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#### ORIGINAL RESEARCH ARTICLE

# Baltic herring prey selectively on older copepodites of *Eurytemora affinis* and *Limnocalanus macrurus* in the Gulf of Riga<sup>\*\*</sup>

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Received 23 October 2014; accepted 29 September 2015 Available online 6 November 2015

#### **KEYWORDS**

Clupea harengus membras; Zooplankton; Selective feeding; Condition factor; The Gulf of Riga Summary Zooplankton availability is a major factor affecting herring body condition that in turn describes its well-being. As herring feeding is known to be selective, it is relevant to access its preferences upon zooplankton species and particular copepod developmental stages to forecast possible intraspecific competition for resources in the species scarce environment of the Gulf of Riga where herring stock size due to successful recruitment has almost doubled since 1989. This study tries to answer whether the small-sized plankters dominated zooplankton community permits herring to be a selective eater. Also how herring body condition has changed in connection to environment driven zooplankton community changes. The time series of zooplankton abundance and herring condition from 1995—2012 were studied; and a detailed study of herring diet was performed monthly by stomach content analysis during the main feeding season in 2011 and 2012. We found that herring selectively prey on *Limnocalanus macrurus* and older copepodite stages of *Eurytemora affinis*, and moreover these were species of whose selected copepodite stages explained most of variation in herring condition factor. The found

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Peer review under the responsibility of Institute of Oceanology of the Polish Academy of Sciences.



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<sup>\*</sup> The study was supported by ERDF project "Development of a mechanistic model of the Gulf of Riga ecosystem in support of efficient national policy to ensure the protection of the Baltic Sea and to promote the sustainable use of its ecosystem" (Ref. No. 010/0287/2DP/2.1.1.1.0/10/APIA/VIAA/040). No involvement in study design by the financial supporters was provided.

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relationship between herring feeding selectivity and long-term variation of herring condition allows applying spring zooplankton abundance of *E. affinis* and *L. macrurus* to estimate favourable feeding conditions for herring, and could also require the revision of currently used model for herring recruitment estimations, where only biomass of *E. affinis* is taken into account. In recent years, the high condition of herring can be associated with a considerable increase of lipid-rich copepod species *L. macrurus*.

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#### 1. Introduction

Herring Clupea harengus membras L. is one of the most important zooplanktivorous pelagic fish species in the Baltic Sea fishery, where a considerable decrease of its weight-atage and condition has been detected since 1980/90s (Cardinale and Arrhenius, 2000). The Gulf of Riga herring, a separate population of the Baltic Sea herring, is characterized by the lowest growth rates compared with herring stocks of the remaining Baltic Sea (Arrhenius and Hansson, 1993). Two paired explanations can be connected to this issue (Casini et al., 2006). Both are determined by prey availability: density dependent factors of increased herring stock size, a pattern of stock shift inverse to that of the Central Baltic since the late 80s (ICES, 2009); and hydro-climatic condition driven changes in the zooplankton community (Cardinale and Arrhenius, 2000; Kornilovs et al., 1992).

A considerable amount of literature has been published on zooplankton predation by clupeid fish in the Baltic Sea. Sandström (1980) was first to demonstrate selective feeding by herring. Then, in a zooplankton species and copepod development stage-resolved study Flinkman et al. (1992) identified that herring feeding is limited by the availability of suitably sized plankters, not the total amount of zooplankton, thus, herring mainly controls older copepodite stages and adult specimens. Long-term studies have outlined that the climate change induced salinity decrease has affected food availability, emphasizing decline in Pseudocalanus sp., main prey item of herring and sprat (Sprattus sprattus L. 1758) of the Central Baltic (Kornilovs et al., 2001; Möllmann et al., 2000, 2004b, 2005). Therefore, food availability has been also coupled with inter- and intraspecific competition as a result of the sprat stock increase after predation release by collapsed cod (Gadus morhua L. 1758) stock (Alheit et al., 2005; Casini et al., 2010; Margonski et al., 2010; Möllmann et al., 2004a; Möllmann and Köster, 2002; Rudstam et al., 1994).

Unlike in the Central Baltic, sprat stock is assessed to be at a low level in the Gulf of Riga where it does not control zooplankton biomass but instead, herring strongly dominates in commercial catches at about 90% of total values (Kotta et al., 2008). Therefore, the gulf is a pleasingly simple, few-species ecosystem for pelagic trophic studies. Due to large freshwater runoff and restricted water exchange to the Baltic Proper, low salinity (5–7 psu) (Berzinsh, 1995) determines the zooplankton community in the gulf. That consists of a limited number of occurring species, dominated by small-sized plankters, such as cladocerans (in summer) and

few taxa of copepods (Ikauniece, 2001; Ojaveer et al., 1998). Lankov et al. (2010) showed Eurytemora affinis prevailing herring diet by annual summer investigations on pooled data basis. Whereas, detailed studies on zooplankton stageselective and season-specific feeding in the Gulf of Riga are unknown so far. Recognizing herring as a selective feeder (Flinkman et al., 1992) in this few-species environment, it is important to assess its preferences upon both zooplankton species and particular copepod developmental stages. This is to forecast possible intraspecific competition for resources in the light of almost doubled stock size since the late 1980s (ICES, 2009). In this study we analyse: (1) juvenile and adult herring selective predation on cladocerans and development stage-resolved copepods, (2) and the zooplankton community relation to the changes in herring condition in the Gulf of Riga, using a time series of 18 years (1995–2012).

#### 2. Material and methods

#### 2.1. Study area and sampling in 2011 and 2012

Herring was collected in monthly cruises along the main feeding season from May to October in 2011 and 2012 in the coastal area of the Gulf of Riga. One trawl haul per month was performed, using OTM pelagic mid-water trawl (duration: 15-30 min; depth range: 23-30 m), close to the thermocline (20-30 m) (Stipa et al., 1999). On the basis of diurnal feeding cycle, the hauls were conducted only during second half of the day. The total fish length was measured to the nearest 0.5 cm and mean wet body weight per length class determined to a precision of 0.1 g. Stomachs of 5 randomly chosen fish per sampling time and length class were removed and preserved in 4% formaldehyde solution immediately on board (n < 5, where number of fish per 0.5 cm length class was not reached). Otoliths were removed for age determination later in laboratory using a stereomicroscope.

To evaluate prey availability, zooplankton sampling was performed on each hauling station, as well as on additional stations representing the central part of the Gulf of Riga from the bottom to the surface with a 160  $\mu$ m Juday net (diameter of the upper aperture: 37 cm; diameter of the middle section: 50 cm) (UNESCO, 1968).

#### 2.2. Sample analysis

Every herring stomach was cut open, and the complete content weighed to a precision of 0.001 g and analysed using

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a light microscope (magnification  $50-100\times$ ). If a stomach contained a large number of prey, a subsample of at least 100 individuals was analysed. Each of the prey was determined to the lowest possible taxonomic level. The following stages were distinguished for copepods: early copepodites C1-3, older copepodites C4-5, adult females C6 and adult males C6, and cladocerans measured to 0.2 mm. Nauplii and rotifers were excluded from analyses as herring consumed an inconsiderable number of them. A total of 797 stomachs were analysed.

Zooplankton samples were preserved and analyses were performed according to the standard protocol of the Manual for Marine Monitoring in the COMBINE Programme of HELCOM (2013). Biomasses were estimated from values on individual wet weight (Hernroth, 1985; Simm and Ojaveer, unpubl. data).

#### 2.3. Data series for 1995 to 2012

To assess historical zooplankton abundance and biomass trends, and variability of herring condition factor, monitoring data collected in the Gulf of Riga by the Institute of Food Safety, Animal Health and Environment "BIOR" from 1995—2012 were used.

Zooplankton was sampled from the bottom to the surface with a 160  $\mu$ m Juday net (UNESCO, 1968) and analysed according to internal procedures (Kornilovs et al., 2001) and the standard protocol of the Manual for Marine Monitoring in the COMBINE Programme of HELCOM (2013). Mean abundance and biomass (Hernroth, 1985; Simm and Ojaveer, unpubl. data) values of stations sampled in May were used.

Fish condition was estimated by Fulton's (1904) condition factor, an index assuming heavier fish of a given length are in better condition (Froese, 2006). To determine herring condition, on average about 1000 individuals were analysed based on fish individual biological data in commercial trawl fishery each year, and mean condition in June and July was used.

Zooplankton species dynamics are related to water and air temperature. Freimane (1967, 1968) found a tight correlation between Copepoda abundance and a sum of daily negative values of air temperature, and that a particular species, *L. macrurus*, abundance depended on water temperature, salinity and amount of solar radiation. Severe winters are associated with sharp environmental changes that could be major drivers of zooplankton dynamics. To describe winter severity, the data used were a sum of daily negative values of air temperature [°C] in Riga, measured by the Latvian Environment, Geology and Meteorology Centre from 1995—2012. These data were further used in a correlation with main forage zooplankton species.

#### 2.4. Data analysis

All statistical analyses were done using the software package R 3.0.2 (R Core Team, 2013). Feeding selectivity on sizeranged zooplankton species- and season-specific individual wet weights (Hernroth, 1985; Simm and Ojaveer, unpubl. data) (Table 1) was described using a Yates' corrected chisquare  $(\chi_y^2)$  test based (abundance of individuals was expressed as percentage of total wet weight of stomach

Table 1 Identification categories and mean individual wet weight [WW,  $\mu g$  ind. $^{-1}$ ] (Hernroth, 1985; Simm and Ojaveer, unpubl. data) of mesozooplankton studied in the Gulf of Riga in 2011 and 2012. For calculations of *C*-index (Pearre, 1982) herring prey data were used as an average number of an identification category per length class and sampling time, and zooplankton abundance expressed as ind.  $m^{-3}$  according to the same identification categories. C, copepodite stages.

Species	Mean WW [μg ind. <sup>–1</sup> ]	Prey category
Evadne nordmanni	6	
Podon/Pleopis spp.	6	Cladoc
Bosmina coregoni	7	
Cyclopoida C1-5	4	
Acartia spp. C1-3	4	
Eurytemora affinis C1–3	5	Cop_C1-6
Cyclopoida C6	9	
Acartia spp. C4-5	10	
Eurytemora affinis C4–5	14	Eury_C4-5
Acartia spp. C6	22	Acar_C6
Eurytemora affinis C6	30	Eury_C6
Limnocalanus macrurus C1–5	50	Limn_C1-5
Cercopagis pengoi	120	Cercop
Limnocalanus macrurus C6	652	Limn_C6

content or zooplankton sample; see the supplementary material) *C*-index (Pearre, 1982) (Eq. (1)):

$$C = \pm \left(\frac{\chi_y^2}{n}\right)^{1/2},\tag{1}$$

where n was total percentage (200) of zooplankton in the sea and in the stomachs. The index is zero-valued for no selection and ranges between -1 and +1, wherein negative values was associated with rejection and positive values with selection. C-index is not sensitive to rare prey species and is statistically testable. The prey data used was an average number of a zooplankton identification category per herring length class and sampling time. Zooplankton abundance was expressed per  $m^3$  according to the same identification categories.

The potential influence of the factors: (i) season, (ii) herring age group, (iii) prey category, and (iv) combination of herring age group and prey category, as well as (v) combination of season and prey category on the differences in selectivity index was evaluated using Linear mixed-effects (lme) model fit with the REML method as implemented in the package nlme of the program R (Pinheiro et al., 2013). A combination of multiple samples from each month and year (same sampling occasion) was used as a random effect. Due to variable haul locations throughout the study area and therefore a limitation of simultaneous spatial data, analyses that were performed assumed no differences between trawl sites. As herring is known to actively search for its food items, we expected it to school in locations where the desired food was most available. Therefore, the trawl sites varied along the coastal area of the Gulf of Riga making it possible to sample respective to occurrence of herring.

If the model showed a statistically significant effect of factor or factor combination, simultaneous tests with adjusted p values for general linear hypothesis (post-hoc test) of the package multcomp in the program R were used to assess which levels showed statistically significant difference (Hothorn et al., 2008). A selectivity value for each prey category level was compared to 0. In the "prey category and age" combination and the "prey category and season" combination, comparisons were performed at each prey level between age classes and between seasons.

As zooplankton species dynamics are related to water and air temperature, the Pearson correlation was applied to relate *L. macrurus* and *E. affinis* long-term abundance in May with winter air temperatures from 1995—2012. Correlation was used to relate long-term changes in the body condition of herring with May abundance of these dominant prey species.

#### 3. Results

## 3.1. Juvenile and adult herring selective predation on zooplankton

The overall model resulted in a "prey category", a combination of "herring age group and prey category", and a combination of "season and prey category" influencing differences in herring selectivity index (lme model, p < 0.0001) (Table 2). Further tests for these significant interactions (Table 3) revealed that both juvenile and adult herring rejected small-sized early copepodites (Cop\_C1-  $6 \times \text{age}, p < 0.0001$ ). All herring selectively preyed on large cold-water calanoid L. macrurus C1-5 (Limn\_C1-5, p = 0.01) and C6 stages (Limn\_C6, p < 0.001).

## 3.2. Seasonal variation of herring feeding selectivity

In absolute numbers, the herring diet was dominated by copepods *L. macrurus* during all the main feeding periods and *E. affinis* in spring and summer; and along with an invasive opportunistic cladoceran *Cercopagis pengoi* in summer and autumn, when it is available in the zooplankton community. Proportion of mysids increased with a reduced zooplankton biomass in autumn period.

**Table 2** The overall linear mixed-effects model results (ANOVA table) of variables (i) season, (ii) herring age, (iii) prey categories, (iv) combination of herring age group and prey category, and (v) combination of season and prey category (p < 0.0001).

Interactions between variables	F-value	d.f.	<i>p</i> -value
Season	0.32	2	0.7308
Age	1.97	1	0.1609
Prey category	51.53	7	< 0.0001
Age × Prey category	17.61	7	< 0.0001
$Season \times Prey \ category$	24.62	14	< 0.0001

Seasonal variation of prey abundance largely did not correspond to herring consumption though. Highly abundant small copepodites of *E. affinis* up to C3, *Acartia* spp. up to C5 and Cyclopoida up to C6 were truly rejected along the main feeding season. *Acartia* spp. C6 despite its relatively large mean individual mass of 22  $\mu$ g ind. did not seem to be desirable prey for herring. An inconsiderable amount of fish eggs and extremely abundant rotifers and copepod nauplii were consumed.

In spring, herring selectively fed on both *E. affinis* C4–6 and *L. macrurus* C1–6 and in summer on *E. affinis* C4–5 and *L. macrurus* C1–6. Invasive cladoceran *C. pengoi* was positively selected in the autumn, along with *L. macrurus* copepodites and adults (Fig. 1). Unfortunately, nectobenthos was not sampled during this study; therefore, selectivity on mysids could not be calculated.

#### 3.3. Long-term relation of herring condition, Limnocalanus macrurus and Eurytemora affinis

We became particularly interested in long-term variation of *E. affinis* and *L. macrurus*, as herring consumed a considerable biomass of these copepods along the feeding study in 2011 and 2012 (43% of herring had *L. macrurus* and 66% had *E. affinis* in their stomachs that made up 45 and 12% of total consumed biomass respectively). Moreover, *L. macrurus* C1–5 (Limn\_C1–5, p = 0.01) and adults (Limn\_C6, p < 0.001) were zooplankton groups herring indicated selective predation on throughout the period of May to October, while *E. affinis* C4–5 was positively selected by adult herring both in spring and summer, without a significant difference between these two seasons (Eury\_C4–5 × age, p < 0.0001) (Fig. 1).

Since the last peak of *L. macrurus* in the 1980s, afterwards it had almost disappeared from the zooplankton community in the gulf (Yurkovskis et al., 1999). Fig. 2 provides an anomaly of May data 1995—2012 that indicates a shift has occurred. Since 2005 mostly positive abundance anomalies of *L. macrurus* have dominated and in recent years it has reached the long-term mean abundance of 20 800—79 730  $\mu g$  m<sup>-3</sup>, while *E. affinis* spring abundance has oscillated mostly inversely to *L. macrurus*.

In order to describe winter severity (conditions influencing spring productivity), a sum of daily negative values of air temperature in winter was used, and that correlated with L. macrurus abundance in May (r = 0.58, p < 0.012), while negative correlation with E. affinis was found (r = -0.61, p < 0.008).

Selectivity estimates indicate that herring preys on older copepodites of *E. affinis* and *L. macrurus* (Fig. 1). An abundance sum of *E. affinis* C4–5 and *L. macrurus* C1–6 stages in May had the tightest correlation with the herring condition factor in June and July, as a response to feeding conditions in spring (r = 0.70, p = 0.007) (Table 4).

#### 4. Discussion

We found that herring selectively targets older copepodites of *E. affinis* and large-sized *L. macrurus*. These findings further support the idea that herring feeding is strictly zooplankton species- and copepod stage-selective (Flinkman et al., 1992).

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**Table 3** Mean and standard deviation of selectivity values (C-index) (Pearre, 1982) for each prey category and each prey category by age groups. The index ranges between -1 and +1, wherein negative values are associated with rejection and positive values with selection; p-values given for the comparison of mean selectivity values with 0 for prey categories and between age groups. Juveniles are 1 year and adults 2-12 year old fish. For prey categories refer to Table 1.

Prey category	Prey category		Prey category $\times$ Ag	e	_
	Mean $\pm$ S.D.	p-value	Mean $\pm$ S.D.		p-value
			Juveniles	Adults	
Cladoc	$-0.04 \pm 0.23$	0.22	$0.07 \pm 0.23$	$-0.10 \pm 0.21$	<0.0001
Cop_C1-6	$\mathbf{-0.28} \pm 0.29$	< 0.001	$-0.26\pm0.31$	$\mathbf{-0.29} \pm 0.28$	< 0.0001
Eury_C4-5	$-\textbf{0.03} \pm \textbf{0.24}$	1	$-0.12\pm0.24$	$\textbf{0.01} \pm \textbf{0.23}$	< 0.0001
Acar_C6	$-\textbf{0.04} \pm \textbf{0.06}$	1	$-0.05\pm0.06$	$-0.04\pm0.06$	0.97
Eury_C6	$-0.01\pm0.14$	0.9	$-0.06\pm0.11$	$\textbf{0.01} \pm \textbf{0.14}$	0.59
Limn_C1-5	$\textbf{0.05} \pm \textbf{0.22}$	0.01	$-\textbf{0.07} \pm \textbf{0.26}$	$\textbf{0.09} \pm \textbf{0.17}$	0.88
Cercop	$\textbf{0.08} \pm \textbf{0.47}$	< 0.001	$\textbf{0.22} \pm \textbf{0.52}$	$-0.00\pm0.41$	< 0.0001
Limn_C6	$\textbf{0.13} \pm \textbf{0.34}$	<0.001	$-0.06 \pm 0.38$	$\textbf{0.20} \pm \textbf{0.29}$	0.73

Herring avoids small early copepodites, nauplii and rotifers even in the species scarce environment of the Gulf of Riga, prevailed by small sized plankters. The particulate-feeding we have identified, consequently assists in our understanding of the role of changes in the well-being of the herring, as these were zooplankton species whose abundance sum of selected copepodite stages explained most of the variation in a historical time series of herring condition factor.

As small-sized plankters prevailed in the Gulf of Riga, we expected diet overlap between adult and juvenile herring towards larger but restricted food fractions, what was indeed true. The main difference was in juveniles consuming cladocerans, both small- (Bosmina coregoni, Evadne nordmanni, Podon/Pleopis spp.) and large-sized (C. pengoi), while adults

preferred older copepodites of *E. affinis*. Therefore, body size of the prey was not the only determining cause of selection. For length classes studied here (>8 cm), the feeding of herring might not be limited by gape-size (Arrhenius, 1996) but rather by prey motility. Because of their low escape response, cladocerans were more likely to be captured (Drenner, 1978; Viitasalo et al., 2001) so that an opportunistic shift to cladocerans in summer could be energetically advantageous. Most likely adult herring had a greater capture success on far more motile copepods, as *E. affinis*, attained through learning to forage, as shown for other fish species (Brown and Laland, 2003). As there were no differences in diet between herring juveniles and adults towards mature *E. affinis* and all stages of large-sized *L. macrurus* suggesting

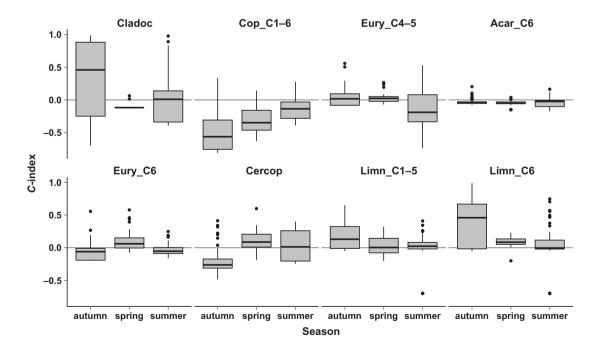


Figure 1 Seasonal variation of herring feeding selectivity (*C*-index) (Pearre, 1982) in each prey category. The index ranges between -1 and +1, wherein negative values are associated with rejection and positive values with selection. For prey categories refer to Table 1.

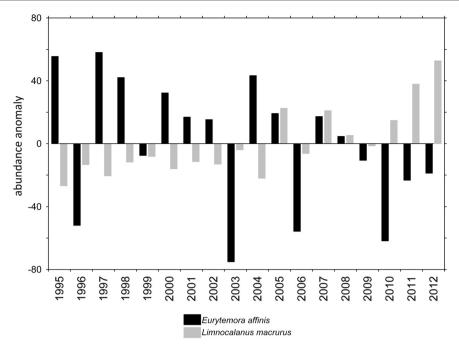


Figure 2 Abundance [ind. m<sup>-3</sup>] anomaly of Eurytemora affinis and Limnocalanus macrurus in the Gulf of Riga in May 1995–2012.

dietary overlap at some level, we address the point that mature herring do not feed in spring while spawning (Link, 2001; Slotte, 1999). In the meantime, juveniles feed actively and could be considerable consumers of the shared food resources of copepods in the season when cladocerans are not widely available in the zooplankton community yet.

A striking finding to emerge from our study was that both the juvenile and adult herring strongly preferred *L. macrurus* species only lately recovered in the Gulf of Riga. Increased herring condition in recent years could be associated with a considerable increase of *L. macrurus*. A distinct characteristic of *L. macrurus* is its lipid content of 67% of dry weight, one of the highest among zooplankton species (Vanderploeg et al., 1998) combined with individual size and weight largest among holoplankton species in the Baltic Sea (Hernroth, 1985).

As already mentioned, since late 1980s *L. macrurus* was almost extinct in the gulf. No significant relationship with herring predation was found at previous studies (Kornilovs

**Table 4** Pearson correlations between abundance of major development stage-resolved prey copepods *Eurytemora affinis* and *Limnocalanus macrurus* in spring and herring condition factor (CF) in successive summer studied in the Gulf of Riga in 1995–2012. C, copepodite stages. For prey categories refer to Table 1.

Prey category	r	<i>p</i> -value
Eury_C1-3	0.39	0.182
Eury_C4-5	0.68	0.011
Eury_C6	0.33	0.266
Limn_C1-3	0.05	0.869
Limn_C4-5	0.37	0.208
Limn_C6	0.20	0.514
Eury_C4-5 + Limn_C1-6	0.70	0.007

et al., 2004). Our study was in contrast to earlier findings by Lankov et al. (2010) who conducted annual summer investigations from 1999—2006, and detected no evidence of *L. macrurus* in herring stomachs. Therefore, extremely low numbers of *L. macrurus* or even an absence in the gulf could not be explained by herring predation for the named period but rather abiotic factors.

In spring, zooplankton abundance increases mostly as a response to abiotic factors (e.g. water temperature) and a subsequently increased food availability (Jurgensone et al., 2011). As predation rates are still relatively low, due to herring spawning, zooplankton community is comparatively unaffected by fish (Rudstam et al., 1994). Although the species development could be affected by food availability in spring, we explained the recent increase of L. macrurus by the positive correlation between its abundance in spring and sum of daily negative values of air temperature in previous winter. Evidently, more frequent cold winters in the last decade have contributed recovery of L. macrurus, a glacial relict species. It should be noted that in 1990s there was only one cold winter with the gulf frozen, as ice occurrence due to a sharp environmental change is the factor affecting species development in spring. L. macrurus is known to be restricted between narrow environmental limits of upper temperature limit of 14°C, and a lower limit of dissolved oxygen of  $5.6 \text{ mg L}^{-1}$  (Kane et al., 2004; Strøm, 1946). Accordingly, the possible interference of oxygen levels (even though dependent on temperature) cannot be ruled out, as the critical combination could be the case in August, when water temperature is often high, water stratified, and oxygen levels lower than optimal under the thermocline (most regular habitat of L. macrurus) (LHEI unpubl. monitoring data, 2012). Yet, the situation in summer and later in autumn can hardly be described by direct link between copepods and hydrological conditions, as it disappears due to predation pressure by fish (Casini et al., 2009).

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Cold winters have benefited L. macrurus development, but those winters also have resulted with lower water temperature in successive springs, delaying development of more thermophilic species like E. affinis. As E. affinis abundance explained most of variation in the herring condition, without a doubt these findings will be much scrutinized, but dependable conclusions for significant L. macrurus impact on high condition in last years can be made. One caveat in interpreting our results is that the herring condition failed to be explained by biomass of these zooplankton species. The biomass of L. macrurus increased towards the end of the time series, therefore the period of its higher biomass is rather short. The biomass appears to be of a great importance, as these two copepod species have considerably different individual weights: L. macrurus is about tenfold heavier than E. affinis (Hernroth, 1985).

However, more research on this topic needs to be undertaken before the association between herring condition and variation of its preferred food items is more clearly understood. Investigating the effects of density-dependent mechanisms on herring growth and condition with the association of biotic factors, as young and adult herring should compete for the available zooplankton specimens (Casini et al., 2006). It will be curious to survey future trends of L. macrurus abundance in the light of changing climate, as it (while being restricted between narrow environmental limits) plays an important role in pelagic food web. Although, a common viewpoint is that higher temperature ensures higher zooplankton biomass and better feeding conditions in the Baltic Sea (Cardinale et al., 2009), we suggest that a pronounced seasonality (cold winters with ice cover) could benefit herring feeding conditions and ensure higher body condition, as in the Norwegian Sea, where a cold water copepod Calanus finmarchicus is the most important prey species for herring (Engelhard and Heino, 2006). Body condition of a fish is the "fast line" to explain its well-being (Froese, 2006) that in turn, is provided by availability of desired food items. High condition is linked to better recruitment thereafter, due to higher fecundity (Arula et al., 2012), lower mortality rates (Engelhard and Heino, 2006) and indirectly indicates a magnitude of possible intraspecific competition.

So far herring recruitment in the Gulf of Riga has been forecasted using Ricker model approach by using two complementary factors: *E. affinis* biomass in May and average water temperature in August that has encountered issue of poor predictions of rich year classes during the last years (ICES, 2013). We speculate that the combination of our findings provides some support for the conceptual premise that the found relationship between the herring feeding selectivity and long-term variation in the herring condition factor has implications to use spring abundance trends of selected copepodite stages of *E. affinis* and *L. macrurus* to estimate feeding situation and, therefore, body condition of herring in the successive year.

#### Acknowledgments

We thank the anonymous reviewers as well as Juris Aigars and Georgs Kornilovs for constructive comments on earlier drafts of the manuscript, and Tyson Duffy for revising the English.

#### Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/doi:10.1016/j.oceano.2015.09.001.

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