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Toward the Morphometric Calibration of the Environmental Biorecorder *Arctica islandica*

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ABSTRACT

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Owing to its extremely long life span and occurrence in the entire North Atlantic, the Arctic boreal *Arctica islandica* has become of particular significance for monitoring the environment, because information on past environmental conditions is archived in morphological and biogeochemical properties of the calcareous shell. To evaluate whether such properties are comparable between different localities, shell and soft body morphometry of six *A. islandica* populations, Norwegian Coast, Kattegat, Kiel Bay (Baltic), White Sea, German Bight (North Sea), and off NE Iceland, were compared. Discriminant analysis indicated distinct differences between populations, albeit not related to geographical distance, but more likely to local hydrography, bottom morphology, and food regime.

ADDITIONAL INDEX WORDS: *Population, mollusc, morphometry, soft body mass, environment.*

INTRODUCTION

The Arctic boreal *Arctica islandica* is among the longest-lived and slowest growing marine bivalves (Jones, 1980; Murawski, Ropes, and Serchuk, 1982; Thompson, Jones, and Dreibelbis, 1980). Individuals over 100 years old are common (Kraus *et al.*, 1992; Ropes and Murawski, 1983) and a maximum age above 400 years is reported from Iceland (Abele *et al.*, 2008). *Arctica islandica* can live at temperatures between 6 and 16°C (Butler *et al.,* 2013; Mann, 1982) and shows a correspondingly wide distribution across the boreoarctic continental shelves on either side of the North Atlantic Ocean. At the east Atlantic Coast it ranges from the White Sea and Barents Sea to Iceland and the Får Islands and to the Bay of Biscay in the south, and at the west Atlantic Coast it is found from Labrador to North Carolina (Abbott, 1974; Brey *et al.*, 1990; Nicol, 1951; Witbaard, Duineveld, and de Wilde, 1999). *Arctica islandica* occurs at depths down to 482 m (Nicol, 1951), although it is commonly found between 10 and 280 m (Kennish and Lutz, 1995; Merrill and Ropes, 1969; Rowell and Chaisson, 1983; Thompson, Jones, and Ropes, 1980).

There is considerable knowledge on anatomy (Boretto *et al.*, 2014; Morton, 2011; Palmer, 1979), behaviour (Taylor, 1976), ecophysiology (Ballesta-Artero *et al.*, 2017; Bayne, 1971; Tschischka, Abele, and Portner, 2000), and population dynamics (Brey *et al.*, 1990; Murawski, Ropes, and Serchuk, 1982; Thompson, Jones, and Ropes, 1980), the latter being particularly interesting for the management of commercial fisheries of *A. islandica*. Recently, longevity of *A. islandica* was the focus of interest in this species: on the one hand, physiologists study the cellular mechanisms of ageing (Abele *et al.*, 2008; Strahl *et al.*, 2007); on the other hand climatologists and ecologists are interested in the calcareous archive provided by the shell that contains morphological and biogeochemical information on past environmental conditions (Bonitz *et al.*, 2018; Lohmann and Schöne, 2013; Marali and Schöne, 2015; Milano *et al.*, 2017). It is important for determining which conditions will assist conservation managers in their global effort to calibrate this biorecorder species and to predict the future environmental scenario (*e.g.,* Finkl and Makowski, 2015; Makowski, Finkl, and Rusenko, 2013; Makowski, Seminoff, and Salmon, 2006; Von Leesen *et al.,* 2017).

Owing to its extremely long life span and wide geographical distribution, *A. islandica* is a prospective model organism for studies of climate change effects on northern boreal marine ecosystems (Jones, 1980; Murawski, Ropes, and Serchuk, 1982). To make *A. islandica* a "standard" biorecorder of northern boreal coastal and shelf systems, it is necessary to check whether individuals from different populations are comparable in their biology throughout the distributional range. Begum *et al.* (2009) have measured the ecophysiological requirement of *A. islandica* from similar populations; the authors proposed a general respiration model that links individual metabolic rates. Again, on the basis of the von Bertalanffy growth models and size–mass relationships, the authors showed that *A.islandica* populations differed distinctly in maximum life span, but less in growth performance; lifetime energy investment distinctly shifted from somatic to gonad production with increasing life span (Begum *et al.,* 2010). Therefore an important step is to check for differences in body size and mass among populations. Size differences were found in many bivalve species (see *e.g.*, Abbot, 1974; Daniels, Stewart, and Gibbons, 1998; Hateley *et al.*, 1992; Papadopoulou *et al.*, 2002; Schwaninger, 1999) and also in *A. islandica* by Holmes, Witbaard, and Van der Meer (2003).

This research intends (1) to compare several *A. islandica* populations by means of shell and soft tissue parameters and

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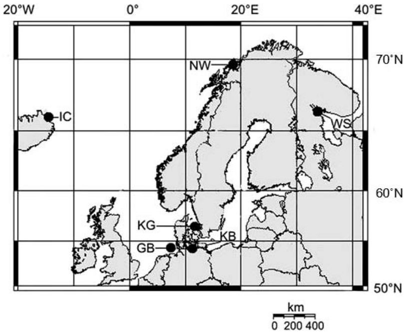

Figure 1. Sample locations of *Arctica islandica*. NW: Norwegian Coast; KG: Kattegat; GB: German Bight; WS: White Sea; IC: Iceland; KB: Kiel Bay. Map redrawn from www.aquarius.geomar.de.

(2) to evaluate whether differences in body size and mass can be related to differences in salinity and temperature regime.

METHODS

Arctica islandica samples were collected using dredges from six different sites: Norwegian Coast, Kattegat, Kiel Bay (Baltic), White Sea, German Bight (North Sea), and off NE Iceland (Figure 1). All samples were collected in 2006 except those from NE Iceland, which were collected in 2004 and 2005. From NE Iceland, only shells were available, whereas animals from the other sites were transported alive to the Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany, where they were used in physiological experiments before morphological analysis.

Statistical and Morphometric Analysis

Different parameters were determined (Figure 2), *e.g.,* shell length (L; greatest anteroposterior distance) shell height (H; greatest distance from umbo to ventral shell margin, not perpendicular to L), shell width (W; greatest distance through both valves to the lower 0.1 mm), and shell mass (M; air-dried mass of both valves) with 0.001-g precision. Wet mass (WM; soft tissue drained on paper), dry mass (DM; 48 h at 60°C), and ash mass (Ash; 24-h incineration at 500°C) were determined with 0.001-g precision. Water fraction was computed as (WM – DM)/WM.

Before comparative analysis, the effect of animal size on the selected parameters in question had to be removed from the data. The approach applied by Krzanowski (1993) and Holmes, Witbaard, and Van der Meer (2003), *i.e.* dividing the shell parameter in question by shell width, did not remove all size effects (tested by analysis of variance). Therefore a more elaborate approach was chosen in a first step and computed for each animal standard size SS and standard volume SV for each animal as:

$$\mathrm{SS} = (L \times W \times H)^{1/3} \tag{1}$$

and

$$\mathrm{SV} = (L \times H \times W). \tag{2}$$

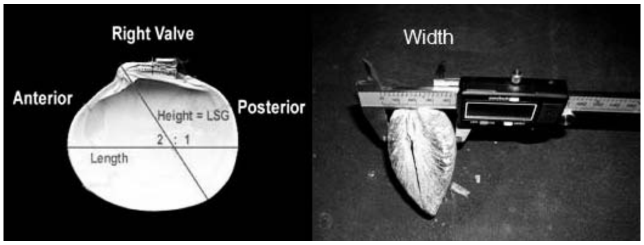

Figure 2. Shell measurements (height, length, width) technique of *Arctica islandica* from six different populations of NE Atlantic Ocean (Norwegian Coast, Kattegat, German Bight, White Sea, Iceland, Kiel Bay).

Then, linear regressions of size measures on SS and of mass measures on SV were established using all data from all populations, where a is intercept and b the slope of the respective regression:

$$\text{size measure} = a + b \times \mathrm{SS} \tag{3}$$

$$\text{mass measure} = a + b \times \mathrm{SV}. \tag{4}$$

The residuals $Y_{\mathrm{R}} = (Y_{\mathrm{measured}} - Y_{\mathrm{estimated}})$ of these regressions proved to be independent of animal size and thus were used as unbiased shell morphometric and soft tissue parameters (L_{R}, H_{R}, W_{R}, M_{R}, residual water fraction [$\mathrm{WF_R}$], $\mathrm{Ash_R}$, residual ash-free dry mass [$\mathrm{AFDM_R}$]) in the following analysis.

Analysis

For each parameter (L, H, W, M, WF, Ash, AFDM), differences between populations were analysed by analysis of covariance (ANCOVA with covariate SS or SV, respectively) with subsequent post hoc test on differences between means. Then, discriminant analysis was used to compare populations on the basis of all parameters (L_{R}, H_{R}, W_{R}, M_{R}, $\mathrm{WF_R}$, $\mathrm{Ash_R}$, $\mathrm{AFDM_R}$) simultaneously (Fraley and Raftery, 2002). Owing to the fact that no soft body data were available for the NE Iceland population, two analyses were performed, one on the basis of shell parameters including all six populations ($N = 427$), and one on the basis of shell and soft body parameters ($N = 223$) excluding the NE Iceland population. Multivariate outliers in the sample space were identified by Mahalanobis jackknife distances (Barnett and Lewis, 1994) and excluded from further analysis.

RESULTS

Mahalanobis analysis identified 9 outliers in the first data set (shell parameters) and 10 outliers in the second data set (shell and soft body parameters). The number of data available for analysis was reduced to 418 and 213, accordingly.

Shell size distributions differ distinctly between populations (Figure 3). Smaller animals <30 mm are completely missing in German Bight and Kattegat, whereas White Sea is restricted to animals <40 mm. The majority of Norway animals were >60 mm.

ANCOVA identified significant differences between populations in every parameter, but there was no consistent overall

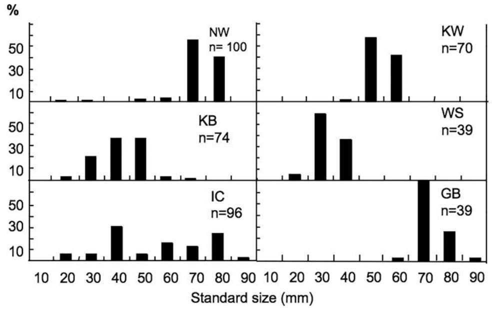

Figure 3. Standard size $(L \times H \times W)^{1/3}$ frequency distribution of *Arcrtica islandica*. NW: Norwegian Coast; KG: Kattegat; GB: German Bight; WS: White Sea; IC: Iceland; KB: Kiel Bay.

pattern, *i.e.* populations did not group similarly for each parameter (Table 1).

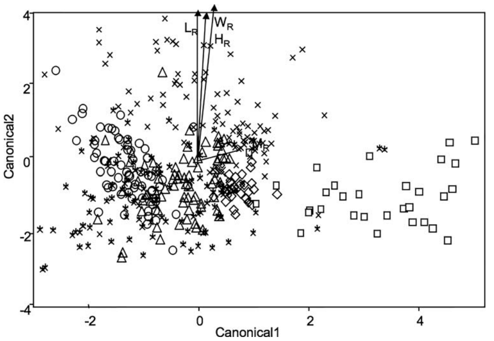

Figure 4. Discrimination analysis on the basis of shell parameters. L_R: length residuals; W_R: width residuals; H_R: height residuals; and M_R: shell mass residuals. Data plotted on the first and second canonical axes. Lines indicate strength and direction of parameter effects (arrowheads indicate that lines are longer than shown). Triangles: Kiel Bay; diamonds: White Sea; squares: German Bight; stars: Norwegian Coast; circles: Kattegat; crosses: Iceland.

Discriminant plot (Figure 4) and corresponding match–mismatch tables (Tables 2, 3) indicate distinct differences between populations on the basis of shell morphology. In terms of the share of animals classified correctly, White Sea has the most distinct population (100%), followed by German Bight (82%). Iceland, Kattegat, and Norway at a similar level (77, 75, and 74%), whereas Kiel Bay is distinctly less well defined (38%). In terms of animals misclassified into a certain population, German Bight takes the lead (only 0.8% of total), followed by Kiel Bay (1.4%), Iceland (5.3%), Kattegat (7.4%), Norway (8.8%), and White Sea (9.5%). Judging from the number of animals misclassified in either direction (Table 3), Kattegat and Norway are most similar (13.5% of Kattegat + Norway), followed by Kiel Bay and White Sea (11.6%). German Bight and Iceland (0.7%), German Bight and Kattegat (0%), as well as Kattegat and White Sea (0%) do not mix at all. Shell width W_R has the strongest discriminative effect, followed by H_R and L_R, which all point in nearly the same direction (Figure 4). The effect of shell mass M_R is distinctly weaker and independent of shell size effects (about 90° in Figure 4).

Table 1. *Analysis of covariance (ANCOVA) of differences in shell and soft tissue parameters between populations. Populations not separated by the post hoc test are marked with the same letter. NW = Norwegian Coast, KG = Kattegat, GB = German Bight, WS = White Sea, IC = Iceland, KB = Kiel Bay.* L = *shell length,* H = *shell height,* W = *shell width,* M = *shell mass, AFDM = ash-free dry mass, WF = water fraction, Ash = ash fraction, SS = standard size, SV = standard volume; n/a = not applicable.*

Parameter	Covariate	ANCOVA p	Post hoc test KB	KG	GB	NW	IC	WS
L	SS	<0.001	—	—	—	—	A	—
			—	B	B	B	—	B
			C	—	C	C	—	C
H	SS	<0.001	—	A	—	—	—	—
			B	—	—	B	—	B
			—	—	C	—	—	C
			—	—	D	—	D	—
W	SS	<0.001	A	—	A	A	A	A
				B				B
M	SV	<0.001	—	—	A	—	A	A
			—	—	—	B	—	B
			C	C	—	—	—	C
AFDM	SV	<0.001	—		A	A	n/a	A
			—	B	B	—		B
			C	C	—	—		C
WF	SV	<0.001	A	—	—	—	n/a	A
			—	B	—	—		—
			—	—	—	C		—
			—	—	D	—		—
Ash	SV	<0.001	A	A	A	A	n/a	—
			—	—	—	—		B

Discriminant analysis indicates a quite similar pattern when based on both shell and soft tissue parameters (Figure 5, Tables 4, 5). The most remarkable difference is the much better definition of Kiel Bay, where 58% (Table 4) were correctly classified compared with 38% (Table 2) above. Overall separation between populations increases slightly in terms of animals correctly classified (79% *vs.* 71%, Tables 4 and 2).

Again, shell width W_R has the strongest discriminative effect, followed by H_R and L_R, which all point in about the same direction (Figure 5). The effects of shell mass M_R and of soft tissue mass parameters WF_R, Ash_R, and $AFDM_R$ are distinctly

Table 2. *Match–mismatch matrix derived from the discriminant analysis on the basis of shell morphology. Each row shows how the animals of one population are placed into each of the six populations compared. % MM is the number of animals wrongly placed into this population in terms of all animals analysed minus the number of animals in this population; % TF is total match and mismatch fraction; % CM is the number of animals of this population matched correctly in terms of total number of animals in this population. Each column shows how many animals of each of the six populations have been grouped into one particular population. NW = Norwegian Coast, KG = Kattegat, GB = German Bight, WS = White Sea, IC = Iceland, KB = Kiel Bay.*

Population	Total	KB	GB	IC	KG	NW	WS	% CM	% TF
KB	73	28	0	9	10	13	13	38.4	72.0
GB	39	0	32	1	0	0	6	82.1	
IC	97	1	0	75	9	1	11	77.3	
KG	70	2	0	1	53	14	0	75.7	
NW	100	2	3	6	9	74	6	74.0	
WS	39	0	0	0	0	0	39	100.0	
% MM		1.4	0.8	5.3	7.4	8.8	9.5		28.0

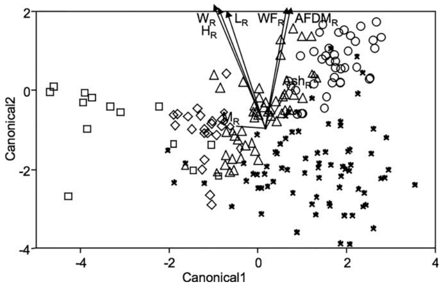

Figure 5. Discrimination analysis on the basis of shell and soft tissue parameters. L_R: length residuals; W_R: width residuals; H_R: height residuals; M_R: shell mass residuals; WF_R: water fraction residuals; $AFDM_R$: ash-free dry mass residuals; Ash_R: ash fraction residuals. Data plotted on the first and second canonical axes. Lines indicate strength and direction and of parameter effects (arrowheads indicate that lines are longer than shown). Triangles: Kiel Bay; diamonds: White Sea; squares: German Bight; stars: Norwegian Coast; circles: Kattegat.

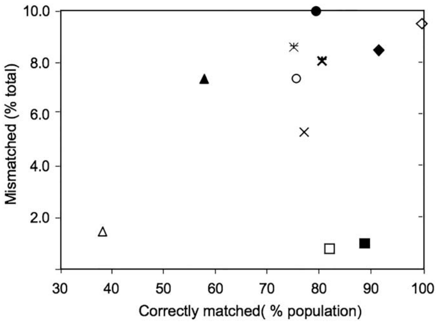

Figure 6. Two-dimensional match–mismatch plot for all populations and both analyses. Triangles: Kiel Bay; diamonds: White Sea; squares: German Bight; stars: Norwegian Coast; circles: Kattegat; and crosses: Iceland. Open symbols: discriminant analysis on the basis of shell parameters; closed symbols: shell and soft tissue parameters.

weaker and apparently independent of the shell size effects, but the effects are in opposition (Figure 5).

DISCUSSION

The research was done on the basis of the morphometric data set of *Arctica islandica* from six different sites. Though the stepwise methods were well defined throughout the research, there are still some concerning steps to make the research more meaningful for calibrating the *A. islandica* populations.

Methodology

The linear regression approach removed all detectable size effects from shell and soft tissue parameters. Nevertheless, the distinct differences in sample shell size range between populations (Figure 3) may have introduced further, albeit undetectable, bias into our analysis, if the relationships between analysed parameters and SS (or SV) change with size and if the mode of this change differs between populations. Such bias can be avoided only by comparing identical size ranges across populations, which was not possible here.

The comparison of populations on the basis of single parameters produced a rather inconsistent picture (Table 1). Nevertheless, the "holistic" approach by means of discriminant analysis indicated distinct separation between populations (Figures 4 and 5). Moreover, adding soft tissue parameters to the analysis improved the level of separation between populations. The following will discuss two questions: (1) which parameters contribute most to the separation of populations, and why; and (2) how are the six populations related to each other morphologically, and which external factors may force morphological differentiation.

Table 3. *Reciprocal mismatch matrix derived from the discriminant analysis on the basis of shell morphology. Each value indicates the rate of mismatch for a particular pair of populations in either direction in terms of percentage of the sum of both populations. NW = Norwegian Coast, KG = Kattegat, GB = German Bight, WS = White Sea, IC = Iceland, KB = Kiel Bay.*

Population	GB (%)	IC (%)	KG (%)	NW (%)	WS (%)
KB	0	5.89	8.39	8.67	11.60
GB	—	0.73	0	2.15	7.69
IC	—	—	5.99	3.56	8.09
KG	—	—	—	13.53	0
NW	—	—	—	—	4.32

Both discriminant analyses (shell parameters only, and shell + soft tissue parameters) indicate that shell width W_R is the most significant factor, followed by the other two shell dimensions (Figures 4 and 5), *i.e.* shells differ most distinctly in shape, whereas shell mass M_R is less distinctive. Soft tissue WF_R and $AFDM_R$ are almost as important as shell shape (Figure 4). Their inclusion increases overall accuracy just slightly from 72% to 79% correct matches, but enhances the definition of Kiel Bay dramatically (Figure 6), except in comparison with White Sea. Contrary to the findings of ANCOVA (Table 1), shell mass has the least discriminating power (Figures 4 and 5). On the other hand, soft tissue mass is as important as shell shape in separating populations (Figure 5). The most likely explanation might be the synergistic effects of salinity and temperature that affect the organism's somatic mass (*e.g.,* Heilmeyar *et al.*, 2008; Shumway, 1996).

Table 4. *Match–mismatch matrix derived from the discriminant analysis on the basis of shell and soft tissue parameters. Each row shows how the animals of one population are placed into each of the five populations compared. % CM is the number of animals of this population matched correctly in terms of total number of animals in this population. Each column shows how many animals of each of the five populations have been grouped into one particular population. % MM is the number of animals wrongly placed (matched) into this population in terms of all animals analysed minus the number of animals in this population. % TF is total match and mismatch fraction. NW = Norwegian Coast, KG = Kattegat, GB = German Bight, WS = White Sea, IC = Iceland, KB = Kiel Bay.*

Population	Total	KB	GB	KG	NW	WS	% CM	% TF
KB	50	29	0	6	2	13	58.0	78.9
GB	18	1	16	0	1	1	88.9	
KG	44	2	0	35	8	0	79.5	
NW	77	7	2	11	61	2	79.2	
WS	24	2	0	0	0	22	91.7	
% MM		7.4	1.0	10.0	8.0	8.5		21.1

Table 5. *Reciprocal mismatch matrix derived from the discriminant analysis on the basis of shell and soft tissue parameters. Each value indicates the rate of mismatch for a particular pair of populations in either direction in terms of percentage of the sum of both populations. NW = Norwegian Coast, KG = Kattegat, GB = German Bight, WS = White Sea, IC = Iceland, KB = Kiel Bay.*

Population	GB	KG	NW	WS
KB	0	8.51	7.09	20.27
GB	—	0	3.15	2.38
KG	—	—	15.70	0
NW	—	—	—	1.98

Relations between Populations

Generally, the six populations appear to be well separated morphologically (72% and 79% correct matches, Tables 2 and 4), but a pairwise comparison reveals obvious differences in definition. The reciprocal mismatch matrices (Tables 3 and 5) indicate that two pairs of populations are quite similar, Kiel Bay and White Sea (11.60% and 20.27% reciprocal mismatch in the first and second analyses, respectively), and Kattegat and Norway (13.53% and 15.70%). Kiel Bay and White Sea populations live in similar distinctly polyhaline environments with an average salinity of 25 (Table 6). Salinity is known to affect morphology in many organisms (*e.g.,* Cuesta and Anger, 2005; Grieve, Shannon, and Dierig, 1999; Marali and Schöne, 2015). In bivalve molluscs, primarily shell thickness and mass have been reported to correlate with salinity, but the findings of this research indicate that shell shape may be affected, too, thus confirming observations of Zettler, Bonsch, and Gosselck (2001). Regarding the similarity of Kattegat and Norway, there is no obvious explanation. Information on environmental conditions is insufficient to identify a common feature that separates these two sites from the remaining ones. Besides, and in combination with salinity, temperature may be significant (*e.g.,* Davis and Calabrese, 1964; Lohmann and Schöne, 2013; Schöne *et al.*, 2003a,b; Shumway, 1996), but even more important are bottom topology and sediment properties (*e.g.,* Hiebenthal *et al.*, 2012; Sejrup *et al.*, 2000; Witbaard, Jansma, and Sass Klaassen, 2003). Finally, the food regime (amount and variability) may also have an effect (Ballesta-Artero *et al.*, 2017, 2018). One might speculate that the setting of these two sites is rather similar, *e.g.*, semiprotected coastal transitional sites (*e.g.,* Berggrena *et al.*, 1999), but complete evidence is still missing. Eventually the outcome of complex interactions of many factors may cause the apparent morphological similarity, as described in several studies (*e.g.,* Bataller, Boghen, and Burt, 1999; Lohmann and Schöne, 2013; Witbaard, Jansma, and Sass Klaassen, 2003). Local environment forcing such as salinity, temperature, and soft bottom sediment (Von Leesen *et al.*, 2017) and food (Ballesta-Artero *et al.*, 2018) is assumed to be the major reason for the coordination/harmony between populations. Therefore, and owing to an understanding of the underlying mechanisms, soft bottom morphology must be taken into account in future relevant research.

The same holds true for the other extreme in the data set, German Bight. These animals have a very distinct and unique morphology *(e.g.,* Figures 3 and 4), but there is no obvious explanation for this finding. The German Bight is a hydrodynamically very active and variable area, strongly affected by tidal currents, storms, and riverine input (Epplé *et al.*, 2006; Marali and Schöne, 2015). The causal links between these features and *Arctica* morphology, however, are still unclear.

Overall, the morphological differences between populations do not correlate with geographical distance (Figures 1, 4, and 5). Holmes, Witbaard, and Van der Meer (2003) observed a similar pattern in a different set of *A. islandica* populations (four North Sea: Oyster Ground, Fladen Ground, Outer Gullmarsfjord, Inner Gullmarsfjord, and one Canadian: Nova Scotia). The authors found that genetic distance was independent of geographical distance, as well as little evidence that morphological differences coincide with genetic differentiation. Obviously, shell morphology of *A. islandica* is forced by local environmental conditions (Epplé *et al.,* 2006; Holmes, Witbaard, and Van der Meer, 2003; Kröncke *et al.*, 2004; Schöne *et al.,* 2003c), and rather not controlled by specific genes. Similar findings in Antarctic limpets (Mauro, Arcuelo, and Parrinello, 2003) support the idea that this might be a general feature in benthic molluscs. Consequently, Dahlgren, Weinberg, and Halanych (2000) also compared the morphological and genetic variations of different *A. islandica* populations from the western Atlantic Coast and found that the morphological variation is forced by local environment too! The authors' next research approach will be to check whether or not morphological distances reflect genetic distances between *A. islandica* populations.

CONCLUSIONS

The present research confirms distinct morphological differences among populations of *A. islandica* that are environmentally but possibly not genetically driven. Discriminant analyses (shell parameters only, and shell + soft tissue parameters) indicate that shell width was the parameter that contributed more to the separation of populations. Nevertheless, they may be accompanied by population-specific physiological adaptations that affect the shell formation process and thus morphological and biogeochemical shell properties. Thus, a

Table 6. *Arctica islandica sample size and site information.*

					Sample Size (total number)	
Population	Site Coordinates	Depth (m)	Salinity (annual mean)	Temp. (annual mean)	Shell Morphometrics	Tissue Mass
Norwegian Coast	69°39′N, 18°57′E	10–30	33	4	100	77
Kattegat	56°09′N, 11°48′E	33	31	8	70	44
Kiel Bay	54°32′N, 10°42′E	25	25	10	73	50
White Sea	66°18′N, 33°38′E	10	25	4	39	24
German Bight	54°09′N, 07°47′E	40	31	10	39	18
Iceland	66°02′N, 14°48′W	14–22	35	5	97	—

comparative calibration of such properties is recommended to make archives from different populations comparable.

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