

# Population structure of *Isoetes lacustris* with respect to life history and environment -results of field studies

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## Abstract

Life history phases of the quillwort *Isoetes lacustris* are described by means of the development of corm, roots, leaf rosette and sporangia. Lowest and mean number of leaves per rosette of fertile plants from a multitude of habitats proved to be correlated significantly and dependent on water transparency, pH or conductivity. The correlation allowed distinguishing between juvenile and adult individuals. The developmental stages sporeling, juvenile, adult fertile, adult infertile and senescent were defined and their abundances characterise the structure of the study populations. The distribution of the sporelings appeared at random, juvenile individuals varied distinctly among the populations and senescent plants were extremely rare. The share of adult fertile individuals was between 50 and 63 % in the Norwegian populations, but 20 % in the population of Lough Corrib, suffering from eutrophication, and 4% in a very dense population. The portion of adult infertile plants was established between 3 and 33 % and was highest in Lough Corrib.

**Key words:** *Isoetes lacustris* - life history - leaf number – pH – conductivity – Secchi depth - development stage - demography - population structure - monitoring

## 1 Introduction

*Isoetes*, comprising approximately 200 extant species, is an ancient cosmopolitan genus of primarily aquatic lycopsids and is phylogenetically isolated from all other living plants (Schuettpeitz and Hoot, 2006). Modern *Isoetes* typically produce only fertile leaves thereby minimizing the vegetative phase (Pigg, 2001). Within *Isoetes*, there is a remarkable morphological uniformity (Taylor and Hickey, 1992).

*Isoetes lacustris* is characterised by a short stem and the usually 2-lobed corm. Roots grow from grooves between the lobes, branching dichotomously. The leaves, microphylls, arising from the corm, are spirally arranged. Each leaf is a potential sporophyll, bearing either a microsporangium or a megasporangium, which is embedded in the base on the adaxial side of the leaf.

The quillwort *Isoetes lacustris* is a submerged evergreen perennial, inhabiting mainly nutrient-poor lakes. Quillworts have evolved various adaptations to these habitats (Keeley and Busch, 1984, Boston and Adams, 1987), and they do not tolerate competition.

The quillwort inhabits soft water lakes throughout Northern Europe; in Central Europe the populations have declined dramatically, mainly due to eutrophication and acidification (Rørslett and Brettum, 1989, Rintanen, 1996, Murphy, 2002). The decrease of individual fitness within populations, experiencing difficult growing conditions, has been demonstrated by Vöge (1997a, b, 2003, 2004).

In the late 1960s botanists began to recognise the necessity of plant demographic research, particularly on endangered species. The aim of demography is to obtain information on the structure of populations. Demographic research requires the knowledge of the life history and plasticity of the particular species. Phases concerning the life history of *Isoetes lacustris* have not yet been defined; plasticity was established in a multitude of habitats (Garcia and Ballesteros, 1993, Szmeja, 1994a, Vöge, 1997a, b). The knowledge of the demography of quillwort is rather limited.

Demographic studies, which are performed only once, result in demographic inventories, demonstrating the actual situation. They are appropriate for comparing populations from different lakes. Garcia and Ballesteros (1993) established plant density and the distribution of leaf length classes on quillwort populations from Lake Baciver in the Spanish Pyrenees. Research on population dynamics requires repeated studies. Szmeja (1994b) observed slow changes of *Isoetes lacustris* populations of the deep water habitats in Polish Lake Krasne during six study years, most individuals being adult, with many leaves. Ctvrtlikova (2008) studied the abundances of sporelings, juvenile and adult plants of the *Isoetes lacustris* population of Bohemian Forest Lake Cerné between 2004 and 2007. However, the criterion for separating juvenile and adult individuals seems unclear.

It was the aim of this study

1. to characterise phases of the life history of quillwort
2. to relate the individual performance to the environment
3. to define developmental stages
4. to describe the structure of quillwort populations

## **2. Methods**

### **2.1. Study area**

In the course of three decades, the vegetation was studied in more than 150 lakes throughout Europe, with special regard to quillwort (Vöge, 1988). For this study, lakes were selected in which the populations of *Isoetes* experience different climate and environmental conditions. Populations of quillwort were studied in six lakes, in five Norwegian sites and one Irish lake, Lough Corrib. The lakes Svavatnet and Revurdjtjørni are situated in Southern Norway, the lakes Abborvann and Rundvann in Northern Norway. Lake Stugusjön is in Central Norway.

### **2.2. Environmental assessment**

The environmental conditions of the study lakes were assessed by measuring water conductivity and pH (WTW). Water transparency was characterised by means of Secchi depth. These data proved expressive in earlier quillwort studies (Vöge, 1997a, b, 2004).

### **2.3. Realization of quillwort life phases**

Plants of distinctive age were sampled in Lake Stugusjön. Number and length of leaves and roots were established, and the development of sporangia was examined. The seasonal change of the mean number of leaves of fertile plants was determined for a population from Lake Rundvann, between spring and autumn; the water temperature was measured.

### **2.4. Demographic studies**

Demographic research on quillwort populations requires the use of diving equipment. For this study, in the centre of the quillwort populations from Lake Revurdjtjørni, Lough Corrib and Lake Abborvann samples of 800 cm<sup>2</sup> were taken at random, between 2,5 and 2,8m in the Norwegian lakes and at 1,6 m in Lough Corrib. These samples were chosen

as reasonable and necessary for the determination of reliable results from very large populations. For each population the leaves of each individual were counted and the existence of mega- and microsporangia was recorded. The lowest number of leaves of a fertile plant was noted and the mean number of leaves of the fertile individuals was calculated.

### **3. Results and discussion**

#### **3.1. Lake characteristics**

Lake position and water characteristics are given in Table 1. With the exception of Lake Revurdjtjørni, the Norwegian study lakes are electrolyte-poor, their conductivity ranges between 36 and 64  $\mu\text{S cm}^{-1}$ . In Lough Corrib (Ireland), under continued eutrophication (Krause and King, 1994), the electrolyte content was extremely high. Further to this, alkaline water and low transparency characterise the lake conditions. The lakes Svåvatnet and Revurdjtjørni, with high water transparency, are situated in a temperate climate, the lakes Rundvann and Abborvann, north of Polar Circle, experience a boreal climate with short summers. Water is less transparent than that of the sites in southern Norway. After a period of acidification (Vöge, 1989), the water of Lake Svåvatnet is slightly acid now.

#### **3.2. Phases of the life history**

As in other Lycophyta an alternation of generations between a small, sex-cell-producing phase (gametophyte) and a conspicuous, spore-producing phase (sporophyte) is observed. Several hundred thousands of microspores are produced in the microsporangium, more than hundred megaspores in the megasporangium. Both male and female gametophytes are microscopic and most of their development is endosporic. Megaspores store copious amounts of food. After fertilization the growing embryo uses this store.

*Isoetes* individuals from Lake Stugusjön were assigned to different life history phases. They are presented in Table 2. Tiny plants with up to 5 very thin leaves without any sporangia represent the first, the sporeling's phase. In the subsequent juvenile phase the plants possess up to 9 leaves, often with some immature megasporangia. During the third phase the number of leaves per individual increases distinctly; up to 22 leaves are formed.. All 6 leaf types that can be distinguished in quillwort are present: immature and mature mega- and microsporophylls, sporophylls that have released their spores, and sporophylls, on which sporangia were not (yet) developed. A last phase, the senescent phase, was identified: plants with few leaves, mainly with empty or without sporangia.

Most plants in populations of quillwort represent the adult phase; this is the annual succession of the loss of many sporophylls during autumn and winter and the production of new leaves during following spring and summer. According to Karfalt and Eggert (1977) an adult quillwort plant produces the same number of leaves each year. The seasonal changes of the mean leaf number of adult plants between spring and autumn were determined in Lake Rundvann (Table 3). Following the rise of temperature the leaf number increases from 10 to 21 leaves and decreases to 14 leaves with the drop in temperature. Consistently, Gacia and Ballesteros (1994) stressed, that the leaf production of quillworts in Lake Baciver was maximum in July, but not noticeable during winter. Another seasonal change was observed in the structure of the leaf rosette (Vöge, 2006). In late winter sporophylls, which have released their spores, make up the majority in the rosette. They are at their minimum in early summer. In contrast, mega- plus microsporophylls are at their minimum in late winter and make up about 80% in early summer.

### 3.3. Quillwort plasticity and environment

Phenotypic plasticity is the ability of a single genotype to express itself in adaptation to different environments. Variability of fertile quillwort individuals was possible to study within lake and between lakes. Plasticity is perceptible in corm width, lowest and means number of leaves, leaf width, megaspore number and diameter, and leaf length (Vöge, 1997a, 2003). The mean number of leaves per fertile plant proved to be a reliable character for describing the population performance, because the mean leaf number is correlated significantly with the corm diameter, the leaf width, the number of spores per megasporangium, and with the lowest leaf number. Electrolyte content, pH and light availability of the particular habitat proved helpful in explaining the mean number of leaves per plant in a population (Vöge, 1997a, b).

The mean and the lowest leaf number per fertile plant present most clearly the quillwort plasticity, depending on the environment. Both leaf numbers are correlated significantly, the correlation is given in Figure 1. The data (unpublished) were determined on plant samples from a multitude of lakes throughout Europe. 6 and 4 leaves, respectively, were the lowest leaf numbers counted, under rather difficult growing conditions. 46 and 31 leaves, respectively, were the highest data, obtained under optimal growing conditions. The lowest leaf number indicates the beginning of the adult, fertile phase. Starting with this leaf number, under optimal growing conditions all plants proved to be fertile. Populations of *Isoetes lacustris* with a mean number of leaves about 30, which is observed rarely, nowadays, the growing conditions appear optimal (a). Mean numbers about 10 can be counted more frequently, in distinctly deteriorated sites, where the species is close to extinction. The growing conditions are called strenuous (c). Populations with about 20 leaves on average are most frequent, indicating suboptimal conditions (b).

In Figure 2 the ranges of conductivity, pH and Secchi depth are shown in which populations of optimal (a), suboptimal (b) or limited (c) performance occurred. Optimal growth was observed in sites with about  $50 \mu\text{Scm}^{-1}$ , pH 6-7 or 4-10m Secchi depth, suboptimal growth in lakes showing up to  $110 \mu\text{Scm}^{-1}$ , up to pH 7,5 or 2-4m Secchi depth, and limited growth in water of up to  $240 \mu\text{Scm}^{-1}$ , up to pH 8,5 or down to 1m Secchi depth. A single lake parameter may decide about the growing conditions; e.g., though conductivity and pH may allow a suboptimal plant development, the individual performance may be rather limited due to low Secchi depth. The lake data measured may explain the mean numbers of leaves that were established for the study populations, with the use of Figure 2.

### 3.4. Explaining developmental stages

Sporelings possess about 5 thread-like leaves, of about 4cm, growing on a thin corm of 3-4mm width. The roots are longer and more numerous than the leaves. The characteristics of the sporelings seemed to be independent from the environmental conditions.

Juvenile plants may develop between 3 and 30 leaves, depending on the growing conditions of the particular habitat (Figure 2). Correspondingly, corm width, leaf length and width may vary distinctly between populations from different sites. However, not all infertile plants are juvenile. The more deteriorated a lake, the more adult plants were observed infertile. Figure 1 allows determining the leaf number per rosette that separates the juvenile phase from the adult, fertile phase in a particular lake, if the mean of leaves was counted.

Adult plants experiencing different growing conditions may differ conspicuously in their mean leaf number, which was counted between 6 and 46 (Figure 2). Usually, their micro- and megasporangia release mature micro- and megaspores during late summer and autumn.

Definitely senescent individuals appear to be rare. Restricted leaf renewal and reproduction are to be expected. Because corm width and leaf number are correlated, a

plant showing an extensive corm supporting only some few leaves is assumed to age. Another indication of senescence may be a leaf rosette, consisting mainly of leaves with empty or undeveloped sporangia.

### 3.5. Structure of the study populations

The demographic inventories of the quillwort populations studied are presented in Figures 3-5, giving the abundances in the leaf number classes. Furthermore, the abundance of the fertile plants is described for each class. Within-lake variation of populations is shown in Figure 3a-c, from Lake Svåvatnet. The populations (b) and (c) are similar in their leaf number distribution. Furthermore, their plant density and their smallest leaf numbers are alike. Population (a) is characterised by a lower density (Table 4) and the plants become fertile supporting more leaves. The leaf number distribution is rather uneven in the population from Lake Revurdjtjørni, one leaf number class embracing nearly 60% of the plants. The plants turn fertile, as soon as they support 20 leaves. Quillwort individuals from Lough Corrib and Abborvann (a) possess distinctly fewer leaves due to eutrophication or to boreal/subarctic climate, respectively (Figure 4). The plants are fertile with 9 or 8 leaves, respectively (Table 4).

Plant density of the above mentioned populations (between 533 and 783 plants per m<sup>2</sup>) seems to correspond to the common density of the colonized lake floor of Norwegian sites (Rørslett and Brettum 1989). The population from Abborvann (b) is of 10 fold density and the plants possess less than 12 leaves (Figure 5). The sporelings support up to 3 leaves, the juvenile plants up to 5 leaves. Fertility begins with 6 leaves, but there are plants as well, in which either micro- or megasporangia are developed. According to Harper (1977), distinct phenotypic plasticity enables plants to reduce their growth, instead of the plant number, in dense populations.

The structure of the study populations is presented in Table 5. Within-lake variation is demonstrated in Table 5a-c. The abundance of the sporelings appears incidental: Most of them are observed as groups of 10-20 individuals on the corm of a fertile plant, sometimes between the leaves. Occasionally, as within the population from Lough Corrib, sporelings were not examined. It is assumed that not all sporelings survive, and so the abundance of the juvenile plants is uncertain, depending on sporelings and the chance of further development between large, adult plants. The abundances of sporelings + juvenile plants range between 32 and 43 %. The percentages of the adult fertile individuals are rather similar and about 50%. The average abundance of adult infertile plants proved 10%.

Regarding the abundance of the developmental stages, the populations from Lake Revurdjtjørni and Lake Abborvann (a) show some similarity. More than half of the plants are fertile, but about 20% are adult infertile. In the population from Lough Corrib, only 20% of the individuals are fertile, but some 30% are adult infertile. Experiencing suboptimal / strenuous growing conditions, the development of sporangia is limited (Vöge, 1997a, b). It is assumed that fertile quillwort individuals may lose their reproductive performance with a suddenly increasing impact. In a sample of 43 adult plants from an Irish lake with brown water of low transparency due to peat cutting, all plants were infertile (Vöge 1997b).

The population from Lake Abborvann (b) shows a divergent structure, due to the particular plant density. 80% of the individuals are classified as sporelings or juveniles. On some of the juvenile plants mega- or microsporangia are developed; only 4% are fertile. Plant growth appears to suffer extremely from intraspecific competition.

Another interesting question is: to determine the life span of *Isoetes* individuals. Two different opinions exist. According to Szmeja (1994b) the life span is 8-10 years, resulting from studies on populations from Lake Krasne. However, the breakdown of the populations was observed some years later. Following Karfalt (pers. com.), the life span may be 100 years. It is supposed, that the life span depends on the growing conditions in the particular habitat.

Little is known on the length of the four life phases. The small number of leaves of the sporelings gives evidence for a development within one growing season. The sporelings develop into the juvenile phase in the following year until the leaf number reaches about 70 % of the average leaf rosette in the particular fertile population (Fig. 1). The increasing leaf number within one year agrees with Szymeja (1994b) when he claims that juvenile plants become adult fertile in their second year. The length of the adult phase is as uncertain as that of the life span. Hanlon (1982) investigated the scarcity of senescent individuals within a population: Plants may disappear within 1-2 years, because vegetative parts decompose very rapidly. Rørslett (1985) emphasizes that dead plants decay fast, leaving only an impression in the sediment layer. Thus, the adult phase characterizes the life span of *Isoetes*. The periods of sporeling and juvenile phases are assumed to be longer in extremely dense populations in which they are predominant.

Other than on *Isoetes lacustris* in cool/temperate climate no seasonality in leaf and spore production was noticed on aquatic quillworts inhabiting alpine lakes in tropical regions, for instance in Papua New Guinea (J. Croft, pers. com.) or in Venezuela (J. Hickey, pers. com.). These observations give reason to assume the continued growth year-round to be the natural life of aquatic quillworts in suited environment.

#### 4. Conclusions

Quillwort adapts the individual growth to the growing conditions in the particular lake. Further to this, in extremely dense populations the individuals impede each other in their development, due to intraspecific competition.

This study and earlier investigations of *Isoetes* populations have demonstrated the distinct effect of the deterioration of habitats. Increasingly the individuals possess fewer leaves, the megasporangia contain fewer spores, which are smaller than they normally are; so the source of food which the embryo uses, is reduced. Therefore, reproduction can be restricted.

Within populations the increasing abundance of adult, infertile plants and decreasing plant density were observed. *Isoetes* goes less deep, so interspecific competition is a further problem, because quillwort does not tolerate competition (Rørslett and Brettum, 1989). A shortening of the life span is assumed.

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Table 1: Lakes under study

Lake	Position		Conductivity ( $\mu\text{S cm}^{-1}$ )	pH	Secchi depth (m)
Stugusjøen	62° 23' 57" N	010° 25' 16" E	42	7.1	5.5
Rundvann	69° 40' 46" N	030° 04' 16" E	64	6.1	3.8
Svåvatnet	58° 23' 39" N	006° 05' 43" E	58	6.0	10
Revurdjtjørni	58° 29' 28" N	005° 48' 54" E	101	7.1	7
Lough Corrib	53° 30' 59" N	009° 24' 18" W	236	8,1	3
Abborvann	69° 40' 56" N	030° 02' 15" E	36	6.9	4.2

Table 2: Leaf number and rosette structure of quillwort individuals during different life phases; in Lake Stugusjøen

Leaf type	Sporeling	Juvenile	Adult	Senescent
Mature Megasporengia	0 0 0	0 0 0 0 0	3 1 3 3 1	0 0 0 0 0 0
Immature Megasporengia	0 0 0	3 4 6 4 2	0 2 2 3 6	0 0 0 1 0 0
Mature Microsporengia	0 0 0	0 0 0 1 0	2 3 2 2 4	0 0 0 2 0 0
Immature Microsporengia	0 0 0	0 0 0 1 0	2 0 2 1 2	0 0 0 0 0 0
Empty Sporengia	0 0 0	0 0 0 0 0	1 4 2 6 6	4 3 2 6 3 1
Undeveloped Sporengia	2 3 5	2 3 3 3 7	3 3 4 3 3	4 5 3 7 5 6
	2 – 5 leaves	5 – 9 leaves	11 – 22 leaves	5 – 16 leaves

Table 3: Seasonal changes in water temperature and mean number of leaves per plant between spring and autumn, in Lake Rundvann

Water temperature (°C)	Mean number of leaves / rosette
8.0	10.3 ± 1.6
14.9	13.7 ± 3.3
18.1	18.4 ± 2.4
12.7	21.0 ± 4.9
9.4	13.9 ± 2.2

Table 4: Populations under study: Plant density and leaf number per rosette of fertile plants

Population data	Lake						
	Svåvatnet			Revurdjtjørni	Lough Corrib	Abborvann	
	a	b	c			a	b
Number of plants per m <sup>2</sup>	617	688	700	533	449	783	7200
Smallest leaf number	20	13	15	20	9	8	6
Mean leaf number	30.7 ± 6.3	25 ± 6.0	27.1 ± 6.4	29.6 ± 9.7	14.5 ± 2.2	14.4 ± 4.3	7.6

Table 5: Population structure: Abundances of development stages

Development stage	Svåvatnet			Revurdjtjørni	Lough Corrib	Abborvann	
	a	b	c			a	b
% Sporeling	8.2	27.3	10.7	0	43.6	3.3	29.8
% Juvenile	35.1	12.7	21.4	18.8	3.6	10.0	50.2
% Adult, fertile	54.0	49.1	51.8	53.1	20	63.3	4.2
% Adult, infertile	2.7	10.9	16.1	28.1	32.8	23.4	15.8

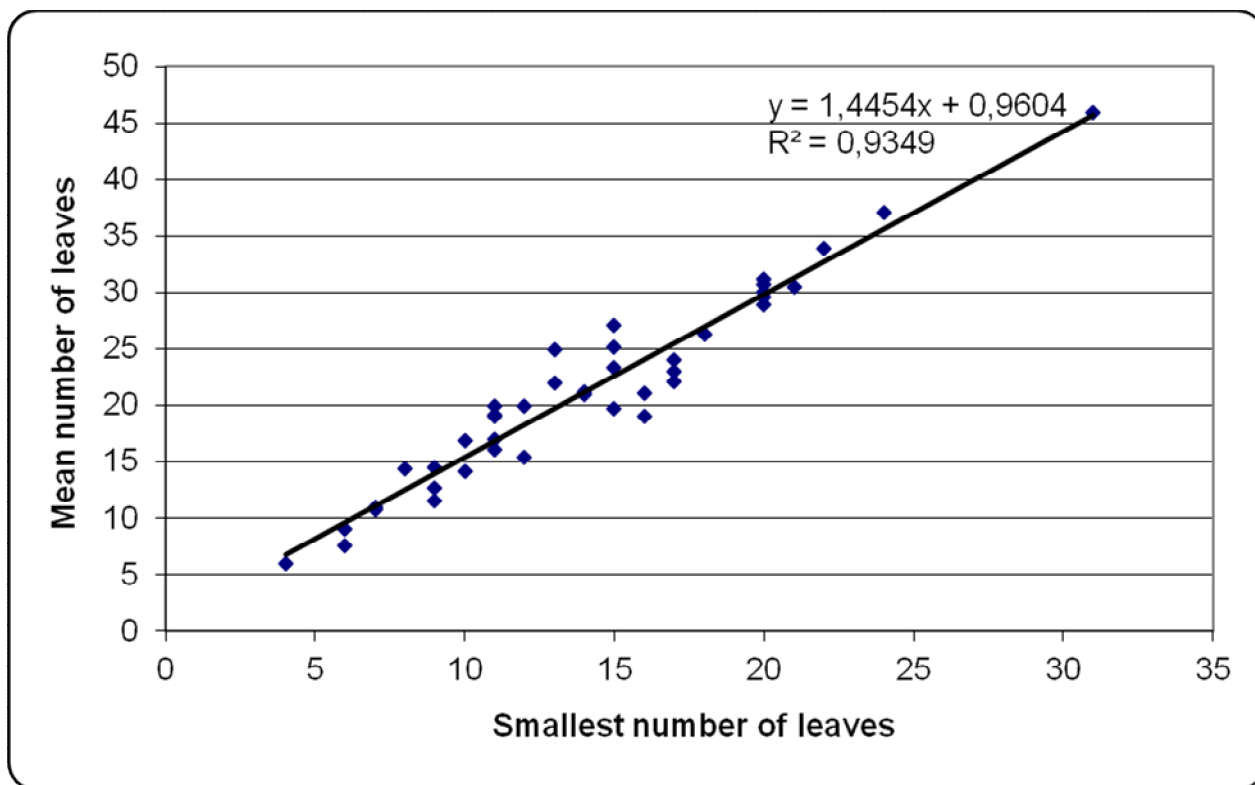


Figure 1: Relationship between the smallest and the mean number of leaves of fertile plants for quillwort populations from 38 lakes throughout Europe

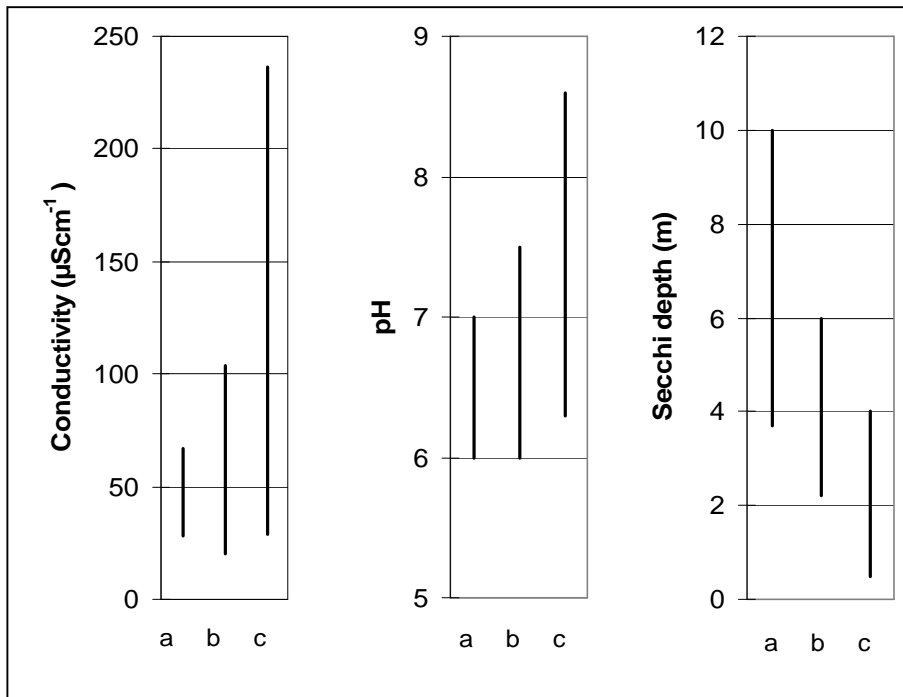


Figure 2: Quillwort populations with a particular mean number of leaves per fertile plant observed in different ranges of conductivity, pH and Secchi depth  
 a: about 30 leaves/rosette, b: about 20 leaves /rosette, c: about 10 leaves/rosette

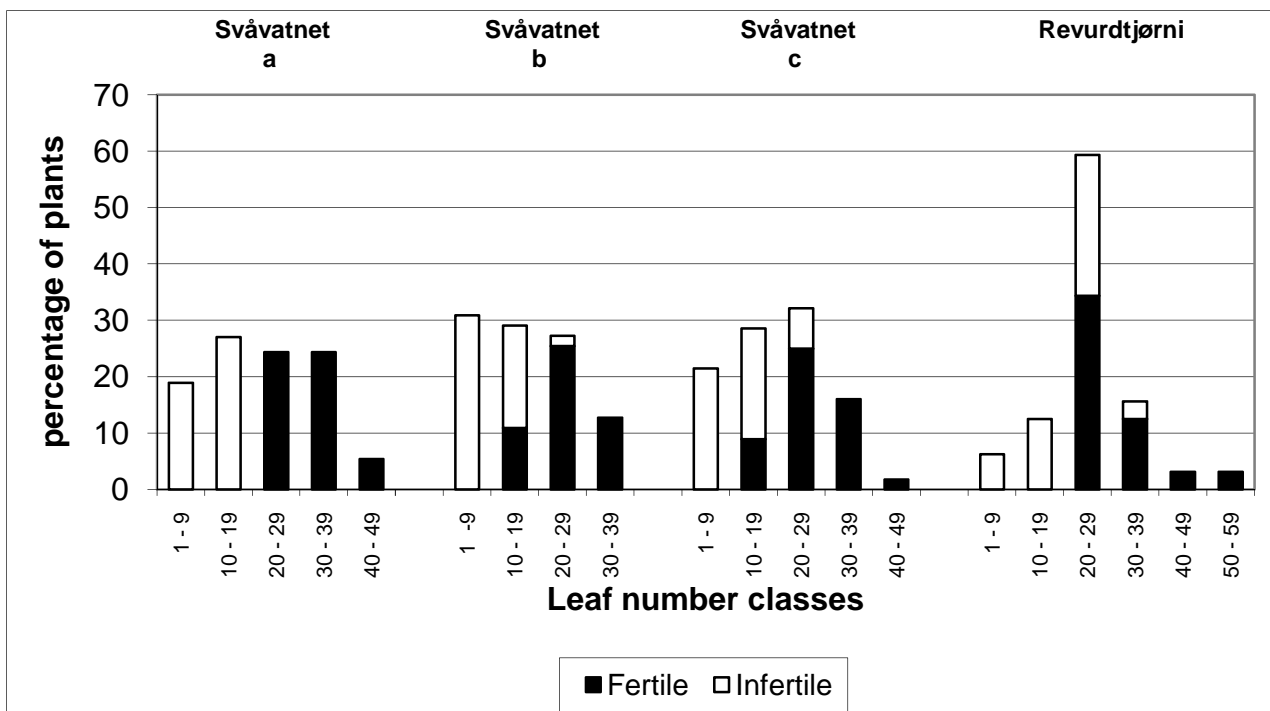


Figure 3: Abundances of leaf number classes for quillwort populations from 2 lakes of Southern Norway

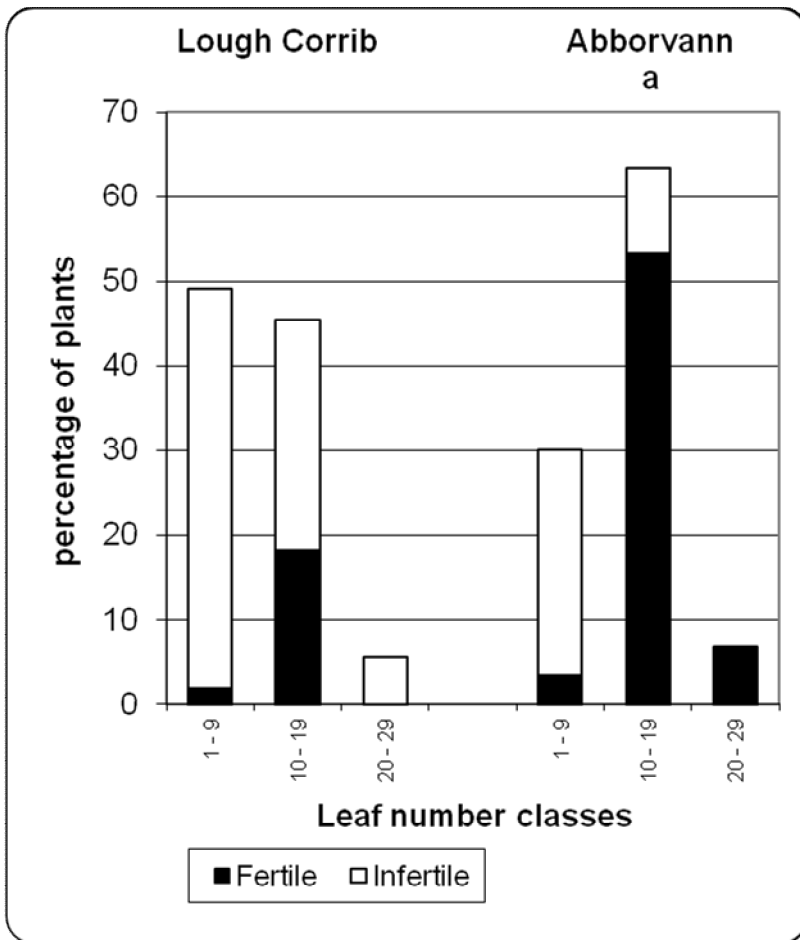


Figure 4: Abundances of leaf number classes for quillwort populations from Lough Corrib (Ireland) and Lake Abborvann (Northern Norway)

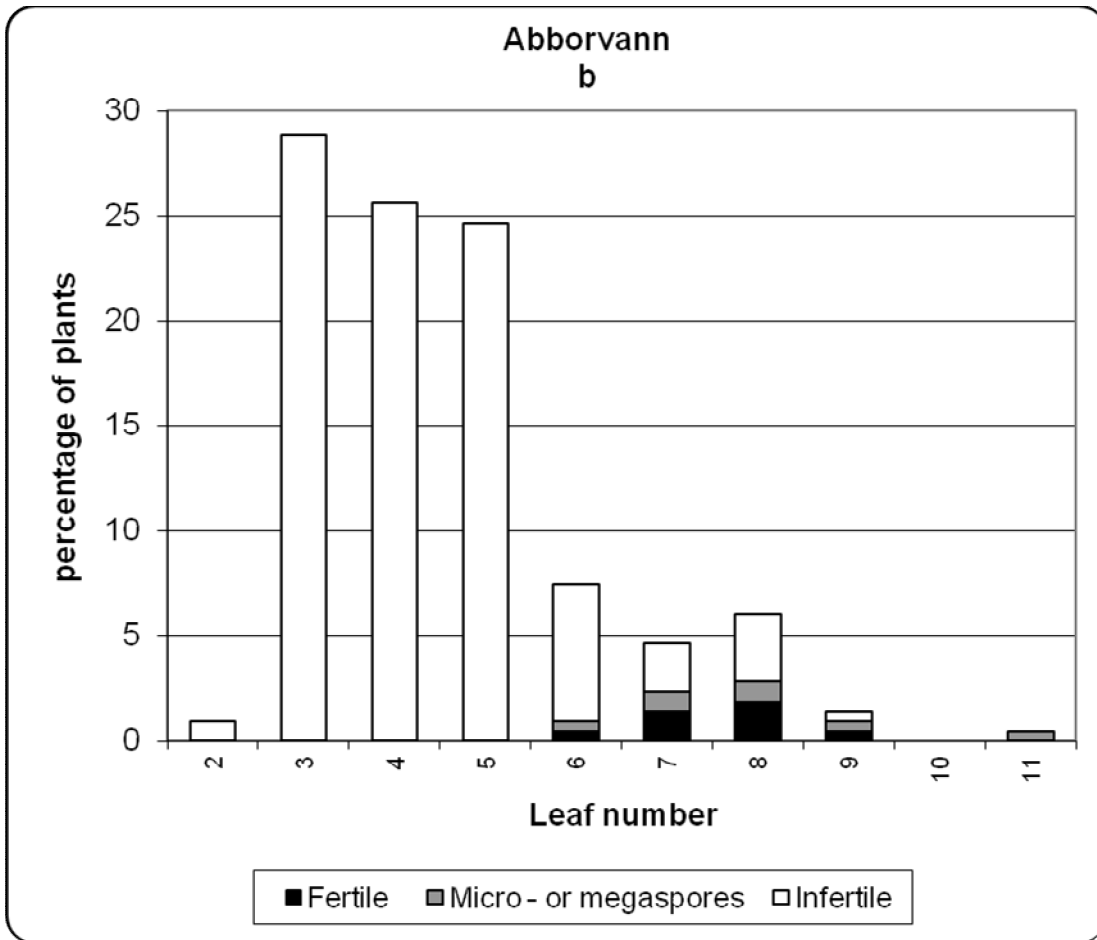


Figure 5: Abundances of leaf numbers for a dense population from Lake Abborvann