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Periodic events of *Potamogeton alpinus* in NW Poland (Pomerania region)

by

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Abstract

We have determined the timing of periodic events, such as leaf formation, flowering, fruiting and wintering of the aquatic plant *Potamogeton alpinus*. This study was performed in 15 watercourses situated in NW Poland in 2014–2015. Characteristics of the age stages were determined on the basis of 728 modules and phenological data were collected from permanent plots. In the study area, the plant appeared in week 12 of the calendar year, when water temperature in the streams was 5.4 ± 0.16°C. At that time, the first leafy juvenile shoots developed from winter buds. In week 22 (water temperature 13.9 ± 0.85°C), juvenile shoots became mature, whereas the first flowers were formed in week 24 (15.6 ± 1.04°C). The generative phase lasted twelve weeks with water temperature from 15.6 ± 1.04°C to 18.9 ± 3.23°C. Between weeks 37 and 44 (water temperature from 13.7 ± 0.77°C to 6.3 ± 1.05°C), senile shoots dominated in the population. From week 45 until week 11 of the next year (water temperature $< 5.4 \pm 0.16$°C), the plants were in the winter resting stage. In our view, climate warming might disturb the phenology of *P. alpinus*, decreasing the probability of sexual reproduction of the species and the phenological distance between the Central European Plain and the Scandinavian populations.

Key words: phenology, boreal aquatic plant, geographic range limit, phenological phases

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Introduction

Potamogeton alpinus (alpine pondweed, red pondweed) is a submerged aquatic plant with a boreal-mountain type of distribution in the Northern Hemisphere, which occurs in the northern parts of Europe (Meusel et al. 1965), North America and NW Asia (Hultén & Fries 1986), and even beyond the polar circle (Preston 1995; Bobrov & Chemeris 2009). The species occurs mostly in Scandinavia, whereas it is much less common in Central and Northwest Europe (Baattrup-Pedersen et al. 2008) (Fig. 1). The plant usually grows in watercourses which are small, not particularly fertile and exposed to full sunlight (Boedeltje et al. 2005) as well as in shallow, slightly acidic or alkaline rivers (Wiegleb & Todeskino 1983). In NE Poland, it usually grows on a thick layer of organic sediment in slowly flowing waters and in oligotrophic flow-through lakes (Zalewska-Gałosz 2008). In Central and Northwest Europe, the persistence of many of the *P. alpinus* sites is threatened by climate changes and human impact on water bodies (Sand-Jensen et al. 2000; Riis & Sand-Jensen 2001). According to Velichkevich and Zastawniak (2006), the presence of *P. alpinus* endocarps in wetland deposits is characteristic of the beginning or the end of interglacial periods. During paleoecological studies, the presence of *P. alpinus* was recorded in NE Poland (Gałka & Sznel 2013; Gałka 2014; Gałka et al. 2014), SE Poland (Kołaczek et al. 2014), the Czech Republic (Gálová et al. 2016) and Romania (Gałka et al. 2017) in sediments accumulated between 14 400 and 4500 cal yr BP, but usually during cooler climate stages. Alpine pondweed propagates mainly vegetatively (Wiegleb & Todeskino 1983; 1985), i.e. similarly to other perennial and clonal aquatic plants (Grace 1993; Szmeja & Gałka 2008; Szmeja 2010). Moreover, the species is also characterized by high phenotypic plasticity (Kaplan 2002; 2008; Kaplan & Zalewska-Gałosz 2004; Robionek et al. 2015), which together with its phenological reactions provides an opportunity to follow the adaptation of the species to changes in environmental conditions. It is worth emphasizing that changes and disruptions to habitat conditions have a major impact not just on the size of modular structures of plant individuals (Bociąg et al. 2013; Robionek et al. 2015), but also on the underwater community structure (Chmara et al. 2014; 2015).

Phenological studies could be used, for example, in research on the coexistence of species (Fargione & Tilman 2005), their invasion (Wolkovich & Cleland 2011), expansion (Szmeja et al. 2016) and reaction of populations and communities to climate change (Fitter & Fitter 2002; Menzel at al. 2006; Cleland et al. 2007; Święta-Musznicka et al. 2011), especially close to their geographic range limits (Chuine & Beaubien 2001; Schwartz 2003). The main focus of research has been on the timing of periodic events, such as leaf formation, flowering, fruiting or wintering, which in the case of aquatic plants is mainly dependent on temperature (Hutchinson 1975; Szmeja & Bazydło 2005; Gałka & Szmeja 2013; Szmeja 2010). Shifts in species phenology can occur due to a rise in temperature (Walther et al. 2002; Cleland 2007); therefore, phenological data could be useful for estimating the biological effects of the recent climate warming.

Although there are various conceptions regarding the cause of global warming, we suggest that in NW Poland it could be associated with an increase in the intensity and frequency of the positive phase of the North Atlantic Oscillation (NAO), during which warmer and moister air has been flowing from above the Atlantic to Northwest Europe, Scandinavia and the Baltic Sea region since 1989, especially in colder seasons (Hurrell 1995; 1996). One of the consequences of the recent climate warming in the studied area, i.e. near Gdańsk, is the expansion of *Salvinia natans* (Gałka & Szmeja 2013; Szmeja & Gałka 2013; Szmeja et al. 2016), which started in the late 1990s (Gałka & Szmeja 2012) with an intensity not observed since

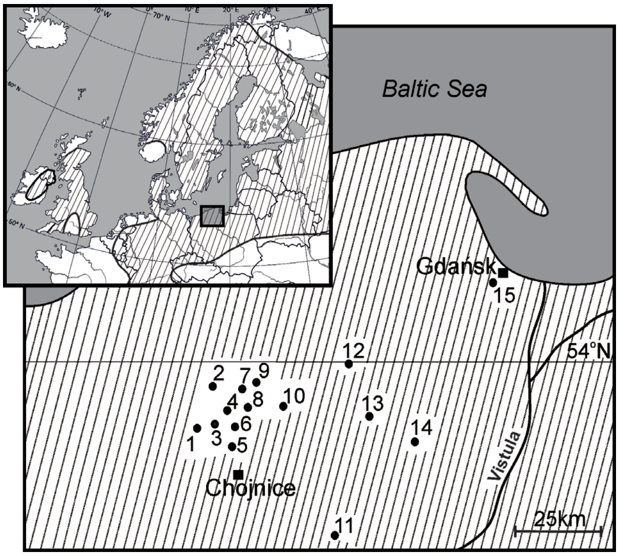

Figure 1

The geographic range of *Potamogeton alpinus* in North and Central Europe (left, hatched area), and the distribution of the study sites (right, 1–15 watercourses). Study sites (streams): 1 – Ruda; 2, 11 – Brda; 3 – Lipczynka; 4 – Chocina; 5 – Stawek; 6 – Czerwonka; 7 – Kulawa; 8, 10 – Zbrzyca; 9 – Kłonecznica; 12 – Graniczna; 13 – Wierzyca; 14 – Święta Struga; 15 – Oliwa the early Middle Ages (Święta-Musznicka et al. 2011). The rapid population growth, like in the case of *S. natans*, applies only to species at most sites located in Southern Europe (Casper & Krausch 1980; Rothmaler et al. 1986), i.e. in areas warmer than the Baltic Sea region. It should be noted, however, that reactions to climate warming of boreal aquatic plants such as *P. alpinus* at the southern limit of their geographic range in the studied region are still unknown. As a result, there is an urgent need to update the scientific basis for the legal protection of boreal aquatic plants and their habitats in European countries close to the Baltic coast.

Our objective was to examine the timing of periodic events in the population of *P. alpinus* close to the southern limit of the geographic range of the species on the Central European Plain. Such data would be the basis for assessing the impact of global warming on the phenology of alpine pondweed and could be used to protect boreal aquatic plant species and their habitats in this part of Europe as well as for comparative analyses of the Scandinavian population. The results presented in this paper have also a potential for palaeoecological reconstructions.

Materials and methods

This study was performed in 15 watercourses with *P. alpinus*, between 1 and 120 km south of the Baltic coast (54°26′–53°48′N, 17°01′–18°32′E) in NW Poland (Pomerania region; Fig. 1). This terrain was formed during the last glaciation event and is characterized by the presence of numerous lakes, rivers and watercourses; the latter are usually small, shallow and slow flowing. This area is close to the south-eastern limit of the geographic range of *P. alpinus* and is separated from its central part by the Baltic Sea.

Three 0.5 dm^3 samples of water and sediment per site were collected from aggregations of *P. alpinus* in 15 watercourses, on one occasion in the middle of the growing season (July or August, 2014–2015). The measured environmental variables of water are as follows: 1 – pH; 2 – conductivity (μS cm^{-1}); 3 – concentration of calcium (mg Ca^{2+} dm^{-3}); 4 – total nitrogen (mg TN dm^{-3}, for $\lambda = 340$ nm); 5 – total phosphorus (mg TP dm^{-3}), spectrophotometrically, for $\lambda = 880$ nm; 6 – water color (mg Pt dm^{-3}); 7 – water flow (m s^{-1}), measured with a Valeport M-801 Electromagnetic Flow Meter; 8 – PAR light intensity (photosynthetic active radiation, as %, measured with a LiCOR Li-250 light meter). The following parameters were measured in the sediment: 8 – organic matter content (%), 9 – mineral matter content (%), 10 – sediment water content (%), 11 – granulometry (fractions: f1 < 0.1, f2 0.1–0.25, f3 0.25–0.5, f4 0.5–1.0, f5 1.0–2.0, f6 > 2.0 mm), and 12 – concentration of calcium (mg Ca g^{-1} d.w. – dry weight). The measurements were performed according to the methods suggested by Eaton et al. (2005). The environmental conditions of watercourses with *P. alpinus* were described in more detail by Robionek et al. (2015).

Characteristics of the age stages (morphological development stages) were determined on the basis of 728 modules of *P. alpinus*, i.e. a repeating structural unit consisting of an aboveground shoot (leaves, stem, inflorescence) and the stretch of a rhizome to the nearest aboveground shoot. Plants were collected randomly by hand from 15 watercourses and transported to the laboratory for measurements. We measured the following traits: 1 – height of shoot (cm) and 2 – the number of leaves on the fresh material as well as on the dry material (drying at 80°C for 48 h); 3 – biomass (mg d.w.); 4 – allocation of biomass to shoot (%); 5 – allocation of biomass to rhizome with roots (%); 6 – allocation of biomass to leaves (%); and 7 – allocation of biomass to generative structures (inflorescence with peduncle, as %). The data were used to characterize the following age stages: juvenile (young, not fully developed), mature (fully developed), generative (flowering and/or fruiting), senile (dieback of the aboveground shoot and fragmentation of the rhizome) and winter buds.

Phenological data were collected from permanent plots (0.5 × 0.5 m) every 14 days during the whole growing season (from March to November) in 2014 and 2015. In winter, samples were collected every 30 days. On each sampling occasion, the temperature of water was measured and the number of modules as well as their age stages (juvenile, mature, generative, senile, winter bud) were counted (without plant removal). On the basis of the quantitative dominance of the age stages, the phenological phases were established in the development of the studied population.

Results

Characteristics of the watercourses

The watercourses with *P. alpinus* varied from slow to fast flowing (0.3 ± 0.2 m s^{-1}; 0.05–0.7 m s^{-1}). They were usually exposed to full sunlight (56.2 ± 15.6% PAR; 36.8–94.9% PAR) and were slightly colored (22.1 ± 12.3 Pt dm^{-3}; median 19 mg Pt dm^{-3}). The water in the streams was alkaline (pH 7.2–8.7; median 7.7), calcium rich (54.7 ± 10.3 mg Ca dm^{-3}; 41.7–77.0 mg Ca dm^{-3}), and characterized by high conductivity (250.5 ± 46.4

μS cm^{-1}; 185–340 μS cm^{-1}) and low concentrations of total nitrogen (1.5 ± 0.7 mg dm^{-3}; 0.4–2.9 mg dm^{-3}) and total phosphorus (0.3 ± 0.1 mg dm^{-3}; 0.1–0.5 mg dm^{-3}; Table 1). Sediment in patches of *P. alpinus* was fine-grained (with the dominant fraction of 0.25–0.50 mm), poorly hydrated (23.2 ± 6.5%; 11.4–38.4%), as well as poor in organic matter (1.8 ± 2.4%; 0.2–9.5%) and calcium (20.9 ± 35.4 mg Ca g^{-1} d.w.; 1.5–114.2 mg Ca g^{-1} d.w.).

Age stages

Alpine pondweed is a non-evergreen submerged perennial plant. We described five age stages during its development: juvenile, mature, generative, senile and the resting stage as a winter bud (Table 2, Figs 2 & 3).

In spring, the winter bud develops into the juvenile stage, which is 4.5 ± 2.0 cm high. The shoot consists of a thin stem with a few small leaves, together with a fragment of the rhizome. The fragment of the rhizome constitutes most of the biomass of an individual (53.2 ± 20.8%), the rest being the stem and leaves.

Adult *P. alpinus* (mature stage of development) consists of the underground rhizome and the aboveground unbranched shoot with several leaves. Most of the biomass of the shoot is allocated to leaves, much less to the stem and the rhizome. The arithmetic mean of the dry weight of this developmental stage is 43.1 ± 23.4 mg.

The generative stage of development, i.e. flowering and fruiting, consists of the underground rhizome and the aboveground shoot, which grows to a height of 54.9 ± 32.4 cm, consisting of the inflorescence spike and 14.2 ± 3.2 leaves, including 3.3 ± 1.7 leaves floating on the water surface. The arithmetic mean of the dry weight of this developmental stage is 70.3 ± 29.9 mg, including 54.7 ± 9.8% leaves, 28.9 ± 8.0% the stem, 4.9 ± 5.2% the inflorescence (with peduncle), and 9.3 ± 6.4% the rhizome with roots.

Dieback of the aboveground shoot, fragmentation of the rhizome and formation of the winter buds is characteristic of the senile stage. The dry weight of the shoot is 16.8 ± 14.9 mg, where leaves accounts for 17.5 ± 24.3%, the stem for 44.4 ± 20.8% and the rhizome for 38.5 ± 23.0%. The resting stage of the studied plant is the winter bud, and it plays the functional role of the turion. The latter stage, which develops on the rhizome, lasts throughout the winter and is small (1.3 ± 1.1 cm) and light (2.4 ± 3.5 mg d.w.).

Phenological phases

During the year, five phenological phases were identified in the populations of *P. alpinus* (Fig. 4): growth, maturation, reproduction, senescence and winter dormancy (resting stage).

The growth phase starts in week 12 (early spring), at a water temperature of 5.4 ± 0.16°C. It lasts approximately ten weeks and the mean water temperature during this period is 8.5 ± 2.41°C (5.2–11.8°C). At this time, juvenile shoots grow from winter buds, forming rhizomes and consequently modules, i.e. repeating structural units of clones (individuals). In the growth

Table 1

Water characteristics at the sites (1–15) of *P. alpinus*

Trait	pH	Cond.	Calcium	Total nitrogen	Total phosphorus	Water color	Flow	PAR
Site		(μS cm^{-1})	(mg Ca dm^{-3})	(mg N dm^{-3})	(mg P dm^{-3})	(mg Pt dm^{-3})	(m s^{-1})	(%)
1	7.7	272 ± 25	59.4 ± 1.2	2.6 ± 0.2	0.1 ± 0.0	20 ± 3	0.5 ± 0.01	42.4 ± 1.2
2	7.9	257 ± 8	57.8 ± 1.0	2.2 ± 0.2	0.4 ± 0.0	19 ± 1	0.2 ± 0.00	58.3 ± 4.6
3	7.2	197 ± 13	44.4 ± 0.3	0.7 ± 0.3	0.1 ± 0.0	28 ± 3	0.3 ± 0.02	43.4 ± 3.2
4	7.6	290 ± 23	58.6 ± 0.0	1.1 ± 0.2	0.3 ± 0.1	26 ± 8	0.4 ± 0.06	50.2 ± 3.4
5	7.3	206 ± 9	54.8 ± 3.5	0.4 ± 0.1	0.4 ± 0.1	18 ± 6	0.1 ± 0.01	73.5 ± 2.6
6	7.3	270 ± 23	67.3 ± 1.1	1.0 ± 0.1	0.1 ± 0.0	40 ± 6	0.2 ± 0.03	94.9 ± 3.3
7	7.8	220 ± 35	41.7 ± 1.2	1.5 ± 0.9	0.2 ± 0.2	7 ± 1	0.5 ± 0.09	44.8 ± 1.6
8	7.5	255 ± 28	45.2 ± 1.7	1.5 ± 0.8	0.5 ± 0.2	21 ± 1	0.2 ± 0.06	45.9 ± 5.1
9	7.8	185 ± 19	46.0 ± 0.2	1.5 ± 0.3	0.1 ± 0.0	20 ± 2	0.1 ± 0.01	70.7 ± 2.7
10	7.5	214 ± 19	42.2 ± 0.4	1.7 ± 0.2	0.2 ± 0.1	55 ± 4	0.7 ± 0.02	68.8 ± 6.0
11	8.0	220 ± 12	77.0 ± 0.3	1.6 ± 0.5	0.3 ± 0.1	15 ± 5	0.3 ± 0.02	49.9 ± 2.4
12	7.7	269 ± 21	61.3 ± 4.3	2.9 ± 2.2	0.4 ± 0.3	13 ± 3	0.3 ± 0.07	64.6 ± 1.4
13	7.7	340 ± 47	62.1 ± 0.3	0.9 ± 0.1	0.2 ± 0.1	29 ± 6	0.3 ± 0.05	54.0 ± 0.4
14	7.2	231 ± 16	45.5 ± 0.4	1.0 ± 0.1	0.2 ± 0.1	15 ± 3	0.1 ± 0.01	44.3 ± 0.8
15	8.7	332 ± 24	56.6 ± 0.8	1.7 ± 0.3	0.3 ± 0.1	25 ± 2	0.1 ± 0.01	36.8 ± 1.7

Explanations: Cond. – conductivity, PAR – light intensity, median for pH; mean ± standard deviation for remaining traits

Table 2

Characteristics of age stages (J–S, where: J – juvenile, M – mature, G – generative, S – senile) and the time of their residence in the population, on the basis of 728 plant samples

Trait/Age stage	J	M	G	S
No. of samples	79	482	125	42
Height of shoot (cm)	4.5 ± 2.0	32.1 ± 23.6	54.9 ± 32.4	15.0 ± 15.9
	(1.2–13.0)	(3.5–185.5)	(19.5–173.5)	(1.1–66.0)
Number of leaves	2.3 ± 2.4	11.5 ± 3.3	14.2 ± 3.2	2.3 ± 3.1
	(0–7)	(4–22)	(7–23)	(0–9)
Biomass (mg d.w.)	13.4 ± 12.3	43.1 ± 23.4	70.3 ± 29.9	16.8 ± 14.9
	(1.8–62.3)	(5.6–136.1)	(13.7–180.5)	(2.0–68.5)
Allocation of biomass to stem (%)	28.7 ± 21.5	22.3 ± 9.2	28.9 ± 8.0	44.4 ± 20.8
	(4.0–95.5)	(3.3–62.7)	(13.6–57.1)	(7.4–90.4)
Allocation of biomass to rhizome with roots (%)	53.8 ± 20.2	20.9 ± 14.4	9.3 ± 6.4	38.5 ± 23.0
	(4.5–96.0)	(2.1–82.1)	(1.2–47.0)	(7.9–92.6)
Allocation of biomass to leaves (%)	17.5 ± 19.9	56.9 ± 13.4	57.4 ± 9.8	17.5 ± 24.3
	(0–71.4)	(12.0–88.0)	(24.4–77.4)	(0–71.5)
Allocation of biomass to generative structures (%)	0	0	4.9 ± 5.2	0
			(0.1–38.0)	
Residence time (weeks)	28	18	12	16
Week in the year	12–40	22–40	24–36	30–44
Temperature of water (°C)	13.9 ± 5.23	16.3 ± 4.23	18.2 ± 3.46	13.1 ± 6.12
	(5.2–24.5)	(8.3–24.5)	(13.0–24.5)	(3.4–24.4)

Explanations: n – number of samples, ± – arithmetical mean with standard deviation, and min.–max value of the trait

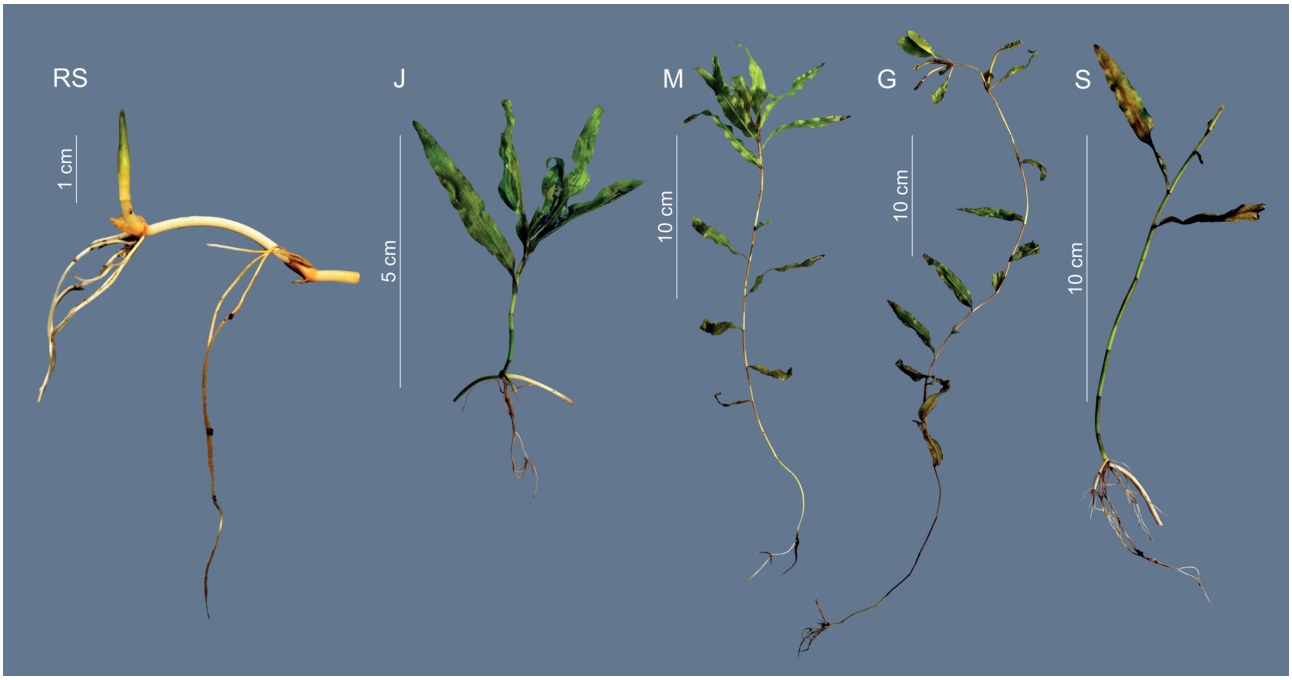

Figure 2

Age stages of *Potamogeton alpinus*, where RS – resting stage (winter bud), J – juvenile, M – mature, G – generative, S – senile

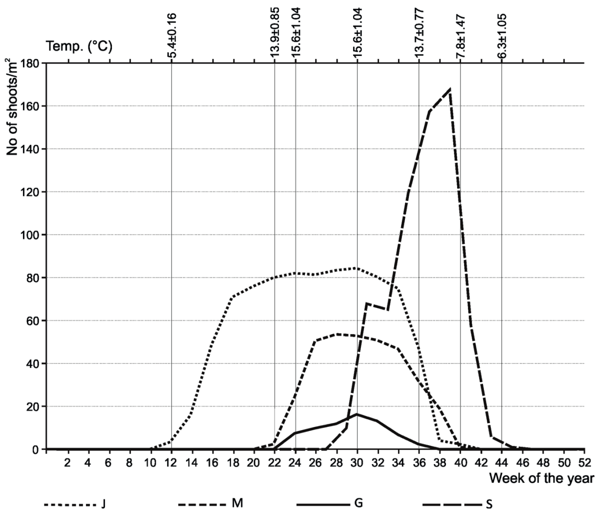

Figure 3

The number of age stages in the populations, where: J – juvenile, M – mature, G – generative, S – senile age stage

phase, juvenile shoots proliferate and dominate in the population.

The maturation phase begins in week 22 at a water temperature of 13.9 ± 0.85°C. It lasts only approximately two weeks, with a median water temperature of 13.7 ± 1.28°C. In this phase, new young modules are formed; their height and the number quickly increase and the rhizome becomes thicker. Consequently, the population density increases, whereas patches of *P. alpinus* are already fully developed and clearly visible in the water bodies. The proliferation of clones ends in week 40 at a water temperature of 7.8 ± 1.5°C.

Reproduction starts in week 24 at a water temperature of 15.6 ± 1.04°C, and it lasts approximately twelve weeks, with a median water temperature of 18.9 ± 3.23°C (14.0–24.5°C). At this time, the predominance of fully developed flowering and fruiting shoots with floating leaves is observed in the population, which stabilize the inflorescence stem and keep it over the water surface. During this phase, patches of *P. alpinus* have the largest surface and are usually very dense.

The first clear signs of senescence in the populations are observed in week 36 at a water temperature of 13.7 ± 0.77°C. At this time, there are juvenile and mature modules in the population, but no longer generative ones, because the inflorescences and infructescences detach from the shoot. In week 40, senile modules with yellowed leaves occur in the population, which eventually decompose (decomposition of leaves, fragmentation of the rhizome). The last aboveground senile shoots occur in the population up to week 44 (water temperature 6.3 ± 1.05°C), when the season comes to an end.

From week 44 to week 12 of the next year, the winter dormancy phase (diapause) occurs in the population. At that time, the plant overwinters as winter buds with fragments of the rhizome. The environmental trait that significantly separates the presented phenological phases is water temperature ($X^2 = 31.4$, $p = 0.01$).

Discussion

Areas located in temperate climates are characterized by seasonal phenomena in plant populations, which very often makes them the object of phenological studies. An example of such research might be the course of periodic events in the development of *P. alpinus*, as described by Brux et al. (1987, 1989) and Germ et al. (2002). Nevertheless, to the best of our knowledge, the complete phenological spectrum of this species in undisturbed conditions has never been determined. Recording the timing of periodic events in plant populations, especially close to the limit of their geographic range, becomes vitally important because of the increasing human impact and, most of all, the recent climate warming (Walther et al. 2002). Phenological analysis of aquatic populations has shown that the timing of life history events responds to changes in global environmental conditions (Gałka & Szmeja 2013).

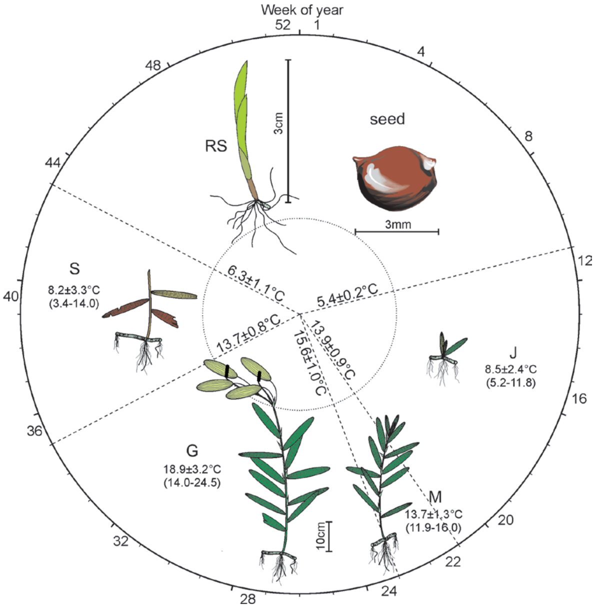

Figure 4

Development of *P. alpinus* population in one year in the study area, where: RS – resting stage (winter bud), J – juvenile, M – mature, G – generative, S – senescent

An increase in global air temperature does not raise serious concerns (Hurrell 1995; 1996; Stocker 2014). The globally averaged, combined land and ocean surface temperature data show a warming of 0.85°C during the 1880–2012 period (Stocker 2014). In N Poland, as in most of the Baltic basin, the warming has been particularly strong since 1980. In the period from 1980 to 2010, the annual air temperature at the weather stations located along the south Baltic coast rose by 0.104°C per decade (Marsz & Styszyńska 2010). The mean annual air temperature near Gdańsk rose from +7.0°C (during the period of 1851–1988) to +8.2°C (between 1989 and 2009). The increase in annual temperature during the present warming (after 1989) is largely due to a sharp temperature rise in winter and spring, mostly in March and April (Szmeja et al. 2016). Air temperature influences environmental conditions in water bodies, for example by regulating the length and timing of the period of ice, temperature of the surface layer of water (Wetzel 2001), and duration of the growing season of plants, as well as the rate of growth and development (Szmeja et al. 2016). There is a close relationship between air temperature and water temperature. The correlation coefficient between the average monthly temperature of the air near Gdańsk and that of the Baltic waters in the area is high and usually 0.85–0.90 (Marsz & Styszyńska 2010). The correlation between the temperatures of air and water in watercourses with *P. alpinus* is equally high.

Terrestrial plant species growing in similar regions have developed a similar phenology (Thuiller et al. 2004). Additionally, previous studies on aquatic plants, as presented by e.g. Santamaria et al. (2003), show that patterns in the phenology of plant species usually correlated with certain environmental variables, such as temperature, precipitation, latitude or altitude. The results of these studies show that most *P. pectinatus* genets can grow and reproduce asexually at distant latitudes. Subarctic and temperate genets have been found to grow and produce tubers at sites, for instance, in Norway, the Netherlands, and Spain. For all genets, regardless of the region and population of origin, the biomass yield and tuber production increased when grown at a decreasing latitude. This might suggest that in Europe, optimal conditions for the growth of *P. pectinatus* are found in the Mediterranean. For populations of *P. alpinus,* i.e. a species with a boreal geographic coverage, the trend of changes along the north-south gradient is probably the opposite. In N Poland, the species flowers and fruits, but probably does not reproduce sexually, because seedlings have never been found (personal observation). Similar observations of the reaction of this plant were recorded in other localities on the Central European Plain and Western Europe (Wiegleb & Todeskino 1985; Brux et al. 1987). There is nothing unusual in this reaction, because some species of remnant populations in the periphery of their geographic range, such as *Decodon verticillatus*, lose their capacity for sexual reproduction, and permanent inability of a population to reproduce sexually is defined as sexual extinction (Eckert et al. 1999; Eckert 2002; Honnay & Bossuyt 2005; Eckert et al. 2008). Also *Stratiotes aloides* is known to reproduce mainly in the vegetative way in Europe (Cook & Urmi-König 1983), which might be attributed to the climatic conditions; a relationship between its fructification and thermal conditions can be observed while analyzing fossil distribution (Gałka 2010). Clonal reproduction as well as a shift in the duration of the development of age stages offer a safe escape route for many species under suboptimal environmental conditions. In our view, climate warming might disturb the timing of *P. alpinus* development, reducing the probability of sexual reproduction of the species and the phenological distance between the Central European Plain and the Scandinavian populations.

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