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The red alga *Hildenbrandia rivularis* is a weak indicator of the good ecological status of riverine habitats

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ABSTRACT

Our knowledge about the size of benthic red alga populations inhabiting European freshwater ecosystems is still insufficient. For many years, in Europe, *Hildenbrandia rivularis* (Rhodophyta, Hildenbrandiaceae) was believed to be a very rare species of crustaceous red algae, valuable for oligotrophic system biomonitoring. In this paper, we challenge this assumption and show the phenomenon of *H. rivularis* expansion (i.e., from mountains and highlands to lowlands) in Europe based on detailed data from Poland. We collected over 311 records of *H. rivularis* occurring in rivers, streams and lakes (not typical habitats for this alga) across the country, including historical data. Here, we show the detailed distribution of this endangered species in Poland, one of the largest European countries. To examine the mechanism of *H. rivularis* population expansion, physicochemical data from 122 aquatic ecosystems were investigated. A comparison between three subperiods (1860–1944, 1945–1999, and 2000–2019) revealed an increase in the average abundance of the *H. rivularis* population in the lowlands area. However, the studied species seems to be disappearing in mountain and upland ecosystems. We found altitude and water flow and quality (i.e., alkalinity, oxygenation and biogens) to be the main determinants of *H. rivularis* occurrence within the study area. The results indicate that this red alga can be described as an expansive species, and its occurrence does not always indicate good water quality and fast water flow. Surprisingly, in contrast to observations from the last century, the population of *H. rivularis* in Poland currently occurs mainly in habitats with eu- and hypertrophic waters. We point out here that in the zone with temperate climate influence, *H. rivularis* is no longer an obvious indicator for oligotrophic ecosystems. We suggest that climate warming and eutrophication–reoligotrophication may have contributed to the increased spread of *H. rivularis* in Europe over recent decades. In addition, we see no reason to classify *H. rivularis* as an endangered species in Poland. This species most often inhabits anthropogenic water systems and occurs at high abundance in waters with high concentrations of biogens. For these reasons, *H. rivularis* is more ubiquitous than a cosmopolitan species (i.e., with a wide range of occurrence but associated with only a specific type of habitat and specific environmental parameters). Thus, the value of *H. rivularis* as a bioindicator for oligotrophic water ecosystems is very low.

1. Introduction

Research on the biology of rare and endangered macroalgal species is key to their protection. Traditionally, studies of the distribution and changes in the extent of occurrence of macroscopic algae in freshwater ecosystems have focused on heavily transformed or estuary habitats

Abbreviations: Asl, above sea level; ATPOL, Atlas of Poland; CGIAR-CSI, Consultative Group on International Agricultural Research – Consortium for Spatial Information; DCA, detrended correspondence analysis; EC, European Commission; ESMI, Ecological State Macrophyte Index; GAM, generalized additive models; GPS, Global Positioning System; HR, *Hildenbrandia rivularis*; IUCN, The International Union for Conservation of Nature; MIR, Macrophyte Index for Rivers; WFD, Water Framework Directive; V-plan., velocity of water between plant associations; V-surf., surface velocity of the water.

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where human activities such as transportation or fish farming are prevalent (Cantonati and Lowe, 2014; Diop et al., 2016; Nelson et al., 2015; Preisler et al., 2009; Råberg and Kautsky, 2007). Lotic ecosystems (such as rivers and streams) are usually characterized by lower plant species diversity than lakes and sustain stable populations of rare species while facilitating natural expansion to new areas along with water flow (Van Donk et al., 2008; Wasson et al., 2005). On the other hand, the reoligotrophication (the process of reverting to the original state of riverine ecosystems, i.e., before anthropogenic pressure, by nutrient reduction) and thermal pollution of water systems are the leading causes of the range of species spread (Gunkel et al., 2013; Makri et al., 2018; Shatwell et al., 2019; Van Donk et al., 2008). However, the mechanisms and factors that induce changes in population sizes and expansion of most macroscopic algae in freshwater remain unknown.

Hildenbrandia rivularis (HR) is one of the most threatened red algal species in Europe (Didukh, 2010; Jakubas et al., 2014; Marhold and Hindák, 1998; Rassi et al., 2010; Temniskova et al., 2008). This red alga is included on the Red List of threatened algae in Slovakia (Marhold and Hindák, 1998) and has been recognized as an endangered plant in Finland and a nearly threatened plant in Bulgaria (Cantonati et al., 2016; Rassi et al., 2010). On the other hand, according to the German Red List of red and brown algae, HR is an unthreatened species (Rudolph et al., 2017). In Poland, HR has been protected by law since 2004 and is categorized as a "vulnerable" species according to the IUCN (The International Union for Conservation of Nature) criteria (Siemińska et al., 2006). Various authors have attempted to summarize the species' distribution, especially in Nordic countries (Eloranta et al., 2016; Eloranta and Kwandrans, 2007; Israelson, 1942; Kann, 1978; Lindstrøm and Rueness, 2009; Rinne and Kostamo, 2022), but data from Central Europe are scarce or absent. In recent decades, interesting data have emerged regarding the occurrence of HR in southeastern Europe, a region where this species has not been previously observed (Barinova et al., 2011; Blagojević et al., 2017; Koletić et al., 2020; Krasznai et al., 2006).

Over the past few decades, HR was believed to be a very rare species of Rhodophyta that occurred chiefly in two unconnected, partially closed areas of Poland: (1) the southern, mountainous area and (2) the northern area of the Baltic Sea environs (Jakubas et al., 2014; Krawiec, 1935; Starmach, 1969a, 1969b; Żelazna-Wieczorek and Ziułkiewicz, 2008). However, new stands of this red alga have recently been recorded in diverse habitats across Poland (especially in lowland areas). Several reports from phycologists have indicated a similar situation in other European countries (Kwandrans and Eloranta, 2010). The latter may be attributed to the more abundant and frequent European hydrobiological research, especially after 2000, when Water Framework Directive (WFD) 2000/60/EC was implemented for environmental monitoring in Europe.

With respect to ecological characteristics, this freshwater red alga prefers streams and rivers with a hard bottom substrate, alkaline pH, and clean hard water (Caisová, 2006; Eloranta and Kwandrans, 2007, 2004; Kitayama, 2014; Simić, 2008; Simić et al., 2010; Żelazna-Wieczorek and Ziułkiewicz, 2008). This red alga is usually reported in shaded and fast-flowing streams. Some data indicate the possible occurrence of HR in the littoral zones of lakes and flow-through lakes (Jakubas et al., 2014). In the case of standing waters, HR occupies particularly shady lakes or ponds (Eloranta, 2019; Eloranta and Kwandrans, 2004).

H. rivularis is a useful indicator of the saprobity of riverine ecosystems. According to the saprobity zone framework, Fjerdingstad (1965, 1964) classified this species as oligosaprobic or katharobic. Ecological classifications of freshwater red algae concerning the trophic state and pH level indicate that HR occurs under eutrophic and alkaline conditions (Rott et al., 1999). In northern Europe, this species is considered an important indicator of hard waters (Eloranta and Kwandrans, 2007, 2004). In Poland and other European countries, the presence of HR, together with other species of algae, liverworts, mosses, pteridophytes and vascular plants, is an element of the biological methods used to assess water quality and the ecological status of flowing waters (according to the Water Framework Directive guidelines); in this respect, HR is considered an indicator of good ecological status (Jakubas et al., 2014; Szoszkiewicz et al., 2010; Żelazna-Wieczorek and Ziułkiewicz, 2008). Furthermore, HR, for example, has been employed by some researchers to classify streams of Austria, and in these cases, this red alga is associated with lowland rivers characterized by relatively high levels of nutrients (Pipp and Rott, 1994).

The primary goal of our study was to explore the factors that potentially influence the distribution and abundance of *H. rivularis* in Poland. We aimed to (1) define the range of expansion of HR in Polish rivers, streams, and lakes and its geographical spread and abundance; (2) determine the habitat requirements of HR; (3) identify the environments for which the species displays the greatest preference; and (4) challenge the belief in the literature about the value of *H. rivularis* as a good bioindicator for oligotrophic, fast-flowing water ecosystems.

2. Material and methods

2.1. Study species

Hildenbrandia rivularis (Liebmann) J. Agardh is a freshwater red alga growing on hard natural and artificial substrates, e.g., stones or concrete and steel structures. The thalli are crustose, bright red, and strongly attached to the substrate. Sometimes, wart-like protuberances are visible on the surface of the thalli, but most often, the thallus is smooth to the touch. The thallus consists of two layers of cells: (i) a basal layer firmly adhering to the substrate and (ii) a pseudoparenchymatic layer built from erect filaments. The basal layer is thin and formed by branched filaments densely aggregated laterally. In contrast, erect filaments are formed by cubic or short-cylindrical cells (Fig. 1). In freshwater ecosystems, sexual reproduction and the presence of tetrasporangia have not been confirmed. Asexual reproduction proceeds by gemmae, consisting of small and dense packets of filaments that release and germinate into new crusts. Vegetative reproduction by fragments of older thalli is predominant (Eloranta, 2019; Kamiya and West, 2008; Necchi, 2016; Starmach, 1977, 1969b, 1969a). This red alga forms a colony, e.g., on stones and rocks that are easy to see, even in very fast-flowing rivers and streams (Fig. 1**B**). Due to the ease of identifying a red crust of this species in the field by the naked eye, even by nonspecialists (there is no need to collect thallus samples and analyze them in the laboratory), *H. rivularis* has been adopted in water monitoring methodologies (Gebler et al., 2017; Kelly et al., 2015; Muratov et al., 2015; Szoszkiewicz et al., 2020).

2.2. Data collection

Data concerning this threatened red alga species were collected from sites across the entire territory of Poland. The available herbarium collections and literature relating to the occurrence of HR in Poland were collected from a range of bibliographic databases and archival materials and subsequently critically reviewed. The database has been supplemented by records from the national monitoring programs under WFD 2000/60/EC (surveys conducted in 2007–2019, encompassing 513 lakes and 1.038 rivers), as well as by the authors' collections and other national research projects (12 lakes surveyed in 2005–2006) (Table A.1 **and Appendix A.2**). In total, the analysis spanned 157 years. Detailed GPS (Global Positioning System) coordinates were recorded for the contemporary stand; in the case of historical stands, the locations were estimated based on herbarium labels, field notes, or descriptions from publications (Table A.1).

A review of all known records of HR in freshwater ecosystems (with running and standing waters) helps to establish the number of stands of this red alga in all 16 administrative regions of Poland (Poland is divided into 16 units) (Fig. 2). The description of the HR distribution in Poland relied on a grid with 10 km × 10 km squares. Each record was assigned to one of the grid squares plotted for the territory of Poland according to

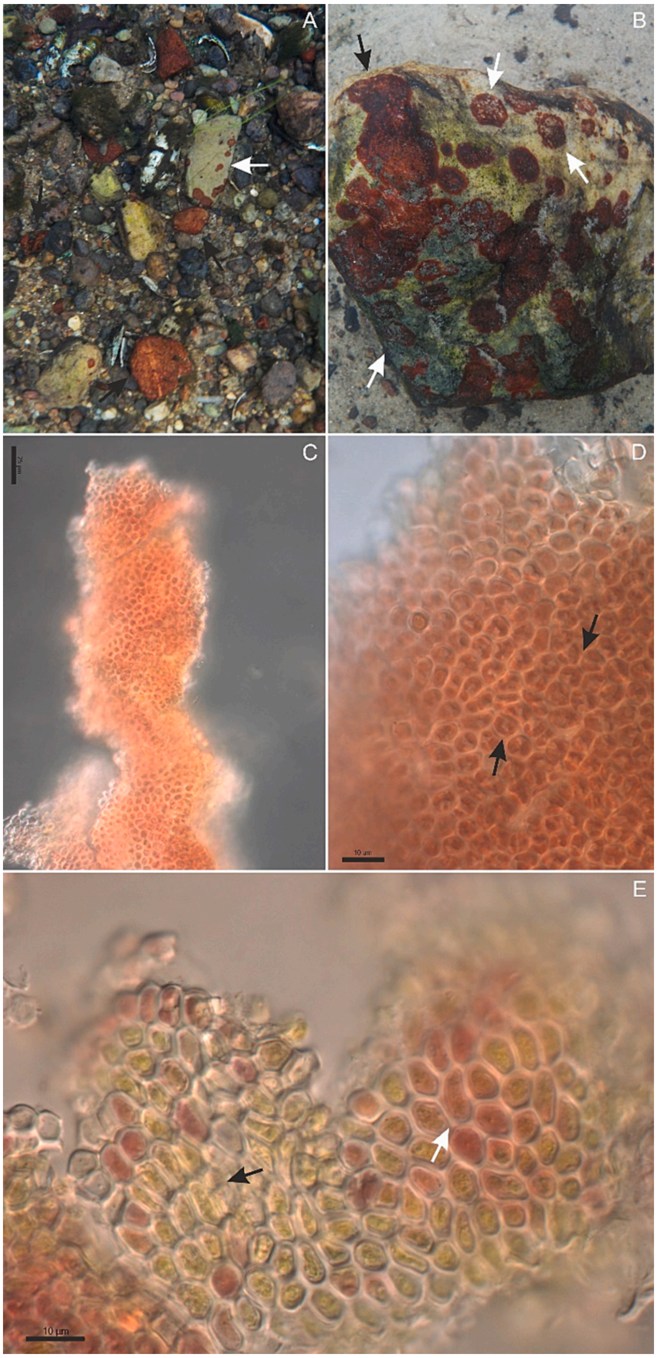

Fig. 1. Habitat and thalli of *Hildenbrandia rivularis*. A – macroscopic view of an HR colony in a natural habitat (white arrow indicates the colony), B – HR colonizes submerged stones (black arrow: overlapping colonies, white arrows: single central colonies), C – microscopic view of the colony crust, D – details of cell morphology (arrow: irregular shape of cells), E – magnification of the marginal part of the crust with a bottom layer of cells (black arrow: elongated cells, white arrows: thick cell walls). Scale bars represent: C – 25 µm; D and E – 10 µm. Photo credits: A and B, M. Gąbka; C-E, A.S. Rybak.

the Atlas of Poland (ATPOL) system (Komsta, 2016).

2.3. Altitudinal distribution

To define HR altitudinal profiles, the range of altitudes for 311 records was divided into five classes while considering altitude data for every record. Class brackets were delimited in such a way that each class would comprise at least 5 % of the records. The subsequent analyses were performed using five resulting classes: (1) ≤ 200 m, (2) 201–300 m, (3) 301–400 m, (4) 401–500 m, and (5) 501–1.000 m. The following altitude classification was adopted for given terrain forms: lowland areas (from 0 to 300 m above sea level [m asl]), uplands (300–500 m asl) and mountains (more than 500 m asl). The HR profile was expressed as the difference between the species frequency within an altitudinal class and its frequency in the entire set of data (total frequency).

2.4. Temporal changes altering temporal distributions

In light of the collected data, the changing temporal distributions of HR stands clearly indicate three periods in which the red alga species were investigated: (1) 1860–1944, (2) 1945–1999 and (3) 2000–2019. To examine changes between two periods, HR frequency was calculated as the number of sites in a grid square relative to the total number of samples collected in each period. Frequency variations between two periods were then computed for each grid square.

2.5. Environmental data

Data related to water quality in 6 lakes and 12 rivers were analyzed. Environmental data from the national lakes and rivers monitoring program (the data in question are made available by the Chief Inspectorate of Environmental Protection in Poland) have also been included. Water samples from lakes and rivers intended as material for physical and chemical assessments were obtained in the same year when studies of aquatic plants were conducted. Sampling occurred four times over the vegetative season, i.e., from March to October. Habitat parameters and species composition were verified for a total of 122 sites where HR occurred.

Water temperature, pH, electrical conductivity, and oxygenation were measured in the field using the Professional Plus multiparameter instrument (YSI, Yellow Springs, OH, USA). The chemical analyses of other parameters of water (i.e., total phosphorus, total nitrogen, total hardness, sulfate, chloride, calcium and magnesium) were performed in the laboratory using a HACH DR 2800 spectrophotometer (Fairborn, OH, USA) according to standard hydrochemical methods (Baird et al., 2017) and specific standards (ISO 9297:1989, ISO 9280:2002, ISO 6878:2006, PN-82/C-04576/08 and PN-76/C-04576/01). The Quality Assurance and Quality Control (QAQC) rules were followed for all sampling steps, including the physicochemical analysis of water and collection of data. Furthermore, the abiotic type of rivers and lakes and their ecological status were assessed according to Annex II of the WFD 2000/60/EC (Lyche Solheim et al., 2019; Spänhoff et al., 2012). This means that the typology of rivers was defined by (i) ecoregion, i.e., lowland or upland, (ii) river landscape types, depending on geological and chemical characteristics (e.g., carbonate or siliceous), (iii) catchment size (large, medium-sized and small rivers), and (iv) type of substrate on the bottom (e.g., organic, sand, or gravel).

2.6. Phytobenthos and vegetation analysis

Field studies on HR ecological requirements and autecology were performed in 2013–2019 on five flowing water ecosystems (i.e., Pilica River with a length of 319 km, Łeba River – 117 km, Wełna River 118 km, Płytnica River – 59 km, and Flinta River – 27 km) during the maximum vegetative period, which in this part of Europe falls in March-October. In these rivers, a numerically stable population of HR has occurred yearly since the late 1990 s. Thalli of this red alga grow on natural/hard substrates, such as river stones/pebbles and artificial materials (e.g., bricks and concrete). In each river, the structure of aquatic plant communities was analyzed. For this purpose, 58 vegetation plots of 16 m^2 (i.e., 4 m × 4 m) were analyzed in the HR microhabitat. The field research relied on the identification of plant species (including

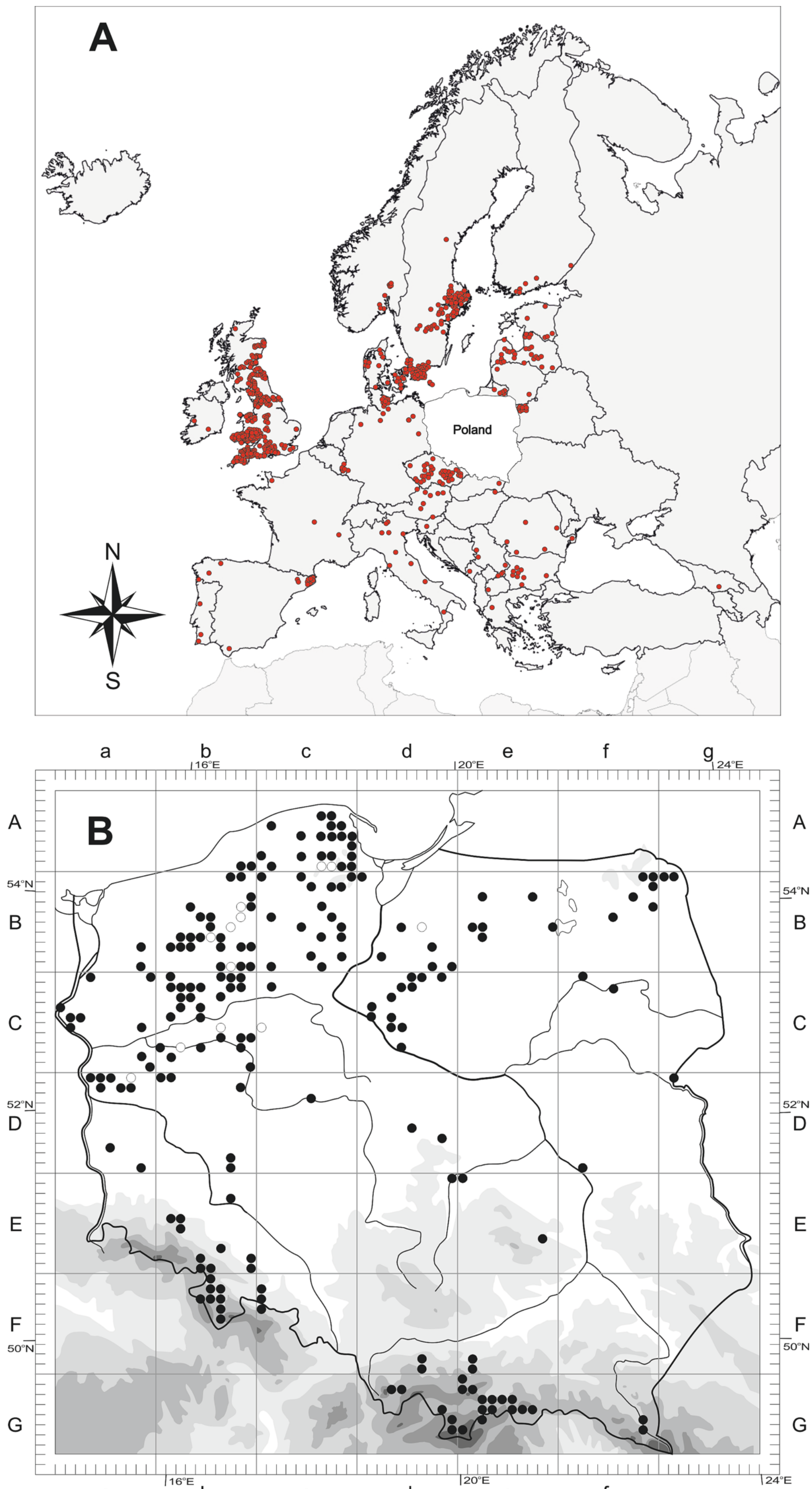

Fig. 2. A. Distribution of *Hildenbrandia rivularis* in Europe. B. The map of Poland shows the main locations of *H. rivularis* presented in the ATPOL system. Black circle – running waters, empty circle – standing waters. ATPOL (Atlas of Poland): grid square system for plant cartography.

mosses, pteridophytes, and macroalgae), assessment of plant percent cover on van der Maarel's 9-degree scale (where 1 = 0.5 %, 2 = 0.5–1.5 %, 3 = 1.5–3 %, 4 = 3–5 %, 5 = 5–12.5 %, 6 = 12.5–25 %, 7 = 25–50 %, 8 = 50–75 % and 9 = 75–100 %), and the determination of species composition (van der Maarel, 1979).

The following parameters were measured in each vegetation plot: depth and temperature of the water, surface velocity of the water (V-surf.), and water velocity between plants (V-plan.), i.e., in the central part of the association. The water velocity was measured at the surface layer (approx. 0.1 m) and in the plant associations using a hydrometric universal current meter (CM-32, Akim Hydrometyry, Seyhan – Adana, Türkiye).

The identification of macroalgae, mosses, and vascular plants relied on examining the morphological features according to taxonomic keys (Jusik, 2012; Müller et al., 2021; Sheath and Vis, 2015). The nomenclature of the plants presented here has been verified to comply with AlgaeBase, IPNI, and WFO Plant List (Guiry and Guiry, 2023; International Plant Names Index, 2023; World Flora Online, 2023).

2.7. Numerical analyses

The pattern of species dominance in all vegetation plots was determined based on the summary status of the plots and the species composition, illustrated by a species dominance curve (McCune and Mefford, 1999). We applied detrended correspondence analysis, DCA (ter Braak and Šmilauer 1998), to explore the main gradients governing the plant species distribution. To determine the most critical variables, automatic forward selection of environmental parameters was used with the Monte Carlo permutation test (with 999 permutations) (Lepš and Šmilauer, 2003). Response curves of HR and cooccurring species to water velocity were modeled by generalized additive models (GAMs) (Hastie and Tibshirani, 1990). The Poisson distribution and smooth term complexity were selected using the Akaike information criterion (Lepš and Šmilauer, 2003). Statistical analyses were performed using CANOCO software, except for species dominance curves, for which the PC-ORD package was used (McCune and Mefford, 1999; ter Braak and Smilauer, 2002).

3. Results and discussion

3.1. Temporal and spatial distributions of H. Rivularis in Poland

Freshwater populations of HR are widely distributed in European stream and lake ecosystems and have been reported in several countries. Specifically, this red alga has been registered in more than 20 countries in diverse locations, including Austria, Belgium, Bulgaria, the Czech Republic, Denmark, Germany, Finland, France, Georgia, Great Britain, Italy, Latvia, Luxembourg, Norway, Poland, Romania, Serbia, Slovenia, Spain, and Sweden (Sherwood et al., 2002). The first-ever graphic summary of the HR distribution in Europe is shown in Fig. 2**A**. The distribution map was created based on published data (Baláži and Hrivnák, 2015; Barinova et al., 2011; Baxová, 2016; Blagojević et al., 2017; Bolpagni et al., 2016; Caisová and Kopecký, 2008; Cantonati et al., 2016; Caraus, 2017, 2012; Ceschin et al., 2013; Chapuis et al., 2014; Eloranta et al., 2016, 2011; Eloranta and Kwandrans, 2007, 2004; Fritsch, 1929; Kohler et al., 2000; Koletić et al., 2020; Kostkevičienė and Laučiūtė, 2009; Kostkevičienė and Sinkevičienė, 2008; Krasznai et al., 2006; Kwandrans and Eloranta, 2010; Lindstrøm and Rueness, 2009; Luther, 1954; Nienhuis, 2003; Pakulnicka and Nowakowski, 2012; Sabater et al., 1989; Serbănescu, 1962; Sherwood et al., 2002; Simić, 2008; Simić et al., 2010; Stoyneva et al., 2003; Tarnavschi, 1941; Temniskova et al., 2008; Vitonyte and Kostkeviciene, 2009; Zidarova et al., 2011).

A review of all published reports shows that the center of occurrence of this alga is located in the Baltic region and Great Britain. Altogether, 311 records with HR stands in Poland, both in rivers and lakes, were obtained (Fig. 2**B**).

The temporal distribution of HR in Poland was mapped based on historical sources, our own research and monitoring data, using data spanning 157 years, as the earliest known mention of HR in Poland dates to 1860 (Hilse, 1862; Kirchner, 1878). The temporal variation in the abundance of the species is shown in Fig. 3. The graph demonstrates that the quantity of HR in Polish running and standing waters has significantly increased over time. Regarding the first investigated period, i.e., 1860–1944, there are 31 records indicating the presence of HR in the country. This small number of reported stands at this time may be attributable not only to the limited algological field work but also to the rarity of this species in the country. Then, considering the small number of these red alga stands in the country, the first proposals to include *H. rivularis* under species protection appeared (Starmach, 1969b, 1969a). In the subsequent period, i.e., 1945–1999, the number of *H. rivularis* stands increased twofold to 78 stands. This is most likely due to the increasing awareness of the algal flora and improved scientific investigations after World War Two, resulting in seminal studies published from 1945 to 1979 (Chudyba, 1970; Kępczyński, 1972, 1963; Lisowski et al., 1971; Siemińska, 1962; Żukowski, 1963). Finally, the number has increased fourfold since 1999 to 311 stands. The records of the species appeared to soar due to the introduction of the WFD in 2000 and more intense biomonitoring-oriented research. On the other hand, extensive searches for *H. rivularis* (by scientists and employees of environmental monitoring units) in the indicated above period (in the upland and mountain areas of Poland) failed. *H. rivularis* has not been observed even in southern Poland's historic sites since the 1960 s (Starmach, 1969b, 1969a).

The greatest abundance of HR is found in the northwest part of Poland, especially in the seaside regions close to the Baltic Sea. The fact that the species is concentrated in areas that are heavily influenced by coastal waters confirms that HR belongs to the group of alkaliphilic species (with preferred pH values ranging from 7.24 to 8.03) (Grant et al., 1990). Similar observations regarding the correlation between HR and pH have been made in other studies (Chudyba, 1970; Jakubas et al., 2014; Necchi and Zucchi, 2001; Żelazna-Wieczorek and Ziułkiewicz, 2008). Furthermore, the occurrence of HR in the mountainous areas in the south, where it is found in streams of cold, alkalescent water, also confirms a positive relationship between the occurrence of this species and high pH levels (Eloranta and Kwandrans, 2007; Jakubas et al., 2014; Kwandrans and Eloranta, 2010). It may be noted that certain genera of freshwater red algal species, e.g., *Bangia* spp., occur only in highly conductive brackish ecosystems (Kwandrans and Eloranta, 2010). The authors of the latter study subscribe to the earlier algological theory (Sheath, 1984; Skuja, 1938), which presumes that species that migrated

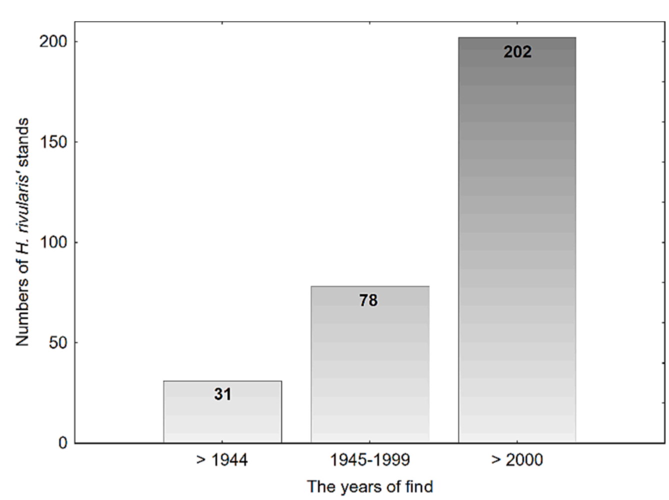

Fig. 3. Temporal abundance fluctuations of *Hildenbrandia rivularis*.

originally from marine habitats are distinguished by the red pigment phycoerythrin (Kwandrans and Eloranta, 2010).

The most significant number of stands with HR was noted in 3 regions: the Zachodniopomorskie, the Pomorskie and the Wielkopolskie voivodships (the highest level of administrative division of Poland, corresponding to a province in other European countries), all of which are located in northwestern Poland (Table 1, Fig. 4). HR appears to be absent only in 1 region, the Lubelskie voivodship. Single stands were found in 2 regions: the Mazowieckie and Świętkorzyskie voivodships (Fig. 4).

Our analyses indicate a decrease in the number of HR stands in the mountain and upland areas or even the total disappearance of this red alga population in historical sites. (Starmach, 1969b, 1969a). Nonetheless, the numerous records showing that this species can be found across the entire country led us to conclude that HR should not be treated as a sporadically occurring species of red alga that prefers only a few particular habitats, e.g., slow-flowing carbonate waters (Barinova, 2013), mountain streams and rivers (Caisová, 2006; Eloranta and Kwandrans, 2007, 2004; Simić, 2008; Simić et al., 2010; Żelazna-Wieczorek and Ziułkiewicz, 2008), as previous studies suggested.

Furthermore, the abundance of this species in the north, where coastal waters strongly influence its habitat, confirms that freshwater HR occurs in stands characterized by high salinity and conductivity (Sherwood and Sheath, 1999; Sherwood et al., 2002). Similar patterns were observed in North America and Europe, where the occurrence of marine species of *Hildenbrandia*, such as *H. rubra*, was strictly connected with ocean basins, and marine niches appeared to be the origin of expansion into freshwater ecosystems (Sherwood et al., 2002; Sherwood and Sheath, 2003). The next step for clarifying the relationship between marine and freshwater specimens and examining their biogeographic patterns is detailed gene sequence analyses.

3.2. Altitudinal distribution

In addition to the precise determination of GPS coordinates, the altitudinal position was obtained for each record. In the entire set of stands, the greatest occurrence was observed in the lowland areas, with 142 stands below 100 m. Upland and mountainous areas showed the lowest frequencies, with only 11 records for 401–500 m and 20 for the 501–1.000 m range (Fig. 4). Detailed information is presented in Table 2 and Fig. 5**A, B**. The obtained outcomes differ from previous findings from, e.g., Nordic countries, where HR occurs mainly in unpolluted mountain areas (Kwandrans and Eloranta, 2010). Similar studies of the distribution patterns and ecology of other species of freshwater red algae in Europe, such as *Paralemanea* spp., also indicate that this genus prefers high-lying mountain rivers at, e.g., 1.400 m in Italy and 700 m in Spain (Simić and Dordević, 2017). Authors have reported that in Central Europe, optimum environmental conditions for HR population development exist in mountain areas, especially during summertime (Eloranta et al., 2016; Starmach, 1982). The majority of Polish studies on this algal species show that HR displays the greatest preference for two thoroughly distinct landscapes in Poland: (i) mountainous and upland areas (Krawiec, 1935; Starmach, 1982, 1969a) and (ii) the western Pomerania region (Kukwa, 2005; Starmach, 1969b; Żukowski, 1963). However, most recent data indicate the possibility of a strongly increased occurrence of this red alga in the central part of Poland (Dąmbska, 1961; Gołdyn, 1965; Jakubas et al., 2014; Kępczyński and Peplińska, 1995; Krawiec, 1935; Żelazna-Wieczorek and Ziułkiewicz, 2008). HR appears to be retreating (i.e., the number of stands or population size is declining) from the mountain to lowland areas, according to the numerous records below 100 m asl. This phenomenon may be connected with the changes following global warming and the increase in water temperature (Arai, 2009; Dąbrowski et al., 2004; Thompson et al., 2005) and implies the high adaptability of some ecotypes of HR to changing habitat conditions (Sherwood et al., 2002) or the existence of still unknown factories responsible for expanding this species to the lowlands. Solving these issues will undoubtedly require extensive ecological research, including molecular techniques and physiological measurements (e.g., photosynthesis rate or protein activity under a given stress condition).

3.3. Habitat conditions

The aim of this study was to examine and elucidate the relationships between the occurrence of *H. rivularis* and the abiotic profiles of rivers, lakes and environmental parameters. The types of rivers and lakes were identified based on a combination of abiotic characteristics specified in WFD 2000/60/EC. Stream and river typology relies on altitude, catchment size and dominant geology (Sandin and Verdonschot, 2006; Verdonschot and Nijboer, 2004), while the division of lakes is informed by morphometric, hydrographic and physicochemical data (Kolada et al., 2005); in our study, the latter was derived from the Polish national monitoring dataset. The examined freshwater red alga populations from Poland were more frequently noted in flowing waters, having been identified in 17 types of rivers or streams and in standing waters in 3 types of lakes. *H. rivularis* occurred 39 times in mid-sized gravel-bottom streams (type 18) and 38 times in sand-bottom rivers (type 19). HR occurred at high abundance in 10 lacustrine lakes classified as type 3a (lowland, high calcium content, high Schindler's ratio, stratified). Types 3a, 3b (high calcium content, high Schindler's ratio, unstratified) and 2b (high calcium content, low Schindler's ratio, unstratified) are the most widespread types in the western part of Poland

Table 1
Numbers (N) and percentages of *H. rivularis* records per administrative unit (voivodship) in two periods of collection (before 2000 and after 2000).

Region/voivodeship	Number of records before 2000	Frequency (%)	Number of records after 2000	Frequency (%)	Total number of records	Frequency (%)	Number of grid squares	Frequency (%)
pomorskie	**43**	39.4	**23**	11.5	**66**	21.2	**36**	17.1
zachodniopomorskie	**10**	9.1	**45**	22.0	**55**	17.7	**34**	16.2
wielkopolskie	**11**	10.1	**31**	15.5	**42**	13.5	**30**	14.4
małopolskie	**15**	13.8	**13**	6.5	**28**	9.0	**20**	9.5
dolnośląskie	**4**	3.7	**22**	11.0	**26**	8.4	**15**	7.1
kujawsko-pomorskie	**17**	15.6	**8**	4.0	**25**	8.0	**19**	9.0
lubuskie	**5**	4.6	**17**	8.0	**22**	7.1	**17**	8.2
warmińsko-mazurskie	**3**	2.7	**18**	9.0	**21**	6.7	**16**	7.6
podlaskie	**1**	0.9	**9**	4.5	**10**	3.2	**9**	4.3
łódzkie	**0**	0	**5**	2.5	**5**	1.6	**4**	1.9
podkarpackie	**0**	0	**3**	1.5	**3**	1.0	**2**	0.9
opolskie	**0**	0	**3**	1.5	**3**	1.0	**3**	1.4
śląskie	**0**	0	**3**	1.5	**3**	1.0	**3**	1.4
mazowieckie	**0**	0	**1**	0.5	**1**	0.3	**1**	0.5
świętokrzyskie	**0**	0	**1**	0.5	**1**	0.3	**1**	0.5
Total	**109**	100	**202**	100	**311**	100	**210**	100

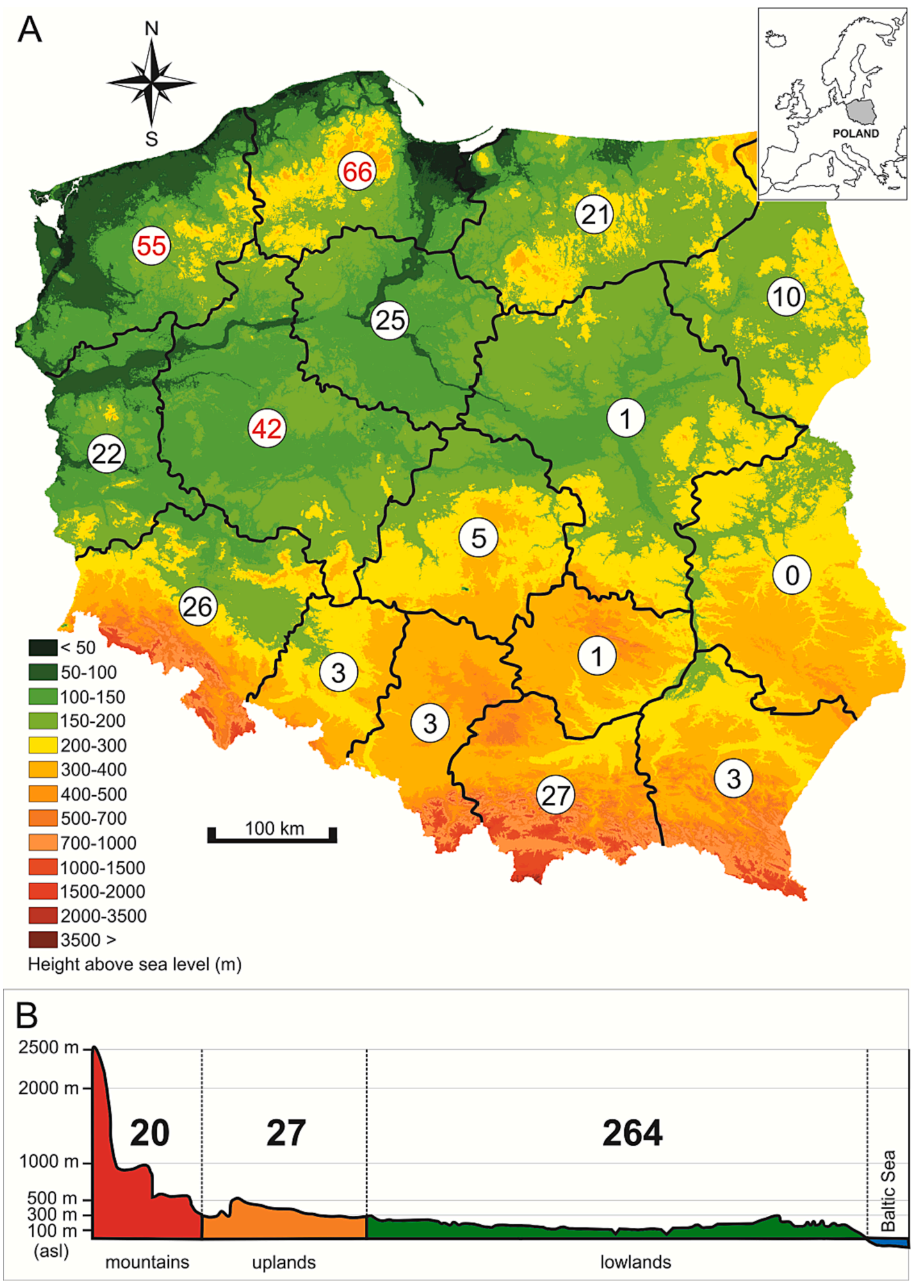

Fig. 4. A. Hypsometric and administrative map of Poland showing the total number of stands with *Hildenbrandia rivularis* (numbers in circles) within the boundaries of the 16 Polish voivodships. Numbers in red: the most abundant stands with *H. rivularis*. Hypsometric map downloaded from the CGIAR-CSI (Consultative Group on International Agricultural Research – Consortium for Spatial Information). B. Number of *H. rivularis* stands in particular landforms. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Altitudinal distribution of *H. rivularis* in Poland.

Altitude class (m)	N	%
A (≤ 100)	**142**	**45.6**
B (101 – 200)	**110**	**35.3**
C (201 – 300)	12	3.8
D (301 – 400)	16	5.1
E (401 – 500)	11	3.5
F (501 – 1000)	20	6.4
Total	311	100.0

N – number of *Hildenbrandia rivularis* records within six altitudinal classes.

(Kolada et al., 2005). In the territory of Poland, HR prefers alkaline, hard, Ca^{2+}- and Mg^{2+}-rich, highly oxygenated waters. The water in these habitats was rich in nutrients, specifically TN and TP, and showed medium conductivity values (Table 3).

The characteristics of the habitat niches of *H. rivularis*, inhabited by cooccurring plant species, are also worthy of interest, which requires detailed autecological studies. In addition, it is worth noting that when this red alga dominates in a given ecosystem, it creates its own association - *Hildenbrandietum rivularis* Luther 1954 (Täuscher, 2013; Täuscher and Krumbiegel, 2020). Most often, however, HR creates communities of several species together with other species of macroalgae (e.g., *Heribaudiella fluviatilis,* which belongs to Ochrophyta, Phaeophyceae) and aquatic lichens, such as members of the *Verrucaria* genus. The analysis of vegetation accompanying *H. rivularis* populations presented here was performed in the microhabitats of five Polish rivers with a total length of 640 km. The analysis of 58 vegetation plots with HR indicates a species-rich composition. The total number of all recorded taxa was 63 species, which indicates a high species richness. The dominance curve of plants shows that mosses, such as *Leptodictyum riparium* and *Fontinalis antipyretica*; vascular plants, i.e., *Nuphar lutea*, *Sagittaria sagittifolia,* and *Potamogeton crispus*; and the brown macroalga *Heribaudiella fluviatilis* were dominant species in the riverine habitats of HR. On the other hand,

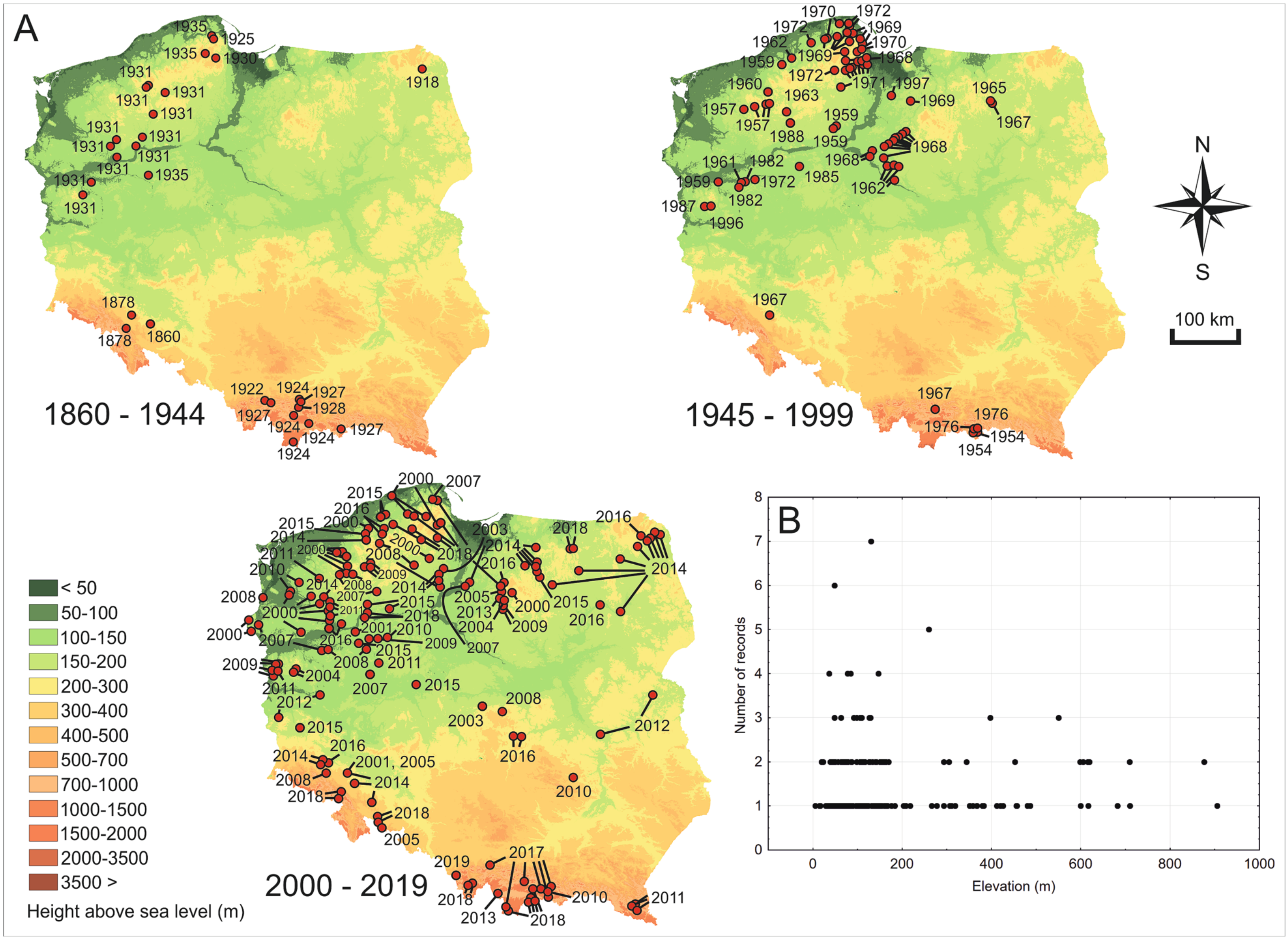

Fig. 5. A. Occurrence of *Hildenbrandia rivularis* populations in three time intervals on the hypsometric map of Poland (the dates indicate when the site was found). B. Number of records of grid squares in relation to the elevation (m) of each square.

Table 3
Environmental conditions in the studied *H. rivularis* microhabitats. Sample size N = 122.

Parameter, unit	Medium	Minimum	Maximum
Temperature (°C)	11.2	7.6	15.6
Oxygen (mg $O_2 \cdot L^{-1}$)	9.5	0.6	19.8
Conductivity (µS · cm^{-1})	384	201	928
Sulphate (mg $SO_4 \cdot L^{-1}$)	24.7	11.1	53.7
Chloride (mg $Cl^- \cdot L^{-1}$)	15.1	5.2	135.0
Calcium (mg $Ca^{2+} \cdot L^{-1}$)	61.0	39.3	90.2
Magnesium (mg $Mg^{2+} \cdot L^{-1}$)	8.5	4.4	17.0
Total hardness (mg $CaCO_3 \cdot L^{-1}$)	209	115	389
pH (−)	8.0	7.8	8.1
Total nitrogen (mg N · L^{-1})	1.81	0.51	8.65
Total phosphorus (mg P · L^{-1})	0.12	0.01	0.47

the fern *Equisetum fluviatile* and vascular plants such as *Scirpus sylvaticus* and *Lycopus europaeus* were very rare in the analyzed vegetation plots and very rarely inhabited the same niches as HR (Fig. 6**A**).

Detrended correspondence analysis (DCA) provided information on species composition, including the autecological niche of HR, among other plant species/communities inhabiting all examined rivers (Fig. 6**B**). The biodiversity of the flora was determined based on the length of the first DCA axis. The studied plot areas were arranged based on species composition and their occurrence along the 2nd DCA axis. The first ordination axis explains 21.3 % of the vegetation variation, while the second axis explains 11.8 %. Axis 1 shows the aggregation of the species associated with the water flow gradient, i.e., living in microhabitats where low water flow or water stagnation has been recorded. This group includes *Lemna trisulca*, *Potamogeton nodosus*, *Nuphar lutea*, *Scirpus lacustris,* and *Fontinalis antipyretica.* The group of species related to the higher water flow includes macroalga, moss, and vascular plant species such as HR, *Leptodictyum riparium*, *Potamogeton pusillus*, *Heribaudiella fluviatilis,* and *Sagittaria sagittifolia*. The analysis of riverine vegetation structure showed the separation of a small group of stands dominated by the filamentous green macroalga *Rhizoclonium riparium* and the vascular plant *Bidens tripartita* (Fig. 6**B**).

The quantitative response curves of HR and the most common aquatic species at the water flow level show some differences. Regarding the functional type of vegetation, HR belongs to the phytobenthic species that mainly prefer parts of rivers with the highest water current velocity (Eloranta and Kwandrans, 2012, 2004). This environmental parameter had the most critical influence on the floristic structure of all macrophyte functional groups ($p < 0.001$, according to the Monte Carlo permutation test). According to the GAM obtained, *H. rivularis* achieved optimum growth in habitats (featuring the highest percentage of colony coverage) with water velocity flow in the range from 0.7 to 1 m · s^{-1} (Poisson distribution, $F = 18.04$ for $p < 0.001$) (Fig. 6**C**). In the rivers in which the water flow velocity was estimated, this physical parameter ranged from 0.5 to 1.5 m · s^{-1} (Table 4). This is in line with other results, where populations of HR accrued only in stands with a flow of water above 0.6 m · s^{-1}(Jakubas and Gąbka, 2015; Laplace-Treyture et al., 2014).

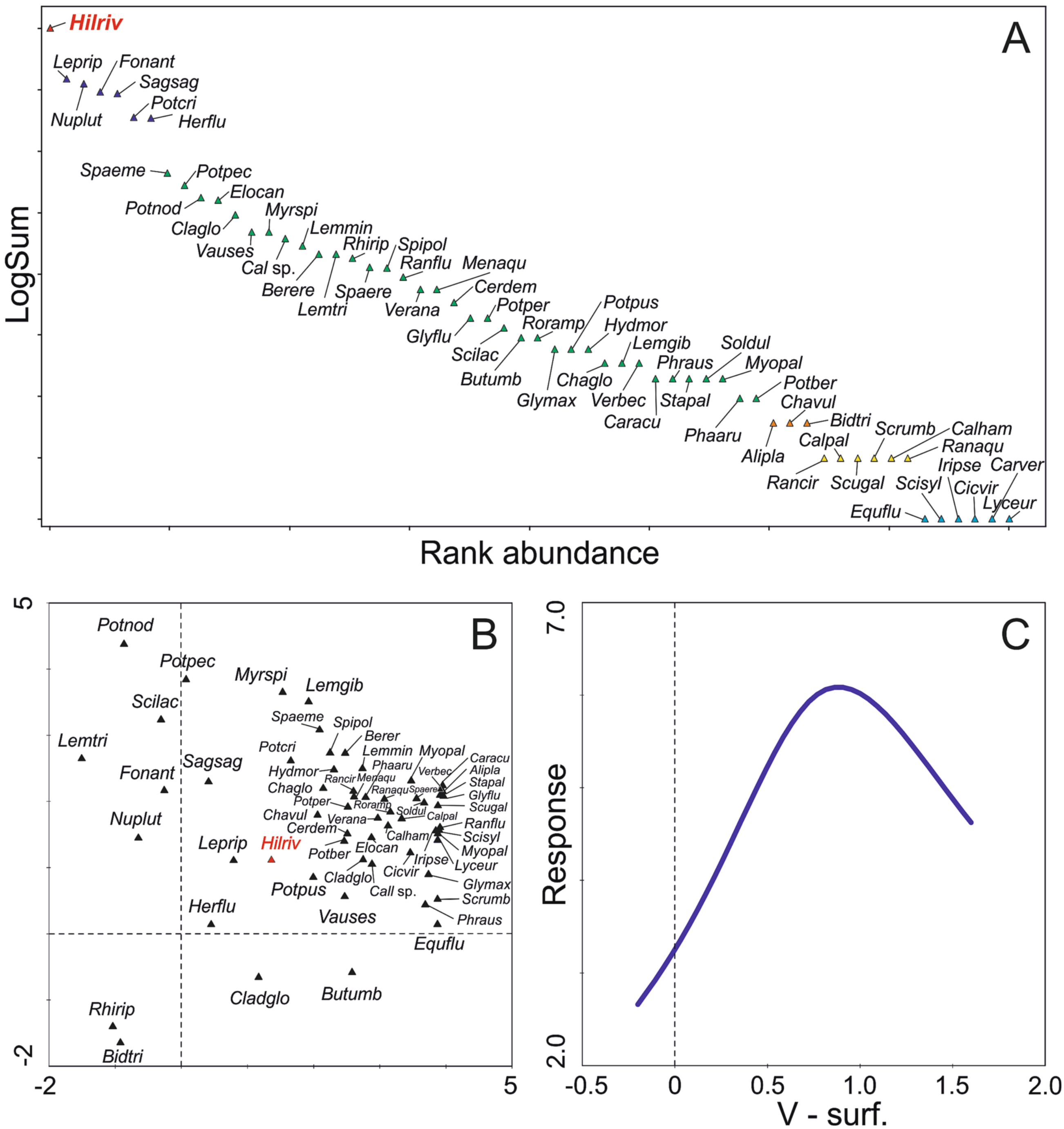

Fig. 6. Numerical analyses of the relations between *Hildenbrandia rivularis*, vegetation, and water flow velocity. **A.** Dominance curves of aquatic plants along 640 km of rivers in 58 vegetation plots. LogSum – log base 10 of the column (species) sum. **B.** Detrended correspondence analysis (DCA) of species optima along the first two axes. **C.** Response curves of *Hildenbrandia rivularis* concerning the water velocity gradient modeled by the generalized additive model using Poisson distribution smooth term complexity selected according to the AIC. The first axis represents the surface velocity of water values (V-surf.), and the second axis represents the cover-abundance codes of van der Maarel's scale. Species abbreviations (in alphabetical order): Alipla – *Alisma plantago-aquatica*, Berere – *Berula erecta*, Bidtri – *Bidens tripartite*, Butumb – *Butomus umbellatus*, Calham – *Callitriche hamulata*, *Cal* sp. – *Callitriche* species, Calpal – *Caltha palustris*, Caracu – *Carex acutiformis*, Carver – *Carex versicaria*, Chaglo – *Chara globularis*, Chavul – *Chara vulgaris*, Cerdem – *Ceratophyllum demersum*, Cicvir – *Cicuta virosa*, Claglo – *Cladophora glomerata*, Elocan – *Elodea canadensis*, Equflu – *Equisetum fluviatile*, Fonant – *Fontinalis antipyretica*, Glyflu – *Glyceria fluitans*, Glymax – *Glyceria maxima*, Herflu – *Heribaudiella fluviatilis*, Hilriv – *Hildenbrandia rivularis*, Hydmor – *Hydrocharis morsus-ranae*, Iripse – *Iris pseudacorus*, Lemgib – *Lemna gibba*, Lemmin – *Lemna minor*, Lemtri – *Lemna trisulca*, Leprip – *Leptodictyum riparium*, Lyceur – *Lycopus europaeus*, Menaqu – *Mentha aquatica*, Myopal –*Myosotis palustris*, Myrspi – *Myriophyllum spicatum*, Nuplut – *Nuphar lutea*, Phraus – *Phragmites australis*, Phaaru – *Phalaris arundinacea*, Potber – *Potamogeton berchtoldii*, Potcri – *Potamogeton crispus*, Potnod – *Potamogeton nodosus*, Potpec – *Potamogeton pectinatus,* Potper – *Potamogeton perfoliatus*, Potpus – *Potamogeton pusillus*, Rancir – *Ranunculus circinatus*, Ranflu – *Ranunculus fluitans*, Rhirip – *Rhizoclonium riparium*, Roramp – *Rorippa amphibia*, Sagsag – *Sagittaria sagittifolia*, Scilac – *Scirpus lacustris*, Scisyl – *Scirpus sylvaticus*, Scrumb – *Scrophularia umbrosa*, Scugal – *Scutellaria galericulata*, Soldul – *Solanum dulcamara*, Spaeme – *Sparganium emersum*, Spaere – *Sparganium erectum*, Spipol – *Spirodela polrhiza*, Stapal – *Stachys palustris*, Vauses – *Vaucheria sessilis*, Verbec – *Veronica beccabunga*, and Verana – *Veronica anagallis-aquatica*.

Table 4
The levels of the most important factors recorded in riverine habitats of *H. rivularis*. Sample size N = 58 from 5 rivers (i.e., Pilica, Wełna, Łeba, Płytnica, and Flinta Rivers).

Parameter, unit	Medium	Minimum	Maximum
Temperature (°C)	21.6	17.1	34
Average water depth (m)	0.39	0.06	1.1
The velocity of water ($m \cdot s^{-1}$)	0.53	0.061	1.508
The velocity of water in plant associations ($m \cdot s^{-1}$)	0.363	0.004	0.69

However, as independent field studies show, this red alga also inhabits ecosystems with very weak water currents (Żelazna-Wieczorek and Ziułkiewicz, 2008). Here, HR populations were recorded in rivers with water flow velocities ranging from 0.006 to 0.295 $m \cdot s^{-1}$. Thus, *H. rivularis* is a rheophilic species that lives in a wide range of water velocity conditions in riverine ecosystems and flow lakes (Cantonati and Lowe, 2014; Eloranta and Kwandrans, 2007; Sheath and Hambrook, 1988).

In the case of the examined rivers, other functional types of vegetation, with dominant species from the *Lemna*, *Potamogeton,* and *Nuphar* genus, preferred the riverine microhabitats with the lowest water velocity (approx. 0.20 $m \cdot s^{-1}$) (Fig. 6**B**). This ecological group includes free-floating plants (i.e., lemnids) or species rooted on the bottom with free-floating leaves on the water surface (e.g., *N. lutea* as a representative of nympheids) (Willby et al., 2000).

Interestingly, studies of freshwater HR populations in Nordic countries (Finland and Sweden) yielded similar results to our observations, namely, that this red alga is common in streams and rivers with a particular current velocity (Eloranta et al., 2016; Israelson, 1942; Sherwood and Sheath, 1999). As early as the 1940 s, Israelson (1942) distinguished five diverse biogeographical red algae groups in Sweden, categorized in relation to the bottom material. A study of red alga distributions in Italian rivers also indicates that this group of Rhodophyta prefers lotic waters, i.e., small or mid-sized rivers and streams (Ceschin et al., 2013). However, the most recent occurrence records of HR in Poland are associated with the country's largest rivers – the Vistula and the Warta (where the stands of HR have been monitored since 2016). Moreover, HR in these two rivers was found in places transformed by human activity: in an old marina on the Vistula and on the concrete structure of a road bridge. To date, there have been limited data indicating the presence of HR in anthropogenic areas, such as limestone reservoirs and old bridge structures (Dąmbska, 1961; Jakubas et al., 2014; Nichols, 1965).

The ecological status of water was assessed for 122 records based on hydrobotanical surveys and records from 2000 to 2016 in the national monitoring database, the latter of which were collected by voivodship inspectorates of environmental protection as part of the country-wide scheme implemented by the Chief Inspectorate of Environmental Protection. The monitoring research was conducted in line with the Polish Macrophyte Index for Rivers (MIR) (Kałuza et al., 2014; Szoszkiewicz et al., 2010) and the Ecological State Macrophyte Index for lakes (ESMI) (Ciecierska and Kolada, 2014). In the lakes, depth and Secchi disc visibility were also examined. The resulting data made it possible to assess the ecological status of the investigated ecosystems, which can be described as "moderate" and "good" in most cases. In the case of watercourses, only 1 stand with HR was classified as having a "bad" and 16 as having a "poor" ecological status. Stands of red algae in standing waters experienced better ecological conditions. It might seem that lotic water systems (i.e., running waters with a continuous flow) would offer better microhabitats for HR. Nevertheless, gradient changes in abiotic properties, turbidity, longitudinal temperature gradation and dissolved material have a significant impact on water parameters, ecological conditions and aquatic vegetation communities in subsequent sections of a given watercourse (from the source to the mouth) (Allan and Castillo, 2007; Gilvear et al., 2013; Jakubas and Gąbka, 2015). The better ecological conditions in the investigated standing waters should be attributed to the fact that the riparian zone provides a biofilter protecting aquatic environments from sedimentation, polluted surface runoff and erosion (Jakubas and Gąbka, 2015). Furthermore, the physicochemical parameters are more stable than in fast-flowing rivers and streams. However, the habitats of phytobenthic communities, such as those formed by HR in rivers and lakes, are affected by geology, altitude, basin morphometry, and level of human activity. This is evidenced by the fact that the sections of rivers designated as having a "bad" and "poor" ecological status were mostly hydromorphologically transformed due to the construction of bridges, dams, or marinas or the concrete reinforcement of riverbanks.

It has been argued in several previous studies that HR tends to grow extensively in places such as artificial surfaces connected with, e.g., road infrastructure (Dąmbska, 1961; Jakubas et al., 2014; Nichols, 1965; Żelazna-Wieczorek and Ziułkiewicz, 2008) and in urban areas (Kitayama 2014). Furthermore, another study of freshwater algae confirmed that certain Rhodophyta, including HR, are highly capable of developing under moderate to polluted conditions (Peerapornpisal et al., 2006). All relevant findings allow this freshwater red alga to be described as a synanthropic species becoming more widespread in Poland. The abundance of HR, which has long been considered a rare and endangered species, made it a good indicator of water quality in many European countries, including Poland, which may mean that it adapts to anthropogenic pressure and aligns its distribution accordingly.

4. Conclusions

The main findings of our study are as follows: (1) in the last decade, significant expansion of HR populations in Polish water ecosystems has been observed, especially in running water and lakes, with a significant simultaneous decline in the numbers of stands of this red alga in the mountain and upland areas; (2) the distribution of HR is not determined by biogeographic barriers, as demonstrated in previous studies; and (3) the distribution of this species is instead related to altitude (a moderate distribution trend has been demonstrated).

Notably, the populations of HR that we studied were most often recorded in flowing shallow waters in very well-lit stands. To date, the literature has reported that red crusts of HR are typical in shaded habitats (Eloranta et al., 2011; Eloranta and Kwandrans, 2007, 2004). Thus, HR also shows considerable plasticity concerning the intensity of light reaching the substrate on which this red alga grows. Clarifying this aspect will require further research on the expression of pigments (i.e., chlorophyll *a*, phycoerythrin and phycocyanin) in HR cells growing at different depths.

Our research shows that HR is a species resistant to substantial nutrient concentrations (often reaching very high levels); it usually inhabits rivers and lakes that have been strongly altered by humans. This is in line with previous observations where, e.g., changes in the thermal properties of rivers (the effect of hydropower plant operation) likely significantly impacted the expansion of HR populations (Jakubas et al., 2014). Further research should confirm whether this is a common feature of this macroalga across various European ecoregions. Additionally, in the next century and with the continuing effects of global climate change caused by human activity, it will be possible to verify the impact of rising water temperatures on the expansion of *H. rivularis* in Europe and on other continents.

Moreover, we emphasize that not all macroalgal species adopted in environmental monitoring protocols are helpful in accurately evaluating the ecological status of water ecosystems in Europe because some of them, such as *H. rivularis,* are not sensitive bioindicators for water contamination (e.g., overfertilization of waters by biogens).

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Table A1
Specification of *H. rivularis* stands in natural and seminatural water ecosystems of Poland. ATPOL: grid square codes system for Poland.

Source	Year of finding	Longitude	Latitude	Alitude (m. above sea level)	Voivodeship	ATPOL	Ecosytem	Name (another known name)
Hilse, 1862; Kirchner, 1878	1860	50°46′41.90″N	17° 4′20.72″E	161.33	dolnośląskie	BE-89	river	Oława
Kirchner, 1878	1878	50°53′3.91″N	16°40′59.92″E	203.93	dolnośląskie	BE-76	mountain stream	Strumień Ślęża
Kirchner, 1879	1878	50°42′33.71″N	16°34′40.53″E	306.80	dolnośląskie	BE-95	mountain stream	Pieszycki Potok
Lingelsheim and Schroder, 1918	1918	54° 6′29.52″N	22°59′13.37″E	146.61	podlaskie	FB-09	river connecting the lakes	Kamionka
Lingelsheim and Schroder, 1919	1918	49°16′14.65″N	20° 0′16.76″E	905.24	małopolskie	EG-50	spring	Potok Olczyski
Namysłowski, 1922	1922	49°48′9.88″N	19°31′20.65″E	344.13	małopolskie	DF-96	mountain stream	Jaszczurówka
Rouppert, 1924	1924	49°50′38.69″N	20° 7′8.09″E	277.39	małopolskie	EF-81	brook	Krzyworzeka
Starmach, 1927	1924	49°30′20.32″N	20°20′20.07″E	452.43	małopolskie	EG-22	mountain stream	non name stream 1
Starmach, 1927	1924	49°37′46.24″N	19°58′57.78″E	480.29	małopolskie	EG-10	mountain stream	Śmietanowy Potok
Starmach, 1927	1924	49°30′30.42″N	20°19′5.76″E	811.66	małopolskie	EG-22	mountain stream	non name stream 2
Starmach, 1927	1925	54°35′37.85″N	18°14′33.48″E	48.72	pomorskie	CA-68	struga	Cedron (Cedronka)
Starmach, 1927	1927	49°48′33.03″N	19°27′11.46″E	484.31	małopolskie	DF-96	brook	Ponikiewka
Starmach, 1927	1927	49°25′50.27″N	20°57′58.46″E	709.75	małopolskie	EG-25	brook	non name brook 1
Starmach, 1927	1927	49°49′16.99″N	20° 8′33.35″E	710.16	małopolskie	EF-91	brook	non name brook 2
Starmach, 1969	1928	49°42′0.51″N	20° 6′10.60″E	605.55	małopolskie	EG-00	river	Potok Lubogoszcz
Koppe, 1929	1930	54°18′20.19″N	18°18′31.29″E	146.67	pomorskie	CA-98	river	Radunia
Frase, 1931	1931	52°36′3.97″N	15°39′54.16″E	40.97	lubuskie	BC-70	river	Męcinka
Frase, 1931	1931	52°57′16.68″N	16°11′55.36″E	52.17	wielkopolskie	BC-34	river	Zbrzyca
Frase, 1931	1931	52°25′46.94″N	15°29′45.28″E	59.58	lubuskie	AC-99	river	Jeziorna
Frase, 1931	1931	53° 5′38.05″N	16° 1′57.66″E	61.34	zachodniopomorskie	BC-23	river	Cieszynka
Frase, 1931	1931	53° 6′28.29″N	16°36′1.83″E	65.25	wielkopolskie	BC-26	river	Krępica
Frase, 1931	1931	53°13′36.11″N	16°44′23.61″E	76.90	wielkopolskie	BC-17	river	Struga Ruda
Frase, 1931	1931	53°11′7.56″N	16° 9′45.82″E	87.88	zachodniopomorskie	BC-14	river	Runica (Młynówka)
Frase, 1931	1931	53°32′2.88″N	16°57′10.89″E	108.64	wielkopolskie	BB-79	river	Debrzynka
Frase, 1931	1931	53°49′48.08″N	17°12′21.28″E	127.57	pomorskie	CB-41	river	Brda
Frase, 1931	1931	53°50′49.08″N	17°10′46.94″E	132.11	pomorskie	CB-41	river	Modra
Frase, 1931	1931	53°55′18.09″N	16°49′2.70″E	154.07	zachodniopomorskie	BB-38	lake	Cieszęcino
Krawiec,1935	1935	54°35′37.85″N	18°14′33.48″E	48.72	pomorskie	CA-68	stream	Cedron (Cedronka)
Krawiec,1935	1935	52°43′22.02″N	16°54′51.13″E	65.07	wielkopolskie	BC-68	river	Wełna
Krawiec,1935	1935	54°18′20.19″N	18°18′31.29″E	146.67	pomorskie	CA-98	river	Radunia
Krawiec,1936	1936	54°21′19.68″N	18° 4′42.29″E	164.06	pomorskie	CA-87	river	Łeba
Starmach,1982	1954	49°24′44.50″N	20°55′45.03″E	598.60	małopolskie	EG-37	river	Czarny Potok
Starmach,1982	1954	49°23′36.50″N	20°54′29.16″E	615.34	małopolskie	EG-36	river	Jastrzębik
Siemińska,1962	1957	53°32′8.39″N	15°52′17.81″E	66.12	zachodniopomorskie	BB-72	river	Drawa
Siemińska,1962	1957	53°35′28.02″N	16° 7′13.49″E	112.83	zachodniopomorskie	BB-73	river	Drawa
Siemińska,1962	1957	53°36′48.13″N	16°23′44.78″E	132.79	zachodniopomorskie	BB-65	lake	Brody
Siemińska,1962	1957	53°36′39.91″N	16°22′43.60″E	134.45	zachodniopomorskie	BB-65	lake	Rakowo
Szafrański, 1960	1959	52°34′22.90″N	15°25′29.10″E	31.57	lubuskie	AC-88	river	Obra
Żukowski, 1963	1959	54°14′11.62″N	16°53′42.30″E	45.33	pomorskie	BA-99	river	Wieprza
Bohr and Giziński, 1960	1959	53°20′37.63″N	17°57′54.52″E	81.79	kujawsko-pomorskie	CB-96	river	Brzeźniczka
Bohr and Giziński, 1960	1959	53°20′37.63″N	17°57′54.52″E	88.77	kujawsko-pomorskie	CB-85	river	Brda
Żukowski, 1963	1960	53°47′21.29″N	16°25′2.10″E	72.65	zachodniopomorskie	BB-45	river	non name river 1
Dąmbska, 1961	1961	52°36′28.88″N	15°59′55.14″E	36.46	wielkopolskie	BC-72	river	Bielina
Kępczyński, 1963	1962	52°51′2.89″N	19° 5′53.29″E	73.89	kujawsko-pomorskie	DC-53	river	Mień
Żukowski, 1963	1962	54° 9′21.88″N	16°42′2.09″E	77.08	zachodniopomorskie	BB-07	river	non name river 2
Kępczyński, 1963	1962	52°39′34.42″N	19°15′56.78″E	79.73	kujawsko-pomorskie	DC-74	river	Świnka
Kępczyński, 1963	1962	52°51′22.90″N	19°15′4.24″E	105.13	kujawsko-pomorskie	DC-54	river	Młynarka
Kępczyński, 1963	1962	52°51′10.01″N	19°17′5.81″E	111.64	kujawsko-pomorskie	DC-54	river	Mień
Żukowski, 1963	1963	53°32′1.54″N	16°51′3.36″E	126.24	wielkopolskie	BB-78	river	Czarna (Glinka)
Chudyba, 1970	1965	53°41′14.05″N	21°25′43.22″E	126.28	warmińsko-mazurskie	EB-59	river connecting the lakes	Krutynia
Rajewski, 1966	1966	54°18′20.19″N	18°18′31.29″E	146.67	pomorskie	CA-98	river	Radunia
Chudyba, 1970	1967	53°41′14.05″N	21°25′43.22″E	126.28	warmińsko-mazurskie	EB-59	river connecting the lakes	Krutynia
The Regional Directorate for Environmental Protection, not published	1967	50°53′3.91″N	16°40′59.92″E	454.20	dolnośląskie	BE-76	stream	non name stream 3
Starmach, 1969	1967	49°42′0.51″N	20° 6′10.60″E	605.55	małopolskie	EG-00	river	Lubogoszcz
Kępczyński, 1972	1968	53° 1′48.22″N	18°45′49.14″E	44.49	kujawsko-pomorskie	DC-31	river	Drwęca
Kępczyński, 1972	1968	52°58′59.61″N	18°44′31.18″E	46.79	kujawsko-pomorskie	DC-41	river	Drwęca
Starmach, 1969	1968	54°35′37.85″N	18°14′33.48″E	48.72	pomorskie	CA-68	stream	Cedron (Cedronka)

(continued on next page)

Table A1 (*continued*)

Source	Year of finding	Longitude	Latitude	Alitude (m. above sea level)	Voivodeship	ATPOL	Ecosytem	Name (another known name)
Markowski, 1980	1968	54°33′26.41″N	18°22′1.26″E	50.91	pomorskie	CA-68	river	Zagórska Struga
Kępczyński, 1972	1968	53° 6′46.77″N	19° 3′5.79″E	56.50	kujawsko-pomorskie	DC-23	river	Drwęca
Kępczyński, 1972	1968	53° 7′24.31″N	19° 6′25.24″E	59.48	kujawsko-pomorskie	DC-23	river	Drwęca
Kępczyński, 1972	1968	53°12′51.00″N	19°17′51.21″E	64.98	kujawsko-pomorskie	DC-15	river	Drwęca
Kępczyński, 1972	1968	53°11′13.46″N	19°14′48.96″E	66.67	kujawsko-pomorskie	DC-14	river	Drwęca
Kępczyński, 1972	1968	53°12′15.77″N	19°15′38.64″E	66.86	kujawsko-pomorskie	DC-14	river	Drwęca
Kępczyński, 1972	1968	53°16′45.76″N	19°28′43.90″E	69.15	kujawsko-pomorskie	DC-06	river	Drwęca
Kępczyński, 1972	1968	53°15′26.47″N	19°23′47.48″E	72.73	kujawsko-pomorskie	DC-05	river	Drwęca
Kępczyński, 1972	1968	53°16′54.67″N	19°28′36.41″E	73.35	kujawsko-pomorskie	DC-06	river	Drwęca
Kępczyński, 1972	1968	52°57′7.23″N	19° 2′4.92″E	78.74	kujawsko-pomorskie	DC-43	river	Drwęca
Markowski, 1980	1968	54°36′31.28″N	18°14′56.32″E	131.91	pomorskie	CA-58	river	Cedron
Markowski, 1980	1968	54°17′30.56″N	18° 2′49.54″E	159.30	pomorskie	CA-96	lake	Raduńskie
Markowski, 1980	1969	54°34′12.51″N	18°18′26.88″E	21.91	pomorskie	CA-68	river	Cedron
Markowski, 1980	1969	54°31′32.56″N	18°25′33.41″E	41.52	pomorskie	CA-69	river	non name river 3
Markowski, 1980	1969	54°33′57.10″N	17°58′59.82″E	46.29	pomorskie	CA-66	river	Łeba
Markowski, 1980	1969	54°35′31.05″N	18°10′11.07″E	46.34	pomorskie	CA-67	river	Gościcina
Markowski, 1980	1969	54°31′13.89″N	18°12′14.03″E	77.92	pomorskie	CA-67	river	Gościcina
Bohr, 1969	1969	53°43′15.34″N	19°35′57.29″E	98.91	warmińsko-mazurskie	DB-56	lake	Jeziorak
Markowski, 1980	1969	54°27′59.88″N	18°29′33.98″E	105.14	pomorskie	CA-79	river	Potok Źródło Marii
Markowski, 1980	1969	54°33′13.75″N	18°11′17.05″E	135.99	pomorskie	CA-67	river	Gościcina
Markowski, 1980	1969	54°21′19.68″N	18° 4′42.29″E	164.06	pomorskie	CA-87	river	Łeba
Markowski, 1980	1970	54°36′20.75″N	18° 9′34.80″E	37.35	pomorskie	CA-57	river	Bolszewka
Markowski, 1980	1970	54°43′25.38″N	17°58′38.76″E	39.13	pomorskie	CA-46	river	Bychowska Struga
Markowski, 1980	1970	54°44′27.87″N	17°58′21.39″E	43.86	pomorskie	CA-46	river	Bychowska Struga
Markowski, 1980	1970	54°34′19.23″N	18° 7′12.46″E	65.98	pomorskie	CA-67	river	Bolszewka
Markowski, 1980	1970	54°23′22.79″N	18°25′21.57″E	110.03	pomorskie	CA-89	river	Strzelenka
Markowski, 1980	1970	54°20′19.15″N	18°23′44.09″E	126.25	pomorskie	CA-89	river	Strzelenka
Markowski, 1980	1971	54°11′54.96″N	18°35′11.49″E	43.02	pomorskie	BD-00	river	Kłodawa
Markowski, 1980	1971	54°15′46.42″N	18°24′43.09″E	91.67	pomorskie	CA-99	river	Reknica
Markowski, 1980	1971	54°11′50.22″N	18°30′47.32″E	105.16	pomorskie	CB-09	river	Kłodawa
Tobolski, 1971	1971	53°53′29.54″N	18° 2′1.70″E	123.60	pomorskie	CB-36	river	Wda
Markowski, 1980	1971	54°16′15.82″N	18°27′24.37″E	144.10	pomorskie	CA-99	river	Reknica
Markowski, 1980	1971	54°15′35.76″N	18°23′24.69″E	148.90	pomorskie	CA-99	river	Reknica
Markowski, 1980	1971	54° 8′38.97″N	18°14′36.34″E	161.31	pomorskie	CB-18	river	Wietcisa
Markowski, 1980	1971	54° 8′5.42″N	18°13′51.61″E	169.51	pomorskie	CB-17	river	Wietcisa
Markowski, 1980	1971	54° 7′52.09″N	18° 7′7.18″E	175.53	pomorskie	CB-17	river	Wierzyca
Markowski, 1980	1972	54°30′10.28″N	17°37′57.32″E	16.46	pomorskie	CA-64	river	Pogorzelica
Markowski, 1980	1972	54°41′26.32″N	18° 9′13.08″E	28.54	pomorskie	CA-47	river	Piaśnica
Keffermüller, 1978	1972	52°37′44.72″N	16°12′53.78″E	46.93	wielkopolskie	BC-74	river	Koszyca
Markowski, 1980	1972	54°41′3.18″N	18°11′52.87″E	88.18	pomorskie	CA-57	river	non name river 4
Markowski, 1980	1972	54° 6′48.49″N	17°51′8.18″E	150.28	pomorskie	CB-15	river	Pilica
Starmach, 1982	1976	49°24′44.50″N	20°55′45.03″E	598.60	małopolskie	EG-37	river	Czarny Potok
Starmach, 1982	1976	49°23′36.50″N	20°54′29.16″E	615.34	małopolskie	EG-36	river	Jastrzębik
Markowski, 1980	1977	54°15′13.03″N	18° 6′24.41″E	159.71	pomorskie	CA-97	lake	Ostrzyckie
Stępczak and Musiał, 1984	1982	52°31′45.96″N	15°52′35.55″E	70.80	wielkopolskie	BC-81	river	non name river 5
Gołdyn, 1985	1982	52°36′17.54″N	15°56′49.02″E	134.77	zachodniopomorskie	BC-72	lake	Koleńskie (Kolno)
administrative document, 1983	1983	54°32′7.52″N	18°25′1.96″E	95.52	pomorskie	CA-69	stream	Cisowska Struga
Gołdyn, not published	1985	52°49′11.81″N	17°11′49.33″E	77.53	wielkopolskie	CC-50	lake	Durowo
Król, 1987	1987	52°15′23.98″N	15°11′2.35″E	86.88	lubuskie	AD-16	river	Pliszka
Górski, 2007; Jasnowska and Jasnowski, 1988	1988	53°23′31.42″N	16°56′49.54″E	114.27	wielkopolskie	BB-99	lake	Górzno Dolne
administrative document, 1996	1996	52°17′24.02″N	15°14′6.53″E	97.90	lubuskie	AD-17	river	Pliszka
Kukwa, 2005; Markowski, 1997	1997	53°46′20.95″N	19°10′54.55″E	83.23	pomorskie	DB-54	river	Liwa
Gąbka, 2000	2000	54°39′41.62″N	17°12′53.26″E	5.17	pomorskie	CA-51	river	Łupawa
Kowalski, these studies	2000	52°47′10.76″N	14°17′35.98″E	14.85	zachodniopomorskie	AC-41	river	Słupia
Kowalski, these studies	2000	53°19′4.40″N	15° 3′53.06″E	19.54	zachodniopomorskie	AB-96	river	Kąpiel
Kowalski, these studies	2000	52°55′26.22″N	14°12′57.62″E	32.09	zachodniopomorskie	AC-30	river	Świergotka
Kowalski, these studies	2000	54°12′53.07″N	16°42′47.17″E	36.74	pomorskie	BA-97	river	Grabowa
Kowalski, these studies	2000	53° 0′22.39″N	15°57′12.12″E	40.33	wielkopolskie	BC-32	river	Drawa
Kowalski, these studies	2000	53°53′39.26″N	16° 3′57.21″E	43.42	zachodniopomorskie	BB-33	river	Bukowa
Kowalski, these studies	2000	53° 2′32.03″N	15°57′51.78″E	43.67	lubuskie	BC-13	river	Płociczna
Kowalski, these studies	2000	53°53′52.07″N	16° 5′26.22″E	44.20	zachodniopomorskie	BB-33	river	Bukowa
Kowalski, these studies	2000	53°50′57.06″N	16°15′22.54″E	54.45	zachodniopomorskie	BB-39	river	Brzeźniczka
Kowalski, these studies	2000	52°49′5.38″N	15°23′24.96″E	59.83	lubuskie	AC-58	river	Santoczna
Kowalski, these studies	2000	53°17′16.54″N	15°32′45.61″E	70.84	zachodniopomorskie	AC-09	river	Ina
Kowalski, these studies	2000	53°11′27.15″N	15°50′59.24″E	77.21	zachodniopomorskie	BC-11	river	Słopica
Kowalski, these studies	2000	53°12′32.57″N	15°42′56.28″E	87.39	lubuskie	BC-11	river	Sitna
Kowalski, these studies	2000	53°42′51.64″N	16°16′58.69″E	107.08	zachodniopomorskie	BB-55	river	Dębnica
Kowalski, these studies	2000	53°38′23.04″N	16°12′41.82″E	126.92	zachodniopomorskie	BB-64	river	Drawa
Kowalski, these studies	2000	53°34′31.88″N	16° 4′28.71″E	139.94	zachodniopomorskie	BB-64	river	Drawa

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Table A1 (*continued*)

Source	Year of finding	Longitude	Latitude	Alitude (m. above sea level)	Voivodeship	ATPOL	Ecosytem	Name (another known name)
Gąbka, these studies	2000	54° 4′30.15″N	17°53′52.96″E	147.13	pomorskie	CB-15	river	Trzebiocha
administrative-tourist document, 2000	2000	53°24′47.73″N	19°56′14.73″E	159.52	warmińsko-mazurskie	DB-99	river	Rynkówka
Ciechanowski, Fałtynowicz and Zieliński, 2004	2000	54°23′43.99″N	18° 1′19.77″E	159.79	pomorskie	CA-86	river	Struga Mirachowska
administrative document, 2000	2000	54°16′59.46″N	18°15′37.04″E	169.54	pomorskie	CA-96	stream	Strużka
Gąbka, these studies	2001	52°51′10.25″N	16°32′24.61″E	77.46	wielkopolskie	BC-56	lake	Lubasz Wielki (Lubaskie Duże)
Gąbka, 2001	2001	50°53′3.91″N	16°40′59.92″E	493.20	dolnośląskie	BE-76	stream	non name stream 4
Gąbka, 2002	2002	53°50′29.25″N	18° 5′31.51″E	116.99	pomorskie	CB-58	river	Wda
Gąbka, 2003	2003	52°46′7.53″N	16°52′36.33″E	66.31	wielkopolskie	BC-68	river	Flinta
Gąbka and Owsianny, 2004, 2010	2003	53°23′1.12″N	16°36′2.26″E	85.99	zachodniopomorskie	BB-97	river	Rurzyca
Kukwa, 2005	2003	53°42′32.97″N	18°22′39.98″E	88.19	pomorskie	CB-58	river	Wda
Żelazna-Wieczorek and Ziułkiewicz, 2008	2003	51°55′29.01″N	19°19′43.96″E	141.16	łódzkie	DD-56	river	Ciosna
administrative document, 2004	2004	53°38′30.41″N	17°57′10.11″E	102.54	kujawsko-pomorskie	CB-66	river	Bielska Struga
Maciantowicz and Jermaczek, 2004	2004	52°17′44.92″N	15°15′58.01″E	104.49	lubuskie	AD-17	river	Łagowa
Maciantowicz and Jermaczek, 2004	2004	52°19′43.09″N	15°17′25.15″E	107.42	lubuskie	AD-07	lake	Łagowskie
administrative document, 2004	2004	53°20′2.59″N	19°45′56.94″E	111.72	warmińsko-mazurskie	DB-97	river	Wel
administrative document, 2004	2004	53°40′44.86″N	16°18′24.03″E	142.24	zachodniopomorskie	BB-55	river	Dębnica
Gąbka and Owsianny, 2004, 2010	2005	53°13′5.18″N	16°47′30.43″E	62.88	wielkopolskie	BC-18	river	Głomia
Gąbka and Owsianny, 2004, 2010	2005	53°12′21.9″N	16°47′08.3″E	63.28	wielkopolskie	BC-18	river	Gwda
Gąbka and Owsianny, 2004, 2010	2005	53°21′8.11″N	16°37′19.84″E	82.49	wielkopolskie	BB-97	lake	Trzebieszki
administrative document, 2005	2005	53°22′16.07″N	19°46′36.47″E	114.40	warmińsko-mazurskie	DB-98	river	Kiełpińska Struga
administrative-tourist document, 2005	2005	50°53′3.91″N	16°40′59.92″E	259.80	dolnośląskie	BE-76	river	Strumień Ślęża
Spałek, not published	2005	50°19′58.43″N	17°16′29.78″E	318.58	opolskie	CF-30	brook	Maruszka
Gąbka and Owsianny, 2004, 2010	2006	53°14′48.64″N	16°47′17.48″E	75.40	wielkopolskie	BC-08	river	Pankawa (Pękawica)
Gąbka and Owsianny, 2004, 2010	2006	53°13′31.15″N	16°44′22.48″E	77.02	wielkopolskie	BC-17	river	Ruda
Gąbka and Owsianny, 2004, 2010	2006	53°19′25.71″N	16°45′58.62″E	84.52	wielkopolskie	BC-08	river	Płytnica
Gąbka and Owsianny, 2004, 2010	2006	53°16′52.87″N	16°44′39.13″E	85.77	wielkopolskie	BC-07	river	Rurzyca
Gąbka and Owsianny, 2004, 2010	2006	53°16′17.91″N	16°36′43.83″E	87.16	zachodniopomorskie	BC-07	river	Dobrzyca (Debrzyca)
Gąbka and Owsianny, 2004, 2010	2006	53°22′8.03″N	17°15′8.88″E	105.14	kujawsko-pomorskie	CB-91	river	Łobżonka
Gąbka and Owsianny, 2004, 2010	2006	53°20′58.59″N	16°34′18.91″E	132.68	wielkopolskie	BB-96	river	Piława
Jusik, 2007	2007	54°36′9.54″N	18°14′41.33″E	27.57	pomorskie	CA-68	stream	Cedron (Cedronka)
Pietruczuk, not published	2007	52°36′17.63″N	15°54′52.00″E	35.53	wielkopolskie	BC-72	river	Kamionka
administrative document, 2007	2007	53°30′57.80″N	18°56′57.30″E	46.30	kujawsko-pomorskie	DB-82	river	Gardęga
administrative document, 2007	2007	52°52′28.95″N	14°25′4.83″E	58.07	zachodniopomorskie	AC-42	river	Słubia
Pietruczuk, not published	2007	52°19′11.31″N	16°54′48.95″E	58.29	wielkopolskie	BD-18	river	Kopel
administrative document, 2007	2007	54°22′48.88″N	17°37′32.86″E	114.04	pomorskie	CA-84	river	Bukowina
Górski, 2007	2007	53°23′31.42″N	16°56′49.54″E	114.27	wielkopolskie	BB-99	lake	Górzno Górne
Waloch, 2008	2008	53°13′12.48″N	14°31′8.07″E	33.14	zachodniopomorskie	AC-03	river	Tywa
Gąbka, 2008	2008	52°35′55.80″N	15°56′36.59″E	36.87	wielkopolskie	BC-72	river	Kamionka
Jusik, not published	2008	53°29′58.97″N	18°22′27.97″E	41.27	kujawsko-pomorskie	CB-88	river	Wda
Jakubas et al., 2014	2008	52°38′47.61″N	16°48′23.42″E	49.06	wielkopolskie	BC-78	river	Wełna
Gąbka, 2008	2008	52°57′0.54″N	16°13′58.65″E	60.22	wielkopolskie	BC-44	river	Bukówka
administrative document, 2008	2008	54°21′7.03″N	17°37′37.78″E	109.15	pomorskie	CA-84	river	Łupawa
Jusik, not published	2008	53°45′3.78″N	17°46′20.60″E	111.03	pomorskie	CB-54	river	Brda
administrative document, 2008	2008	54° 0′12.32″N	16°58′59.99″E	121.89	pomorskie	BB-29	river	Studnica
Gąbka, 2008	2008	53°30′16.50″N	16°28′52.52″E	125.62	zachodniopomorskie	BB-76	river	Piława
Hachułka, 2011	2008	51°51′8.95″N	19°43′37.96″E	167.09	łódzkie	DD-68	river	Strumień Kamienna

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Table A1 (*continued*)

Source	Year of finding	Longitude	Latitude	Alitude (m. above sea level)	Voivodeship	ATPOL	Ecosytem	Name (another known name)
Cedro, Mianowicz, and Zawadzki, 2008	2008	51° 0′55.27″N	16° 6′3.03″E	310.64	dolnośląskie	BE-52	brook	Jawornik
Smoczyk, 2011	2009	52°12′21.36″N	14°53′9.36″E	47.52	lubuskie	AD-16	river	Pliszka
Smoczyk, 2011	2009	52°18′31.38″N	14°49′18.21″E	49.25	lubuskie	AD-04	river	Ilanka
Pietruczuk, not published	2009	52°45′15.85″N	17° 0′15.81″E	67.93	wielkopolskie	BC-69	river	Mała Wełna
Smoczyk, 2011	2009	52°21′54.78″N	14°55′7.26″E	71.32	lubuskie	AD-05	river	Cierniczka
Gąbka and Owsianny, 2004, 2010	2009	53°47′40.89″N	16°24′31.98″E	74.17	zachodniopomorskie	BB-45	river	Parsęta
Śledzińska and Wieloch, 2009	2009	53° 9′17.79″N	15°53′2.10″E	75.59	zachodniopomorskie	BC-12	river	Słopica
Okrągła, Kamińska and Chmielewski, 2012	2009	53°13′46.52″N	19°43′56.36″E	104.80	warmińsko-mazurskie	DC-17	river	Brynica
Okrągła, Kamińska and Chmielewski, 2012	2009	53°12′30.95″N	19°43′41.19″E	123.80	warmińsko-mazurskie	DC-17	river	Brynica
Gąbka and Owsianny, 2004, 2010	2009	53°36′57.78″N	16°25′30.26″E	129.27	zachodniopomorskie	BB-65	lake	Strzeszyn
Gąbka and Owsianny, 2004, 2010	2009	53°36′52.08″N	16°25′20.29″E	130.27	zachodniopomorskie	BB-65	river	non name river 6
Gąbka and Owsianny, 2004, 2010	2009	53°41′19.91″N	16°51′36.84″E	131.67	zachodniopomorskie	BB-58	river	Gwda
Gąbka and Owsianny, 2004, 2010	2009	53°37′2.25″N	16°22′12.83″E	132.38	zachodniopomorskie	BB-65	lake	Komorze
Gąbka and Owsianny, 2004, 2010	2009	53°35′18.42″N	16°27′10.25″E	132.68	zachodniopomorskie	BB-66	river	Piława
Gąbka and Owsianny, 2004, 2010	2009	53°36′48.13″N	16°23′44.78″E	132.79	zachodniopomorskie	BB-65	lake	Brody
Gąbka and Owsianny, 2004, 2010	2009	53°36′39.91″N	16°22′43.60″E	132.79	zachodniopomorskie	BB-65	lake	Rakowo
Gąbka and Owsianny, 2004, 2010	2009	53°42′18.02″N	16°41′18.87″E	133.67	zachodniopomorskie	BB-57	lake	Trzesiecko
Gąbka and Owsianny, 2004, 2010	2009	53°42′32.48″N	16°41′39.97″E	136.05	zachodniopomorskie	BB-57	river	Niezdobna
Gąbka and Owsianny, 2004, 2010	2009	53°46′22.07″N	16°48′56.36″E	137.11	zachodniopomorskie	BB-48	lake	Dołgie (Długie)
Smoczyk, 2011	2009	52°18′38.4″N	14°49′10.7″E	50.10	lubuskie	AD-04	river	Ilanka
administrative document, 2010	2010	53°19′4.40″N	15° 3′53.06″E	19.54	zachodniopomorskie	AB-98	river	Krępiel
Jusik, not published	2010	53°28′2.09″N	15°14′26.13″E	64.45	zachodniopomorskie	AB-78	river	Krępiel
Messyasz et al. (2010)	2010	52°49′11.81″N	17°11′49.33″E	77.53	wielkopolskie	CC-50	lake	Durowskie (Durowo)
Czekaj, not published)	2010	50°58′48.65″N	21°14′52.45″E	183.65	świętokrzyskie	EE-68	river	Świślina
Jusik, not published)	2010	49°29′20.38″N	20°40′52.36″E	346.23	małopolskie	EG-25	brook	Rytrzanka
Gąbka, 2011	2011	53°2′5.23″N	15°57′7.91″E	42.66	lubuskie	BC-32	river	Drawa
Gąbka, 2011	2011	53°35′28.02″N	16° 7′13.49″E	42.77	wielkopolskie	BB-73	river	Drawa
Gąbka, 2011	2011	53° 5′16.61″N	15°59′46.68″E	60.25	lubuskie	BC-32	river	Płociczna
Gąbka, 2011	2011	53° 5′35.19″N	16° 0′31.09″E	62.84	zachodniopomorskie	BC-22	river	Cieszynka
Gąbka, 2011	2011	53° 8′42.94″N	15°52′30.94″E	63.01	zachodniopomorskie	BC-12	river	Korytnica
Miężalska, not published	2011	53°15′47.97″N	16°46′39.19″E	68.42	wielkopolskie	BC-08	river	Rurzyca
Gąbka, 2011	2011	53° 3′10.50″N	15°57′26.40″E	69.30	lubuskie	BC-22	river	non name river 7
Gąbka, 2011	2011	52°27′42.32″N	17° 4′38.07″E	79.61	wielkopolskie	BC-99	river	Główna
Gąbka, 2011	2011	53°31′16.06″N	15°41′39.06″E	83.59	zachodniopomorskie	BB-71	river	Brzeźnicka (Węgorza)
Bylak and Kukuła, 2011	2011	49°16′0.42″N	22°28′50.19″E	455.68	podkarpackie	FG-48	brook	Tworylczyk
Bylak and Kukuła, 2011	2011	49°12′5.99″N	22°31′30.60″E	619.55	podkarpackie	FG-58	brook	Rzeka
Bylak and Kukuła, 2011	2011	49°13′4.99″N	22°30′31.00″E	632.68	podkarpackie	FG-58	brook	Hulski Potok
Smoczyk, 2011	2011	52°22′07.5″N	14°55′12.9″E	54.50	lubuskie	AD-05	river	Cierniczka
Gąbka, these studies	2012	52°22′3.20″N	15°52′49.06″E	51.65	lubuskie	BD-01	river	Obra
Jachimek-Michaś, not published	2012	53°18′14.15″N	16°47′32.98″E	76.59	wielkopolskie	BC-08	river	Płytnica
Miężalska, not published	2012	53°20′45.24″N	16°48′58.33″E	79.58	wielkopolskie	BB-98	river	Gwda
Lachowska, not published	2012	51°31′52.83″N	21°50′2.95″E	112.28	mazowieckie	FD-92	river	Wisła
Rosadzinski, not published	2012	51°41′32.63″N	15° 1′30.29″E	117.22	lubuskie	AD-75	river	Lubsza
Kowalski, these studies	2012	53°50′7.59″N	22°59′53.58″E	120.65	podlaskie	FB-39	river	Rospuda
Krawczewska, not published	2013	53°20′52.36″N	19°44′38.46″E	108.92	warmińsko-mazurskie	DC-08	river	Wel
Nosek, not published	2013	49°28′50.34″N	19°41′39.05″E	616.83	małopolskie	DG-38	brook	Czarna Orawa
Smoczyk, these studies	2013	50°25′22.4″N	16°33′51.0″E	310.40	dolnośląskie	BF-25	river	Bystrzyca Dusznicka
Gąbka, these studies	2014	53°29′57.70″N	18°53′48.57″E	35.07	kujawsko-pomorskie	DB-82	river	Osa
Figiel, not published	2014	53°29′58.97″N	18°22′27.97″E	41.27	kujawsko-pomorskie	CB-68	river	Wda
Friedensberg, not published	2014	53° 8′42.94″N	15°52′30.94″E	63.01	zachodniopomorskie	BC-12	river	Korytnica
Figiel, not published	2014	53°37′2.18″N	18°16′14.40″E	68.38	kujawsko-pomorskie	CB-68	river	Prusina
Gąbka, these studies	2014	54°7′54.02″N	16°40′55.35″E	71.86	zachodniopomorskie	BB-07	river	Grabowa
Gąbka, these studies	2014	53°39′18.09″N	18°18′59.76″E	76.49	kujawsko-pomorskie	CB-68	river	Wda
Friedensberg, not published	2014	53°17′6.00″N	15°49′57.97″E	83.34	zachodniopomorskie	BB-63	river	Drawica

(continued on next page)

Table A1 (*continued*)

Source	Year of finding	Longitude	Latitude	Alitude (m. above sea level)	Voivodeship	ATPOL	Ecosytem	Name (another known name)
Czachorowski, 2014	2014	54°0′48.12″N	20°28′6.42″E	85.76	warmińsko-mazurskie	EB-22	river	Kirsna
Czachorowski, 2014	2014	53°40′46.70″N	20°30′25.13″E	103.96	warmińsko-mazurskie	EB-62	river	Łyna
Tyl, not published	2014	53°9′7.62″N	22°18′42.33″E	104.33	podlaskie	FC-15	river	Łojewek
Gąbka, these studies	2014	53°44′49.72″N	20°14′4.91″E	104.48	warmińsko-mazurskie	EB-51	river	Giławka
Czachorowski, 2014	2014	53°43′3.13″N	20°28′19.64″E	105.60	warmińsko-mazurskie	EB-62	river	Łyna
Czachorowski, 2014	2014	53°46′28.76″N	20°28′40.78″E	115.55	warmińsko-mazurskie	EB-52	river	Łyna
Czachorowski, 2014	2014	53°49′57.31″N	22°23′0.24″E	124.21	warmińsko-mazurskie	FB-45	river	Ełk
Czachorowski, 2014	2014	53°41′14.05″N	21°25′43.22″E	126.28	warmińsko-mazurskie	EB-59	river connecting the lakes	Krutynia
Friedensberg, not published	2014	53°31′47.93″N	16°29′24.97″E	126.88	zachodniopomorskie	BB-76	river	Piława
Friedensberg, not published	2014	53°35′29.36″N	16° 5′6.36″E	128.85	zachodniopomorskie	BB-63	river	Drawa
Gąbka, these studies	2014	54°8′9.00″N	23°17′37.76″E	133.35	podlaskie	GB-01	river	Marycha
Gąbka, these studies	2014	54°4′56.36″N	23° 5′26.68″E	133.37	podlaskie	FB-19	river	Piertanka
Gąbka, these studies	2014	54°3′35.76″N	23° 0′24.11″E	138.85	podlaskie	FB-19	river	Czarna Hańcza
Gąbka, these studies	2014	54°9′45.30″N	23°12′49.75″E	143.98	podlaskie	GB-00	river	Czarna
Gąbka, these studies	2014	53°59′24.65″N	22°47′11.94″E	151.38	podlaskie	FB-27	river	Hańcza
Kosina and Tomaszewska, 2014	2014	50°53′3.91″N	16°40′59.92″E	203.93	dolnośląskie	BE-76	stream	non name stream 5
Kosina and Tomaszewska, 2014	2014	50°39′19.04″N	17° 3′6.66″E	217.82	dolnośląskie	BE-99	brook	Zuzanka
Smoczyk and Wierzcholska, 2014	2014	50°24′16.81″N	16°23′48.92″E	550.00	dolnośląskie	BF-24	river	Bystrzyca Dusznicka
Smoczyk, these studies	2014	51°08′17.0″N	16°00′31.0″E	155.20	dolnośląskie	BE-42	river	Kaczawa
Smoczyk, these studies	2014	51°07′51.2″N	15°58′32.4″E	163.00	dolnośląskie	BE-41	river	Kaczawa
Smoczyk, these studies	2014	50°22′05.7″N	16°38′17.0″E	314.70	dolnośląskie	BF-36	river	Nysa Kłodzka
Smoczyk, these studies	2014	50°25′18.2″N	16°38′50.3″E	293.50	dolnośląskie	BF-16	river	Nysa Kłodzka
Gąbka, these studies	2015	54°22′40.03″N	17° 3′5.10″E	44,615	pomorskie	CA-80	river	Słupia
Gąbka, these studies	2015	54°22′14.26″N	17° 1′17.05″E	25.58	pomorskie	CA-80	river	Kwacza
Gąbka, 2015	2015	52°43′6.13″N	16°36′58.07″E	52.68	wielkopolskie	BC-66	river	Kończak
Gąbka, 2015	2015	53° 9′21.35″N	17°15′25.66″E	67.42	wielkopolskie	CC-11	river	Łobzonka
Gąbka and Rybak, these studies	2015	52°12′2.01″N	17°53′36.36″E	74.75	wielkopolskie	CD-25	river	Warta
Gąbka, these studies	2015	52°12′13.26″N	17°53′10.76″E	78.80	wielkopolskie	CD-25	river	Warta
administrative document, 2015	2015	54° 9′28.32″N	16°42′35.78″E	79.41	zachodniopomorskie	BB-08	river	Warta
Gąbka, 2015	2015	53°18′35.77″N	16°30′5.39″E	97.21	zachodniopomorskie	BC-06	river	Zdbica
Gąbka, 2015	2015	53°18′28.39″N	16°29′4.66″E	97.95	zachodniopomorskie	BC-06	river	Piławka
Gąbka, 2015	2015	53°18′19.58″N	16°28′59.77″E	102.19	zachodniopomorskie	BC-06	river	Żydówka
Wąsicki, not published	2015	51°34′55.96″N	15°27′35.45″E	118.33	lubuskie	AD-98	river	Iławka (Szprotawka, Młynówka)
administrative document, 2015	2015	53°39′1.56″N	20°30′22.10″E	128.72	warmińsko-mazurskie	EB-62	river	Łyna
Smoczyk, these studies	2015	50°24′50.3″N	16°31′14.7″E	343.50	dolnośląskie	BF-25	river	Bystrzyca Dusznicka
Kissler, not published	2016	52°53′6.74″N	15°58′38.13″E	31.39	lubuskie	BB-63	river	Drawa
Gąbka, these studies	2016	54° 8′52.29″N	17° 2′0.42″E	78.88	pomorskie	CB-00	river	Wieprza
Gąbka, these studies	2016	54°12′29.57″N	17° 5′23.40″E	85.84	pomorskie	CB-00	river	Pokrzywna
Krawczewska, not published	2016	53°32′14.62″N	19°40′15.62″E	89.48	warmińsko-mazurskie	AD-04	river	Iławka
Dzierzgowska, not published	2016	53°14′5.10″N	21°52′3.29″E	96.99	podlaskie	FC-02	river	Pisa
Gąbka, 2016	2016	53°32′1.54″N	16°51′3.36″E	126.24	wielkopolskie	BB-78	river	Czarna (Glinka)
Gąbka and Rybak, these studies	2016	51°32′15.00″N	20° 7′56.72″E	148.35	łódzkie	EE-00	river	Pilica
Gąbka and Rybak, these studies	2016	51°32′26.12″N	20° 8′24.33″E	152.15	łódzkie	EE-00	river	Gać
Gąbka and Rybak, these studies	2016	51°32′24.01″N	19°58′55.37″E	161.30	łódzkie	DE-09	river	Wolbórka
Zega and Sztelmach, not published	2016	54° 8′1.10″N	22°52′53.53″E	175.81	podlaskie	FB-08	river	Czarna Hańcza
Rosadzinski, not published	2016	50°32′53.57″N	16°29′48.57″E	420.37	dolnośląskie	BF-05	river	Włodzica
Smoczyk, these studies	2016	51°08′35.8″N	16°04′17.5″E	141.50	dolnośląskie	BE-42	river	Nysa Szalona
Smoczyk, these studies	2016	50°24′13.9″N	16°28′54.9″E	397.50	dolnośląskie	BF-25	river	Bystrzyca Dusznicka
Smoczyk, these studies	2017	50°25′19.2″N	16°24′40.6″E	510.50	dolnośląskie	BF-24	river	Kamienny Potok
Smoczyk, these studies	2017	50°25′54.8″N	16°26′20.2″E	575.80	dolnośląskie	BF-24	river	Czerwona Woda
Smoczyk, these studies	2017	50°24′52.9″N	16°38′08.0″E	305.00	dolnośląskie	BF-26	river	

(*continued on next page*)

Table A1 (*continued*)

Source	Year of finding	Longitude	Latitude	Alitude (m. above sea level)	Voivodeship	ATPOL	Ecosytem	Name (another known name)
								Bystrzyca Dusznicka
Smoczyk, these studies	2017	50°14′25.8″N	16°37′48.4″E	358.10	dolnośląskie	BF-46	river	Nysa Kłodzka
Panek, these studies	2017	49°51′30.53″N	19°30′57.73″E	266.31	małopolskie	DF-86	river	Skawa
Panek, these studies	2017	49°31′49.43″N	20°31′27.52″E	266.16	małopolskie	EG-24	river	Dunajec
Panek, these studies	2017	49°26′31.71″N	20°43′6.27″E	379.47	małopolskie	EG-35	river	Poprad
Panek, these studies	2017	49°38′1.23″N	20°13′35.15″E	600	małopolskie	EG-11	brook	Kamienica
Panek, these studies	2017	49°18′4.53″N	19°50′57.13″E	876.36	małopolskie	DG-59	brook	Czarny Dunajec
Panek, these studies	2017	49°33′40.85″N	20°45′18.16″E	367.47	małopolskie	EG-25	river	Kamienica
Panek, these studies	2018	49°24′3.15″N	20°20′51.37″E	426.11	małopolskie	EG-32	river	Dunajec
Panek, these studies	2018	49°23′33.70″N	20°24′15.94″E	457.10	małopolskie	EG-33	river	Dunajec
Panek, these studies	2018	49°22′12.43″N	20°17′33.57″E	486.90	małopolskie	EG-42	brook	Niedziczanka
Panek, these studies	2018	49°32′29.94″N	20°24′15.83″E	367.13	małopolskie	EG-23	brook	Kamienica
Panek, these studies	2018	49°17′7.44″N	19°51′32.11″E	879.29	małopolskie	DG-59	brook	Lejowy Potok
Panek, these studies	2018	53° 6′22.76″N	16°47′14.79″E	54.00	wielkopolskie	BC-28	river	Gwda
Panek, these studies	2018	53° 3′42.83″N	16°44′15.96″E	48.08	wielkopolskie	BC-27	river	Gwda
Panek, these studies	2018	50°24′20.08″N	17°11′47.20″E	208.36	opolskie	CF-20	brook	Widna
Panek, these studies	2018	50°27′41.72″N	17°10′47.29″E	203.41	opolskie	CF-10	brook	Widna
Panek, these studies	2018	50°46′9.57″N	16°25′51.33″E	350.88	dolnośląskie	BE-84	brook	Młynówka
Panek, these studies	2018	50°41′8.22″N	16°22′11.08″E	293.08	dolnośląskie	BE-94	brook	Złotnica
Panek, these studies	2018	53°59′6.52″N	21°14′0.44″E	114.80	warmińsko-mazurskie	EB-27	brook	Dejna
Panek, these studies	2018	54°36′4.62″N	18°10′5.21″E	48.20	pomorskie	CA-57	river	Gościcina
Panek, these studies	2018	54°13′43.6″N	17°40′25.8″E	127.80	pomorskie	CB-05	river	Słupia
Panek, these studies	2018	54°23′37.1″N	17°41′56.9″E	128.00	pomorskie	CA-84	river	Bukowina
Panek, these studies	2018	54°18′23.8″N	18°18′31.1″E	138.80	pomorskie	CA-98	river	Reknica
Panek, these studies	2018	54°6′20.4″N	18°15′8.6″E	131.60	pomorskie	CB-18	river	Wietcisa
Panek, these studies	2018	54°13′19.9″N	17°39′30.0″E	126.61	pomorskie	BB-29	river	Stropna
Panek, these studies	2018	54°16′27.9″N	17°13′5.1″E	73.25	pomorskie	BB-29	river	Brodek
Panek, these studies	2018	53°25′46.9″N	19°43′30.1″E	106.00	warmińsko-mazurskie	DC-33	river	Wólka
Panek, these studies	2018	53°25′46.9″N	19°43′30.1″E	106.01	warmińsko-mazurskie	DC-33	river	Wólka
Panek, these studies	2018	49°36′11.5″N	19°6′27.2″E	411.66	śląskie	DG-83	river	Żabniczanka
Panek, these studies	2018	49°37′25.8″N	19°09′09.4″E	382.74	śląskie	DG-83	river	Cięcinka
Krajewski, not published	2019	49°43′30.0″N	18°49′51.6″E	682.50	śląskie	GD-01	brook	Gościeradowiec
Smoczyk, these studies	2019	50°27′54.5″N	16°38′36.0″E	285.10	dolnośląskie	BF-16	river	Ścinawka

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ecolind.2023.109918.

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