



Original Article

Multidecadal dynamics of the Arctic copepod *Limnocalanus macrurus* in relation to environmental variability in the Baltic Sea

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The Arctic *Limnocalanus macrurus* is a prominent representative of large copepods which performs several essential functions in freshwater and marine ecosystems. Being a cold stenotherm species, its distribution is primarily confined to deeper water layers. Based on the long-term observations from one of the largest spatially confined natural populations of this species in the Baltic Sea, we detected profound long-term variability of *L. macrurus* during 1958–2016: high abundances before the 1980s, then nearly disappearance in the 1990s and recovery in the 2000s. The main environmental parameters explaining the interannual variability of *L. macrurus* in spring were herring spawning stock biomass in preceding year, winter severity, and bottom water temperature in preceding summer. The effect of winter severity and water temperature was also non-linear. The sliding window correlation analysis pointed to a non-stationary relationship between the abundance of *L. macrurus* and the key variables. Given the observed pronounced seasonality in the population structure of *L. macrurus* (young stages dominated in the beginning of the year and only adults were left in the population in summer and autumn) we identified the dynamics of key environmental variables to understand this species under different ecosystem configurations and different combinations of drivers of change.

Keywords: annual abundance, Gulf of Riga, herring spawner biomass, hydro-climatic conditions, non-linear and non-stationary relationships

Introduction

The response of marine species and populations to external drivers of change can be either linear or non-linear. While linear systems behave additively (i.e. they are equal to the sum of their parts) and can therefore be disassembled, non-linear systems are non-additive (i.e. antagonistic or synergistic effects prevail) and thus cannot be studied through disaggregation (Klein and Thurstan, 2016). Furthermore, the relationship (i.e. linear or non-linear) between the driver(s) and the affected biota can

also be non-stationary, i.e. change over time. For example, non-stationary links have been documented between recruitment, spawning stock biomass (SSB) and water temperature for multiple fish stocks (Ottersen *et al.*, 2013). Only long-term time-series, which enable to capture a wide range of variability of drivers and encompass different combinations of their relative roles, allow to learn both the type of the effect on the species or populations of interest, as well as the potential dynamics over time.

One of the ecologically relevant but relatively poorly studied species in many marine and freshwater environments of the northern hemisphere is the calanoid copepod *Limnocalanus macrurus*. *L. macrurus* is a large lipid-rich copepod with high content of polyunsaturated fatty acids, serving thereby as a high-quality prey for fish (Hiltunen et al., 2014). Bearing in mind the absolute key role of the species in aquatic pelagic ecosystems, mechanistic understanding of its population ecology and the primary drivers of its abundance in different aquatic ecosystems from a long-term perspective is imperative. As a cold stenotherm species (Van Hove et al., 2001; Apollonio and Saros, 2013; Jackson et al., 2013; Drits et al., 2016), the distribution of *L. macrurus* is usually restricted to deeper colder water masses (Carter and Goudie, 1986), with ability to penetrate the seasonal thermocline to the upper water layers at night when stratification is weak (Wells, 1960). The species is characterized by continuous and plastic feeding (Warren, 1985; Barbiero et al., 2009; Dahlgren et al., 2012; Jackson et al., 2013), thereby efficiently exploiting the available food resource and transferring the energy from lower trophic levels to fish.

Limnocalanus macrurus is considered as a glacial relict in the Baltic Sea (Segerstråle, 1966), being the largest widely distributed copepod species (up to 3 mm in length) in its northern part: Gulf of Bothnia, Gulf of Finland, and Gulf of Riga (GoR). All these basins are characterized by relatively harsh climate conditions in winter and relatively low salinity, hosting therefore several glacial relicts (Järvekülg, 1973). However, the ecology of *L. macrurus* in the Baltic Sea is poorly documented. Based on the long-term records, the species was very abundant in the GoR before the 1980s but nearly disappeared in the late 1980s, allegedly due to mild winters which resulted in warmer water during the winter/spring period (Kornilovs et al., 2004). In addition, abundance of the species has been suggested to change in relation to variations in salinity in Bothnian Sea (Rajasilta et al., 2014), where it may dominate in the copepod community most of the year, constituting often >50% of the biomass (Dahlgren et al., 2010). *Limnocalanus macrurus* is the highly preferred prey item of the most abundant pelagic fish species—herring (*Clupea harengus membras*)—in both the Gulf of Bothnia (Flinkman et al., 1992) and GoR (Livdåne et al., 2016), while other abundant planktivorous fish consume *L. macrurus* only marginally (Ojaveer et al., 1997).

To enhance our understanding of the long-term dynamics of *L. macrurus* at the edge of its distribution area in the Baltic Sea as a response to the dynamics of the key drivers of change, and to test the hypothesized effect of each variable (see Table 1), we have: (i) established multidecadal abundance dynamics of the species in the GoR (Baltic Sea) and associated environmental and biological factors that have been previously suggested to influence its population size. These are winter severity (Ojaveer et al., 1998), water temperature (Kornilovs et al., 2004), oxygen content (Roff, 1973; Kane et al., 2004), salinity (Rajasilta et al., 2014), and predator stock size (Barbiero et al., 2009), (ii) identified the key environmental variables potentially affecting *L. macrurus* abundance dynamics, (iii) investigated the non-linear interactions between the explanatory variables that drive the interannual abundance dynamics of *L. macrurus*, and (iv) looked for the evidence of non-stationary links between the key environmental variables and interannual abundance variability of *L. macrurus*.

Table 1. Expected effects of the studied environmental drivers on the abundance of *L. macrurus* in the GoR.

Variable	Expected effect	References
SSB of the predator	Strong negative	Kane et al. (2004) and Barbiero et al. (2009)
Winter air temperature	Strong negative	Ojaveer et al. (1998)
Summer water temperature	Weak negative	Kornilovs et al. (2004)
Salinity	Weak negative	Rajasilta et al. (2014) and Segerstråle (1966)
Oxygen content	Weak positive	Roff (1973) and Kane et al. (2004)

Material and methods

The study area

The GoR is a shallow partly landlocked sub-basin in the northeastern Baltic Sea, separated from the Baltic Proper by the shallow and narrow Irbe Strait. The main influx of fresh water from the vast drainage area of 134 000 km² occurs primarily in the southern part of the basin. In most parts, salinity ranges between 5.0 and 6.5 PSU with the absence of a permanent halocline. Due to its shallowness, the dynamics of both surface and near-bottom temperatures are directly coupled with air temperatures. Due to strong vertical mixing, dissolved oxygen concentration is in most areas higher than 5 ml L⁻¹, while values below 2 ml L⁻¹ have been found in the deepest part of the GoR (>45 m; Kotta et al., 2008).

Data

Data of *L. macrurus* abundances, derived from the database of the Institute of Food Safety, Animal Health and Environment, BIOR, were obtained from seven stations in the central GoR (Figure 1), covering years from 1958 to 2016 (299 samples in May, 275 in August, and 152 in October, 726 profiles in total). Samples were collected with vertical tows by a Juday net (mesh size 160 µm, opening diameter of upper ring 36 cm) and fixed in 4% formaldehyde solution. Sample collection and analysis procedure was based on UNESCO (1968) and remained the same throughout the survey period. Abundances were initially reported as individuals per m³, but transformed in this analysis to individuals per m² by multiplying the densities with depth of entire profile.

List of environmental variables tested by the statistical models was limited to these that were previously suggested to drive *L. macrurus* abundance dynamics either in the Baltic Sea or elsewhere (Kornilovs et al., 1992; Sidrevics et al., 1993; Kane et al., 2004) and for which we had reliable long-term data available: (i) winter severity (measured as a sum of negative daily mean air temperatures from November to March; data from Estonian Weather Service, 1958 to 2016), (ii) temperature, (iii) salinity, and (iv) oxygen content of the bottom water (data from BIOR, 1963 to 2016, average value measured from the depth range of 30–50 m in August), and (v) SSB of autumn and spring herring together [data from Ojaveer (2003), Ojaveer et al. (2004), and ICES (2018), 1958 to 2016].

Data analysis

Time series of comparable annual mean abundances of *L. macrurus*, accounting for all sampling artefacts (interannual differences in the number of samples, time of sampling, or spatial

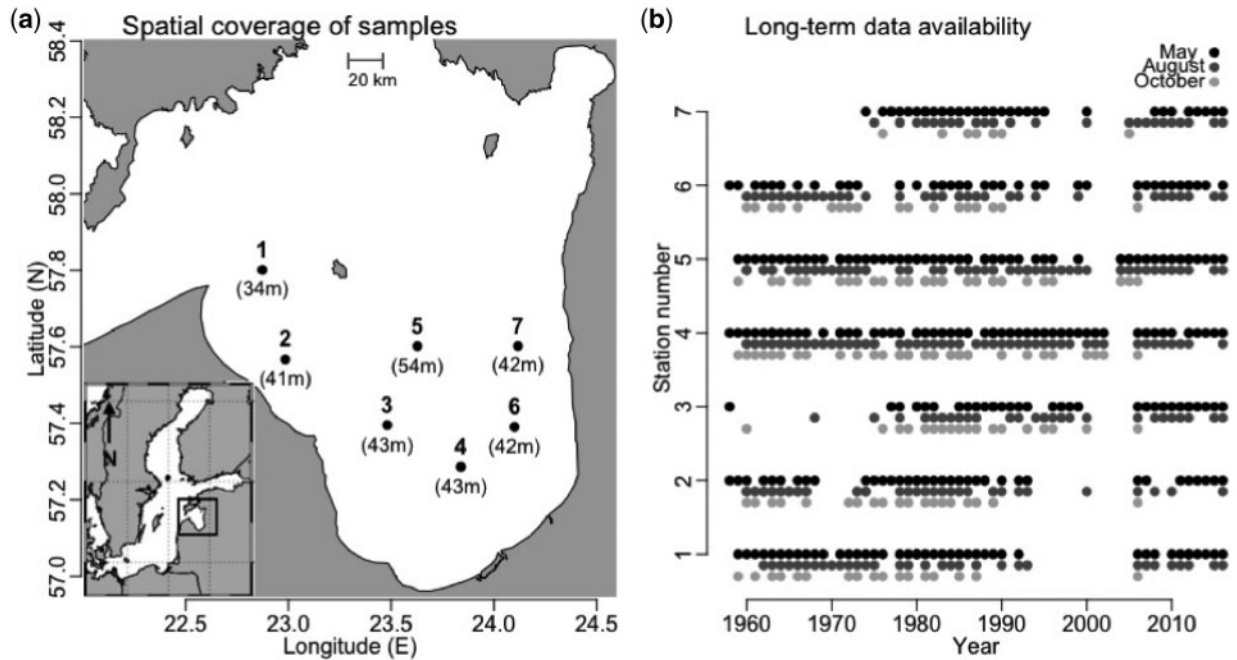


Figure 1. Location of sampling stations of *L. macrurus* in the GoR and availability of data during 1958–2016.

distribution of data) were calculated as marginal means of categorical variable “year” with generalized additive model (GAM), where year was combined with the sampling depth and Julian day, following to Carstensen *et al.* (2006). The best model was determined through the forward selection, and annual means were estimated with the final model setting other significant terms at their all time mean values. The long-term sampling was more consistent in spring (May) and summer (August) than in autumn (October) (Figure 1b), therefore autumn data were left out from this study, apart from one visualization of seasonal dynamics in community maturity. Since the population structure was very different between the months (mostly juveniles in spring, and adults in summer), time series of annual abundances were estimated for spring and summer independently. The maturity of population was visualized through a variable “mean stage,” calculated as a weighted mean of the sequence from 0 to 6, corresponding to nauplii, copepodites I–V, and adults. Each value was weighted by the abundance of respective stage in the sample, resulting in a single number measure of the population age composition. Initial inspection of results indicated that *L. macrurus* is univoltine in the GoR, therefore, generally higher abundances of younger stages in spring was considered most reliable indicator of the long-term dynamics of this species.

To quantify the relative importance of selected environmental variables, and the reliability of the model results, we used the multimodel inference method (Burnham and Anderson, 1998), following the same procedure as described in Everaert *et al.* (2018). In this procedure, all possible models from single predictor to a full model of all five variables were fitted, using again GAM, resulting in 31 models in total. For each model, an Akaike Information Criterion for small sample sizes (AICc) was found. Models were ranked in increasing order of AICc, and the Δ_i was calculated as the difference between AICc of *i*th candidate model minus the AICc of best model. A *relative likelihood* of all models was first calculated as $\exp(-0.5 \cdot \Delta_i)$, and the Akaike weight of

each model was found dividing the relative likelihood of each model with the sum of relative likelihoods of all models. A 95% confidence set of models was determined as the set of models with highest Akaike weight whose accumulative Akaike weight was up to 95% (i.e. excluding all models starting from the first model whose accumulative Akaike weight exceeded 95%). For the presentation of results, the Akaike weights were re-calculated for this 95% confidence set, dividing the relative likelihood of each model by the sum of relative likelihoods of the 95% set of models only. Evidence ratio (ER) was calculated as $\exp(0.5 \cdot \Delta_i)$, and it describes the likelihood that the best model is better than model *i*. Relative importance of the explanatory variables was found by summing the Akaike weights of each model in 95% confidence set that included the respective variable. Furthermore, to compare the expected effects based on the previous knowledge of the ecology of this species (Table 1), all GAMs fitted during multimodel inference were visually assessed by plotting the partial effects of all variables, and assessing their significance. In the total of 31 models, each variable was included in 16 models, and all occasions when the actual effect agreed with the effect in Table 1, were recorded.

Finally, to detect and visualize the non-stationarity in the links between *L. macrurus* and most important explanatory variables, chronological sliding window analysis was used. Linear models were fitted to the 15-year subsets of data, and slopes and *p*-values of the models fitted to these subsets were recorded. The subsets (44 in total) were selected with a sliding window of 15 years, moving stepwise from the start and to the end of time series (i.e. 1959–1973, 1960–1974, ..., 2002–2016).

Results

The multidecadal dynamics of hydroclimate and the main predator (herring SSB) are displayed in Figure 2. While winters have become milder and bottom water temperatures in summer (measured as a mean of 30–50 m depth profile) increased, bottom

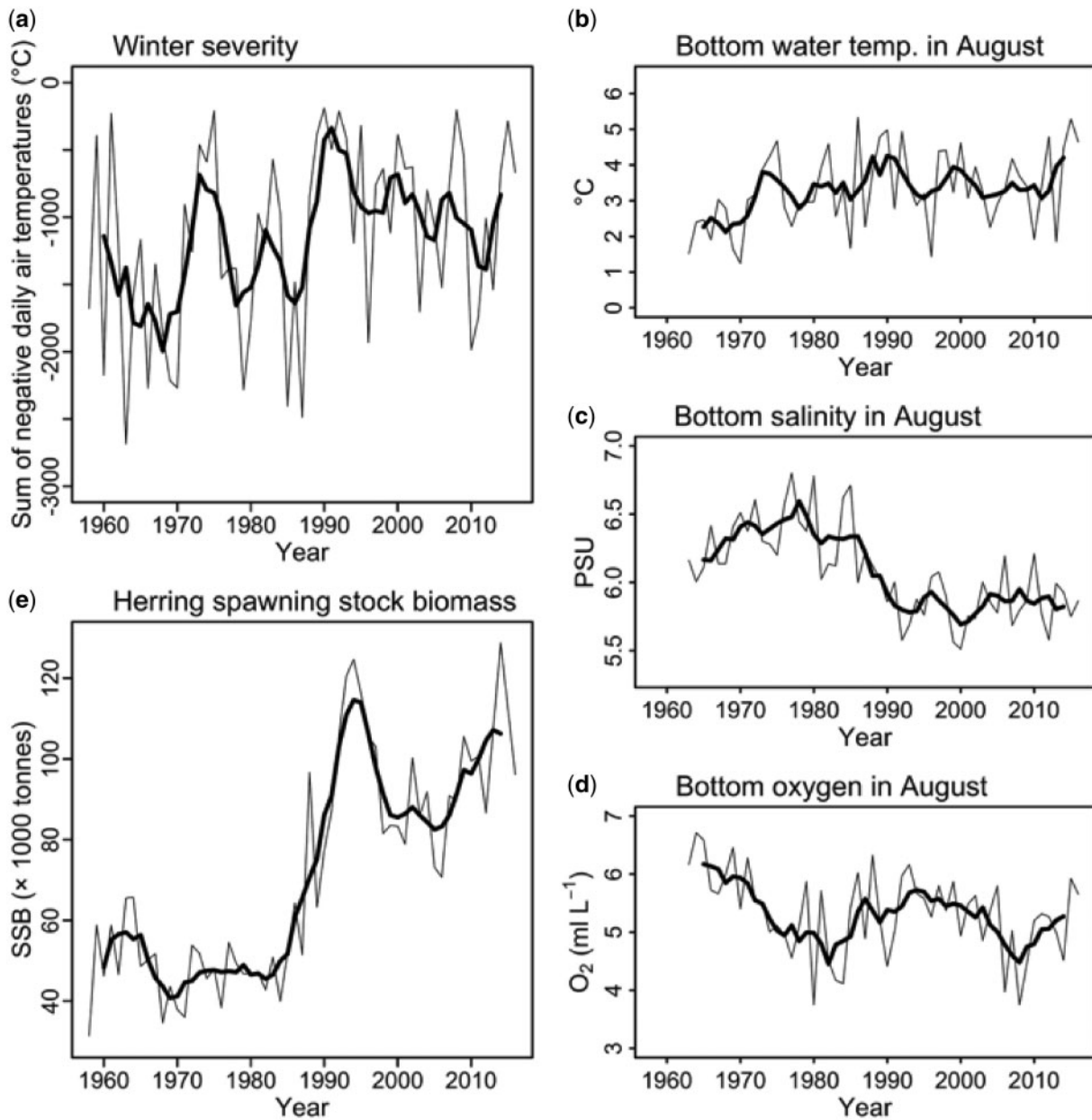


Figure 2. Long-term changes of environmental parameters in the GoR during 1958–2016. For data sources, see Material and methods section. Thin line: annual values; bold line: running 5-year average.

oxygen concentration in summer (variability range ca. 3.5–7 ml L⁻¹ O₂) has decreased over time. Salinity was generally higher until the mid-1980s (PSU 6.5 and higher) and has decreased since then (generally below 6.0). Herring SSB was low until the mid 1980s, and increased afterwards with values during the past three decades often being two times higher than previously (Figure 2).

Total abundances of *L. macrurus*, including all stages, reached up to 10 500 ind m² in spring and up to 1650 ind m² in summer during the period of 1958–2016, with monthly mean values of 153 ± 14 and 403 ± 69 m², respectively. In spring, the abundance was higher in the beginning of the time series until the end of 1980s, after which it suddenly dropped to very low levels for few years (Figure 3a). In summer, the long-term decline in the abundance started nearly a decade earlier than in spring—already in

the 1970s—and the species was absent in summer samples also for a longer period than in spring (Figure 3b). The abundances in spring and summer recovered in the 1990s, although not to the levels comparable to those observed in the 1960s and 1970s, and seem to decline again in the recent most years of time series (after 2010).

Interannual variability (defined in the model by the categorical explanatory variable “year”) was the main source of variability in both spring and summer (Table 2, Figure 3a and b). Noteworthy is also the very clear seasonality in the mean stage of *L. macrurus*: young stages dominated in the beginning of the year, and only adults were left in the community in summer and autumn (Figure 3c), indicating that the species is univoltine in the GoR.

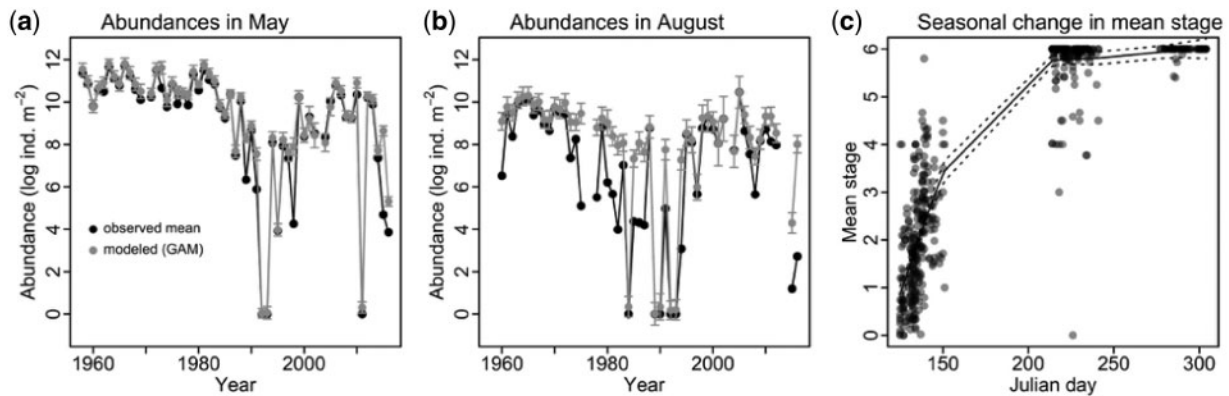


Figure 3. Initial modelling of the abundance (individuals m^{-2} in logarithmic units) of *L. macrurus* in the GoR during 1958–2016: (a) annual mean abundances in spring (black) and the spatially balanced annual values estimated with the model 1 (Table 2, grey); (b) annual mean abundances in summer and the annual values estimated with the model 2 (Table 2); (c) seasonal development of the community maturity (mean stage = 0—all nauplii, mean stage = 6—all adults).

Table 2. Results of the forward selection LM/GAM modeling to that was used to calculate the comparable annual mean abundances of *L. macrurus*.

Model 1: spring
Dependent variable: <i>Limnocalanus macrurus</i> abundance (individuals m^{-2}), explanatory variables: year, sampling depth, Julian day. $n = 299$, family Gamma, link = "log".
Step 1: \sim as.factor (year) ($R^2 = 0.62$, AIC = 6 296)
Step 2: (final model): \sim as.factor (year) + s(sampling depth) ($R^2 = 0.67$, AIC = 4 967)
Model 2: summer
Dependent variable: <i>Limnocalanus macrurus</i> abundance (individuals m^{-2}), explanatory variables: year, sampling depth, Julian day. $n = 275$, family Gamma, link = "log".
Step 1: \sim as.factor (year) ($R^2 = 0.44$, AIC = 1 360)
Step 2 (final model): \sim as.factor (year) + s(sampling depth) ($R^2 = 0.51$, AIC = 4 946.)

Model 1, spring; model 2, summer. Data from 1958 to 2016.

Table 3. Significance of the explanatory variables in best ranking model of the multimodel inference procedure.

Final model: herring SSB + winter severity + bottom water temperature

p -values:
 Herring SSB: 0.00003
 Winter severity: 0.05
 Bottom water temp: 0.02
 AICc: 228

The main environmental parameters linked to the interannual variability of *L. macrurus* in spring were (in the declining order of importance) herring SSB of preceding year, winter severity and bottom water temperature in preceding summer ($R^2 = 0.47$, Table 3). Abundance of *L. macrurus* declined with the herring SSB increasing from 60 to 100 thousand tonnes, but was stable at very low and very high herring SSB values in the beginning and end of the observation period (Figure 4a). The severity of preceding winter and bottom water temperatures of the preceding summer appeared to have negative effect on *L. macrurus* abundance during the mildest winters and at highest water temperatures, respectively (Figure 4b and c). The Figure 4d indicates that there were at least three outliers in the time series, which probably affected the shapes of fitted curves as well as their significance. These outliers belonged to the years 1992, 1993, and 2011, which all were characterized by good sampling coverage (7, 4, and 5 stations, respectively),

implying that these years were indeed characterized by low abundance of *L. macrurus*, and there is no good reason to exclude them. Furthermore, leaving these years out only improved the model "fit" and significance of the individual terms.

The multimodel inference procedure indicated that herring SSB in previous year, severity of preceding winter, and bottom water temperatures in previous summer were the most important predictors to explain the variability of abundance of *L. macrurus*, as their summed Akaike weights exceed 0.80 (Figure 5). The best model had a w_i of 0.404 (Table 4), which must be interpreted as that there is 40.4% chance that a model including herring SSB, severity of preceding winter and bottom water temperatures in previous summer as covariates is truly the best approximating model. However, the model that included also bottom water salinity (Table 4), was not significantly worse based on the ER, since for the best model to clearly outperform others, ER of every other model should be >2 (Everaert et al., 2018).

The close inspection of all 31 models fitted during multimodel inference indicated that the strong and negative correlation between SSB and the *L. macrurus* was the only relation consistent with the expectation (detected in all 16 models that included the SSB). The correlation to the winter air temperature was non-linear and negative (as in Figure 4b) in 50% of the fitted models (8). Although the salinity came often significant (based on p -value <0.05), the expected negative effect was seen in only 1 model. The water temperature followed the same non-linear shape as in Figure 4c in most of the fitted models. Oxygen

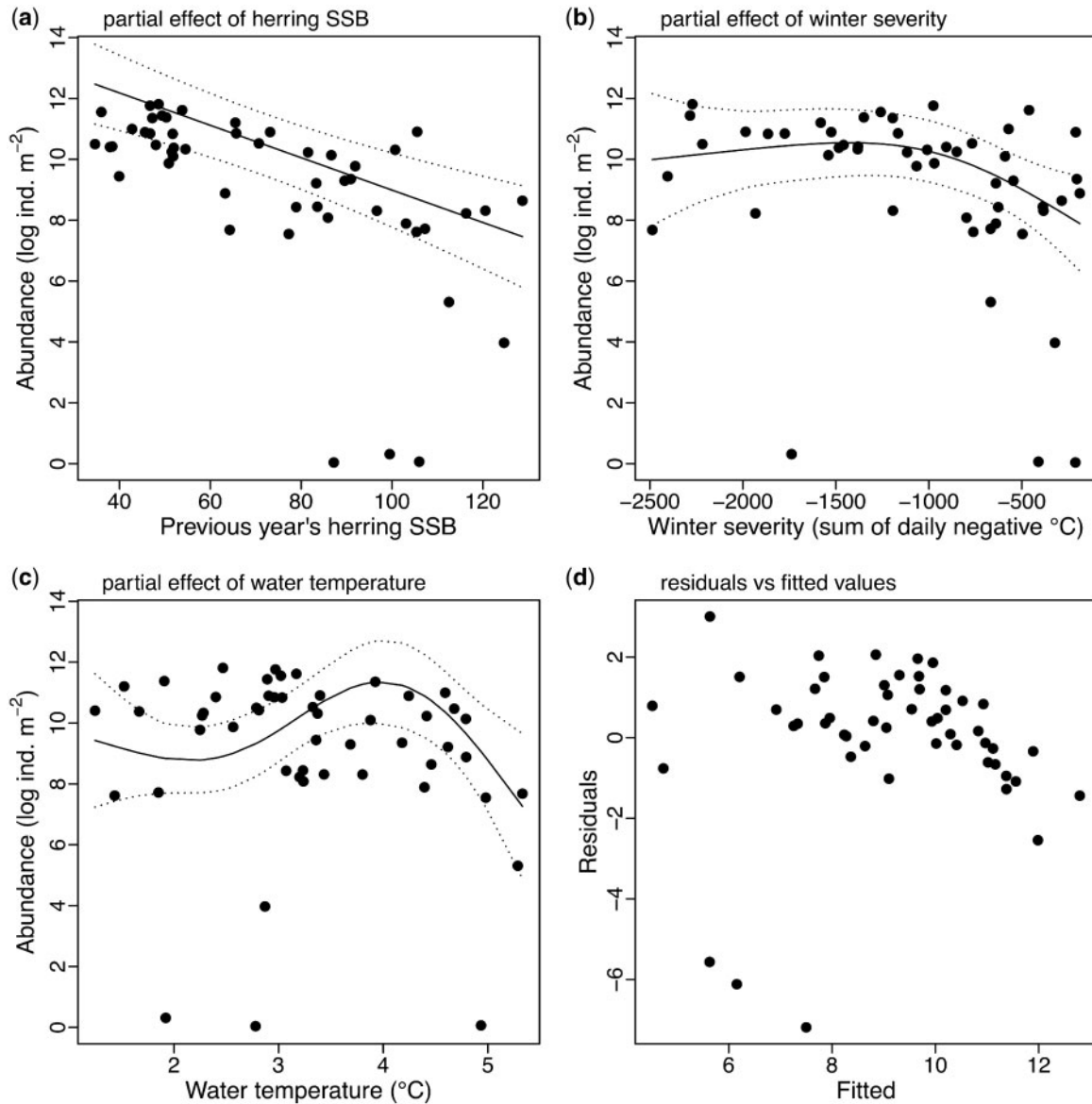


Figure 4. The non-linear smooth terms of the best ranking GAM identified by multimodel inference procedure (herring SSB in previous year, winter severity and bottom water temperature in summer of the previous year) (see Tables 3 and 4). Panel d serves as a diagnostics of model fit, showing the residual distribution along the fitted values.

content had no detectable correlation to the *L. macrurus* abundance in any of the models.

The chronological sliding window analysis (Figure 6) depicts non-stationarity of the relationship between the herring SSB and *L. macrurus* abundance (Figure 6a): a weak positive link in the beginning of the time-series, when herring SSB was low and *L. macrurus* abundance high (until the mid-1970s), followed by negative and often also stronger effect during the period of the rapid increase in herring SSB (Figure 6a). The effect of winter severity was not very strong in any of the sliding window steps, although the slopes became more negative during the mildest winters in the record (between the mid-1980s until early 2000). During colder winters, until the mid-1980s and since the mid-2000s, the effect of winter severity was weak and often positive (Figure 6b). The effect of

bottom water temperature in preceding summer became more negative during periods of generally warmer bottom water.

Discussion

This study of *L. macrurus*, investigating the interannual dynamics of the species and its links to the key explanatory variables—hydroclimate and predation—in over six decades of continuous data, is the most comprehensive analysis of this Arctic species to date. Despite several related interests and scientific efforts (Vuorinen *et al.*, 1998; Kane *et al.*, 2004; Mäkinen *et al.*, 2017), the data compiled for this study covered longer time-scale than any study performed so far and thereby not only enables to describe the long-term dynamics of the species, but also better to understand its ecology under different ecosystem configurations

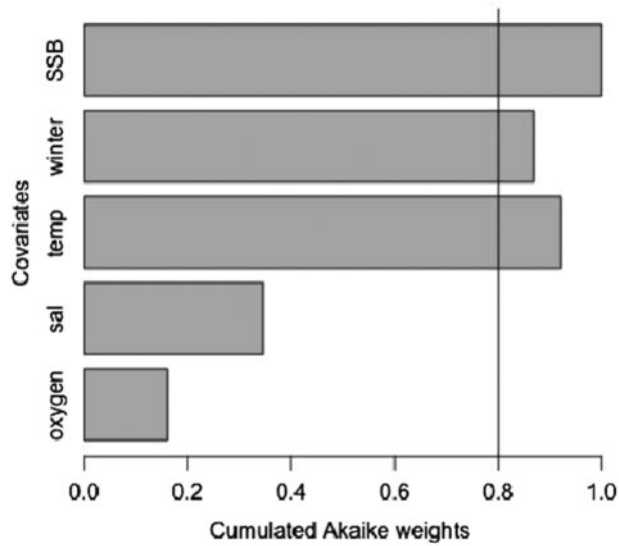


Figure 5. Relative importance of herring spawning stock biomass (“SSB”) in previous year, winter severity (“winter”), and the bottom water temperature (“temp”), salinity (“sal”), and oxygen (“ox”) in previous summer on the annual abundance of *L. macrurus* in the GoR. A variable that shows up in models with large weights will receive a high summed Akaike weight and is considered important. Vertical line is drawn at 0.8, which is used as a cut-off to differentiate between important and less important variables.

Table 4. The 95% of confidence set of best-ranked models in the multimodel inference (the models whose summed Akaike weight, acc *wi* is <0.95 of all models).

Candidate model	AICc	Δ_i	<i>wi</i>	acc <i>wi</i>	ER
SSB + winter severity + temp	228.57	0.000	0.404	0.404	
SSB + winter severity + temp + sal	229.33	0.761	0.276	0.680	1.46
SSB + winter severity + temp + ox	231.48	2.912	0.094	0.774	4.29
SSB + temp	232.37	3.803	0.060	0.834	6.70
SSB + winter severity + temp + sal + ox	232.72	4.154	0.051	0.885	7.98
SSB + winter severity	233.05	4.479	0.043	0.928	9.39
SSB	233.41	4.840	0.036	0.964	11.24
SSB + temp + sal	234.67	6.099	0.019	0.983	21.11
SSB + temp + ox	234.93	6.358	0.017	1.000	24.03

Variables assessed were herring spawning stock biomass (SSB) in previous year, winter severity, bottom water temperature (temp), salinity (sal), and oxygen (ox) in previous summer. The metrics used to quantify the relative strength of each model are based on the difference between the AICc for small datasets of the best models and AICc of the model *i* (Δ_i). The ER quantifies how likely it is that the best mode is better than model *i*.

and different combinations of drivers of change. Furthermore, and in contrast to all previous studies, we explicitly sought for the evidence of the existence of non-linear and non-stationary links in the interannual variability of *L. macrurus*, and thereby opened new challenges towards interpretation of the partly contrasting results compared to previous studies.

The observed long-term trend in *L. macrurus* abundance should be interpreted in the context of the known ecosystem regime shifts. The major, and mostly climate driven, regime shift in

the Baltic Sea took place in the late 1980s and early 1990s, when the abundance and biomass levels of several key taxa changed (Möllmann *et al.*, 2009; Arula *et al.*, 2014, and references therein). While *L. macrurus* abundance exhibited historical lows during that period, the abundance levels before and after the regime shift were broadly similar, in contrast to other key players in pelagic ecosystem (e.g. *Sprattus sprattus*, *Acartia* spp., *Pseudocalanus acuspes*; Möllmann *et al.*, 2009). However, functioning of the pelagic food web might have changed, due to the likely trophic decoupling of zooplankton–herring (Bernreuther *et al.*, 2018). Also, and importantly, the lowest population sizes were observed during the highest herring SSB level associated with the warmest hydro-climatic conditions in the record, i.e. under the conditions of the strongest pressures.

The seasonal pattern of mean stage implies that *L. macrurus* is univoltine in the GoR and its main reproduction period is winter and early spring. This finding agrees with some previous studies from the lakes and the Baltic Sea (Roff and Carter, 1972; Doubek and Lehman, 2011; Dahlgren *et al.*, 2012), but disagrees with the studies that reported a continuous reproduction of *L. macrurus* in the Baltic Sea (e.g. Kankaala, 1987). As early life stages were dominating in *L. macrurus* community in spring, our findings on the almost linear negative relationship between herring SSB and *L. macrurus* abundance, negative impact of mild winters on *L. macrurus* abundance above the sum of negative daily air temperature of -1000°C , and inhibition of *L. macrurus* abundance by bottom water temperature in previous summer above 4°C , may help to identify the key processes responsible for formation of recruitment of the species. Thus, our results suggest that conditions related to both parent individuals during previous year (survival due to predation by herring and ambient water temperature in summer affecting the condition of adults) and the reproduction process (temperature conditions in winter; as *L. macrurus* reproduces during winter in the Baltic Sea) are the factors jointly affecting *L. macrurus* abundance in spring.

As became evident from the analysis, neither salinity nor oxygen concentration likely affected *L. macrurus* abundance in the GoR. The basin lacks a halocline and due to its shallowness, hydrothermal mixing ensures good oxygenation of even near-bottom water layers. And even if the deepest water layers are oxygen depleted, the species still finds suitable thermal habitat. However, large oxygen-depleted zones in other areas of the Baltic Sea with haloclines may significantly affect the standing stock of the species, as has been observed for other large-bodied copepod *P. acuspes* (Renz and Hirche, 2004). Although the immigration history of *L. macrurus* to the Baltic Sea is unknown, it has been documented that some glacial relict species of marine origin in the Baltic Sea have a wide salinity tolerance as their immigration includes first adaptation to freshwater conditions (immigration via rivers) and then back to the marine conditions in the Baltic Sea (Segerstråle, 1966). Thus, they are primarily under thermal control and some of them have Baltic-wide distribution at contrasting salinity levels, while only a very few of them have broken the thermal barrier and permanently colonized shallow coastal areas.

The fact that the long-term decline in summer abundances started nearly a decade earlier than decline in spring abundances, may reflect a sampling artefact, as the adult *L. macrurus* may be concentrated in deeper near-bottom layer not representatively sampled during summer. The near-bottom copepod communities have rarely been studied despite numerous reports of potentially

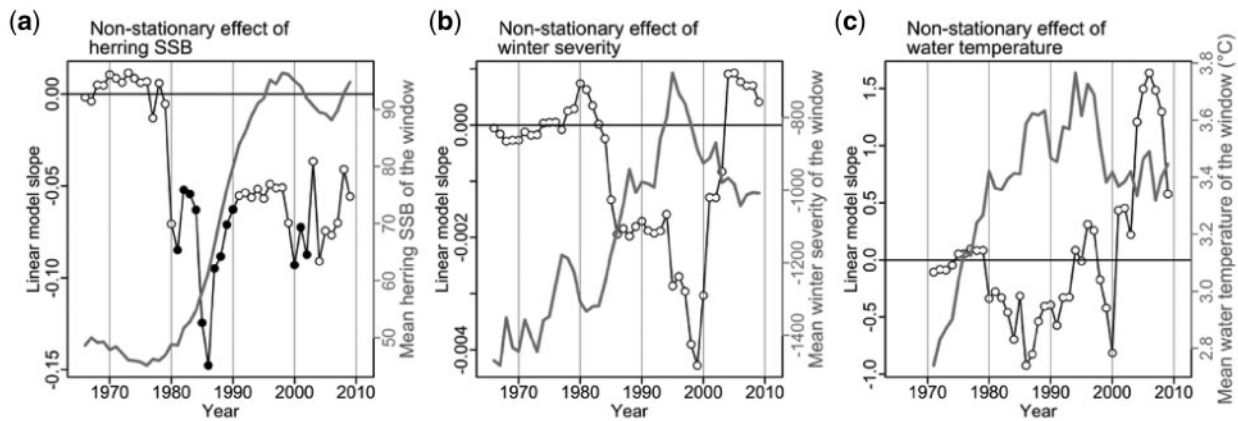


Figure 6. Results of the chronological sliding window analysis: time trends in linear slopes of *L. macrurus* abundance ($\ln(\text{ind m}^{-2})$) with herring SSB (1000 tonnes) in previous year (a), winter severity (mean air temperature during November–March) (b), and the bottom water temperature in summer of the previous year (c). Filled points denote values where the slope was significant at $p < 0.05$. Grey line is the mean values of the respective explanatory variable in each 15-year subset (1958–1972, 1959–1973, . . . , 2002–2016). On the x-axis is the middle year of each 15-year subsets.

very high zooplankton concentrations (exceeding 50 000 ind per m^3), probably due to methodological constraints, and neglecting this community may cause severe underestimates of the stock of pelagic zooplankton (Hirche *et al.*, 2016). While the sampling design and protocol has remained unchanged over the years, we cannot retrospectively evaluate whether or not it has been always precisely followed historically. The uncertainty in historical information and data is important and has been discussed in multiple occasions (Eero *et al.*, 2007).

The Baltic Sea is a semi-enclosed basin, and therefore influenced by multiple human-induced drivers of change. Amongst those, eutrophication and pollution have been and still are important stressors affecting the structure and dynamics of the Baltic Sea ecosystems since the late 1950s to early 1960s (Murray *et al.*, 2019). GoR ecosystem is currently one of the most eutrophic areas in the Baltic Sea (HELCOM, 2018). In addition, some areas of the Baltic Sea stand out negatively for very high levels of acidification compared to other coastal regions worldwide, however, several populations within the Baltic Sea have evolved to locally adapted populations that show enhanced resilience towards acidification (Reusch *et al.*, 2018, and references therein). These factors were not taken into account in this work, due to lack of suitable long-term time-series, and may, in addition to those identified in our work, additionally affect *L. macrurus*.

The interpretation of the chronological sliding window can easily be biased by the researcher's expectation. From Figure 6, it seems that the negative effect of herring SSB on the abundance of *L. macrurus* appeared only when the SSB itself was drastically increasing—implying a non-linear effect, depending on the level of the driver. As the shift in herring SSB also coincided with warming winters and elevated water temperature in summer, the low period of *L. macrurus* could have also been caused by either of those thermal variables or in combination with herring SSB. Since herring SSB remains very high to date, but winter air and bottom water temperatures have decreased during the last two decades, the temperature effect as a primary driver behind the recovery of *L. macrurus* from the early 2000s seems more plausible, essentially due to the very strong positive effect of summer water

temperature. However, there also remains a possibility that something changed in the coupling between predators and their prey in the meantime, as found in the pelagic realm for the central Baltic Sea (Bernreuther *et al.*, 2018). The possible trophic decoupling (i.e. low utilization of prey production relative to the predator abundance) might have occurred due to the drastic reduction in herring individual size over time (ICES, 2018) or due to the dietary shifts of the herring population. Specifically, smaller herring consumes smaller-sized prey (Ojaveer *et al.*, 2017), which might have resulted in reduced predation pressure on *L. macrurus*. It is also possible that spatial distributions of *L. macrurus* and herring have changed, leading to the reduced spatial overlap between the species. However, while the correlations observed inspire several alternative scenarios as explanations, some involving non-linear effects, others non-stationarity of the links, it does not provide solid evidence for any of these suggestions.

It is generally accepted that biota (incl. glacial relict species) in the Baltic Sea is primarily under the abiotic stress (as most organisms are living at the edge of their ecophysiological tolerance limits and distribution area), and biotic interactions play a less important role in structuring biotic communities. While our findings undoubtedly indicate that *L. macrurus* is under temperature stress in the study area, results from two different modelling approaches (multimodel inference method and chronological sliding window analysis) both point to the fact that herring SSB in preceding year is actually the most important variable to explain the multiannual abundance dynamics of *L. macrurus*. In other words, based on our study we could conclude that trophic interactions (i.e. predation) are more important than abiotic conditions to explain the long-term annual-scale abundance dynamics of *L. macrurus* even at the edge of its distribution area that is also characterized by a high density of planktivorous fish. However, before making any far-reaching conclusions about the functioning of the pelagic food web and the relative role of the main planktivorous fish—herring—in the relatively simple and species-poor ecosystem, causality of the identified key drivers of change (Sugihara *et al.*, 2012; Ye *et al.*, 2015) in shaping *L. macrurus* abundance needs to be investigated.

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