PRIMARY RESEARCH PAPER



# The cycle of mussels: long-term dynamics of mussel beds on intertidal soft bottoms at the White Sea

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**Abstract** Dense blue mussel assemblages are unstable, their structure changing from year to year. Three types of models can be used to describe this instability: (1) "exogenous" model based on regional temperature fluctuations, (2) "endogenous" deterministic model associated with negative impact of adult mussels on juveniles and (3) "density-linked stochasticity" model based on positive feedbacks resulting in overcrowding and destabilizing the settlement. We compared predictions deduced from these models with a time series based on the results of long-term (18 years)

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N. V. Lentsman Department of Ichthyology and Hydrobiology, St Petersburg State University, St Petersburg, Russia e-mail: arcella1@yahoo.com monitoring of abundance and demographic structure of three mussel beds at the White Sea. Most of our findings agreed well with the predictions deduced from the endogenous model. In particular, (1) longterm changes in mussel abundance and demographic structure were strictly cyclic, with non-matching periods (5–9 years) at different sites; (2) stages with the dominance of old mussels alternated with those where juveniles dominated and (3) some signals of delayed density dependence were revealed. However, the time series also contained elements of long-term trends, which may testify to the involvement of some exogenous factors (probably long-term climate changes).

**Keywords** *Mytilus* · Mussel beds · Population dynamics · Long-term changes

## Introduction

Long-term monitoring data on marine ecosystems present a challenge for researchers trying to explain and forecast changes in populations and communities. Models emulating the dynamics of ecological systems are the distillation of our knowledge in this respect as well as an indispensable forecasting tool. While researchers studying plankton have already made headway in the construction of dynamic models (Franks, 2002), similar studies of benthic systems are just starting. A key to a successful development of a model is the choice of suitable objects, which should show clear structural and dynamical patterns and be easy to study. Communities associated with dense assemblages of ecosystem engineers such as marine shallow-water bivalves are the best candidates for this role.

Dense assemblages of blue mussels (*Mytilus edulis* L., *M. trossulus* Gould, and other related species) are a strong presence in marine shallow-water bottom communities (Buschbaum et al., 2009). These sessile bivalves are influential ecosystem engineers, and changes in their populations may be crucial for numerous associated species (Khaitov, 2013). Mussel assemblages are unstable systems, that is, their population structure (McGrorty et al., 1990; Khaitov, 2013), abundance (Beukema et al., 2010), recruitment (Beukema & Dekker, 2014) and cover (Wootton & Forester, 2013) may change dramatically from year to year.

In general, temporal fluctuations in natural populations can be explained by an exogenous regulation, an endogenous regulation or a combination of the two (Berryman, 1989). Correspondingly, three types of models can be developed. (1) Purely exogenous, or stochastic, models are usually proposed if there is a strong correlation between population parameters and some external factor or factors. The correlation between population parameters and sunspots cycles or hydrologic cycles is a famous example (Gray & Christie, 1983). To note, calling a factor "exogenous" or "external", we mean that there is no feedback to it in the population (Berryman, 1989). (2) Purely endogenous, or deterministic, models apply if there are internal regulatory mechanisms (positive or negative feedbacks). These models usually predict a strongly specific pattern of the population time series (e.g. population cycles). By the same token, if such a pattern is found, there are good reasons to consider an endogenous model for the system. (3) The models of the third type apply if external stochastic impacts are effective only when, owing to some intra-population processes, the population parameters achieve critical values (see Wootton & Forester, 2013 and examples therein).

In this paper, we consider those models of these three types that have been specially developed for long-term dynamics of *Mytilus* populations on the basis of long-term monitoring. It should be noted that numerous models of this kind have been extensively used for land ecosystems (Berryman, 1996; Ginzburg & Taneyhill, 1994 and references therein) and some of them might be applicable to mussels. Such an extrapolation, however, was outside the scope of our study.

Within the "exogenous" approach, the instability of mussel populations has been explained as a consequence of climate changes. In particular, the role of regional temperature was highlighted during long-term monitoring of intertidal mussel populations in the Wadden Sea (Beukema & Dekker, 2014), where mussel recruitment success was shown to be closely correlated with temperature fluctuations.

The "endogenous" approach to mussel population dynamics focuses on the role of density-dependent regulatory processes, that is, negative feedbacks. There is ample evidence of a negative correlation between adults and juveniles in dense mussel assemblages (Okamura, 1986; Lehane & Davenport, 2004; Khaitov, 2013). Since the negative influence of adult animals upon conspecific juveniles leads to endogenous population instability (Claessen et al., 2004), the population will change even without any external influence.

Instability based on negative interactions within a population often manifests itself in population cycles (Claessen et al., 2004). Such cycles have been revealed in populations of the zebra mussel Dreissena polymorpha (Strayer & Malcom, 2006), the freshwater counterpart of Mytilus. Mathematical models based on negative adult-juvenile interactions in D. polymorpha predict regular endogenous cyclic changes in abundance and demographic structure (Maclsaac et al., 1991; Strayer & Malcom, 2006; Casagrandi et al., 2007). A model, which is very similar to that of Casagrandi et al. (2007), has been independently developed for Mytilus edulis populations in the White Sea (Lukanin et al., 1986; Naumov, 2006). It is also based on the negative influence of adult mussels upon juveniles and predicts cyclic patterns in long-term changes in abundance and age/size structure of local mussel settlements. To note, the models by Casagrandi et al. (2007) and Naumov (2006) can be considered as particular cases within the framework of the demographic theory for an open population with spacelimited recruitment (Roughgarden et al., 1985).

According to the "endogenous" model (in the version of Lukanin et al., 1986; Naumov, 2006),

mussel demographic structure should change in a cyclic fashion, with several distinct types of size/age composition substituting each other in the course of time (Fig. 1). To begin with, adult mussels strongly inhibit recruitment. This negative impact could be direct (through filtering out of larvae) or indirect (through organic pollution of the biotope by faecal and pseudo-faecal pellets produced by adults). The recruitment can occur only after most or all old molluscs die. Then the population is dominated by young small mussels (Stage 1: unimodal size/age distribution with small sizes/ages as modal classes; Fig. 1). As mussels grow, the intensity of the negative influence upon recruits increases, recruitment stops and the population starts to be dominated by middle-aged individuals (Stage 2: unimodal size/age distribution with meddle sizes/ages as modal classes; Fig. 1). At Stage 3 (Fig. 1), the population is dominated by old large mussels, which still inhibit recruitment. After that two scenarios are possible. If larval supply is high, the recruitment starts when most (but, importantly, not all) old mussels die, leading to the bimodal size/age distribution (Stage 4-a; Fig. 1). If larval supply is weak (for example, in areas with slow water currents), the settlement may be expected to dwindle or collapse (Stage 4-b; Fig. 1). It remains to be said that this "cyclic" model, though well developed theoretically (Naumov, 2006; Casagrandi et al., 2007), has never been tested "in action" so far.

The model of the third type, referred to as "densitylinked stochasticity" (DLS), was developed for *Mytilus californianus*, which forms dense assemblages on exposed rocks (Wootton & Forester, 2013). DLS model, contrary to the previous one, is based on positive interactions between old mussels and juveniles. This positive feedback leads to an increase of population density up to the point when most mussels are attached to each other rather than to the primary rock surface. When the population reaches this critical stage, stochastic exogenous forces (e.g. wave impact) come into play destroying the settlement. Thus, this model takes into account the effects of random environmental impacts superimposed upon the deterministic skeleton of population changes.

In spite of the long history of mussel population monitoring (Wootton & Forester, 2013; Beukema & Dekker, 2014), no attempts have been made to compare the predictions of the different models with the behaviour of time series observed. This study aimed to fill this gap by testing predictions that could be deduced from the purely exogenous, purely endogenous and DLS approaches.

The predictions deduced from the "exogenous" model were based on the assumption about the key

**Fig. 1** Scheme of longterm dynamics of mussel size/age structure according to the "endogenous" model (after Lukanin et al., 1986). *L* mussel size or age, *N* abundance



role of the regional temperature (or, more precisely, the key role of climatic factors associated with regional temperature) in driving long-term changes in mussel populations (Beukema et al., 2001; Beukema & Dekker, 2014). The role of climatic factors is expected to be even higher for intertidal mussel beds in the Arctic, where disturbances associated with ice impact (Naumov, 2013) and the availability of planktonic primary producers mussels feed on (Leu et al., 2011) strongly depend on regional temperature.

So, the predictions deduced from the "exogenous" model (we will consider them as hypotheses to be tested) were as follows. Since all mussel beds are influenced by the same climatic factors, the long-term changes in the abundance and size structure should be coordinated in the neighbouring mussel beds (Exo1). Long-term changes in the abundance and size structure of mussel populations should show some correspondence with the long-term changes in the regional temperature (Exo2).

The predictions deduced from the "endogenous", deterministic model (Naumov, 2006; Casagrandi et al., 2007) were as follows. Since changes regulated by biotic interactions act at a small spatial scale (Zajac et al., 1998), they should be independent (that is, noncoordinated) in spatially distant mussel beds (Endo1). The time series should be stationary, i.e. population parameters should fluctuate around an invariable equilibrium value (Endo2), as this is the main assumption for models based on density-dependent regulation (Turchin & Taylor, 1992). Regular cycles should be present in the dynamics of abundance and size structure of any given mussel population (Endo3), since it is the only possible pattern of changes predicted by this model (Naumov, 2006; Casagrandi et al., 2007). The patterns of inter-annual changes in the size structure of a mussel bed should be similar to those presented in Fig. 1: long-term dynamics of mussel beds could be described as the cyclic interchanges of stages with small mussels as dominants followed by stages dominated by large mussels (Endo4). Since the endogenous model is based on density-dependent regulation, the density dependence could be revealed in analysis of structure of the time series (Endo5).

Finally, we deduced one general prediction from the DLS model. This model forecasts a very special pattern of changes in mussel abundance: a sharp drop followed by a steady increase followed by another sharp drop and so on (Wootton & Forester, 2013). Thus, the strongest changes in abundance should occur after periods of population density peaks (*DLS*).

In this study, we compare these predictions with data on abundance and demographic structure (assessed as the composition of different size classes) of mussel populations collected annually for 18 years at three mussel beds located in a small fjord-like bay at the White Sea.

## Materials and methods

#### Collection design

The study was conducted in the Voronya Bay (Kandalaksha Bay, White Sea, Fig. 2), where 3 mussel beds (denoted as Vor2, Vor4 and Vor5) were monitored annually. The mussel beds had a very small area (less than 0.5 ha), which is typical of permanent mussel beds at the intertidal of the White Sea. The detailed description of the study area and the sampling procedure can be found in our previous work (Khaitov, 2013). Briefly, the sampling procedure was as follows. Six samples placed inside haphazardly chosen mussel patches were taken at each of the three beds between August 1 and August 15 annually in 1996-2013 (in 1996, 5 samples were taken at each bed; in 1998, Vor5 was not sampled and only 5 samples were taken at Vor4). A round core with an area of  $55 \text{ cm}^2$  was thrown at random onto the mussel bed. The same person (V.Kh.) made all the collections, so we can be fairly sure that the sampling was carried out in a uniform way throughout the study period. If a randomly thrown core landed on a mussel-free area, the nearest mussel patch was sampled. The samples were washed through a sieve with a 0.5-mm mesh, all the mussels were picked out and their length was measured using a calliper or a stereo-microscope (with ocular micrometer) to the nearest 1 mm. The validity of this sampling design is discussed in the electronic supplement (Appendix 1 in Supplementary material).

#### Quantitative data representation

To assess the mussel population structure, we used two types of quantitative data: univariate and multivariate. The mussel size scale was divided into 6 classes (with a 10 mm step) and the abundance of mussels of each class in each sample was calculated. In this way, the



Fig. 2 Voronya Bay and the positions of the three mussel beds under study

Size-Class Abundance Matrix (SCAM, see Khaitov, 2013) was constructed: it contained 6 variables (size classes) and 314 samples. So, SCAM is the multivariate representation mussel size structure in each sample. The sum of all variables for each sample in SCAM represents the total mussel abundance in each sample. The average total abundance was also calculated for each mussel bed in each year. The total abundance (and annually averaged one) was considered as univariate datasets describing mussel population. For all statistical procedures (see bellow), the total mussel abundances and elements of SCAM were log-transformed  $(\ln(N + 1))$ . This transformation is needed to meet the assumptions in regression (Zuur et al., 2009) and in distance-based multivariate analysis (Clarke & Gorley, 2006).

On the basis of SCAM, the Average Size-Class Abundance Matrices (ASCAM) were calculated separately for each mussel bed. Each ASCAM contained the mean abundances of mussels from different size classes in a particular bed in a given year. Years were considered as samples and size classes as variables in the ASCAM. Each sample in ASCAM describes the mussel size structure at particular mussel bed in given year. Thus, ASCAMs were considered as multivariate datasets describing averaged mussel size structure. For all followed statistical procedures elements of ASCAM were log-transformed.

Data on averaged monthly air temperature were extracted from the annual reports of the Kandalaksha nature reserve ("The Chronicle of Nature of the Kandalaksha Reserve") for 1995-2000 and from the archives stored in the Internet site http://www.rp5.ru (2001–2013) for Kandalaksha weather station (WMO station index 22217; 18 km from the Voronya Bay). The averaged monthly temperature matrix (AMT matrix) was constructed, where months were treated as variables and years as samples. To note, the AMT matrix contained temperatures for January-August of the calendar year of sampling and for September-December of the previous calendar year. In this way, an AMT matrix represented a temperature during mussel "biological" year (see above). The AMT matrix was used as a multivariate and annually averaged temperature as a univariate characteristic of the temperature conditions in the region in different years.

In several further analyses, we transformed our initial data (multivariate and univariate) into form of matrices of Euclidian Distances between pairs of time

points (years). The calculation of these matrices is discussed in detail in electronic supplement (Appendix 1 in Supplementary material). In sum, we calculated two types of matrices: Euclidean Distances Multivariate (EDM) and Euclidean Distances Univariate (EDU) matrices. EDM is the usual triangular matrix containing Euclidean Distances between pairs of years, calculated on the basis of Multivariate datasets. EDM was calculated for each mussel bed separately on the basis of elements of their ASCAM. EDU is a matrix of the same type as EDM but calculated on the basis of only singular, univariate variable. Additionally, we calculated EDM and EDU on the basis of temperature data.

Mathematical formulation of deduced predictions and statistical approaches to test them

## Prediction Exol

If the parameters of changes in mussel beds are strongly coordinated, then (1), in the case of the univariate dataset, the general additive regression model (GAM) containing only one smoother, common for all mussel beds, should be better than the regression model containing three different smoothers calculated for each particular mussel bed; (2), in the case of multivariate dataset, no significant interactions between factors "Site" and "Year" should be found in two-factor PERMANOVA. Otherwise the prediction *Endo1* would be confirmed.

To test this prediction for univariate dataset (total mussel abundance in each sample), we calculated the parameters of two GAM (Zuur et al., 2009):

GAM1 : 
$$L_{ij} = \beta_0 + f_{com}(Year_i) + \beta_1 Site + \varepsilon_{ij}$$
(1)

$$GAM2 : L_{ij} = \beta_0 + f_1(\text{Year}_i \text{ in Vor2}) + f_2(\text{Year}_i \text{ in Vor4}) + f_3(\text{Year}_i \text{ in Vor5}) + \beta_1 \text{Site} + \varepsilon_{ij}.$$
(2)

Here  $L_{ij}$  is the log-transformed total mussel abundance in sample *j* in year *i*,  $\beta_0$  is the intercept,  $\beta_1$  slope coefficient for Site, as factor,  $f_{com}$  is the common smoother for all sites,  $f_1, f_2, f_3$  is the smoothers for each particular mussel bed,  $\varepsilon$  is the residuals. These two models were compared using the Akaike information criterion (AIC). If *Exol* is correct, the AIC for GAM1 should be lower than AIC for GAM2, i.e. the first regression model should be better. R-statistical environment version 2.15.0 (R Development Core Team, 2012) was used for these and all the following statistical calculations (if not indicated otherwise). For the GAM calculations, above "gam()" function from package "mgcv" was used.

Two-factor PERMANOVA (Anderson, 2005) was performed with "Site" (3 levels: Vor2, Vor4, Vor5) and "Year" (16 levels; to balance the complex, the data of 1998, when Vor5 was not sampled, were excluded; the data of 1996, when only 5 samples were taken at each bed, were also excluded) as fixed orthogonal factors. As a dependent dataset we used log-transformed elements of SCAM (Euclidean Distance was used as dissimilarity metric). The function "adonis()" from the package "vegan" was used for the above analysis. The homogeneity of dispersion was checked by PERMDISP software (Anderson, 2001) before the PERMANOVA analysis.

#### Prediction Exo2

If mussel population parameters depend on regional temperature, then there should be some congruence between the two time series.

To test this association, cross-correlation analvsis between the mean total abundance time series and the time series reflecting the annually averaged temperature was performed. The temperature was lagged back (negative lags) in relation to mussel abundance and for each lag, the correlation coefficients were calculated. The significance of correlation coefficients was assessed by Bartlett's criterion  $2/\sqrt{n}$ , where n is the length of the time series. It should be noted that significant correlations revealed in the cross-correlation analysis are not true correlations between mussel abundance and temperature. Rather, they indicate some congruence in the dynamics of these two parameters. This congruence, predicted by Exo2, may be obscure due to weak associations and strong noise in the time series. Therefore, in order not to miss any possible signals of congruence, we took into account all correlations that meet Bartlett's criterion, even low ones. The function "ccf()" from the package "stats" was used for the calculations.

To analyse the association between regional temperature and the size structure of a mussel bed, we used Mantel correlation approach (Clarke & Gorley, 2006; Legendre & Legendre, 2012). For the analysis, we used EDM matrices calculated on the basis of both temperature data and ASCAM. These Euclidean distance matrices were then compared to test the match between them using Mantel correlation. Spearman's rank correlation coefficient was used as a statistic in the procedure with the permutation test for significance assessment (here and in the following analyses 999 permutations were run). The function "mantel()" from the package "vegan" was used.

### Prediction Endo1

If changes in the population parameters of different mussel beds are non-coordinated, then (1), for univariate dataset, AIC for GAM2 should be smaller than AIC for GAM1, i.e. the regression model containing only smoothers calculated for each mussel bed separately should be better than the regression model including common for all mussel beds pattern of changes; (2), for multivariate dataset, significant interaction between factors "Year" and "Site" should be revealed in two-factor PERMANOVA. The test of this prediction was described earlier (*Exo1*).

#### Prediction Endo2

If the time series is stationary, then no significant trend in population parameters (either abundance or size structure) should be present.

To reveal the presence of trends, if any, in both univariate and multivariate time series, we used a "model matrix" approach (Clarke & Gorley, 2006; Legendre & Legendre, 2012). This technique, proven to be effective in the analysis of the spatial data series (Clarke & Warwick, 2001; Borcard & Legendre, 2012), is applicable to the time series as well (Clarke & Warwick, 2001; Clarke & Gorley, 2006).

We constructed the gradient matrix as the Euclidean distance matrix between 18 successive time points as described in Clarke & Gorley (2006). Then EDU and EDM matrices computed for each mussel bed were compared with the gradient model matrix by Mantel correlation. If the analysis revealed significant results, it was considered as an evidence of the presence of a trend in a particular time series. This analysis was also applied to EDU and EDM matrices calculated for temperature data.

## Prediction Endo3

If regular cyclic components are present in the dynamics of abundance and size structure, the congruence between time series (univariate or multivariate) and periodic cos-like or sin-like function should be found.

We used, again, the "model matrix technique" to test this prediction but cyclic matrices instead gradient ones were constructed. The general procedure of cyclic matrix calculation was described in detail by Clarke and Gorley (2006). The algorithm used in our investigation is given in the electronic supplement (Appendix 1 in Supplementary material). Shortly, the cyclic matrices are the matrices of Euclidean distances between points evenly distributed around a circle with some period. We constructed 16 cyclic matrices for the periods of 3-18 years. After the matrices were constructed, the Mantel correlation was used to compare each cyclic matrix with EDU and EDM matrices representing interannual variations of population parameters. However, since some trends could be found in both univariate and multivariate time series, we used the partial Mantel correlations (Legendre & Legendre, 2012) with gradient matrix (see above) as covariate. The same analysis was applied to EDU and EDM matrices based on temperature data to reveal cyclic components in the long-term temperature dynamics.

The results of the analysis described could be presented as a periodogram (the period of cyclic matrix as the abscissa and the partial Mantel correlation as the ordinate). The significance of the partial Mantel correlation was assessed by permutation procedure as described in Legendre & Legendre (2012). If permutation test revealed a significant match between the EDU or EDM matrix with the cyclic matrix of particular period, it was considered as an evidence of the presence of the cyclic component with the corresponding oscillation period. We considered results as significant at both P < 0.05 and P < 0.1.

# Prediction Endo4

If the endogenous model is appropriate for the observed time series, then the size structure of

mussel beds should demonstrate a corresponding temporal sequence of size structures. Unimodal sizefrequency distribution with small mussels as dominants should change over to unimodal distribution with large mussels as dominants. The latter size structure should change over to bimodal size distribution. The latter should change over to the unimodal distribution with small mussels as dominants. So, the phase portrait of the system should look like a set of loops, with the points moving between the stages described above.

To test this prediction, we used EDMs reflecting inter-annual variation in size structure of each mussel beds for non-metric multidimensional scaling (nMDS) ordination performed for all mussel beds separately, so that a long-term trajectory in their size structure dynamics could be visualized. We considered the size structure of mussel beds at extreme positions of the nMDS ordination.

# Prediction Endo5

If the observed time series are based on densitydependent negative feedbacks, as predicted by the deterministic model, then the Partial Rate Correlation Function (PRCF, Berryman & Turchin, 2001) should include several non-zero components.

PRCF analysis was performed according to the recommendations of Berryman & Turchin (2001). Before the analysis, all total mussel abundance time series were detrended by subtracting the linear regression line (Legendre & Legendre, 2012). The algorithm of the subsequent analysis is described in the electronic supplement (Appendix 1 in Supplementary material). Briefly, PRCF provides information on the dependence of the rate of changes in mussel abundance in time t on the abundance of mussels in time t-d. High and significant negative PRCF values denote a decreased rate of changes as a response to a high abundance of mussels in the previous time (negative feedback). Positive values, if any, denote increased population growth as a response to a high abundance (positive feedback).

The significance of the PRCF values were assessed by Bartlett's criterion  $(2/\sqrt{n})$ , where *n* is the length of the time series (Berryman & Turchin, 2001). Additionally, we assessed the 99% confidence intervals for each PRCF values using bootstrapping of time series (999 bootstrap replicates). The bootstrapping of time series was performed by function "tsboot()" from the package "boot". We consider the PRCF values as significant if zero value was not included into the confidence intervals.

## Prediction DLS

If the strongest changes in population parameters are associated with the periods following the population density peaks, then  $L_t$  (log-transformed population density in time *t*) being regressed versus  $L_{t-1}$  (log-transformed population density in the previous time period) should demonstrate a highly heteroscedastic pattern (Wootton & Forester, 2013).

To test this prediction, we fitted the linear regression  $L_t = b_0 + b_1L_{t-1} + \varepsilon$  (for each mussel bed separately) and assessed it for the homogeneity of dispersion using Breusch–Pagan test. The test was performed by function "bptest()" from the package "Imtest".

## Results

The test for the predictions of Exo1 and Endo1

The mean total mussel abundance varied broadly from year to year and between sites (Fig. 3B–D). The AIC for GAM1 was greater than that for GAM2 (393.1 and 303.2 correspondingly). This means that GAM2 is a better regression model. It predicts different tendencies in long-term changes for different mussel beds and, hence, there is no obvious tendency common for all the three mussel beds. All the smoothers fitted by GAM2 were significant (F = 19.7; P < 0.001 for Vor2; F = 10.2; P < 0.001 for Vor4; F = 3.1; P = 0.0054 for Vor5) and in a good agreement with the changes in mean total abundance (Fig. 3).

In the case of size structure dynamics (multivariate case), the interaction between factors Year and Site was significant (PERMANOVA, pseudo $F_{\text{Year}^*\text{Site}} = 12.67$ , P < 0.001). Hence, long-term changes in size structure did not show any pattern of long-term changes common for all mussel beds (see also electronic supplement, Appendix 2).

The test for the prediction of Exo2

The average annual temperature followed a clear upand-down pattern (Fig. 3A), with minimums in 1996, 1998, 2003, 2007, 2010–2011 and 2013 and maximums in 1997, 2000 2001, 2006, 2008 and 2012. A significant positive cross-correlation between the mussel abundance and the average annual temperature in the same year (that is, with a zero lag) was observed only in the case of Vor2 (Table 1). However, three significant positive cross-correlations with negative lags were found for two mussel beds: -1 and -4 years for Vor2 and -3 years for Vor5. The highest (though marginally significant; r = 0.448) positive correlation at Vor4 was also associated with the lag of -3 years.

Mantel correlations between multivariate Euclidean distance (EDM) matrices calculated on the basis of temperature data (AMT matrix) and ASCAMs were not significant for all the mussel beds ( $\rho = 0.12$ ;  $\rho = 0.01$ ;  $\rho = 0.06$  for Vor2, Vor4 and Vor5 respectively; P > 0.1 in all cases). Hence, there were no clear correspondence between the patterns of temperature dynamics and those of size structure dynamics.

The test for the prediction of Endo2

The Mantel correlations between univariate Euclidean distance (EDU) matrices and gradient matrix were significant only in the case of annual mean temperature ( $\rho = 0.28$ ; P = 0.013) and total mussel abundance at Vor2 ( $\rho = 0.59$ ; P < 0.001). The same analysis in the case of multivariate Euclidean distance matrices (EDM) revealed significant matches with gradient matrix for all the mussel beds ( $\rho = 0.61$ , P < 0.001 for Vor2;  $\rho = 0.22$ , P = 0.022 for Vor4;  $\rho = 0.40$ , P = 0.002 for Vor5). However, no matches with gradient matrix were revealed for EDM matrix describing variations in temperature ( $\rho = 0.12$ , P = 0.114).

Thus, some elements of trends were found in all the parameters involved in the analysis, both those related to mussel beds and those related to the regional temperature.

The test for the prediction of Endo3

Periodogramms based on partial Mantel correlations between univariate Euclidian distance matrices (EDU) and cyclic matrices (Fig. 4) were sufficiently close to Fig. 3 Long-term changes in A annually averaged regional temperature; B-D total mussel abundance (mean  $\pm$  SE). The *dotted lines* represent the values predicted by GAM2 (see text for details)



 Table 1 Results of cross-correlation analysis of dependence

 between mussel abundance and average annual temperature

Lag	Vor2	Vor4	Vor5
0	0.475	-0.072	0.009
-1	0.529	-0.184	0.008
-2	0.373	0.226	0.284
-3	0.377	0.448	0.535
-4	0.490	0.21	0.394
-5	0.185	0.115	0.047
-6	-0.132	0.172	0.004
-7	0.037	0.081	0.282
-8	0.134	0.124	0.314
-9	0.156	-0.073	-0.254

Significant correlations are shown in bold

those calculated on the basis of multivariate Euclidean distance matrices (EDM). The temperature time series (univariate as well as multivariate) clearly signalled the presence of a cyclic component with a period of 4 years. In the case of multivariate time series of Vor2 (i.e. the long-term changes in size structure), a high, though marginally significant (0.05 < P < 0.1), Mantel correlation was found for comparison of EDM with the cyclic matrix with a period of 9 years. Univariate time series (i.e. total mussel abundance dynamics) for Vor4 signalled the presence of cyclic components with a period of 5–6 years. In the case of Vor5, both EDM (size structure) and EDU (total abundance) showed the presence of some cyclic components with a period of 7–9 years. A weak, marginally significant signal of the presence of a 4-year cycle was revealed in the case of the univariate time series at Vor5.

#### The test for the prediction of Endo4

The size structure varied clearly from year to year in all the beds (Fig. 5), the trajectory of point movement being obviously different in all the cases. At the same time, several features of the size structure dynamics were common for all the mussel beds. Firstly, the Fig. 4 Partial Mantel correlations between Euclidian distance matrices (based on univariate and multivariate data) and cyclic model matrices of different periods. The gradient model matrix was used as the third (covariate) matrix for partial correlation calculations. A Analysis based on time series of regional temperature; **B–D** analysis based on population parameters



cyclic character of the size-structure changes was noticeable in all the cases, being reflected in the loops of the trajectory of point movement. Secondly, all the mussel beds showed, at different times, three similar types of size-frequency distributions: (1) unimodal distribution with the dominance of large mussels and the lack of small ones (e.g. Vor2 in 1998; Vor4 in 1999; Vor5 in 1999), (2) virtually unimodal distribution with the dominance of small mussels and the lack of large ones (e.g. Vor2 in 2009; Vor4 in 2011; Vor5 in 2008) and (3) bimodal distribution, with small and large mussels as co-dominants (e.g. Vor2 in 2006; Vor4 in 2001; Vor5 in 2006). The size-frequency histograms for



Fig. 5 nMDS ordination reflecting the changes in mussel size structure at different mussel beds. A Vor2, B Vor4, C Vor5 (note that the point corresponding to Vor5 in 1998 is absent on the diagram). *Black circles* mark the points in polar (minimal or

each mussel bed in all the years are given in the electronic supplement (Appendix 2 in Supplementary material).

The test for the prediction of Endo5

Significant negative values of PRCF[1] were found for all the mussel beds (Fig. 6). Some other PRCF values were close to the significance threshold: PRCF[2] and

maximal) positions according to the correspondent nMDS axis. Histograms on the margins of nMDS chart reflect the size-frequency distribution in the mussel population during the stages marked by *filled circles* 

PRCF[3] for Vor2, PRCF[2] and PRCF[4] for Vor4 and PRCF[2] for Vor5. The bootstrapped 99% confidence intervals calculated for these values do not include zero.

The test for the prediction of DLS

The relationship between mussel abundance in a given year  $(L_t)$  and the abundance in the previous year  $(L_{t-1})$ 



#### Fig. 5 continued

did not show any traits of heteroscedasticity (Breusch– Pagan test, P > 0.1 in the case of all the three mussel beds investigated). Hence, no strong changes in the years following the periods of the highest mussel abundance were observed.

### Discussion

The mussel beds in our study were unstable systems, demonstrating significant inter-annual variations in abundance and demographic structure. Having analysed the time series of the mussel population parameters, we found that (1) changes in different mussel beds were not coordinated, the oscillation patterns being different at different sites. (2) There were no clear direct correlations between the mussel bed parameters (abundance and size structure) and the regional temperature. (3) However, the abundance and the regional temperature showed a positive correlation with a time lag of -1, -3 and -4 years. (4) All the time series had some manifestations of long-term



Fig. 5 continued

trends. (5) However, detrending exposed the presence of a regular cyclic component in each of them. (6) These cyclic components had different periods in all the time series. (7) The demographic structure (expressed as size-frequency distribution) was represented by a succession of three typical stages: the unimodal distribution with the dominance of large mussels, the unimodal distribution with the dominance of small mussels and the bimodal distribution, with small and large mussels as co-dominants. (8) As shown by PRCF analysis, all mussel beds demonstrated a direct density dependence (with a lag of 1 year), which is trivial, since the time series were detrended before the analysis; but there was also some evidence of delayed density dependence (with lags of 2 and more years). (9) The strongest changes in the total abundance were not associated with the periods of the highest abundance.

These findings are now to be compared with the predictions of the "exogenous", the "endogenous"

and the "density-linked stochasticity" model (see "Introduction" section).

The density-linked stochasticity model (DLS) (1)seems to be the less applicable in our case. This model, developed for mussel populations on exposed rocks (Wootton & Forester, 2013), is conceptually based on the positive interaction between adults and juveniles. This positive interaction stems from the fact that old mussel facilitates recruitment: juveniles attach their byssus threads to shells more readily than to any other surface (Commito et al., 2014). According to the DLS model, this positive feedback inevitably leads to an increase in abundance and at some moment recruits have to attach themselves exclusively to the shells of older mussels, all the primary hard substrate being occupied. The resulting multilayered assemblages may be easily dislodged by stochastically occurring large waves. Thus, mussel populations are prone to collapses after periods of the highest abundance.

Our findings, especially finding #9, do not agree with the *DLS* prediction. The strongest changes were not associated with the periods of the highest abundance. These contradictions may be due to the fact that the mussel beds in our study were situated in sheltered areas with a weak wave impact. Under these conditions, nothing prevents mussel assemblages from becoming multilayered structures and when a certain density level is reached some negative feedbacks (see below) become important. Conversely, in an environment where gales are frequent, mussels are unlikely to achieve this critical density level.

It cannot be entirely ruled out that we failed to recognize some indications of DLS because of the sampling design. To remind, we sampled only mussel patches, avoiding gaps. If a gap in a local area of a mussel bed was created by a stochastic impact at a time t, it could not be compared with the abundance in this local area in the previous year (t - 1).

However, mussel beds in our study were very small. Each of them might be expected to respond to a stochastic impact as a whole. In such a case, DLS model should predict the changes in the abundance of all the mussels at local mussel beds. If, which is unlikely, different parts of a small mussel bed respond to a stochastic impact differently, DLS model would describe changes in these small parts rather than those in a whole population. In that case, DLS model can be considered as a model of gap formation but not as a model of population dynamics.

(2) At first glance, our findings do not agree with the exogenous model, either, at least, the one based on regional temperature (see Introduction). In particular, findings #1 and #2 clearly disagree with predictions *Exo1* and *Exo2* 

The exogenous model based on the regional temperature as the most important driver of long-term fluctuations was proposed for intertidal soft-bottom mussel beds in the Wadden Sea (Beukema et al., 2001; Beukema & Dekker, 2014). A strong negative correlation between mussel abundance and regional temperature was observed there (but see Folmer et al., 2014 who did not find this correlation): mussel recruitment (in spring) was found to be higher after a cold winter than after a mild one (Beukema et al., 2001; Beukema & Dekker, 2014). The authors explain it by the low abundance of predators or competitors after severe winters.

In our study, the association between regional temperature and mussel populations was clearly different. The only significant non-lagged correlation between mussel abundance and regional temperature found for Vor2 was positive (Table 1). In addition, the period of cyclic fluctuations in the regional temperature time series was usually shorter than the periods revealed in the mussel population time series (4 years vs. 5–9 years, respectively; Fig. 4).

Thus, we have not found any clear correspondence between the changes in mussel populations and the patterns predicted by this particular exogenous model. At the same time, an indication of a 4-year periodic cycle was found at Vor5, pointing to some correspondence between the periodicity of mussel population dynamics and climatic changes. Additionally, the long-term trends found in all ecological time series (result #4) could be considered as a manifestation of a tendency common for all the mussel beds (*Exo1*). The presence of long-term trends in the temperature time series is in line with this statement.

(3) Most our results (especially #1, 6, 7 and 8) are in good agreement with the predictions of an endogenous, deterministic model.

As applied to mussels, endogenous models are based on the negative effect of adults upon larvae and juveniles (Naumov, 2006; Casagrandi et al., 2007). It should be noted that there are also abundant data on the *positive* effect of adult mussels upon recruits, which tend to settle near adults (e.g. Commito et al., 2014 and references therein). Nevertheless, the negative effect is well documented: field studies have demonstrated negative correlations between abundance of adults and juveniles (Khaitov, 2013), while experiments have shed light on the inhibition mechanisms by competition (Okamura, 1986) or filtering out of larvae (Lehane & Davenport, 2004; Dolmer & Stenalt, 2010). We may, therefore, be fairly sure that some negative feedback does exist. A seeming contradiction with the data on positive interactions calls for a special study. (At the same time, these two mechanisms are not necessarily incompatible since juveniles attracted by adults inevitably encounter face stiff competition in their dense assemblages.) Whether this negative feedback is powerful enough to drive long-term changes can only be revealed by statistical tests of a given time series.

If a population is regulated endogenously, the time series should exhibit only two patterns of population dynamics: (1) stability (equilibrium) and (2) cyclic oscillations (Turchin & Taylor, 1992). Leaving aside the issue of stability (since changes were statistically significant, see GAM2 results), we will turn to the consideration of the cyclic pattern. Its presence was observed and statistically proven for all the mussel beds in our study (finding #5, Fig. 4). Similar patterns of changes in mussel populations were described in other areas, where oscillations of biomass (Beukema et al., 2010) and mussel cover (Folmer et al., 2014) were revealed. Thus, the predictions of the endogenous model (Endo3) agree well with our findings as well as those of other authors.

Further, since biological interactions act at a restricted spatial scale (Zajac et al., 1998), we should expect that local mussel assemblages, if regulated endogenously, should have uncoordinated patterns of long-term changes. In fact, we revealed just this: the periods of the regular cyclic fluctuations were clearly different at different mussel beds (finding #1 and #6, Figs. 3, 4). This observation is in good agreement with *Endo1*.

The predictions of endogenous model are also realized in the size structure dynamics (Fig. 1).

Negative feedback leads us to expect a periodical emergence of settlements lacking juveniles (Fig. 1, stage 2 and 3). Indeed, such "gerontocratic" stages, reflected in the unimodal size distributions with the dominance of large mussels, were found in the longterm dynamics of all the mussel beds (Fig. 5 and Appendix 2 in Supplementary material). As predicted by the endogenous model (Endo4; Fig. 1, stages 1 and 4A), they alternated with stages characterized by the bimodal distribution and with those characterized by the unimodal juvenile-dominated one (Fig. 5; Appendix 2 in Supplementary material). Neither of these two findings is unusual. An "abnormal" population structure, dominated by the "rule by elders", has often been recorded in mussel beds (Commito & Boncavage, 1989; Dankers et al., 2001; Commito et al., 2005). Alternations similar to those found by us have been described in the studies where size structure of mussel beds was monitored for several years (Dankers et al., 2001). All this suggests that the endogenous model, well suited for the explanation of the long-term dynamics of the mussel beds in our study, may also be applicable to that in other areas.

One cannot rule out, however, that the cyclic nature of the long-term dynamics results from the periodic influence of some exogenous factors rather than the density-dependent regulation. The best tool for recognizing the density-dependent basis of a time series is the analysis of partial rate correlation function (PRCF, Berryman & Turchin, 2001).

Since a high negative PRCF[1], testifying to direct, first-order, negative feedbacks (Berryman & Turchin, 2001), is trivial and uninformative for detrended time series that were used in our analysis, we will discuss the PRCF of higher order. The time series generated by multi-component systems are usually based on delayed feedbacks, and thus, represent second- or higher-order autoregressive processes (Berryman, 1992). These processes should be reflected in high negative PRCF values for lag 2 or greater (Berryman, 1992; Berryman & Turchin, 2001). However, using the Bartlett's significant threshold, which is recommended for PRCF analysis (Berryman & Turchin, 2001), we recognized the dominance of the first-order feedback only. At the same time, the confidence intervals revealed by bootstrapping of the time series (Fig. 6) show that PRCF[2] is not equal to zero in the case of all the mussel beds. Some higher-order feedbacks are also present in the system (see the Fig. 6 Partial rate correlation functions (PRCF) for the mussel mean abundance time series at the mussel beds. *Dashed horizontal lines* represent the Bartlett's significance band. *Error bars* represent 99% bootstrap's confidential intervals



negative PRCF[3] for Vor2 and PRCF[4] for Vor4). Thus, the system appears to be based on some delayed feedbacks. An analysis of a longer time series might yet reveal an even greater role of the delayed regulatory feedbacks in dynamics of mussel beds.

It is now time to address the issue that an endogenously regulated population should exhibit stationary dynamics, in other words, that the population parameters should oscillate around an unchangeable mean (Turchin & Taylor, 1992). This was not the case in our study (finding #4). All the mussel beds contained some elements of long-term trends and the time series were not perfectly stationary. Thus, *Endo2* was not confirmed. This means that besides the density dependence, the populations were influenced by some other factor or factors (intrinsic or exogenous) unaccounted for in the purely endogenous model.

For a start, let us address the possibility that trending changes can be driven by some exogenous factors. The best candidate for the role of such a driver of the population dynamics trends is climate. Longterm temperature dynamics in our study showed a clear trend: the mean regional temperature increased in the last decade (Fig. 3). At the same time, a tendency towards an increase in the total mussel abundance could be traced at all the mussel beds (Fig. 3). This correspondence, however, seemed to be delayed: the total mussel abundance was positively correlated with the temperature in the previous years (finding #3). We found that the mussel abundance increased several years after warmer years and, vice versa, decreased several years after colder ones.

The key to understanding the correlations observed in our study may be the fact that, while the summer temperature in the study region is rather stable, the winter temperature is highly variable (Skazina et al., 2013). Most of the changes in the annually averaged temperature could be explained by the temperature of cold periods. The lagged positive correlation could be then interpreted as an increase in mussel abundance

during periods following the years with mild winters. There are no reliable data on the biological basis of this phenomenon. To venture a guess, it may be associated with the niche shifts of mussel recruits. It is known that primary settlers usually avoid dense assemblages of adult mussels, settling instead in other biotopes, for example, on subtidal filamentous algae near intertidal mussel beds (see Bayne, 1964). In fact, we inspected some subtidal mussel beds in the study area and all of them were carpeted with ephemeral filamentous algae densely inhabited by mussel juveniles (our unpublished observations). We suppose that existing intertidal mussel beds are colonized not by primary settlers but by older juveniles, which can redistribute from the areas of primary settlement into mussel beds by crawling (see Hunt & Scheibling, 1998). This means that the success of recruitment at intertidal mussel beds may depend on whether primary settlers do well in their subtidal refuges. This, in turn, may depend on the winter temperature: if the winter was mild, more primary settlers survive their first year. When, after 1-4 years spent in such refuges, these juveniles finally obtain a "permanent position" at the intertidal mussel beds, they provide the observed increase in the mussel abundance. The growth of subtidal filamentous algae seems to be positively related with the temperature (Connell & Russell, 2010). If so, a high algal biomass in warmer years (i.e. after mild winters) would be reflected in a higher abundance of secondary recruits.

At the same time, there might still be a way to explain the revealed trends without resorting to the exogenous influences. This possibility is associated with the fact that delayed feedbacks usually produce cycles with much longer periods than direct (not delayed) ones (Turchin, 2009). If delayed regulation is present in the mussel population (and this is not to be ruled out, see above), then the trends can be interpreted as manifestations of cycles with longer periods, which cannot be recognized because of the short observation span. These "lingering" cycles may be driven by some still unknown mechanisms. These hypothetical mechanisms, in turn, may arise from the presence of an additional important element of the system (intrapopulation or inter-specific interactions), which was left out of this analysis.

To sum up, our results suggest that the models describing the long-term dynamics of intertidal softbottom mussel beds should take into account endogenous regulations based on negative feedbacks. These regulations are likely to produce regular longterm cycles, "constant inconstancies" as Lukanin et al. (1990) put in. At the same time, three limitations should be explicitly considered.

Firstly, the features of long-term dynamics agreeing with an endogenous model (cyclic changes, delayed feedbacks, negative intra-population interactions etc.) were revealed in a study of very special systemssmall intertidal mussel beds in an Arctic environment. Paradoxically enough, their long-term existence is possible only under very stable conditions, with severe environmental impacts being smoothed by local conditions. Otherwise they would perish fast, not to be observed for decades. Intra-population interactions in such a stable environment may be powerful enough to drive cyclic changes. Large mussel beds in European and American soft bottom flats exist under more unpredictable conditions and may be much more sensitive to external impacts. Therefore, it is possible that the patterns predicted by endogenous models would not be recognizable in their dynamics.

Secondly, our sampling design entailed an assumption that all parts of mussel bed had the same population structure and the same dynamical properties as the central parts of large mussel patches that were sampled. While we believe that this is true of small mussel beds in the White Sea, this may not be so in case of large heterogeneous mussel beds in other seas. Moreover, since the negative impact of adults upon juveniles (the basis of endogenous models) is higher inside the dense patches than on their edges, the intensity of negative feedbacks may depend on the spatial heterogeneity of a mussel bed, with lower feedbacks to be expected in more heterogeneous assemblages. It would be interesting to compare the dynamical properties (regular cycles presence, the shape of PRCF and so on) of the mussel time series in our study with those obtained under differ conditions by other designs, though this is likely to turn out an extremely challenging task.

Thirdly, regular oscillations of local mussel beds may obviously be shifted by some exogenous impacts, including climatic ones. They may also be combined with the changes arising from other biological interactions, both intra- and inter-specific. The complete model should be prepared to incorporate these possibilities. A more complex mathematical processing of longer time series may then be needed. However that may be, we suppose that endogenous regulation is a possibility to be seriously considered when analysing long-term dynamics of mussel beds. In our opinion, mussels can be invited to the club of species with cyclic population dynamics, where they would find themselves in the company of small rodents and forest insects.

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