deteriorated, either because of reduced food production or increased competition with other organisms, (ii) increased fish biomass is restricting its feeding rates, (iii) food it consumes is of lowered quality, or (iv) a combination of the above.

Vertical size distribution in relation to light and temperature

Based on an earlier study on vertical differences in the size distribution of *M. mixta* (Rudstam *et al*. 1989) and mysids' responses to light and temperature [Beeton 1960, Bowers 1988, Boscarino *et al*. 2009 (*M. diluviana*), Rudstam *et al*. 1989 (*M. mixta*)], we expected that mysid size would increase with depth and that smaller specimens would occur in warmer water. We had also expected that larger individuals would respond to higher light intensity by staying deeper during bright nights, as predation risk increases with prey size and light intensity (Vinyard and O'Brien 1976).

For *N. integer*, we found the expected increase in size with depth which was explained more by *in situ* light than temperature (Table 5). For *M. relicta* and *M. mixta*, no such relationships were detected.

With the one year life cycle of both *Mysis* species in this part of the Baltic Sea (Rudstam *et al*. 1986), the relative size-differences within these species were small at any one time of sampling. In addition to this, *Mysis* spp. also restricted their occurrence to reasonably great depths (mainly below the thermocline) with light levels well below the threshold for visual feeding by herring, 10^{-4} lux (Batty *et al*. 1990). If visual predation is low at these depths, there would be no fitness advantage to separate vertically by size. Considering these factors, it is not surprising that we were able to explain more of the vertical size structure in *N. integer* (size increase with depth/light) than in *Mysis* spp. With several cohorts each year, the former species has a wider size distribution, it occurred over a larger depth range and this also resulted in more trawl samples containing *N. integer* (more length measurements; Table 6). As the relationships between size and light and temperature found for this species were linear, it means that light affects the size distribution along the entire range of sampled depths, even where temperature is near constant, i.e. above and below the thermocline. Reciprocally, had the temperature effect been the main one, a nonlinear response would have been found, but it was not.

A recent study by Boscarino (2010a) showed that juvenile *Mysis diluviana* (formerly *Mysis relicta*) prefer higher temperatures (10–12 °C) than larger subadults and adults (6–8 °C) suggesting that there are ontogenetic temperature preferences. Juveniles also tolerated light better, although the preferred light levels were comparable to those of larger individuals. Similar size-dependent differences in temperature preferences are common in both invertebrates (Moore *et al*. 1996) and fish (Jobling 1981, Larsson 2005).

Thus, even though juvenile mysids may prefer higher temperatures to optimize growth, there also seems to be a predation avoidance component within those temperature ranges; be it caused by visual predators or cannibalism avoidance (Quirt and Lasenby 2002). The increasing size with depth and light in *N. integer* could thus be explained as a response to predation, since small individuals occur where light intensity is sufficient for feeding by herring whereas larger, more conspicuous individuals (Vinyard and O'Brien 1976) are found deeper. However, we always found the smallest juveniles to be distributed higher in the water than larger specimens, even during isothermal conditions. This suggests that the vertical size-distribution in at least *N. integer* is driven more by light- (fish predation) than size-related temperature preferences.

A general problem in explaining the vertical size structure of mysids in response to depth, temperature and light, is that these three explanatory variables are correlated to some extent (Federle *et al*. 1982). Temperature conditions vary with depth, although the correlations differ over the sampling period. *In situ* light intensity decreases consistently with depth, but differ on an absolute scale due to nighttime light conditions and water transparency. The correlation between temperature and light was low and acceptable (VIF < 2), which indicates that our results should be reliable.

In conclusion, our results show that *M. mixta* has decreased both in proportion to other mysids, and in absolute abundance as compared with studies in the same area in the mid-1980s, and anecdotal knowledge from the mid-1990s. The proportion of *N. integer* has increased considerably and *M. relicta* is now as abundant as *M. mixta* and seems to have increased somewhat since the mid-1980s. Although we could not determine the reasons for the general decrease in *M. mixta*, contributing factors could be increased pelagic fish abundance, i.e. intensified predation and kairomone-induced feeding restrictions and/or decreased quality of the food. The stable isotope analyses suggest significant diet differences among the three mysid species, in particular between *N. integer* and *Mysis* spp. *Neomysis integer* appears to feed at a lower trophic level, supposedly primarily on phytoplankton. Although this result may be influenced by ontogenetic differences as *N.* integer was substantially smaller, the fact still remains that small, phytoplanktivorous *N. integer* are abundant in today's pelagic community and that their presence may affect food-web processes. The size of *Mysis* spp. did not change significantly with depth which may be expected as their presence was limited to deep, dark waters where predation risk by visual predators is low. *N. integer* on the other hand increased linearly with depth and decreased with *in situ* light throughout the sampled depths irrespective of temperature, indicating that light affects vertical size structure in juvenile and subadult *N. integer* relatively more than temperature.

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