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

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13 **Abstract**

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

31 **Key words:** Annual abundance, Gulf of Riga, hydro-climatic conditions, herring spawner
32 biomass, non-linear and non-stationary relationships.

33 **Introduction**

34 The response of marine species and populations to external drivers of change can be either linear
35 or non-linear. While linear systems behave additively (i.e. they are equal to the sum of their
36 parts) and can therefore be disassembled, nonlinear systems are non-additive (i.e. antagonistic or
37 synergistic effects prevail) and thus cannot be studied through disaggregation (Klein *et al.*,
38 2016). Furthermore, the relationship (i.e. linear or non-linear) between the driver(s) and the
39 affected biota can also be non-stationary, i.e. change over time. For example, non-stationary
40 links have been documented between recruitment, spawning stock biomass and water
41 temperature for multiple fish stocks (e.g. Ottersen *et al.*, 2013). Only long-term time-series,
42 which enable to capture a wide range of variability of drivers and encompass different
43 combinations of their relative roles, allow to learn both the type of the effect on the species or
44 populations of interest, as well as the potential dynamics over time.

45 One of the ecologically relevant but relatively poorly studied species in many marine and
46 freshwater environments of the northern hemisphere is the calanoid copepod *Limnocalanus*
47 *macrurus*. *L. macrurus* is a large lipid-rich copepod with high content of polyunsaturated fatty
48 acids, serving thereby as a high-quality prey for fish (Hiltunen *et al.*, 2014). Bearing in mind the
49 absolute key role of the species in aquatic pelagic ecosystems, mechanistic understanding of its
50 population ecology and the primary drivers of its abundance in different aquatic ecosystems from
51 a long-term perspective is imperative. As a cold stenotherm species (e.g. van Hove *et al.* 2001;
52 Apollonio and Saros, 2013; Jackson *et al.*, 2013; Drits *et al.*, 2016)), the distribution of *L.*
53 *macrurus* is usually restricted to deeper colder water masses (Carter and Goudie, 1986), with
54 ability to penetrate the seasonal thermocline to the upper water layers at night when stratification
55 is weak (Wells, 1960). The species is characterized by continuous and plastic feeding (Warren,
56 1985; Barbiero *et al.*, 2009; Dahlgren *et al.*, 2012; Jackson *et al.*, 2013), thereby efficiently
57 exploiting the available food resource and transferring the energy from lower trophic levels to
58 fish.

59 *L. macrurus* is considered as a glacial relict in the Baltic Sea (Segerstråle, 1966), being the
60 largest widely distributed copepod species (up to 3 mm in length) in its northern part: Gulf of
61 Bothnia, Gulf of Finland, and Gulf of Riga. All these basins are characterized by relatively harsh
62 climate conditions in winter and relatively low salinity, hosting therefore several glacial relicts
63 (Järvekülg, 1973). However, the ecology of *L. macrurus* in the Baltic Sea is poorly documented.
64 Based on the long-term records, the species was very abundant in the Gulf of Riga before the
65 1980s but nearly disappeared in the late 1980s, allegedly due to mild winters which resulted in
66 warmer water during the winter/spring period (Kornilovs *et al.*, 2004). In addition, abundance of
67 the species has been suggested to change in relation to variations in salinity in Bothnian Sea
68 (Rajasilta *et al.*, 2014), where it may dominate in the copepod community most of the year,
69 constituting often more than 50% of the biomass (Dahlgren *et al.*, 2010). *L. macrurus* is the
70 highly preferred prey item of the most abundant pelagic fish species – herring (*Clupea harengus*
71 *membras*) – both in the Gulf of Bothnia (Flinkman *et al.*, 1992) and Gulf of Riga (Livdāne *et al.*,
72 2016), while other abundant planktivorous fish consume *L. macrurus* only marginally (Ojaveer
73 *et al.*, 1997).

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

86 Table 1. Expected effects of the studied environmental drivers on the abundance of
87 *Limnocalanus macrurus* in the Gulf of Riga.

Variable	Expected effect	References
Spawning stock biomass of the predator	Strong negative	Kane <i>et al.</i> , 2004; Barbiero <i>et al.</i> , 2009;
Winter air temperature	Strong negative	Ojaveer <i>et al.</i> , 1998
Summer water temperature	Weak negative	Kornilovs <i>et al.</i> , 2004
Salinity	Weak negative	Rajasilta <i>et al.</i> , 2014; Segerstråle, 1966
Oxygen content	Weak positive	Roff, 1973; Kane <i>et al.</i> , 2004

88

89 **Material and Methods**

90 *The study area*

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

99 *Data*

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

107 transformed in this analysis to individuals per m² by multiplying the densities with depth of
108 entire profile.

109 List of environmental variables tested by the statistical models was limited to these that were
110 previously suggested to drive *L. macrurus* abundance dynamics either in the Baltic Sea or
111 elsewhere (Kornilovs *et al.*, 1992; Sidrevics *et al.*, 1993; Kane *et al.*, 2004) and for which we had
112 reliable long-term data available: i) winter severity (measured as a sum of negative daily mean
113 air temperatures from November to March; data from Estonian Weather Service, 1958–2016), ii)
114 temperature, iii) salinity and iv) oxygen content of the bottom water (data from BIOR, 1963–
115 2016, average value measured from the depth range of 30–50 m in August), and v) spawning
116 stock biomass of autumn and spring herring together (data from Ojaveer (2003), Ojaveer *et al.*
117 (2004), and ICES (2018), 1958–2016).

118 *Data analysis*

119 Time series of comparable annual mean abundances of *L. macrurus*, accounting for all sampling
120 artefacts (interannual differences in the number of samples, time of sampling, or spatial
121 distribution of data) were calculated as marginal means of categorical variable “year” with with
122 generalised additive model (GAM), where year was combined with the sampling depth and
123 julian day, following to Carstensen *et al.* (2006). The best model was determined through the
124 forward selection, and annual means were estimated with the final model setting other significant
125 terms at their all time mean values. The long-term sampling was more consistent in spring (May)
126 and summer (August) than in autumn (October) (Figure 1b), therefore autumn data were left out
127 from the current study, apart from one visualization of seasonal dynamics in community
128 maturity. Since the population structure was very different between the months (mostly juveniles
129 in spring, and adults in summer), time series of annual abundances were estimated for spring and
130 summer independently. The maturity of population was visualized through a variable “mean
131 stage”, calculated as a weighted mean of the sequence from 0 to 6, corresponding to nauplii,
132 copepodites I–V, and adults. Each value was weighted by the abundance of respective stage in
133 the sample, resulting in a single number measure of the population age composition. Initial
134 inspection of results indicated that *L. macrurus* is univoltine in the GoR, therefore, generally

135 higher abundances of younger stages in spring was considered most reliable indicator of the
136 long-term dynamics of this species.

137 To quantify the relative importance of selected environmental variables, and the reliability of the
138 model results, we used the multimodel inference method (Burnham and Anderson, 1998),
139 following the same procedure as described in Everaert *et al.* (2018). In this procedure, all
140 possible models from single predictor to a full model of all five variables were fitted, using again
141 GAM model, resulting in 31 models in total. For each model, an Akaike Information Criterion
142 for small sample sizes (AICc) was found. Models were ranked in increasing order of AICc, and
143 the Δ_i was calculated as the difference between AICc of *i*th candidate model minus the AICc of
144 best model. A *relative likelihood* of all models was first calculated as $\exp(-0.5*\Delta_i)$, and the
145 Akaike weight of each model was found dividing the relative likelihood of each model with the
146 sum of relative likelihoods of all models. A 95% confidence set of models was determined as the
147 set of models with highest Akaike weight whose accumulative Akaike weight was up to 95%
148 (i.e. excluding all models starting from the first model whose accumulative Akaike weight
149 exceeded 95%). For the presentation of results, the Akaike weights were re-calculated for this
150 95% confidence set, dividing the relative likelihood of each model by the sum of relative
151 likelihoods of the 95% set of models only. Evidence ratio (ER) was calculated as $\exp(0.5*\Delta_i)$,
152 and it describes the likelihood that the best model is better than model *i*. Relative importance of
153 the explanatory variables was found by summing the Akaike weights of each model in 95%
154 confidence set that included the respective variable. Furthermore, to compare the expected
155 effects based on the previous knowledge of the ecology of this species (Table 1), all GAMs fitted
156 during multimodel inference were visually assessed by plotting the partial effects of all variables,
157 and assessing their significance. In the total of 31 models, each variable was included in 16
158 models, and all occasions when the actual effect agreed with the effect in Table 1, were recorded.

159 Finally, to detect and visualize the non-stationarity in the links between *L. macrurus* and most
160 important explanatory variables, chronological sliding window analysis was used. Linear models
161 were fitted to the 15-year subsets of data, and slopes and p-values of the models fitted to these
162 subsets were recorded. The subsets (44 in total) were selected with a sliding window of 15 years,
163 moving stepwise from the start and to the end of time series (i.e. 1959–1973, 1960–1974, ...,
164 2002–2016).

165 **Results**

166 The multi-decadal dynamics of hydroclimate and the main predator (herring SSB) are displayed
167 in Figure 2. While winters have become milder and bottom water temperatures in summer
168 (measured as a mean of 30–50 m depth profile) increased, bottom oxygen concentration in
169 summer (variability range ca. 3.5–7 ml L⁻¹ O₂) has decreased over time. Salinity was generally
170 higher until the mid-1980s (PSU 6.5 and higher) and has decreased since then (generally below
171 6.0). Herring SSB was low until the mid 1980s, and increased afterwards with values during the
172 past three decades often being two times higher than previously (Figure 2).

173 Total abundances of *L. macrurus*, including all stages, reached up to 10 500 ind m² in spring and
174 up to 1650 ind m² in summer during the period of 1958–2016, with monthly mean values of 153
175 ± 14 and 403 ± 69 m², respectively. In spring, the abundance was higher in the beginning of the
176 time series until the end of 1980s, after which it suddenly dropped to very low levels for few
177 years (Figure 3a). In summer, the long-term decline in the abundance started nearly a decade
178 earlier than in spring – already in the 1970s – and the species was absent in summer samples also
179 for a longer period than in spring (Figure 3b). The abundances in spring and summer recovered
180 in the 1990s, although not to the levels comparable with those observed in the 1960s and 1970s,
181 and seem to decline again in the recent most years of time series (after 2010).

182 Interannual variability (defined in the model by the categorical explanatory variable “year”) was
183 the main source of variability both in spring and summer (Table 2, Figure 3a, b). Noteworthy is
184 also the very clear seasonality in the mean stage of *L. macrurus*: young stages dominated in the
185 beginning of the year, and only adults were left in the community in summer and autumn (Figure
186 3c), indicating that the species is univoltine in the GoR.

187 The main environmental parameters linked to the interannual variability of *L. macrurus* in spring
188 were (in the declining order of importance) herring SSB of preceding year, winter severity and
189 bottom water temperature in preceding summer ($R^2 = 0.47$, Table 3). Abundance of *L. macrurus*
190 declined with the herring SSB increasing from 60 to 100 thousand tonnes, but was stable at very
191 low and very high herring SSB values in the beginning and end of the observation period (Figure
192 4a). The severity of preceding winter and bottom water temperatures of the preceding summer

193 appeared to have negative effect on *L. macrurus* abundance during the mildest winters and at
194 highest water temperatures, respectively (Figure 4b, c). The Figure 4d indicates that there were at
195 least three outliers in the time series, which probably affected the shapes of fitted curves as well
196 as their significance. These outliers belonged to the years 1992, 1993, and 2011, which all were
197 characterized by good sampling coverage (7, 4, and 5 stations, respectively), implying that these
198 years were indeed characterised by low abundance of *L. macrurus*, and there is no good reason to
199 exclude them. Furthermore, leaving these years out only improved the model “fit” and
200 significance of the individual terms.

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

210 The close inspection of all 31 models fitted during multimodel inference indicated that the strong
211 and negative correlation between SSB and the *L. macrurus* was the only relation consistent with
212 the expectation (detected in all 16 models that included the SSB). The correlation to the winter
213 air temperature was non-linear and negative (as in Figure 4b) in 50% of the fitted models (8).
214 Although the salinity came often significant (based on p -value < 0.05), the expected negative
215 effect was seen in only 1 model. The water temperature followed the same non-linear shape as in
216 Figure 4c in most of the fitted models. Oxygen content had no detectable correlation to the *L.*
217 *macrurus* abundance in any of the models.

218 The chronological sliding window analysis (Figure 6) depicts non-stationarity of the relationship
219 between the herring SSB and *L. macrurus* abundance (Figure 6a): a weak positive link in the
220 beginning of the time-series, when herring SSB was low and *L. macrurus* abundance high (until
221 the mid-1970s), followed by negative and often also stronger effect during the period of the rapid

222 increase in herring SSB (Figure 6a). The effect of winter severity was not very strong in any of
 223 the sliding window steps, although the slopes became more negative during the mildest winters
 224 in the record (between the mid-1980s until early 2000). During colder winters, until the mid-
 225 1980s and since the mid 2000s, the effect of winter severity was weak and often positive (Figure
 226 6b). The effect of bottom water temperature in preceding summer became more negative during
 227 periods of generally warmer bottom water.

228 **Table 2.** Results of the forward selection LM/GAM modeling to that was used to calculate the
 229 comparable annual mean abundances of *Limnocalanus macrurus*. Model 1: spring; model 2:
 230 summer. Data from 1958–2016.

<p>Model 1: Spring</p> <p>Dependent variable: <i>Limnocalanus macrurus</i> abundance (individuals m⁻²), explanatory variables: year, sampling depth, julian day. n = 299, family Gamma, link = “log”.</p> <p>Step 1: ~as.factor (year) (R² = 0.62, AIC = 6296)</p> <p>Step 2: (final model): ~as.factor (year) + s(sampling depth) (R² = 0.67, AIC = 4967)</p>
<p>Model 2: Summer</p> <p>Dependent variable: <i>Limnocalanus macrurus</i> abundance (individuals m⁻²), explanatory variables: year, sampling depth, julian day. n = 275, family Gamma, link = “log”.</p> <p>Step1: ~as.factor (year) (R² = 0.44, AIC = 1360)</p> <p>Step 2 (final model): ~as.factor (year) + s(sampling depth) (R² = 0.51, AIC = 4946.)</p>

231

232 **Table 3.** Significance of the explanatory variables in best ranking model of the multimodel
 233 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

234

235 **Table 4.** The 95% of confidence set of best-ranked models in the multimodel inference (the
236 models whose summed Akaike weight, $acc\ wi$ is less than 0.95 of all models). Variables assessed
237 were herring spawning stock biomass (SSB) in previous year, winter severity, bottom water
238 temperature (temp), salinity (sal), and oxygen (ox) in previous summer. The metrics used to
239 quantify the relative strength of each model are based on the difference between the Akaike
240 Information Criterion for small datasets (AICc) of the best models and AICc of the model I (Δi).
241 The evidence ratio (ER) quantifies how likely it is that the best mode is better than model i .

Candidate model	AICc	Δi	w_i	$acc\ w_i$	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

242

243 **Discussion**

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

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

255 The observed long-term trend in *L. macrurus* abundance should be interpreted in the context of
256 the known ecosystem regime shifts. The major, and mostly climate driven, regime shift in the
257 Baltic Sea took place in the late 1980s and early 1990s, when the abundance and biomass levels
258 of several key taxa changed (Möllmann *et al.*, 2009; Arula *et al.*, 2014, and references therein).
259 While *L. macrurus* abundance exhibited historical lows during that period, the abundance levels
260 before and after the regime shift were broadly similar, in contrast to other key players in pelagic
261 ecosystem (e.g. *Sprattus sprattus*, *Acartia* spp., *Pseudocalanus acuspes*; Möllmann *et al.*, 2009).
262 However, functioning of the pelagic food web might have changed, due to the likely trophic
263 decoupling of zooplankton-herring (Bernreuther *et al.*, 2018). Also, and importantly, the lowest
264 population sizes were observed during the highest herring SSB level associated with the warmest
265 hydro-climatic conditions in the record, i.e., under the conditions of the strongest pressures.

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

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

294 The fact that the long-term decline in summer abundances started nearly a decade earlier than
295 decline in spring abundances, may reflect a sampling artifact, as the adult *L. macrurus* may be
296 concentrated in deeper near-bottom layer not representatively sampled during summer. The near-
297 bottom copepod communities have rarely been studied despite numerous reports of potentially
298 very high zooplankton concentrations (exceeding 50 000 ind per m³), probably due to
299 methodological constraints, and neglecting this community may cause severe underestimates of
300 the stock of pelagic zooplankton (Hirche *et al.*, 2018). While the sampling design and protocol
301 has remained unchanged over the years, we cannot retrospectively evaluate whether or not it has
302 been always precisely followed historically. The uncertainty in historical information and data is
303 important and has been discussed in multiple occasions (e.g. Eero *et al.*, 2007).

304 The Baltic Sea is a semi-enclosed basin, and therefore influenced by multiple human-induced
305 drivers of change. Amongst those, eutrophication and pollution have been and still are important
306 stressors affecting the structure and dynamics of the Baltic Sea ecosystems since the late 1950s
307 to early 1960s (e.g. Murray *et al.*, 2019). Gulf of Riga ecosystem is currently one of the most
308 eutrophic areas in the Baltic Sea (HELCOM, 2018). In addition, some areas of the Baltic Sea
309 stand out negatively for very high levels of acidification compared to other coastal regions
310 worldwide, however, several populations within the Baltic Sea have evolved to locally adapted

311 populations that show enhanced resilience toward acidification (Reusch *et al.*, 2018, and
312 references therein). These factors were not taken into account in the current work, due to lack of
313 suitable long-term time-series, and may, in addition to those indentified in our work, additionally
314 affect *L. macrurus*.

315 The interpretation of the chronological sliding window can easily be biased by the researcher's
316 expectation. From Figure 6, it seems that the negative effect of herring SSB on the abundance of
317 *L. macrurus* appeared only when the SSB itself was drastically increasing – implying a non-
318 linear effect, depending on the level of the driver. As the shift in herring SSB also coincided with
319 warming winters and elevated water temperature in summer, the low period of *L. macrurus* could
320 have also been caused by either of those thermal variables or in combination with herring SSB.
321 Since herring SSB remains very high to date, but winter air and bottom water temperatures have
322 decreased during the last two decades, the temperature effect as a primary driver behind the
323 recovery of *L. macrurus* from the early 2000s seems more plausible, essentially due to the very
324 strong positive effect of summer water temperature. However, there also remains a possibility
325 that something changed in the coupling between predators and their prey in the meantime, as
326 found in the pelagic realm for the central Baltic Sea (Bernreuther *et al.*, 2018). The possible
327 trophic decoupling (i.e. low utilization of prey production relative to the predator abundance)
328 might have occurred due to the drastic reduction in herring individual size over time (e.g. ICES,
329 2018) or due to to the dietary shifts of the herring population. Specifically, smaller herring
330 consumes smaller-sized prey (Ojaveer *et al.*, 2017), which might have resulted in reduced
331 predation pressure on *L. macrurus*. It is also possible that spatial distributions of *L. macrurus* and
332 herring have changed, leading to the reduced spatial overlap between the species. However,
333 while the correlations observed inspire several alternative scenarios as explanations, some
334 involving non-linear effects, others non-stationarity of the links, it does not provide solid
335 evidence for any of these suggestions.

336 It is generally accepted that biota (incl. glacial relict species) in the Baltic Sea is primarily under
337 the abiotic stress (as most organisms are living at the edge of their ecophysiological tolerance
338 limits and distribution area), and biotic interactions play a less important role in structuring biotic
339 communities. While our findings undoubtedly indicate that *L. macrurus* is under temperature
340 stress in the study area, results from two different modeling approaches (multimodel inference

341 method and chronological sliding window analysis) both point to the fact that herring SSB in
342 preceding year is actually the most important variable to explain the multiannual abundance
343 dynamics of *L. macrurus*. In other words, based on our study we could conclude that trophic
344 interactions (i.e. predation) are more important than abiotic conditions to explain the long-term
345 annual-scale abundance dynamics of *L. macrurus* even at the edge of its distribution area that is
346 also characterised by a high density of planktivorous fish. However, before making any far-
347 reaching conclusions about the functioning of the pelagic food web and the relative role of the
348 main planktivorous fish – herring – in the relatively simple and species-poor ecosystem,
349 causality of the identified key drivers of change (Sugihara *et al.*, 2012; Ye *et al.*, 2015) in
350 shaping *L. macrurus* abundance needs to be investigated.

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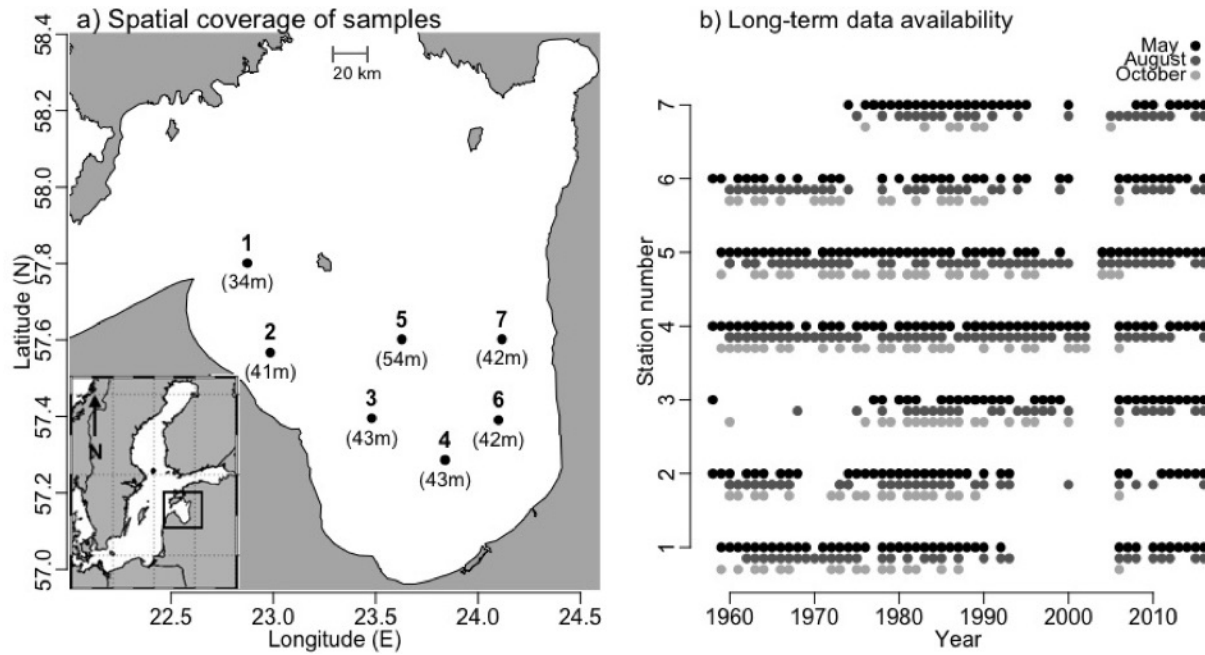
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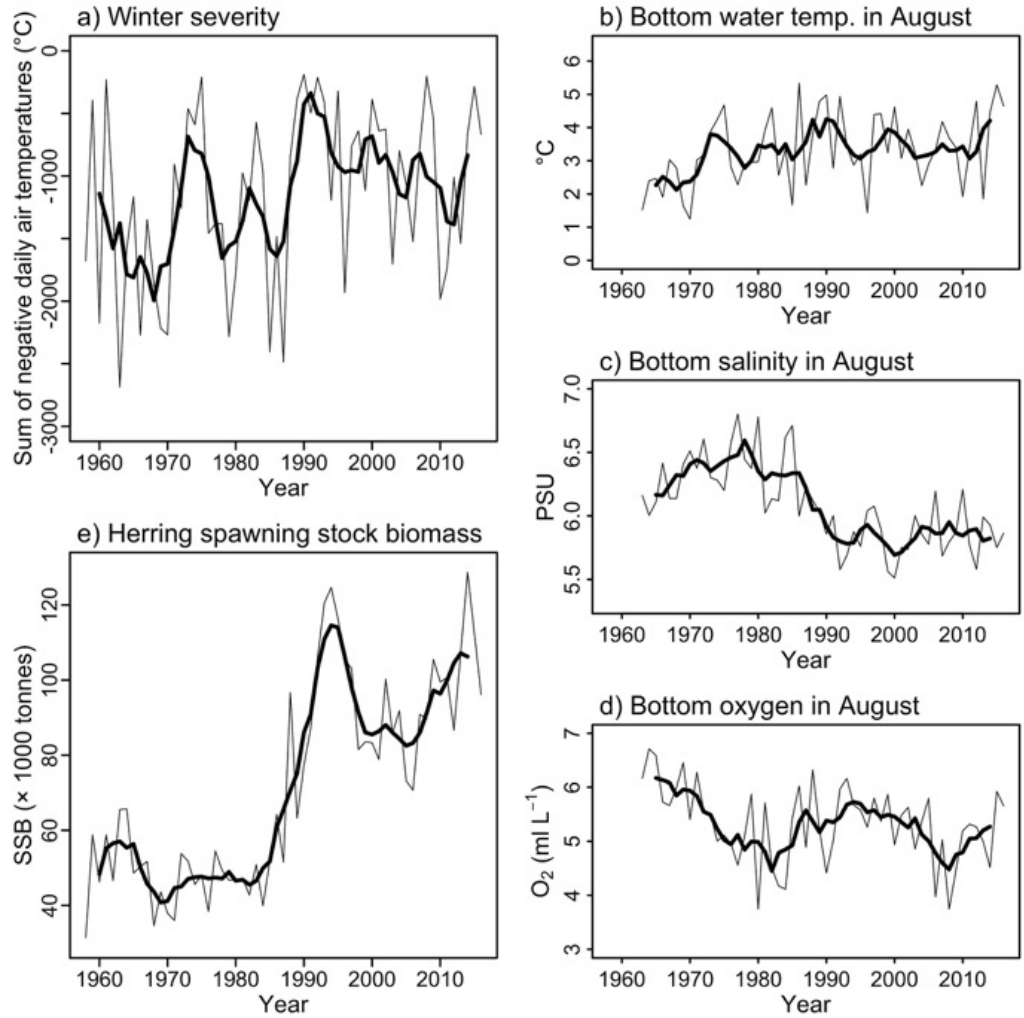
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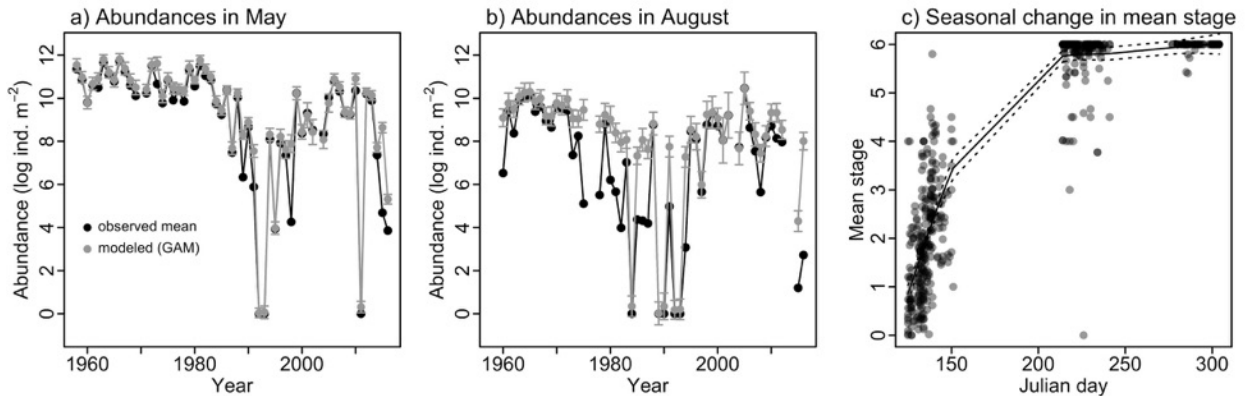
501 **Figure 1.** Location of sampling stations of *L. macrurus* in the GoR and availability of data
 502 during 1958-2016



503

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

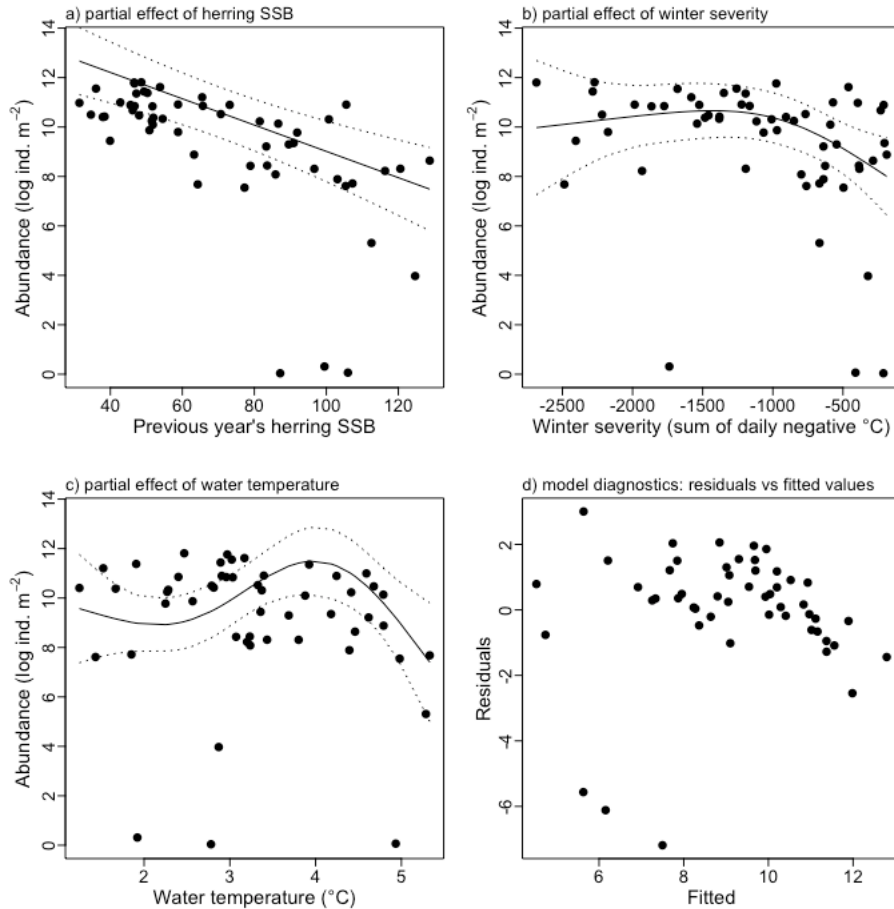
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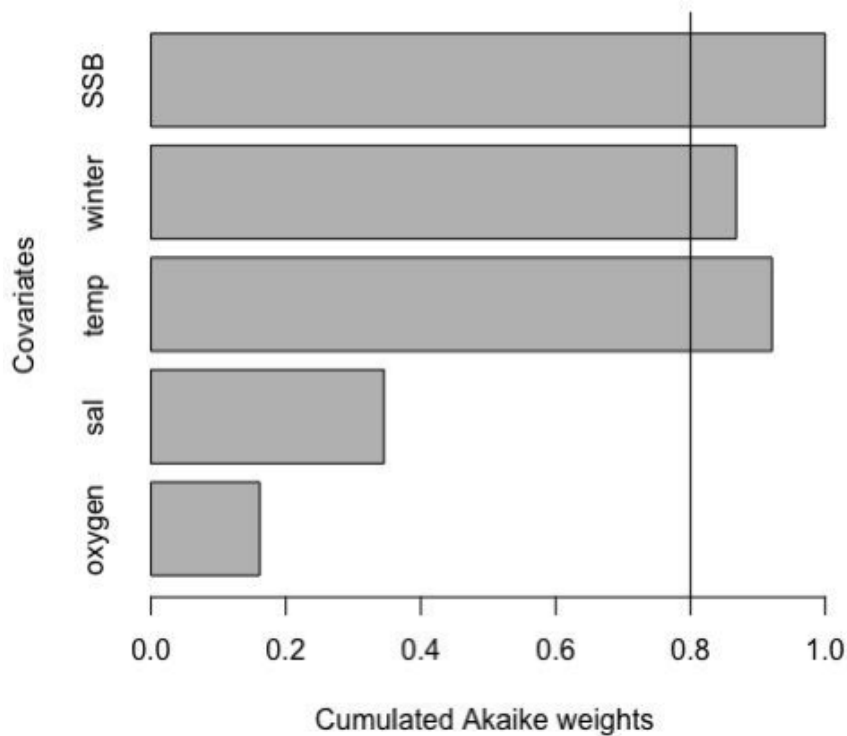
508

509 **Figure 3.** Initial modelling of the abundance (individuals m^2 in logarithmic units) of *L. macrurus*
 510 in the GoR during 1958–2016: (a) annual mean abundances in spring (black) and the spatially

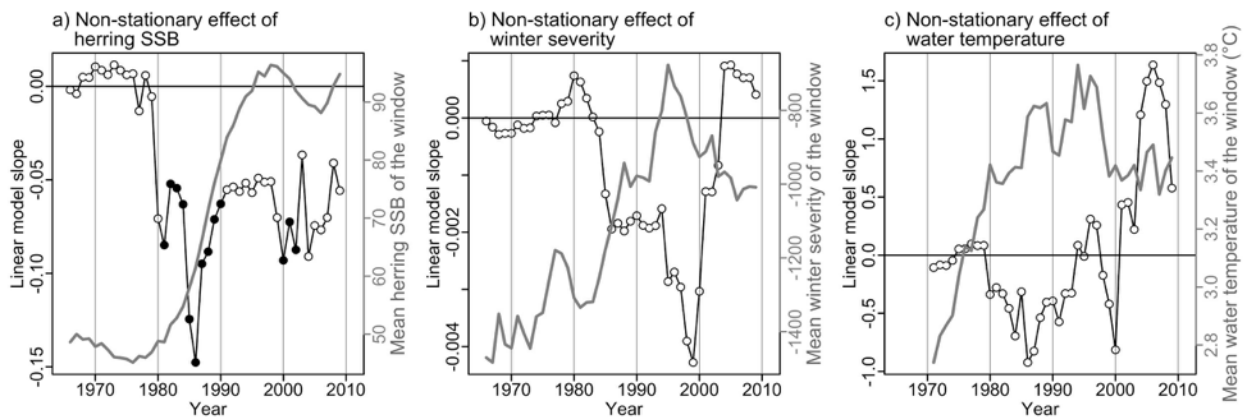
511 balanced annual values estimated with the model 1 (Table 2, grey); (b) annual mean abundances
512 in summer and the annual values estimated with the model 2 (Table 2); (c) seasonal development
513 of the community maturity (mean stage . 0—all nauplii, mean stage. 6—all adults).
514



515
516 **Figure 4.** The non-linear smooth terms of the best ranking GAM identified by multimodel
517 inference procedure (herring SSB in previous year, winter severity and bottom water temperature
518 in summer of the previous year) (see Tables 3 and 4). Panel d serves as a diagnostics of model
519 fit, showing the residual distribution along the fitted values.



520
 521 **Figure 5.** Relative importance of herring spawning stock biomass (“SSB”) in previous year,
 522 winter severity (“winter”), and the bottom water temperature (“temp”), salinity (“sal”), and
 523 oxygen (“ox”) in previous summer on the annual abundance of *L. macrurus* in the GoR. A
 524 variable that shows up in models with large weights will receive a high summed Akaike weight
 525 and is considered important. Vertical line is drawn at 0.8, which is used as a cut-off to
 526 differentiate between important and less important variables.
 527



528
 529 **Figure 6.** Results of the chronological sliding window analysis: time trends in linear slopes of *L.*
 530 *macrurus* abundance ($\ln(\text{ind m}^2)$) with herring SSB (1000 tonnes) in previous year (a), winter
 531 severity (mean air temperature during November–March) (b), and the bottom water temperature
 532 in summer of the previous year (c). Filled points denote values where the slope was significant at

533 $p < 0.05$. Grey line is the mean values of the respective explanatory variable in each 15-year
534 subset (1958–1972, 1959–1973, . . . , 2002–2016). On the x-axis is the middle year of each 15-
535 year subsets.