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# At the north-eastern extremity: variation in *Cepaea nemoralis* around Gdańsk, northern Poland

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**Abstract:** Variation in the shell colour and banding polymorphism in the land snail *Cepaea nemoralis* was studied in 260 populations in the region of Gdańsk, northern Poland. Unlike in other regions of Poland, many populations contain brown shells. Populations from shaded habitats have higher frequencies of brown than those from open and intermediate habitats, largely at the expense of yellow shells. Nearly all brown shells are also unbanded. Apart from this disequilibrium, banding morphs among yellow and pink shells show no relationship to habitat. There are no broad geographical trends in morph-frequencies, but there are very strong correlations among populations very close together, revealed both by pairwise analysis and Moran's I. Principal Component Analyses show that these correlations relate to overall genetic similarity at the loci involved. The populations are at the north-eastern limits of the species' range; habitats are mostly anthropogenic, and comparisons with studies in two urban areas (Wrocław, SW Poland, and Sheffield, central England) suggest that the patterns of variation seen are a product of human transport of propagules followed by local dispersal. The effect of habitat here is much less marked than in regions much further west, but it indicates that natural selection has occurred.

**Key words:** *Cepaea nemoralis;* polymorphism; natural selection; founder effects

## Introduction

The striking shell polymorphism of the European land snail *Cepaea nemoralis* (L., 1758) has been a subject of study for well over a century. A bewildering variety of patterns of variation have been discovered (Jones et al. 1977; Cook 1998), involving, in varying proportions, forms of natural selection, founder effects, genetic drift and gene flow. Patterns vary with locality, and although there are some trends visible across the whole geographical range (from Scotland and S Sweden in the north to central Spain and N Italy in the south, and from Ireland and Portugal in the west to Hungary, the Baltic Republics and E Poland to the east) (Jones et al. 1977; Silvertown et al. 2011), there are many deviations from these very broad trends, and some very local patterns, often reversing those seen elsewhere.

While sometimes recorded from forests, and especially from their fringes, *C. nemoralis* also flourishes in more open, usually anthropogenic habitats: hedges, roadside verges, various grasslands, gardens, parks and orchards. It has been accidentally or deliberately transported to such environments outside its natural range, including several locations in N America. Within its natural range, it has colonised previously inhospitable areas in towns and cities where pollution has declined, and waste ground or gardens are plentiful (Cameron et al. 2009). Within Poland, nearly all populations of the species are in highly modified habitats. In the southeast of the country, these populations are certainly introduced (Ożgo 2005). Elsewhere in the country it seems likely that the same is true; in Silesia the species seems to be confined to cities or the immediate vicinity of roads and villages, while *Cepaea hortensis* (Müller, 1774) occupies more natural habitats (Cameron et al. 2009; Pokryszko et al., unpublished data). Despite the obvious opportunities for founder effects and drift to influence morph frequency variation, Ożgo (2005), Ożgo & Kinnison (2008) and Ożgo (2011) have shown that natural selection related to the shadiness of the habitat can work powerfully over relatively short periods of time, although there are strong indications that neighbouring populations retain similar morph frequencies by common descent (Cameron et al. 2009). This supports the finding of Ożgo (2011) that selective responses to habitat vary with locality and the initial genetic composition of the source population.

Preliminary investigations of *C. nemoralis* populations near Gdańsk revealed some with high frequencies of brown shells. While brown shells (and especially the dark brown, generally unbanded ones) are a feature of northern populations, they are virtually absent from the western part of Pomerania at the same latitudes, as they are in more southerly parts of Poland (Megalab database; Ożgo unpublished). These populations are among the most north-easterly known, at least

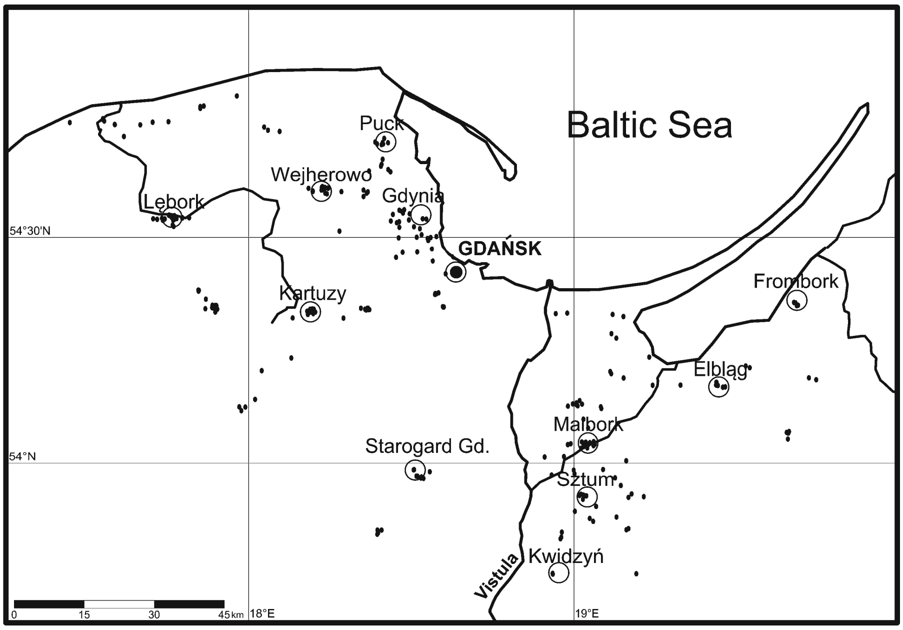


Fig. 1. A map of the study area, showing the position of the samples made in this study.

among those occurring frequently (there are scattered populations, certainly introduced, in S Sweden and the Baltic republics). Hence, we surveyed *C. nemoralis* populations around the city and its hinterland to determine patterns of variation, and their possible causes at the edge of the range within which the species is abundant, and, if introduced, of long standing.

### Area and habitats sampled

Figure 1 shows the study area and the positions of samples within it. The area reaches approximately 120 km west to east and north to south. While sampling was opportunistic, samples are spread over the area, with some clusters. Only localities where the species was present at high densities were sampled.

Sites were classified as follows: open habitats had only grasses and herbs; intermediate habitats included hedges and areas with scattered trees or bushes; in shaded ones trees or bushes were dense enough to give shade throughout the day. The open sites were mostly road verges and derelict sites; shaded sites ranged from fairly natural woods, through old tree stands in parks or cemeteries to areas relatively recently grown with trees and bushes. Those recent tree stands constituted the majority of shaded sites in the area. We categorized the habitats on the basis of their present condition, but it was apparent that most were unstable and short-lived.

### Material and methods

At each site, adult *C. nemoralis* were collected from an area of no more than 400 m$^2$, or of up to 30 m long in linear habitats such as roadsides, within a single habitat category. Both live and fresh empty shells were considered. The shells were scored for colour (yellow, pink or brown) and for the presence or absence of bands. For yellow and pink shells those with bands were allocated to midbanded (00300), to trifasciate (00345) or to many-banded, where more than three bands were present (Jones et al. 1977). Brown banded shells, which were rare (1.1% of all shells), are hard to score for number of bands, which are often very faint. Midbanded and trifasciate frequencies are expressed as a proportion of the relevant banding categories in yellow and pink shells only. Sites were marked on topographical maps or town plans, and locations later defined in decimal degrees. Appendix 1 gives the geographical coordinates of each.

In all analyses we have used morph frequencies, not estimated allele frequencies. For midbanded the frequencies are those within the banded shells; for trifasciate they are those within shells with more than one band, reflecting the dominance hierarchy at these loci (Jones et al. 1977). Unbanded shells are much more frequent among brown shells than others, and this may be an epistatic effect (Cook 1998). Hence we have also used the frequency of unbanded among yellow and pink shells only in some analyses. Where regression or least squares correlation has been used all these frequencies have been arcsine transformed. Besides such tests of association of morphs with each other and with position and habitat, we have examined the linkage disequilibrium between shell colour and banding, taking simply the proportion of unbanded shells within each colour class.

The effect of habitat has been examined in more detail by taking nearest neighbour pairs of shaded versus open or intermediate sites. For each shaded site the nearest open or intermediate site has been used. If more than one shaded site shared the same nearest neighbour, the next nearest open or intermediate site was found for the second or subsequent shaded sites, thus ensuring that no sample is used more than once. Only pairs with distances of less than 8 km have been used; two shaded sites lacked nearest neighbours within this distance, and have been excluded from this analysis.

Following Cameron et al. (2009), we have used the Nei index of genetic similarity (Nei 1972) using the frequencies of yellow, brown, unbanded and midbanded in banded for clustering, and for Mantel tests of association with distance. Spatial pattern has also been examined using Moran's I for each morph. Overall pattern has been analysed by Principal Components Analysis (PCA) using the same four frequencies to assess autocorrelation among populations on the basis of overall genetic similarity; Moran's I was calculated

Table 1. Mean frequencies (%) of morphs in the samples overall and by habitat, with the overall range of frequencies for each morph and the number of samples in which it was not found.

| | *n* | Yellow | Pink | Brown | Unbanded | Mid in banded | 00345 in many banded |
|---|---|---|---|---|---|---|---|
| Overall mean | 260 | 43.3 | 39.6 | 17.1 | 29.0 | 53.9 | 10.8 |
| Range | | 0–93.4 | 0–100 | 0–90.6 | 0–99.1 | 0–100 | 0–87.6 |
| Samples without | | 2 | 2 | 35 | 19 | 2 | 105 |
| Mean open | 89 | 45.5 | 40.4 | 14.0 | 26.6 | 55.3 | 12.5 |
| Mean intermediate | 110 | 45.9 | 38.4 | 15.7 | 26.9 | 52.7 | 10.2 |
| Mean shaded | 61 | 35.3 | 40.7 | 24.0 | 36.2 | 53.7 | 9.4 |

Table 2. Paired samples. A – The numbers of pairs in which each morph was in excess in each habitat category, and the probability of the result being due to chance. Note that 18 pairs lacked 00345 altogether. B – Mean values for morph frequencies in the pairs of shaded versus open or intermediate samples, and the probabilities of the difference being due to chance (paired sample *t*-test, arcsine transformed).

| A – Pairs | Yellow | Pink | Brown | Unbanded | Mid in Banded | 00345 in many banded |
|---|---|---|---|---|---|---|
| Shaded | 24 | 25 | 43 | 31 | 24 | 18 |
| Open & intermediate | 35 | 34 | 16 | 28 | 35 | 23 |
| $P$ ($\chi^2$) | ns | ns | <0.001 | ns | ns | ns |
| **B – Pairs** | **Yellow** | **Pink** | **Brown** | **Unbanded** | **Mid in Banded** | **00345 in many banded** |
| Shaded | 35.45 | 39.96 | 24.59 | 37.17 | 53.18 | 9.61 |
| Open & intermediate | 41.42 | 40.81 | 17.77 | 30.82 | 55.43 | 8.34 |
| $P$ ($t$-test) | 0.067 | ns | 0.0011** | 0.015* | ns | ns |

for sites' scores on the first two PCA axes. Variation within and among populations has been estimated via the Simpson index of diversity (Southwood & Henderson 2000), by the proportions of samples with different numbers of morphs present, and by estimating $F_{ST}$ based on morph frequencies (Cameron et al. 2009). We estimated means and standard deviations of these $F_{ST}$ values using a bootstrapping procedure with 1000 permutations. The software used for the analyses comprised: SAM (Rangel et al. 2006) for Moran's I; PC-ORD (McCune & Mefford 1999) for Mantel test and clustering; CANOCO, version 4.5 (ter Braak & Šmilauer 2002) for PCA; and STATISTICA, version 7.1 (StatSoft Inc. 2010) for all the other one-dimensional tests.

## Results

*Morph frequencies and habitat*

We made 260 samples with a mean number of 116.7 shells per sample (SE. ± 2.2). Details of location, habitat and composition are given in Appendix 1 and the distribution of sites is shown in Fig. 1. Table 1 shows the mean frequencies and ranges for each major colour or banding morph in the whole array, the number of samples lacking the morph, and the mean frequencies for each habitat class considered separately.

While the mean frequencies of morphs differ, frequencies of each at individual sites span all or nearly all the range from 0 to 100%. Very few samples lack yellow, pink or midbanded shells, but 40% lack trifasciate (00345) shells, 13% lack brown shells and 7% lack unbanded shells. Differences in means between open and intermediate habitats are very slight and in no case do they differ significantly. Shaded habitats, however, have a lower mean frequency of yellow and higher frequencies of brown and unbanded than in the other two habitats. In all these cases the differences between shaded habitats and each of the others are significant ($P < 0.01$, *t*-tests, arcsine transformed). Unbanded has a much higher mean frequency in brown shells (90.6%) overall than in yellow (6.1%) or pink (29.3%) shells (see below). The frequency of unbanded in yellow and pink shells only shows no relationship to habitat. Only one shaded site lacks brown (1.6%), while 34 open and intermediate sites do so (17.1%). Other morphs show no significant differences among habitats, nor does the category "effectively unbanded" (unbanded, midbanded and trifasciate combined) as used by Cain & Sheppard (1954). The difference between shaded and other habitats also shows up in the PCA analysis (Appendix 2), where shaded habitats differ from both the others on Axis 1 ($P < 0.001$, *t*-test).

To check that these differences are not a product of different geographical distributions of samples from different habitats, 59 nearest neighbour pairs of open/intermediate and shaded samples were analysed (Table 2). While the same trends persist, they are weaker than in the overall comparison. In particular, variation in yellow fails to achieve significance in either of the tests used. This suggests that the effects of habitat and location are partly confounded in the overall analysis.

*Morph frequencies and location*

With one exception, no morph shows any correlation with either latitude or longitude. Yellow shows a barely significant decline eastwards ($P < 0.05$, *t*-test, arcsine transformed), which explains only 3.8% of variance;

Table 3. Correlation between members of the 59 shaded/open or intermediate pairs for each morph considered (data arcsine transformed). 36 pairs have distance between members less than 1 km, 23 have greater distances (greatest 6.9 km.). R squared shows the proportion of variation explained by the relationship.

| Pairwise correlations | | *r* squared | *r* | *P* |
|---|---|---|---|---|
| Yellow | overall | 0.082 | 0.290 | 0.06 |
| | < 1 km | 0.233 | 0.483 | < 0.01 |
| | > 1 km | 0.022 | 0.148 | ns |
| Brown | overall | 0.283 | 0.532 | < 0.001 |
| | < 1 km | 0.387 | 0.622 | < 0.001 |
| | > 1 km | 0.196 | 0.443 | < 0.05 |
| Pink | overall | 0.320 | 0.566 | < 0.001 |
| | < 1km | 0.404 | 0.636 | < 0.001 |
| | > 1 km | 0.283 | 0.532 | < 0.01 |
| Unbanded | overall | 0.161 | 0.401 | < 0.01 |
| | < 1 km | 0.419 | 0.647 | < 0.001 |
| | > 1 km | 0.055 | 0.234 | ns |
| mid in banded | overall | 0.008 | 0.090 | ns |
| | < 1 km | 0.127 | 0.356 | < 0.05 |
| | > 1 km | –0.021 | –0.145 | ns |
| 00345 in many banded | overall | 0.023 | | ns |

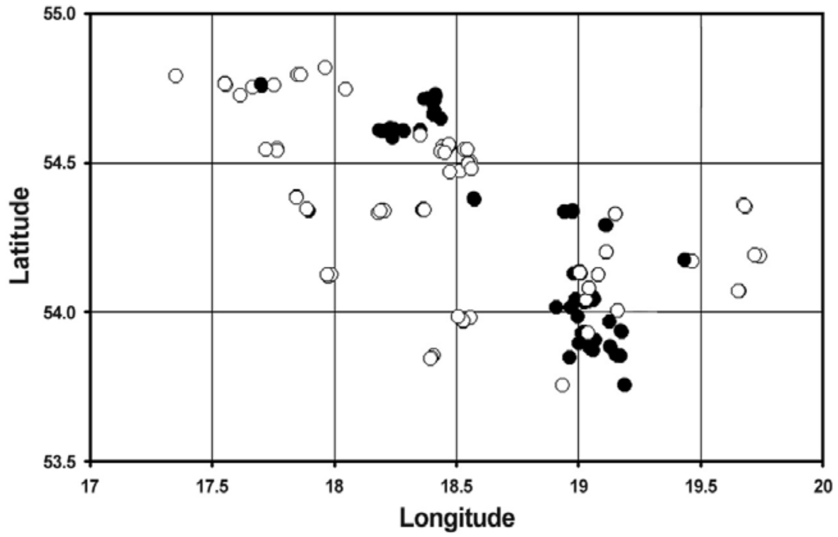


Fig. 2. The distribution of samples in the top (filled circles) and bottom (open circles) quartiles of sample scores on the second PCA axis. Small clusters can be seen.

given the number of tests, this result could be accidental.

Despite this lack of large scale pattern, there is evidence of smaller-scale geographical patterning. Among the habitat pairs, there are some strong within-pair correlations (Table 3), and these are stronger among pairs with the shortest distances between members. This small-scale pattern is also shown by Moran's I using all samples (Table 4); only over short distances (< 1.5 km) does this indicate strong associations, and in both analyses midbanded shows less structure than the colour morphs or unbanded. Trifasciate similarly shows little sign of geographical structure on either large or small scales (data not shown).

Mantel tests using estimates of Nei's I among all possible pairs show a significant but very weak decay of genetic similarity with distance ($R$ = –0.072, $P$ = 0.002). Neither these similarities (data not shown), nor the positions of samples on the first axis of the PCA (Appendix 2 and Table 4, Moran's I) show any geographical pattern other than at a very small scale. The second PCA axis shows stronger spatial structure (Table 4), but even here significant positive correlations disappear after ca. 20 km apart, and the lack of significant relationships with latitude or longitude suggests that there are clusters of similar sites separated by distances at least as great as this, as suggested by the pattern in Fig. 2.

Table 4. Values of Moran's I for each of seven distance classes defined by upper limits (column 3, km.), with probabilities estimated from 1999 Monte Carlo simulations. I/I (max) gives I as a proportion of the maximum possible for the data set in each case.

| D.Class | Count | Up.Limit | Moran's | *P* | I (max) | I/I (max) |
|---|---|---|---|---|---|---|
| **Yellow** | | | | | | |
| 1 | 488 | 1.5 | 0.356 | <0.001 | 0.816 | 0.436 |
| 2 | 646 | 5 | 0.125 | 0.003 | 0.601 | 0.205 |
| 3 | 855 | 10 | 0.105 | 0.004 | 0.601 | 0.174 |
| 4 | 2540 | 20 | 0.086 | <0.001 | 0.453 | 0.189 |
| 5 | 6696 | 40 | –0.034 | 0.005 | 0.189 | –0.179 |
| 6 | 13217 | 80 | –0.033 | <0.001 | 0.159 | –0.208 |
| 7 | 9227 | 171 | –0.003 | 0.621 | 0.156 | –0.018 |
| **Brown** | | | | | | |
| 1 | 488 | 1.5 | 0.296 | <0.001 | 0.747 | 0.396 |
| 2 | 646 | 5 | 0.103 | 0.012 | 0.526 | 0.197 |
| 3 | 855 | 10 | 0.038 | 0.236 | 0.538 | 0.072 |
| 4 | 2540 | 20 | –0.060 | 0.003 | 0.295 | –0.204 |
| 5 | 6696 | 40 | –0.001 | 0.899 | 0.229 | –0.006 |
| 6 | 13217 | 80 | –0.011 | 0.018 | 0.101 | –0.195 |
| 7 | 9227 | 171 | 0.005 | 0.408 | 0.143 | 0.035 |
| **Unbanded** | | | | | | |
| 1 | 488 | 1.5 | 0.309 | <0.001 | 0.822 | 0.375 |
| 2 | 646 | 5 | –0.02 | 0.586 | 0.539 | –0.037 |
| 3 | 855 | 10 | 0.076 | 0.024 | 0.518 | 0.147 |
| 4 | 2540 | 20 | –0.039 | 0.047 | 0.235 | –0.165 |
| 5 | 6696 | 40 | –0.031 | 0.002 | 0.174 | –0.228 |
| 6 | 13217 | 80 | –0.004 | 0.454 | 0.081 | –0.056 |
| 7 | 9227 | 171 | 0.01 | 0.140 | 0.095 | 0.106 |
| **Midbanded in banded** | | | | | | |
| 1 | 488 | 1.5 | 0.128 | 0.006 | 0.548 | 0.233 |
| 2 | 646 | 5 | 0.105 | 0.006 | 0.591 | 0.178 |
| 3 | 855 | 10 | 0.148 | 0.001 | 0.646 | 0.221 |
| 4 | 2540 | 20 | 0.074 | 0.001 | 0.375 | 0.197 |
| 5 | 6696 | 40 | –0.024 | 0.032 | 0.209 | –0.115 |
| 6 | 13217 | 80 | –0.027 | 0.002 | 0.131 | –0.206 |
| 7 | 9227 | 171 | –0.006 | 0.352 | 0.163 | –0.037 |
| **Sample scores on the first PCA axis** | | | | | | |
| 1 | 488 | 1.5 | 0.184 | 0.002 | 0.681 | 0.271 |
| 2 | 646 | 5 | <0.001 | 0.987 | 0.478 | –0.002 |
| 3 | 855 | 10 | 0.077 | 0.028 | 0.452 | 0.171 |
| 4 | 2540 | 20 | –0.019 | 0.294 | 0.239 | –0.081 |
| 5 | 6696 | 40 | –0.017 | 0.101 | 0.168 | –0.104 |
| 6 | 13217 | 80 | –0.006 | 0.332 | 0.084 | –0.075 |
| 7 | 9227 | 171 | –0.004 | 0.532 | 0.115 | –0.034 |
| **Sample scores on the second PCA axis** | | | | | | |
| 1 | 488 | 1.5 | 0.205 | 0.001 | 0.634 | 0.323 |
| 2 | 646 | 5 | 0.175 | <0.001 | 0.632 | 0.278 |
| 3 | 855 | 10 | 0.188 | <0.001 | 0.727 | 0.259 |
| 4 | 2540 | 20 | 0.101 | <0.001 | 0.439 | 0.229 |
| 5 | 6696 | 40 | –0.037 | 0.003 | 0.236 | –0.157 |
| 6 | 13217 | 80 | –0.034 | 0.001 | 0.145 | –0.233 |
| 7 | 9227 | 171 | –0.007 | 0.292 | 0.188 | –0.038 |

### *Associations, disequilibria and variability*

Only two associations between morphs across samples are significant: brown and unbanded ($R = +0.677$, $P < 0.001$), and, negatively, between yellow and unbanded ($R = -0.268$, $P < 0.05$). Both these trends are a product of the strong linkage disequilibrium between colour and banding (Table 5). Unbanded is almost always at a higher frequency in brown than in the other colours;

Table 5. The direction of disequilibria between colour and banding in the samples, and the frequency distribution of unbanded in brown shells. Null samples lack one or other of the colour or banding morphs altogether.

| Mean % unbanded | In yellow | In pink | In brown |
|---|---|---|---|
| | 6.07% | 29.3% | 90.6% |
| | Excess in yellow | Null | Excess in pink |
| Unbanded, number of samples | 38 | 39 | 188 |
| | Excess in yellow | Null | Excess in brown |
| Unbanded, number of samples | 1 | 40 | 219 |
| | Excess in pink | Null | Excess in brown |
| Unbanded, number of samples | 4 | 53 | 203 |
| Unbanded in brown | 100% | Both banded and unbanded | All banded |
| Number of samples | 155 | 67 | 3 |

Table 6. Estimates of $F_{ST}$ for the whole array, corrected for sampling error. The first row gives the direct estimate, the lower rows give the results of bootstrapping with 1000 permutations.

| | Yellow | Unbanded | Mid in Banded | Brown |
|---|---|---|---|---|
| Mean of $F_{ST}$ | 0.1647 | 0.1846 | 0.1687 | 0.1736 |
| Estimated mean of $F_{ST}$ | 0.1648 | 0.1829 | 0.1689 | 0.1743 |
| Estimated SD of $F_{ST}$ | 0.0133 | 0.0152 | 0.0139 | 0.0193 |
| Estimated mean ± SD | (0.1515; 0.1781) | (0.1677; 0.1981) | (0.1550; 0.1828) | (0.1550; 0.1936) |
| Estimated variance | 0.000177 | 0.000231 | 0.000194 | 0.00037 |

in a majority of samples all brown shells are unbanded. It is also at a higher frequency in pink than in yellow in the great majority of cases. Within the yellow and pink classes, there are no significant overall associations of midbanded and trifasciate with colour (data not shown).

The overall variation between samples for each morph except trifasciate, estimated by $F_{ST}$ calculated on morph frequencies following Cameron et al. (2009), is shown in Table 6, together with the standard deviations of each. All have similar values in the range 0.16–0.19. Estimates for shaded and for open and intermediate habitats considered separately give very similar values (data not shown); habitat contributes very little to the overall variation. Table 7 shows the results of three methods of estimating the amount of within population variation: the number and proportion of samples monomorphic at the various loci, the number of morphs present in each, and the Simpson Index of Diversity (1 – D) (Cameron et al. 2009). These are compared with other results below.

Table 7. Estimates of polymorphism. A – the number and percentage of samples containing given numbers of morphs; here, the morphs recognised are unbanded, midbanded, trifasciate and five-banded within pink and yellow shells, and unbanded or banded within brown shells (see methods). B – the number and percentage of samples monomorphic at the given loci. C – the mean Simpson Index of Diversity (as D – 1), here taking eight morphs (unbanded, midbanded and many banded in both yellow and pink, unbanded and banded in brown). For eight morphs, the maximum value the Index can take is 0.875.

| A – Number of morphs | Samples | % of samples |
|---|---|---|
| 1 | 0 | 0 |
| 2 | 1 | 0.4 |
| 3 | 6 | 2.3 |
| 4 | 11 | 4.2 |
| 5 | 22 | 8.5 |
| 6 | 45 | 17.3 |
| 7 | 65 | 25.0 |
| 8 | 67 | 25.8 |
| 9 | 34 | 13.1 |
| 10 | 9 | 3.5 |
| **B – Monomorphic** | **Samples** | **% of samples** |
| colour | 1 | 0.4 |
| banding | 19 | 7.3 |
| mid in b | 3 | 1.2 |
| all three | 0 | 0 |
| **C – Simpson Index** | **(D-1)** | |
| mean | 0.712362 | |
| SD | 0.112449 | |
| SE | 0.0069 | |
| % of Maximum | 81.4 | |

## Discussion

Comparison of the many regional surveys of polymorphism in *C. nemoralis* shows a very wide range in the patterns of variation revealed (see review in Cook 1998). In some, variation with habitat is strong and affects more than one locus (Cain & Sheppard 1954; Cameron & Pannett 1985; Ożgo 2011); in others, the relationship is weak or absent (Cain & Currey 1963, 1964). Although not examined in all these studies, microgeographical variation (populations close to one another tending to have similar morph-frequencies at some or all loci) appears to be pervasive, reflecting the common immediate ancestry of adjacent populations, or the homogenising effects of gene flow in the case of very close populations (Cameron & Dillon 1984;

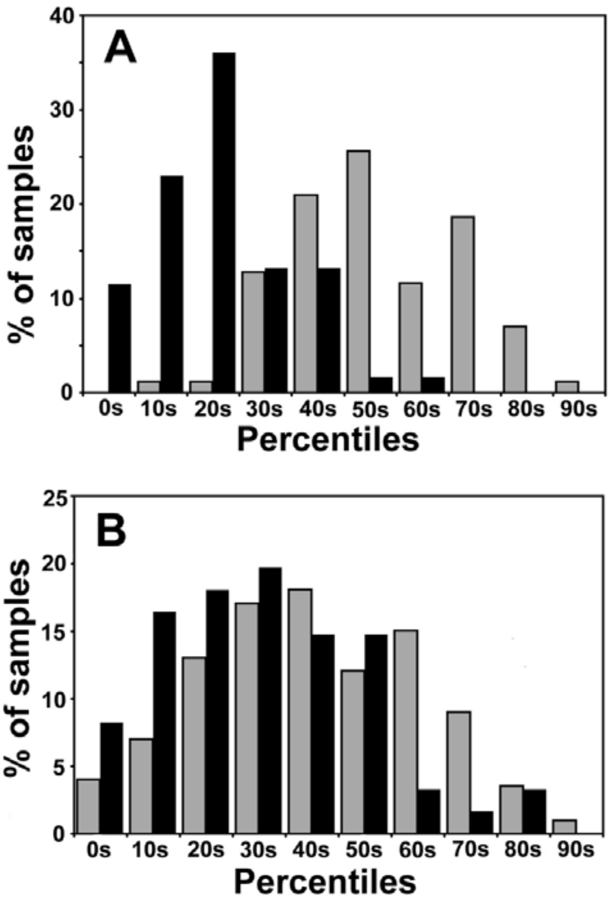


Fig. 3. The frequencies (%) of samples falling into 10% frequency categories for yellow in open/intermediate (grey) and shaded habitats (black): A – for central England (between c. 51.5 and 53.0 degrees N) ($n$ = 147); B – for Gdańsk ($n$ = 260). Data for England come from the Megalab database and unpublished records of R.A.D. Cameron and B.M. Pokryszko.

Cameron & Pannett 1985; Cook 1998; Ożgo 2011). This is not a product of large scale geographical variation; we can note the wide range of frequencies recorded at all loci in this study, covering only a tiny part of the known geographical range. The balance between these elements appears to relate to landscape history and the stability of habitats occupied by the snail (Cameron & Dillon 1984).

In the region around Gdańsk, there is an effect of habitat. It is, however, weak compared to that seen, for example, in the English Midlands (Cain & Sheppard 1954; Currey et al. 1964; Cameron & Pannett 1985). Fig. 3 demonstrates the difference between the two regions in the distribution of frequencies of yellow between habitats overall. In general, variation in yellow between habitats is the most consistent over the species' range (Cook 2008). This effect of habitat is seen here only in variation in the relative proportions of yellow and brown shells (pink being unaffected) and, allowing for the very strong association of brown with unbanded shells, it appears not to apply to other variation in the number or presence of bands.

By contrast, there is a strong microgeographical pattern; samples close to one another are more similar than those further apart. This is a purely local effect, as there are no larger scale relationships with geographical position that might result from climatic gradients. Paired samples show that this relationship decays rapidly with distance and is weakest in mid-banded and trifasciate, while the Moran's I analyses confirm the small scale of spatial effects. There are no blocks of the region in which a set of samples with very similar morph frequencies can be found, corresponding to the "Area Effects" of Cain & Currey (1963).

While we have no direct evidence about the length of time the region has been occupied by *C. nemoralis,* we do have evidence that it has expanded its range and abundance in the 20$^{th}$ century. Schumann (1881) searched for snails in the environs of Gdańsk, west of the Vistula River. *Cepaea hortensis* was frequent everywhere, but he found *C. nemoralis* only in isolated sites in Gdańsk, in Gdańsk-Oliwa, Gdańsk-Westerplatte and Sopot. The species was frequent in those places, but Schuman states clearly that he did not find it in other places. Protz (1897) recorded species found during an excursion in the districts of Świecie, Tuchola, Chojnice and Starogard, an area somewhat to the south of our study (Starogard is included in both). In all, he records over 80 species of snails found, some of them with a note "common" or "frequent". *Cepaea nemoralis* was recorded in only two out of many locations. Today *C. nemoralis* is widespread, but *C. hortensis* is uncommon. The region today is at the north-eastern extremity of the range within which *C. nemoralis* occurs in large numbers and it is probable that most populations in their present locations originate from accidental human introductions, many of them in recent times. They are certainly in anthropogenic habitats subject to change, with implications for the balance between selection, drift and founder effects.

We can examine this by comparing the variation seen here with that recorded by Cameron et al. (2009) in two cities with different patterns of colonisation and population connectivity (Table 8, Fig. 4). Values of $F_{ST}$, and of all three measures of within population variation are intermediate between those in Wrocław, with dense and frequently connected populations, probably established for at least 60 years, and those in Sheffield, scattered, isolated and of very recent origin (within the last 20–30 years). The area involved in this study is much larger than that in either city. This might explain some, but not all of the differences with Wrocław, but fails to do so in the case of Sheffield, where populations vary much more and contain fewer morphs. Values of $F_{ST}$ in this study are also lower than those seen in classic Area Effects, where many populations may originate from a single refugial source (Cameron & Dillon 1984; Cameron et al. 2009). As in these cities, a model of human transport, over varying distances, followed by very local dispersal and migration seems the most parsimonious explanation for the geographical patterns. This follows, at a very small scale, the model of leptokurtic dispersal of propagules in northern Europe during the Holocene proposed by Ibrahim et al. (1996). Evidently,

Table 8. Measures of variation among and within populations. A – Values of $F_{ST}$ (with standard deviations) for variation at three loci. B – Percentage of samples monomorphic at three loci, and in all three at once, and of the mean of the Simpson Index of Polymorphism (with standard errors) in Wrocław, Gdańsk and Sheffield. Data for Wrocław and Sheffield from Cameron, Pokryszko and Horsák (2009). Note that mean sample sizes are similar in all three regions, and that brown is very rare in both Sheffield and Wrocław.

| A | $F_{ST}$ Y | SD | $F_{ST}$ U | SD | $F_{ST}$ Mid | SD |
|---|---|---|---|---|---|---|
| Wrocław | 0.086 | 0.019 | 0.091 | 0.015 | 0.123 | 0.021 |
| Gdańsk | 0.165 | 0.013 | 0.183 | 0.015 | 0.169 | 0.014 |
| Sheffield | 0.205 | 0.024 | 0.341 | 0.078 | 0.281 | 0.036 |

| B | Colour | Banding | Mid in Banded | All Three | Simpson | SE |
|---|---|---|---|---|---|---|
| Wrocław | 0 | 0 | 9.6 | 0 | 0.730 | 0.004 |
| Gdańsk | 0.4 | 7.3 | 1.2 | 0 | 0.712 | 0.007 |
| Sheffield | 5.6 | 53.3 | 28.0 | 2.8 | 0.553 | 0.027 |

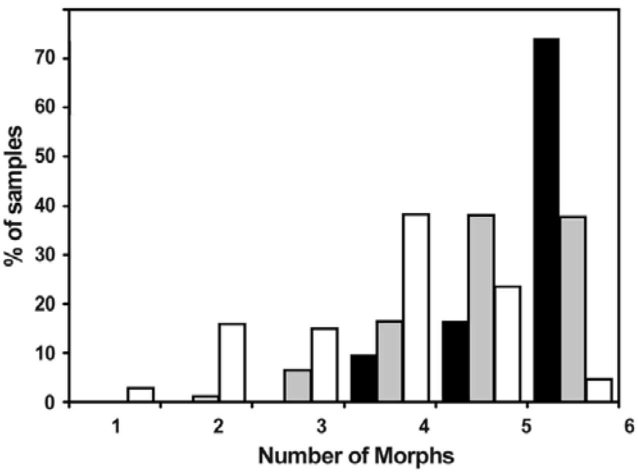


Fig. 4. Frequency distributions of samples containing different numbers of morphs in Wrocław (black), Gdańsk (grey) and Sheffield (white), based on the occurrence of yellow, pink, unbanded and midbanded in banded shells (six possible morphs). Brown shells, frequent in Gdańsk, are very rare in the other two regions.

connectivity has been greater than in Sheffield suggesting a longer period of occupancy. As Ożgo (2011) points out, hermaphroditism, obligatory outcrossing, multiple matings and sperm storage serve to reduce the tendency of founder effects to remove genetic variation, while retaining significant effects on morph frequencies.

In this study variation with habitat is limited. While the combination of habitat and position effects is not unknown elsewhere (Cameron & Pannett 1985), the modest level of habitat effects relative to location has not been reported previously. Ożgo (2011) has shown that when pairs separated from each other by great distances are considered, geographical variation masks overall habitat effects even when these are manifest on a pair-by-pair comparison. Contrary to some earlier analyses, Ożgo (2011) has also shown that marked frequency differences between habitats may develop over very short periods (a few generations of two to three years only). Her study included samples within the region considered here. This might suggest very recent colonisation or spread in the Gdańsk region, a possibility enhanced by the historical evidence above. Our study did not record the proportion of shells with fused bands, an important component of difference in many of her pairs, so we may have underestimated the speed at which adaptive change is occurring.

In this context, the brown shell morph is of particular interest. While the overall incidence of brown is similar to that recorded in other surveys at the same latitudes much further west, it differs markedly from the adjacent area of Pomerania immediately to the west (Megalab database; Ożgo unpublished), in which brown shells are extremely infrequent (present in only three out of 50 samples). They are also very rare elsewhere in Poland occurring in only 17 out of 200 samples in the Megalab database. We note that brown shells are frequent in the Netherlands and that Dutch engineers were used for land drainage and reclamation along the lower Vistula River and its tributaries and especially in the Vistula Delta in the 16th and 17th centuries. There was a strong religious component to this migration. Mennonites were persecuted in the Netherlands and free in Poland, and were encouraged to settle because of their engineering abilities which allowed them to prosper in areas considered agriculturally unusable. Whole families with all their possessions migrated, which increased the likelihood of transporting snails. While brown shells are clearly favoured in shaded habitats, their very presence in the region may result from human transport. In addition to data presented here, we note that populations of *C. nemoralis* in the Czech Republic are certainly introduced, are spreading (Honěk 1995; Dvořák & Honěk 2004), and have anomalously low frequencies of yellow shells when compared with populations at the same latitudes further west or with Hungarian populations to the east (Megalab database). Founding populations and their genetic co-adaptations may have a profound effect on the composition of descendent populations even in the face of selection.

This study thus reinforces an emerging view that even when dealing with a few loci in a single species, the causes of patterns of variation, or the balance of importance of each, varies with region, and is associated with patterns of colonisation and with the details of land use and habitat stability in each. Further, the same selective forces operating on populations differing greatly in genetic structure may promote responses involving different loci having similar phenotypic effects (Ożgo 2011). The search for range-wide trends and general rules, while useful, needs to be moderated by understanding regional peculiarities. A simple one effect, one cause hypothesis is unlikely to explain variation across the whole range of any species.

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Appendix 1. Geographical co-ordinates, habitat and morph composition of samples used in this study.

| No | Site | Habitat | long | lat | YU | YM | YT | YF | PU | PM | PT | PF | BU | BB | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Czernin | O | 19.0686 | 53.9044 | 45 | 11 | 0 | 3 | 23 | 11 | 0 | 3 | 0 | 0 | 96 |
| 2 | Dąbrówka Mal. | S | 19.0900 | 53.9864 | 0 | 8 | 0 | 7 | 42 | 8 | 0 | 3 | 9 | 0 | 77 |
| 3 | Gościszewo | I | 18.9994 | 53.9847 | 0 | 27 | 0 | 2 | 0 | 24 | 5 | 15 | 0 | 0 | 73 |
| 4 | Gościszewo | I | 19.0019 | 53.9764 | 0 | 23 | 0 | 13 | 0 | 8 | 3 | 11 | 0 | 2 | 60 |
| 5 | Kalwa | S | 19.1447 | 53.9506 | 0 | 19 | 0 | 13 | 45 | 14 | 0 | 5 | 6 | 0 | 102 |
| 6 | Kołoząb | I | 19.1311 | 53.8808 | 0 | 6 | 0 | 2 | 42 | 2 | 2 | 1 | 18 | 0 | 73 |
| 7 | Kwidzyn | O | 18.9350 | 53.7539 | 2 | 7 | 5 | 10 | 10 | 5 | 5 | 11 | 10 | 0 | 65 |
| 8 | Kwidzyn | I | 18.9347 | 53.7556 | 0 | 8 | 12 | 17 | 2 | 10 | 1 | 3 | 30 | 0 | 83 |
| 9 | Łabuń | S | 19.1267 | 53.9678 | 0 | 15 | 0 | 1 | 9 | 0 | 0 | 0 | 81 | 0 | 106 |
| 10 | Malbork | I | 19.0494 | 54.0456 | 0 | 22 | 1 | 1 | 19 | 4 | 0 | 26 | 16 | 0 | 89 |
| 11 | Malbork | O | 19.0303 | 54.0425 | 6 | 5 | 0 | 3 | 48 | 8 | 0 | 3 | 1 | 0 | 74 |
| 12 | Malbork | S | 19.0325 | 54.0436 | 7 | 5 | 0 | 16 | 22 | 10 | 0 | 13 | 22 | 0 | 95 |
| 13 | Malbork | I | 19.0225 | 54.0336 | 0 | 40 | 0 | 13 | 20 | 11 | 0 | 0 | 25 | 4 | 113 |
| 14 | Malbork | O | 19.0347 | 54.0456 | 8 | 19 | 0 | 14 | 32 | 25 | 0 | 7 | 16 | 0 | 121 |
| 15 | Malbork | I | 19.0411 | 54.0342 | 0 | 6 | 0 | 0 | 0 | 32 | 0 | 16 | 0 | 0 | 54 |
| 16 | Mikołajki Pom. | O | 19.1683 | 53.8550 | 1 | 35 | 0 | 10 | 0 | 40 | 0 | 11 | 0 | 0 | 97 |
| 17 | Mikołajki Pom. | I | 19.1617 | 53.8525 | 0 | 7 | 0 | 5 | 0 | 32 | 0 | 15 | 0 | 0 | 59 |
| 18 | Postolin | S | 19.0486 | 53.8778 | 0 | 8 | 0 | 5 | 1 | 70 | 0 | 23 | 1 | 0 | 108 |
| 19 | Postolin | I | 19.0594 | 53.8711 | 0 | 29 | 1 | 6 | 0 | 24 | 0 | 6 | 0 | 0 | 66 |
| 20 | Prabuty | O | 19.1922 | 53.7547 | 0 | 2 | 1 | 1 | 6 | 28 | 2 | 16 | 1 | 11 | 68 |
| 21 | Ryjewo | S | 18.9633 | 53.8472 | 0 | 2 | 0 | 0 | 0 | 26 | 0 | 17 | 0 | 0 | 45 |
| 22 | Ryjewo | S | 18.9589 | 53.8325 | 0 | 54 | 0 | 22 | 0 | 13 | 0 | 3 | 0 | 1 | 93 |
| 23 | Ryjewo | O | 18.9617 | 53.8358 | 0 | 16 | 0 | 21 | 0 | 12 | 0 | 21 | 0 | 16 | 86 |
| 24 | Stary Targ | O | 19.1778 | 53.9321 | 0 | 4 | 0 | 0 | 0 | 29 | 0 | 18 | 0 | 0 | 51 |
| 25 | Stary Targ | I | 19.1681 | 53.9244 | 1 | 38 | 2 | 9 | 0 | 25 | 0 | 17 | 0 | 0 | 92 |
| 26 | Szropy | O | 19.1611 | 54.0056 | 0 | 0 | 0 | 64 | 0 | 0 | 0 | 10 | 33 | 0 | 107 |
| 27 | Sztum | I | 19.0222 | 53.9314 | 0 | 3 | 0 | 3 | 0 | 43 | 1 | 11 | 0 | 0 | 61 |
| 28 | Sztum | I | 19.0169 | 53.9286 | 0 | 18 | 0 | 2 | 0 | 29 | 0 | 8 | 0 | 0 | 57 |
| 29 | Sztum | O | 19.0367 | 53.9275 | 0 | 3 | 1 | 8 | 0 | 33 | 0 | 26 | 0 | 0 | 71 |
| 30 | Sztum | I | 19.0278 | 53.9200 | 0 | 0 | 0 | 0 | 0 | 82 | 0 | 10 | 0 | 0 | 92 |
| 31 | Sztum | I | 19.0386 | 53.9278 | 0 | 2 | 0 | 17 | 0 | 2 | 0 | 69 | 0 | 0 | 90 |
| 32 | Sztum | S | 19.0292 | 53.9294 | 0 | 25 | 0 | 1 | 2 | 45 | 0 | 7 | 0 | 0 | 80 |
| 33 | Sztumska Wieś | O | 19.0033 | 53.8933 | 0 | 13 | 0 | 3 | 0 | 25 | 1 | 8 | 19 | 0 | 69 |
| 34 | Waplewo | I | 19.2153 | 53.9261 | 1 | 6 | 1 | 10 | 0 | 24 | 1 | 28 | 36 | 0 | 107 |
| 35 | Malbork | I | 19.0294 | 54.0978 | 0 | 35 | 0 | 12 | 13 | 7 | 0 | 3 | 9 | 4 | 83 |
| 36 | Malbork | S | 19.0294 | 54.0369 | 1 | 26 | 0 | 15 | 0 | 6 | 0 | 13 | 29 | 2 | 92 |
| 37 | Malbork | I | 19.0369 | 54.0469 | 15 | 33 | 0 | 14 | 19 | 7 | 0 | 8 | 16 | 0 | 112 |
| 38 | Malbork | I | 19.0647 | 54.0428 | 0 | 53 | 0 | 4 | 5 | 8 | 0 | 0 | 11 | 7 | 88 |
| 39 | Malbork | I | 19.0603 | 54.0392 | 0 | 52 | 3 | 5 | 7 | 20 | 0 | 0 | 4 | 8 | 99 |
| 40 | Malbork | S | 19.0245 | 54.0475 | 2 | 8 | 2 | 10 | 9 | 31 | 0 | 15 | 16 | 9 | 102 |
| 41 | Malbork | O | 19.0611 | 54.0481 | 0 | 54 | 0 | 4 | 8 | 11 | 0 | 0 | 6 | 8 | 91 |
| 42 | Malbork | S | 19.0453 | 54.0425 | 1 | 1 | 0 | 2 | 15 | 5 | 0 | 1 | 61 | 8 | 94 |
| 43 | Mikoszewo | I | 18.9797 | 54.3336 | 3 | 72 | 2 | 8 | 0 | 2 | 0 | 2 | 2 | 0 | 91 |
| 44 | Mikoszewo | I | 18.9444 | 54.3328 | 3 | 76 | 0 | 2 | 7 | 8 | 1 | 0 | 7 | 0 | 104 |
| 45 | Świerki | O | 19.0844 | 54.1219 | 4 | 62 | 0 | 25 | 8 | 5 | 0 | 3 | 0 | 0 | 107 |
| 46 | Świerki | I | 19.0831 | 54.1256 | 0 | 8 | 0 | 78 | 0 | 5 | 0 | 9 | 0 | 0 | 100 |
| 47 | Trępnowy | S | 18.9819 | 54.1269 | 0 | 4 | 0 | 0 | 10 | 49 | 0 | 0 | 24 | 7 | 94 |
| 48 | Sztutowo | I | 19.1525 | 54.3261 | 1 | 9 | 0 | 33 | 0 | 0 | 0 | 27 | 3 | 1 | 74 |
| 49 | Nowy Dwór | I | 19.1150 | 54.1992 | 0 | 32 | 0 | 34 | 5 | 4 | 0 | 17 | 4 | 0 | 96 |
| 50 | Nowy Dwór | I | 19.1119 | 54.2039 | 5 | 54 | 0 | 16 | 8 | 12 | 0 | 6 | 2 | 4 | 107 |
| 51 | Nowy Staw | I | 19.0178 | 54.1392 | 7 | 27 | 1 | 6 | 27 | 4 | 0 | 9 | 6 | 2 | 89 |
| 52 | Nowy Staw | I | 19.0250 | 54.1317 | 0 | 21 | 0 | 6 | 7 | 0 | 0 | 6 | 48 | 1 | 89 |
| 53 | Nowy Staw | S | 19.0117 | 54.1278 | 0 | 9 | 0 | 4 | 30 | 26 | 0 | 2 | 31 | 7 | 109 |
| 54 | Nowy Staw | S | 19.0069 | 54.1308 | 0 | 8 | 0 | 30 | 5 | 5 | 0 | 12 | 32 | 1 | 93 |
| 55 | Nowy Staw | I | 18.9969 | 54.1319 | 0 | 0 | 0 | 4 | 25 | 13 | 0 | 0 | 44 | 8 | 94 |
| 56 | Kałdowo | I | 18.9903 | 54.0433 | 3 | 56 | 0 | 10 | 11 | 1 | 0 | 2 | 7 | 1 | 91 |
| 57 | Kałdowo | I | 18.9814 | 54.0414 | 7 | 35 | 0 | 22 | 5 | 2 | 0 | 16 | 6 | 0 | 93 |
| 58 | Kmiecin | I | 19.1531 | 54.1894 | 1 | 52 | 2 | 19 | 3 | 28 | 0 | 7 | 2 | 0 | 114 |
| 59 | Tragamin | S | 19.0439 | 54.0786 | 0 | 0 | 0 | 0 | 9 | 0 | 0 | 1 | 96 | 0 | 106 |
| 60 | Pogorzała Wieś | O | 18.9314 | 53.9739 | 5 | 54 | 0 | 29 | 10 | 4 | 0 | 1 | 8 | 2 | 113 |
| 61 | Kraśniewo | I | 18.9694 | 54.0147 | 6 | 19 | 1 | 9 | 30 | 10 | 0 | 4 | 20 | 1 | 100 |
| 62 | Stegna | I | 19.1192 | 54.3306 | 0 | 24 | 8 | 14 | 0 | 10 | 0 | 1 | 56 | 1 | 114 |
| 63 | Jazowa | I | 19.2422 | 54.1733 | 1 | 47 | 0 | 35 | 1 | 19 | 0 | 12 | 6 | 0 | 121 |
| 64 | Miłoradz | I | 18.9100 | 54.0142 | 0 | 7 | 0 | 8 | 41 | 22 | 0 | 2 | 14 | 6 | 100 |
| 65 | Tujsk | I | 19.1308 | 54.2781 | 0 | 37 | 0 | 16 | 13 | 18 | 0 | 9 | 15 | 0 | 108 |
| 66 | Rybina | I | 19.1158 | 54.2881 | 1 | 28 | 2 | 15 | 19 | 20 | 0 | 4 | 22 | 0 | 111 |
| 67 | Marzęcino | S | 19.2319 | 54.2358 | 0 | 1 | 1 | 8 | 31 | 11 | 2 | 1 | 6 | 3 | 64 |
| 68 | Nowy Staw | I | 19.0078 | 54.1344 | 0 | 14 | 1 | 7 | 0 | 14 | 0 | 0 | 54 | 0 | 90 |
| 69 | Borowo | O | 18.1350 | 54.3228 | 0 | 28 | 26 | 17 | 1 | 43 | 22 | 14 | 1 | 0 | 152 |
| 70 | Bieszkowice | O | 18.2794 | 54.5158 | 0 | 60 | 9 | 31 | 15 | 21 | 5 | 10 | 17 | 0 | 168 |
| 71 | Wejherowo | O | 18.2450 | 54.6114 | 1 | 27 | 0 | 5 | 2 | 49 | 0 | 6 | 10 | 0 | 100 |

Appendix 1. (continued)

| No | Site | Habitat | long | lat | YU | YM | YT | YF | PU | PM | PT | PF | BU | BB | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 72 | Gdańsk | O | 18.6003 | 54.3472 | 0 | 32 | 0 | 14 | 11 | 29 | 1 | 35 | 6 | 0 | 128 |
| 73 | Wejherowo | I | 18.2278 | 54.6139 | 4 | 12 | 0 | 20 | 4 | 26 | 0 | 35 | 4 | 0 | 105 |
| 74 | Gdańsk | O | 18.6056 | 54.4211 | 0 | 10 | 1 | 16 | 2 | 35 | 0 | 20 | 10 | 0 | 94 |
| 75 | Wejherowo | O | 18.1972 | 54.6050 | 11 | 13 | 0 | 12 | 8 | 24 | 1 | 27 | 12 | 0 | 108 |
| 76 | Borowo | I | 18.2914 | 54.3225 | 3 | 47 | 0 | 26 | 0 | 41 | 0 | 48 | 50 | 0 | 215 |
| 77 | Wejherowo | I | 18.1972 | 54.6039 | 1 | 11 | 0 | 11 | 1 | 15 | 1 | 9 | 32 | 0 | 81 |
| 78 | Wejherowo | I | 18.2244 | 54.6131 | 0 | 16 | 0 | 20 | 3 | 34 | 0 | 30 | 31 | 0 | 134 |
| 79 | Gdańsk | I | 18.5983 | 54.3472 | 1 | 20 | 0 | 24 | 4 | 27 | 0 | 17 | 28 | 0 | 121 |
| 80 | Gdańsk | I | 18.5728 | 54.3753 | 2 | 30 | 0 | 25 | 1 | 46 | 0 | 32 | 31 | 1 | 168 |
| 81 | Gdańsk | I | 18.5750 | 54.3764 | 0 | 32 | 0 | 3 | 5 | 22 | 4 | 15 | 13 | 0 | 94 |
| 82 | Gdańsk | I | 18.5772 | 54.3767 | 1 | 9 | 0 | 18 | 18 | 43 | 0 | 19 | 24 | 3 | 135 |
| 83 | Gdańsk | I | 18.5972 | 54.3481 | 0 | 22 | 1 | 21 | 0 | 27 | 0 | 19 | 41 | 0 | 131 |
| 84 | Wejherowo | S | 18.2269 | 54.6150 | 0 | 27 | 0 | 37 | 2 | 26 | 0 | 40 | 23 | 0 | 155 |
| 85 | Wejherowo | S | 18.2342 | 54.6130 | 6 | 28 | 0 | 53 | 8 | 62 | 0 | 60 | 56 | 0 | 273 |
| 86 | Sopot | S | 18.5658 | 54.4497 | 13 | 27 | 0 | 29 | 16 | 45 | 1 | 31 | 38 | 0 | 200 |
| 87 | Wejherowo | S | 18.2353 | 54.6000 | 5 | 7 | 0 | 0 | 14 | 41 | 1 | 9 | 22 | 0 | 99 |
| 88 | Gdańsk | S | 18.5733 | 54.3769 | 1 | 14 | 0 | 19 | 2 | 25 | 0 | 23 | 30 | 0 | 114 |
| 89 | Gdańsk | S | 18.5836 | 54.3786 | 0 | 13 | 0 | 13 | 13 | 22 | 0 | 28 | 46 | 0 | 135 |
| 90 | Kartuzy | O | 18.1889 | 54.3422 | 23 | 63 | 6 | 12 | 3 | 5 | 0 | 2 | 22 | 0 | 136 |
| 91 | Kartuzy | S | 18.1956 | 54.3431 | 2 | 44 | 0 | 18 | 3 | 6 | 0 | 2 | 48 | 0 | 123 |
| 92 | Kartuzy | O | 18.2003 | 54.3422 | 1 | 111 | 1 | 12 | 5 | 19 | 0 | 6 | 15 | 0 | 170 |
| 93 | Kartuzy | S | 18.2050 | 54.3361 | 0 | 24 | 0 | 40 | 20 | 2 | 0 | 4 | 45 | 0 | 135 |
| 94 | Kartuzy | O | 18.1814 | 54.3344 | 9 | 56 | 1 | 23 | 5 | 0 | 0 | 0 | 61 | 0 | 155 |
| 95 | Kartuzy | O | 18.1819 | 54.3306 | 24 | 32 | 2 | 36 | 0 | 0 | 0 | 0 | 34 | 0 | 128 |
| 96 | Kartuzy | S | 18.1794 | 54.3381 | 14 | 44 | 2 | 39 | 14 | 3 | 0 | 9 | 50 | 0 | 175 |
| 97 | Kartuzy | S | 18.1986 | 54.3328 | 14 | 74 | 1 | 38 | 9 | 1 | 0 | 0 | 74 | 0 | 211 |
| 98 | Kartuzy | I | 18.1897 | 54.3361 | 89 | 69 | 1 | 85 | 5 | 0 | 0 | 2 | 82 | 0 | 333 |
| 99 | Żukowo | S | 18.3667 | 54.3447 | 0 | 25 | 4 | 7 | 32 | 37 | 3 | 15 | 6 | 2 | 131 |
| 100 | Żukowo | S | 18.3692 | 54.3417 | 0 | 9 | 0 | 18 | 30 | 11 | 0 | 22 | 33 | 0 | 123 |
| 101 | Żukowo | S | 18.3644 | 54.3442 | 0 | 12 | 0 | 2 | 8 | 65 | 0 | 43 | 53 | 0 | 183 |
| 102 | Żukowo | S | 18.3452 | 54.3447 | 0 | 12 | 2 | 9 | 34 | 24 | 5 | 24 | 20 | 0 | 130 |
| 103 | Żukowo | O | 18.3672 | 54.3444 | 3 | 31 | 0 | 12 | 16 | 60 | 1 | 18 | 5 | 3 | 149 |
| 104 | Żukowo | O | 18.3711 | 54.3414 | 0 | 7 | 1 | 28 | 77 | 11 | 1 | 38 | 31 | 0 | 194 |
| 105 | Żukowo | O | 18.3603 | 54.3406 | 0 | 117 | 1 | 23 | 5 | 8 | 0 | 2 | 0 | 0 | 156 |
| 106 | Żukowo | S | 18.3617 | 54.3408 | 0 | 26 | 2 | 8 | 16 | 60 | 1 | 21 | 1 | 2 | 137 |
| 107 | Starogard Gd. | S | 18.5086 | 53.9858 | 1 | 33 | 0 | 21 | 2 | 1 | 0 | 2 | 53 | 0 | 113 |
| 108 | Starogard Gd. | I | 18.5194 | 53.9711 | 4 | 63 | 17 | 19 | 12 | 0 | 0 | 0 | 13 | 0 | 128 |
| 109 | Starogard Gd. | S | 18.5378 | 53.9667 | 0 | 32 | 1 | 17 | 2 | 15 | 3 | 14 | 41 | 0 | 125 |
| 110 | Starogard Gd. | S | 18.5156 | 53.9717 | 0 | 65 | 8 | 28 | 5 | 0 | 0 | 0 | 20 | 0 | 126 |
| 111 | Starogard Gd. | O | 18.5072 | 53.9853 | 0 | 10 | 0 | 72 | 0 | 0 | 0 | 2 | 35 | 0 | 119 |
| 112 | Starogard Gd. | I | 18.5294 | 53.9675 | 0 | 35 | 0 | 50 | 1 | 0 | 0 | 1 | 50 | 0 | 137 |
| 113 | Starogard Gd. | O | 18.5314 | 53.9697 | 0 | 20 | 1 | 58 | 1 | 0 | 0 | 0 | 44 | 0 | 124 |
| 114 | Starogard Gd. | O | 18.5567 | 53.9814 | 0 | 18 | 7 | 23 | 1 | 2 | 6 | 4 | 59 | 2 | 122 |
| 115 | Lubichowo | I | 18.3961 | 53.8519 | 26 | 38 | 0 | 28 | 0 | 0 | 0 | 0 | 30 | 0 | 122 |
| 116 | Lubichowo | I | 18.3981 | 53.8450 | 1 | 16 | 2 | 62 | 24 | 0 | 0 | 1 | 15 | 0 | 121 |
| 117 | Lubichowo | I | 18.3953 | 53.8425 | 0 | 11 | 0 | 67 | 1 | 0 | 0 | 0 | 46 | 0 | 125 |
| 118 | Lubichowo | O | 18.4089 | 53.8519 | 0 | 13 | 38 | 19 | 4 | 4 | 22 | 12 | 11 | 0 | 123 |
| 119 | Wejherowo | S | 18.2439 | 54.6111 | 8 | 17 | 0 | 9 | 5 | 28 | 0 | 27 | 32 | 0 | 126 |
| 120 | Wejherowo | S | 18.2433 | 54.6117 | 14 | 23 | 3 | 22 | 5 | 28 | 1 | 15 | 14 | 0 | 125 |
| 121 | Wejherowo | O | 18.1964 | 54.6042 | 13 | 31 | 0 | 12 | 6 | 41 | 0 | 9 | 11 | 0 | 123 |
| 122 | Wejherowo | O | 18.1839 | 54.6108 | 3 | 16 | 0 | 16 | 6 | 44 | 0 | 37 | 1 | 0 | 123 |
| 123 | Wejherowo | O | 18.2233 | 54.6069 | 0 | 2 | 1 | 1 | 17 | 86 | 11 | 8 | 0 | 0 | 126 |
| 124 | Wejherowo | O | 18.2850 | 54.6036 | 12 | 22 | 0 | 7 | 7 | 50 | 9 | 8 | 5 | 0 | 120 |
| 125 | Wejherowo | O | 18.2322 | 54.6067 | 6 | 16 | 1 | 14 | 55 | 24 | 0 | 6 | 5 | 0 | 127 |
| 126 | Nadole | O | 18.0950 | 54.7373 | 0 | 10 | 14 | 11 | 48 | 25 | 13 | 12 | 0 | 0 | 133 |
| 127 | Nadole | O | 18.0472 | 54.7469 | 0 | 10 | 0 | 102 | 0 | 6 | 0 | 17 | 0 | 0 | 135 |
| 128 | Nadole | O | 18.0594 | 54.7400 | 1 | 11 | 0 | 15 | 46 | 18 | 1 | 21 | 34 | 0 | 147 |
| 129 | Wejherowo | S | 18.2261 | 54.6136 | 2 | 29 | 0 | 37 | 8 | 36 | 0 | 43 | 20 | 0 | 175 |
| 130 | Wejherowo | S | 18.2406 | 54.5986 | 12 | 12 | 0 | 5 | 10 | 47 | 3 | 6 | 38 | 0 | 133 |
| 131 | Frombork | I | 19.6767 | 54.3575 | 0 | 5 | 6 | 1 | 111 | 6 | 14 | 9 | 0 | 0 | 152 |
| 132 | Frombork | I | 19.6853 | 54.3503 | 0 | 8 | 3 | 7 | 54 | 8 | 17 | 27 | 7 | 0 | 131 |
| 133 | Frombork | S | 19.6817 | 54.3564 | 0 | 1 | 7 | 15 | 70 | 1 | 7 | 19 | 13 | 0 | 133 |
| 134 | Frombork | S | 19.6900 | 54.3511 | 0 | 5 | 0 | 19 | 18 | 25 | 35 | 10 | 10 | 1 | 123 |
| 135 | Milejewo | I | 19.5411 | 54.2125 | 0 | 25 | 6 | 12 | 0 | 33 | 10 | 7 | 2 | 0 | 95 |
| 136 | Milejewo | I | 19.5289 | 54.2161 | 0 | 25 | 3 | 23 | 0 | 7 | 3 | 6 | 13 | 0 | 80 |
| 137 | Młynary | O | 19.7453 | 54.1856 | 12 | 22 | 4 | 20 | 4 | 0 | 0 | 6 | 20 | 2 | 90 |
| 138 | Młynary | S | 19.7231 | 54.1900 | 4 | 24 | 4 | 39 | 3 | 10 | 0 | 21 | 33 | 7 | 145 |
| 139 | Pasłęk | O | 19.6592 | 54.0672 | 0 | 14 | 0 | 13 | 32 | 0 | 0 | 0 | 0 | 0 | 59 |
| 140 | Pasłęk | O | 19.6611 | 54.0689 | 1 | 66 | 0 | 6 | 59 | 0 | 0 | 0 | 5 | 0 | 137 |
| 141 | Pasłęk | S | 19.6581 | 54.0539 | 0 | 18 | 0 | 18 | 65 | 8 | 0 | 8 | 9 | 0 | 126 |
| 142 | Pasłęk | S | 19.6547 | 54.0686 | 1 | 10 | 0 | 29 | 77 | 0 | 0 | 0 | 24 | 0 | 141 |

Appendix 1. (continued)

| No | Site | Habitat | long | lat | YU | YM | YT | YF | PU | PM | PT | PF | BU | BB | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 143 | Pasłęk | S | 19.6619 | 54.0705 | 1 | 52 | 1 | 14 | 6 | 26 | 1 | 7 | 14 | 1 | 123 |
| 144 | Sierakowice | O | 17.8972 | 54.3361 | 0 | 38 | 0 | 29 | 0 | 22 | 1 | 14 | 23 | 0 | 127 |
| 145 | Sierakowice | O | 17.8978 | 54.3364 | 1 | 26 | 1 | 6 | 2 | 80 | 6 | 8 | 0 | 0 | 130 |
| 146 | Puzdrowo | O | 17.8664 | 54.3433 | 3 | 45 | 7 | 25 | 7 | 20 | 2 | 18 | 0 | 0 | 127 |
| 147 | Sierakowice | O | 17.9011 | 54.3503 | 0 | 47 | 0 | 17 | 0 | 11 | 0 | 6 | 46 | 1 | 128 |
| 148 | Sierakowice | O | 17.8875 | 54.3458 | 0 | 14 | 14 | 44 | 0 | 18 | 20 | 21 | 0 | 0 | 131 |
| 149 | Sierakowice | O | 17.8908 | 54.3453 | 0 | 19 | 1 | 10 | 5 | 34 | 5 | 41 | 7 | 0 | 122 |
| 150 | Sierakowice | I | 17.8978 | 54.3378 | 0 | 14 | 0 | 14 | 1 | 65 | 0 | 30 | 0 | 0 | 124 |
| 151 | Sierakowice | I | 17.8894 | 54.3456 | 0 | 11 | 25 | 24 | 0 | 13 | 25 | 23 | 4 | 0 | 125 |
| 152 | Sierakowice | I | 17.8897 | 54.3456 | 1 | 26 | 8 | 22 | 6 | 31 | 6 | 15 | 6 | 0 | 121 |
| 153 | Sierakowice | I | 17.8886 | 54.3511 | 1 | 7 | 0 | 10 | 6 | 14 | 1 | 20 | 63 | 0 | 122 |
| 154 | Sierakowice | I | 17.8881 | 54.3456 | 0 | 20 | 4 | 41 | 6 | 14 | 8 | 28 | 10 | 0 | 131 |
| 155 | Sierakowice | I | 17.8875 | 54.3456 | 0 | 40 | 5 | 17 | 2 | 25 | 4 | 14 | 19 | 0 | 126 |
| 156 | Sierakowice | S | 17.9033 | 54.3425 | 9 | 29 | 14 | 19 | 1 | 23 | 2 | 11 | 14 | 0 | 122 |
| 157 | Sierakowice | I | 17.8969 | 54.3508 | 0 | 62 | 0 | 41 | 0 | 8 | 0 | 10 | 0 | 0 | 121 |
| 158 | Załakowo | O | 17.8444 | 54.3847 | 0 | 67 | 0 | 20 | 6 | 18 | 0 | 12 | 4 | 0 | 127 |
| 159 | Załakowo | O | 17.8461 | 54.3839 | 0 | 73 | 2 | 16 | 2 | 18 | 0 | 4 | 9 | 0 | 124 |
| 160 | Załakowo | O | 17.8450 | 54.3842 | 2 | 46 | 1 | 24 | 3 | 15 | 2 | 9 | 21 | 0 | 123 |
| 161 | Załakowo | O | 17.8458 | 54.3833 | 1 | 32 | 3 | 48 | 2 | 4 | 4 | 9 | 33 | 0 | 136 |
| 162 | Załakowo | I | 17.8464 | 54.3831 | 2 | 45 | 6 | 51 | 2 | 7 | 4 | 6 | 27 | 1 | 151 |
| 163 | Załakowo | I | 17.8467 | 54.3844 | 0 | 49 | 1 | 23 | 3 | 5 | 0 | 6 | 28 | 0 | 115 |
| 164 | Załakowo | I | 17.8458 | 54.3825 | 1 | 29 | 3 | 42 | 4 | 4 | 2 | 2 | 40 | 0 | 127 |
| 165 | Migi | S | 17.8683 | 54.3647 | 0 | 57 | 0 | 17 | 2 | 13 | 0 | 9 | 35 | 0 | 133 |
| 166 | Lubowidz | I | 17.8169 | 54.5458 | 2 | 85 | 4 | 20 | 1 | 2 | 0 | 0 | 19 | 0 | 133 |
| 167 | Lębork | O | 17.7544 | 54.5511 | 1 | 36 | 1 | 21 | 24 | 20 | 0 | 13 | 15 | 0 | 131 |
| 168 | Lębork | O | 17.7550 | 54.5519 | 0 | 46 | 4 | 19 | 26 | 19 | 2 | 9 | 6 | 0 | 131 |
| 169 | Mosty | I | 17.7956 | 54.5447 | 12 | 17 | 1 | 14 | 15 | 7 | 0 | 9 | 59 | 0 | 134 |
| 170 | Mosty | O | 17.7961 | 54.5458 | 10 | 23 | 9 | 12 | 6 | 7 | 2 | 7 | 48 | 4 | 128 |
| 171 | Lębork | I | 17.7186 | 54.5422 | 24 | 13 | 0 | 27 | 17 | 10 | 1 | 11 | 17 | 1 | 121 |
| 172 | Mosty | O | 17.7781 | 54.5436 | 3 | 22 | 3 | 33 | 15 | 15 | 1 | 9 | 22 | 10 | 133 |
| 173 | Lębork | I | 17.7706 | 54.5419 | 6 | 22 | 4 | 20 | 33 | 17 | 1 | 13 | 13 | 2 | 131 |
| 174 | Lębork | O | 17.7058 | 54.5433 | 12 | 27 | 4 | 21 | 23 | 22 | 0 | 4 | 24 | 1 | 138 |
| 175 | Lębork | O | 17.7361 | 54.5400 | 35 | 45 | 2 | 10 | 8 | 16 | 1 | 2 | 3 | 0 | 122 |
| 176 | Lębork | I | 17.7708 | 54.5494 | 1 | 20 | 7 | 23 | 13 | 33 | 5 | 20 | 0 | 0 | 122 |
| 177 | Lębork | I | 17.7675 | 54.5400 | 3 | 18 | 7 | 24 | 34 | 5 | 2 | 8 | 15 | 4 | 120 |
| 178 | Lębork | I | 17.7658 | 54.5450 | 0 | 8 | 3 | 9 | 3 | 10 | 3 | 8 | 13 | 1 | 58 |
| 179 | Lębork | S | 17.7672 | 54.5464 | 0 | 18 | 6 | 21 | 38 | 1 | 2 | 7 | 37 | 0 | 130 |
| 180 | Lębork | I | 17.7333 | 54.5444 | 25 | 22 | 0 | 21 | 9 | 10 | 0 | 8 | 26 | 0 | 121 |
| 181 | Lębork | I | 17.7417 | 54.5428 | 0 | 27 | 3 | 27 | 5 | 37 | 2 | 20 | 5 | 0 | 126 |
| 182 | Lębork | S | 17.7694 | 54.5261 | 0 | 29 | 4 | 35 | 16 | 18 | 4 | 11 | 4 | 0 | 121 |
| 183 | Lębork | I | 17.7661 | 54.5292 | 7 | 22 | 3 | 15 | 3 | 40 | 3 | 20 | 13 | 2 | 128 |
| 184 | Lębork | I | 17.7622 | 54.5467 | 1 | 23 | 0 | 32 | 31 | 15 | 0 | 9 | 15 | 0 | 126 |
| 185 | Lębork | O | 17.7711 | 54.5503 | 2 | 19 | 7 | 13 | 22 | 34 | 2 | 18 | 3 | 0 | 120 |
| 186 | Gdynia | O | 18.4369 | 54.5383 | 0 | 31 | 3 | 59 | 8 | 6 | 0 | 10 | 13 | 0 | 130 |
| 187 | Gdynia | O | 18.4631 | 54.5242 | 0 | 16 | 1 | 16 | 1 | 44 | 6 | 45 | 1 | 0 | 130 |
| 188 | Gdynia | O | 18.4553 | 54.5344 | 19 | 17 | 14 | 31 | 20 | 5 | 7 | 9 | 8 | 0 | 130 |
| 189 | Gdynia | O | 18.4628 | 54.5367 | 0 | 16 | 8 | 15 | 2 | 37 | 7 | 39 | 6 | 0 | 130 |
| 190 | Gdynia | O | 18.4436 | 54.5528 | 1 | 10 | 3 | 19 | 39 | 9 | 0 | 41 | 7 | 1 | 130 |
| 191 | Gdynia | O | 18.4631 | 54.5622 | 0 | 31 | 2 | 28 | 2 | 13 | 1 | 29 | 24 | 0 | 130 |
| 192 | Gdynia | I | 18.5461 | 54.5425 | 0 | 16 | 16 | 37 | 17 | 5 | 5 | 11 | 23 | 0 | 130 |
| 193 | Gdynia | I | 18.4533 | 54.4578 | 1 | 42 | 2 | 39 | 17 | 13 | 0 | 7 | 9 | 0 | 130 |
| 194 | Gdynia | O | 18.4736 | 54.4692 | 0 | 13 | 3 | 25 | 35 | 3 | 3 | 6 | 42 | 0 | 130 |
| 195 | Gdynia | S | 18.5594 | 54.5017 | 3 | 20 | 3 | 24 | 22 | 7 | 1 | 19 | 31 | 0 | 130 |
| 196 | Gdynia | O | 18.4611 | 54.5008 | 0 | 14 | 2 | 8 | 26 | 44 | 8 | 25 | 3 | 0 | 130 |
| 197 | Gdynia | O | 18.4744 | 54.5561 | 10 | 18 | 1 | 5 | 19 | 61 | 0 | 16 | 0 | 0 | 130 |
| 198 | Gdynia | O | 18.4714 | 54.5597 | 5 | 2 | 1 | 16 | 6 | 10 | 0 | 35 | 55 | 0 | 130 |
| 199 | Gdynia | O | 18.4928 | 54.5406 | 0 | 35 | 2 | 20 | 9 | 23 | 3 | 12 | 26 | 0 | 130 |
| 200 | Gdynia | O | 18.5319 | 54.5078 | 3 | 24 | 2 | 13 | 13 | 14 | 4 | 19 | 37 | 1 | 130 |
| 201 | Gdynia | I | 18.5631 | 54.4769 | 0 | 15 | 9 | 68 | 4 | 0 | 0 | 12 | 22 | 0 | 130 |
| 202 | Gdynia | I | 18.5083 | 54.5256 | 0 | 30 | 1 | 17 | 3 | 21 | 0 | 29 | 12 | 7 | 120 |
| 203 | Gdynia | I | 18.5169 | 54.5022 | 5 | 33 | 1 | 41 | 28 | 9 | 0 | 10 | 3 | 0 | 130 |
| 204 | Gdynia | I | 18.4781 | 54.5633 | 7 | 28 | 4 | 26 | 1 | 10 | 2 | 18 | 35 | 0 | 131 |
| 205 | Gdynia | S | 18.5350 | 54.5433 | 0 | 27 | 6 | 31 | 25 | 10 | 1 | 17 | 12 | 0 | 129 |
| 206 | Gdynia | I | 18.4950 | 54.5547 | 5 | 19 | 1 | 30 | 31 | 14 | 1 | 17 | 12 | 0 | 130 |
| 207 | Gdynia | I | 18.5186 | 54.4700 | 0 | 31 | 4 | 35 | 20 | 9 | 0 | 22 | 8 | 0 | 129 |
| 208 | Gdynia | S | 18.5264 | 54.5211 | 0 | 38 | 1 | 35 | 11 | 18 | 0 | 16 | 1 | 0 | 120 |
| 209 | Reda | I | 18.3664 | 54.6033 | 3 | 25 | 0 | 9 | 37 | 15 | 0 | 21 | 22 | 0 | 132 |
| 210 | Reda | I | 18.3528 | 54.5927 | 1 | 25 | 12 | 18 | 12 | 11 | 17 | 17 | 3 | 0 | 116 |
| 211 | Reda | I | 18.3625 | 54.6000 | 2 | 13 | 0 | 35 | 13 | 18 | 0 | 11 | 27 | 3 | 122 |
| 212 | Reda | S | 18.3528 | 54.6072 | 2 | 51 | 0 | 18 | 23 | 24 | 0 | 5 | 6 | 0 | 129 |

Appendix 1. (continued)

| No | Site | Habitat | long | lat | YU | YM | YT | YF | PU | PM | PT | PF | BU | BB | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 213 | Połchowo | O | 18.3700 | 54.6494 | 0 | 16 | 0 | 19 | 10 | 34 | 0 | 44 | 8 | 0 | 131 |
| 214 | Mrzezino | I | 18.4292 | 54.6528 | 0 | 13 | 0 | 21 | 72 | 7 | 0 | 7 | 8 | 0 | 128 |
| 215 | Mrzezino | I | 18.4358 | 54.6475 | 0 | 1 | 0 | 0 | 70 | 22 | 3 | 2 | 23 | 0 | 121 |
| 216 | Smolno | I | 18.4089 | 54.6642 | 0 | 25 | 0 | 6 | 23 | 51 | 0 | 19 | 0 | 0 | 124 |
| 217 | Smolno | I | 18.4067 | 54.6600 | 0 | 46 | 0 | 2 | 0 | 72 | 0 | 4 | 0 | 0 | 124 |
| 218 | Żelistrzewo | O | 18.4117 | 54.6756 | 0 | 23 | 0 | 8 | 22 | 51 | 0 | 19 | 0 | 0 | 123 |
| 219 | Puck | I | 18.4117 | 54.7131 | 0 | 22 | 0 | 16 | 7 | 28 | 0 | 20 | 37 | 0 | 130 |
| 220 | Puck | O | 18.3889 | 54.7139 | 0 | 12 | 0 | 2 | 0 | 32 | 0 | 0 | 77 | 3 | 126 |
| 221 | Puck | S | 18.3947 | 54.7097 | 0 | 32 | 0 | 7 | 1 | 16 | 2 | 3 | 93 | 0 | 154 |
| 222 | Puck | S | 18.4089 | 54.7081 | 1 | 22 | 0 | 26 | 8 | 25 | 0 | 33 | 16 | 0 | 131 |
| 223 | Puck | O | 18.4286 | 54.7122 | 0 | 9 | 0 | 13 | 21 | 13 | 0 | 15 | 47 | 1 | 119 |
| 224 | Puck | O | 18.4167 | 54.7219 | 0 | 21 | 0 | 13 | 5 | 13 | 0 | 5 | 71 | 0 | 128 |
| 225 | Puck | O | 18.4136 | 54.7097 | 1 | 27 | 1 | 11 | 4 | 45 | 0 | 12 | 17 | 0 | 118 |
| 226 | Wieżyca | O | 18.1309 | 54.2341 | 0 | 24 | 4 | 10 | 0 | 9 | 1 | 2 | 2 | 1 | 53 |
| 227 | Gołobie | O | 18.0399 | 54.2060 | 2 | 26 | 0 | 19 | 3 | 33 | 0 | 26 | 15 | 0 | 124 |
| 228 | Żukowo | I | 18.3578 | 54.3421 | 0 | 30 | 0 | 27 | 25 | 27 | 0 | 24 | 13 | 8 | 154 |
| 229 | Kościerzyna | I | 17.9776 | 54.1168 | 20 | 17 | 0 | 29 | 6 | 14 | 2 | 15 | 7 | 17 | 127 |
| 230 | Kościerzyna | O | 17.9899 | 54.1249 | 20 | 17 | 3 | 34 | 49 | 1 | 1 | 4 | 8 | 6 | 143 |
| 231 | Kościerzyna | I | 17.9712 | 54.1256 | 31 | 6 | 0 | 33 | 1 | 4 | 0 | 11 | 13 | 1 | 100 |
| 232 | Kościerska Huta | O | 18.0196 | 54.1419 | 17 | 31 | 5 | 32 | 10 | 7 | 0 | 7 | 16 | 11 | 136 |
| 233 | Gdynia | S | 18.5772 | 54.5038 | 7 | 11 | 0 | 4 | 1 | 0 | 0 | 0 | 7 | 0 | 30 |
| 234 | Gdynia | S | 18.5528 | 54.4954 | 5 | 18 | 1 | 14 | 7 | 14 | 1 | 18 | 4 | 0 | 82 |
| 235 | Gdynia | I | 18.5523 | 54.4950 | 11 | 8 | 0 | 24 | 9 | 14 | 0 | 22 | 6 | 0 | 94 |
| 236 | Gdynia | I | 18.5497 | 54.4997 | 1 | 7 | 2 | 13 | 1 | 7 | 1 | 7 | 3 | 0 | 42 |
| 237 | Elbląg | O | 19.4383 | 54.1803 | 1 | 7 | 2 | 7 | 0 | 2 | 0 | 0 | 1 | 5 | 25 |
| 238 | Elbląg | O | 19.3281 | 54.1736 | 3 | 8 | 1 | 5 | 1 | 0 | 0 | 0 | 3 | 5 | 26 |
| 239 | Elbląg | O | 19.4383 | 54.1747 | 2 | 23 | 0 | 16 | 0 | 10 | 0 | 0 | 11 | 3 | 65 |
| 240 | Elbląg | I | 19.4372 | 54.1742 | 1 | 53 | 4 | 18 | 0 | 13 | 0 | 5 | 53 | 36 | 183 |
| 241 | Elbląg | I | 19.4392 | 54.1797 | 1 | 24 | 2 | 16 | 1 | 6 | 0 | 7 | 25 | 5 | 87 |
| 242 | Elbląg | I | 19.4414 | 54.1733 | 1 | 3 | 0 | 2 | 0 | 2 | 0 | 0 | 4 | 3 | 15 |
| 243 | Elbląg | S | 19.4658 | 54.1697 | 0 | 0 | 2 | 6 | 0 | 1 | 1 | 1 | 8 | 6 | 25 |
| 244 | Elbląg | S | 19.4581 | 54.1692 | 0 | 5 | 3 | 3 | 0 | 1 | 1 | 0 | 6 | 11 | 30 |
| 245 | Elbląg | S | 19.4433 | 54.1731 | 2 | 10 | 0 | 6 | 0 | 4 | 0 | 4 | 12 | 15 | 53 |
| 246 | Białogóra | O | 17.9633 | 54.8164 | 6 | 9 | 0 | 31 | 43 | 15 | 2 | 12 | 10 | 0 | 128 |
| 247 | Kopalino | O | 17.8508 | 54.7883 | 2 | 16 | 0 | 20 | 12 | 27 | 0 | 34 | 9 | 0 | 120 |
| 248 | Kopalino | I | 17.8506 | 54.7894 | 0 | 9 | 0 | 37 | 29 | 8 | 0 | 37 | 0 | 0 | 120 |
| 249 | Kopalino | S | 17.8508 | 54.7925 | 0 | 10 | 0 | 38 | 12 | 9 | 0 | 37 | 15 | 0 | 121 |
| 250 | Lubiatowo | I | 17.8619 | 54.7939 | 0 | 2 | 0 | 29 | 2 | 1 | 0 | 85 | 1 | 0 | 120 |
| 251 | Ciekocino | I | 17.4497 | 54.7569 | 4 | 18 | 0 | 15 | 16 | 21 | 1 | 21 | 20 | 2 | 118 |
| 252 | Sasino | I | 17.7531 | 54.7589 | 0 | 9 | 0 | 40 | 28 | 5 | 3 | 20 | 8 | 7 | 120 |
| 253 | Ulinia | O | 17.7042 | 54.7578 | 3 | 105 | 7 | 7 | 0 | 15 | 1 | 1 | 0 | 0 | 139 |
| 254 | Sarbsk | S | 17.6664 | 54.7522 | 0 | 26 | 64 | 11 | 6 | 18 | 28 | 5 | 22 | 0 | 180 |
| 255 | Szczenurze | I | 17.6161 | 54.7261 | 0 | 25 | 0 | 81 | 0 | 23 | 0 | 0 | 5 | 1 | 135 |
| 256 | Nowęcin | I | 17.5883 | 54.7525 | 3 | 53 | 3 | 34 | 7 | 3 | 0 | 3 | 21 | 0 | 127 |
| 257 | Nowęcin | O | 17.5878 | 54.7528 | 2 | 48 | 7 | 38 | 11 | 1 | 0 | 1 | 28 | 0 | 136 |
| 258 | Łeba | I | 17.5519 | 54.7631 | 11 | 7 | 10 | 49 | 12 | 4 | 0 | 0 | 34 | 0 | 127 |
| 259 | Łeba | O | 17.5558 | 54.7606 | 15 | 9 | 11 | 38 | 18 | 13 | 0 | 0 | 25 | 0 | 129 |
| 260 | Łeba | I | 17.5514 | 54.7656 | 11 | 19 | 13 | 60 | 10 | 13 | 0 | 0 | 14 | 0 | 140 |

Explanations: Details of the sites sampled in this study. O – open habitat; I – intermediate habitat; S – shaded habitat.. Y – yellow; P – pink; B – brown. U – unbanded; M – midbanded (00300); T – trifasciate (00345); F – many banded. BB – all banded browns. Longitude and latitude in decimal degrees.

Appendix 2. Scores of each site on each axis of a Principal Components Analysis using frequencies of yellow, brown, unbanded and midbanded in banded shells in the samples.

| | Eigenvalue | 0.4255 | 0.2933 | 0.2058 | 0.0754 | |
|---|---|---|---|---|---|---|
| Site name | Site no. | PCA AX 1 | PCA AX 2 | PCA AX 3 | PCA AX 4 | Habitat |
| Czernin | 1 | 0.2723 | –0.7761 | –1.7766 | 3.8375 | O |
| Dąbrówka Mal. | 2 | 1.3676 | –0.6573 | 0.1676 | 2.3555 | S |
| Gościszewo | 3 | –1.113 | –0.8222 | 0.9643 | –0.3291 | I |
| Gościszewo | 4 | –1.3848 | 0.226 | 0.2656 | –0.4934 | I |
| Kalwa | 5 | 0.5507 | –0.6433 | 0.1092 | 1.9687 | S |
| Kołoząb | 6 | 2.214 | –0.7592 | –0.1261 | 2.229 | I |
| Kwidzyn | 7 | 0.3997 | 1.0725 | 0.6142 | 0.2618 | O |
| Kwidzyn | 8 | 0.6901 | 0.8737 | –0.4147 | –0.9371 | I |
| Łabuń | 9 | 2.9293 | –2.1156 | –2.0473 | –1.3229 | S |
| Malbork | 10 | 0.6804 | 0.0211 | 0.5407 | 0.3794 | I |
| Malbork | 11 | 1.3677 | –0.9669 | 0.1269 | 3.5995 | O |
| Malbork | 12 | 1.1949 | 0.7132 | 0.202 | 0.7693 | S |
| Malbork | 13 | 0.206 | –1.0842 | –1.0135 | 0.0876 | I |
| Malbork | 14 | 0.5103 | –0.7412 | –0.1262 | 1.242 | O |
| Malbork | 15 | –0.5019 | –1.2834 | 2.2037 | –0.5276 | I |
| Mikołajki Pom. | 16 | –1.3024 | –1.0734 | 0.4736 | –0.1879 | O |
| Mikołajki Pom. | 17 | –0.6731 | –0.9506 | 1.8691 | –0.4782 | I |
| Postolin | 18 | –0.4816 | –1.44 | 2.0316 | –0.4708 | S |
| Postolin | 19 | –1.4968 | –1.0634 | 0.1526 | –0.1882 | I |
| Prabuty | 20 | 0.2703 | –0.9294 | 1.925 | –1.3401 | O |
| Ryjewo | 21 | –0.3075 | –1.0201 | 2.6235 | –0.6032 | S |
| Ryjewo | 22 | –2.0137 | –0.3113 | –0.9377 | –0.1045 | S |
| Ryjewo | 23 | –0.6603 | 0.5752 | 0.8748 | –1.7954 | O |
| Stary Targ | 24 | –0.3961 | –1.0794 | 2.436 | –0.5706 | O |
| Stary Targ | 25 | –1.3766 | –0.5435 | 0.3491 | –0.1753 | I |
| Szropy | 26 | 0.2818 | 2.6767 | –0.2193 | –0.9954 | O |
| Sztum | 27 | –0.5062 | –1.529 | 2.1793 | –0.5186 | I |
| Sztum | 28 | –1.0926 | –1.4581 | 0.9668 | –0.3168 | I |
| Sztum | 29 | –0.5025 | –0.3127 | 2.2632 | –0.557 | O |
| Sztum | 30 | –0.3814 | –2.2951 | 2.3905 | –0.5386 | I |
| Sztum | 31 | –0.3018 | 1.8267 | 2.8133 | –0.692 | I |
| Sztum | 32 | –1.0156 | –1.821 | 0.9056 | –0.1684 | S |
| Sztumska Wieś | 33 | 0.4413 | –1.2994 | 0.3237 | –0.9217 | O |
| Waplewo | 34 | 1.0862 | 0.1024 | 0.8246 | –1.1421 | I |
| Malbork | 35 | –0.5038 | –0.6895 | –0.8056 | 0.129 | I |
| Malbork | 36 | 0.3493 | 0.0714 | –0.5534 | –1.0177 | S |
| Malbork | 37 | 0.0445 | –0.2717 | –0.9976 | 1.2098 | I |
| Malbork | 38 | –0.9431 | –1.4792 | –1.3939 | –0.5667 | I |
| Malbork | 39 | –1.1701 | –1.3843 | –0.7982 | –0.3876 | I |
| Malbork | 40 | 0.4992 | –0.5686 | 0.7556 | –0.8281 | S |
| Malbork | 41 | –1.0899 | –1.5173 | –1.1748 | –0.3531 | O |
| Malbork | 42 | 3.1975 | –1.0726 | –1.0075 | –1.4394 | S |
| Mikoszewo | 43 | –2.1796 | –0.7167 | –1.8105 | 0.2498 | I |
| Mikoszewo | 44 | –1.5386 | –1.4079 | –1.6562 | 0.4518 | I |
| Świerki | 45 | –1.7881 | –0.1412 | –1.2841 | 0.6212 | O |
| Świerki | 46 | –1.7486 | 2.4372 | –0.1512 | –0.2073 | I |
| Trępnowy | 47 | 1.0273 | –2.6511 | 0.444 | –0.888 | S |
| Sztutowo | 48 | –0.9071 | 2.018 | 0.8159 | –0.5003 | I |
| Nowy Dwór | 49 | –1.2293 | 0.9154 | –0.1623 | –0.0097 | I |
| Nowy Dwór | 50 | –1.3187 | –0.5645 | –0.8951 | 0.2732 | I |
| Nowy Staw | 51 | 0.1474 | –0.4804 | –0.5031 | 1.5607 | I |
| Nowy Staw | 52 | 1.7843 | –0.5739 | –1.2128 | –1.0348 | I |
| Nowy Staw | 53 | 1.5215 | –1.8474 | –0.1633 | 0.0868 | S |
| Nowy Staw | 54 | 0.8644 | 1.3412 | –0.0816 | –0.8862 | S |
| Nowy Staw | 55 | 2.5806 | –1.5321 | –0.5565 | –0.5386 | I |
| Kałdowo | 56 | –1.1883 | –0.8034 | –1.549 | 0.6131 | I |
| Kałdowo | 57 | –0.971 | 0.5753 | –0.5761 | 0.4104 | I |
| Kmiecin | 58 | –1.5068 | –0.6168 | –0.363 | 0.0277 | I |
| Tragamin | 59 | 4.4792 | 1.8844 | –0.5521 | –2.0181 | S |
| Pogorzała Wieś | 60 | –1.1995 | –0.027 | –1.3113 | 0.4106 | O |
| Kraśniewo | 61 | 0.8899 | –0.6955 | –0.5733 | 1.2173 | I |
| Stegna | 62 | 1.162 | –0.2623 | –1.1759 | –1.3158 | I |
| Jazowa | 63 | –1.3932 | 0.1456 | –0.3788 | -0.1646 | I |
| Miłoradz | 64 | 1.2307 | –1.3141 | 0.2348 | 1.12 | I |
| Tujsk | 65 | –0.3583 | –0.5855 | –0.3445 | 0.1578 | I |
| Rybina | 66 | 0.2281 | –0.7191 | –0.4368 | 0.3362 | I |
| Marzęcino | 67 | 1.3391 | –0.2102 | 0.662 | 1.6373 | S |

Appendix 2. (continued)

| Site name | Site no. | PCA AX 1 | PCA AX 2 | PCA AX 3 | PCA AX 4 | Habitat |
|---|---|---|---|---|---|---|
| Nowy Staw | 68 | 1.8626 | –1.2991 | –1.2496 | –1.4945 | I |
| Borowo | 69 | –1.0739 | 0.2975 | 0.9715 | –0.3352 | O |
| Bieszkowice | 70 | –0.7779 | –0.0247 | –0.4086 | 0.0917 | O |
| Wejherowo | 71 | –0.5483 | –1.6868 | 0.4509 | –0.3263 | O |
| Gdańsk | 72 | –0.4958 | –0.1903 | 0.9498 | –0.0102 | O |
| Wejherowo | 73 | –0.4374 | 0.4135 | 1.3085 | –0.1108 | I |
| Gdańsk | 74 | –0.247 | –0.2957 | 1.1435 | –0.5324 | O |
| Wejherowo | 75 | 0.1345 | 0.1046 | 0.6677 | 0.3368 | O |
| Borowo | 76 | 0.1618 | –0.1467 | 0.3013 | –0.7577 | I |
| Wejherowo | 77 | 1.0642 | –0.266 | –0.1825 | –1.0367 | I |
| Wejherowo | 78 | 0.3883 | –0.0818 | 0.7255 | –0.7828 | I |
| Gdańsk | 79 | 0.1965 | –0.0738 | 0.1769 | –0.592 | I |
| Gdańsk | 80 | –0.0202 | –0.3032 | 0.5165 | –0.6929 | I |
| Gdańsk | 81 | –0.3021 | –0.8801 | 0.2948 | –0.2936 | I |
| Gdańsk | 82 | 0.5846 | –0.5454 | 0.7782 | –0.1983 | I |
| Gdańsk | 83 | 0.5228 | –0.1662 | 0.0396 | –0.9936 | I |
| Wejherowo | 84 | –0.2617 | 0.5363 | 0.6461 | –0.6177 | S |
| Wejherowo | 85 | 0.2765 | 0.2482 | 0.6501 | –0.5579 | S |
| Sopot | 86 | 0.3426 | –0.1401 | 0.2304 | 0.0498 | S |
| Wejherowo | 87 | 0.9141 | –1.7539 | 0.4945 | 0.2004 | S |
| Gdańsk | 88 | 0.4901 | 0.0531 | 0.4707 | –0.8042 | S |
| Gdańsk | 89 | 1.2672 | 0.01 | 0.4448 | –0.6325 | S |
| Kartuzy | 90 | –0.7066 | –0.5333 | –1.9445 | 0.7367 | O |
| Kartuzy | 91 | 0.4768 | –0.6249 | –1.4836 | –0.7155 | S |
| Kartuzy | 92 | –1.4563 | –1.0624 | –1.2727 | 0.008 | O |
| Kartuzy | 93 | 0.8252 | 0.8471 | –0.7282 | –0.1621 | S |
| Kartuzy | 94 | 0.5187 | –0.4704 | –1.827 | –0.4095 | O |
| Kartuzy | 95 | 0.0141 | 0.8546 | –1.78 | 0.3945 | O |
| Kartuzy | 96 | 0.3752 | 0.473 | –1.1161 | 0.0951 | S |
| Kartuzy | 97 | 0.3434 | –0.2444 | –1.728 | –0.2224 | S |
| Kartuzy | 98 | 0.1967 | 0.9415 | –1.8774 | 0.9552 | I |
| Żukowo | 99 | 0.0517 | –0.8872 | 0.71 | 0.7564 | S |
| Żukowo | 100 | 1.361 | 0.6298 | 0.5168 | 0.3024 | S |
| Żukowo | 101 | 1.0377 | –0.9504 | 1.0379 | –0.8562 | S |
| Żukowo | 102 | 0.8971 | –0.0838 | 0.9641 | 0.6289 | S |
| Żukowo | 103 | –0.4222 | –1.1441 | 0.7778 | 0.1324 | O |
| Żukowo | 104 | 1.436 | 1.1362 | 1.0021 | 1.2915 | O |
| Żukowo | 105 | –2.1954 | –0.6208 | –1.524 | 0.2517 | O |
| Żukowo | 106 | –0.4698 | –1.1446 | 1.1634 | 0.1226 | S |
| Starogard Gd. | 107 | 0.9392 | –0.1354 | –1.479 | –1.0028 | S |
| Starogard Gd. | 108 | –1.1554 | 0.1186 | –1.4715 | 0.453 | I |
| Starogard Gd. | 109 | 0.4777 | –0.1916 | –0.3919 | –0.8758 | S |
| Starogard Gd. | 110 | –1.1259 | 0.0798 | –1.5325 | –0.1299 | S |
| Starogard Gd. | 111 | –0.0526 | 2.2794 | –0.7389 | –0.8635 | O |
| Starogard Gd. | 112 | 0.2518 | 0.8972 | –1.2387 | –0.8964 | I |
| Starogard Gd. | 113 | 0.2693 | 1.6108 | –1.0227 | –0.9168 | O |
| Starogard Gd. | 114 | 1.3507 | 0.9027 | –0.716 | –1.4132 | O |
| Lubichowo | 115 | –0.1226 | 0.3528 | –2.0234 | 0.6302 | I |
| Lubichowo | 116 | –0.2685 | 1.8958 | –0.4794 | 0.6207 | I |
| Lubichowo | 117 | 0.427 | 2.0962 | –0.848 | –0.9901 | I |
| Lubichowo | 118 | –0.6518 | 1.89 | 0.5869 | –0.3803 | O |
| Wejherowo | 119 | 0.67 | –0.3131 | 0.3396 | –0.3488 | S |
| Wejherowo | 120 | –0.3215 | 0.0194 | –0.1067 | 0.3407 | S |
| Wejherowo | 121 | –0.4672 | –1.0329 | –0.1801 | 0.4452 | O |
| Wejherowo | 122 | –0.532 | –0.2307 | 1.5132 | –0.0708 | O |
| Wejherowo | 123 | –0.0336 | –1.8501 | 2.07 | 0.2125 | O |
| Wejherowo | 124 | –0.4124 | –1.1068 | 0.5639 | 0.4653 | O |
| Wejherowo | 125 | 0.6112 | –0.7144 | 0.1909 | 2.2114 | O |
| Nadole | 126 | 0.3268 | 0.3118 | 1.1605 | 1.5047 | O |
| Nadole | 127 | –1.6762 | 2.4422 | –0.0006 | –0.2327 | O |
| Nadole | 128 | 1.409 | 0.1033 | 0.4975 | 0.8085 | O |
| Wejherowo | 129 | –0.2692 | 0.3171 | 0.741 | –0.3098 | S |
| Wejherowo | 130 | 0.9325 | –1.5107 | –0.1265 | –0.0027 | S |
| Frombork | 131 | 1.8067 | 0.7272 | 1.3279 | 3.402 | I |
| Frombork | 132 | 1.0903 | 0.9583 | 1.634 | 1.5433 | I |
| Frombork | 133 | 1.639 | 1.8835 | 1.3081 | 2.0626 | S |
| Frombork | 134 | 0.3337 | 0.6071 | 1.7138 | 0.0098 | S |
| Milejewo | 135 | –1.09 | –0.3972 | 0.7451 | –0.3551 | I |
| Milejewo | 136 | –0.7591 | 0.5676 | –0.4785 | –0.5338 | I |

Appendix 2. (continued)

| Site name | Site no. | PCA AX 1 | PCA AX 2 | PCA AX 3 | PCA AX 4 | Habitat |
|---|---|---|---|---|---|---|
| Młynary | 137 | 0.0474 | 0.8609 | –1.162 | 0.1781 | O |
| Młynary | 138 | 0.1501 | 0.9483 | –0.1472 | –0.889 | S |
| Pasłęk | 139 | 0.3306 | 0.1575 | –0.2807 | 2.6993 | O |
| Pasłęk | 140 | –0.1983 | –1.5214 | –1.1636 | 2.2402 | O |
| Pasłęk | 141 | 0.9611 | –0.0133 | 0.2321 | 2.294 | S |
| Pasłęk | 142 | 1.6632 | 1.1001 | 0.0866 | 2.237 | S |
| Pasłęk | 143 | –0.8137 | –0.8842 | –0.5047 | –0.1405 | S |
| Sierakowice | 144 | –0.502 | –0.0428 | –0.2422 | –0.6091 | O |
| Sierakowice | 145 | –0.8451 | –1.6369 | 1.2863 | –0.2459 | O |
| Puzdrowo | 146 | –1.3105 | 0.1875 | –0.0071 | 0.2257 | O |
| Sierakowice | 147 | 0.2852 | –0.6754 | –1.1787 | –0.9599 | O |
| Sierakowice | 148 | –1.1542 | 1.4491 | 1.0207 | –0.384 | O |
| Sierakowice | 149 | –0.2834 | –0.065 | 1.6088 | –0.3855 | O |
| Sierakowice | 150 | –0.6878 | –0.831 | 1.7822 | –0.4238 | I |
| Sierakowice | 151 | –0.832 | 1.5544 | 1.2501 | –0.507 | I |
| Sierakowice | 152 | –0.7853 | 0.0749 | 0.5506 | –0.1026 | I |
| Sierakowice | 153 | 2.0844 | 0.2223 | 0.0157 | –1.2212 | I |
| Sierakowice | 154 | –0.6054 | 1.1578 | 0.7147 | –0.2838 | I |
| Sierakowice | 155 | –0.5458 | –0.2895 | –0.0522 | –0.4748 | I |
| Sierakowice | 156 | –0.6673 | 0.2478 | –0.2928 | –0.0064 | S |
| Sierakowice | 157 | –2.0119 | 0.4121 | –0.8243 | –0.054 | I |
| Załakowo | 158 | –1.4795 | –0.4935 | –0.5895 | 0.0909 | O |
| Załakowo | 159 | –1.533 | –0.769 | –1.0433 | –0.0963 | O |
| Załakowo | 160 | –0.6134 | –0.1708 | –0.6594 | –0.2971 | O |
| Załakowo | 161 | –0.2228 | 1.0829 | –0.6249 | –0.6106 | O |
| Załakowo | 162 | –0.687 | 0.8355 | –0.7892 | –0.4422 | I |
| Załakowo | 163 | –0.423 | –0.1588 | –1.1615 | –0.4769 | I |
| Załakowo | 164 | 0.1803 | 0.8671 | –0.9466 | –0.6481 | I |
| Migi | 165 | –0.2503 | –0.6639 | –1.0212 | –0.5988 | S |
| Lubowidz | 166 | –1.4024 | –0.5041 | –1.7858 | –0.1245 | I |
| Lębork | 167 | –0.1462 | –0.3181 | –0.1069 | 0.5444 | O |
| Lębork | 168 | –0.6243 | –0.3976 | –0.2075 | 0.7798 | O |
| Mosty | 169 | 1.6816 | 0.075 | –0.9126 | –0.1121 | I |
| Mosty | 170 | 1.0378 | 0.1961 | –0.9121 | –0.5909 | O |
| Lębork | 171 | 0.3691 | 0.9254 | –0.5455 | 1.2363 | I |
| Mosty | 172 | 0.1579 | 0.4597 | –0.1475 | –0.4735 | O |
| Lębork | 173 | 0.2836 | 0.1019 | 0.0846 | 0.9834 | I |
| Lębork | 174 | 0.2661 | –0.3345 | –0.6214 | 0.7499 | O |
| Lębork | 175 | –0.8851 | –0.6857 | –1.6928 | 1.8953 | O |
| Lębork | 176 | –0.7179 | 0.1588 | 0.9353 | 0.2569 | I |
| Lębork | 177 | 0.475 | 0.8246 | –0.0245 | 0.8354 | I |
| Lębork | 178 | 0.3408 | 0.312 | 0.4159 | –0.7013 | I |
| Lębork | 179 | 1.2852 | 0.7796 | –0.2425 | 0.638 | S |
| Lębork | 180 | 0.3652 | 0.2921 | –1.1209 | 0.9155 | I |
| Lębork | 181 | –0.8537 | –0.0656 | 0.6821 | –0.1914 | I |
| Lębork | 182 | –0.8153 | 0.502 | 0.1554 | 0.3871 | S |
| Lębork | 183 | –0.2925 | –0.4036 | 0.5647 | –0.2452 | I |
| Lębork | 184 | 0.1414 | 0.2856 | –0.0363 | 0.8393 | I |
| Lębork | 185 | –0.2619 | –0.296 | 0.8287 | 0.6657 | O |
| Gdynia | 186 | –0.9547 | 1.3039 | –0.4558 | –0.0691 | O |
| Gdynia | 187 | –0.6052 | –0.0084 | 1.9008 | –0.4819 | O |
| Gdynia | 188 | –0.2408 | 1.5239 | –0.3161 | 1.2505 | O |
| Gdynia | 189 | –0.4891 | 0.2246 | 1.5595 | –0.4882 | O |
| Gdynia | 190 | 0.5728 | 1.1077 | 1.3464 | 0.9802 | O |
| Gdynia | 191 | –0.2228 | 0.5607 | 0.204 | –0.6245 | O |
| Gdynia | 192 | 0.0405 | 1.5215 | 0.0024 | 0.014 | I |
| Gdynia | 193 | –0.8598 | 0.3308 | –0.501 | 0.4399 | I |
| Gdynia | 194 | 1.4894 | 0.9317 | –0.1619 | 0.4016 | O |
| Gdynia | 195 | 0.7138 | 0.7282 | 0.0046 | 0.1931 | S |
| Gdynia | 196 | 0.0638 | –0.5566 | 1.5152 | 0.5608 | O |
| Gdynia | 197 | –0.2737 | –1.3722 | 0.9021 | 0.8602 | O |
| Gdynia | 198 | 1.7947 | 1.236 | 0.5619 | –0.95 | O |
| Gdynia | 199 | –0.0605 | –0.3164 | –0.1556 | –0.3044 | O |
| Gdynia | 200 | 0.7959 | 0.0266 | –0.0089 | –0.3321 | O |
| Gdynia | 201 | –0.587 | 2.1762 | –0.3586 | –0.4423 | I |
| Gdynia | 202 | –0.3847 | 0.0061 | 0.586 | –0.8647 | I |
| Gdynia | 203 | –0.6358 | 0.6829 | –0.2864 | 1.1199 | I |
| Gdynia | 204 | 0.208 | 0.585 | –0.4131 | –0.4951 | I |
| Gdynia | 205 | –0.2117 | 0.7297 | 0.1202 | 0.5502 | S |
| Gdynia | 206 | 0.1783 | 0.6036 | 0.2506 | 0.9739 | I |

Appendix 2. (continued)

| Site name | Site no. | PCA AX 1 | PCA AX 2 | PCA AX 3 | PCA AX 4 | Habitat |
|---|---|---|---|---|---|---|
| Gdynia | 207 | –0.5386 | 0.792 | 0.1634 | 0.4247 | I |
| Gdynia | 208 | –1.1864 | 0.3368 | 0.041 | 0.2609 | S |
| Reda | 209 | 0.783 | –0.3553 | 0.2026 | 0.9462 | I |
| Reda | 210 | –0.6656 | 0.8488 | 0.748 | 0.1938 | I |
| Reda | 211 | 0.4165 | 0.5852 | 0.0202 | –0.3177 | I |
| Reda | 212 | –0.7529 | –0.8496 | –0.4754 | 0.8075 | S |
| Połchowo | 213 | –0.1926 | 0.1499 | 1.4789 | –0.1925 | O |
| Mrzezino | 214 | 1.142 | 0.3348 | 0.3839 | 2.5287 | I |
| Mrzezino | 215 | 2.0565 | –1.8487 | 0.2408 | 2.3515 | I |
| Smolno | 216 | –0.3315 | –1.2622 | 1.0874 | 0.6301 | I |
| Smolno | 217 | –1.2503 | –1.9725 | 0.6074 | –0.2462 | I |
| Żelistrzewo | 218 | –0.3412 | –1.1712 | 1.1254 | 0.5873 | O |
| Puck | 219 | 0.6105 | –0.3961 | 0.1753 | –0.6568 | I |
| Puck | 220 | 2.1293 | –2.3021 | –1.0565 | –1.7214 | O |
| Puck | 221 | 1.8647 | –1.3836 | –1.3563 | –1.4509 | S |
| Puck | 222 | –0.1686 | 0.3199 | 0.749 | –0.2709 | S |
| Puck | 223 | 1.7713 | 0.1124 | 0.0558 | –0.355 | O |
| Puck | 224 | 1.7965 | –0.7136 | –1.0286 | –1.222 | O |
| Puck | 225 | –0.2585 | –1.1088 | 0.3764 | –0.3742 | O |
| Wieżyca | 226 | –1.5713 | –0.1513 | –0.584 | –0.3276 | O |
| Gołobie | 227 | –0.3389 | –0.2326 | 0.6024 | –0.3808 | O |
| Żukowo | 228 | –0.0371 | –0.0558 | 0.4695 | –0.035 | I |
| Kościerzyna | 229 | –0.1492 | 0.7388 | –0.1331 | –0.2923 | I |
| Kościerzyna | 230 | 0.5057 | 1.2328 | –0.4066 | 1.9137 | O |
| Kościerzyna | 231 | 0.0239 | 2.0161 | –0.9084 | 1.1901 | I |
| Kościerska Huta | 232 | –0.2447 | 0.6361 | –0.8419 | 0.0488 | O |
| Gdynia | 233 | –0.0895 | –0.3802 | –2.2502 | 0.9956 | S |
| Gdynia | 234 | –0.5073 | 0.2685 | 0.449 | 0.3759 | S |
| Gdynia | 235 | –0.1466 | 0.9955 | 0.5065 | 0.6606 | I |
| Gdynia | 236 | –0.785 | 0.8649 | 0.3775 | –0.1993 | I |
| Elbląg | 237 | –0.9467 | 0.5233 | –0.6812 | –1.5362 | O |
| Elbląg | 238 | –0.304 | 0.1934 | –1.2753 | –0.9682 | O |
| Elbląg | 239 | –0.6715 | –0.3136 | –0.9666 | –0.6511 | O |
| Elbląg | 240 | 0.5129 | –0.7812 | –0.9177 | –2.2688 | I |
| Elbląg | 241 | 0.2325 | 0.0729 | –0.7181 | –1.134 | I |
| Elbląg | 242 | 0.6103 | –0.8205 | –0.9033 | –1.9165 | I |
| Elbląg | 243 | 1.3067 | 1.8547 | 0.2549 | –2.9631 | S |
| Elbląg | 244 | 0.6624 | 0.2466 | –0.271 | –3.5231 | S |
| Elbląg | 245 | 0.7132 | –0.3341 | –0.3671 | –2.7124 | S |
| Białogóra | 246 | 0.5707 | 0.7638 | 0.4325 | 1.5311 | O |
| Kopalino | 247 | –0.1281 | 0.2306 | 1.1036 | 0.044 | O |
| Kopalino | 248 | –0.1106 | 1.4874 | 1.272 | 0.8383 | I |
| Kopalino | 249 | 0.0248 | 1.4415 | 0.9533 | –0.1728 | S |
| Lubiatowo | 250 | –0.309 | 1.9874 | 2.5601 | –0.587 | I |
| Ciekocino | 251 | 0.4321 | –0.0614 | 0.4109 | 0.0666 | I |
| Sasino | 252 | 0.2214 | 1.5618 | 0.7528 | 0.2527 | I |
| Ulinia | 253 | –2.2018 | –0.907 | –1.472 | 0.1939 | O |
| Sarbsk | 254 | –0.5681 | 1.2917 | 0.2599 | –0.3937 | S |
| Szczenurze | 255 | –1.5604 | 1.244 | –0.3957 | –0.2958 | I |
| Nowęcin | 256 | –0.8043 | 0.2507 | –1.2565 | 0.0078 | I |
| Nowęcin | 257 | –0.4618 | 0.512 | –1.2277 | –0.0185 | O |
| Łeba | 258 | 0.4699 | 2.0033 | –0.7405 | 0.1584 | I |
| Łeba | 259 | 0.3294 | 1.2536 | –0.6418 | 0.7384 | O |
| Łeba | 260 | – 0.7384 | 1.5036 | –0.6962 | 0.4303 | I |

Explanations: Habitat: O – open; I – intermediate; S – shaded.