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Introduction of the amphipods *Pallasea quadrispinosa* and *Gammaracanthus lacustris* into lakes in northern Sweden

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Two species of glacial relict amphipods have been stocked as fish-food organisms in impounded lakes in Sweden since the 1970s. *Pallasea quadrispinosa* now populates at least ten lakes in the River Umeälven and *Gammaracanthus lacustris* has established sparse populations in two lakes in the River Indalsälven.

The distribution of *P. quadrispinosa* in reservoirs was similar to that in the donor lake, with adults moving to deeper, cooler water in summer. The amphipods had an omnivorous diet, with a preference for zooplankton. They were in turn consumed by the major fish species. They were most important as prey in autumn and winter. Brown trout and Arctic char have become more numerous in the reservoirs, but the mean size of these fish has decreased. Introductions of *P. quadrispinosa* have spread the fish parasite *Cystidicola* sp.

G. lacustris was found in small numbers on deep bottoms in the Håckren reservoir. This species seems to have a two-year life cycle, with the reproductive period starting in summer and ending in winter when the young are released. The adults of this species preyed on zooplankton, chironomid larvae and *P. quadrispinosa*. The only fish species to prey regularly on *G. lacustris* was burbot.

1. Introduction

Several glacial relict crustaceans have been introduced into northern Swedish lakes as part of a scheme to improve food resources for fish in impounded reservoirs. The new organisms include the oppossum shrimp *Mysis relicta* Lovén and the gammarid amphipods *Pallasea quadrispinosa* Sars and *Gammaracanthus lacustris* Sars (Fürst 1981). In Sweden, these glacial relicts usually occur in fresh waters that lie below or just above the former highest shoreline of the Baltic (Segerstråle 1957). The aim was to provide an alternative to the shallow-water invertebrates that had been exterminated by the fluctuations in water level associated with lake impoundment.

The results of the introduction of *Mysis relicta* have been reported by Fürst et al. (1984, 1985, and 1986) and by Lasenby et al. (1986). This paper describes the ecology of the introduced amphipods

in reservoirs, in comparison to that in lakes where they occur naturally. A brief account is given of their importance as prey organisms for fish, and the effects observed so far on the fish populations.

P. quadrispinosa is of freshwater origin and its closest relatives are found in Lake Baikal (Segerstråle 1957). The species reaches a length of 15 to 20 mm and is chararacterized by two pairs of subdorsal spines (Sars 1895). This amphipod is found on the bottom at all depths in lakes and also makes excursions into the water (Sars 1895, Samter & Weltner 1900,1904, Ekman 1915, Decksbach 1927, Thienemann 1928, Valle 1936, Berg 1938, Gordeev 1949, Mathisen 1953, Särkkä 1979). It is sensitive to acidification (Kinsten 1986).

G. lacustris is a large, long-legged amphipod of marine origin, closely related to the arctic species *G. loricatus* (Lomakina 1952, Segerstråle 1957). Bousfield (1989) assigned *G. lacustre* to the new genus *Relictacanthus*. The females, which are larger than the males, reach a length of about 35 mm, and a row of spines runs along the lower part of the back (Sars 1895). These animals are found in lakes deeper than about 30 m (Sars 1895, Ekman 1915, Gordeev 1949, Lundberg 1957, Kinsten 1986). They live on the bottom in the deeper zones and are also found swimming.

2. Material and methods

P. quadrispinosa was stocked in 25 lakes in northern Sweden, and became established in at least 16 (Fürst 1981). The species has spread downstream (Fürst et al. 1986) and may also have been transferred to other lakes by local inhabitants. The donor lake for most of the *P. quadrispinosa* that were stocked was Lake Stora Öfsjön in the province of Jämtland.

G. lacustris was stocked in five lakes (Fürst 1981), became established in the Håckren reservoir in the River Indalsälven and spread downstream to Lake Storsjön (Fürst et al. 1986). The donor lake was Lake Vättern in southern Sweden.

The results presented here are based primarily on studies carried out from 1979 to 1984 in lakes Abelvattnet, Ajaure and Gardiken in the upper stretches of the River Umeälven, where *P. quadrispinosa* is now widespread, and from June to October 1984 in the Håckren reservoir, which has both *P. quadrispinosa* and *G. lacustris* (Table 1).

Amphipods were collected with a beam trawl towed along the bottom, in traps baited with fish-food pellets and in bundles of fishing net left overnight on the bottom. Fish populations were monitored by standardized fishing with gillnets. The most important fish species are brown trout (*Salmo trutta*), Arctic char (*Salvelinus alpinus*) and whitefish (*Coregonus* sp.).

3. Results and discussion

As in the donor lake, water temperature determined the depth at which *Pallasea quadrispinosa* was found. In Lake Stora Öfsjön, in summer the adult amphipods migrated to deeper water where temperatures were below 10°C (Hill 1988b). In the impounded lakes, juveniles were found from 5 to 50 m depth in July and August, while adults

Table 1. Lakes in northern Sweden where the effects of introductions of *Pallasea quadrispinosa* (*P.q.*) and *Gammaracanthus lacustris* (*G.l.*) have been studied.

	Area km²	Depth m	Year impounded	Water level fluctuation, m	Organisms introduced
River Umeälven					
Abelvattnet	34	74	1969	16	*P.q.* 1971
Ajaure	49	37	1967	10	*P.q.* 1971
Gardiken	84	80	1961	20	*P.q.* 1971
River Indalsälven					
Håckren	43	60	1966	27	*P.q.* 1968 *G.l.* 1971

were below 10 m depth at temperatures less than about 11°C. In September, adults were found in water as shallow as 2.5 m. This was reflected in the diet of Arctic char. In summer, only char caught in the deepest parts of the lakes fed on adult *P. quadrispinosa*, while in autumn and winter, char from shallow bottoms also ate the large amphipods (Hill & Forsberg 1986).

The diet of *P. quadrispinosa* in the reservoirs was similar to that in lakes where they occur naturally (Mathisen 1953, Jacobson 1954, Hill 1988b). They mainly consumed cladocerans and copepods, but also diatoms, detritus, mineral particles and chironomid larvae.

P. quadrispinosa was most important as a food organism for fish in autumn and winter (Fürst et al. 1978, Hill & Forsberg 1986). Not only brown trout, Arctic char and whitefish, but also perch (*Perca fluviatilis*), grayling (*Thymallus thymallus*) and burbot (*lota lota*) fed on the amphipods. The quality of the flesh of shallow-dwelling char in impounded lakes seems to be better where *P. quadrispinosa* has been introduced (Hill 1988a).

In lakes Abelvattnet, Ajaure and Gardiken, the introduction of the amphipod has resulted in an increase in the number of brown trout and Arctic char, but a decrease in the mean size of individual fish (Fürst et al. 1986). In particular, the population of stunted deep-dwelling char in Lake Ajaure seems to have become more numerous.

Another consequence of the introductions of *P. quadrispinosa* has been the spread of the nematode *Cystidicola* sp., a parasite of the swimbladder of fish. The worm, which is probably *C. farionis* (Smith & Lankester 1979), infests Arctic char in lakes Ajaure and Gardiken (Fürst et al. 1986) and in some other lakes where *P. quadrispinosa* has been introduced from Lake Stora Öfsjön (Hammar unpubl.). Larvae of *Cystidicola* sp. were found in *P. quadrispinosa* from Lake Öfsjön, and adult worms infest whitefish from the same lake (Hill 1988b).

Gammaracanthus loricatus was caught in the deeper parts of the Håckren reservoir, and the population seems to be sparse. From June to October, most juveniles and all adults were found at or below 40 m, where temperatures were not higher than 8°C. This agrees with earlier descriptions of the species as a cold-water form that lives at great depths (Ekman 1915, Valle 1929, Gordeev 1949, Lomakina 1952). The littoral and sublittoral zones of this lake are also likely to be a highly inhospitable environment, as the amplitude of the water fluctuations may be as much as 27 m (Table 1).

The reproductive period of *G. lacustris* older than one year started in June, when the gonads of both males and females were clearly visible under the dorsal cuticle. Females carried eggs in the brood pouch in August and October, and the young were probably released in winter, as females with empty brood pouches were caught in February (Hill, unpubl.). Previous authors have also concluded that the life cycle lasts at least two years, and that the young hatch in winter (Ekman 1915, 1920, Gordeev 1949, Lomakina 1952).

Adult *G. lacustris* (15–24 mm) were mainly carnivorous. They had eaten cladocerans such as *Daphnia* sp. and *Bosmina* sp., calanoid and cyclopoid copepods, chironomid larvae and *P. quadrispinosa* (Hill, unpubl.).

G. lacustris was eaten by burbot and brown trout, but burbot was the only fish species that fed regularly on the amphipod. Several authors have reported that burbot preys on *G. lacustris* (Nybelin 1935, Gordeev 1949, Vøllestad 1983). The fish populations in the Håckren reservoir are so sparse that no conclusions can be drawn about the effect of the introduction of the two glacial relict crustaceans in this lake.

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