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Porella obtusata: distribution, ecology and threats at the west coast of Norway, the northern fringe of its European distribution

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Porella obtusata is a liverwort with a southwestern distribution in Europe. In Norway it is confined to areas with oceanic climate along the west coast, where it also reaches its northern limit. Typically it is growing on sunlit, base rich rocks at sea level in southwestern Norway, a scarce habitat in these coasts dominated by granitic bedrock. There are some old records, but investigations after year 2000 have yielded much new information. *Porella obtusata* is a rare species in Norway, and the new information shows that its habitat is threatened by exploitation and shrub encroachment of the shoreline.

The liverwort *Porella obtusata* (Tayl.) Trev. has status as a threatened species in Norway, and is evaluated as endangered (EN) in the Norwegian red list (Hassel et al. 2010). The size of the Norwegian population is estimated to be about 2000 individuals, and no subpopulations have more than 250 individuals, combined with an ongoing decline in number of individuals (Hassel et al. 2010). The reasons for decline are twofold; first there is encroachment of areas earlier used for livestock grazing and second, human exploitation of the species habitat by e.g. boathouses, harbors, roads etc. Thus, the rarity and decline of *P. obtusata* in Norway does not seem to result from natural fluctuations of populations at the edge of their distribution.

The traditional view was that *P. obtusata* had a wide Palearctic distribution, reported from two main areas, East Palearctic (China and Japan), and West Palearctic (Europe, North Africa and Asia Minor; Gökler 1998, Damsholt 2002). However, the Asian taxon *Porella obtusata* var. *macroloba* (Steph.) S.Hatt. et. M.X.Zhang has proven not to be conspecific with the European *P. obtusata* (Hentschel et al. 2007), and is better treated as *Porella macroloba* (Steph.) S.Hatt. et. Inoue. In the West Palearctic *P. obtusata* s.s. is recorded from most of the states bordering the Mediterranean Sea (Ros et al. 2007). In addition the distribution includes Macaronesia and the Atlantic coast of the Iberian Peninsula, France, Great Britain and Ireland, and with the northern limit at the southwestern coast of Norway (Paton 1999, Damsholt 2002).

The wide Mediterranean distribution of *P. obtusata* may indicate survival during the last glacial maximum in several refugial areas like Asia Minor, Italy, Spain, and one or more of the Macaronesian Islands (Taberlet et al. 1998, Ansell et al. 2011, Hutsemékers et al. 2011). Based on current distribution the source populations for northward dispersal after the last glaciation were most likely situated on the southwestern European mainland or Macaronesia (Kyrkjeeide et al. 2014). Whether the northward dispersal resulted from spores or vegetative fragmentation is not known, but today spore production in the Atlantic region seems to be restricted to Macaronesia (Paton 1999, Damsholt 2002, Fontinha et al. 2010).

The first record of *P. obtusata* in Norway was made in 1889. Early knowledge on the species was compiled by Jørgensen (1934), as *P. thuja*. In total only five localities were mentioned; Sogn og Fjordane, Askvoll, Alden (1889); Sogn og Fjordane, Flora, Kinn (1898, very sparse, no specimens known – needs confirmation); Rogaland, Kvitsøy, Ystabø (1912); Hordaland, Austevoll, the islands of Møkster and Litlakalsøy (1919). Few records have been added after Jørgensen (1934) until the year 2000, but

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thereafter the species has been searched for more systematically, especially in the period 2008–2015.

In its typical form, *P. obtusata* is easily separated from other Scandinavian *Porella* species by its underleaves twice as wide as the stem, broadly rounded leaf lobes with lobules about as wide as the underleaves, and the lack of acrid taste (Paton 1999, Damsholt 2002, Atherton et al. 2010). It is the only Scandinavian species of the genus that mainly is found on sea cliffs. In the field the flat glossy patches, yellowish green with a secondary brownish pigmentation are characteristic (Fig. 1). *Porella platyphylla* (L.) Pfeiff. and *P. cordaeana* (Huebener) Moore are not glossy, but dull green, normally without brown pigmentation. *Porella arboris-vitae* (With.) Grolle is glossy, but has the characteristic strong acrid taste; a modification of *P. arboris-vitae* (syn. *P. laevigata* var. *thuja* Nees) with strong acrid taste, was recorded (Arnell 1956) with a range from Vest Agder to Sogn og Fjordane, similar in range to *P. obtusata*. These plants were described as having an acrid taste and can therefore not belong to *P. obtusata,* although they mimic that species.

The aim of the current study is to compile information on the distribution and ecology of *P. obtusata* at the northern limit of its distribution in Europe. We also evaluate the status of the populations and current threats to populations of *P. obtusata* in Norway.

Material and methods

Collections of *Porella obtusata* in Norwegian herbaria were examined by the first author. Both old and new collections and field notes are available at "Artskart" (Artsdatabanken and GBIF 2015). During recent years, the species has been systematically searched for in areas where it could be expected to grow. This field work has been conducted in important areas for nature management and partly on contract for the management authorities. In particular we have searched for *P. obtusata* in areas with calcareous or other base-rich bedrocks close to the sea in the oceanic southwestern districts of the counties Rogaland and Hordaland. Geographic coordinates of all registered populations were taken with handheld GPS with an accuracy of ± 10 m. Notes on habitat, substrate and altitude were made at each locality. Associated species were registered at some localities. Collections from new localities are deposited in public herbaria, mainly TRH.

Figure 1. *Porella obtusata* growing in yellowish green glossy patches with a characteristic secondary brownish pigmentation. (Photo: J. B. Jordal).

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Nomenclature of bryophytes, lichens and vascular plants follows Artsnavnebasen (Artsdatabanken 2015).

Results

Distribution

Porella obtusata is reported from five new municipalities: Rennesøy in Rogaland, Bømlo and Stord in Hordaland and Selje and Bremanger in Sogn og Fjordane (Fig. 2a). We have also found many new localities close to earlier known localities, and got hold of much more information about the occurrence of *P. obtusata* at the old localities reported by Jørgensen (1934), especially in the southern part of the distribution area. Based on current knowledge Kvitsøy (Rogaland) and Bømlo (Hordaland) have most localities, the largest populations, and are the core areas for *P. obtusata* in Norway (Table 1).

Rogaland district

Porella obtusata has for a long time been known from Kvitsøy County, and here it is now recorded from many localities. In the Kvitsøy archipelago *P. obtusata* occurs both on the main island and many of the smaller islands (Fig. 2c; Jordal and Johnsen 2009). All old records labelled "Rennesøy" belong to Kvitsøy (Ystabø). The species is widespread and rather common in the Kvitsøy archipelago, which is in contrast to all neighboring areas that also seem to have suitable habitats. Rennesøy and Finnøy are two islands with rather large areas of suitable habitat, but intensive field investigations have resulted in only two records of *P. obtusata.*

Hordaland district

Field investigations at potential localities of *Porella obtusata* in Bømlo, Stord and Austevoll, shows that it

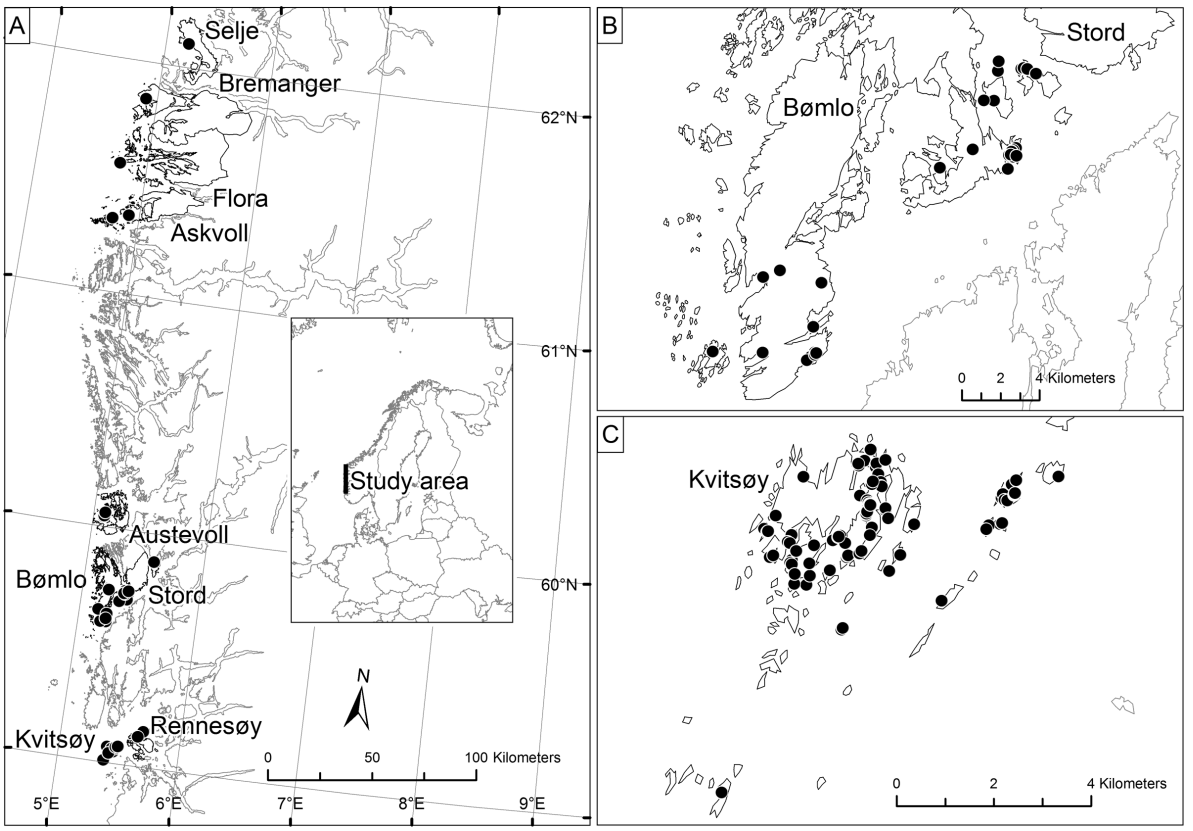

Figure 2. Distribution of *Porella obtusata* in (A) Norway, (B) Bømlo County and (C) Kvitsøy County (based on data from Artsdatabanken and GBIF 2015, Jordal and Johnsen 2009).

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Table 1. Known localities (>500 m apart) of *P. obtusata* with information on population size. Shrub encroachment, is a general threat that applies to most localities of *P. obtusata* and therefore not specified under threats.

Locality	County	District	Altitude m a.s.l.	No. of records	Year	Population size	Threats
Litla Kalsøy, near the harbour	Austevoll	Hordaland	1–19	7	1919–2008	medium	habitat loss
Litla Kalsøy, northeastern part	Austevoll	Hordaland	2-3	3	2008	small	unknown
Møkster south	Austevoll	Hordaland	1–5	9	1919–2008	small	habitat loss
Mosterhamn	Bømlo	Hordaland	1–10	49	1967–2014	large and important	habitat loss
Mosterhamn, Hestavikjo	Bømlo	Hordaland	-	1	1967	unknown	destroyed
Bømlahamn	Bømlo	Hordaland	1–5	14	2008–2014	medium	habitat loss
Eidesvika	Bømlo	Hordaland	2–5	2	2013–2014	small	habitat loss
Holmen	Bømlo	Hordaland	5	1	2011	small	unknown
Litle Trettholmen	Bømlo	Hordaland	5	1	2009	small	unknown
Store Nappaholmen	Bømlo	Hordaland	2–5	1	2014	medium to large	unknown
Spyssøya, Vedneset	Bømlo	Hordaland	1–5	5	2008–2014	small	habitat loss
Spyssøya, west of Klubbaskeia	Bømlo	Hordaland	2-4	5	2008–2014	small	unknown
Steinsvåg	Bømlo	Hordaland	4	1	2011	small	unknown
Vestre Vika	Bømlo	Hordaland	1–10	6	2008–2014	small	habitat loss
Vorland: Rundøya	Bømlo	Hordaland	3-5	1	2013	small	unknown
Espevær	Bømlo	Hordaland	2-5	1	2015	small	unknown
Nautøya with islands near by	Stord	Hordaland	2-5	7	1995–2015	medium	unknown
Storsøy	Stord	Hordaland	-	1	1972	unknown	unknown
Kvitsøy mainland with nearby islands	Kvitsøy	Rogaland	1–8	79	1912–2013	large and very important	habitat loss
Bussholmen	Kvitsøy	Rogaland	3	1	2008	small	unknown
Hestholmen	Kvitsøy	Rogaland	-	3	2011	small	unknown
Higgelen	Kvitsøy	Rogaland	5	1	2011	small	unknown
Håland	Kvitsøy	Rogaland	2	1	2009	small	unknown
Krågøy	Kvitsøy	Rogaland	3	1	2011	small	unknown
Sandholmen and Lyngholmen	Kvitsøy	Rogaland	1–3	4	2008–2011	small	unknown
Sandholmen, western	Kvitsøy	Rogaland	-	2	2011	small	unknown
Sandøya	Kvitsøy	Rogaland	1–3	10	2008	medium	unknown
Ternøy	Kvitsøy	Rogaland	6	1	2008	small	unknown
Ertensøy, eastern part	Rennesøy	Rogaland	1–10	3	1987–2015	small	unknown
Sørbø church	Rennesøy	Rogaland	20	1	1985	small	destroyed
Alden	Askvoll	Sogn og Fjordane	0–300	9	1889	unknown	unknown
Atløyna: Brurastakken south	Askvoll	Sogn og Fjordane	-	1	2003	small	unknown
Ytre Grotle, Storholmen	Bremanger	Sogn og Fjordane	4	2	2014	small	unknown
Kinn, sydsiden nær stranden	Flora	Sogn og Fjordane	<10	1	1898	small (old info. 1898)	unknown
Geitnesvika, between Drage and Indre Fure	Selje	Sogn og Fjordane	5	2	1967–2014	small	unknown

is restricted to areas with base-rich bedrock, although other substrates have been investigated (Jordal and Gaarder 2009, Jordal 2010, Fadnes 2013, Flynn and Gaarder 2013). Most records are from Bømlo (Table 1, Fig. 2b) and this area seems together with Kvitsøy in Rogaland district to be the main area for *P. obtusata* in Norway.

Sogn og Fjordane district

In this region we have not searched systematically for *P. obtusata*. Altogether five localities are known. There are two old localities, Alden Island in Askvoll County and Kinn Island in Flora County, which have not been revisited. The three more recent localities are from Selje County between Drage and Indre Fure on the Stadtlandet peninsula, discovered in 1967 and refound in 2014, from Atløyna island, Brurastakken sør in Askvoll County, discovered in 2003, and from Ytre Grotle in Bremanger County, discovered in 2014 (Table 1). The localities in Selje are the northernmost known for *P. obtusata* in Europe.

Habitat and substrate

Porella obtusata is usually found growing in thick patches or small carpets on sunlit calcareous rocks or other base-rich rocks close to the sea (Fig. 3). The substrates of *P. obtusata* along the Norwegian coast are different base-rich bedrocks like greenstone, marble and limestone. In Bømlo the species seems to have preference for greenstone and is not very frequent in the areas with limestone and marble. The Kvitsøy area is also rich in greenstone. The tendency of the rock to create fissures and small cavities may be of higher significance to the species than the kind of rock itself. Exposure varies between east/southeast and northwest, but most localities are southerly to westerly exposed. All new sites are below 20 m a.s.l., and most records are below 6–7 m a.s.l. At Alden island in Askvoll, Jørgensen (1934) cites B. Kaalaas 1889 on *P. obtusata* growing "up to 300 m". This is very different from all other known Norwegian localities and should be confirmed. In Kvitsøy and Bømlo *P. obtusata* often grows in small fissures with trickling water, or protected against the wind and sun in small cavities made by erosion of the rocks. Sometimes it is found

Figure 3. *Porella obtusata* is typically growing in small patches on sunlit base rich rocks close to the sea, like here at Bømlo, Hordaland. (Photo: K. Hassel).

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slightly sheltered by small bushes like *Juniperus communis* or graminoids. This shelter seems to be important during dry windy periods like the winter 2013/14 where many of the exposed patches got dried out and color changed to brown, whereas the patches below *J. communis* looked green and healthy.

Associated species

Among mosses and liverworts many associated species have been noted. In Kvitsøy associated bryophytes noted were e.g. *Pterogonium gracile, Bryum alpinum, B. capillare, Trichostomum brachydontium, Hypnum jutlandicum, Frullania tamarisci* and *Homalothecium sericeum*. Other less frequent species were e.g. *Hedwigia stellata, Polytrichum piliferum, Hypnum lacunosum, Scapania compacta, Riccia sorocarpa, Frullania fragilifolia, Mnium hornum, Dicranum scoparium, Tortula subulata, Gymnostomum aeruginosum, Grimmia pulvinata* and *Schistidium maritimum*. In Bømlo *Ptycomitrium polyphyllum, Tortella bambergeri* and *T. tortuosa* were also noted.

Also some lichens were observed to co-occur with *P. obtusata,* one of the most remarkable was the rare *Leptogium britannicum* at some of the localities in Kvitsøy, Bømlo and Austevoll. The ecological demands of this species seem very much to resemble those of *P. obtusata*. Other lichens recorded together with *P. obtusata* were e.g. *Parmotrema crinitum* and different *Collema* spp. and *Scytininum* spp. and further *Parmelia saxatilis, Dermatocarpon* spp., *Enchylium tenax, Nephroma laevigatum, Peltigera collina,* and *Cladonia* spp. (e.g. *C. portentosa, C. furcata, C. strepsilis* and *C. subcervicornis*).

Commonly associated vascular plants in Bømlo and Kvitsøy were e.g. *Asplenium adianthumnigrum, A. ruta-muraria, Sagina subulata, Geranium columbinum, G. sanguineum, Viola tricolor, Hylotelephium maximum, Rhodiola rosea, Aira praecox, Sedum anglicum, S. acre, Armeria maritima, Plantago maritima* and *P. lanceolata*.

Threats

Two of the 34 localities were destroyed due to fertilization by use of wet manure, and building of houses. At

Figure 4. At least eight localities of *P. obtusata* are threatened by habitat loss due to construction work, like here at Litla Kalsøy in Austevoll, Hordaland. (Photo J. B. Jordal).

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Figure 5. Shrub encroachment, due to reduced grazing by livestock, is a general threat that applies to most localities of *P. obtusata,* like here at Bømlo, Hordaland. (Photo J. B. Jordal).

least eight localities are threatened by habitat loss due to construction work (Fig. 4, Table 1).

Shrub encroachment, due to reduced grazing by livestock, is a general threat that applies to all localities (Fig. 5). This also applies to the few localities in protected areas. In Kvitsøy, Rogaland, one locality lies within Higgelen nature reserve (created to protect seabirds), and five of the localities (Ternøya, Sandøya, Sandholmen, Lyngholmen, Bussholmen) lie in the Higgelen-Eime bird protection area, which offers only weak protection, mainly prohibition of hunting.

Discussion

Distribution and ecology

The Norwegian distribution of *Porella obtusata* is confined to the southwestern coast, an area which is characterized by an oceanic climate with mild winters and cool summers (Størmer 1969). We show that the main areas for *P. obtusata* in Norway, with most localities and the largest populations, are found in the southern part of the distribution area. Most populations are found close to sea level, which seems to be an effect of latitude as it is recorded from higher altitudes further south, e.g. from sea level to 650 m a.s.l. in the British Isles (Blockeel et al. 2014), 370–980 m a.s.l. and 900–1850 m a.s.l. in Portugal and Madeira (Fontinha et al. 2010, Hespanhol et al. 2010). *Porella obtusata* belongs to an oceanic southern-temperate element sensu Hill and Preston (1998). They include in this element 18 species from the British Isles, six of which are also known from the Norwegian southwestern coast, i.e. *Glyphomitrium daviesii, Ptycomitrium polyphyllum, Ulota calvescens, Lophocolea fragrans, Porella obtusata* and *Saccogyna viticulosa*. The only species that may grow together with *P. obtusata* is *Ptycomitrium polyphyllum*, which is also the only other species with relatively large local populations. Large local populations of *P. polyphyllum* can be explained by efficient dispersal, as *P. polyphyllum* is commonly found with sporophytes. This is also reflected in a

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more even distribution along the Norwegian southwestern coast. All the other species of this oceanic southern-temperate element occupy other habitats and have small and scattered distributions.

The restriction of *P. obtusata* to low altitudes is an important factor contributing to its evaluation as a threatened species in Norway. Low altitude areas are under high pressure by human exploitation. Impacts of land-use changes on habitats during the last 50 years are by far the most important reason for putting species at risk of dying out in Norway, especially physical disturbances (i.e. house building, roads and other infrastructure) and land-use changes associated with farming and forestry (Kålås et al. 2010).

In earlier times human exploitation probably had a positive influence on the populations of *P. obtusata.* The agricultural practice of the first half of the 20th century with high densities of livestock and a high grassing pressure kept the vegetation open and favorable for a weak competitor like *P. obtusata* (Austrheim et al. 2011). Thus both change in agricultural practice and increased exploitation of lowland areas leads to loss of *P. obtusata* habitat.

The habitat preference of *P. obtusata* is rather narrow and limited to base-rich bedrocks. The available areas for population establishment is highly restricted along the acidic bedrock dominating the southwestern coast of Norway (Norges Gologiske Undersøkelser 2015). Sexual reproduction by spores is not known in the North Atlantic part of the distribution area, and only sterile and female plants are observed (Jørgensen 1934, Paton 1999, Damsholt 2002). Spore production in the Atlantic region is only reported from Madeira, where it seems to be common (Fontinha et al. 2010). Thus dispersal and establishment in possible habitats along the Norwegian coast, probably rely mainly on vegetative diaspores. The current distribution of *P. obtusata* in Norway could be hypothesized to have originated from a few long-distance dispersal events by wind leading to establishment of isolated populations along the Norwegian west coast. From these populations local dispersal could take place. The success of local dispersal would depend on distance to available habitats and potential dispersal vectors. The reason for finding the large populations at Bømlo and Kvitsøy is probably due to old human settlements in the region (Alsaker 1987), and large sheep populations that has been moved from the main islands and out to smaller island during the season to utilize available resources. Sheep are known to be effective vectors for local dispersal of bryophyte fragments (Pauliuk et al. 2011), and with the help of human boat transport between islands, the dispersal could be very effective.

In a historic perspective it is likely that *P. obtusata* has had more numerous and larger populations in its main distribution area (Kvitsøy and Bømlo) up to the mid-20th century. Up to this time the landscape was kept open due to high utilization by sheep grazing. Later the grazing pressure of unimproved land has decreased by as much as 50% in western Norway (Austrheim et al. 2011). During the second half of the 20th century managed grazing with the use of fertilizers to increase grass production are of growing importance (Asner et al. 2004, Austrheim et al. 2011). This lead to shrub encroachment in abandoned areas with subsequent increased competition from vascular plants. Formerly grazed *Calluna vulgaris* heath areas and grazed pastures in upper parts of the sea shore are transformed by tall herbs, bushes and trees, like *Juniperus communis*, *Rosa* spp., *Betula pubescens*, *Sorbus aucuparia, Salix* spp. and others. This reduces the light conditions and the possible habitat where *P. obtusata* can survive. In the more intensively used grassland areas a more dense grass vegetation develop leading to increased competition from vascular plants due to fertilization.

In addition increased pressure on lowland areas due to a larger human population and demands of roads, marinas, buildings etc. lead to direct loss of available habitats. In Kvitsøy filling with rock masses from underwater tunnel construction also may become a threat, if the plans become realized. Stone and gravel may be used for different purposes like building roads, e.g. to connect different islands. The coastal areas are popular in many ways and there is an increasing human population and pressure to exploit it.

Climate change can offer increasing problems. In the winters 2012–2014 most of the distribution area had periods with very dry conditions without a protecting snow cover. After this, it was observed that a large part of the populations in Bømlo were strongly reduced due to drought.

Red list status

The species is listed as endangered (EN) in Norway (Hassel et al. 2010), and this is not changed in the proposal for the 2015 Norwegian red list, based on the above mentioned knowledge on the current population and the actual threats. The species is not known in Sweden, Finland, Denmark or Germany. In other European countries *P. obtusata* is listed as vulnerable (VU) in Serbia, near threatened (NT) in Canary Island and Italy, and data deficient (DD) in San Marino and Bulgaria (Hodgetts 2014).

State of knowledge

The investigations of the last years have given a more thorough picture of the distribution and ecology in the most important areas in Rogaland and Hordaland. In Sogn og Fjordane the situation is more uncertain. We know that the distribution of suitable rocks for the species is limited, but we still have work to do here. There is also a possibility that the species could occur further north, e.g. in the southern part of Møre og Romsdal. However, areas with

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suitable rocks are scarce here. The areas with appropriate rocks near the sea in the right climate are as a whole very limited in Norway. Therefore it is not expected that the number of known localities with *P. obtusata* will rise much in the future.

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