Published on paper: 1982. Published online: 2024-10-27.
ISSN 1502-4873 (paper). ISSN 1891-5396 (electronic).
doi: https://doi.org/10.5324/fn.v3i0.6139.

Zoogeography of *Triturus vulgaris* (L.) and *T. cristatus* (Laurenti) (Amphibia) in Norway, with notes on their vulnerability

DAG DOLMEN

Dolmen, D. 1982. Zoogeography of *Triturus vulgaris* (L.) and *T. cristatus* (Laurenti) (Amphibia) in Norway, with notes on their vulnerability. *Fauna norv. Ser. A. 3,* 12—25.

The distribution of *Triturus vulgaris* (L.) in Norway is separated into a southeastern distribution area, extending westwards along the coast, and a central Norwegian area in the Trøndelag region. *T. cristatus* (Laurenti) has three separate distribution areas: a southeastern, a southwestern, and a central Norwegian area.

It is thought that *T. cristatus* reached southwestern Norway through mountain passes from southeastern Norway. Possibly *T. vulgaris* also reached this region, but it did not tolerate the change to a colder and more humid, atlantic climate. The many fjords and the high mountains in southwestern Norway may today be an important dispersal barrier for the species. Hydrochore dispersal by rafts seems to be fairly common. Both newts reached central Norway from Jämtland, Sweden, probably also from southeastern Norway. The later climate deteriorations have reduced the maximum distribution area of the species, as has also human activity.

Summer, and possibly also winter temperature, precipitation, length of activity season, day length and the amount of direct sun radiation all cooperate in the limitation of the newts' distribution and abundance. With respect to growth in the larvae, long day conditions in central Norway are thought to compensate for the higher average temperatures further south.

In Norway the newts may disperse locally, but *T. cristatus* is threatened, and locally even in danger of extinction, especially in central and southwestern Norway, by forestry practices and introduction of fish to newt localities. The better dispersal abilities of *T. vulgaris* vs. *T. cristatus* can be explained by the wider ecological amplitude, less nocturnal habits and more terrestrial way of life of *T. vulgaris*.

Dag Dolmen, Department of Zoology, University of Trondheim, N-7000 Trondheim, Norway.

INTRODUCTION

In a recent survey Dolmen (in press b) gives detailed information on the distribution and habitat of the newts, *Triturus vulgaris* (L.) and *T. cristatus* (Laurenti), in Norway, as part of a much wider European project on herpetile mapping and conservation of their habitats. The present paper discusses newt distribution in Norway in relation to immigration, climate and dispersal barriers, and also to more recent human interference. Since both newts, and especially *T. cristatus* are vulnerable to extinction in many parts of Europe, and since the reasons in many cases have not been known, special emphasis has been put on the most serious threats to newts in Norway today.

DISTRIBUTION AND HABITATS

Triturus vulgaris (L.) in Norway is distributed in two discrete areas: a) Southeastern- and southern Norway, mostly in the lowland, from the Swedish border along the coast to Stavanger. In the Østerdal valley district it is found as far north as Ytre Rendal, in the Gudbrandsdal valley up to Fron and it is also found at Lesja, while in upper Telemark it goes as far east as Tokke and Vinje at 700 m altitude. b) Central Norway from Surnadal and Oppdal, mainly in the inland, east of the Trondheimsfjord to Grong and Namsskogan. An apparently isolated population exists at Vefsn. The distribution of *T. vulgaris* in Scandinavia and Finland is shown in Fig. 1.

T. cristatus (Laurenti) is distributed in three

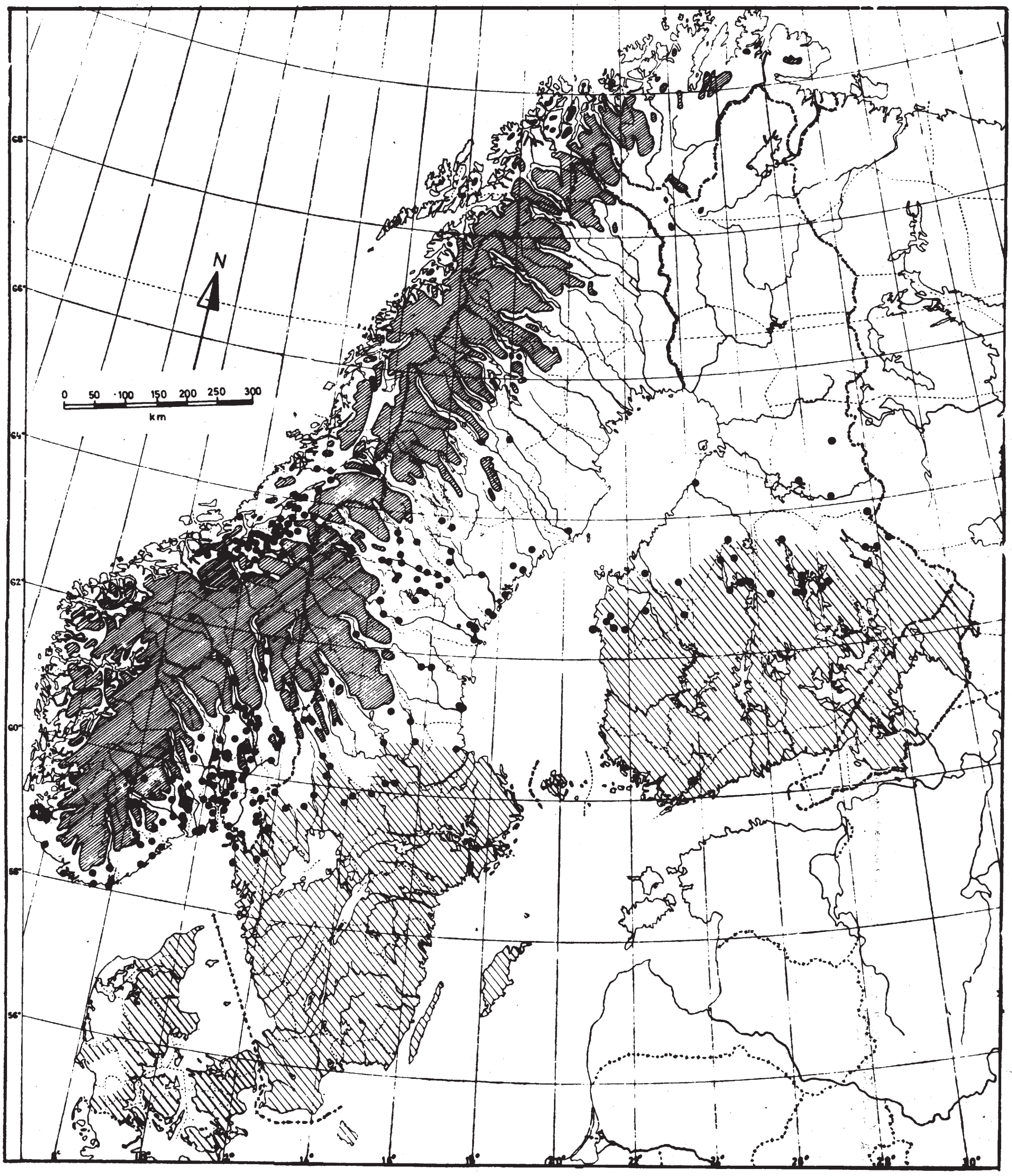


Fig. 1. The distribution of *Triturus vulgaris* in Scandinavia and Finland. Areas in Denmark, South Sweden and Finland where the newt is common, are loosely hatched. For Denmark the map is based on Pfaff (1943), for Sweden on Gislén & Kauri (1959) (plus one find by Olsen 1974 and one by Dolmen 1981a), for Finland on Terhivuo (1981). Areas more than 500 m above sea level are densely hatched.

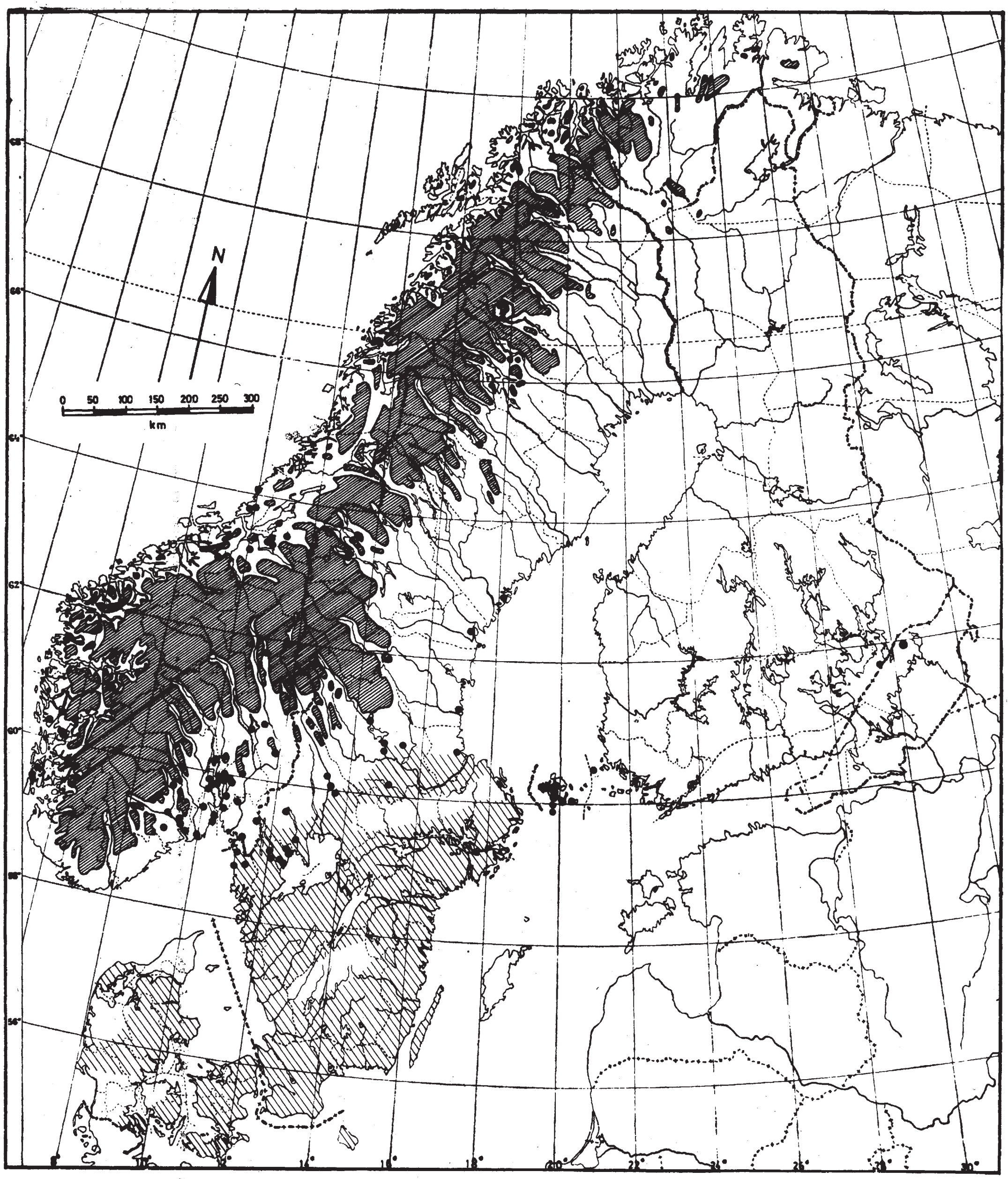


Fig. 2. The distribution of *Triturus cristatus* in Scandinavia and Finland. See legend to Fig. 1.

areas: a) Southeastern Norway, in the lowland, from the Swedish border, on both sides of the Oslofjord, to the Skien area. Northwards it is found as far as Helgøya at Mjøsa, and Løten and most northerly at Ytre Rendal. In Telemark it goes as far as Seljord and Kviteseid at 600 m altitude. b) Southwestern Norway between Haugesund and Bergen. c) Central Norway from Rindal, sporadically inland, to Levanger, and, at the coast, on the Fosen Peninsula. In addition to the abovementioned local areas some uncertain finds of newts are reported further north. The distribution of *T. cristatus* in Scandinavia and Finland is shown in Fig. 2. Further details of Norwegian distribution are given elsewhere (Dolmen, in press b).

With respect to pool size and water quality, *T. vulgaris* has been shown, in both areas, to live and breed in a variety of different locality types. *T. cristatus* is apparently somewhat less euryecious, but both species occur within wide ranges of e.g. H^+-ion concentration, dystrophy, and Ca^{++} content. In southeastern Norway *T. cristatus* is found in many eutrophic localities (cattle-ponds and clay basins) in the lowland, but in Telemark further west and in southwestern Norway, in dystrophic localities. In central Norway *T. cristatus* has been found only in dystrophic, and often acid, localities. *T. cristatus* is a markedly more aquatic species than *T. vulgaris*, and on land it seems to prefer the damper hiding-places (cf. Dolmen 1981b, and in press b).

IMMIGRATION AND DISPERSAL BARRIERS

The immigration to the Scandinavian Peninsula

From their refuges in the Mediterranean, in their dispersal period after the Ice Ages, *T. vulgaris* and *T. cristatus* have been thought to have reached the Scanian area by a land bridge during the early Boreal age (Boreal age: 7500—5500 B.C.) (Johnsen 1935, Gislén & Kauri 1959, see also Dolmen 1976). The favourable climate (Hafsten 1960, 1963, Berglund 1968), together with the existence of many favourable habitats, allowed the newts to prosper and disperse rapidly north- and westwards from South Sweden during the next millennia.

As a result of the climatic conditions during the Atlantic age (5500—3000 B.C.), and the following relatively warm and dry Sub-boreal age (3000—500 B.C.), the lower parts of the Scandinavian alpine region were forested, the upper timber-line being situated at least 400—500 metres higher up than today. Bogs and marshes also grew during the Atlantic age (cf. Hafsten 1960, 1963). Newts should therefore be able to force the mountain passes from southeastern Norway to southwestern Norway, and also from southeastern Norway and from Jämtland, Sweden, to central Norway. The latter passes are partly forested also today (by *Pinus silvestris* and *Betula pubescens*). Even though *T. vulgaris* and *T. cristatus* are mainly lowland animals, they can, as shown by the present investigations, also be found at localities in Norway more than 600—700 m above sea level. In Central- and South Europe they may often reach altitudes of more than 1000 m and even 2000 m (Steward 1969, Arnold et al. 1978); for *T. vulgaris* in the Carniche Alps 2250 m is mentioned by Freytag (1954).

The immigration to southwestern Norway

Both newt species have been found in upper Telemark, at least as far up as 600—640 m above sea level (a.s.l.), and *T. vulgaris* at 700 m a.s.l. In all likelihood they have also survived until recently (or still?) at about 900 m a.s.l. (Dolmen, in press b).

The mountain passes from the southeastern parts of Norway to the southwestern parts, e.g. via Haukeligrend — Haukelisæter, are situated about 1000 m a.s.l. These areas would, during the Atlantic age (see Hafsten 1960, 1963), have an even better climate for the newts than newt localities 400 m lower down have today. *T. cristatus* therefore probably dispersed to southwestern Norway through these passes; its absence from southern Norway also supports this theory. *T. vulgaris*, however, has shown that it can go higher up in the highland and has a greater ability to disperse than *T. cristatus* (Steward 1969). The question is therefore why *T. vulgaris* is absent from (or extremely rare in) southwestern Norway. Its path over the mountain passes would have been shorter and easier than for *T. cristatus*. One possible answer is that it did cross the mountains, but was later eliminated by a worsening of the climate during the Sub-atlantic age (500 B.C. up to present time).

The immigration to central Norway

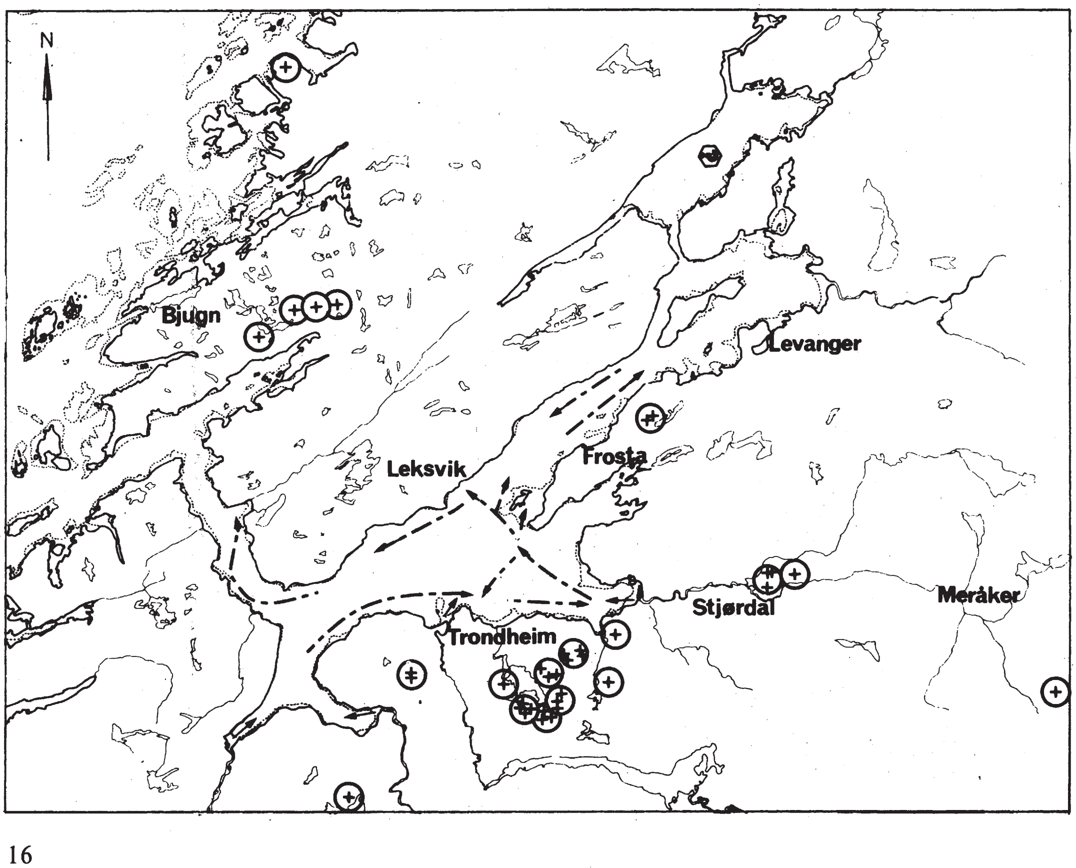
The immigration theory of Johnsen (1935) and Kauri (1959, 1970), viz. that *T. vulgaris* has dispersed to central Norway from Jämtland, is strengthened by the fact that both species have earlier been found in the Meråker border mountains, just on the watershed (Dolmen, in press b). The actual lakes, Småvannene, are today situated a few tens of metres above the local upper timber-line *(Pinus silvestris)*. Further northwestwards from this atypical newt locality, down the valley, there are numbers of ponds and tarns, where newts have not been found, but which could apparently keep a newt population today. Most probably the apparent absence of newts in the Småvannene lakes today is due to the introduction of fish (Bjerna Bendiksen, Stordalen, pers.comm. 1972). The lakes are situated approximately 40 km from the nearest known Norwegian locality for *T. vulgaris* and *T. cristatus* (at Flora, Stjørdal), and about 70 km from the nearest Swedish find of the species (Undersåker, see Gislén & Kauri 1959).

Probably more than one pass between Jämtland and central Norway was forced by the newts, while some possibly also came in from southeastern Norway. The lowest passes from Jämtland to Trøndelag, are not higher than 500—600 m a.s.l. Some mountain passes from southeastern Norway to Trøndelag are lower than 700 m altitude, and may also have been suitable dispersal routes. An uncertain record of newts exists from Røros (Dolmen, in press b).

Fig. 3. The current-situation in parts of the Trondheimsfjord, and the distribution of *Triturus cristatus*. A raft drifting from Stjørdalen can easily end up at Frosta/Levanger or on the Fosen Peninsula, e.g. Leksvik.

The crossing of sea barriers

In which way *T. cristatus* reached the Fosen Peninsula in central Norway is difficult to say. The distribution pattern does not indicate a dispersal route around the Trondheimsfjord. Crossing the fjord on floating trees or logs is, however, a possibility: Some of the great water masses from the Stjørdalselva River flow right across the fjord (Fig. 3), and it is possible that a log coming down the Stjørdalselva River would run aground on the north side (Per Jacobsen, NTH Trondheim; pers.comm. 1976). It is also known that many individuals of *T. cristatus* may hide together between the bark and the wood of dead, fallen trees (Dolmen 1976). If such a tree was taken by the river during the spring flood (or a clay slide) in Stjørdalen, where both newts are present, it might easily carry newts across the fjord to where *T. cristatus* also in fact has been found. The salt content in the surface layer of the Stjørdalselva fjord current today, during the spring flood, may be less than 5—10 ‰, even at a distance of several kilometres from the river mouth.



The tolerance to salinity in *T. vulgaris,* which is probably a bit hardier than *T. cristatus* (Dolmen 1981b), can be seen from the fact that *T. vulgaris* larvae have been found to live even in water with about 4 ‰ salinity (Dolmen, in press b): Two living *T. vulgaris* larvae were discovered in a rock-pool in southeastern Norway, but three or four additional larvae were newly dead (probably because of increasing salinity due to evaporation, or the very high temperature in the pond). Lönnberg (1920, 1925) has shown that adult *T. vulgaris* can even tolerate a sojourn in 6 ‰ salt water (brackish water in the Baltic Sea east of Stockholm, Sweden) for more than a day and night, without seeming to take any harm.

T. vulgaris has also been found in small rock-pools exposed to splash from the sea on some small skerries outside Kristiansand in southern Norway. The newts lived here together with marine elements like coelenterates. The specific conductivity, however, of the pond water was not more than 350 µS/cm, and the pH 6,4 (Ingvar Spikkeland, Oslo; pers.comm. 1977). The localities are situated some six-eight kilometres out from the Otra River mouth at Kristiansand, and the dispersal may have occurred by passive floating on trees or logs out to the small islands.

According to Lönnberg (1920) a similar hydrochore dispersal may have brought *T. vulgaris* out to the outer islands of the archipelago east of Stockholm, Sweden, more than ten kilometres from the mainland. Johnsen (1935) supposes that the occurrence of *T. vulgaris* at the Hvaler Archipelago, outside the mouth of the Glomma River, in southeastern Norway, even as far out as Akerøya, can be ascribed to dispersal by rafts.

The crossing of sea barriers such as fjords and coastal waters thus seems to have taken place in many instances near the outlet of big rivers.

It is also highly probable that the occurrence of *T. cristatus* (perhaps also *T. vulgaris*) on the Åland Archipelago, between Sweden and Finland, should be attributed to a similar passive dispersal. The first islands of this archipelago would effectively reduce the chances of a successful rafting from Sweden further to the Finnish mainland. This may explain why *T. cristatus* has been found so frequently in the western, main parts of Åland, but not on the great many islands further east and on the Finnish mainland, a problem mentioned by Terhivuo (1981).

It is also worth mentioning that at the northwestern outpost of the distribution of *T. vulgaris* in southern Norway, in the Stavanger/Jæren area, no big rivers exist. The adjacent fjord area (Boknafjord) is, moreover, very broad and with numerous small islands, which theoretically would have hindered newts on a drifting raft from crossing successfully.

Possible climate dispersal barriers in southwestern Norway

In southwestern Norway, and also in the coastal part of central Norway, *T. vulgaris* is rare or absent. *T. cristatus,* however, is present in both areas. Possibly *T. vulgaris* tolerates the coastal climate less well than *T. cristatus.*

Olsen (1974) showed that at Stavanger/Jæren in the western part of southern Norway, *T. vulgaris* needs as much as four months for larval development, before the metamorphosis in mid-September. Larval hibernation under the ice cover of the pond is quite common, but not favourable. He therefore assumed that southwestern Norway (here defined as the area right north of Stavanger: Haugesund-Bergen), which on average has slightly lower temperatures than Stavanger and Jæren, is too hard climatically for *T. vulgaris.*

A climate barrier for *T. vulgaris* north of Stavanger can hardly be fully proved, however; in contrast to the finds by Olsen (1974), a few larvae collected at Klepp, Jæren 1971, had attained full metamorphosis size as early as the end of July (cf. Dolmen, in press c). It is reasonable to assume that the many fjords, especially Boknafjord with its many branches, and the many high mountains in the Ryfylke area, constitute the most serious dispersal barriers northwards for *T. vulgaris.*

The average winter temperature may be much the same in the Stavanger/Jæren area and in southwestern Norway, but the number of days with a temperature above 0°C is lower in the southwestern Norwegian fjord area (in which *T. vulgaris* does not live, but *T. cristatus* does) (Pedersen 1968). The Stavanger/Jæren area has also a slightly longer summer (the number of days warmer than 10°C) (Pedersen 1968, Sund 1968), but locally the summer average temperature in southwestern Norway may be as high as — or even higher — than at Stavanger/Jæren (Ekman 1922, Johannessen 1963). There is no noticeable difference in the number of yearly plant growth days (Johannessen 1977). From Table 1 it is seen that on the average the climate stations in inner southwestern Norway have the same number of clear days as Stavanger/Jæren during the summer; the number of fully overcast days, however, is higher,

Table 1. Monthly number of days with various weather phenomena, and mm precipitation; standard normals from 1931—60, according to Bruun & Håland (1970).

Locality	Monthly number of days with rain . .					overcast days . . .				
	M	J	J	A	S	M	J	J	A	S
Stavanger/Jæren										
Obrestad	13.1	15.0	15.7	16.9	20.1	7.2	7.8	10.6	10.1	10.7
Klepp	12.7	15.3	16.5	17.7	20.5	7.7	9.0	10.6	10.1	10.0
Sola	13.5	15.1	15.6	18.3	20.8	8.8	11.0	12.2	10.5	9.2
Stavanger	13.3	15.2	16.3	17.8	19.9	9.9	11.9	11.6	12.8	12.6
Southwestern Norway										
Sauda	12.8	16.7	18.2	18.6	20.6	11.3	14.1	15.8	15.2	16.1
Indre Matre	14.9	17.6	19.7	19.2	20.5	11.9	14.4	16.5	14.5	16.1
Bergen. Fr.berg	15.5	18.5	19.6	19.3	21.4	12.5	14.3	16.6	15.4	16.3

Locality	clear days					mm precipitation				
	M	J	J	A	S	M	J	J	A	S
Stavanger/Jæren										
Obrestad	5.9	3.4	1.8	2.2	2.1	51	72	90	108	153
Klepp	7.5	5.2	3.2	3.8	3.3	—	—	—	—	—
Sola	5.4	2.9	1.9	2.3	2.0	98	69	89	108	122
Stavanger	5.8	4.5	2.3	2.5	2.1	51	78	97	111	140
Southwestern Norway										
Sauda	5.6	3.3	2.0	2.8	2.8	83	120	121	155	217
Indre Matre	6.1	4.0	3.0	2.9	2.8	110	180	173	228	—
Bergen, Fr.berg	4.5	3.4	1.9	2.6	2.0	83	125	141	168	228

and also the number of days with rain slightly higher. The monthly averages of the daily minimum temperature are also distinctly lower in southwestern Norway than in the Stavanger/Jæren area during the summer (Bruun 1967, see also Ekman 1922). The most conspicuous climatic feature of the fjord area in southwestern Norway, however, is the great amount of monthly precipitation, which may be more than twice that of Stavanger/Jæren e.g. (see also Wallén 1968, Johannessen 1977). All these factors naturally work on the flora elements e.g.: the Nemoral biotic zone ends exactly in the Stavanger area (Sjörs 1963).

There are two or three factors which may disfavour *T. vulgaris* compared to *T. cristatus* in a cool and humid climate (southwestern Norway): its preference for a high water temperature (23,5°C, against 20,6°C for *T. cristatus*, according to Strübing 1954), and the fact that *T. vulgaris* is a relatively short-lived animal (Hagström 1977, 1979a,b; Dolmen, in press c). Probably it cannot therefore put up with successive breeding failures. A third possible factor is the difference in hygro- and hydrophily of the two species (Dolmen, in press b).

The influence of the climate on the distribution of newts on the Scandinavian Peninsula

The distribution of newts in Norway falls within the areas where the last frost night is normally recorded some time between 21 May and 1 June (cf. Myklebost & Strömme 1963). Terhivuo (1981) points out that most records of *T. vulgaris* in Fennoscandia refer to regions where the annual length of the vegetation period (a daily mean temperature of ⩾ 6°C) is 140 days or longer. This, however, does not apply so well to Norway, especially coastal Norway, where 160 days seems more appropriate. One of the factors, perhaps the most important, for growth and distribution of the newts is thought to be the heat sum of the summer half-year, and — especially for the metamorphosis — the maximum temperatures in the water. This is only partly reflected through the July isotherms (see Ekman 1922); towards west (milder spring and autumn) and north (longer daily radiation- and twilight periods) the newts seem to tolerate a lower July temperature (longer hunting-day; see Dolmen, in press a). In southeastern and southern Norway the main distribution of the species roughly follows the 15°C-isotherm for July (cf. Ekman 1922), but *T. cristatus* does not go further west than Skien. It is possible that certain edaphic factors are involved in the distribution of *T. cristatus*, e.g. Ca-content underground (see Dolmen 1981b). *T. vulgaris* goes further west, to Stavanger, and its area crosses the 14°C-isotherm at Lista/Lindesnes. In southwestern Norway *T. cristatus* also lives within the 14°C zone, in central Norway even partly within the 13°C zone. Like *T. vulgaris* the other part of its distribution area comes to lie within the 14°C zone: around central parts of the Trondheimsfjord. In Sweden the main distribution areas of both *T. vulgaris* and *T. cristatus* lie within the 14°C-isotherm, except for some isolated records in the far north, and also the area around Lake Storsjöen, Östersund, which has an average temperature of about 13°C in July.

For the diurnal larvae, beside the daily air temperature, also the amount of sunshine should be important, as this increases the water temperature. Central Norway and the Storsjöen/Östersund area in Jämtland, Sweden, have the same normal temperature in June (cf. Ekman 1922); the plant growth season, however, is much shorter at Storsjöen (120—140 days compared to 160—180 days in the central Norwegian lowland (cf. Johannessen 1977). Nevertheless, the growth of *T. vulgaris* larvae is just as good at Storsjöen as at the best localities in central Norway, and metamorphosis may even take place earlier (Dolmen, in press c; see also Olsen 1974). The reason is probably the larger amount of clear weather in Jämtland (cf. Wallén 1968; for further discussion see Dolmen, in press c).

It has been shown (Dolmen, in press c) that the growth of newt larvae in central Norway is not much slower than in southeastern Norway. Moreover, larval hibernation as described from South Scandinavia (e.g. Collett 1918, Gislén & Kauri 1959, Hagström 1927b, Olsen 1974) has never been observed in the northern distribution area (even though the latest *T. vulgaris* larvae have been collected as late as 30 October, and a few times from under thin ice cover in the autumn), nor in north central Sweden (cf. Olsen 1974; Dolmen, in press c). Metamorphosis thus generally takes place relatively early in central Norway. The mid-summer light condition in the north presumably compensates for the higher temperatures further south, both influencing the growth.

The maturity of newts in central Norway is reached one year later, at least, than at similar biotopes in southeastern Norway. In *T. vulgaris* the first breeding takes place when 3 + and 2 + years old, respectively, in the two areas (Dolmen, in press c). At the northernmost localities (Vefsn), however, the growth and maturing processes are much slower. Unfavourable climatic conditions, the absence of a real dark/twilight period (night < 5 lux) e.g., thus possibly limit the distribution of the species further north.

One of the northermost Swedish populations of newts, at Stensele (now eradicated; see Dolmen 1978b), situated at 470 m altitude, probably survived because of neoteny (Kauri 1959). The climatic conditions so far north and so high above sea level in a dry region have probably favoured neoteny instead of the normal aquatic/terrestrial alternation. Neoteny is otherwise very rare in Scandinavia, and has been found only once in Norway (see Dolmen 1978b). At the Vindelgransele locality, not far from Stensele, but situated at only 340—350 m altitude, the size of the *T. vulgaris* larvae seemed to be no less than for central Norwegian larvae from the same time of the year (mid-July), but little is known about the adults (Dolmen, 1981a, and in press c).

PROFITS AND THREATS
Man's influence on the amphibian fauna

Human activity, especially in earlier times, may have had a positive influence on the amphibian fauna and also, locally, on the dispersal of the newts. The digging of numerous drinking-water basins and wells for man and cattle, in southeastern Norway e.g., as mentioned by Dolmen (1980), has given both newts splendid breeding conditions. There is also a possibility that newt eggs and larvae could have been carried, involuntarily, by man from one district to another, during the transport of live fish fry for introduction to new areas: Johnsen (1935) guessed that the anthropochore dispersal of *Carassius vulgaris, Cyprinus carpio,* and possibly *Esox lucius,* may have taken newts to new areas; it has also been proposed (Lund 1964) that aquarium keepers might have set out newts in new areas after having kept them for some time as pets. These hypotheses, however, were put forth at a time when the distribution of the newts was still little known and appeared to be very discontinuous and scattered. Although a few attempts of anthropochore, voluntarily long-distance dispersal of newts are known (both unsuccessful; see Dolmen, in press b), it is believed that any such transports take place mainly within the area already occupied by the species.

Human activity has also in different ways made the newts *less* common. The detrimental effect of the introduction of fish to a newt locality is mentioned in a separate section. Otherwise, intensive cultivation and afforestation have destroyed many newt localities (cf. Hagström 1981a). Dolmen (1976) mentions that 35 known newt localities in central Norway have been destroyed by draining and filling-in during the last thirty years (see also Dolmen 1978a). For *T. cristatus* this makes up to 22 % of all localities known, and some more are threatened (additional 12 %) (cf. Dolmen 1981b). Even where the pools have been destroyed the newts may return for breeding, however. The philopatry of *T. vulgaris* for its particular breeding-pond (cf. Dolmen 1981c) has been illustrated by an example by Dolmen (1976). The newts still gathered year after year in the springtime, although never getting an opportunity to reproduce before the partly filled-in pools dried out.

Acid precipitation is probably a great problem to newts, especially in southern Norway, in the acid bedrock complex region, where *T. vulgaris* occurs very scantily. *T. cristatus*, however, has probably never existed in this area (cf. Collett 1918). During the last few years acid precipitation has become a serious problem in most of this region (see Økland 1969, 1979, Brække 1976, Statistisk Sentralbyrå 1976 e.g.). Even though the acidity destroys the fish in these lakes (cf. Leivestad et al. 1976), giving the newts a chance to occupy new areas (cf. Andrén et al. 1978, Hagström 1981b), the water would very soon get too acid for the newts as well (Dolmen, in press b).

In southern Sweden changes of the landscape and a lowering of the ground-water level, together with acid precipitation have caused a serious decline in the amphibian populations (Hagström 1972a, 1975, 1981b). Declines of the amphibian fauna and changes in density, however, can also be ascribed to the fact that many of our herpetile species in Scandinavia live at the northern margins of their distributional areas, and therefore may show density fluctuations even with small climate changes.

The impact of fish predation

One of the most serious problems for local newt populations in Scandinavia today is fish introduction to ponds and tarns. The impact of fish predation on a newt population may be fatal. Even though *T. vulgaris* has been reported to live in fish ponds (Vogel 1966), and both species are said to cause great harm to fish fry (Sjögren 1947, 1973), the experience of the author is that introduction of fish to a newt locality usually is catastrophic for the newts. This effect has been noticed with *Salmo trutta* in a number of cases (cf. Dolmen 1976, 1981b).

Newts have in Norway very rarely been found in fish-ponds or -tarns. Only in about 12 localities in central Norway has *T. vulgaris* been found (only one or a few specimens) together with *S. trutta*. Most of these localities are referred to by Dolmen (1976). In only four of the lakes is the newt population of any size, and in these lakes the amphipod *Gammarus lacustris* is also found to be fairly abundant and possibly being preferred as a prey by the fish («search image» cf. Svärdson & Nilsson 1964, Pianka 1978). No population of *T. cristatus* in central Norway has ever been found together with *S. trutta*. When *S. trutta* has been successfully introduced to a newt locality *T. cristatus* has always disappeared shortly afterwards.

T. cristatus has proved to be much more vulnerable to predation from *S. trutta* than *T. vulgaris*, probably because the *T. cristatus* larvae, at least for a time, live a nectonic life and are easily detected by the fish. Those of *T. vulgaris* are benthic, more cryptically coloured, and usually keep to the shallow near-shore parts of the lake, relatively rich in vegetation, where the fish occur less commonly. As shown from stomach examinations of *S. trutta*, not only newt larvae, but also adults, at least of *T. vulgaris*, are eaten by fish (some cases are mentioned by Dolmen 1976).

The occurrence of *Gasterosteus aculeatus* seems to have a similar detrimental influence on newt populations. *T. cristatus* in central Norway has never been found together with *G. aculeatus*, and of more than 180 localities for *T. vulgaris* in central Norway only 4 or 5 of them are known to keep a population of *G. aculeatus*, and these localities are quite special (for details see Dolmen 1976). The detrimental impact of this fish on newt populations is also mentioned by Smith (1964) e.g., who states that «introduction of sticklebacks into a pond has been known to clear it of newt larvae in a few months».

G. aculeatus is very common in the central Norwegian lowland, up to the upper postglacial marine limit, which is at about 200 m altitude in central parts of Trøndelag (Holtedahl & Andersen 1960). But the fish has reached even higher up some places, and may inhabit ponds or tarns in forest or bog areas. The distribution of *G. aculeatus* in ponds and tarns on floors of the lowland valleys in central Norway is probably the main reason for the absence of *T. vulgaris* from these valleys (for three exceptions, see Dolmen, Sæther & Aagaard 1975; Dolmen 1976). In the Gudbrandsdal valley in southeastern Norway, the distribution of *T. vulgaris* is associated with the valley floor, and according to Collett (1918) the newt is not found in the hills above. In central Norway, however, the newt localities are almost exclusively situated in the hills above the valley floor, at a fairly long distance from the rivers, since most of the ponds and oxbow-lakes historically have a near connection to the rivers, which have a population of *G. aculeatus*. In the Gudbrandsdal valley, however, this fish is absent (Huitfeldt-Kaas 1918). The occurrence of certain species of fish in an area may probably act as an effective barrier for the newts.

Many of the clay basins and cattle-ponds in southeastern Norway, however, which keep a population of newts, also have non-*Cyprinus* cyprinid fish. These localities probably have no big newt populations, but the impact of such fish in many cases does not seem to be catastrophic, not even for *T. cristatus* (cf. Beebee 1979).

The present dispersal capacity of the newts

The distribution of the newts in Norway can partly be explained by the dispersal abilities of the species in different parts of the country, although the landscape has changed in various ways in appearance through the ages. Knowledge about the ecological and geographic factors involved in the dispersal of the newts is also very important when considering conservation of these animals and their habitats.

When the amphibians invaded the Scandinavian Peninsula after the Ice Ages, they took advantage of a great number of excavated or dammed-up ponds and lakes, which made dispersal easy. Over the years the number of suitable breeding localities in many parts of the country has diminished considerably, either by natural processes or by human interference. The distribution area of the newts has therefore become subdivided on several occasions, and many localities are now isolated.

The success for pioneer populations depends usually on the number of individuals involved; population density and pressure, and reproductive rate are therefore important factors contributing to dispersal phenomena (Udvardy 1969). According to Hagström (1979b) a female newt (both species) lays some 100—200 eggs. Because newts live a very unobtrusive life at least on land, they may live more than 10—15 years in nature (Hagström 1977, 1979a; Dolmen, in press c) and the population can grow quickly when first established, provided aquatic predators are not too numerous.

It is also known that, even though newts are very philopatric animals (Dolmen 1981c, cf. Terhivuo 1981), and the terrestrial dwellings are usually situated close to the breeding pond (Dolmen 1981c), some (mostly young?) newts will be on the move. *T. vulgaris* and *T. cristatus* have been discovered up to half an English mile ($\approx$ 800 m) away from their breeding pond (Simms 1969, Viertel 1976), and spring migrations to the pond have been observed from a distance of several hundred metres (Heusser 1956, Vilter & Vilter 1962, Dolmen 1976 and unpublished). At a locality in central Norway the newts *(T. vulgaris)* «immediately» invaded a new pond formed in a slate quarry. The nearest known newt pond is situated 400 m away (Dolmen 1976). Similar examples have been reported by Warwick (1949), and Smith (1964) explains this new-colonization as due to random movements of the newts from a nearby pond. Dispersal can therefore easily occur from one suitable locality to another more than one half kilometer away, and probably much further. This applies also when newts lose their way to the home breeding pond, as recorded by Cummings (1912) (cf. Dolmen 1976, 1981c). The newts' olfactory sence may probably be of great help in the orientation (the smell of certain pond algae?) (cf. Dolmen 1981c). The chance to reach another suitable breeding locality depends, however, also on the number of such localities, their size and form («catching angle») and the distance (cf. Udvardy 1969). The success of dispersal and colonizing of a new breeding area for newts is very much similar to island colonizing, as dealt with by MacArthur (1972).

Dispersal is slower and gene flow between populations less frequent in central Norway than in the lowland southeastern Norway. A look at the map (series M-711, 1:50000) reveals that in 30 randomly chosen 1-km-squares in a region near Drøbak (Oslofjord district in southeastern Norway) at least 10 apparently suitable ponds can be found, and in the Horten — Tønsberg region, in the same district, 25 ponds, while e.g. Verdal (central Norway) and Stjørdal show only 2 and 3 ponds, respectively. It is known that none of these last mentioned ponds have newts (a few smaller ponds not visible on the map have), but almost all the cattle-ponds and clay basins in the Oslofjord district have newts. While most newt localities around the Oslofjord thus are within relatively easy reach for newts from other localities, a great many localities in the central Norwegian lowland have, in practice, become isolated from each other. Especially the relatively aquatic *T. cristatus* would have great problems to disperse to and through this cultivated land. Most of the difference, — both areas are mainly arable, clayey lowland — is probably partly due to more hilly landscape in central Norway, but also to different farming strategies and water storage practices in the two areas (see Dolmen 1980); only a few farmers in central Norway usually dig out cattle-ponds. In the boggy regions of central Norway the number of suitable ponds and tarns are often far higher, e.g. 30 1-km squares show 32 bog ponds and tarns for Skaun near Trondheim. Another important aspect is that eutrophic ponds, as those in the Oslofjord district, seem to be more favourable with respect to growth and maturing processes, both for newt larvae and adults, than oligotrophic or dystrophic biotopes (Dolmen, in press c). The reasons (food supply, pH, altitude/temperature etc.) are not fully known.

Big or small stands of trees, bushes, ditches and uncultivated land between the many man-made ponds, as seen e.g. in many parts of southeastern Norway, are splendid dispersal corridors. The boggy areas in central Norway are probably also fit for use, judging from the high frequency of newt localities among bog ponds and tarns. It should also be mentioned, as pointed out by Johan F. Willgohs, Bergen (pers.comm. 1978) that although southwestern Norway generally is characterized by mountains and many fjords, the distribution area of *T. cristatus* there is covered by more or less continuous pine *(Pinus silvestris)* forest with boggy areas, forming what can be looked upon as a broad dispersal «corridor» between the newt localities.

Dispersal takes place probably most often by terrestrial juvenile newts (Bell 1977, Andrén et al. 1978, Dolmen 1981c), but also dispersal by aquatic newts along water-courses is thought to take place. The positive rheotaxis shown for newts during the breeding season (Dolmen 1981c), together with a tendency for newts to climb uphill after breeding (Cummings 1912), may have led many animals up into the upper valleys and highlands. Newt localities on hill tops are in fact surprisingly common in all parts of the Scandinavian Peninsula. Terhivuo (1981), too, stresses the possible importance of river valleys for the dispersal of newts and other herpetiles in Sweden and Norway.

The greater dispersal ability of *T. vulgaris,* compared to *T. cristatus* (cf. Steward 1969), can easily be explained from the relatively wide ecological amplitude, less nocturnal habits, and more terrestrial way of life in *T. vulgaris*. In addition this species is less vulnerable to fish predation. In Norway, like in other European countries, it is more common and has a slightly wider distribution than *T. cristatus*.

T. cristatus has only a relatively short period of terrestrial dispersal each year (cf. Dolmen, in press b). Also its aquatic habits and its relatively short activity period each night in central Norway must hamper the species in dispersal from its bog areas, to occupy e.g. cattle-ponds (which are very short-lived, geologically speaking) in its northern area.

Small isolated populations of any animal species (usually in the periphery of the distribution area) are in danger of extinction, by natural causes like competition, predation, disease, changes in habitat, or population fluctuations (MacArthur 1972). Many such newt localities could be mentioned (see maps). In addition, it appears to be only a question of time until these localities are destroyed by human interference: fish introduction, draining, or filling-in.

Since the late 1800s up to the present time the climate of Scandinavia has become milder (Johannessen 1963, 1970); but although many species of homoiotherm vertebrates have shown a clear dispersal northwards during this period of time, no corresponding widening of area has been observed in amphibians and reptiles. European herpetiles with their northern distribution border in southern Sweden seem to be more or less of relic nature (Terhivuo 1981). In Norway, too, a decline in the northern herpetile populations and an extinction from the northermost districts seems to take place (Dolmen 1978a, Terhivuo 1981). As in Finland, the northern marginal populations of *T. vulgaris* in Norway are isolated from each other. Terhivuo (1981) suggests that the site tenaciousness of this newt means a low rate of dispersal, and hypothesizes that in the long run many of the marginal populations of *T. vulgaris* perhaps died out. A similar situation seems to be present in Sweden (cf. Gislén & Kauri 1959, Dolmen 1978b, 1981b).

Nothing in the situation seems to indicate an expansion of the distribution of *T. vulgaris* in the northern region — the area has been thoroughly investigated. Since an anthropochore dispersal by *T. vulgaris* to the Vefsn localities is very improbable — they are not situated close to any former or recent human dwelling — it is highly probable that this northernmost local population of *T. vulgaris* has relic status. The newts in this area become sexually mature two or three years later than in southeastern parts of the country and in the district around the Trondheimsfjord, and few newts seem to reach the adult stage.

As seen from the summer isotherms (see e.g. Ekman 1922) the Vefsn — Rana district, the newts' northern outpost, forms a «pocket» of favourable climate which may have enabled the species to survive a period of climatical deterioration. At least four other herpetile species appear to have their northern distribution border in this region, although the populations are very sparse (Dolmen 1978a).

It should be mentioned that the Stortjørna locality, Vefsn, is surrounded on three sides by lakelets/tarns in which *Gasterosteus aculeatus* is abundant. The occurrence of this small predatory fish in an area may probably act as an effective dispersal barrier for the newts. It also makes the fate of the newt population in Stortjørna uncertain. Unintentional introduction of *G. aculeatus* may come to be catastrophic for the newts.

ACKNOWLEDGEMENTS

Thanks are due to Kåre Elgmork and Hans Kauri, for having critically read parts of the manuscript, to Carolyn Baggerud for language consultation and to Gerd Herjuaune and Sylvi Bjørn for typewriting the manuscript.

REFERENCES

Andrén, C., Hagström, T. & Nilson, G. 1978. Hasselsnok, sandödla, «strandpadda» — några viktiga herpetologiska naturvårdsfrågor. *Sveriges Natur 1978*, 291—293.

Arnold, E.N., Burton, J.A. & Ovenden, D.W. 1978. *A field guide to the reptiles and amphibians of Britain and Europe*. Collins, London.

Beebee, T.J.C. 1979. Habitats of the British amphibians (2): suburban parks and gardens. *Biol. Conserv. 5*, 241—257.

Bell, G.A.C. 1977. The life of the smooth newt *(Triturus vulgaris)* after metamorphosis. *Ecol. Monogr. 47*, 279—299.

Berglund, B.E. 1968. Vegetasjonsutviklingen i Norden efter istiden. *Sveriges Naturs Årsbok 1968*, 31—53.

Brække, F.H. 1976. Impact of acid precipitation on forest and freshwater ecosystems in Norway. *SNSF Research Report (Oslo) 1976—6*, 1—111.

Bruun, I. 1967. *Climatological summaries for Norway. Standard normals 1931—60 of the air temperature in Norway*. Det Norske Meteorologiske Institutt, Oslo.

Bruun, I. & Håland, L. 1970. *Climatological summaries for Norway. Standard normals 1931—60 of number of days with various weather phenomena*. Det Norske Meteorologiske Institutt, Oslo.

Collett, R. 1918. (publ.: Wollebæk, A.) *Norges krybdyr og padder*. Aschehoug, Kristiania (Oslo).

Cummings, B.F. 1912. Distant orientation in Amphibia. *Proc. zool. Soc. Lond. 1912*, 8—19.

Dolmen, D. 1976. Biologi og utbredelse hos *Triturus vulgaris* (L.), liten salamander, og *T. cristatus* (Laurenti), stor salamander, i Norge, med hovedvekt på Trøndelagsområdet. *K. norske Vidensk. Selsk. Mus. Rapport Zool. Ser. 1976—6*, 1—164.

Dolmen, D. 1978a. Norske padder og krypdyr, en foreløpig utbredelsesoversikt. *Fauna 31*, 165—174.

Dolmen, D. 1978b. De neotene salamanderne («skrattabborrene») ved Stensele. *Fauna och Flora 73*, 171—177.

Dolmen, D. 1980. Padder og krypdyr i Vestfold. *Natur i Vestfold 1980*, 35—42.

Dolmen, D. 1981a. Et nytt «Skrattabborrtjärn» i Lappland. *Fauna och Flora 76*, 89—92.

Dolmen, D. 1981b. Distribution and habitat of the smooth newt, *Triturus vulgaris* (L.), and the warty newt, *T. cristatus* (Laurenti), in Norway. — In: Coborn, J. (ed.). *Proc. Euro. Herp. Symp. C.W.L.P. Oxford 1980*, pp. 127—139.

Dolmen, D. 1981c. Local migration, rheotaxis, and philopatry by *Triturus vulgaris* within a locality in central Norway. *Brit. J. Herpet. 6*, 151—158.

Dolmen, D. in press a. Diel rhythms of *Triturus vulgaris* (L.) and *T. cristatus* (Laurenti) (Amphibia) in central Norway. *Gunneria*.

Dolmen, D. in press b. A survey of the Norwegian newts (Triturus, Amphibia); their distribution and habitats. *Gunneria*.

Dolmen, D. in press c. Growth and size of *Triturus vulgaris* (L.) and *T. cristatus* (Laurenti) (Amphibia) in different parts of Norway, with special emphasis on central Norway. *Holarct. Ecol.*

Dolmen, D., Sæther, B. & Aagaard, K. 1975. Ferskvannsbiologiske undersøkelser av tjønner og evjer langs elvene i Gauldalen og Orkdalen, Sør-Trøndelag. *K. norske Vidensk. Selsk. Mus. Rapport Zool. Ser. 1975—5*, 1—47.

Ekman, S. 1922. *Djurvärldens utbredningshistoria på Skandinaviska halvön*. Bonnier, Stockholm.

Freytag, G. 1954. *Der Teichmolch*. Ziemsen, Wittenberg.

Gislén, T. & Kauri, H. 1959. Zoogeography of the Swedish amphibians and reptiles with notes on their growth and ecology. *Acta vertebratica 1*, 193—397.

Hafsten, U. 1960. Pollen-analytic investigations in South Norway. — In: Holtedahl, O. (ed.). Geology of Norway. *Norges Geol. Undersøkelse 208,* pp. 434—462.

Hafsten, U. 1963. *Oslotrakten gjennom 10.000 år.* Universitetsforlaget, Bergen.

Hagström, T. 1972a. Göteborgstraktens amfibiefauna. *Göteborgs Djurskyddsför. Årsskr. 1972:* 22—27.

Hagström, T. 1972b. Vattenövervintring hos västsvenska salamanderlarver. *Fauna och Flora 67,* 261—263.

Hagström, T. 1975. Herpetilerna och naturvården. *Sveriges Natur 1975,* 131—140.

Hagström, T. 1977. Growth studies and ageing methods for adult *Triturus vulgaris* L. and *T. cristatus* Laurenti (Urodela, Salamandridae). *Zool. Scripta 6,* 61—68.

Hagström, T. 1979a. Population ecology of *Triturus cristatus* and *Triturus vulgaris* (Urodela) in SW Sweden. *Holarct. Ecol. 2,* 108—114.

Hagström, T. 1979b. *Studies of the population ecology of two newt species* (Urodela, *Triturus) in southwestern Sweden.* Dissertation, University of Göteborg.

Hagström, T. 1981a. A note on amphibian conservation in central and northern Fennoscandia. — In: Coborn, J. (ed.). *Proc. Euro. Herp. Symp. C.W.L.P. Oxford 1980,* p. V.

Hagström, T. 1981b. Reproductive strategy and success of amphibians in waters acidified by atmospheric pollution. — In: Coborn, J. (ed.). *Proc. Euro. Herp. Symp. C.W.L.P. Oxford 1980,* pp. 55—57.

Heusser, H. 1956. Biotopansprüche und Verhalten gegenüber natürlichen und künstlichen Umweltveränderungen bei einheimischen Amphibien. Beobachtungen am mittleren Zimmerberg. *VierteljSchr. Naturforsch. Ges. Zürich 101,* 189—210.

Holtedahl, O. & Andersen, B.G. 1960. Glacial map of Norway. — In: Holtedahl, O. (ed.). Geology of Norway. *Norges Geol. Unders. 208.*

Huitfeldt-Kaas, H. 1918. *Ferskvannsfiskenes utbredelse og indvandring i Norge.* Centraltrykkeriet, Kristiania (Oslo).

Johannessen, T.W. 1963. Vær og klima i Norge. — In: Ruud, J.T. (ed.). *Dette er Norge 1814—1964 1.* Gyldendal, Oslo, pp. 65—92.

Johannessen, T.W. 1970. The climate of Scandinavia. — In: Wallén, C.C. (ed.). Climates of Northern and Western Europe. *World survey of climatology 5.* Elsevier, Amsterdam, pp. 23—79.

Johannessen, T.W. 1977. Vær- og klimaforhold. — In: Gjessing, J. *Norges geografi.* Universitetsforlaget, Oslo, pp. 61—126.

Johnsen, S. 1935. Om utbredelsen av vannsalamandrene *(Triton)* i Norge. *Naturen 59,* 97—111.

Kauri, H. 1959. *Triturus vulgaris* (Laurenti). Smooth newt. Mindre vattenödla. — In: Gislén, T. & Kauri, H. Zoogeography of the Swedish amphibians and reptiles with notes on their growth and ecology. *Acta vertebratica 1,* 209—242.

Kauri, H. 1970. Amfibiene. — In: Frislid, R. & Semb-Johansson, A. (eds.). *Norges dyr 3.* Cappelen, Oslo, pp. 314—333.

Leivestad, H., Hendrey, G., Muniz, I.P. & Snekvik, E. 1976. Effects of acid precipitation on freshwater organisms. — In: Brække, F.H. (ed.). Impact of acid precipitation on forest and freshwater ecosystems in Norway. *SNSF research report (Oslo) 1976—6,* pp.87—111.

Lönnberg, E. 1920. Egendomlig förekomst av vattenödla. *Fauna och Flora 15,* 143.

Lönnberg, E. 1925. Et litet bidrag til kännedomen om groddjurens utbredningsförmåga. *Fauna och Flora 20,* 241—249.

Lund, Hj. Munthe-Kaas. 1964. *Dyreliv i vann og vassdrag.* 2. ed. Cappelen, Oslo.

MacArthur, R.H. 1972. *Geographic ecology.* Harper & Row, New York.

Myklebost, H. & Strømme, S. 1963. Land og folk. *Norge 1.* Cappelen, Oslo.

Økland, J. 1969. Om forsuring av vassdrag og betydning av surhetsgrader (pH) for fiskens næringsdyr i ferskvann. *Fauna 22,* 140—147.

Økland, J. 1979. Kalkinnhold, surhetsgrad (pH) og snegler i norske innsjøer. *Fauna 32,* 96—111.

Olsen, O. Dreyer. 1974. *Intraspecifikk variasjon hos liten salamander,* Triturus vulgaris *(Linnaeus), i Skandinavia.* Cand.real. Thesis, University of Bergen.

Pedersen, F. 1968. Maps 4—5. — In: Sømme, A. (ed.). *A geography of Norden.* Cappelen, Oslo.

Pfaff, J.R. 1943. De danske padders og krybdyrs utbredelse. *Flora og Fauna 49,* 49—123.

Pianka, E.R. 1978. *Evolutionary ecology.* 2 ed. Harper & Row, New York.

Simms, C. 1969. Indications of the decline of breeding amphibians at an isolated pond in marginal land. *Brit. J. Herpet. 4,* 93—96.

Sjögren, B. 1947. Vattenödlor skadegörare i fiskdammar. *Svensk Fisk-Tidsk. 1947,* 9—11.

Sjögren, B. 1973. *Våra groddjur, ödlor och ormar.* Zinderman, Uddevalla.

Sjörs, H. 1963. Amphi-Atlantic zonation, Nemoral to Arctic. — In: Löve, A. & Löve, D. (eds.). *North Atlantic biota and their history.* Pergamon Press, Oxford, pp. 109—125.

Smith, M.A. 1964. *The British amphibians and reptiles.* 3 ed. Collins, London.

Statistisk Sentralbyrå 1976. *Environmental statistics 1976. Statistiske analyser (Oslo) 22,* 1—233.

Steward, J.W. 1969. *The tailed amphibians of Europe.* David & Charles, Newton Abbot.

Strübing, H. 1954. Über Vorzugstemperaturen von Amphibien. *Z. Morph. u. Ökol. Tiere. 43,* 357—386.

Sund, T. 1968. Norway. — In: Sømme, A. (ed.). *A geography of Norden.* Cappelen, Oslo, pp. 235—291.

Svärdson, G. & Nilsson, N.A. 1964. *Fiskeribiologi.* Tema, Halmstad.

Terhivuo, J. 1981. Provisional atlas and population status of the Finnish amphibian and reptile spe-

cies with reference to their ranges in northern Europe. *Ann. Zool. fenn. 18,* 139—164.
Udvardy, M.D.F. 1969. *Dynamic zoogeography.* Van Nostrand Reinhold, New York.
Viertel, B. 1976. Die Amphibien Rheinhessens unter besonderer Berücksichtigung der Umgebung von Oppenheim. *Mz. Naturw. Arch. 15,* 183—221.
Vilter, V. & Vilter, A. 1962. Migration de reproduction chez le triton alpestre des Alpes vaudoises. *C.r. Séanc. Soc. Biol. 156,* 2005—2008.
Vogel, Z. 1966. (Transl.: Schierl, M.) *Reptiles and amphibians.* Hamlyn, London.
Wallén, C.C. 1968. Map. 6. — In: Sømme, A. (ed.). *A geography of Norden.* Cappelen, Oslo.
Warwick, T. 1949. The colonization of bomb-crater ponds at Marlow, Buckinghamshire. *J. Anim. Ecol. 18,* 137—141.