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Testing the hypothesis of tolerance strategies in *Hiatella arctica* L. (Mollusca: Bivalvia)

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Abstract The physiological and biocenotic optima of *Hiatella arctica* L. inhabiting shallow water fouling communities of the White Sea were compared. The biomass and proportion of *H. arctica* in communities were used for the estimation of biocenotic optima or community success. The physiological state of populations was assessed by means of the fluctuating asymmetry. The fluctuating asymmetry of *H. arctica* was calculated using the valve weights. It was determined that the shell of *H. arctica* possesses a slight directional asymmetry, the right valve usually being larger (and heavier) than the left one. The relationship between fluctuating and directional asymmetries is discussed. High biomass and proportion of *H. arctica* in the community generally correspond with high levels of fluctuating asymmetry. Thus, a discrepancy between physiological and ecological optima is observed, which is recognised as being characteristic of a tolerance strategy. However, in the absence of pressure from major filter-feeding competitors such as the mussel *Mytilus edulis* L. and the solitary ascidian *Styela rustica* L., populations of *H. arctica* possess a high biomass and low levels of fluctuating asymmetry. It appears that *H. arctica* prefers to inhabit shelters or depressions, or to be covered by other organisms. Populations of *H. arctica* existing in the absence of shelter had extremely high levels of fluctuating asymmetry despite the absence of filter-feeding competitors. Thus, the strategy adopted by *H. arctica* L. in the investigated upper 5 m layer of water in the White Sea can be described as a stress- and competitor-tolerant strategy.

Keywords Fluctuating asymmetry · Directional asymmetry · *Hiatella arctica* · Biofouling · Tolerance strategy · The White Sea

Introduction

Ramenskii (1935) described three main survival strategies in terrestrial plants: tolerance (S), ruderal (R) and competitive (K) strategies. This classification was adopted in the Russian literature, but received little attention elsewhere. Almost 40 years later the classification of survival strategies was “rediscovered” by Grime (1974), became widely adopted by plant ecologists, and was then developed further. Tolerance strategies were divided into two categories, referring to plants that are tolerant to unfavourable abiotic environmental conditions and to a high degree of competitive pressure from other species, respectively (Mirkin and Rosenberg 1983). Another classification scheme of tolerance strategies was suggested by Campbell and Grime (1992) who distinguished species following a disturbance (D)—and a stress-tolerance (S) strategy, respectively.

It appears that the classification of plant survival strategies also may be applied to sedentary marine animals. Knowledge of the distribution of these strategies among populations may provide a useful explanation of succession patterns in benthic and fouling communities. Studies on the succession of fouling communities in the White Sea indicate that the survival strategies of fouling organisms indeed are similar to those of plants (Sirenko et al. 1978; Oshurkov 1985, 1992; Khalaman 1989, 2001a,b).

Hiatella arctica, a widespread bivalve, is one of the main fouling organisms in the White Sea, and research into its competitive strategy is required in order to understand its population dynamics and role in fouling communities. In contrast to mussels, *H. arctica* does not form a uniform fouling community: The

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settlements of *H. arctica* are usually interspersed by those of other species. At least within the upper 3–5 m water layer, *H. arctica*, although numerous, is not the sole dominant of most fouling communities (Oshurkov 1985; Kulakovskii et al. 1993; Khalaman 1998, 2001a).

The distribution patterns of *H. arctica* in the upper water layer in the White Sea, and the proportion of this mollusc in fouling communities, appear to be the result of a tolerance strategy. The presence of large filter-feeding competitors such as mussels (*Mytilus edulis* L.) and solitary ascidians (*Styela rustica* L.) in shallow-water fouling communities in the White Sea is widely documented. Thus, the strategy of *H. arctica* might be expected to be both stress- and competitor-tolerant.

It has been suggested that the physiological and biocenotic (community success) optima in species with tolerance strategies do not coincide (Lopatin 1963; Vasilevich 1987). Thus, tolerant species might be expected to attain a high biomass and abundance rank within a community where the environmental factors are sub-optimal for this species and vice versa. Therefore, there is a strong need to compare the biocenotic success and the physiological state of *H. arctica* in different communities.

The biomass and abundance rank of *H. arctica* within communities reflect the biocenotic or community success of the population. The physiological state of the population can be estimated using the fluctuating asymmetry (FA) of the shells, i.e., random deviations from perfect bilateral symmetry. FA is the most widely used measure of developmental stability, which in turn is a sensitive indicator of the physiological state of individuals within a population. In other words, developmental stability refers to the ability of a developing organism to produce a consistent phenotype in a given environment (Leary and Allendorf 1989; Palmer and Strobeck 1992; Freeman et al. 1993; Graham et al. 1993a; Palmer 1996; Møller 1997). In recent years, FA has been used extensively as an indicator of genetic and environmental stress at the population level and to estimate the prevailing environmental conditions (Alados et al. 1993; Graham et al. 1993a; Møller et al. 1995; Bonn et al. 1996; Vollestad and Hindar 1997; Carrascal et al. 1998; Lajus and Sukhotin 1998; Smith 1998; Lajus 2001; and many others). Thus, high levels of FA in a population of *H. arctica* would indicate sub-optimal environmental conditions and vice versa.

The main goal of the present study was to test the hypothesis that *H. arctica* L. adopts a tolerance strategy within shallow-water fouling communities in the White Sea. It was decided to carry out statistical analyses of bilateral valve asymmetry FA as an indicator of the environmental conditions under which the population exists. Based on information and on data of biomass and abundance rank, the tolerance strategy of *H. arctica* was assessed.

Methods

Sampling and laboratory procedures

H. arctica and fouling communities containing this species were sampled from artificial substrata in mussel culture farms situated in Kandalaksha Bay in the White Sea in July–August 1997 and August–September 1998 (Fig. 1). Vertically suspended substrata (nylon rope or fish net ribbon) in the upper water layer are used for cultivation of blue-mussels (*M. edulis* L.) in the White Sea. The length of the artificial substrata is 3 m (Kulakovskii and Kunin 1983). Besides the mussel community, some other fouling organisms such as ascidians (*S. rustica*), sponges (*Halichondria panicea*) and *H. arctica* can develop on the artificial substrata of culture farms (Oshurkov 1992; Khalaman 2001a). The location of the

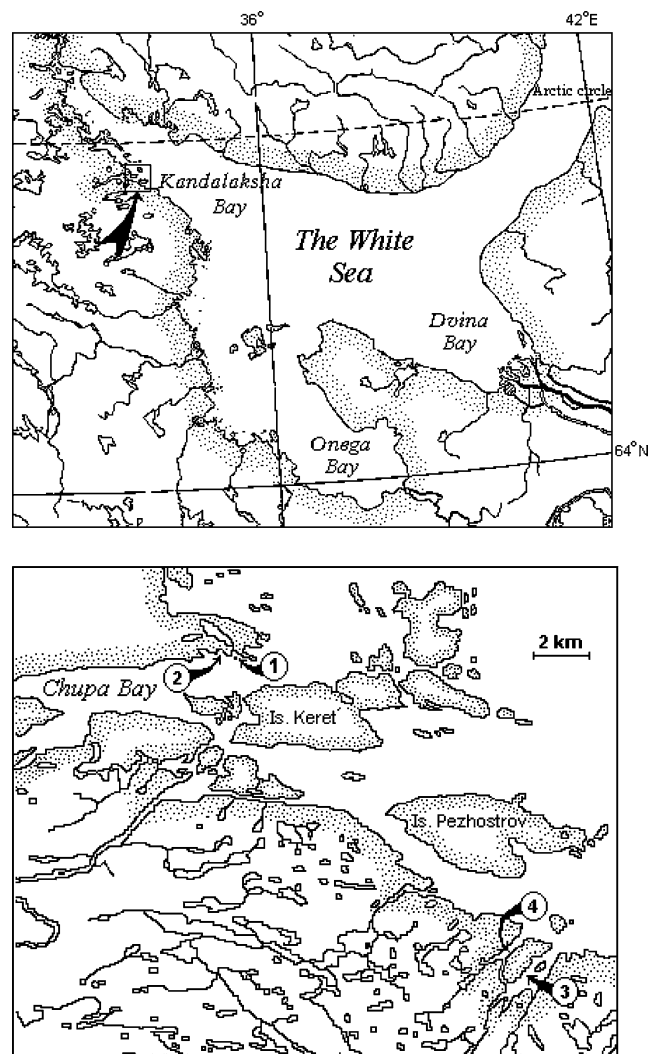


Fig. 1 Study area and location of mussel culture farms where sampling was carried out; 1 Krivozjorskaya Bay, 2 Kruglaya Inlet, 3 Nikolskaya Inlet, 4 Osechkova Inlet

mussel culture farm, volume of sampled material and types of fouling community are given in Table 1.

Sampling of all species present in the fouling communities was carried out at nine stations. For each sample, artificial substrate (ribbon of fish net) of 0.1 m length was taken, with all associated organisms. At four stations, only specimens of *H. arctica* were picked from the fouling communities. In these cases, the type of fouling community was determined visually. At four additional stations, specimens of *H. arctica* were picked from vertically suspended experimental plastic plates measuring 0.5×0.7 m. Sampling of the entire fouling community was not carried out from these plates. Where the entire community was sampled, the numbers of *H. arctica* necessary for statistical analysis of FA were taken from these samples. However, at two stations (nos. 4 and 5; see Table 1) with extremely low densities of *H. arctica*, it was necessary to pick additional specimens from neighbouring areas of the same fouling community. The number of replicate samples per station ranged between two and five, dependent on the length of the substrate occupied by a homogenous fouling community. Sorting, species identification, counting of specimens and biomass determinations were carried out in the laboratory. Wet weight biomass of the communities sampled and of *H. arctica* populations were converted to units per 1 m length of substrate. After weighing, the FA of *H. arctica* was analysed for each sample.

The relative weight of the two valves of *H. arctica*, subsequently referred to as the “trait”, was used to estimate FA. Approximately 50 individuals of *H. arctica* were taken from each population (see Table 1). The shells of *H. arctica* are fragile, and the extremely thin outer part of the valves is often broken during handling. However, such slight damage does not significantly influence the weight, while length measurements are greatly affected by shell injury. Nonetheless, badly damaged specimens were excluded from the analyses. To dissolve soft tissue, molluscs were immersed in a 5% solution of NaOH for 24 h at 40°C. The shells were then rinsed in fresh water and the remaining soft tissue was removed. All valves were numbered, air-dried until a constant weight was attained and weighed to the nearest 0.5 mg.

Numerical analyses

Data were subjected to linear regression and correlation analyses. Parameters for linear regressions were calculated out by both least squares and maximum likelihood methods (Casella and Berger 1990). Where both variables show random variation, the second method is more appropriate for regression analysis. There is solid criticism against using the least squares regression technique for asymmetry analysis (Graham et al. 1998). For this reason, the subsequent data analysis was based on the maximum likelihood technique.

Table 1 Sampling locations and some characteristics of *Hiatella arctica* populations

Station	Type of substrate	Location	T (years)	D (m)	Type of fouling community	N_c	N_i	FA	DA	B (g/m)	P (%)	D (ind./m)
1	Fish net	Nikolskaya Inlet	5	1.5	Mytilus edulis	5	50	0.004107	0.939	96 ± 50.3	1.57	22 ± 98
2	Fish net	Nikolskaya Inlet	5	2.5	<i>Hiatella arctica</i>	3	55	0.003648	0.906	515 ± 145.4	56.8	653 ± 200
3	Fish net	Krivozjorskaya Bay	6	1.5	Mytilus edulis	3	59	0.008318	0.929	133 ± 6.3	4.39	527 ± 235
4	Fish net	Osechkova Inlet	9	2	Mytilus edulis + <i>Laminaria saccharina</i>	3	56	0.005204	0.89	12 ± 2.92	0.17	90 ± 20
5	Fish net	Nikolskaya Inlet	6	1.5	Mytilus edulis	3	75	0.003396	0.874	10 ± 8.6	0.12	67 ± 65
6	Fish net	Kruglaya Inlet	9	2.5	<i>Syella rustica</i>	2	59	0.005699	0.881	120 ± 8.3	5.35	375 ± 7
7	Fish net	Kruglaya Inlet	9	2.5	<i>Syella rustica</i>	2	70	0.00352	0.912	485 ± 153.6	16.09	815 ± 304
8	Fish net	Kruglaya Inlet	6	2.5	<i>Syella rustica</i>	3	54	0.00704	0.9	73 ± 38.6	8.49	477 ± 136
9	Fish net	Kruglaya Inlet	6	2	<i>Haliichondria panicea</i>	3	56	0.007997	0.894	213 ± 67.7	15.41	195 ± 50
10	Fish net	Nikolskaya Inlet	8	2.5	<i>Syella rustica</i>	46	50	0.003353	0.977			
11	Fish net	Nikolskaya Inlet	3	1.5	Mytilus edulis	50	50	0.002962	0.883			
12	Fish net	Krivozjorskaya Bay	5	1.5	Mytilus edulis	49	49	0.002915	0.92			
13	Fish net	Osechkova Inlet	8	3	<i>Syella rustica</i>	72	72	0.011601	0.902			
14	Plastic plate	Kruglaya Inlet	3	3	Mytilus edulis	55	55	0.006545	0.949			
15	Plastic plate	Kruglaya Inlet	4	1.5	<i>Hiatella arctica</i> + Bryozoa gen. sp.	52	52	0.021839	0.924			
16	Plastic plate	Kruglaya Inlet	4	3	Mytilus edulis	33	33	0.005207	0.884			
17	Plastic plate	Kruglaya Inlet	4	5	Mytilus edulis	22	22	0.010818	0.915			

T Exposure time of artificial substrata. D depth, N_c number of fouling samples taken, N_i number of *H. arctica* individuals taken for analysis, FA fluctuating asymmetry, DA directional asymmetry (regression coefficient), B biomass of *H. arctica*, P proportion of *H. arctica* in community, D density of *H. arctica*

The analysis of FA was based on the following reasoning: The FA of bilaterally symmetrical animals can be expressed as the variance of individual asymmetries (d_i): $FA = \text{Var}(d_i)$ with $d_i = r_i - l_i$, where r_i is the dimension of the trait on the right side of individual i , and l_i is the dimension of the same trait on the left side of individual i . The average value of d_i should be zero, if the right and left sides are symmetrical.

Directional asymmetry (DA) appears if the average of d_i is not equal to zero (Graham et al. 1993b, 1998; Palmer 1996). This means that the dimension of the trait on one side is, on average, larger than on the other side. In this case, individual asymmetries are the result of both FA (d_{iFA}) and DA (d_{iDA}):

$$d_i = d_{iFA} + d_{iDA}$$

Let us assume that the weight of the right valve (Wr) is an independent variable and that the relationship between the left and right valves is expressed by a linear equation. Then,

$$Wl_{\text{exp}} = a + bWr,$$

where Wl_{exp} is the theoretical expected weight of the left valve at a given weight of the right part of the shell (Wr).

If the intercept (a) does not differ from zero and the regression coefficient (b) is equal to 1, DA is absent. When the right valve is heavier than the left valve, the regression coefficient is less than 1. In this case, the absolute difference between the opposite valves is dependent on the size of the mollusc. If $b=1$, but a does not equal zero, the difference between the valves is constant.

From $d_i = Wr - Wl_i$, and $d_i = d_{iFA} + d_{iDA}$ follows

$$d_{iFA} + d_{iDA} = Wr_i - Wl_i \quad (1)$$

It is essential to note that d_{iDA} in fact denotes the difference between the observed weight of the right valve (Wr_i) and the theoretically predicted weight of the left valve ($Wl_{i\text{exp}}$):

$$d_{iDA} = Wr_i - Wl_{i\text{exp}}.$$

Hence, Eq. 1 may be expressed as:

$$d_{iFA} + (Wr_i - Wl_{i\text{exp}}) = Wr_i - Wl_i,$$

which is equivalent to

$$d_{iFA} = Wl_{i\text{exp}} - Wl_i \quad (2)$$

Equation 2 allows a simple calculation of individual FA. In the present study, the FA was estimated as the normalised to the expected weight of left valve Wl_{exp} . variance of d_{iFA} :

$$FA = \text{Var}(d_{iFA}/Wl_{\text{exp}})$$

In the literature, the use of total residual variance as an estimation of FA is recommended (Graham et al. 1998). However, since total residual variance computed

by the maximum likelihood method is closely associated with the average size of the tested object (weight of shells in this case), the method is here considered inappropriate for this purpose. There was a high correlation ($r=0.83$) between total residual variance and the weight of the shell in *H. arctica*. For correct assessment of FA and the relationship between FA and the ecological success of *H. arctica*, it is essential to avoid these auto-correlation effects. Thus, the present study uses a new method which allows an assessment of FA independent of shell weight.

Results and discussion

Differences between right and left valves

In the literature, it is often stated that shells of *H. arctica* L. have equally sized valves (Skarlato 1987). In reality, the right valve of this mollusc commonly is somewhat larger than the left one and weighs more. However, specimens of *H. arctica* with a larger left valve can also be found, although in the present study, the percentage of these individuals per sample did not exceed 24%. In the populations studied, differences between the relative weight of the valves were maximally 40%, with an average of 10%. In some individuals, there were no demonstrable differences in valve weights. However, the number of such individuals was comparatively low (< 10%).

The distribution of the differences in weight between right and left valve normalised to the average weight of a valve (D_i) is shown in Fig. 2.

$$D_i = (Wr - Wl) / [(Wr + Wl)/2].$$

The distribution differs from normal only in having a significant positive kurtosis ($k=2.5$). The average of D_i does not equal zero but is positive, with a value of 0.095 and SD=0.076 ($n=913$). Thus, the specimens of *H. arctica* studied possess a slight DA, with the right part of the shell being normally larger than the left one.

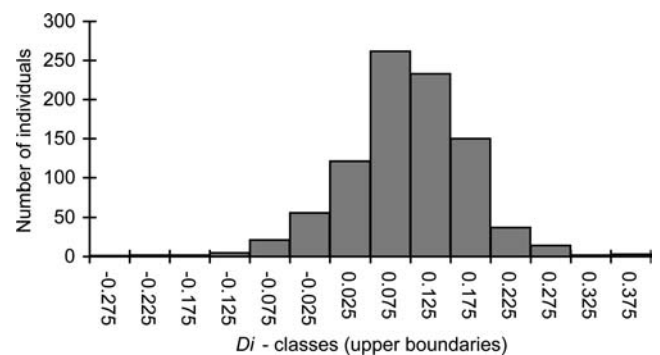


Fig. 2 Frequency distribution of the differences in weight between right and left valves normalised to the average weight of a valve: $D_i = (Wr - Wl) / [(Wr + Wl)/2]$

Analysis of directional asymmetry

The relationship between the weights of the left and right valves is well described by a linear regression. All samples show a correlation coefficient (r) of not less than 0.99. No significant differences were observed between results obtained by the least squares technique and the maximum likelihood technique. This is illustrated by the high correlation ($r=0.96$) between regression coefficients obtained by the different techniques. Moreover, the results of the investigation as a whole do not depend on the chosen method of calculation. This is likely to reflect the very close relationship between right and left valves.

The regression coefficient (b) varies from 0.87 to 0.98 for different settlements of *H. arctica*. Calculated for pooled data, the value is 0.906. Intercept (a) fluctuates slightly around zero from -0.0044 to $+0.0036$ for different samples, and is almost equal to zero (0.0002) for pooled data. Thus, in the present study, the level of DA is assessed in terms of the regression coefficient which was calculated for each population of *H. arctica* separately. It must be borne in mind at this point that the regression coefficient is inversely related to DA.

Analysis of fluctuation asymmetry

FA varies from 0.0029 to 0.0218 for different settlements of *H. arctica*. The highest value was detected for populations of *H. arctica* inhabiting one of the four investigated plastic plates (station 15, see Table 1). This plate was submerged at 1.5 m depth and was covered by a poor settlement of different bryozoans and a well-developed population of *H. arctica*. At this station, there was no organic or inorganic shelter available to the molluscs. It must be noted that the preference of *H. arctica* for shelters or depressions or for being covered by other organisms has prompted some authors to consider this species as a drilling mollusc (Zevina 1972), although this is unlikely due to the fragile nature of the shell. The high value of FA in the *Hiatella* population at station 15 probably was caused by the absence of suitable shelters. As is evident from Table 1, settlements of *H. arctica* located on other plates which were covered by a well-developed mussel fouling population (stations 14, 16 and 17) show a moderate level of FA.

Relationship between the proportion of “left-valve” individuals and directional and fluctuating asymmetries

As stated above, the proportion of individuals where the left valve is larger than the right one (left-valve individuals) varied from 0 to 24% among the sampling stations. It is clear that an increase in the proportion of left-valve individuals can result from either an increase in FA, or a decrease of DA, or a combination of both.

The relationship between the proportion of left-valve specimens and the regression coefficient is shown in

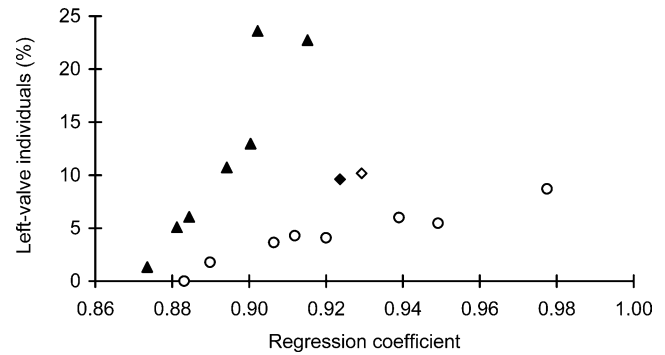


Fig. 3 Proportion of left-valve individuals vs regression coefficient of the relationship between left and right valves in populations of *H. arctica*. Symbols as follows: empty circles and solid triangles—first and second groups of *H. arctica* populations, respectively; empty and solid rhombus—intermediate populations

Fig. 3. On average, with an increased proportion of left-valve specimens, the regression coefficient also increases and, therefore, the DA declines. This result is clear and as might have been expected. However, the dispersion of the data points is extremely high. Moreover, there seem to be two different groups of *H. arctica* settlements: one of them, marked on Fig. 3 and subsequent figures by empty circles, shows a comparatively low proportion of left-valve molluscs. Even slight increases in the proportion of left-valve individuals corresponds to considerable decreases in DA, with the regression coefficient tending to 1. In the other group of settlements, marked by solid triangles, sharp increases in the proportion of left-valve individuals correspond with only slight increases in the regression coefficient, i.e., with slight decreases in DA. The regression coefficient does not reach such high values as in the other group. As can be seen from Fig. 4, the first group of settlements does not show a close relationship between FA and the proportion of left-valve individuals, whereas there is a high positive correlation between these parameters in the second group. Thus, both processes which can result in an increase in the proportion of left-valve individuals (i.e., increase in FA and decrease in DA, respectively) is demonstrated in the

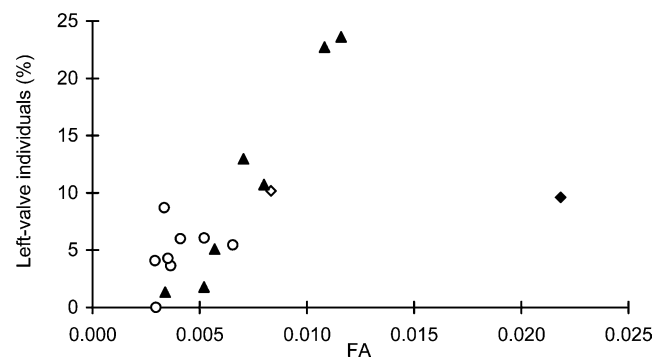


Fig. 4 Relationship between the proportion of left-valve individuals and the fluctuating asymmetry of shells in populations of *H. arctica* (symbols as in Fig. 3)

present study, although a certain degree of overlap is evident.

The clear separation of the two groups of *Hiatella* settlements is interesting (see Fig. 3). Only two intermediate points are evident. The first one (solid rhombus) represents a *H. arctica* settlement with an extremely high FA value, located on a plastic plate (station 15). The second one (empty rhombus) refers to a settlement with an unusual history of development (station 3). In this area, there was a low initial colonisation and growth rate of mussels (*M. edulis*), and thus a low competition pressure for settled *H. arctica*. However, during the last 2 years prior to sampling, secondary fouling of juvenile mussels had taken place on this substrate and extensively covered the settlement of *H. arctica*. It is highly probable that the comparatively high FA observed for this population of *H. arctica* is due to these events. The level of DA and the proportion of left-valve individuals in both settlements appear to be closely linked.

The relationship between the regression coefficient (inverse estimation of DA) and FA is shown in Fig. 5. Two discrete types of *H. arctica* populations can be distinguished: Within the first group (empty circles), there is a high variation of the regression coefficient, but the variance in FA was low. FA remained comparatively low and independent of the regression coefficient. The second group (solid triangles) shows a positive linear relationship between the regression coefficient and FA. The general pattern is that FA increases (and thus DA declines) with increasing regression coefficients. However, above regression coefficients of 0.9, FA shows a tendency to remain constant or even to decrease. It should be noted that the maximum of FA (except for one outlier) approximately corresponds to the regression coefficient calculated for pooled data (0.906).

The observed relationship between fluctuating and directional asymmetries suggests that the deviation from a hypothetical normal level of DA is a response to a decrease in FA. If this is the case, it is proposed that the estimation of developmental instability should involve both FA and the deviation of DA from its hypothetical normal level. However, this proposal is in conflict with the widely accepted opinion that DA is developmentally

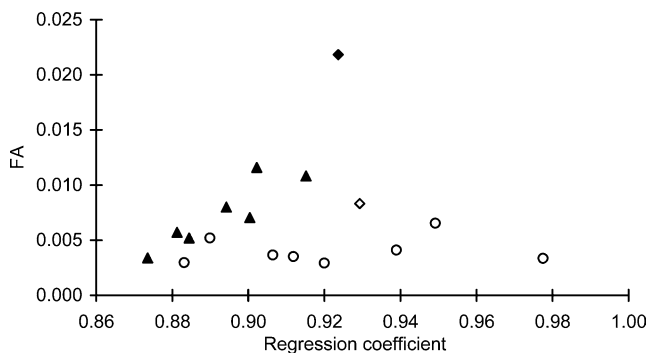


Fig. 5 FA of shells versus the coefficient of regression between left and right valves (symbols as in Fig. 3)

controlled and cannot be used to evaluate developmental instability (Van Valen 1962; Palmer and Strobek 1992, 1997; Palmer 1996). The data of the present study do not allow an unequivocal rejection of the above hypothesis, because DA is not constant among populations. In addition, populations of *H. arctica* with extreme values of DA show low levels of FA. Thus, the present results support the view that DA may in some cases reflect developmental instability (Leary and Al-lendorf 1989; Graham et al. 1993b; Møller 1994).

Some additional questions arise from the proposed interaction between fluctuating and directional asymmetries: e.g., how can the “normal” level of DA be determined and how can a combination of FA and DA be used to assess development instability? However, addressing these issues is beyond the scope of the present work and remains for future studies. Therefore, for the time being, only FA is used as an indicator of development instability.

Relationships between ecological characteristics of *H. arctica* settlements and directional and fluctuating asymmetries of populations

A clear relationship between the type of fouling community and FA or DA of *H. arctica* was not observed. The relationships between the biomass of *H. arctica* and its proportion in fouling communities, respectively, and

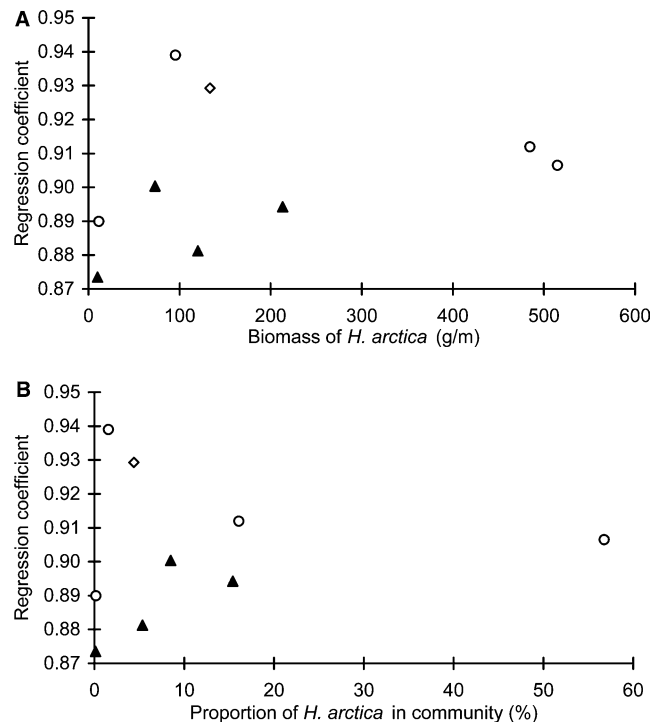


Fig. 6 Coefficient of regression between left and right valves versus some characteristics of *H. arctica* populations: **A** biomass of *H. arctica*, **B** proportion of *H. arctica* in community (symbols as in Fig. 5)

the regression coefficient are shown in Fig. 6. The regression coefficient for each community approximates the value calculated for pooled data (0.906) as biomass (or the proportion of *H. arctica* within the community) increases.

FA generally increases with increasing biomass of *H. arctica*, but two populations with an extremely high biomass show low values of FA (Fig. 7a). A similar relationship exists between the proportion of *H. arctica* in the community and FA (Fig. 7b). Populations of *H. arctica* show a low values of FA both when the biomass of *H. arctica* is extremely high and low (Fig. 7a).

How do the data obtained correspond to the predicted stress tolerance strategy in *H. arctica*? Species which are tolerant to extreme abiotic factors, will develop high biomasses in such extreme environments, due to the absence of less tolerant competitors. In spite of high community success, the physiological state of the tolerant species may be low due to the fact that the environmental regime is sub-optimal. Apparently, the tolerant species is expelled by competitors from optimal to sub-optimal environments. Species which are tolerant to the impact of competitors demonstrate an analogous relationship between community success and the physiological state of the population. However, the explanation for this is different from that given for species tolerant to extreme abiotic factors.

H. arctica settles among numerous and often large filter-feeding competitors such as the blue mussel

M. edulis or the solitary ascidian *S. rustica*. Under competitive stress, the resources (food and space) can support only very restricted abundances of tolerant species (low biomass but high physiological state of population). If the abundance of a population increases, the intraspecific competition for limiting resources also increases, resulting in a decline of the physiological state of organisms (high biomass but low physiological state of population). Thus, a low physiological state and, consequently, a high level of FA are the cost for ecological success. This phenomenon is illustrated by the left parts of the graphs in Fig. 7.

However, the settlements of *H. arctica* with the highest proportion of the community and an extremely high biomass showed low levels of FA (Fig. 7). It should be noted that these high values may not reflect the species' competitive ability, but rather the absence of competitors. For example, as a result of wave action, patches of mussels drop down from artificial substrata to the bottom, while *H. arctica* remains on the substratum, released from the high competitive pressure by *M. edulis*. This can be seen in Fig. 8, where the relationships between community biomass and biomass of *H. arctica* are shown. Even after removal of mussels, *H. arctica* is not deprived of shelter. It is unlikely that all sedentary organisms disappear from the substrata simultaneously, and in addition, the artificial substrate (fish net) itself may serve as shelter. In the absence of competitors, populations of any species develop as rapidly as resources allow. In the absence of large filter-feeding competitors, food access is not a limiting factor for *H. arctica*. This might explain why the biomass of this mollusc attained so high a value and why this process was not accompanied by a corresponding increase in FA. Such a situation can be observed when the proportion of *H. arctica* within the community exceeded approximately 15% (Fig. 7).

The extremely high level of FA that was measured for one of the *H. arctica* populations inhabiting plastic plates (station 15) where mussels were missing, additionally supports the suggestion that this species requires some form of shelter (organic or inorganic). In spite of absence of the competitors, the environmental

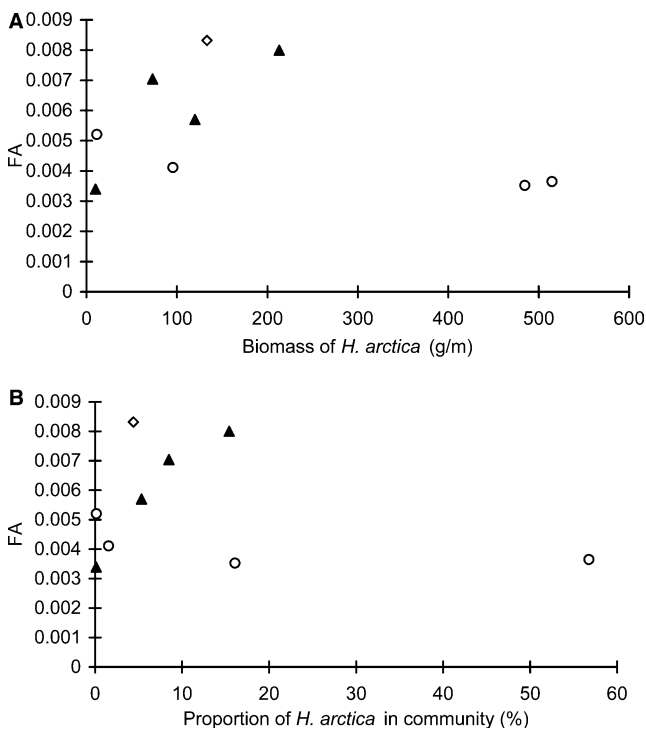


Fig. 7 Relationships between the fluctuating asymmetry of shells and some characteristics of *H. arctica* populations: **A** biomass of *H. arctica*, **B** proportion of *H. arctica* in community (symbols as in Fig. 3)

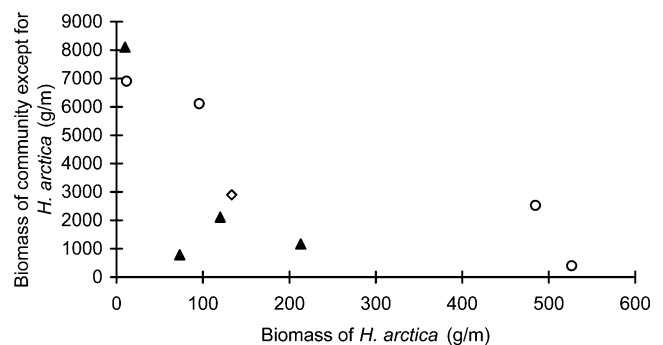


Fig. 8 Relationship between the biomass of fouling communities (except for *H. arctica*) and the biomass of *H. arctica* (symbols as in Fig. 3)

conditions at this site were apparently unfavourable for *H. arctica*. Populations of *H. arctica* inhabiting plates that were covered by mussels (stations 14, 16 and 17) had only moderate FA values.

At to the “normal” levels of DA, there are three main reasons to suggest 0.906 as an estimation of the normal DA value of *H. arctica* in the White Sea. First, the regression coefficient of the relationship between left and right valves calculated for pooled data is equal to 0.906. Second, *H. arctica* inhabiting most optimal environmental conditions (without major competitors) have a similar regression coefficient. Finally, the turning point of the relationship between directional and fluctuating asymmetries is close to this DA value. If 0.906 is a correct estimation of the normal DA value, methods for the use of joint FA and DA parameters can be developed. For this purpose, the regression parameters obtained for pooled data were also applied to calculate FA for each population of *H. arctica*, but it is not yet known whether this approach is the most appropriate. The relationship between this joint parameter and the biomass of *H. arctica* is shown in Fig. 9. The relationship was not markedly different from that resulting from separate parameters (see Fig. 7a), but was less pronounced.

The same species can exhibit different strategies depending on the environmental biotic conditions (Grime 1979; Mirkin and Rosenberg 1983; Vasilevich 1987). The present study shows *H. arctica* to display a tolerance strategy in shallow waters in the White Sea, where the species is not dominant within the community. In deeper waters, the species may adopt a different survival strategy. This is indicated by the observation that *H. arctica* can dominate in fouling communities at 10 m and deeper in the White Sea (Oshurkov 1985). In addition, it is interesting to note the dominance of *H. arctica* within certain benthic communities in Arctic seas (Filatova 1957; Gulliksen et al. 1980).

A summer thermocline is known to develop in the inlets of the White Sea, which commonly lies at depths between 5 and 20 m, depending on the individual hydrological characteristics of the bays (Naumov et al. 1986; Babkov 1995). In deeper and cooler water, there is

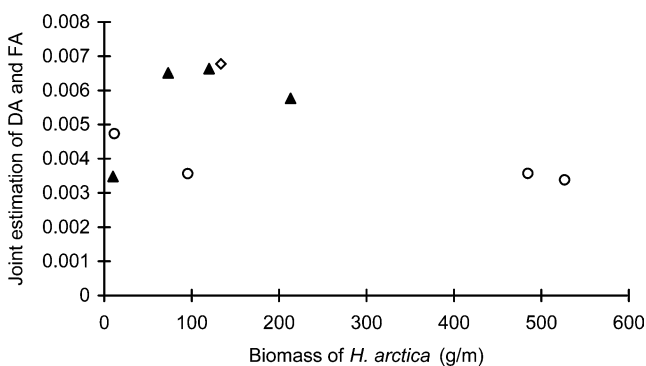


Fig. 9 Relationship between the suggested joint parameter of directional and fluctuating asymmetries and the biomass of *H. arctica* (symbols as in Fig. 3)

a marked decline in the abundance of *H. arctica*'s main competitor, *M. edulis*, and the role of *H. arctica* in such communities differs from that in shallower waters.

Measurement of FA appears to be a comparatively easy, and thus attractive, method for estimating the physiological state of populations, particularly in ecological studies. However, as the present study indicates, this approach is not yet sufficiently developed theoretically as well as methodically. The heated discussions, which still exist in the literature, is clear evidence of this point (Palmer 1996; Møller 1997; Palmer and Strobeck 1997; Clarke 1998; Lajus 2001). Nevertheless, as with all scientific disciplines, such controversy is a normal and necessary step in the development of the technique.

The present study cannot be considered as definite evidence that *H. arctica* L. follows a stress- and competitor-tolerant strategy in shallow waters in the White Sea. The conclusion is based on some more or less proven assumptions: (1) the triangular model of plant survival strategies can be applied to sedentary marine animals, (2) the level of FA reflects the physiological state of population and (3) the physiological and biocenotic optima in species that adopt tolerance strategies do not coincide.

The study was an attempt to test whether these assumptions applied to a concrete species. The results indicate that this may be case in the studied populations of *H. arctica*, and that these really adopt tolerance strategies. However, the additional studies on *H. arctica* and other species are needed.

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