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Freshwater tolerance in the *trachurus* form of three-spined stickleback *Gasterosteus aculeatus* L. in West Norway

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In 1982, an isolated freshwater population of three-spined stickleback *Gasterosteus aculeatus* of the *trachurus* form was found in a park pond within the city of Bergen, Norway. This marine form has hitherto been regarded as unable to survive in freshwater outside the breeding season. Consequently, an experiment was set up to test whether these specimens are physiologically adapted to low-salinity water, also during the winter. Specimens of an estuarine population were used as a control group. No mortality was observed in the park pond population. The estuary control group also showed a better freshwater tolerance than was expected.

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INTRODUCTION

Three-spined sticklebacks *Gasterosteus aculeatus* are well-known for their great phenotypic variation, especially in the number of bony plates along the sides of the body (Bertin 1925, Heuts 1947a, Munzig 1963, Hagen and Gilbertson 1972). According to this characteristic, three different forms have been recognized (Munzig 1959, Hagen 1967). The *trachurus* form has a complete row containing thirty to thirty-five lateral plates. The *leiurus* form has one to nine plates, situated on the anterior part of the body. The third form, *semiarmatus,* covers the range between the two other forms, the plates being divided by a gap into an anterior and a posterior row (Wotton 1976).

Differences in low-salinity adaption capability have been recorded, that are correlated with the differences in body armature. The migratory *trachurus* fish normally do not tolerate low-salinity water outside the breeding season (Koch and Heuts 1943, Baggerman 1957, Lam and Hoar 1967). Heuts (1947b) found that the difference between the two form depended on genetic differences, while Gutz (1970) suggested that the basic mechanism of osmoregulation may be different in *trachurus* and *leiurus* fish due to a difference in their sensitivity to the effects of thyroxine.

In November 1982, we found an isolated freshwater *trachurus* population in a small park pond in the city of Bergen, situated on the coast of West Norway. This finding, apparently in conflict with current conceptions of freshwater tolerance, raised some questions. First, is this population really adapted to a freshwater habitat also outside the breeding season, or is it able to winter in the pond by means of, for instance, the small bottom layer of water with higher salinity? Second, if this is a real adaptation, is this an exclusive property of this population or a general property of the *trachurus* populations in the area? An experiment was set up to answer the questions of low-salinity tolerance, both in the park pond population and in an additional population from an estuary in the area.

MATERIAL AND METHODS

The sample from the estuarine population was taken the 29. Nov. 1982, and the sample from the park pond the 1. Dec. 1982. A fine-meshed seine was used to catch the sticklebacks. The specimens from the estuary were all of the *trachurus* form, and the mean number of lateral plates was 32.79 (SD: 1.24). The fish ranged from 36 to 77 mm. In the sample from the park pond there were in addition to *trachurus* small fractions of *semiarmatus* (3.41 %) and *leiurus* (1.14 %) forms. Only specimens of the *trachurus* type were used in the experiment. The mean

number of plates in the *trachurus* specimens was 31.33 (SD: 1.12), the fish ranging from 49 to 76 mm.

The estuary, situated at Grimstad outside Bergen, is a shallow bay with only a narrow connection to the sea. A brook drains into the bay, creating an estuarine salinity of 17‰ at the time the sample was taken.

The park pond, within the city of Bergen, is a small pond (max. 200 x 20 m), with a maximum depth of 1.5 m. It has an occasionally opened underground outlet to the sea. A permanent connection to the sea was cut off approx. twenty years ago. The salinity is well below 1‰, allowing for a layer of 30 cm just above the bottom in the deepest parts of the pond, in which the salinity goes up to about 9‰. The only other fish species in the pond is a population of Crucian carp *(Carassius carassius).*

In the laboratory, the estuary specimens were kept for one day at a salinity equal to that of the estuary (17‰). The water temperature was allowed to increase from 6.5°C (estuary temperature) to 16°C. This period would enable us to detect mortality caused by stress during catching and transport, or by the rise in temperature. The salinity was then reduced stepwise. After the first day, the concentration was brought down to 10‰, after the second day to 5.5‰, and finally after the fourth day down to 0.8‰.

The park pond specimens were caught two days after estuary ones. They were kept in water of equal salinity to that of the pond (0.6‰) for two days to adjust them to the higher temperature.

When the estuary specimens were acclimatized to the same level of salinity as that of the pond, they were marked by cutting one of the dorsal spines. In each of the two tanks (150 l), 40 to 50 specimens from each population were places together. Mortality was recorded daily, and dead fish removed. The sticklebacks were fed frozen *Daphnia,* which they ate readily. The experiment was terminated after 33 days. However, some specimens from both populations were kept in an aquarium containing water of low salinity all through the winter.

RESULTS

The results of the experiment are given in Figure 1. The park pond population showed no mortality at all from the time they were caught to the time the experiment was terminated.

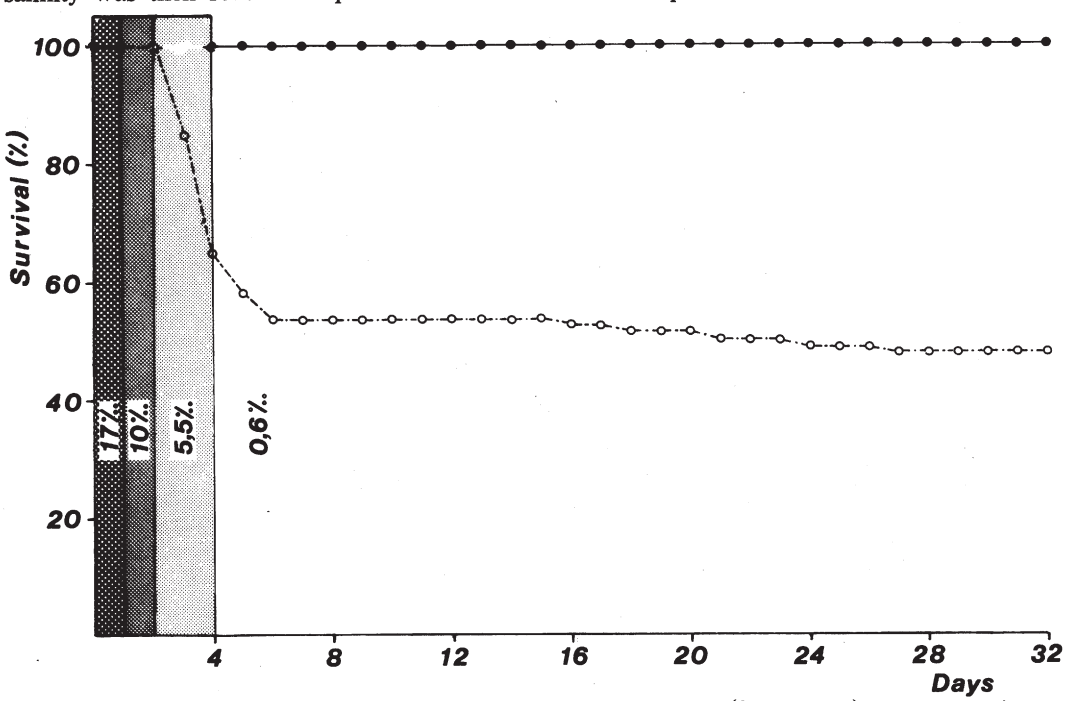

Fig. 1. The figure shows the survival of the isolated park pond population (filled circles) and the estuarine population (open circles) submitted to water of low salinity. The bars represent the period of acclimatization of the estuarine population.

No mortality was observed among the estuary specimens the first day, nor on the second day, with the first salinity reduction. The third and fourth days brought on considerable mortality — 12 and 17 specimens, respectively — when the salinity reduced further.

With salinity down to 0.6 ‰, the fifth and sixth days brought a mortality of five and four specimens respectively. Thus, nearly half of the estuary specimens died during four days of stepwise salinity reduction. From this point on, mortality dropped markedly.

Nine more days brought no deaths, but a slight mortality — five specimens — was recorded from the 16. day to the 27.. Mortality was down to zero for the last five days of the experiment.

After 32 days 100 % of the park pond specimens and 47.6 % of the estuary specimens were still alive. Furthermore, those fish from both populations that were kept in an aquarium for the rest of winter showed no mortality, and specimens from both populations matured in early March.

DISCUSSION

Our results show beyond any doubt that the park pond *trachurus* stickleback population is able to survive in freshwater during the late autumn and early winter. The estuary population also showed a higher survival capacity than was expected, 47.6 % after 33 days. Lam and Leatherland (1969) reported a mortality of about 80 % after only nine days when *trachurus* specimens were transferred from saltwater to freshwater. Furthermore, the mortality among the specimens from the estuary occurred mostly in the period of rapid change in salinity. After the specimens were acclimatized to freshwater, mortality was low. The ability to survive permanently in freshwater seems to be general property also in anadromous *trachurus* populations along the western coast of Norway.

The inconsistency with the current theory can be explained in two ways. First, there is the possibility that high mortality in previous experiments has been misinterpreted as being due to low salinity, when it was in reality caused by rapid salinity changes. For instance, Lam and Leatherland (1969) drew the conclusion of low freshwater tolerance on the basis of a direct transfer of *trachurus* sticklebacks from seawater to freshwater. Our experiment shows mortality occurs just during the period of salinity change. On the other hand, Baggerman (1957) found that *trachurus* sticklebacks reared in the laboratory and kept in freshwater permanently, showed poor survival outside the breeding season. Low survival of the *trachurus* form in freshwater must therefore be a real problem in some populations.

A second explanation is geographical variation in the ability to tolerate water of low salinity. Most of the previous studies have been conducted at the southern coasts of the North Sea, near the southern border of the *trachurus* distribution area in western Europe (Koch and Heuts 1943, Baggerman 1957, Gutz 1970) or in north America (Lam and Hoar 1967, Lam and Leatherland 1969). According to the theory (Munzig 1963) the *trachurus* form has originated in the north. The loss of ability to tolerate freshwater outside the breeding season may be part of the adaptations to survive near the border of its distribution. Therefore, what we observe at the coast of Norway, which is in the centre of the distribution, may be an original property of the *trachurus* form. This is supported by the presence of resident freshwater *trachurus* populations which exist both in southeast Europe (Berg 1949), in north America (Hagen and Gilbertson 1972) and in Norway (pers. obs.).

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