

# Trends and drivers of *Macoma balthica* L. dynamics in Kandalaksha Bay, the White Sea

EVGENY A. GENELT-YANOVSKIY<sup>1,2</sup>, DMITRIY A. ARISTOV<sup>2,3</sup>, ALEXEY V. POLOSKIN<sup>3,4</sup>  
AND SOPHIA A. NAZAROVA<sup>1,2</sup>

<sup>1</sup>Department of Ichthyology and Hydrobiology, Saint-Petersburg State University, Saint-Petersburg, Russia, <sup>2</sup>Zoological Institute of Russian Academy of Sciences, Saint-Petersburg, Russia, <sup>3</sup>Laboratory of Marine Benthic Ecology and Hydrobiology, Saint-Petersburg, Russia, <sup>4</sup>Department of Invertebrate Zoology, Saint-Petersburg State University, Saint-Petersburg, Russia

*Long-term population dynamics of marine invertebrates can be shaped by environmental conditions as well as biotic factors, including predation, diseases, interspecific or intraspecific competition. Towards the northern edge of species ranges the role of biotic interactions gradually decreases while the impact of climate oscillations becomes more important. This study examined the long-term changes in abundance, individual growth rates and shell shape characteristics of *Macoma balthica*, one of the dominant species in White Sea soft-bottom intertidal communities. To test the role of predators in changes in clam abundance, we examined the number of moonsnails *Amauropsis islandica*. *Macoma balthica* exhibited spatially synchronous population dynamics at six sites in Kandalaksha Bay, where densities of clams varied between 140 and 8500 ind. m<sup>-2</sup> during the 21-year period of observations. Statistical modelling using generalized additive models (GAM) shows that a combination of mild winter and warm summer led to an increase in *M. balthica* density the following year. Predation by *A. islandica* had no impact on changes in *M. balthica* density. Growth rates of *M. balthica* were higher during a cool decade, but clams that lived in a warmer period were characterized by more globose shells. Our results suggest that the climate oscillations can be regarded as the key factor causing the shift in abundance of *M. balthica* in the White Sea during the last two decades via recruitment and survival.*

**Keywords:** *Macoma balthica*, *Limecola balthica*, White Sea, population dynamics, linear growth, *Amauropsis islandica*, Naticidae, predator-prey interactions, climate change

Submitted 30 January 2017; accepted 3 July 2017; first published online 22 August 2017

## INTRODUCTION

The White Sea is a mostly enclosed subarctic sea connected to the Barents Sea and surrounded by Kola Peninsula in the north, Karelia in the west, and the Kanin Peninsula to the north-east. Most of the White Sea is situated to the south from the Arctic Circle with the only exception in the north-western corner, the apex of the Kandalaksha Bay. In summer the sea surface warms up to 20°C in small bays (Babkov & Golikov, 1984), but during the winter temperature of the upper water layer falls below zero causing the permanent ice cover from November to mid April (Kuznetsov, 1960).

Kola Peninsula has warmed quickly over recent decades, with a surface area temperature rise of 2.3°C over the past 50 years. While there was no significant change in the annual mean precipitation, spring has become more wet and autumn more dry since the 1960s (Marshall *et al.*, 2016). This change caused the reduced duration of the winter sea ice cover in the White Sea (Parkinson, 2014). Similar temperature rise is typical for the whole Arctic, where the temperature is increasing at a rate of two to three times that of the global trend. Globally, both positive and negative responses of the marine species to the climate change in the Arctic have been

found so far, such as increased annual primary production, changes in zooplankton abundance and species composition, decline in population size of marine mammals and northward range shifts in some fish species (Wassmann *et al.*, 2011). Range shifts and changes in abundance of one species, especially predators, often causes the rearrangement of the whole ecosystem structure. Recent northward expansions of Northern shrimp, Bluefin tuna and Atlantic mackerel took place on the background of both climate change and overfishing of cod near West Greenland (Hamilton *et al.*, 2003; Mackenzie *et al.*, 2014).

Intertidal species respond to climate change in terms of distribution range shifts, variation in abundance and growth of individuals. Along the North-east Atlantic, typical boreal intertidal communities are currently limited at north by 10°C summer isotherm, geographically equal to the White and Barents Seas. Direct observations and statistical modelling show that distribution ranges of common species of the typical Atlantic intertidal communities are shifting northwards (Berge *et al.*, 2005; Helmuth *et al.*, 2006; Jueterbock *et al.*, 2013). Population dynamics of boreal intertidal invertebrates are strongly related to seawater temperatures (Strasser *et al.*, 2003; Wetthey *et al.*, 2011). Among the abundant species on the intertidal of European seas, *Macoma balthica* (Linnaeus, 1758) is often regarded as the most sensitive to elevated ambient temperatures (Beukema *et al.*, 2009). Elevated winter temperatures have been shown to have both direct and indirect impacts on recruitment in intertidal bivalves. Beukema & Dekker (2014) found high

**Corresponding author:**  
S.A. Nazarova  
Email: sophia.nazarova@gmail.com

recruitment in shrimps *Crangon crangon* and shore crabs *Carcinus maenas* after mild winters and concluded that top-down predation is the main regulatory factor for the survival of bivalve juveniles in the Wadden Sea.

In the White Sea *M. balthica* is a common food source for many birds (Pertsov, 1963) and fishes (Azarov, 1963). The role of *M. balthica* in the diet of invertebrate predators is less studied in the region. Since 2001 we have been recording the population densities of the Iceland moonshell *Amauropsis islandica* and *M. balthica* at sites where these species occur simultaneously. Density of *A. islandica* in the White Sea intertidal communities can be high, reaching 50 ind m<sup>-2</sup>, but moonshells are distributed across the tidal flats unevenly, forming relatively permanent summer aggregations with rather distinct upward borders (Aristov, 2013). At the studied locations *A. islandica* feeds on several species of intertidal molluscs, but mainly on *Macoma* (Aristov et al., 2015). It is easy to spot the effects of predation by naticid snails, because they leave boreholes on the victim's shell (see Kabat, 1990 for review). During our survey we found that in 2014 the dominant part of registered mortality in *Macoma* population was due to predation by *Amauropsis* (Aristov et al., 2015). Along with the well-known high consumption rate in other naticid species (Clements & Rawlings, 2014) we can expect that abundance of *A. islandica* snails has an impact on long-term *Macoma* population dynamics.

The dynamics of the White Sea intertidal communities have been studied for almost 30 years (Sergievsky et al., 1997; Sukhotin & Berger, 2013). These studies proposed several causes to describe the changes in species abundances: species interactions (Khalaman, 2013; Naumov et al., 2014), rare weather events (Naumov, 2013) and cyclic character in population recruitment (Khaitov, 2013), although the relationship between abundance and climate oscillations were not discussed.

Another approach to study the impact of climate change on species performance is based on the research of temporal variation in growth rates of individuals. For example, growth rates in Arctic subtidal bivalves *Clinocardium ciliatum* and *Serripes groenlandicus* near Greenland and Svalbard significantly increase during warm years and in sites affected by warm Atlantic currents (Ambrose et al., 2006; Sejr et al., 2009; Carroll et al., 2011). Geographic variation in growth rates of *M. balthica* is well studied (Beukema & Meehan, 1985) which makes it an ideal subject to study how long-term variation in growth rates is related to climate oscillations.

*Macoma balthica* is a widely distributed bivalve in Europe. This species however is now regarded as a complex of two (sub) species with overlapping distribution, different origin and probably, different tolerance range (Nikula et al., 2007; Strelkov et al., 2007; Luttikhuisen et al., 2012; Becquet et al., 2013). While the dynamics of *Macoma* is very well studied in the central part of the distribution range, it is necessary to carry out comparative studies from other regions.

In the present paper we explore whether the population dynamics of *Macoma balthica* in the apex of Kandalaksha Bay during the last 20 years were affected by climate oscillations, and examine the contribution of predator–prey interactions between *M. balthica* and the moonshells *Amauropsis islandica* to the *Macoma* abundance variation. Finally, we compare the growth rates of *M. balthica* during different periods of the study to explore the footprint of climate

change on individual performance of this species in the Subarctic.

## MATERIALS AND METHODS

### Study area

Kandalaksha Bay forms the north-west portion of the White Sea. It is the warmest part of the sea with the annual mean surface water temperature of 4°C at the apex, seasonal mean amplitude of about 20°C (Filatov et al., 2007) and average tidal amplitude of about 2 m. The most typical species of intertidal fauna at the White Sea sandflats are baltic clams *Macoma balthica* [recently *Limecola balthica* has become accepted as the valid scientific name (Sartori, 2016), but here we use *Macoma balthica* as the commonly used synonym], lugworms *Arenicola marina*, sludge-worms *Tubificoides benedii* and mudsnails *Peringia ulvae* (Naumov, 2013).

### Samples

The length of the time series varied from 6 to 21 years for different sites. The samples of *M. balthica* were collected from six tidal flats in the apex of Kandalaksha Bay between 1992 and 2012 (Figure 1). At each site 5–20 core samples with an area of 0.03 m<sup>-2</sup> were collected annually in late July (see Table 1 for details). To address the effect of the predator on *M. balthica* at two sites (YUG, LOM) we counted the number of Iceland moonshell *Amauropsis islandica* from the 0.25 m<sup>2</sup> around each of the *Macoma* core samples.

Samples were sieved through a 0.5 or 1 mm mesh and sorted alive in the laboratory. All *M. balthica* individuals were taken from samples, counted and their greatest shell length was measured with a stereomicroscope to the nearest 0.1 mm. To ensure comparability between cores which were sieved through different mesh, we only used molluscs larger than 1 mm. Thus, we also cut off the spat and analysed the abundance of individuals older than 1 year (Zubakha et al., 2000; Nazarova, unpublished data).

To study the shell shape and growth-related variation, two samples of *Macoma*, collected at Luvenga estuary, were used: (1) a sample from 1997 represented the cool period (N = 55 ind.), and (2) a 2015 sample represented the warm period (N = 57 ind.). Standard measurements of each clam from these samples were done using a stereomicroscope and Vernier callipers (small and large specimens correspondingly) to the nearest 0.1 mm, particularly length *L* (the greatest distance between the posterior and anterior ends), height *H* (the greatest distance perpendicular to the anterior-posterior axis passing through the umbo), width *W* (the greatest distance perpendicular *L* and *H* passing across two valves) of the shells and the width of the external growth rings. Age of clams was determined as number of the growth rings (Maximovich et al., 1992).

### Statistical analysis

All calculations were done using the R statistical software (R Core Team, 2016). We used non-parametric Mann–Whitney test for paired and Kruskal–Wallis test for multiple comparisons. To compare similarity of population dynamics

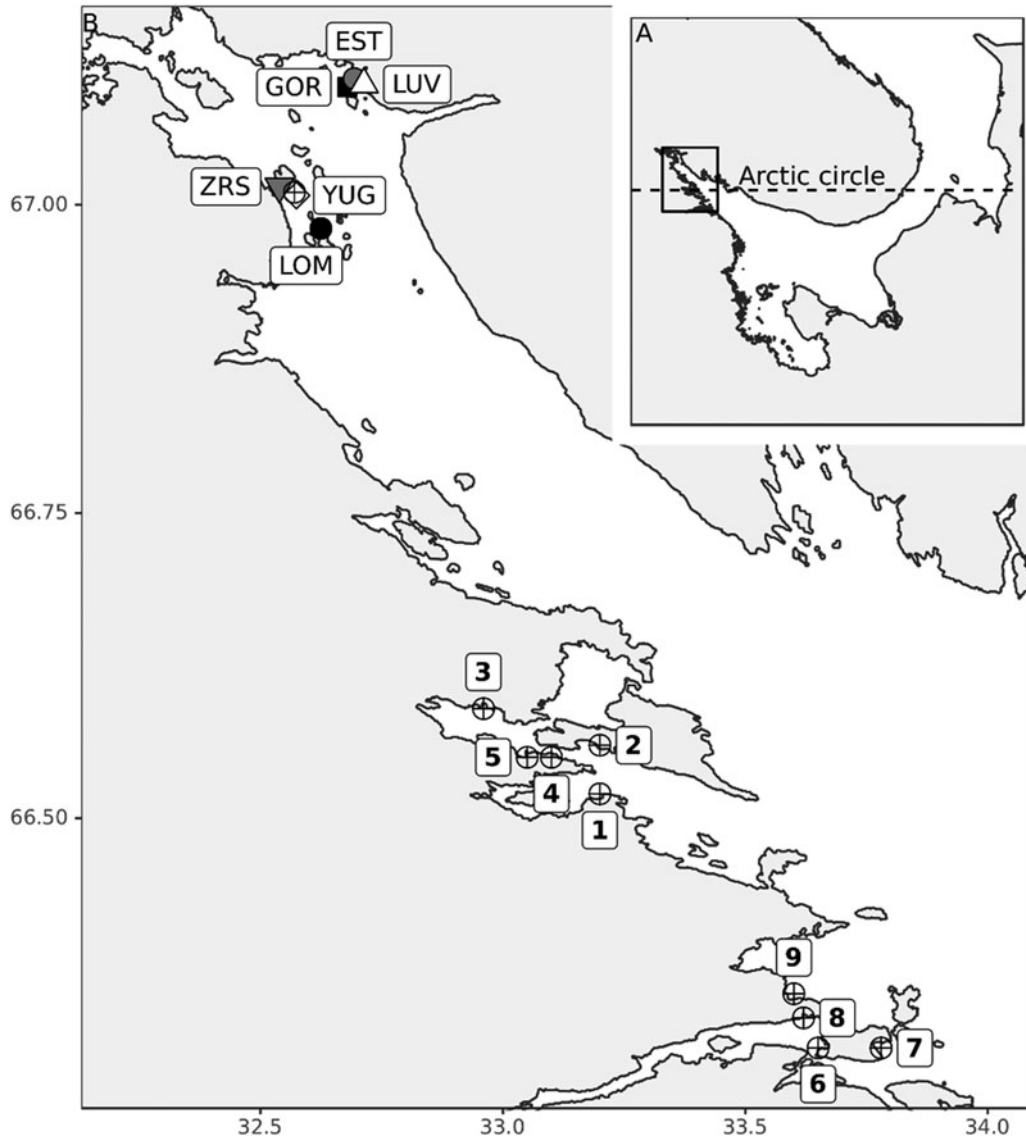


Fig. 1. Map of the study area: the White Sea (A) and Kandalaksha Bay (B). See Table 1 for sampling site details. Numbers mark previously published data (Table 5).

trends for each site initial data were transformed into matrices of Euclidean distances between pairs of time points (years) (see Khaitov & Lentsman, 2015 for details). These matrices were compared by Mantel test from the vegan package (Legendre & Legendre, 2012; Oksanen *et al.*, 2016). Spearman’s rank correlation coefficient was used as a statistic in the procedure with the permutation test for significance assessment (999 permutations were run).

To test whether the temperature oscillations have an effect on population dynamics of *Macoma balthica*, the three longest time-series, namely data from LUV, GOR and ZRS were used. Natural logarithm of *M. balthica* density was used as the modelling value. Records of monthly averaged surface air temperature for the period before 2000 were extracted from the annual reports of the Kandalaksha State Nature Reserve (‘The Chronicle of Nature of the Kandalaksha Reserve’, 1992–

Table 1. Sampling details.

Region	Code	Site	Coordinates	Years of sampling	N cores per sampling	Mesh (mm)
Luvenga skerries	EST	Luvenga Estuary	E 32.69316, N 67.10162	1992–2012	9	0.5
	GOR	Goreliy Island	E 32.67891, N 67.09472	1992–2012	12	0.5
	LUV	Luvenga, mainland	E 32.71333, N 67.09689	1992–2000	15–25	0.5
Severniiy archipelago	ZRS	Zapadnaya Ryashkova Salma Strait, Ryashkov Island	E 32.539, N 67.01463	1994–2012	6	0.5
	YUG	Youzhnaya Inlet, Ryashkov Island	E 32.57397, N 67.00751	2001–2012	10–15	1
	LOM	Bolshoy Lomnishniy Island	E 32.62451, N 66.98088	2007–2012	5–10	1

2000). Monthly temperatures for the period between 2001 and 2012 were taken from web-based archives of Raspisaniye Pogodi Ltd (<http://www.rp5.ru>) for Kandalaksha weather station (WMO station index 22217). These data were commonly applied for all sites, therefore year cannot be isolated as predictor in modelling.

Population dynamics of *M. balthica* are mainly regulated by recruitment success in each year, which is a result of three processes: (1) gonad development, (2) spawning and settlement success and (3) spat survival in the first winter (Maximovich, 1985; Honkoop *et al.*, 1998; Philippart *et al.*, 2003; Beukema *et al.*, 2009). Critical periods for processes are previous winter for the gonads forming, previous summer for spawning and recruitment and current winter for spat survival (Maximovich, 1985). We used temperatures in February and July as a proxy of winter and summer conditions. Since samples were collected in late July, three predictors were used in the model: February temperature of the sampling ( $FEB_t$ ) and of the previous ( $FEB_{t-1}$ ) year, and July temperature ( $JUL_{t-1}$ ) of the previous year. No correlation was revealed between these three predictors.

Autocorrelation function showed significant values at lag 1 for *M. balthica* abundance at all sites. No autocorrelation was found in temperature time-series (Supplementary Table S1). Therefore temperature effects (through thin-spline interpolation) on *M. balthica* abundance was estimated using generalized additive mixed models (GAMM) as implemented in the mgcv package for R (Wood, 2006). These GAMM use the data to determine the underlying linear or non-linear trend and covariate functional form without having to assume any specific functional form (Wood, 2006).

We fitted the following GAMM model:

$$\log(N_t) = \beta_0 + f_1(FEB_{t-1}) + f_2(JUL_{t-1}) + \beta_3(FEB_t) + \beta_1 \text{Site} + \varepsilon$$

with  $\varepsilon \sim \text{AR1}(\rho)$ , where  $\log(N_t)$  is the natural logarithm of *M. balthica* density in year  $t$ ;  $\beta_0$  is the intercept;  $\beta_1$  is the slope coefficient for Site;  $FEB_{t-1}$ ,  $JUL_{t-1}$  and  $FEB_t$  are mean monthly air temperatures in year  $t-1$  and  $t$  correspondingly;  $f_1, f_2, f_3$  are the smoothers for each monthly temperature,  $\varepsilon$  is the residuals. Autoregressive model of residuals (order 1) was included ( $\text{AR1}(\rho)$ ), where residual at time  $t+1$  is the function of residual at time  $t$  (see Pinheiro & Bates, 2006 for details). All model predictors seemed to have significant influence on the dependent variable, so the selection of model was not needed. To check the importance of autoregressive structure we fitted the GAM model with the same predictors and smoothers. Final models were checked with Akaike information criteria (AIC).

To test the predator effect of *Amauropsis islandica* we used data from YUG and LOM sites. We fitted the linear model with similar predictors as in GAMM (see above) and added season mean abundance of *Amauropsis* ( $N_a$ ). The following full model was fitted:

$$\log(N_t) = \beta_0 + \beta_1 F_{EB_{t-1}} + \beta_2 J_{UL_{t-1}} + \beta_3 F_{EB_t} + \beta_4 \text{Site} + \beta_5 N_a + \varepsilon$$

Backward selection was then carried out to fit the optimal model. Akaike information criteria (AIC) was used for better

model choice. Both final models were checked for patterns in the residuals and QQ-plots visually (Zuur *et al.*, 2009). ANOVA was used to estimate the effects of predictors and smoothers. Null hypotheses were rejected at 5% confidence level.

The used shell shape measure can be described as globosity ( $W/L$ ). The evidence of positive allometry of shell shape was tested by Spearman correlation test and corrected by taking the natural logarithm of both shell measures and performing a principal component analysis (PCA) on the two measures (Luttikhuisen *et al.*, 2003). The first principal component was interpreted as size, and the second as size-corrected shape (high value corresponds to flattened shell).

Growth differences between generations in each period were estimated by mean annual shell increments. Shell increments were calculated as the difference between neighbour growth rings. Growth curves were approximated by the von Bertalanffy equation (von Bertalanffy, 1938). The values obtained for  $K$  and  $L_{\max}$  were multiplied to obtain the parameter  $\omega$  ( $\omega = K \times L_{\max}$ ), which is more suitable than either  $K$  or  $L_{\max}$  to investigate growth rate variations (Appeldoorn, 1983).

## RESULTS

### *Macoma balthica* population dynamics

During the 21-year period of regular observations, densities of *M. balthica* varied by 4–40-fold at different sites (Figure 2). Minimum abundance was observed at YUG in 2012 (142 ind.  $m^{-2}$ ), and maximum was at ZRS in 1999 (8530 ind.  $m^{-2}$ ) (Table 2). Maximum variation was observed at ZRS. At LOM (the shortest time-series) abundance did not significantly fluctuate (Kruskal–Wallis test:  $\chi^2 = 9.9$ ,  $P = 0.077$ ) and long-term mean density was 713 ind.  $m^{-2}$ . At other sites mean density before 1998 was lower than after 1998 (Figure 2).

There was an obvious synchrony between sites, that already can be traced from the common peaks of clam density in 1994, 1999, 2004–2005 and 2007–2008 (Figure 2). Mantel test showed that population dynamics at six of 15 pairs of locations demonstrated similar patterns (Supplementary Table S2). Only the recruitment of 1998 (common peak in 1999) caused the shift in the abundance for a long period. The effect from other large recruitment events lasted for only 1 or 2 years (Figure 2). Wilcoxon test supported the significant difference between mean clam abundance before and after the year of 1998 at all sites (Table 2). Therefore the long-term population dynamics of *M. balthica* in the apex of

Table 2. *Macoma balthica* abundance variation.

Site	$N_{\min}$	$N_{\max}$	$N_{\text{mean}}$		$W$	$P$ value
			Before 1998	After 1998		
EST	165	3330	474	1974	1	<0.001
GOR	223	4753	814	1903	2	<0.001
LUV	251	3558	845	2661	0	0.004
LOM	378	1530	–	713	–	–
YUG	142	1913	–	1082	–	–
ZRS	220	8530	435	2303	0	<0.001

$N$ , density, ind.  $m^{-2}$ ;  $W$ , Wilcoxon test between two periods.

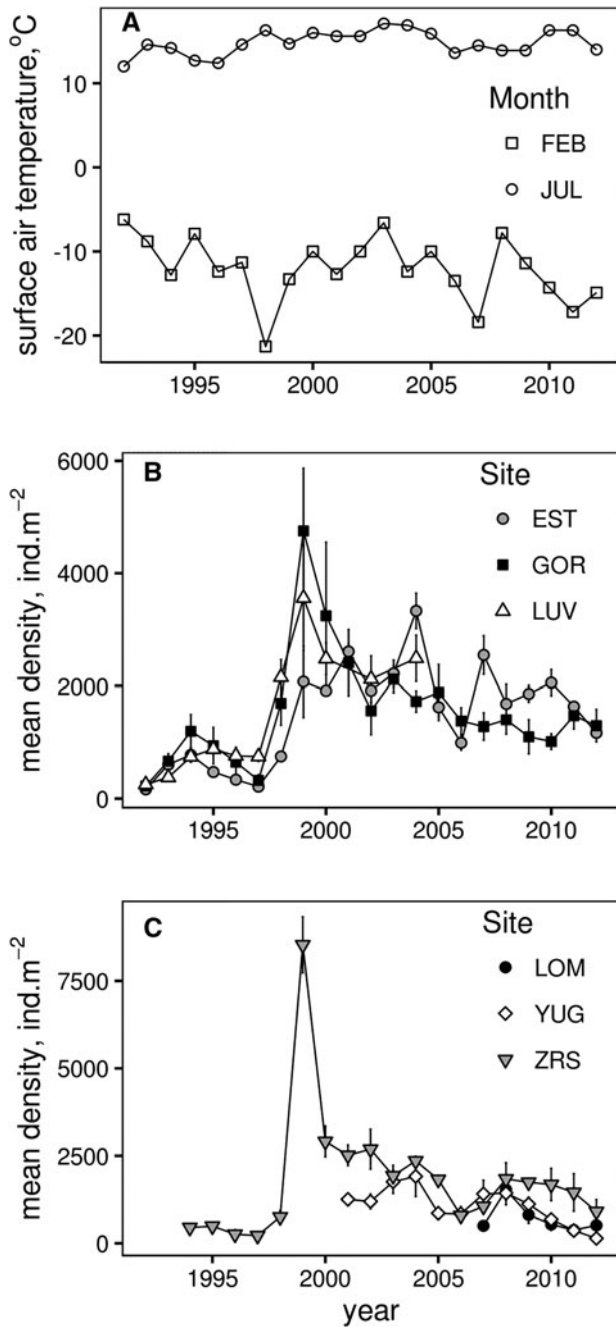


Fig. 2. Dynamics of monthly average air temperatures in Kandalaksha (A), *Macoma balthica* mean density ( $\pm$ SEM) at Luvenga skerries (B) and North archipelago (C).

Kandalaksha Bay during our study can be divided into two periods: (1) low-density period, which lasted between 1992 and 1998, and (2) high-density period from 1999 to 2012.

### Temperature and predator effects

The general additive mixed model (GAMM) that accounted for non-linear effects of temperature and site, fitted abundance dynamics well with 65% deviance explained. The distribution of GAMM residuals showed no obvious patterns. Akaike information criteria (AIC) of GAMM was less than that for GAM (128 vs 139), meaning that GAMM is a better

Table 3. Summary of GAMM results.

Fixed effects				
	Slope	Std	<i>t</i> -value	<i>P</i> -value
Intercept	6.84	0.36	18.81	<0.001***
Site (GOR)	1.46	0.51	2.86	0.0065**
Site (ZRS)	0.09	0.52	0.18	0.86
Smooth terms				
	Edf	<i>F</i> -value	<i>P</i> -value	
<i>s</i> ( $FEB_t$ )	2.84	4.33	0.017*	
<i>s</i> ( $JUL_t$ )	4.55	6.91	<0.001***	
<i>s</i> ( $FEB_{t+1}$ )	2.01	20.14	<0.001***	

The approximate proportion of explained variance (Adj.  $R^2$ ) is 0.65. Edf is estimated degrees of freedom and describes the curves of smoothers. Std is the standard error. \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

regression model. All fitted predictors have a significant effect on the log abundance of *Macoma* larger than 1 mm in length (Table 3).

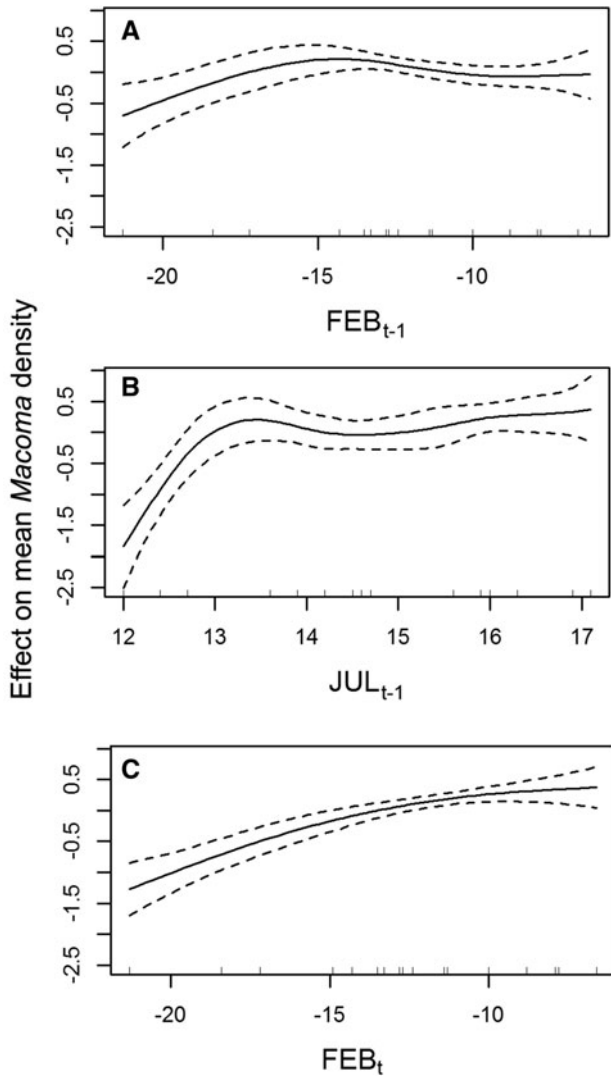
The cross-validation of spline-smoothers in GAMM showed a non-linear pattern for all smoothers (Figure 3). Density seems to increase monotonically with increasing  $FEB_{t+1}$  temperature, meanwhile the maximum modelled abundance of *M. balthica* corresponds to mean values of  $FEB_t$  temperature (Figure 3A, B). Predicted *M. balthica* abundance decreased rapidly with decreasing  $JUL_t$  temperature below +13°C (Figure 3C).

We analysed dynamics of *M. balthica* populations under predator pressure of *A. islandica* at YUG and LOM sites. Fitted linear model explained 54% of variance. Modelling shows that *A. islandica* had no effect on investigated *M. balthica* populations, and population dynamics of this species depends only on winter temperatures (Table 4) just as populations at LUV, GOR and ZRS. The reverse analysis shows that changes in density of *M. balthica* do not alter the dynamics of *A. islandica* either (ANOVA,  $F = 0.72$ ,  $P = 0.42$ ).

### Shell shape and growth rates

To characterize *M. balthica* individuals from cold and warm periods we use shell shape and linear growth as a complex response to different factors. The length of clams, randomly included in the analysis, varied from 5.6 to 15.5 mm in the 1997 sample, and from 3.4 to 14.6 mm in the 2015 sample. Shell shape displayed positive allometry (larger shells are more globose) only in the 1997 sample (Spearman rank test:  $r = 0.62$ ,  $P < 0.0001$  in 1997 and  $r = -0.13$ ,  $P = 0.31$  in 2015). Therefore we used shell shape data corrected for length as described in Materials and methods. Mann-Whitney test showed that *M. balthica* shells, collected in 2015, were more globose compared with those sampled 18 years earlier, in 1997 ( $U = 2384$ ,  $P < 0.0001$ , Figure 4).

To compare growth rates, we used molluscs of ages 3+ to 6+ as most abundant generations in both 1997 and 2015. In both sampling years (i.e. 1997 and 2015), we calculated mean annual shell increment for each growth year in each mollusc generation (e.g. the first, the second and the third growth years for 3+, etc.). In molluscs of one sampling year, this increment appeared to be the same in the same growth year regardless of the generation of molluscs (Supplementary Table S3). Therefore we could combine



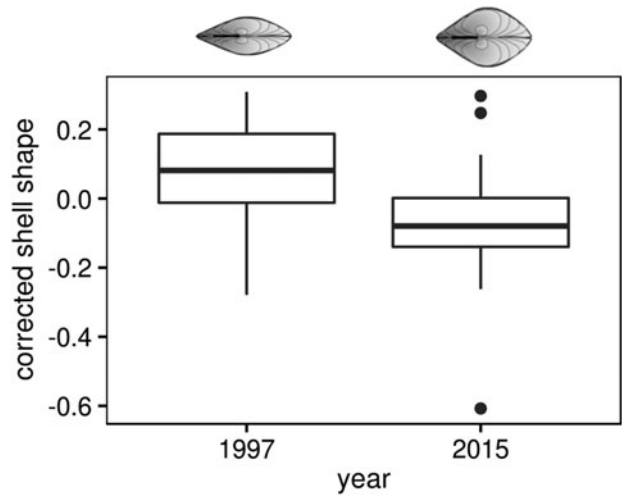
**Fig. 3.** The effects of average monthly temperature of (A) previous year February, (B) previous year July and (C) this year February on the mean *Macoma balthica* abundance. Solid curves are smoothing terms in final GAMM model (given that all other smoothers and parametric part of the model are constant), dashed lines denote 95% confidence bands.

molluscs of all generations of one sampling year to infer one growth curve. To plot these growth curves, we used a growth year instead of age and length of the corresponding growth ring instead of shell length. Figure 5 shows the comparison of growth curves of *M. balthica* collected in 1997 and 2015. The growth rate was similar in young clams (of no more than the third year of growth), but molluscs of the

**Table 4.** ANOVA results for *Macoma balthica* dynamics at the sites with predators.

Factor	Df	SS	MS	F-value	P-value
Site	1	591,788	591,788	4.8778	0.051
$N_a$	1	154,290	154,290	1.2717	0.29
$FEB_t$	1	945,311	945,311	7.7917	0.02*
$FEB_{t+1}$	1	671,628	671,628	5.5359	0.04*
$JUL_t$	1	101	101	0.0008	0.98
Residuals	10	1,213,223	121,322		

Df, degrees of freedom; SS, sum of squares; MS, mean squares. Significance level: \* $P < 0.05$ .



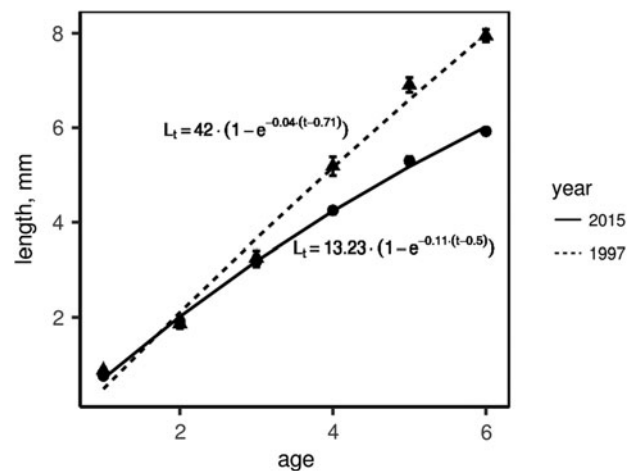
**Fig. 4.** Change of *Macoma balthica* shell shape at Luvenga Estuary (EST) from the 1990s to 2010s. Corrected shell shape means the factor loading of the second principal component of the PCA on log (shell length) and log (shell width).

fourth and greater years of growth grew faster during the 1990s ( $\omega$  is 1.67 in 1997 and 1.46 in 2015).

## DISCUSSION

### *Macoma balthica* population dynamics in the context of climate oscillations

*Macoma balthica* from the northernmost part of Kandalaksha Bay showed strong inter-annual variation in abundance between the years 1992 and 2012. The alternation between the periods of high and low abundance is typical for many White Sea invertebrates, sticklebacks and seagrasses (Khalaman & Naumov, 2009; Gerasimova & Maximovich, 2013; Khalaman, 2013; Varfolomeeva & Naumov, 2013; Ivanova *et al.*, 2016; Khaitov & Lentsman, 2016). This alternation was found to be regular in mussel beds (Khaitov, 2013) and fouling subtidal communities (Khalaman, 2013), but irregular in soft-shell clams *Mya arenaria* (Gerasimova &



**Fig. 5.** Linear growth of *Macoma balthica* at Luvenga Estuary (EST) in the 1990s and 2010s. Dots indicate mean length  $\pm$  SEM, lines are von Bertalanffy approximation of growth.

Maximovich, 2013). Similar densities of *M. balthica* from the same part of the White Sea were observed in late 1940s (Sveshnikov, 1963, Table 5). Unfortunately data on clams density for the period between the 1940s and 1979 are lacking, but in the 1980s *M. balthica* abundance was the lowest among all periods of monitoring studies of this species. After 1979 the density of *M. balthica* has been increasing gradually (Table 5).

The long-term maximum mean density of *M. balthica* (>1+ age) was observed in 1999, representing the unusually successful recruitment after the postlarvae settlement in the summer of 1998. This particular year was characterized by a relatively cool winter (but see Naumov, 2013 for a description of the abnormally early ice melting), warm summer and warm following winter (Figure 2). An unusual increase in density of acorn barnacles *Semibalanus balanoides* was observed in 1998 due to intense settlement of juveniles, but no correlation was observed between the recruit density and adult abundance during the next year (Marfenin *et al.*, 2013). High recruitment after the settlement in 1998 was also observed in *Mya arenaria*, and while the authors suggested the existence of a common mechanism regulating the recruitment rate, no factors were proposed to support the successful recruitment (Gerasimova & Maximovich, 2013). A sudden increase in abundance of *M. balthica* in 1998 and 1999 was reported from the Keret Archipelago (~100 km away from our sampling sites, Varfolomeeva & Naumov, 2013). The authors also mentioned that the density and biomass gradually increased after the peak in 1998 and that the changes were similar among investigated sites. According to our data, population dynamics of *M. balthica* in the apex of Kandalaksha Bay were also synchronized (Figure 2). These findings together suggest that *M. balthica* dynamics in the White Sea are synchronized over large areas as well as in other parts of Europe, particularly in the Wadden Sea (Beukema *et al.*, 1993, 2001; Honkoop *et al.*, 1998), even though these regions are inhabited by two separate subspecies of *M. balthica* (see below).

Statistical modelling shows that a combination of mild winter and warm summer leads to an increase in *M. balthica* density in the next year, including the explosive 40-fold population growth that took place in the late 1990s. Results from the present study reveal the *M. balthica* population size increasing in response to milder than average winters in the north-west White Sea. Our findings seem to contradict all the current knowledge about the climate-driven population

dynamics of intertidal bivalves (*Macoma balthica*, *Cerastoderma edule*, *Mya arenaria* and *Mytilus edulis*) from the NE Atlantic (Philippart *et al.*, 2003; Beukema & Dekker, 2005; Beukema *et al.*, 2015). While abundance of *M. balthica* was increasing in the late 1990s in the north-western White Sea (northern part of Baltic clam distribution range), it was seriously declining in the Wadden Sea from the mid-1980s onward (central part of range) (Beukema *et al.*, 2009; Compton *et al.*, 2016).

We propose several explanations for such opposing trends in population dynamics. To start with, *Macoma balthica* is no longer regarded as one single species in Europe, but a complex including *M. balthica rubra* inhabiting the North Sea and NE Atlantic, and *M. balthica balthica* found in the White, Barents and Baltic Seas (Nikula *et al.*, 2007). Thus, comparing the life history traits of *Macoma* from the Wadden and White Seas should consider the high probability of a different tolerance range in the two subspecies in line with different phenology of these regions.

Our study shows a positive relationship between air temperature in February with the summer density of *M. balthica* in the same and next years. This implies an effect of winter temperature on gonadal development and reproductive output of adults as well as on survival of 0+ recruits during their first winter. Hydrological winter in the White Sea starts in December when the temperature of the upper layer of the water column falls below zero and spans until late March (Usov *et al.*, 2013). Germ cells development of *M. balthica* in the White Sea starts in July and takes nearly 10 months up to the next June when spawning occurs at water temperatures between +10 and +15°C (Maximovich, 1985).

Winter mean water temperature in the Wadden Sea varied between 0 and +7°C during 1965–2010 (Beukema *et al.*, 2009). Gonadal development in *M. balthica* from the Thames Estuary and Wadden Sea takes place between mid-summer till next February, and spawning occurs when water temperature reaches +10°C (Caddy, 1967, 2010; de Wilde, 1975). Reproductive output consists of two components: egg size, positively correlated with summer temperatures, and egg number related to food availability during prolonged period of gonadal development. Lack of food prior to spawning may be an important factor stimulating resorption (Honkoop & Van der Meer, 1997). Winter feeding activity in *Macoma* is generally much lower than in spring and summer. While clams can switch their feeding mode from deposit to suspension-feeding, it was shown that clams

Table 5. *Macoma balthica* abundance in Kandalaksha Bay in different periods.

Code	Site	1948–1949	1962–1966	1979–1989	1990–1997	1998–2012	Source
YUG	Youzhnaya Inlet, Ryashkov Island	1342 (NA)					(1)
1	Podvolochje Bay, Velikaya Salma Strait		NA (120–1240)				(2)
2	Lobanikha Bay, Velikiy Island		NA (20–810)				(2)
3	Pekkelinskaya Bay		NA (43–980)				(2)
4	Rugozerskaya Bay, Cape Kindo		NA (80–2760)				(2)
5	Ermolinskaya Bay		NA (75–400)				(2)
6	Suhaya Salma, Keret Island			471 (5–2013)	210 (33–593)	513 (56–1165)	(3, 4)
7	Klushiha Bay, Keret Island			325 (40–660)	442 (153–990)	702 (284–3028)	(3, 4)
8	Medvezhya Bay			87 (62–112)	282 (53–848)	921 (289–3300)	(5)
9	Seldyanaya Bay			79 (67–102)	267 (42–727)	1034 (452–2089)	(5)

Mean density and its range are shown. NA, no data.

Sources: (1) Sveshnikov (1963); (2) Semenova (1974); (3) Maximovich *et al.* (1991); (4) Gerasimova & Maximovich (2013); (5) Varfolomeeva & Naumov (2013).

depend for their food intake to a great extent on algal food present in the water column (Hummel, 1985; Olafsson, 1986). In the White Sea, the period from late February till mid-March is marked by a gradual increase in chlorophyll-*a* concentration following winter (Usov *et al.*, 2013). Since the reproductive cycle in *Macoma* from the White Sea takes three more months than those from the Wadden Sea, early availability of food might prevent gonadal resorption during unfavourable seasons and, therefore, higher reproductive success after relatively warm winters.

### Predator–prey interactions

The Iceland moonshell *Amauropsis islandica* is a long-living circumpolar species, mainly found in the bathyal, infralittoral and circalittoral zones (Egorova, 2007). In Kandalaksha Bay of the White Sea moonshells also occur in the intertidal zone (Aristov *et al.*, 2015). The knowledge of distribution, abundance, life history and feeding behaviour of *A. islandica* from this region is still fragmentary. *Amauropsis* is dioecious, in May–June females lay the stiff egg-mass covered by sand and mucus and known as ‘sand collars’. This species does not have a pelagic larval stage for dispersal (Golikov, 1987). Two reasons were taken into account for estimating the naticid *Amauropsis islandica* effect on *Macoma* abundance. Firstly, long-term monitoring studies showed that population dynamics of *M. balthica* in the Wadden Sea can be significantly altered by the pressure from the intertidal invertebrate predators, e.g. brown shrimp *Crangon crangon* (Beukema *et al.*, 2009 and references therein). Secondly, naticids are known to regulate the abundance of their prey (Wiltse, 1980). Nevertheless, no significant effect of *A. islandica* on *M. balthica* abundance at sites where these two species simultaneously occur in the apex of Kandalaksha Bay were found. While this result is very unexpected, it is probably not a unique case of interactions between the invertebrate predators and bivalves. The purplemouth moonshell *Cryptonatica janthostoma* from the Pacific does not significantly alter the density of bivalves that it feeds on, namely *Anisocardia venusta* and *Clinocardium californiense* (Selin, 2008). The author suggested that *A. venusta* is too small for the predator and *C. californiense* can actively escape from the attacking predator although direct long-term observations were not conducted. Similarly, the survey of interactions between the blue crab *Callinectes sapidus* and North American relative of the Baltic clam, *Macoma petalum* from Chesapeake bay, did not reveal a top-down predator effect (Seitz & Lipcius, 2001). In our case we assume that the *Macoma* population can easily recover from predator pressure with migrating clams from the unaffected part of the intertidal. Since *Amauropsis* has more restricted preferences than *Macoma* to the various abiotic factors at the intertidal such as low tide exposure, sediment type and salinity, there are many nearby *Amauropsis*-free settlements.

On the other hand, the abundance of *Macoma* clam seems to have no effect on the variation in density of *Amauropsis* at the surveyed tidal flats. Also, there is no clear evidence in the literature of such bottom-up influence of prey species on dynamics of naticids. Naticids demonstrate some species preferences (Vignali & Galleni, 1986) and can shift from one prey to another (Clements & Rawlings, 2014; Aristov *et al.*, 2015), so the bottom-up effect can be less distinct. The lack of top-down predator control and, from the current perspective,

of bottom-up regulation between *M. balthica* and *A. islandica* in Kandalaksha Bay intertidal deserves further research.

### Linear growth and shell shape variation of *M. balthica* in the apex of Kandalaksha Bay

Morphometric and linear growth analysis of *M. balthica* from the White Sea revealed that clams grew faster and had flattened shells during the cool period, but were globose and slow-growing during the warm period. Our findings contradict the data of Luttkhuizen *et al.* (2003) emphasizing spatial variability in *Macoma* shell shape in contrast with its stability over several years. Earlier, Beukema & Meehan (1985) revealed latitudinal clines in *M. balthica* shell shape, particularly clams from northern populations are more globose, while being oblong in southern part of the species range in Europe. We explain such a discrepancy between the results of two studies as follows. Luttkhuizen *et al.* (2003) analysed clam shell shape during three consistent years, while our two samples are not only spaced in time by 18 years, but also represent two periods with different climate conditions.

Luttkhuizen *et al.* (2003) compared the shape of *M. balthica* on both sides of Frisian Islands and found clam shells to be more globose in the enclosed Wadden Sea, where chances to be washed out from the sediment are lower, and where selection pressure from a great number of wintering birds is higher – globose shells are less affected by predation risk from birds, being harder to swallow and containing more salt water, which may energetically be very costly for birds (Zwarts & Blomert, 1992; Visser *et al.*, 2000; Luttkhuizen *et al.*, 2003). Significant numbers of the waders wintering in the Wadden Sea migrate to the White Sea in summer, where they feed on *Macoma* as well (Pertsov, 1963). Predation by birds is a very important factor in the dynamics of marine intertidal bivalves (e.g. Beukema *et al.*, 1993; Nehls *et al.*, 1997; Malham *et al.*, 2012; and references therein), thus it could be expected that changes in bird populations, especially at wintering and nesting areas would have an impact on bivalve populations. Populations of birds feeding mainly on *Macoma* in the White Sea, e.g. turnstones *Arenaria interpres*, oystercatchers *Haematopus ostralegus* and dunlins *Calidris alpina* have been declining during recent decades (Austin & Rehfish, 2005; Koryakin, 2012). Since shell shape is considered as a trait under selection (see above, Luttkhuizen *et al.*, 2003), the predation pressure on flatter shells is expected to decrease and shells are predicted to become less globose on average – the opposite trend to those we observed in Kandalaksha Bay. These species however do not swallow clams whole, but dig them out and open them on the surface of the sediment (Hulscher, 1982). Other species common in Kandalaksha Bay, such as eider ducks *Somateria mollissima* and common gulls *Larus canus* primarily feed on *Mytilus* mussels and not on *Macoma* (Mokievskiy *et al.*, 2012; Tolmacheva, 2013; V.V. Bianki, personal communication). Thus, the observed increased globosity of *Macoma* shells cannot directly be related to the changes in selective pressure from birds feeding on the tidal flats.

Slow-growing bivalves are usually more globose than faster-growing members of the same species (Seed, 1968; Gillmor, 1980; Newell & Hidu, 1982). This trade-off between linear growth and change of mantle cavity volume



matches the eco-physiological dynamic energy budget (DEB) models assuming that food digestion and assimilation of energy in ectotherms is proportional to the organism's surface area (Sarà *et al.*, 2013). Growth in *M. balthica* is restricted to water temperatures from 4 to 16°C with optimal growth conditions considered to be 10°C (Honkoop & van der Meer, 1997). At low tides *Macoma* can be stressed by high air temperatures during summer (Beukema *et al.*, 2009). The long-term mean summer water temperatures in the White Sea during the past 50 years varied around 10–15°C (Usov *et al.*, 2013). The increase in number of years with mean July surface area temperatures higher than 16°C since 1998 (Figure 2; Marshall *et al.*, 2016) offers one of the parsimonious explanations for decrease in linear growth rate in *Macoma* from Kandalaksha Bay.

Sediment type may be another factor responsible for shell shape in bivalves. The sand gaper *Mya arenaria*, often occurring in the same intertidal habitats as *M. balthica*, was shown to have a more globose shell in gravel than in sand or mud sediments (Newell & Hidu, 1982). This hypothesis needs testing since the site chosen to compare shell growth and shape is located in the estuary, where small sedimentation processes are unstable, but the sediment particle size distribution and organic content were not estimated during the *M. balthica* long-term monitoring programme. Hence, further study is required to make similar comparisons, but collections of clams from this part of the White Sea (either dry or preserved in alcohol/formalin) are difficult to find.

## CONCLUSIONS

Densities of *Macoma balthica* observed at different locations across the apex of Kandalaksha Bay (the White Sea) have tended to fluctuate in parallel during recent 20 years. These long-term population dynamics are affected by climatic factors. We conclude that *M. balthica* in the White Sea benefit from mild winters. Year-to-year fluctuations in abundance of the moonshell *Amauropsis islandica*, predated primarily on *M. balthica* at some sites studied, did not affect the general trend of clam dynamics. In addition, elevated seasonal temperatures in the White Sea may lead to changes in shell growth characteristics of *M. balthica*.

## SUPPLEMENTARY MATERIAL

The supplementary material for this article can be found at <https://doi.org/10.1017/S0025315417001473>.

## ACKNOWLEDGEMENTS

We are grateful to all participants of the White Sea expeditions of Laboratory of Marine Benthic Ecology and Hydrobiology in 1992–2012 for their help in the fieldwork and to the administration of Kandalaksha State Nature Reserve and personally to Alexander S. Koryakin for supporting our activity. We would like to thank Dr Vitaliy V. Bianki and Mikhail G. Bass for the productive discussion. We appreciate the comments which helped to enhance this paper of Dr Alexey A. Sukhotin and anonymous referees.

## FINANCIAL SUPPORT

The study was partially supported by RFBR grant No 16-34-00682, and SPbSU Action 2 research project No. 1.38.253.2014.

## REFERENCES

- Ambrose W.G., Carroll M.L., Greenacre M., Thorrold S.R. and McMahon K.W. (2006) Variation in *Serripes groenlandicus* (Bivalvia) growth in a Norwegian high-Arctic fjord: evidence for local-and large-scale climatic forcing. *Global Change Biology* 12, 1595–1607.
- Appeldoorn R.S. (1983) Variation in the growth rate of *Mya arenaria* and its relationship to the environment as analyzed through principal components analysis and the omega parameter of the von Bertalanffy equation [Soft shell clam populations]. *Fishery Bulletin United States, National Marine Fisheries Service* 81, 75–84.
- Aristov D., Varfolomeeva M. and Puzachenko G. (2015) All's good in a famine? *Hydrobia ulvae* as a secondary prey for juveniles of Iceland moonshells *Amauropsis islandica* at the White Sea sandflats. *Journal of the Marine Biological Association of the United Kingdom* 95, 1601–1606.
- Aristov D.A. (2013) The dynamic of predatory gastropod mollusk *Amauropsis islandica* (Gmelin, 1791) (Naticidae: Caenogastropoda) at the Kandalaksha Bay conservation area (White Sea). In Nemova N.N., Murzina S.A. and Mescheryakova O.V. (eds) *Proceedings of the XII Conference on Exploration, Sustainable Use and Protection of Natural Resources of the White Sea*. Petrozavodsk: Kola Research Center, pp. 21–23. [In Russian]
- Austin G.E. and Rehfish M.M. (2005) Shifting nonbreeding distributions of migratory fauna in relation to climatic change. *Global Change Biology* 11, 31–38.
- Azarov V.V. (1963) Fishes feeding at the intertidal zone of Ryashkov and Lodeyniy islands in the White Sea (Kandalaksha Bay). *Proceedings of Kandalaksha Reserve* 4, 35–53. [In Russian]
- Babkov A.I. and Golikov A.N. (1984) *Hydrobiocomplexes of the White Sea*. Leningrad: Zoological Institute AS USSR Publishers. [In Russian]
- Becquet V., Lasota R., Pante E., Sokolowski A., Wolowicz M. and Garcia P. (2013) Effects of fine-scale environmental heterogeneity on local genetic structure in *Macoma balthica* from the Gulf of Gdańsk (southern Baltic Sea). *Hydrobiologia* 714, 61–70.
- Berge J., Johnsen G., Nilsen F., Gulliksen B. and Slagstad D. (2005) Ocean temperature oscillations enable reappearance of blue mussels *Mytilus edulis* in Svalbard after a 1000 year absence. *Marine Ecology Progress Series* 303, 167–175.
- Beukema J.J. and Dekker R. (2005) Decline of recruitment success in cockles and other bivalves in the Wadden Sea: possible role of climate change, predation on postlarvae and fisheries. *Marine Ecology Progress Series* 287, 149–167.
- Beukema J.J. and Dekker R. (2014) Variability in predator abundance links winter temperatures and bivalve recruitment: correlative evidence from long-term data in a tidal flat. *Marine Ecology Progress Series* 513, 1–15.
- Beukema J.J., Dekker R., Essink K. and Michaelis H. (2001) Synchronized reproductive success of the main bivalve species in the Wadden Sea: causes and consequences. *Marine Ecology. Progress Series* 211, 143–155.
- Beukema J.J., Dekker R. and Jansen J.M. (2009) Some like it cold: populations of the tellinid bivalve *Macoma balthica* (L.) suffer in various

- ways from a warming climate. *Marine Ecology Progress Series* 384, 135–145.
- Beukema J.J., Dekker R., van Stralen M.R. and de Vlas J.** (2015) Large-scale synchronization of annual recruitment success and stock size in Wadden Sea populations of the mussel *Mytilus edulis* L. *Helgoland Marine Research* 69, 327–333.
- Beukema J.J., Essink K., Michaelis H. and Zwarts L.** (1993) Year-to-year variability in the biomass of macrobenthic animals on tidal flats of the Wadden Sea: how predictable is this food source for birds? *Netherlands Journal of Sea Research* 31, 319–330.
- Beukema J.J. and Meehan B.W.** (1985) Latitudinal variation in linear growth and other shell characteristics of *Macoma balthica*. *Marine Biology* 90, 27–33.
- Caddy J.F.** (1967) Maturation of gametes and spawning in *Macoma balthica* (L.). *Canadian Journal of Zoology* 45, 955–965.
- Caddy J.F.** (2010) Hydrodynamic sorting in the life history dynamics of *Macoma balthica* in a nursery area in the Thames estuary, England. *Ciencia Pesquera* 18, 14.
- Carroll M.L., Ambrose W.G., Levin B.S., Henkes G.A., Hop H. and Renaud P.E.** (2011) Pan-Svalbard growth rate variability and environmental regulation in the Arctic bivalve *Serripes groenlandicus*. *Journal of Marine Systems* 88, 239–251.
- Clements J.C. and Rawlings T.A.** (2014) Ontogenetic shifts in the predatory habits of the northern moonshell (*Lunatia heros*) on the Northwestern Atlantic Coast. *Journal of Shellfish Research* 33, 755–768.
- Compton T.J., Bodnar W., Koolhaas A., Dekinga A., Holthuijsen S., ten Horn J., McSweeney N., van Gils J.A. and Piersma T.** (2016) Burrowing behavior of a deposit feeding bivalve predicts change in intertidal ecosystem state. *Frontiers in Ecology and Evolution* 4, 1–9.
- de Wilde P.A.W.J.** (1975) Influence of temperature on behaviour, energy metabolism and growth of *Macoma balthica* (L.). In Barnes H. (ed.) *Proceeding of 9th European Marine Biology Symposium*. Aberdeen: Aberdeen University Press, pp. 239–256.
- Egorova E.N.** (2007) New data against the bipolar status of the genus *Amauropsis* (Naticidae, Mollusca) with a description of the new genus *Pseudoamauropsis* from Antarctic region. *Zoological Journal* 86, 16–29. [In Russian]
- Filatov N., Tolstikov A. and Zdorovenov R.** (2007) Features of variability in hydrophysical processes and fields. In Filatov N. and Terzhevik A. (eds) *The White Sea and their watershed under influences of climate and anthropogenic impact*. Petrozavodsk: Karelian Research Center RAS, pp. 189–257. [In Russian]
- Gerasimova A.V. and Maximovich N.V.** (2013) Age–size structure of common bivalve mollusc populations in the White Sea: the causes of instability. *Hydrobiologia* 706, 119–137.
- Gillmor R.B.** (1980) *Intertidal growth in suspension-feeding bivalves*. PhD thesis. University of Maine, Maine, USA.
- Golikov A.N.** (1987) Class Gastropoda. In Starobogatov Y.I. and Naumov A.D. (eds) *Mollusks of the White Sea*. Leningrad: Nauka, pp. 41–204. [In Russian]
- Hamilton L.C., Brown B.C. and Rasmussen R.O.** (2003) West Greenland's cod-to-shrimp transition: local dimensions of climatic change. *Arctic* 56, 271–282.
- Helmuth B., Mieszkowska N., Moore P. and Hawkins S.J.** (2006) Living on the edge of two changing worlds: forecasting the responses of rocky intertidal ecosystems to climate change. *Annual Review of Ecology, Evolution, and Systematics* 37, 373–404.
- Honkoop P.J.C. and Van der Meer J.** (1997) Reproductive output of *Macoma balthica* populations in relation to winter-temperature and intertidal-height mediated changes of body mass. *Marine Ecology Progress Series* 149, 155–162.
- Honkoop P.J.C., Van der Meer J., Beukema J.J. and Kwast D.** (1998) Does temperature-influenced egg production predict the recruitment in the bivalve *Macoma balthica*? *Marine Ecology Progress Series* 164, 229–235.
- Hulscher J.B.** (1982) The oystercatcher *Haematopus ostralegus* as a predator of the bivalve *Macoma balthica* in the Dutch Wadden Sea. *Ardea* 70, 89–152.
- Hummel H.** (1985) Food intake of *Macoma balthica* (Mollusca) in relation to seasonal changes in its potential food on a tidal flat in the Dutch Wadden Sea. *Netherlands Journal of Sea Research* 19, 52–76.
- Ivanova T.S., Ivanov M.V., Golovin P.V., Polyakova N.V. and Lajus D.L.** (2016) The White Sea threespine stickleback population: spawning habitats, mortality, and abundance. *Evolutionary Ecology Research* 17, 301–315.
- Jueterbock A., Tyberghein L., Verbruggen H., Coyer J.A., Olsen J.L. and Hoarau G.** (2013) Climate change impact on seaweed meadow distribution in the North Atlantic rocky intertidal. *Ecology and Evolution* 3, 1356–1373.
- Kabat A.R.** (1990) Predatory ecology of naticid gastropods with a review of shell boring predation. *Malacologia* 32, 155–193.
- Khaitov V.** (2013) Life in an unstable house: community dynamics in changing mussel beds. *Hydrobiologia* 706, 139–158.
- Khaitov V.M. and Lentsman N.V.** (2016) The cycle of mussels: long-term dynamics of mussel beds on intertidal soft bottoms at the White Sea. *Hydrobiologia* 781, 161–180.
- Khalaman V.V.** (2013) Regular and irregular events in fouling communities in the White Sea. *Hydrobiologia* 706, 205–219.
- Khalaman V.V. and Naumov A.D.** (2009) Long-term dynamics of common species of polychaetes in fouling communities of the White Sea. *Russian Journal of Marine Biology* 35, 463–473.
- Koryakin A.S.** (2012) Sea birds monitoring in Kandalaksha Bay of the White Sea (1967–2010 years). *Zoological Journal* 91, 800–808. [In Russian]
- Kuznetsov V.V.** (1960) *The White Sea and biological peculiarities of its flora and fauna*. Moscow-Leningrad: Academy of Sciences Publishers. [In Russian]
- Legendre P. and Legendre L.F.** (2012) *Numerical ecology*. Amsterdam: Elsevier.
- Luttikhuisen P.C., Drent J., Peijnenburg K., Van Der Veer H.W. and Johannesson K.** (2012) Genetic architecture in a marine hybrid zone: comparing outlier detection and genomic clines analysis in the bivalve *Macoma balthica*. *Molecular Ecology* 21, 3048–3061.
- Luttikhuisen P.C., Drent J., Van Delden W. and Piersma T.** (2003) Spatially structured genetic variation in a broadcast spawning bivalve: quantitative vs molecular traits. *Journal of Evolutionary Biology* 16, 260–272.
- MacKenzie B.R., Payne M.R., Boje J., Høyer J.L. and Siegstad H.** (2014) A cascade of warming impacts brings bluefin tuna to Greenland waters. *Global Change Biology* 20, 2484–2491.
- Malham S.K., Hutchinson T.H. and Longshaw M.** (2012) A review of the biology of European cockles (*Cerastoderma* spp.). *Journal of the Marine Biological Association of the United Kingdom* 92, 1563–1577.
- Marfenin N.N., Bolshakov F. and Mardashova M.** (2013) Fluctuations in settlement and survival of a barnacle *Semibalanus balanoides* in the White Sea intertidal. *Hydrobiologia* 706, 51–68.

- Marshall G.J., Vignols R.M. and Rees W.G. (2016) Climate change in the Kola Peninsula, Arctic Russia, during the last 50 years from meteorological observations. *Journal of Climate* 29, 6823–6840.
- Maximovich N.V. (1985) Peculiarities of ecology and reproduction cycle of *Macoma balthica* L. in the Chupa inlet. In Khlebovich V.V. and Skarlato O.A. (eds) *Biocoenosis of Chupa Bay at the White Sea and its seasonal dynamics. The investigations of marine fauna*. Leningrad: Nauka Publishers, pp. 230–243. [In Russian]
- Maximovich N.V., Gerasimova A.V. and Kunina T.A. (1991) Dynamics of structural characteristics in littoral beds of *Macoma balthica* L. in the Chupa Inlet (the White Sea). *Vestnik Leningradskogo Universiteta, Series 3 Biology* 2, 23–31. [In Russian]
- Maximovich N.V., Gerasimova A.V. and Kunina T.A. (1992) Production of *Macoma balthica* population in the Chupa Bay (the White Sea). I. Linear growth. *Vestnik Leningradskogo Universiteta, Series 3 Biology* 4, 12–19. [In Russian]
- Mokievskiy V.O., Popovkina A.B., Poyarkov N.D., Tzetlin A.B., Zhadan A.E. and Isachenko A.Yu. (2012) Foraging of common eider (*Somateria molissima*) wintering in Velikaya Salma strait (Kandalaksha Bay, the White Sea). *Zoological Journal* 91, 881–896. [In Russian]
- Naumov A.D. (2013) Long-term fluctuations of soft-bottom intertidal community structure affected by ice cover at two small sea bights in the Chupa Inlet (Kandalaksha Bay) of the White Sea. *Hydrobiologia* 706, 159–173.
- Naumov A.D., Savchenko O.N., Aristov D.A. and Biyagov K.L. (2014) Twenty-seven-years-long dynamics of biomass in fourteen benthic species from two sites at the White Sea intertidal. In Naumov A.D. (ed.) *49 European Marine Biology Symposium, St-Petersburg. Abstracts*. St-Petersburg: ZIN RAS, p. 54.
- Nehls G., Hertzler I. and Scheiffarth G. (1997) Stable mussel *Mytilus edulis* beds in the Wadden Sea – they're just for the birds. *Helgoland Marine Research* 51, 361–372.
- Newell C.R. and Hidu H. (1982) The effects of sediment type on growth rate and shell allometry in the soft shelled clam *Mya arenaria* L. *Journal of Experimental Marine Biology and Ecology* 65, 285–295.
- Nikula R., Strelkov P. and Väinölä R. (2007) Diversity and Trans-Arctic invasion history of mitochondrial lineages in the North Atlantic *Macoma balthica* complex (Bivalvia: Tellinidae). *Evolution* 61, 928–941.
- Oksanen J., Blanchet F.G., Friendly M., Kindt R., Legendre P., McGlenn D., Minchin P.R., O'Hara R.B., Simpson G.L., Solymos P., Stevens M.H.H., Szoecs E. and Wagner H. (2016) *vegan: community ecology package*. <https://CRAN.R-project.org/package=vegan>.
- Olafsson E.B. (1986) Density dependence in suspension-feeding and deposit-feeding populations of the bivalve *Macoma balthica*: a field experiment. *Journal of Animal Ecology* 55, 517–526.
- Parkinson C.L. (2014) Spatially mapped reductions in the length of the Arctic sea ice season. *Geophysical Research Letters* 41, 4316–4322.
- Pertsov N.A. (1963) Some new data on feeding of birds during breeding season at Northern Archipelago, Kandalaksha State Reserve. *Proceedings of Kandalaksha Reserve* 4, 29–34. [In Russian]
- Philippart C.J., van Aken H.M., Beukema J.J., Bos O.G., Cadée G.C. and Dekker R. (2003) Climate-related changes in recruitment of the bivalve *Macoma balthica*. *Limnology and Oceanography* 48, 2171–2185.
- Pinheiro J. and Bates D. (2006) *Mixed-effects models in S and S-PLUS*. New York, NY: Springer Science & Business Media.
- R Core Team (2016) *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Sarà G., Palmeri V., Montalto V., Rinaldi A. and Widdows J. (2013) Parameterisation of bivalve functional traits for mechanistic eco-physiological dynamic energy budget (DEB) models. *Marine Ecology Progress Series* 480, 99–117.
- Sartori A.F. (2016) *Limecola balthica* (Linnaeus, 1758). In *MolluscaBase*. Accessed through: World Register of Marine Species at <http://www.marinespecies.org/aphia.php?p=taxdetails&id=880017> on 2017-01-19.
- Seed R. (1968) Factors influencing shell shape in the mussel *Mytilus edulis*. *Journal of the Marine Biological Association of the United Kingdom* 48, 561–584.
- Seitz R.D. and Lipcius R.N. (2001) Variation in top-down and bottom-up control of marine bivalves at differing spatial scales. *ICES Journal of Marine Science: Journal du Conseil* 58, 689–699.
- Sejr M.K., Blicher M.E. and Rysgaard S. (2009) Sea ice cover affects inter-annual and geographic variation in growth of the Arctic cockle *Clinocardium ciliatum* (Bivalvia) in Greenland. *Marine Ecology Progress Series* 389, 149–158.
- Selin N.I. (2008) Feeding behavior, ration and size structure of a population of the predatory gastropod *Cryptonatica janthostoma* in Vostok Bay, Sea of Japan. *Russian Journal of Marine Biology* 34, 186–190.
- Semenova N.L. (1974) Distribution of bivalve mollusk *Macoma balthica* (L.) in some inlets of Kandalaksha Bay at the White Sea. *Proceedings of the White Sea Biological Station of Moscow State University* 4, 87–102.
- Sergievskiy S.O., Granovitch A.I. and Sokolova I.M. (1997) Long-term studies of *Littorina obtusata* and *Littorina saxatilis* populations in the White Sea. *Oceanologica Acta* 20, 259–265.
- Strasser M., Dekker R., Essink K., Günther C.-P., Jaklin S., Kröncke I., Madsen P.B., Michaelis H. and Vedel G. (2003) How predictable is high bivalve recruitment in the Wadden Sea after a severe winter? *Journal of Sea Research* 49, 47–57.
- Strelkov P., Nikula R. and Väinölä R. (2007) *Macoma balthica* in the White and Barents Seas: properties of a widespread marine hybrid swarm (Mollusca: Bivalvia). *Molecular Ecology* 16, 4110–4127.
- Sukhotin A. and Berger V. (2013) Long-term monitoring studies as a powerful tool in marine ecosystem research. *Hydrobiologia* 706, 1–9.
- Sveshnikov V.A. (1963) Biocenotic relations and environmental conditions of some food invertebrates of intertidal infauna in the Kandalaksha Bay of the White Sea. *Proceedings of Kandalaksha Reserve* 4, 114–134. [In Russian].
- Tolmacheva E.L. (2013) *Ecology of common species of suborder Lari of the White Sea*. PhD thesis. Petrozavodsk State University, Petrozavodsk, Russia.
- Usov N., Kutcheva I., Primakov I. and Martynova D. (2013) Every species is good in its season: do the shifts in the annual temperature dynamics affect the phenology of the zooplankton species in the White Sea? *Hydrobiologia* 706, 11–33.
- Varfolomeeva M. and Naumov A. (2013) Long-term temporal and spatial variation of macrobenthos in the intertidal soft-bottom flats of two small bights (Chupa Inlet, Kandalaksha Bay, White Sea). *Hydrobiologia* 706, 175–189.
- Vignali R. and Galleni L. (1986) Naticid predation on soft bottom bivalves: a study on a beach shell assemblage. *Oebalia* 13, 157–178.
- Visser G.H., Dekinga A., Achterkamp B. and Piersma T. (2000) Ingested water equilibrates isotopically with the body water pool of a shorebird with unrivaled water fluxes. *American Journal of Physiology – Regulatory, Integrative and Comparative Physiology* 279, R1795–R1804.
- von Bertalanffy L. (1938) A quantitative theory of organic growth (inquiries on growth laws. II). *Human Biology* 10, 181–213.

- Wassmann P., Duarte C.M., Agusti S. and Sejr M.K.** (2011) Footprints of climate change in the Arctic marine ecosystem. *Global Change Biology* 17, 1235–1249.
- Wethey D.S., Woodin S.A., Hilbish T.J., Jones S.J., Lima F.P. and Brannock P.M.** (2011) Response of intertidal populations to climate: effects of extreme events vs long term change. *Journal of Experimental Marine Biology and Ecology* 400, 132–144.
- Wiltse W.I.** (1980) Effects of *Polinices duplicatus* (Gastropoda: Naticidae) on infaunal community structure at Barnstable Harbor, Massachusetts, USA. *Marine Biology* 56, 301–310.
- Wood S.** (2006) *Generalized additive models: an introduction with R*. Boca Raton, FL: CRC Press.
- Zubakha M.A., Poloskin A.V. and Goltsev N.A.** (2000) Peculiarities in reproduction and recruitment of *Macoma balthica* L. population at the White Sea. *Vestnik Sankt-Peterburgskogo Universiteta. Series 3: Biology* 2, 108–115. [In Russian].
- Zuur A., Ieno E.N., Walker N., Saveliev A.A. and Smith G.M.** (2009) *Mixed effects models and extensions in ecology with R*. New York, NY: Springer Science & Business Media.
- and
- Zwarts L. and Blomert A.-M.** (1992) Why knot *Calidris canutus* take medium-sized *Macoma balthica* when six prey species are available. *Marine Ecology Progress Series* 83, 113–128.

**Correspondence should be addressed to:**

S.A. Nazarova

Marine Research Lab, Zoological Institute, Russian Academy of Science, Universitetskaya emb., 1, Saint-Petersburg, 199034, Russia

email: [sophia.nazarova@gmail.com](mailto:sophia.nazarova@gmail.com)