ICES STATUTORY MEETING 1993

C.M.1993/M:21
Anadromous and Catadromous Fish Committee

A METHOD OF OBSERVING THE SPAWNING BEHAVIOUR OF FARMED AND WILD SALMONIDS IN A NATURAL STREAM HABITAT

by

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ABSTRACT

When farmed fish escape from farms, they may compete with wild individuals for a number of resources, such as food, spawning sites, and mates. As a part of a larger study on genetic impact from farmed fish on wild populations, the spawning behaviour of released farmed brown trout was observed. A 6 by 4 m net enclosure with a steel frame (scaffolding) was placed in the middle of the spawning area of wild brown trout in River Øyreselv, and secured well to resist flows and strong currents. The lower part of the net was kept tight to the river bed by a steel chain and lead weights. A Seametrix underwater video camera with remote-controlled focus and tilt was set up in the middle of the enclosure, about 15 cm above the bottom. The camera was connected to a monitor and the behavioural sequences were recorded on a Thomson U-matic portable videocassette recorder. Five male and five female mature farmed brown trout were released within the enclosure together with wild spawners. Both wild and farmed fish were also studied outside the enclosure. The spawning behaviour of farmed trout is described and compared to the behaviour of wild brown trout. The farmed trout displayed basically normal spawning behaviour, though this was less vigorous than that of wild trout. The different behavioural patterns previously reported for spawning brown trout, such as courting and quivering, testing of the spawning substrate, digging, gaping, and release of milt were observed in the farmed brown trout. Aggressive behaviour and sneaking behaviour by small wild males were also recorded. Finally, viable offspring of farmed trout were collected.

Introduction

Observations of escaped farmed salmon in salmon rivers have led to a discussion concerning the spawning success of escaped farmed fish and the potential harmful genetic effects on native populations. In Norway a programme to record the number of farm-origin fish in coastal areas, fjords and rivers is running. In several cases the numbers and proportions of mature fish that originate from farms are substantial (Anon. 1989; Hansen and Jonsson 1990), and in some rivers even spawned escapees have been found (L'Abee Lund, 1988). Is there then any reason to doubt that escaped farmed fish reproduce successfully, and spawn among themselves or with wild fish? Different opinions have been expressed, but so far there are few observations of spawning behaviour of farmed individuals in natural habitats, and little empirical data on the reproductive success of escaped or released farmed fish.

The farm environment could theoretically, influence the spawning behaviour of farmed fish at two different levels. First, the absence of natural stimuli such as predators, and lack of exercise could cause the farmed fish to be less fit and to move more slowely than wild conspecifics. This might in part explain why escapees have been reported to stop in the lower areas of a river (Anon. 1989; Gudjonsson, 1991; Webb et al. 1991). Secondly, to the extent that components of behaviour are influenced by genetic variability, selection and genetic drift in the hatchery population could change the behaviour of the fish. In that case farmed fish would be at a disadvantage in intrasexual competition with wild fish. Vincent (1960) and Moyle (1969) compared the behaviour of wild and farmed brook trout and found behavioural differences between wild and farmed stocks, as the wild fish had a tendency to remain near the bottom of their trough, while domestic fish spread vertically through the water column. Further, it has been found that Atlantic salmon juveniles of farm origin are less aggressive than wild juveniles, and are also less capable of defending territories (Norman, 1987). A study on the timing of migration of rainbow trout revealed a shift towards an earlier return to the river in the cultured population (Rosentreter, 1977).

However, regardless of the ultimate cause of changes in behaviour, be it environmental or genetic, the result on the spawning ground will be the same, a reduction in reproductive capability. The present observations form part of a more comprehensive investigation in which genetic markers are included to quantify gene flow from farmed fish to wild stocks, (Skaala, Dahle, Jørstad & Nævdal 1990; Skaala, Jørstad & Borgstrøm 1992). A prerequisite for genetic impact, however, is adequate spawning behaviour in natural habitats.

Observations conducted under laboratory conditions may suffer from a number of deviations from the conditions in natural habitats, and an extrapolation may sometimes be questioned. On the other hand, experimental studies of behaviour are difficult to conduct in natural habitats. This is partly due to the lack of physical confinement, the large number of individuals, and the possibility of the experimental animals to move in and out of the observation area, and lack of biological information on the observed individuals. As it was not known if the farmed fish would demonstrate a spawning activity at all, the aim of the study was to observe and describe the behaviour of mature farmed brown trout in a natural spawning habitat. As the discussion and the technical solutions may have relevance in several freshwater and anadromous fish species, the technical set-up is described and reported separately.

Materials and methods

The spawning area
The area chosen for the investigation (Fig. 1) is located 200 m above a waterfall, which is impassable to ascending fish. There are both riffles and pools in this part of the river, and the bottom is composed of gravel and stones suitable for spawning. Observations of spawning wild brown trout, and a high concentration of 0+ juveniles detected by electrofishing, indicated that this part of River Øyreselv, western Norway, is a natural spawning area for wild trout. The temperature in the river during the observations was 7-8 degrees C. The current velocity ranged from 30 to 80 cm/sec., and the water depth varied between 0.1 and 1.2 m. during the period of observation.

The technical set-up
In autumn 1989, a 6 by 4 m net enclosure (Fig. 2) with a steel frame (scaffolding) was placed in the middle of the spawning area, and secured well to resist flows and strong currents. The lower part of the net was kept tight to the river bed by a steel chain and lead weights. A Seametrix underwater video camera with remote-controlled focus and tilt was set up in the middle of the enclosure, about 15 cm above the bottom. The camera was connected to a monitor and the behavioural sequences were recorded on a Thomson U-matic portable videocassette recorder. Video recordings were also made outside the enclosure by freehand filming using a neoprene wetsuit with mask and snorkel. The clear water gave good resolution of details on the tapes. The fish were allowed to acclimatize to the new environment for 8 days before recordings began. Observations were mainly carried out between 10 a.m. and 5 p.m., in the period 5th October to 1st November 1989, giving approximately 180 hours of observation. A 24-hour observation period using a light-sensitive video camera was also included in order to obtain an idea of diurnal activity rhythms.

The trout
The farmed fish were chosen from a genetically marked population, kept at the Institute of Marine Research under standard rearing conditions. Prior to the release, the farmed trout had only experienced the inside of a glassfibre tank with a high density of fish, and a low water velocity. Ten mature individuals, 5 males and 5 females, were selected from the cultured population and released into the enclosure, while 8 females and 30 males were tagged and released in the river outside the enclosure. Females ranged in total length from 312 to 370 mm and males from 320 to 363 mm. The condition factor varied from 1.16 to 1.47. Each fish was tagged with Floy anchor tags, males with blue and females with red tags. Further, six wild trout (one female and five males) ranging from 170 to 200 mm in length were captured and released into the enclosure.

Results

Observed behavioural patterns
The following behavioural patterns were observed in connection with spawning (Table 1): *Quivering:* The male quivered his body for some seconds when courting. *Feeling:* The female made repeated contacts with the substrate with the anal and pectoral fins. *Cutting or digging:* The female turned over on her side and dug a nest by beating or flapping her body and caudal fin. *Bouncing:* The female moved slowly up and down in the nest. *Crouching:*

Before spawning the female bent her body and pressed the posterior part towards the substrate. *Gaping:* A fish opened up its mouth widely, just before or during spawning. When spawning, the male and female made synchronous quivering and gaping movements. *Sneaking:* Wild small males stole up on a female in the nest. In addition, aggressive behaviour (attack and lateral display) by the dominant male towards subordinate males was observed.

Observations in the enclosure
During the observation period three of the five farmed females made a nest. Among the farmed males, one dominant male defended and courted the females at the nest, although other males also attempted to do so. The wild males adopted a sneaking strategy. The courting and spawning activity observed lasted from two to eight days for individual females. The wild female did not spawn though she was full of ripe eggs after the observation period. Spawning took place in the day-time, with maximum activity around 13.00 to 16.00. The 24-hour observations revealed that the fish were passive at night and stayed motionless close to the bottom.

A comparison between the behaviour patterns observed in this study and those reported in previous studies on trout and other salmonids is given in Table 1. Most behaviour patterns of wild brown trout described by Jones and Ball (1953) were also recorded in this study of farmed trout. The exception is "covering", when the female "moves upstream immediately after ejaculation and covers up the eggs with vigorous cutting activity" (Jones and Ball, 1953). Covering was not observed in our study in spite of its prevalence in salmonids (Table 1). Another difference concerns sneaking, which was not described by Jones and Ball (1953), as they had no small males in their observations. Sneaking behaviour, however, has since been described in other salmonids (Table 1). With one exception, the farmed trout thus displayed the same behavioural repertoire as has been reported for wild trout.

Courting and spawning
For successful reproduction to occur, it is essential that the male and female also synchronize actual spawning. The farmed male courted the females when they prepared for spawning with cutting, feeling, bouncing and crouching. The male would then swim forwards and quiver in line with the female's pectoral fins, with the body parallel to the female. The female responded by rising above the nest, cutting or doing nothing. This has also been observed in wild trout (Jones and Ball, 1953). Gaping, which is associated with release of eggs and sperm in wild trout, was observed in all farmed females with a nest. The gaping of the female was initiated by quivering and gaping of the male, but the degree of gaping could differ. When the male and female simultanously quivered and gaped with high intensity, it was regarded as a complete spawning. In several cases a faint cloud of milt could be seen. Thus, the farmed males and females appeared to be well synchronized.

Spawning competition and aggressive behaviour
It has been suggested that farmed males might differ from wild fish in their ability to compete successfully for females. In the present study, a dominant male generally did not permit other males in the vicinity of the female in the nest, and approaching males were immediately chased off. However, in three cases a subordinate male courted a spawning female in the absence of the dominant male. It was also observed that the dominant male did

not always attack other males intruding the vicinity of the female, and in 12 out of 75 cases (16%), the dominant male did not attack, but made only lateral displays or no response at all. Furthermore, now and then the subordinate males were observed to bite the female, which sometimes caused her to leave the nest. Aggressive behaviour by female trout was also observed in this study, and attacks by spent females towards males and ripe females were recorded. The dominant male was also observed to attack sneaking wild males, and with the great difference in size between farmed and wild males in this study, farmed males thus competed successfully with wild males.

Sneaking
Some of the small wild males captured in the river and transferred to the enclosure adopted a sneaking strategy. When caught, these wild males had the colouration commonly found in resident trout in running water, but they soon developed a camouflage pattern with large alternating dark and light patches. Watching the courting and spawning of the larger farmed trout, they tried to swim close to the farmed female in the nest. The sneakers were often chased by dominant males, but in several cases when the dominant male was absent, the sneakers were seen courting a female without being attacked. One sneaker resumed its position some distance from the female after several unsuccessful courtings. During 15 incomplete gapings one female was alone with the dominant male outside the field of observation. Sneaking wild males were then sometimes observed beside the female.

Observations outside the enclosure
During the diving survey two hours after the release, the farmed fish were seen mixing with wild fish at the spawning area as well as in the large pool above the spawning area (Table 2). The farmed trout were also seen in the main stream where current velocities ranged between 60 and 80 cm/sec.

Hierarchies including farmed females, a dominant farmed male and several subdominant wild males were observed. The speed of the movements and the intensity of aggression seemed somewhat higher in wild individuals than in farmed fish. The farmed male holding the dominant position close to the female never attacked and was never attacked himself.

In one case, when farmed males were absent, the largest wild male was dominant. He courted a farmed female, and defended his position against other males. On another occasion a farmed male held a dominant position close to a female, while a subdominant wild male positioned close to the farmed male. No attacks were seen between these two males; the farmed male left his position from time to time, and only the wild male was seen to quiver towards the female. Although sneakers were chased by both farmed males and females, they sometimes managed to get close to the female and quiver with high intensity. In one case a farmed male was passive towards the female and seldom approached when the female was cutting. Wild males but no farmed males were observed quivering towards this female. One farmed female was observed redigging a nest, and eggs were carried downstream by the current. In the sample of 0+ fry collected during the summer and autumn the following year, viable offspring of both farmed and wild trout were found.

Discussion and conclusions

The technical set-up worked well, although a few improvements could be made. Organic material carried by the current had to be removed from the net regularly. This problem could be reduced by altering the shape of the enclosure, especially the upstream side, in such a way that the current would hit the net by an angel of 45 degrees or less.

The spawning behaviour of the farmed trout included the same behavioural components as have been described for wild trout (Jones and Ball, 1953), the only possible difference being that covering of spawned eggs by farmed females was not recorded in the present study. However, the lack of covering is, however, not necessarily linked to genetic changes caused by the hatchery environment. It has been observed that females preparing nests stop digging if they encounter a layer of clay which is not suitable for the eggs (Crisp and Carling 1989). In our study, however, the females continued their activity and spawned.

Another prerequisite for successful spawning is the synchronous release of eggs and milt. In connection with spawning of the last female observed, it was repeatedly seen that the female quivered and gaped in the absence of males or that the male was present but responded too slowly or not at all. Jones and Ball (1953) occasionally observed gaping in one wild female trout when alone. This may be an example of bad timing between the sexes. Usually, however, the farmed females responded adequately to the courting of the males.

An important point in the discussion of successful spawning is intrasexual competition. Intense competition for females is common in many salmonids. The farmed males showed aggressive behaviour in the enclosure, and one male managed to monopolize a female. The farmed males also completely dominated the wild males, possibly as a result of the great size difference in this experiment. Outside the enclosure, a large farmed male was seen to have a high rank in the hierarchy around a spawning female, without trying to court her. Although not quantified in our observations, the impression of slow movements and lower intensity in aggressive behaviour would result in a competitive disadvantage for the farmed males. A competitive disadvantage for farmed fish has been observed in a tank experiment with Atlantic salmon (Järvi et al, 1990) and in Pacific salmon (Fleming and Gross, 1990).

Sneaking is regarded as an alternative strategy to fighting for access to females and reproduction. Therefore, small mature males or sneakers (in wild as well as in farmed populations) may represent a mechanism for transfer of genetic material from farmed to wild populations. The presence of small mature males has been reported for several brown trout populations (Jonsson 1989; Crisp and Carling 1989), and sneaking behaviour has been described in brown trout (Crisp and Carling 1989) as well as in several other salmonids (Briggs, 1953; Carlson, 1957; Keenleyside and Dupuis, 1988). However, the dark camouflage patches observed in sneaking brown trout in the present study (Fig. 3), is the first direct observation of this camouflage pattern in brown trout. Wild trout that were not sneaking in the enclosure did not display the pattern. Furthermore, during snorkel surveys made before and after the spawning season, this type of camouflage was not observed. It was only seen at spawning grounds during the spawning season. This camouflage pattern is very different from parr marks which are also believed to have a camouflage function, making the fish more cryptic (Donnelly and Dill 1984). It is possible that two forms

of crypsis have different selective values in different habitats or at different life stages. In the spawning habitat, which included large stones covered with dark moss, the patchy camouflage may be less visible than parr marks.

The overall conclusion of this study is that the mature farmed trout acclimatized rapidly to the natural environment, and that they mixed with wild trout in spawning activity. However, although we did not quantify this, we gained an impression of slower movements and lower intensity in the spawning activity of the farmed males compared to wild males. The farmed trout exhibited largely normal spawning behaviour, as most previously reported behavioural patterns were observed, and viable offspring from the farmed trout were found.

Acknowledgements

Stein Mortensen and Kjærand Nesvik are acknowledged for drawing assistance. Valuable comments from Harald Sægrov on the manuscript were highly appreciated. We would also like to thank Eva Farestveit, Ole Ingar Paulsen, Gunnar Bakke and Harald Næss for helping with the video recordings. We further acknowledge Ola Halrynjo, Laila Unneland and Hari Rudra for their professional care and handling of the genetically marked trout.

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Table 1. The most common components of spawning behaviour reported in three salmonid species, Salmo salar, S. trutta, Oncorhynchus keta. "-" indicates lack of description in referred literature.

Behaviour	S. salar	S. trutta	O. keta
Quivering	2,3	3,5	1,4
Cutting	2,3	3,5	1,4
Crouching	-	3,5	-
Feeling	2	3,5	4
Gaping	2,3	3,5	1,4
Covering	2,3	3	1,4
Aggression	2,3	3,5	1
Sneaking	2	5	-

1: Briggs, 1953; 2: Carlson, 1957; 3: Jones and Ball, 1953; 4: Tautz and Groot, 1975; 5: this study.

Table 2. Observations on behaviour at different sites outside the enclosure during the peak of spawning in 1989. F: dominant farmed fish, W: dominant wild fish, w: satellite male, wh: wild male hierarchy (usually 6-10 males), smc: sneaking male with camouflage.

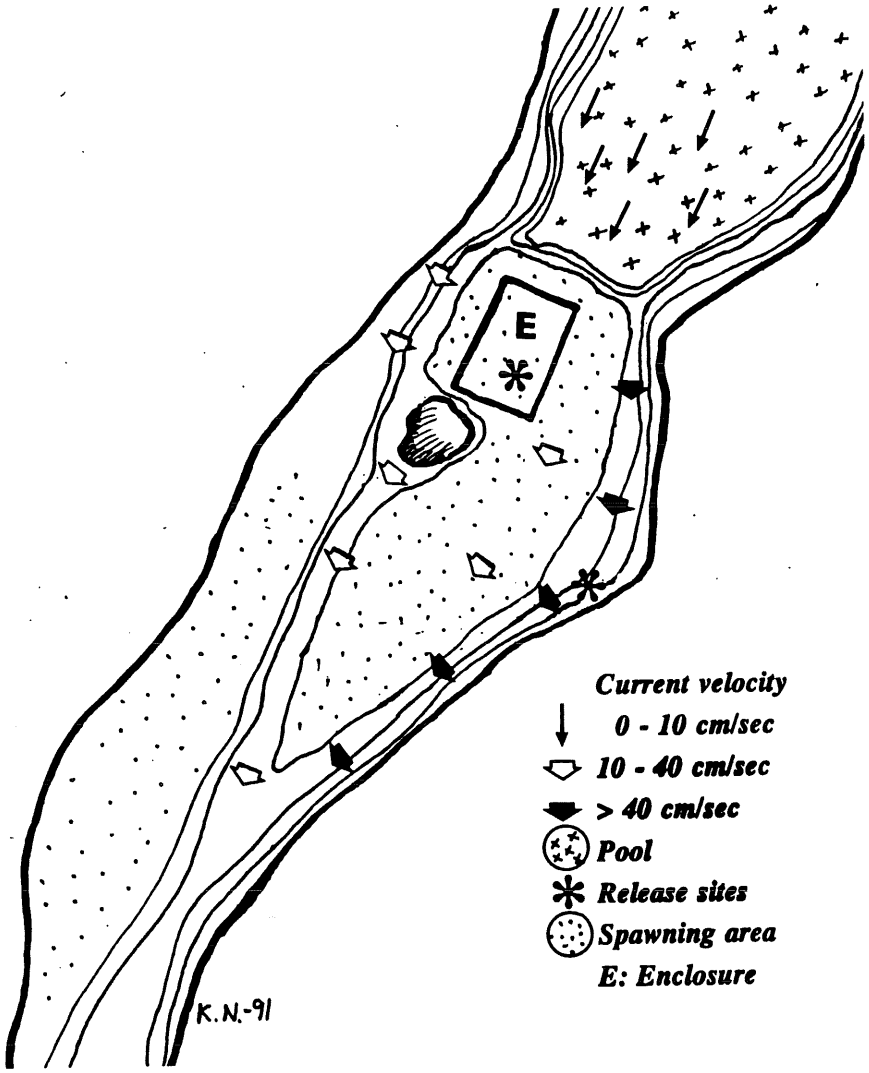
Site no.	Males	Females	Behaviour
1	F, 2-3w	F	Feeling, agression
2	F, wh	F	Feeling, cutting
3	F, W, wh, smc	F	Feeling, cutting agression, quivering sneaker quivering
4	F, wh, smc	F	Feeling, cutting, agression
5	W, 3-5w	F	Feeling, cutting agression, quivering
6	F, wh, smc	F	Feeling, agression
7	Redd		
8	Redd		
9	Redd		
10	F, wh, smc	F	Feeling, cutting, agression
11	F, 3-6w	F	Feeling, cutting, agression
12	F, wh, smc	F	Feeling, agression
13	F, wh, smc	F	Feeling, agression

FIGURES

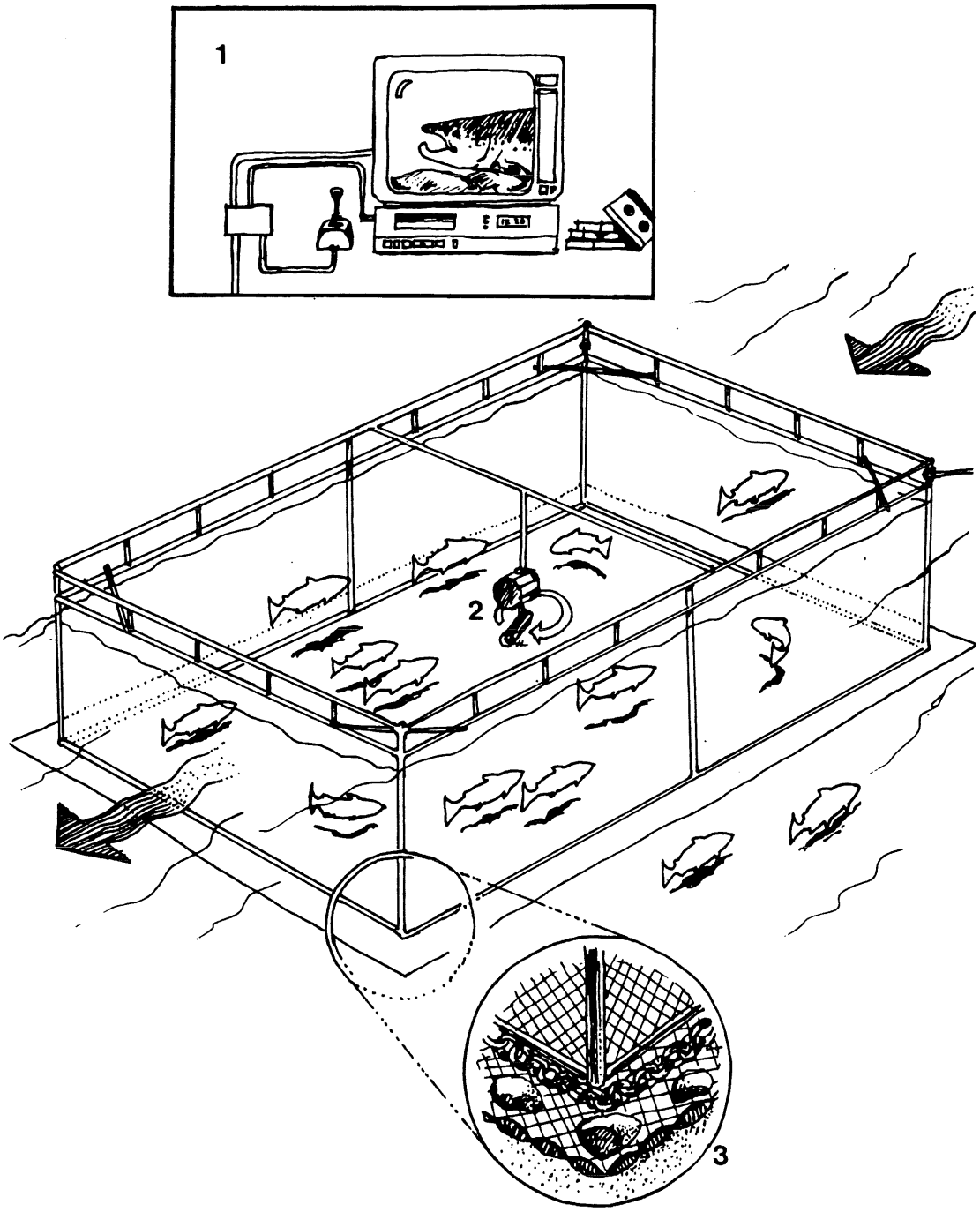
Fig. 1. The spawning area.

Fig. 2. The spawning enclosure in River Øyreselv and the video set-up. 1: monitor and joystick controlling the video camera, 2: position of the camera, 3: steel-chain, stones and lead used as weights to keep the net close to the substrate.

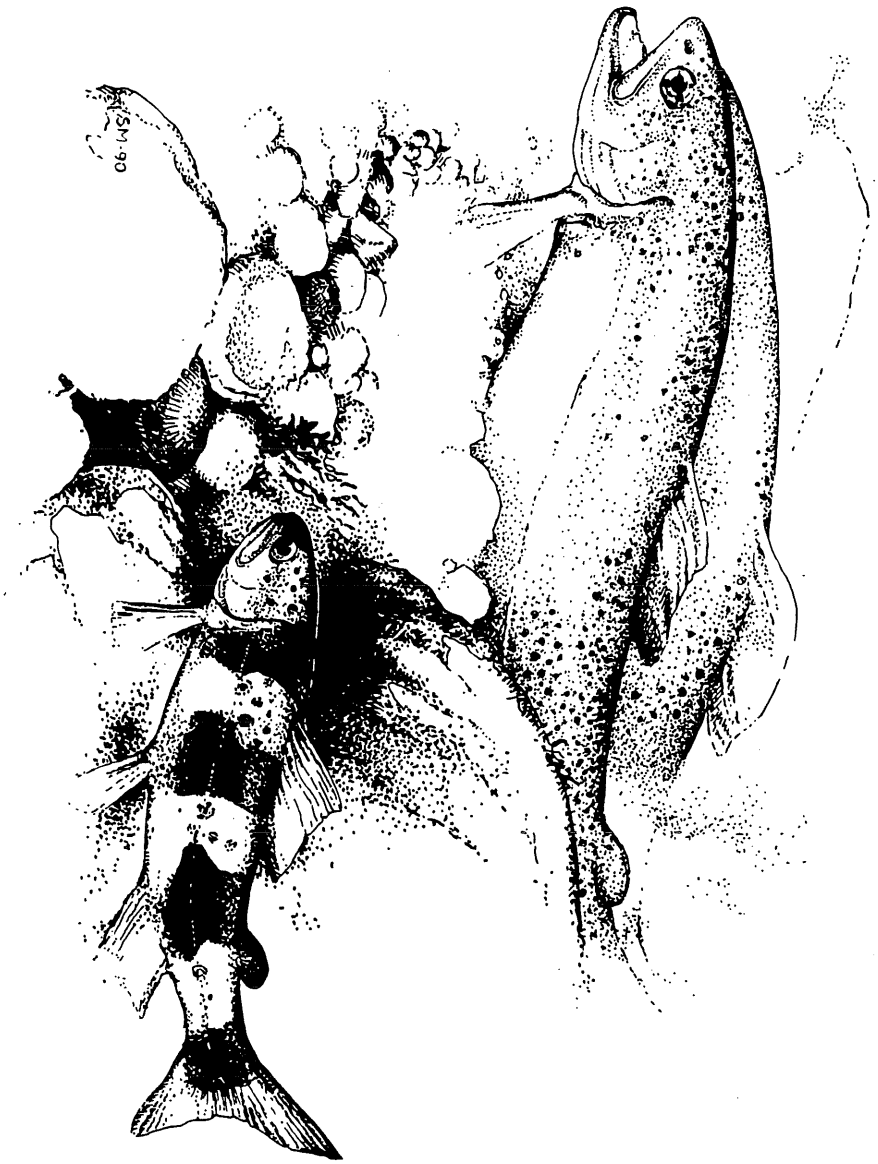
Fig. 3. Wild brown trout sneaker displaying camouflage pattern, and farmed spawners. (Drawn by Stein Mortensen from video recordings).



Skoda et al. Fig 1.



Skala ad fig 2.



Skaala et al fig 3.