ARE REARED JUVENILES FIT FOR RELEASE INTO THE WILD?

by

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ABSTRACT

The main question that has to be raised when planning to enhance natural fish populations is whether reared fish are fitted for a life in the wild, or more specifically, whether there are differences between reared and indigenous fish. There are many published examples of observed differences between reared and wild individuals. The causes and effects of these differences are discussed. Results from the Norwegian enhancement programme, comparing reared and wild individuals of Atlantic salmon, *Salmo salar* L., Atlantic cod, *Gadus morhua* L., and European lobster, *Homarus gammarus* L. are discussed in the light of other results in the literature.

Introduction

A critical phase in sea ranching programmes is the transition from the hatchery to the wild. In the wild, animal will try to optimise their feeding depending on the availability of prey, and the probability of being eaten. An important question is therefore if reared cod or lobsters have developed normal feeding and anti-predator behaviour compared to their wild counterparts. Releases of individuals with unnatural behaviour, may result in reduced survival rates. If the aim of a release programme is to enhance recruitment to overfished populations, the released animals must also have natural spawning behaviour, so that it can contribute to reproduction.

Several factors, such as the price and quality of juveniles and the value of recaptured fish, will decide whether a sea ranching project can be economically feasible or not. Usually, there will be a close correlation between the quality of the juveniles and their prospects of survival in the sea. The quality of the juveniles should then be a key factor in the development of ecologically and economically based sea ranching programmes. It is important to stress here that good quality fry, fit for sea ranching, are not identical to good quality fry for net pen rearing. Some qualities might be the same (e.g. resistance to disease), while many will be different. This is easy to understand when we think of the completely different environments of the hatchery and the wild.

In this paper I will start by looking at morphological and behavioural differences between reared and wild individuals, and at the possible causes of these differences. I then go into more details regarding results with Atlantic salmon, *Salmo salar* L., Atlantic cod, *Gadus morhua* L., and European lobster, *Homarus gammarus* L. I will discuss results from the Norwegian enhancement programme (Anon. 1989) in the light of other results in the literature.

Differences between wild and reared fish

A survey of the literature reveals many well-documented examples of morphological and behavioural differences between wild and reared fish and crustaceans (e.g., Blaxter 1970,1975, Browman 1989). Differences caused by the rearing environment should, however, be separated from differences caused by local adaptation, where populations have evolved different lifehistory strategies that can be attributed to inter- or intra-species interactions, and environmental heterogeneity. Comparative studies should therefore always be carried out using animals from the same area.

Morphological differences

Morphometric characters often change with exposure to different environmental conditions (Browman 1989). It is therefore expected that there will be morphological differences between reared and wild individuals as shown in Table 1. For sea ranching it is of the greatest interest to focus on morphological changes that may affect feeding and anti-predator behaviour. Reared individuals are also often characterised by unusual pigmentation, and altered coloration may

increase the risk of predation. Landeau and Terborgh (1986) showed that dyed silvery minnows, *Hybognathus nuchalis*, in schools of undyed fish were eaten more often than their schoolmates.

Although most of the literature deals with morphological differences that may have negative effects on the reared individuals after release, there are few documented examples of increased mortality that can be attributed to such changes. This may be due to problems of method, and should not be taken as a proof of "no effect". In sea ranching programmes, efforts should, on the contrary, be put into diminishing unnatural morphological development and coloration.

Table 1. Examples of morphological differences between reared and wild individuals.

Species	Morphological characters	Ref.
Lined sole (*Achirus lineatus*)	Incomplete eye migration, Fin abnormalities, ambicoloration, partial albinism.	Houde 1971
Several species	Several morphological characters	Blaxter 1975
Ayu (*Plecoglossus altivelis*)	Morphological deformities	Komada 1980
Red Sea Bram (*Pagrus major*)	Body height, eye diameter, upper jaw length, and other morphometric measures.	Matsumiya *et al.* 1984
Masu salmon (*Oncorhynchus masou*)	Structure of the head skeleton	Romanov 1984
Haplochromis squamipinnis (Pisces, Cichlidae)	Premaxillae	Witte 1984
American lobster (*Homarus americanus*)	Differentiation of the claws	Govind and Pearce 1986
Jack Mackerel (*Trachurus japonicus*)	Several morphometric measures	Suda *et al.* 1987
European lobster (*Homarus gammarus*)	Differentiation of the claws	Wickins 1986
Red Sea Bream (*Pagrus major*)	Numbers of vertebrae, pleural and dorsal ribs and fin rays. Bone abnormality.	Matsuoka 1987

Behavioural differences

The development of any particular item of behaviour is determined by both genetic and environmental factors (Huntingford 1986). Throughout their life cycles, animals must modify their behaviour according to the risk of predation and the availability of prey organisms. Recently released fish show different feeding behaviour from wild fish in the first period after release, and it can take several months before their ability to capture wild prey is as effective as that of wild individuals. This has been documented both for salmonids (Sosiak et al. 1979, Shustov et al. 1981, O'Grady 1983, Bachman 1984, Johnsen & Ugedal 1986; 1989), and for Atlantic cod (Nordeide and Salvanes 1991, Kristiansen and Svåsand 1992).

Normal anti-predator behaviour after release is important in stock enhancement programmes. Several studies have shown that most of the major components of the agonistic repertoire appear in isolated fish at the normal age, although these are often poorly coordinated and wrongly oriented (Huntingford 1886). Experience with predators will often strengthen antipredator behaviour, as has been shown for sockeye salmon (Oncorhynchus nerka), Ginetz and Larkin (1976); zebra danio (Brachydanio rerio), Dill (1974); European minnow (Phoxinus phoxinus), Magurran (1990), coho salmon (Oncorhynchus kisutch), Patten (1977), Olla and Davis (1989), and others. Predator training can therefore be a way of increasing the survival of released fish.

The selection pressure for some traits is often higher and differently directed in nature than in a laboratory tank. Reared individuals might therefore be less well adapted to life after release than their wild conspecifics (Wales 1954).

Another difference is the use of formulated feed in the hatchery. Artificial feed is often different from the natural prey organisms. Romanov (1984) showed that significant differences in the structure of the head skeleton of cultured and wild juveniles of masu salmon, Oncorhynchus masou. He attributed these differences to the culture conditions, and in particular to the diet of artificial feeds used.

Blaxter (1970) suggested that marine larvae reared in tanks are almost certainly deprived of sufficient sensory input for the proper development of their sense organs and their associated areas in the central nervous system, and that social stress in a crowded situation may lead to abnormal behaviour and undesirable morphological consequences. This was followed up by Browman (1989) who discussed ontogenetic critical periods in fish. Critical periods refer to restricted periods during development when the organism is especially sensitive to missing or unnatural types of stimulus. If these natural stimuli are not given during a critical period, lasting changes in the phenotype or behaviour can take place. Browman (1989) provides several examples from critical periods in embryology, ethology and ecology, from both fish and other animal groups.

Conclusion general part

From the above data, we can be conclude that an artificial rearing environment will produce individuals that differ in some traits from wild individuals. However, it is still unclear to what degree these differences affect the survival potential of individuals after release, and how long this effect may last. It is also unclear what is normal and what is unnatural. Nature shows a wide range of diversity within and between populations, and different life history strategies might have similar fitness. A general characteristic of marine organisms is their ability to modify their behaviour according to changes in their environment.

Atlantic salmon (*Salmo salar* L.)

The broodstock used for enhancement purposes consists usually of wild salmon originating from the river to be enhanced, or of ranched fish returning to the site of release. Depending on the ecological traits of the stock in question, the eggs are stripped from October to December. The newly fertilized eggs are thereafter transferred to the hatchery where they hatch after about 400 day-degrees. When the yolk sac nearly is absorbed, the fry are transferred to tanks where they are fed until the time of smoltification,1.5-2.5 years after stripping. The fry or smolts are thereafter released upriver (fry or presmolts), in the rivermouths, in the estuaries or in the sea (smolts).

Before they are released in the wild, the salmon have thus spent a considerable time in artificial rearing. In comparison, reared cod are released from four to eight months after fertilization. With regard to fish densities and feeding regimes, the hatchery environment differs greatly from the natural habitats for salmon. The fry are kept in densities of thousands of fish per m^3 and startfed on formulated feed, and only exceptionally zooplankton may enter the tanks with the incoming water supply. The survival from ova to smolt in hatcheries may surpass 50%, while it is less than 1 % in the wild (e.g. Piggins and Mills 1985). The sheltered hatchery environment thus may produce individuals with low potential for survival in the wild.

Wild salmon spend two to five years in the river before smoltification and migration to the sea (Hansen 1987). At time of smoltification, several physiological changes occur, and the behaviour of the salmon changes (c.f. Hoar 1976). While wild salmon parr have a positively rheotactic and strongly territorial behaviour (Keenleyside and Yamamoto 1962), at smoltification they develop a negative rheotactic response, reduce their aggressive activity and start to shoal (Kalleberg 1958), and usually migrate to the sea in small shoals (Holm and Skilbrei pers. comm.)

Comparative studies

Most of the comparative studies of wild and reared salmon have been performed on salmon parr in river habitats. Laboratory experiments have revealed that high densities and continuous stress in the rearing phase might inhibit development of a normal social behaviour (Fenderson & Carpenter 1971). In a study of the territorial behaviour of a wild and a cultivated parr population, a significantly higher proportion of dominant fish was found in the parr from wild parents (Norman 1987). The difference was explained by different selection pressure in the hatchery compared to the natural habitat of salmon.

Several studies have documented that reared salmon parr have different feeding behaviour for several months after release, compared with wild salmon (E.g., Sosiak *et al.*, 1979; Shustov *et al.*, 1981).

Anti-predator behaviour

During their seaward migration sea-ranched salmon are subject to heavy mortality from predation (e.g. Larsson 1985, Hvidsten and Møkkelgjerd 1987). High mortality of reared smolt migration to the sea might be attributed to a synergistic effect caused by osmotic stress and fright reaction from an unknown predator (Järvi 1989). The physiological stress response was reduced when the fish were acclimatized either to the osmotic conditions or habituated to predators (Järvi 1990). Acclimatization to seawater and predator training before release might therefore help survival. Pol'gen *et al.* (1989) suggests that swimming training affects survival rates after release. Handling stress might inhibit normal anti-predator behaviour, and before release, the smolts should therefore be given possibility to restrain after transport or handling.

Suggestion for improvement

In summary, there are many documented differences between reared and wild salmon, especially in the river phase before migration to the sea. However, we must be aware that most of the comparative studies have been conducted in the rivers, and there is consequently no evidence for fewer differences between wild and reared post smolts during migration to the feeding grounds, or in the sea phase in general.

Relating to the described studies, I will put forward the following three suggestions for improvement in the rearing period;

1. *Production methods that ensure good smolt quality for release* (Stefansson 1991): Production of smolt for stock enhancement demands different strategies than for production of smolt for intensive farming. Environmental factors may be manipulated to control growth rate and to influence the timing of the parr-smolt transformation. However, these manipulations may interfere with the quality of the smolts. Rearing conditions should also be optimal, as suboptimal rearing conditions, e.g. high densities, poor feeding and poor water quality, might reduce the success of smolts after release.

2. *Stamina enforcement* - Use of tanks with sufficiently strong water circulation to enhance the swimming ability of the smolt by simulating river conditions.

3 *Acclimatization* - Seawater acclimatization and predator training prior to release. Acclimatization after handling stress.

European lobster (*Homarus gammarus* L.)

In Norway, lobsters for stock enhancement purposes are produced at Kyrksæterøra, which has a yearly capacity of about 80,000 small lobsters (Grimsen et al. 1987). Wild berried females are captured in the sea and hatching occurs in individual containers with flowing seawater. At hatching the pelagic larvae are transferred to small tanks ("Hughes kreisels") where they are kept until metamorphosis (20°C <temp.< 24°C). The length of this period is about two weeks, after which the postlarvae are collected and transferred to separate ongrowing compartments where they live from six months to a year.

Comparative studies

The environment in the rearing period is very different from the natural habitat for wild lobster. After settlement in the wild, juvenile lobsters (*Homarus americanus*) will hide in the sediment or in crevices (Wahle and Steneck 1992). Here they grow to a size of about 12-15 cm (3-4 years). In this period they prey on the fauna in the sediment and by filtering pelagic plankton (Lavalli and Barshaw 1989). In the rearing unit, the lobsters live singly in small boxes. Their main feed is frozen brine shrimp *(Artemia salina)*. An important question is whether this type of artificially rearing affects the ontogenetic development of the lobsters.

In reared lobsters, differences in morphological development and unnatural behaviour after release have been documented. Earlier, most of the reared lobsters possessed two morphologically similar cutter claws (Wickins 1986, Uglem pers. com.), and their colour has been different from that of wild lobsters. Different coloration may increase the predation risk, and a missing crusher claw may influence feeding behaviour and the social status of the lobsters.

In the first scientific release experiments carried out in Norway, more than 10% of the animals released were eaten within a few hours of release, primarily by labridae. After release

some lobsters swam up and down, while some remained immobile on the sea bottom for several minutes (van der Meeren 1991). This behaviour certainly increased the possibility of being eaten.

The reasons for this behaviour were investigated by van der Meeren (1993). She investigated the effects of environmental parameters, the presence of predators, and the transportation method. The results revealed that acclimatised lobsters which are not stressed showed functional behaviour in relation to light, temperature and predators, and to some degree also to each other.

In later releases in Norway, when the lobsters had been acclimatised to normal sea water for about 15-30 min, the lobsters showed nearly normal behaviour (van der Meeren et al., 1990). In contrast, in earlier releases of lobsters in Norway, they were taken directly from a nearly frozen state in the transportation boxes, and released without further acclimatisation.

Improvement of the rearing methods and new studies

Results from Wales showed that when live oyster spat were added to the rearing chambers, most of the reared lobsters developed a crusher claw (Wickins 1986). This was also done at Kyrksæterøra, and the use of shellsand gave promising results (Uglem pers. com.). The observed differences in coloration may also be normalised by manipulating the content of pigment in the food, and such experiments are now being carried out (Uglem pers. com.).

Small changes in the hatchery practice may then reduce several of the observed differences between reared and wild lobsters. However, there is a need for more detailed comparative investigations including studies of the anti-predator behaviour of reared lobsters in different situations, interactions with other species, density-dependent effects, and selection of the best nursery grounds in the release area.

Atlantic cod (*Gadus morhua* L.)

In contrast with salmon and lobster, cod are reared in semi-natural conditions. The production of cod in enclosed seawater ponds has been documented by Øiestad et al. 1985; Blom et al. 1991. In mid-February the broodstock are transferred to spawning pens where they spawn naturally. The fertilised eggs are then transferred to the hatchery where they hatch after two to three weeks depending on the temperature. Several million cod larvae are released into large sea enclosure[1], where they are startfed on naturally occurring plankton. This environment has many similarities with the natural environment of wild cod larvae. Differences are larger densities of both larvae and prey. In November the year before, potential predators were killed with rothenon (a plant poison). The reared cod accept artificial feed from a size of about 0.5 grams. From this size until the cod are large enough for tagging and release between July and October (size: 10-50 gram), the main diet of the cod consists of formulated feed.

Due to high mortality rate (primarily through cannibalism) less than 5% survive the pond period. The mortality is probably highest for the less fit larvae, and the pond period may thus act as a selection mechanism. This may result in only the most vigorous larvae surviving.

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[1]*Other production units such as large net pens, basin and intensive production methods have been tried.*

Comparative studies

Similar feeding preferences (Svåsand and Kristiansen 1985; Kristiansen 1987) and differences in the weight of the stomach contents of wild and reared cod (Kristiansen 1987) have been reported, based on stomach content analyses of I+ cod (released as 0-group). Released reared cod had learned to catch the same prey types and in the same proportions as wild cod the second week after release, but mean weight of the stomachs contents were smaller (Kristiansen and Svåsand 1992). Nordeide and Salvanes (1991) found differences in feeding behaviour between wild and newly released reared 0-group cod. This indicates that reared fish need some time after release to acclimatise to their new environment. With regard to predation, Nordeide and Salvanes (1991) also found that densely stocked 0-group cod were heavily preyed upon just after release, and Nordeide and Svåsand (1990) reported differences in the behaviour of juvenile reared and wild cod towards a potential predator.

Stengrund (1993) compared the feeding behaviour of wild and reared juvenile cod towards gobies (*Gobiusculus flavescens*) in tank experiments. This study revealed differences in the behaviour of the two groups: the reared fish tried to exhaust their prey, while the wild cod used an "ambush" strategy. Similar number of prey were eaten by wild and reared cod, although the reared cod used more energy to capture their prey. The first period after transfer from the production unit to the release area may, therefore be critical.

However, these differences are small compared with what has been reported for other species. What can be the reason for this? One is obvious; the released cod were produced in a semi-natural production system (Øiestad et al. 1985) and were startfed on the same naturally occurring zooplankton as wild cod. The reared cod fed on natural zooplankton from start feeding until after metamorphosis, and they were only offered artificial feed after about a month past metamorphosis. The production pond also has many similarities with the natural environment with regard to predators and vegetation. Most other species used for enhancement purposes are produced in smaller artificial systems, and they are usually only offered artificial feed. Furthermore, the production environment is often tanks that have little or no resemblance to the natural environment.

Suggestions for improvement and new studies

To summarize, none of the observed differences between reared and wild cod are critical for the further development of the cod enhancement programme. On the other hand, it is important not to ignore these observations. The development of methods that result in more rapid acclimatisation to, and dispersal within the release environment, should be investigated in future enhancement programmes. Thus, the effects of training are confirmed by several authors. Further comparative investigations should also be carried out, and there is a special need for more detailed studies of the behaviour of cod (micro-scale, diurnal behaviour, anti-predator and feeding).

Summary and perspectives

I conclude that exposure to an artificial rearing environment during ontogeny can affect both the phenotype and the behaviour of the reared individuals, and thereby also their potential for survival after release into the wild. Browman (1989) focused on critical periods and suggested that spatial and temporal overlap between the developing organism and specific environmental inputs is essential. From this point of view, the production environment should be as natural as

possible in order to ensure that the fish receive the necessary stimuli at the right time (critical window). All rearing of fish must be artificial to some extent, but the application of a semi-natural production regime and the use of live prey may be an important explanation of why only a few differences were detected in the cod release experiments.

It is, however, important to distinguish between:

a)   *short term differences in behaviour caused by lack of acclimatisation and stress caused by transportation and release into a new environment,*

and

b)   *lasting differences in phenotype and behaviour caused by the rearing environment.*

For both groups, something can be done to reduce or diminish the differences between reared and wild individuals.

For the first type, acclimatising to the release environment, and feeding, and predator training will often give positive effects, and this might be a god investment in sea ranching programmes. Learning is suggested as an important mechanism that provides behavioural flexibility (Dill 1983), and that may increase the ability of salmonids to avoid predators (Patten 1977; Olla and Davis 1989). Moreover, it has been shown in a study with European minnow, *Phoxinus phoxinus*, that anti-predator behaviour is inherited, but that it can be modified by early experience (Magurran 1990).

Lasting (type b) differences might be caused by a lack of, or unnatural, stimuli during periods of ontogeny. To normalise these differences, we must look at the rearing environment. One example is the rearing of lobsters, where the use of particular substrates in the rearing boxes, produces lobster fry with normal claws.

The possible effects of releasing deviant individuals depends on the species and the strategy for the release programme. If the aim is a "put and take fishery", it is not a strict demand that the reared individuals should resemble wild conspecifics. In such cases, it is more important to ensure a high return rate.

In releases where the goal is to enhance overfished populations, as with lobster stocks in Norway, the consequences of releasing diverging lobsters might be serious. Thus, if the aim is enhancement or restocking, strict demands must be made of the individuals that are to be released. The broodstock should be taken from the release area, and the size of the broodstock should be large enough to ensure that rare alleles also are incorporated in the broodstock. The reared lobster must be as similar as possible to wild animals both in the juvenile period, and when recruiting to the spawning stock. Measures of reproductive success are therefore important.

Reproductive success my be studied using genetically marked individuals. In Norway, such studies has been conducted on brown trout (Skaala, 1992). In addition, nearly 150.000 genetically marked cod are released in Norway (Jørstad *et al.*, in press), and several thousand genetically marked salmon have been released in a river in western Norway (Skaala, 1993). We are also trying to find a genetic tag that can be used to identify released lobsters (Jørstad *et al.* 1992).

Finally, I wish to stress that the development of methods for production of high quality juveniles (for sea ranching) is the first step in the development of a large scale sea ranching programme.

Literature

Anon. 1989. St.prp. nr. 95 (1989-90). Gjennomføring av det finanspolitiske opplegget for 1990.

Bachman, R. A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. Trans. Am. Fish. Soc.: 113: 1-32.

Blaxter, J. H. S. 1970. Sensory deprivation and sensory input in rearing experiments. Helgoländer wiss. Meeresunters., 20: 642-654.

Blaxter, J.H.S. 1975. Reared and wild fish - how do they compare? In Proc. 10th Eur. Mar. biol. Symp. Vol. 1, pp. 11-26. Ed. by G. Persone and E. Jaspers. Universal Press, Wettern, Belgium.

Blom, G., Otterå, H., Svåsand, T., Kristiansen, T.S., and Serigstad, B. 1991. The relationship between feeding conditions and production of cod fry (*Gadus morhua* L.) in a marine semi-enclosed ecosystem in western Norway, illustrated by use of a consumption model. ICES mar. Sci. Symp., 192: 176-189

Browman, H. I. 1989. Embryology, ethology and ecology of ontogenetic critical periods in fish. Brain, Behavior and Evolution, 34: 5-12.

Dill, L.M. 1974. The escape response of the zebra danio (*Brachydanio rerio*) II. The effect of experience. Anim. Behav., 22: 723-730.

Dill, L.M. 1983. Adaptive flexibility in the foraging behavior of fishes. Can. J. Fish. Aquat. Sci., 40: 398-408.

Fenderson, O. C., & Carpenter, M. R. 1971. Effects of crowding on the behaviour of juvenile hatchery and wild landlocked Atlantic salmon (*Salmo salar* L.). Anim. Behav., 19: 439-447.

Ginetz, R. M., and Larkin, P. A. 1976. Factors affecting rainbow trout (*Salmo gairdneri*) predation on migrant fry of sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can., 33: 19-24.

Grimsen, S., Jaques, R.N., Erenst, V. and Balchen, J.G. 1987. Aspects of automation in a lobster farming plant. Modelling, Identification and Control, 8(1):61-68.

Govind, C. K., and Pearce, J. 1986. Differential reflex activity determines claw and closer muscle asymmetry in developing lobsters. Science, 233: 354-356.

Hansen, L.P., 1987. Viktige fiskearter - Laks, pp. 50-66, In. Fisk i Fersvann, Økologi og ressursforvatling. Ed. by R. Borgstrøm og L.P. Hansen. Landbruksforlaget Oslo.

Hoar, W.S. 1976. Smolt transformation: evolution, behaviour and physiology. J. Fish. Res. Board Can., 33:1234-1252.

Houde, E.D. 1971. Developmental abnormalities of the flatfish *Achirus lineatus* reared in the laboratory. Fish. Bull. 69(3): 537-544

Huntingford, F. A. 1986. Development of behaviour in fish. pp. 47-68. In The behaviour of teleost fishes. Ed. by Tony J. Pitcher. Croom Helm, London & Sydney.

Hvidsten, N.A., & Møkkelgjerd, P.I. 1987. Predation on salmon smolts, *Salmo salar* L., in the estuary of the River Surna, Norway. J. Fish Biol., 30: 273-280.

Johnsen, B. O., & Ugedal, O. 1986. Feeding by hatchery-reared and wild brown trout, *Salmo trutta*, in a Norwegian stream. Aquaculture and Fisheries Management, 17: 281-287.

Johnsen, B. O., & Ugedal, O. 1989. Feeding by hatchery-reared brown trout, *Salmo trutta* L. released in lakes. Aquaculture and Fisheries Management, 20: 97-104.

Järvi, T. 1989. Synergistic effect on mortality in Atlantic salmon, *Salmo salar*, smolt caused by osmotic stress and presence of predators. Env. Biol. Fish., 26: 149-162.

Järvi, T. 1990. Cumulative acute physiological stress in Atlantic salmon smolts: the effect of osmotic imbalance and the presence of predators. Aquaculture; 89: 337-350.

Jørstad, K.E., Farestveit, E., van der Meeren, G. 1992. Genetic studies in connection with the Norwegian stock enhancement programme of lobster (*Homarus gammarus*). Poster presented at "Genetics and Evolution of Aquatic Organisms", Bangor, September 1992.

Jørstad, K.E., Nævdal, G, Paulsen, O.I., and Thorkildsen, S. *in press*. Release and recapture of genetically tagged fry in a Norwegian fjord system. *In*: Genetics and Evolution of Aquatic

Kallleberg, H. 1958. Observation in a stream tank of territotariality and competition in juvenile salmon and trout (*Salmo salar* L. and *Salmo trutta* L.). Rep. Inst. Freswh. Res. Drottningholm 39:55-98.Organisms, Ed. by A.R. Beaumomt. Chapman & Hall.

Keenleyside, M.H.A, and Yamamoto, F.T. 1962. Territorial behaviour of juvenile Atlantic salmon (*Salmo salar* l.). Behaviour, 19:139-169.

Komada, N. 1980 Incidence of gross malformations and vertebral anomalies of natural and hatchery *Plecoglossus altivelis*. Copeia 1:29-35.

Kristiansen, T.S. 1987. Vekst og ernæring til utsatt, oppdrettet torskeyngel og vill torsk (*Gadus morhua* L.) i Heimarkspollen, Austevoll. Cand. scient. thesis, Department of Fisheries Biology, University of Bergen, Norway. 134 pp. (In Norwegian).

Kristiansen, T.S., & Svåsand, T. 1992. Comparative analysis of stomach contents of cultured and wild cod, *Gadus morhua* L. Aquaculture and Fisheries Management, 23:661-668.

Landeau, L., and Terborgh, J. 1986. Oddity and the 'confusion effect' in predation. Anim. Behav., 34: 1372-1380.

Larsson, P.O. 1985. Predation on migration smolt as a regulating factor in Baltic salmon, *Salmo salar* L, populations. J. Fish Biol.,26: 391-397

Lavalli, K.L. and Barshaw, D.E. 1989. Post-larval American lobsters (*Homarus americanus*) living in burrows may be suspension feeding. Mar. Behav. Physiol. 15:255-264.

Magurran, A.E. 1990. The inheritance and development of minnow anti-predator behaviour. Anim. Behav.: 39:834-842.

Matsumiya, Y., Kanamuru, H., Oka, M., Tateishi, M. Morphometric comparison between artificially-released Red Sea Bream and 0-age wild fish. Bull. Jap. Soc. Sci. Fish. 50: 1173-1178.

Matsuoka, M. 1987. Development of the skeletal tissues and skeletal muscles in the red sea bream. Bull. Seikai. Reg. Fish. Res. Lab.; 65: 1-112.

Nordeide, J. T., and Salvanes, A.G.V. 1991. Observations on reared newly released and wild cod (*Gadus morhua* L.) and their potential predators. ICES mar. Sci. Symp., 192: 139-146.

Nordeide, J.T., and Svåsand, T. 1990. The behaviour of wild and reared juvenile cod, *Gadus morhua* L., towards a potential predator. Aquac. fish. manage., 21: 317-325.

Norman, L. 1987. Akvarieobservationer av revirhävdandet hos laxunger (*Salmo salar* L.) av vild och odlad härstammning. Laxforskningsinstitutet Meddelande 1987:2.

O'Grady, M. F. 1983. Observation on the dietary habits of wild and stocked brown trout, *Salmo salar* L., in Irish lakes. J. Fish Biol.; 22: 593-601.

Olla, B.L. & Davis M.W. 1989. The role of learning and stress in predator avoidance of hatchery-reared coho salmon (*Oncorhynchus kisutch*) juveniles. Aquaculture; 76: 209-214.

Patten, B.G. 1977. Body size and learned avoidance as factors affecting predation on coho salmon, *Oncorhynchus kisutch*, fry by Torrent sculpin, *Cottus rhotheus*. Fish. Bull. U.S. 75: 457-459.

Piggins, D.J.; and Mills, C.P.R., 1985. Comparative aspects of the biology of naturally produced and hatchery-reared Artlantic salmon smolts (*Salmo salar* L.). Aquaculture, 45:321-333.

Pol'gen, A.V.; Kucherov O.A., Popov A.P., Vitvitskaya, L.V.; Nikonorov, S.I. 1989. Experimental rearing of juvenile Atlantic salmon jointly with predators. Rybn. Khoz., 11: 21-23

Romanov, N. S. 1984. Effect of culture conditions on skull morphology in smolts of the masu salmon, *Oncorhyncus masou* (Brevoort). Aquaculture, 41:147-153.

Shustov, Y. A., Shchurov, I. L.; & Smirnov, Y. A. 1981. Adaption times of hatchery salmon, *Salmo salar*, to river conditions. J. Ichtyol. 20:156-159.

Skaala, Ø. 1992. Genetic variation in brown trout *Salmo trutta* L., and application of genetic markers in studies on gene flow from cultured populations. Dr. Scient thesis, department of Fisheries and Marine Biology, University of Bergen, Norway., 96 pp.

Skaala, Ø. 1993. Rømming, havbeite og GMO; Undersøkingar av genetiske og økologiske effektar på ville bestander. Havforskningsinstituttet, senter for havbruk nr 11., 1993. 16 pp. (in Norwegian).

Sosiak, A. J., Randall, R. G., & MacKenzie, J. A. 1979. Feeding by hatchery-reared and wild Atlantic salmon (*Salmo salar*) parr in streams. J. Fish. Res. Boared Can., 36: 1408-1412.

Stefansson, S. 1991. Factors affecting the quality of Atlantic salmon smolts for use in sea ranching. pp. 82-84 In Sea Ranching - Scientific experiences and challenges. Proceedings from the symposium and workshop 21-23 October 1990, Bergen Norway, Ed. by T.N. Pedersen and E. Kjørsvik.

Stengrund, P. 1993. Forskjeller i beiteatferd mellom oppdrettet og vill torsk (*Gadus morhua* L.) og effekt av læring: To ulike beitestategier på tangkutling (*Gobiusculus flavescens* Fabricius).Cand. scient. thesis; Department of Fisheries and Marine Biology, University of Bergen, Norway. 154 pp. (In Norwegian).

Suda, Y., Shimizu; M., Nose, Y. 1987. Morhological difference between cultivated and wild jack mackerel *Trachurus japonicus*. Nippon Suisan Gakkasihi 53: 59-61.

Svåsand, T., and Kristiansen, T.S. 1985. Release of artificially reared 0-group coastal cod (*Gadus morhua* L.) in a landlocked fjord in western Norway. ICES CM 1985/F:10, 12 p.

van der Meeren, G.I. 1991. Out-of-Water transportation effects on the behaviour in newly released juvenile Atlantic lobsters *Homarus gammarus*. Aquaculture Eng., 10: 44-64.

van der Meeren; G.I. 1993. Initial response to physical and biological conditions in naive lobsters *Homarus gammarus*. Mar. Behav. Phys., xx-xxx-xxx.

van der Meeren, G. I.; Svåsand, T., Grimsen, S., Kristiansen, A.; and Farestveit, E. 1990. Large scale release experiments of juvenile lobsters, *Homarus gammarus*, in Norway. ICES C.M. 1990/K:2, 9 pp.

Wahle, R.A. and Steneck. R.S. 1992. Habitat restrictions inn early benthic life: experiments on habitat selection and in situ predation with the American lobster. J. Exp. Mar. Bio. Ecol., 157:91-114.

Wales, J.H. 1954. Relative survival of hatchery and wild trout. Prog. Fish-Cult. 16:125-127.

Wickins, J. F. 1986. Stimulation of crusher claw development in cultured lobsters, *Homarus gammarus* (L.). Aquaculture and Fisheries Management, 17: 267-273.

Witte, F. 1984. Consistency and functional significance of morphological differences between wild-caught and domestic *Haplochromis squamipinnis* (Pisces, Cichlidae).

Øiestad, V., Kvenseth, P.G., and Folkvord, A. 1985. Mass production of Atlantic cod juveniles (*Gadus morhua* L.) in a Norwegian salt water pond. Trans. Am. Fish. Soc., 114: 590-595.