COMPORTEMENT DE FRAYE DE L'OMBLE CHEVALIER, *SALVELINUS ALPINUS* (L.), OBSERVÉ DANS LE LÉMAN A PARTIR DU SOUS-MARIN «F.A.-FOREL».

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RÉSUMÉ

De 1984 à 1989, la fraye de l'omble chevalier, *Salvelinus alpinus* (L.), du Léman a été étudiée à partir du sous-marin «F.A.-FOREL». Ces observations de la fraye naturelle ont été comparées avec celles effectuées par FABRICIUS (1953), FABRICIUS et GUSTAFSON (1954), et FROST (1965), en aquarium ; et celles effectuées par FROST (1965) et SANDLUND *et al.* (1992) dans le milieu naturel. Trois différences principales apparaissent entre les observations effectuées par ces auteurs et celles effectuées dans le Léman : (1) les ombles chevaliers du Léman ne sont pas agressifs, (2) les femelles ne creusent pas de nids, et (3) les femelles sont polygames comme les mâles.

SPAWNING BEHAVIOUR OF THE ARCTIC CHAR, *SALVELINUS ALPINUS* (L.), OBSERVED IN LAKE GENEVA FROM THE SUBMARINE «F.A.-FOREL».

SUMMARY

From 1984 to 1989, the spawning of the Arctic char, *Salvelinus alpinus* (L.), of Lake Geneva, was studied, using the submarine «F.A.-FOREL». The observations made of spawning behaviour in nature were compared with those made by FABRICIUS (1953), FABRICIUS and GUSTAFSON (1954) and FROST (1965) of spawning behaviour in an aquarium, and by FROST (1965) and SANDLUND *et al.* (1992) of spawning behaviour in nature. There are three main differences between the Lake Geneva observations and the ones produced by these authors : (1) the Lake Geneva char is not aggressive, (2) it doesn't dig any nest, and (3) females are polygamous as well as males.

INTRODUCTION

The biology of the Arctic char, *Salvelinus alpinus* (L.), was studied in Lake Geneva from 1984 to 1990 (RUBIN, 1990). Today this population is maintained at its present level by stocking only (RUBIN and BUTTIKER, 1993). The spawning grounds of the Arctic char were described in detail by RUBIN and BUTTIKER (1992). Investigations were performed in order to correlate the success of the natural spawning with the physico-chemical characteristics of the water and the substrate quality of the spawning grounds (RUBIN, 1990). Most of the spawning areas are located at a depth of more than 50 meters, that is to say, beyond the security depth for scuba diving. Therefore, the submarine «F.A.-FOREL» was used, which is operational to a depth of 500 m for several hours without surfacing. During the hours spent on the spawning grounds, Arctic char eggs were sampled and the spawning grounds and spawning behaviour described. This article reports the main observations on the spawning behaviour of the Arctic char in Lake Geneva.

MATERIAL AND METHODS

Location of the study areas

Lake Geneva is situated in the south-west part of Switzerland (Coordinates of the middle of the lake : 46° 27' N, 6° 32' E). Its volume is 88.9 x 10^9 m^3. The maximal depth is 309.7 m and the mean depth is 157.2 m. The «F.A.-FOREL» dived at four different places, where Arctic char usually spawn during winter : Chillon, Veraye, Bouveret and Meillerie (RUBIN and BUTTIKER, 1992).

Dates of the dives

The «F.A.-FOREL» dived two times at Chillon in December 1984. During these dives, the spawning grounds were roughly located and the submarine was tested to establish whether it could be successfully used to observe spawning behaviour. After the success of these test dives, 9 dives took place at Chillon, 2 at Veraye, 5 at Bouveret and 9 at Meillerie. From winter 1984/85 to winter 1988/89, the «F.A.-FOREL» dived 26 times to study the spawning of the Arctic char, remaining submerged for 97 hours 16 minutes.

Technical observation

When the «F.A-FOREL» arrived on a spawning ground, char generally swam away, frightened by the noise of the engine of the submersible and by the light of the projectors. Then, the pilot landed the submarine and stopped the engine, the projectors of the submarine still switched on. The fish came again after a while (2 to 5 minutes) and did not seem to be disturbed. The observation of the spawning behaviour could now begin. The whole dives were recorded on video tapes. Thereby, it was possible to precisely describe each movement of the fish by repeatedly studying the interesting sequences in the laboratory.

RESULTS

On two occasions (Fig. 1A and 1B), during the dives of December 1984 above the PICCARD spawning ground at Chillon, the whole Arctic char spawning behaviour patterns could be observed from courting to spawning. These sequences gave a good example of the general spawning behaviour pattern of the Arctic char observed in Lake Geneva. But on many other occasions, parts of the spawning behaviour patterns were also observed. The following descriptions are a summary of all the observations made on the spawning grounds from 1984 to 1989.

Aggressiveness and territorial behaviour

No aggressiveness between the spawners nor against the other char present was ever observed. It was frequent to see more than 10 fish spawning simultaneously without any fighting. In Fig. 1A, the female was courted by two males, in Fig. 1B by three males. No aggressive acts were ever observed. Neither the males nor the females have any well-defined territories. All the fish swam over the whole spawning ground. Once, the spawning act took place in one area and another time, in another place. No fish seemed to dominate the others.

The Arctic char were only seen to be aggressive towards burbot, *Lota lota*. Burbot live near the spawning grounds and usually predate Arctic char eggs. It was frequent to see Arctic char trying to repel burbot from the spawning grounds. Big females were observed swimming rapidly against the burbot with their gill rakers fully erected. Burbot generally swam away, but came back as soon as the Arctic char had gone away and ate eggs. To find them, burbot often hollowed out the gravel or pushed the stones away. Nevertheless, the stomachs of char caught by fishermen on the spawning grounds often contained some Arctic char eggs too.

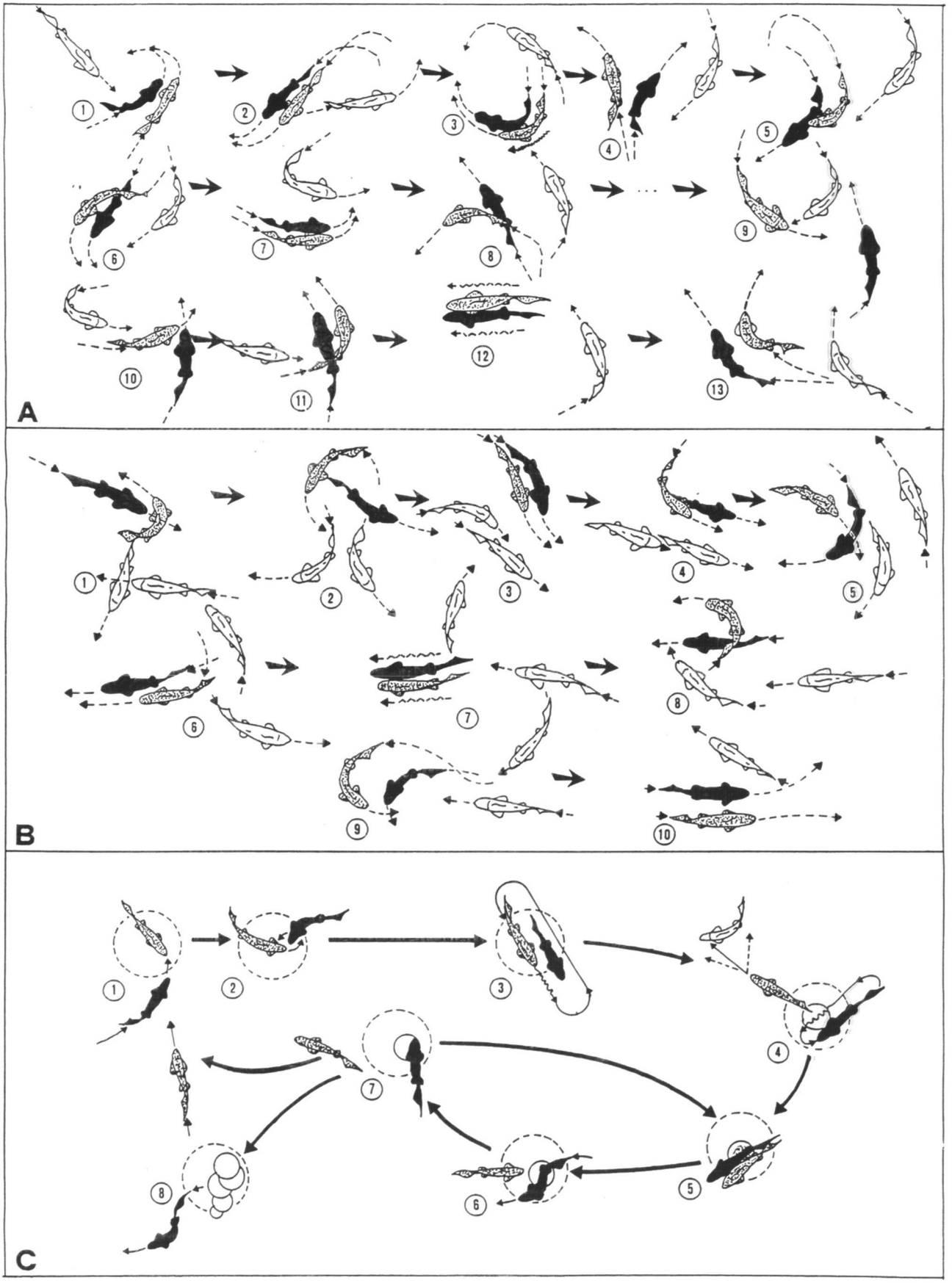
A
B
C

Figure 1 : Spawning behaviour of the Arctic char.
Black fish : spawning female. Dotted fish : spawning male. White fish : other char.

A and B : spawning behaviour observed in December 1984 above the PICCARD spawning ground at Chillon in Lake Geneva. Duration of sequence A : 1 minute 30, B : 1 minute 35. Time between the two sequences : 5 minutes.
C : spawning behaviour observed by FABRICIUS and GUSTAFSON (1954) in aquarium.

C_1 : female entering the territory of the male.
C_2 : fight between the male and the female.
$A_{1\text{-}11}$, $B_{1\text{-}6,\ 8\text{-}10}$, C_3 : pair formation and courting.
C_4 : nest digging.
A_{12}, B_7, C_5 : spawning act.
C_6 : covering of the eggs.
C_7 : if the female still has some eggs to spawn, return to C_5, or C_8.
C_8 : the female guards its nest for some days. The male spawns with another female.

Figure 1 : Comportement de fraye de l'omble chevalier.
Poisson noir : femelle en fraye. Poisson pointillé : mâle en fraye. Poisson blanc : autre omble.

A et B : comportement observé en décembre 1984 sur l'omblière PICCARD à Chillon dans le Léman. Durée de la séquence A : 1 minute 30, B : 1 minute 35. Temps entre les deux séquences : 5 minutes.
C : Comportement observé par FABRICIUS et GUSTAFSON (1954) en aquarium.

C_1 : femelle entrant dans le territoire du mâle.
C_2 : lutte entre le mâle et la femelle.
$A_{1\text{-}11}$, $B_{1\text{-}6,\ 8\text{-}10}$, C_3 : formation du couple et cour.
C_4 : creusement du nid.
A_{12}, B_7, C_5 : fraye.
C_6 : recouvrement des oeufs.
C_7 : si la femelle a encore des oeufs, retour à C_5, sinon C_8.
C_8 : la femelle garde son nid pendant quelques jours. Le mâle fraye avec une autre femelle.

Nest-Digging and spawning substrate

No searching behaviour (FABRICIUS and GUSTAFSON, 1954) or nest digging by females were ever observed. Nevertheless, while diving at the beginning of the spawning season (end of November), floating clouds of sediment were often observed near the spawning grounds. This sediment was deposited during summer over the gravel and swept away by the great swimming activity of the fish over the spawning grounds at the beginning of winter. No Arctic char spawned anywhere except on rocky or gravel bottoms (RUBIN and BUTTIKER, 1992). Substrate samples taken on sand bottoms, or on any substrate other than gravel, never contained any Arctic char eggs.

Courting

Courting was often observed as the trembling, shuddering or quivering movements of the males. The males and the females swam in large circles, about 30 cm above the gravel. The males always swam on the outside of the circles (Fig. 1).

Spawning act and polygamy

Anchoring movements were observed many times. According to FABRICIUS and GUSTAFSON (1954), anchoring is the signal which the female gives when she is ready to spawn. The female swims slowly over the ground, lowering her erected fin down into spaces between the stones and moving forwards until the fin stops against a stone or jams in a narrow crack.

Both male and female Arctic char are polygamous in Lake Geneva. Some big females (30 to 60 cm, TL) were often observed, followed by a cohort of 2 to 8 smaller males (20 to 50 cm, TL). More than one male often seemed to take part successively in the spawning act. When a female had finished spawning, males mated with another female.

The spawning act took place in the same way as described by FABRICIUS and GUSTAFSON (1954) : « *The male approaches the anchored female from behind and glides trembling along her side, but instead of swimming on forwards as in normal courting, he stops or at least swims very slowly when his anal fin comes close by the female one. At this moment he bends his body backwards, trembles vigorously and opens his mouth wide, and both fish simultaneously expel a portion of their sexual products* ». In Lake Geneva, the spawning act lasted 3 to 4 seconds. Spawning acts occurred in series. Female spawned in the gravel, then swam over the spawning ground, being courted again by the males, then spawned again. The time between two successive spawning acts was about 5 minutes. The time between sequence A and B of Fig. 1 was 5 minutes. The spawning act A lasted 1 minute 30 seconds and B, 1 minute 35 seconds.

Protection of the eggs against predators

Females were often observed undulating like a snake after having spawned, sweeping the substrate with their caudal, anal and pelvic fins. The result of this movement was that all the eggs were swept down into the crevices between the stones. After this action, the eggs were less visible to predators, such as burbot.

DISCUSSION

General problems of observing fish spawning behaviour

The studies of FABRICIUS (1953) and FABRICIUS and GUSTAFSON (1954) about the spawning behaviour of the Arctic char are very well documented. These authors captured wild char and described in detail the spawning behaviour of the fish in the aquarium. However, while reading these detailed descriptions there is a question that always arises : is the described spawning behaviour of the fish, observed in the aquarium,

the same as their behaviour would be in nature ? As a matter of fact, the behaviour of an animal is generally differs in nature and in captivity. As far as fish are concerned, it is almost impossible to recreate exactly the same water quality and the same environment in the aquarium as in nature. The size of the tank, for instance, is of the greatest importance. FABRICIUS was, of course, aware of this problem. He wrote in 1954 that the tank used in 1953 was so small (662 dm^3) that the territorial behaviour could not be studied properly. That's why he built a new aquarium in 1954 (5600 dm^3) (FABRICIUS and GUSTAFSON, 1954). FROST (1965) studied the spawning behaviour of the Windermere Arctic char, but the aquarium used was also very small (230 dm^3). Nevertheless, even in very big aquaria, the problem is still the same : the fish are not free.

FROST (1965) had some opportunities to compare nature and aquarium spawning behaviour, because some spawning grounds of Windermere were situated along the shore in shallow water. She found no differences between nature and aquarium spawning behaviour observations. In Lake Thingvallavatn, Iceland, SANDLUND *et al.* (1992) observed the spawning behaviour of the Arctic char in nature by scuba diving.

Because of all the possible behaviour alterations in the aquarium due to the fact that fish are captive, the study of the spawning behaviour in nature appears much more reliable. In the case of the Arctic char of Lake Geneva, the use of a submarine was indispensable, due to the important depth at which the Arctic char spawn. At this depth (60 m and below, RUBIN and BUTTIKER, 1992), no light filters down from the surface. Arctic char spawn in complete darkness. The spawning observations were performed under the light of the submarine projectors. The presence of these lights was the only factor which could have affected the spawning behaviour observed in Lake Geneva.

Aggressiveness

FABRICIUS and GUSTAFSON (1954) observed that males began to show aggressive behaviour very soon after being introduced in the tank (40-55 minutes). FABRICIUS (1953) stated that the frequency of aggressive behaviour increased greatly during the spawning season, particularly among males, but also that aggressive behaviour occurred at all seasons. FROST (1965) observed that males fought and chased one another continually while spawning. In Lake Thingvallavatn, Arctic char showed extremely aggressive behaviour, probably because four different isolated morphs coexist in this lake, some spawning at the same time and on the same spawning grounds (SANDLUND *et al.*, 1992). No aggressiveness between the spawners nor against the other chars present on the Lake Geneva spawning ground was ever observed. FABRICIUS and GUSTAFSON (1954), as FROST (1965), stated that males defended well-defined territories for several days and violently attacked all trespassers. Sometimes, some females also showed this behaviour. In Lake Thingvallavatn, females selected specific spawning sites (SANDLUND *et al.*, 1992). In Lake Geneva, neither the males nor the females have any well-defined territories. FABRICIUS and GUSTAFSON (1954) observed that char were not only aggressive towards each other but also towards the other present species. In Lake Geneva, spawning arctic char are aggressive towards burbot, which is the only other fish species present at this depth during the spawning season.

There are three main reasons to explain this difference in aggressiveness among the studied Arctic char : firstly, all the observations made by FABRICIUS (1953) and FABRICIUS and GUSTAFSON (1954) were performed in aquarium, that is to say in a closed area, where fish could not move anywhere they wanted. In such a context, aggressiveness towards each other probably increases greatly. Secondly, FABRICIUS and GUSTAFSON (1954) and SANDLUND *et al.* (1992) stated that the aggressive behaviour had the double function of keeping the territory free from other char and protecting the eggs against predators. As the Lake Geneva char are not territorial, they do not have to show aggressiveness to chase the other char present. Thirdly, the char studied by FABRICIUS and GUSTAFSON (1954), FROST (1965) and SANDLUND *et al.* (1992) might belong to a more aggressive sub-species than those of Lake Geneva.

Nest-Digging

FABRICIUS and GUSTAFSON (1954) observed that females dug nests and that walnut-sized stones were their favourite material. Before digging, the female always showed a peculiar «searching» behaviour. While searching, females violently fought when they were close to each other. In Lake Geneva, this «searching» behaviour was never observed nor was aggressiveness between the females.

FABRICIUS and GUSTAFSON (1954) described two digging movements and stated that females always dug before spawning, but the result of digging depended on the bottom material. In sand and gravel rather deep circular pits were formed, on bottoms where stones were embedded in sand and gravel the stones were cleaned within a circular patch and the loose material between them was sucked up so that the crevices became very deep, and on rocky bottoms without any loose material no result of the digging movements could be detected. FROST (1965) also observed these digging movements. According to FABRICIUS (1953), all species of the genus *Salmo* dig nests. FABRICIUS and GUSTAFSON (1954) stated that the most important function of the nest-digging movement was to increase the permeability of the bottom material, by sucking up and flinging away the loose material in which the stones were embedded. Nevertheless, FROST (1965) observed that in the genus *Salvelinus* this action seemed to be a poorly developed part of the pattern of the spawning behaviour.

In Lake Geneva, females do not dig nests. Why ? FABRICIUS and GUSTAFSON (1954) indicated that females which were about 30 cm long, were able to throw up stones measuring up to 4 cm in diameter. Once, they observed a stone measuring 9.5 cm in diameter and weighing about 600 g being displaced for about 20 cm by the digging movements of a female, which was 32.5 cm long and weighed 460 g. FROST (1965) observed that eggs were frequently found in spawning grounds where fist-sized, head-sized or even larger stones predominated, but also that the two last-mentioned could not possibly be moved by a char. Most of the Lake Geneva spawners are between 30 and 40 cm long. According to FABRICIUS and GUSTAFSON (1954), they should be able to throw up stones up to 4 to 10 cm in diameter. The substrate of the Lake Geneva spawning grounds is composed of stones generally being 5 cm to fist-sized in diameter (RUBIN and BUTTIKER, 1992). Consequently, these stones are probably too big to be thrown up by the char. That's probably why the Lake Geneva Arctic char does not dig any nests.

This lack of nest digging does not seem to be an exception. The char of Sunapee Lake also spawn without digging nests (KIRCHEIS, 1976). DEMPSON and GREEN (1985) observed that char of Fraser River only dug nests if the stones of the spawning grounds were smaller than 10 to 20 cm in diameter. SANDLUND *et al.* (1992) observed in Lake Thingvallavatn that the females cleaned the substrate from sediment. This behaviour was also observed in Lake Geneva at the beginning of the spawning season. Nevertheless, these authors do not describe any nest digging. As in Lake Geneva, according to the pictures presented in their article, the diameters of the lava stones were probably to big for the fish to be able to dig a nest.

Courting

FABRICIUS and GUSTAFSON (1954), FROST (1965) and SANDLUND *et al.* (1992), described the same courting behaviour as the one observed in Lake Geneva. The only difference between FABRICIUS and GUSTAFSON (1954) observations and the Lake Geneva ones is that in the aquarium the male first attacked the female which invaded the guarded territory and only afterwards courted her more and more. In Lake Geneva, no such aggressiveness was ever observed.

Spawning act

The spawning act described by FABRICIUS and GUSTAFSON (1954), FROST (1965) and SANDLUND *et al.* (1992) was exactly the same as the one observed in Lake Geneva. The spawning act lasted less than 10 seconds according to FABRICIUS and

GUSTAFSON (1954) observations. They also observed that the spawning acts usually occurred in groups of 1 to 5 acts, (4 to 7 according to FROST 1965). The intervals between the successive acts of a group varied from 30 seconds to 9 minutes (mean : 2.5 minutes). That is to say about the same timing as the ones observed in Lake Geneva (5 minutes).

Polygamy

FABRICIUS and GUSTAFSON (1954) indicated that males were polygamous but that females could not spawn with more than one partner because of the high pugnacity between the males. Contrary to this, in the Lake Geneva spawning grounds, males did not show any aggressiveness and thus females were allowed to be polygamous too. KIRCHEIS (1976) also observed for char of Sunapee Lake that «*more than one male (2-4) accompanies each female, swimming just behind and off the side as she moves over the spawning site*». In Lake Thingvallavatn, SANDLUND *et al.* (1992) stated that usually a female was surrounded by a group of males, but one (the guarding male) defended her against potential intruders, the satellites. The satellites employed a sneaking technique both to court the female and to join in with a spawning pair. In Lake Geneva, no marked difference between guarding and satellites males was ever detected.

Protection of the eggs against predators

The particular way the females in Lake Geneva swam, sweeping the eggs down in the substrate after oviposition, was also described by FABRICIUS and GUSTAFSON (1954) and SANDLUND *et al.* (1992). This seems to be a usual behaviour to prevent the predators from finding the spawned eggs.

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