# Enhancement studies of coastal cod, Gadus morhua L. 

## Recruitment, migration, and mortality

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Dr. philos. thesis


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# ENHANCEMENT STUDIES OF COASTAL COD, Gadus morhua L. Recruitment, migration, and mortality 

by

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To ELISABETH
and
GISKE, TORILL, AND RAGNHLD

## PREFACE

This thesis dealing with several aspects concerning sea ranching with coastal cod, Gadus morhua, in Norway, was carried out at the Department of Aquaculture, Institute of Marine Research. Most of the field work were done at the Austevoll Marine Research Station where also the reared cod were produced. Financial support was also provided by the Norwegian Ministry of Local Government and Labour, and the Norwegian Oil/Fish Fund.

Several people have contributed to this thesis. Dr. Victor Øiestad started the cod release project at Austevoll, and he inspired me during the first part of my work. I am grateful to my coauthors (Tore S. Kristiansen, Knut E. Jørstad, and Geir Blom) and to Harald Næss and the several others who took part in the tagging and release operations, fishing surveys, and the registration of tag returns. I am also grateful to professor Ray J.H. Beverton, the editor of the ICES Journal of Marine Science (earlier Journal de Conseil). He contributed significantly to the form of the four papers published in that journal.

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#### Abstract

This thesis is based on an enhancement experiment with coastal cod, started in 1983 at Austevoll in western Norway. The main objectives were to describe the recruitment, migration, and mortality patterns of reared 0 - and 1 -group cod after release, and to evaluate the use of genetically marked yolk-sac larvae for studies of early life stages of cod.


Reared cod released as 0 -group recruited to the local spawning stock in the release area 2.5 years after release. The results suggest that reared cod did not differ from wild cod in growth and survival. When monitoring the genetic variation in broodstock and offspring at different stages, no genetic differences were detected, neither between broodstock and offspring, nor during the period after release, except that two rare alleles, found in the wild population were not present in the broodstock, and consequently not in the offspring. The reared cod were produced in a seawater pond with environmental conditions similar to the natural environment. This might be a reason why successful results were obtained.

Reared cod released in sheltered coastal areas as 0 -group remained in the locality of release both as juveniles and after maturation. No difference in migration patterns of similar sized wild and reared cod was found. The described migration pattern seems general for cod tagged as juveniles in sheltered fjord and coastal areas in Norway.

Natural recruitment in the release area was investigated, and it was shown that reared cod contributed significantly in the corresponding yearclasses. The reared cod recruited to the local fishery as 2 -group at a size of about 30 cm . Less than $35 \%$ of the reared cod released as 0 and 1 -groups survived to the 2 -group stage. The mortality was attributed to predation and cannibalism, and seemed to decrease with increased fish size at release. Indications of density dependent mortality were found. After recruitment to the local fishery as 2 -group the natural mortality of cod decreased to about $20 \%$ year $^{-1}$, while the fishing mortality increased to nearly $50 \%$ year $^{-1}$. The possible negative consequences of today's fishing pattern concerning cod enhancement are discussed.

The last paper describes a pilot experiment that is the first steps in a study aiming to evaluate the effects of mass releases of yolk-sac larvae on local recruitment and the potential of using a genetic marker for estimating survival and growth of early life stages of cod under natural conditions.

## SAMMENDRAG PÅ NORSK

Denne avhandlingen bygger på et utsettingsprosjekt med oppdrettet torsk scm ble startet på Austevoll i 1983. Målet var å beskrive rekrutteringsmønster, vandring og dødelighet til utsatt oppdrettet 0 - og 1 -gruppe torsk, samt evaluere bruken av genetisk merkede plommesekklarver for styrking av lokale torskebestander og for studier av tidlige livsstadier hos torsk.

Utsatt oppdrettet torsk rekrutterte til gytebestanden i utsettingsområdet som 3-gruppe. Resultatene kunne ikke påvise forskjeller i vekst og overlevelse mellom vill og oppdrettet torsk av samme årsklassen. I de genetiske undersøkelsene av stamfisk, avkom og utsatt fisk ble det ikke påvist forandringer. Eneste unntaket var at to sjeldne genvarianter (genotyper) som fantes i den ville populasjonen, manglet i stamfisken, og følgelig også i den utsatte fisken. Den utsatte torsken var oppdrettet i en sjøvannspoll. Miljøet i pollen har mange likhetstrekk med torskelarvenes naturlige miljø i naturen. Polloppdrettet torskeyngel er derfor sannsynligvis bedre rustet til et liv i det fri, enn om den skulle ha vært oppdrettet på kunstig fôr i karmiljø.

Mesteparten av den oppdrettede torsken som ble satt ut som 0-gruppe, var stedegen både som ungfisk og etter kjønnsmodning. Tilsvarende vandringsmønsteret ble også funnet for villfisk i disse områdene. Stedegenhet synes å være et generelt trekk hos kysttorsk i beskyttede fjordog kystområder.

Naturlig rekruttering av torsk i området ble undersøkt, og det ble påvist at utsatt torsk ga et betydelig innslag i sine respektive årsklasser. Mindre enn $35 \%$ av torsken som ble satt ut som 0 - og 1-gruppe, overlevde frem til 2 -gruppe stadiet. Dødeligheten i denne perioden skyldes hovedsakelig predasjon og kannibalisme. Dødeligheten var negativt korrelert med fiskestørrelse ved utsetting, og resultatene synes å indikere en tetthetsavhengig dødelighetskomponent. Etter rekruttering til fisket som 2-gruppe ved en størrelse på ca 30 cm , stabiliserte naturlig dødelighet seg på et relativt lavt nivå (ca. $20 \% \mathrm{pr}$ år), mens fiskedødeligheten $\emptyset k$ kte til nærmere $50 \% \mathrm{pr}$ år. Flere potensielt negative effekter ved dagens beskatningsmønster ble diskutert.

Det siste arbeidet i avhandlingen beskriver et piloteksperiment med genetisk merkede plommesekklarver. Dette er første steget i en studie av effekten av masseutsettinger av plommesekklaryer på lokal rekruttering. Videre kan en genetisk markør brukes til studier av vekst og overlevelse hos tidlige livsstadier hos torsk under naturlige forhold.

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## INTRODUCTION

The oceanic production of fish is probably much higher than the global catch that largely depends on economic factors as supply and demands of fish and fishery products (Rothschild 1981). One possible way to harvest more of this production is trough aquaculture, which covers a variety of forms from shellfish and fish farming to sea ranching (Ryther 1981). Well documented examples of sea ranching are the extensive enhancement programmes in the North Pacific Ocean. In this region more than $4 \cdot 10^{9}$ smolts of different species of Pacific salmon, Oncorhynchus sp., were released yearly in the mid-eighties, and several of these ranching programmes have obtained economic viability (Isaksson 1988). In Japan, there is an extensive research activity to incorporate also marine fish species such as red sea bream, Pagrus major, and hirame, Paralichthys olivaceum, in the ranching programmes (Suda 1991).

Norway has many advantages for aquaculture purposes due to a long coastline and a high mean sea temperature (Braaten and Sætre 1973). Up to now, most of the aquaculture activity in Norway has been cage rearing. The production of Atlantic salmon, Salmo salar, increased from less than 5000 tonnes in 1980 to more than 150,000 tonnes in 1990, and intensive research activities are conducted to incorporate new marine species into fish farming (Tilseth 1990). In recent years sea ranching has also in Norway become an interesting alternative to intensive fish farming as a tool for increasing the yield from the inshore fisheries. Scientific releases of Atlantic cod (Svåsand 1990), Atlantic salmon (Anon. 1989), Arctic charr, Salvelinus alpinus (Heggberget 1991), and lobster, Homarus gammarus (Meeren et al. 1990) have been conducted.

Enhancement experiments on reared juvenile coastal cod have been carried out since 1983 at several sites in Norway (Svåsand 1990). The main purpose of the programme was to find out if it is possible to enhance natural cod populations with reared juveniles and if this is profitable. This is, however, a very complex problem involving research activities in marine and fisheries biology, oceanography, economy, and law. The aim of the present thesis was, therefore, not to try to draw any conclusion on the feasibility of cod enhancement, but to give some of the biological information necessary to unravel the puzzle.

This thesis is based on the data from an enhancement experiment with coastal cod that started in 1983 at Austevoll in western Norway (Svåsand 1990). The main objectives were to describe the recruitment, migration ${ }^{l}$, and mortality patterns of reared 0 - and 1 -group cod after release.

Nearly 100 years before the development of the mass rearing technique of cod fry, large scale releases of artificially hatched yolk-sac larvae were initiated in Norway and USA. Since then more than $90 \cdot 10^{9}$ yolk-sac larvae have been released over a period of 90 years ${ }^{2}$ (for review, see Solemdal et al. 1984). A main drawbacks of these releases was the lack of appropriate tagging methods, and no evidence of any beneficial result has been obtained (Shelbourne 1964; Solemdal et al. 1984). On this background a pilot study aiming to evaluate the effects of mass releases of yolk-sac larvae on local recruitment, and the potential of using a genetic marker for estimating survival and growth of early life stages of cod under natural conditions, was also incorporated into the thesis.

The following six papers are included in the thesis:

I: Svåsand, T., Jørstad, K.E., and Kristiansen, T.S. 1990. Enhancement studies of coastal cod in western Norway. Part I. Recruitment of wild and reared cod to a local spawning stock. J. Cons. int. Explor. Mer, 47: 5-12.

II: Svåsand, T., and Kristiansen, T.S. 1990. Enhancement studies of coastal cod in western Norway. Part II. Migration of reared coastal cod. J. Cons. int. Explor. Mer, 47: 13-22.

III: Svåsand, T. 1990. Comparisons of migration patterns of wild and recaptured reared coastal cod, Gadus morhua L., released in a small fjord in western Norway. Aquac. fish. manage., 21: 491-495.

[^0]IV: Kristiansen, T.S, and Svåsand, T. 1990. Enhancement studies of coastal cod in western Norway. Part III. Interrelationships between reared and indigenous cod in a nearly land-locked fjord. J. Cons. int. Explor. Mer, 47: 23-29.

V: Svåsand, T., and Kristiansen, T.S. 1990. Enhancement studies of coastal cod in western Norway. Part IV. Mortality of reared cod after release. J. Cons. int. Explor. Mer, 47: 30-39.

VI: Svåsand, T., Jørstad, K.E., Blom, G., and Kristiansen, T.S. 1991. Application of genetic markers for early life history investigations on Atlantic cod (Gadus morhua L.). ICES mar. Sci. Symp., 192: 193-199.

## SUMMARY OF PAPERS

## Paper I. Recruitment of wild and reared cod to a local spawning stock

About 3000 reared cod were released near a local spawning ground at Austevoll in 1983. The results showed that the reared cod recruited in a normal way to the local spawning stock in the release area. By sampling the local cod population at different times after release it was found that reared fish contributed $25 \%$ of the 1983 yearclass caught as juveniles in 1984, and $36 \%$ and $35 \%$ of the same yearclass caught on the spawning ground in respectively 1986 and 1987. No differences in growth or survival between reared and wild cod were detected. When monitoring the genetic variation in broodstock and offspring at different stages, no genetic differences were detected, neither between broodstock and offspring, nor during the period after release, except that two rare alleles in the $P G M$ locus, $P G M(150)$ and $P G M(70)$, found in the wild population were not present in the broodstock, and consequently not in the offspring.

## Papers III\&III. Migration of coastal cod

Reared cod released in sheltered coastal areas remained where they were released both as juveniles and after maturation (paper II). In this study nearly 21,000 tagged reared juvenile cod ( 0 -group) were released at three sites in western Norway between September and November 1983. The total tag returns by January 1988 from the three groups were 3268 individuals. More than $96 \%$ of the tag returns were recaptured in shallow nearshore waters less than 10 km from the release site, and only one cod had migrated more than 100 km . No recaptures were recovered from the North Sea. This may be attributed to the deep Norwegian Coastal Trench separating it from the Norwegian coast. The results indicated a weak increase in dispersion rates with fish size. The movement showed no marked preferential directionality, and no indications of spawning migrations were found.

Migration patterns of recaptured reared cod (previously tagged and released in the same area) and tagged wild cod were compared in paper III. A total of 946 wild $\operatorname{cod}$ (mean length $=347$ mm ) and 121 recaptured reared cod (mean length $=342 \mathrm{~mm}$ ) were released in Heimarkspollen between December 1986 and February 1988. By March 1990, 416 (44.0\%) wild and 63 (52.1\%) recaptured reared cod were reported recaptured. More-than $87 \%$ of the tag returns were captured in Heimarkspollen and the study showed no significant differences in displacement between wild and recaptured reared cod. Number of days between release and recapture were
significantly different between the two groups. This divergence might be attributed to unequal numbers in the groups, and future studies with equal-sized groups were suggested.

## Paper IV. Interrelationships between reared and indigenous cod

The variations in the yearclass strength of cod in Heimarkspollen, a $2.9 \mathrm{~km}^{2}$ almost land-locked fjord at Austevoll, western Norway, and the contribution of reared cod in the corresponding yearclasses (1983-1986) was studied. It was not possible to conclude that reared cod were more heavily predated after release than wild cod (Svåsand and Kristiansen 1985). The estimated natural recruitment of wild 0-group cod in September-December in the fjord in the years 19831986. varied from 3000 to 13,700 (corrected for $10 \%$ tag loss). The growth patterns of reared and wild cod of the same yearclass were similar. Reared cod contributed 24-69\% (corrected for $10 \%$ tag loss) of the estimated 0 -group abundances of wild and reared cod in Heimarkspollen in this period. The ratio of reared cod of the 1983-1985 yearclasses seemed to decrease with time after release. However, this decrease was only significant for the 1984-yearclass. The estimated density of wild 0 -group cod in Heimarkspollen ( $1000-4700 \mathrm{~km}^{-2}$ when correcting for $10 \%$ tag loss) was similar to that observed in other investigated coastal areas. A release of about 2000-3000 reared cod $\mathrm{km}^{-2}$ should therefore probably be enough to secure an average yearclass abundance in most areas.

## Paper V. Mortality of reared cod after release

Mortality patterns of reared cod released in Heimarkspollen were investigated. Natural mortality (M) and fishing mortality ( F ) were estimated using Ricker's two-release method and virtual population analysis (VPA). According to paper IV, a tag loss of $10 \%$ was used. Incomplete reporting of recaptured tagged cod was believed to be low in the release area, due to intensive publicity campaigns. However, some allowance for incomplete reporting was made, and it was assumed that only $90 \%$ of recaptured cod were reported.

The survival from release as 0 - and 1 -groups to the 2 -group stage (pre-recruit survival) of different groups of reared cod varied from 13 to $32 \%$, corresponding to total instantaneous mortality rates $(Z)$ of about 1.1-1.8 year ${ }^{-1}$. The mortality in the pre-recruit period was attributed to predation (primarily by pollack, Pollachius pollachius, and cannibalism, and the results suggested both size- and density-dependent effects. The instantaneous coefficient of natural mortality $(M)$ of cod larger than $30 \mathrm{~cm}(\approx 2+\operatorname{cod})$ was estimated as 0.22 year $^{-1}$. Similar values
of natural mortality have been reported for the North Sea cod. After recruitment to the fishery as 2 -group, the mean fishing mortality coefficient was estimated as about 0.6 year $^{-1}$.

## Paper VI. Application of genetic markers for early life history investigations

The first release experiment with genetically marked yolk-sac larvae was carried out in Heimarkspollen in 1988. The larvae used were offspring from a cod broodstock that was homozygous for a rare allele at the PGI- 1 locus. The objectives were to evaluate the contribution of the released larvae compared with the natural cod spawning in the release area and, further, to use genetically marked larvae to measure survival and growth of cod from the yolk-sac stage.

Less than 2 millions larvae were produced and only 1.5 million of these were released. Due to the small release, estimation of growth and survival would have needed a very high sampling effort, and only a restricted sampling programme was carried out. Jørstad et al. (1987) found no clear differences in survival or growth rates between different PGI-1 genotypes under controlled conditions. This suggests no differences in fitness for the genetically marked larvae used in this experiment compared to other PGI-1 genotypes. This was also supported by our study where the estimated contribution of released larvae at the time of release ( $<4 \%$ ) was similar to the estimated contribution at the late larval stage (3.3\%). It was concluded that the method might be useful in future studies, both conceming growth and survival and for evaluating the effects of releases of artificially hatched larvae.

## GENERAL DISCUSSION

## Evaluation of the tag return data

The results presented in papers I-V are based on data obtained from tagged fish (Floy anchor tags and internal steel tags) recaptured by local fishermen, or in fishing surveys. In general, tagging data may contain several intrinsic sources of errors that may influence the results (e.g. Buckley and Blankenship 1990; McFarlane et al. 1990). These errors may be grouped as: shedding of tags, tagging mortality, tagging artifacts such as growth depression or increased predation risk, and under-reporting of recaptured tagged fish.

Floy FD67-C anchor tag ${ }^{3}$ were the most used tags. These tags can be used on cod larger than about 15 cm with low tagging mortality, but shedding of tags has been a problem (Svåsand 1990). Losses of different types of Floy FD anchor tags have been reported for several species: brook trout, Salvelinus fontinalis: 2.0-5.7\% (Carline and Brynildson 1972); channel catfish, Ictalurus punctatus: 19-90\% (Greenland and Bryan 1974); barramundi, Lates calcarifer: estimated to $17 \% 100$ days after tagging (Davis and Reid 1982); lake whitefish, Coregonus clupeaformis: 11.1-20.5\% (Ebener and Copes 1982); blueback herring, Alosa aestivalis: $1 \%$ (Bulak 1983); and others. However, due to large inter-species variation in shedding rates, any direct comparison with cod can not be done. Based on several observations and results from unpublished control group experiments, an underlying assumption of zero tagging mortality and a shedding rate of $10 \%$ were used for the release experiments reported in this thesis (except for paper I). Errors in these estimates will influence the mortality and abundance estimates given in papers IV\&V. However, as discussed in the papers, errors within reasonable limits will not alter the main conclusions.

Growth of untagged wild and tagged reared coastal cod of the same ages were similar, and seldom significantly different (Kristiansen 1987; Svåsand et al. 1987; papers I\&IV). This indicates that use of Floy anchor tags has no apparent effect on the growth of coastal cod. Similar results were reported by Jensen (1967) for larger wild cod tagged with Lea and Petersen disc tags in the waters off New England.

[^1]The oddity of the prey may increase the predation risk, and Landeau and Terborgh (1986) showed that dyed silvery minnows, Hybognathus nuchalis, in schools of undyed fish were eaten more often than their schoolmates. Also, visual tags may increase the oddity of the tagged individuals. However, recapture rates of internally and externally tagged cod of similar sizes were not significantly different (Svåsand et al. 1987), indicating no significant effects on survival of external tags on cod. A possible reason for this is the solitary behaviour of 0-group and older cod. Negative effects of external tags might, however, be a larger problem with schooling species.

Another important aspect is under-reporting of recaptured tagged fish. Reporting rates in tagging experiments are often a function of advertising (Holt 1963). The tagging operation was therefore announced in local newspapers and a pamphlet, including a registration form for recording of information on recaptured cod, was sent to local fishermen and households (paper 1). Due to the extensive information campaigns and regular communications with local fishermen, a reporting rate as high as $90 \%$ was used. The validity of this assumption was not tested, but can be examined by looking at recapture rates of fish released at larger sizes. The predation risk for cod larger than about 30 cm is low, and natural mortality has been estimated to about $20 \%$ year $^{-1}$ (paper V). Between 44 and $52 \%$ of larger tagged cod (length $>30 \mathrm{~cm}$ ) were reported recaptured from releases in Heimarkspollen (paper III). When accounting for $10 \%$ under-reporting, shedding of tags ( $10 \%$ ) and annual natural mortality of $20 \%$ this shows that the assumed reporting rate is reasonable. However, reporting rates may fluctuate, and deviations from the assumed value may have had some influence on the results, mainly on the mortality estimates, as discussed in paper V .

An overall evaluation of the tagging data has revealed several sources of errors. However, none are regarded to influence the main conclusions of this thesis.

## Migration

Migration plays an important part in the life of fish populations. Northcote (1978) suggested that migration of freshwater fish has evolved to (1) optimize feeding, (2) to avoid unfavourable conditions, (3) to enhance reproductive success and (4) possibly to promote colonizations. However, these reasons could easily apply to fish migration in general (McKeown 1984). When reared fish are liberated it is important to investigate whether these fishes have different migratory behaviour than the indigenous fish. Moreover, the migration pattern may also
determine the potential production rate in a population, and thereby also the financial aspects of running an enhancement programme.

Reared cod tagged and released as juveniles are sedentary in southern Norway (Moksness and Øiestad 1984; Nordeide and Salvanes 1988; papers II\&III), and present data on immature cod from northern Norway shows the same pattern (Larsen 1990). Moreover, several studies confirm that most wild coastal cod in these areas also are sedentary (Løversen 1946; Jakobsen 1987; Nordeide and Salvanes 1988; paper III), although some deviations have been reported, especially for wild cod tagged during the spawning season (discussed in paper II). This suggests that the migration patterns of coastal cod are fairly uniform in Norway, at least for reared cod released as juveniles in sheltered areas.

Sedentariness has both positive and negative consequences for cod enhancement. Firstly, it makes it easy to manage the enhanced population. The drawback is that the low mobility might limit the productivity in comparison with migratory populations. If food resources are limiting factors, the cost of migration is potential more serious for small compared to larger fish, and Roff (1988) suggested in a theoretical work that migratory fishes are predicted to grow faster, and to be larger in average than non-migrants. Results from a study with resident and migratory populations of threespine sticklebacks, Gasterosteus aculeatus, in a single drainage in northern California, U.S.A., support this hypothesis (Snyder 1991). Thus, if the trend for migration is connected to growth rate or size, the high and probably size-selective, fishing intensity on the coastal cod populations (paper V) can theoretically select for sedentariness. Indications of differing migratory behaviour of wild coastal cod according to variations in the environment on the nursery and feeding grounds are reported (Godø 1986), although it is not known whether these differences are genetically or environmentally determined. Thus, further studies are needed to determine the factors controlling the migration of coastal cod, whether it is of genetic or environmental nature.

## Natural mortality and density-dependence

Decreased mortality with size is well documented for marine species (Peterson and Wroblewski 1984; Folkvord and Hunter 1986; Anderson 1988; Tsukamoto et al. 1989; and others). Likewise, increased survival with increased size at release for 0\&1-group cod (mean lengths: $16-22 \mathrm{~cm}$ ) are reported in paper V. Moreover, natural mortality seems to stabilize at the end of the 1 -group stage, and instantaneous coefficient of natural mortality of cod larger than about

30 cm was estimated to 0.22 year $^{-1}$ (paper V). The most probable reasons for pre-recruit (0\&1groups) mortality in the investigated locations are cannibalism and predation from pollack. As the cod grow in size the risk of predation will decrease. This suggests that size at release and time spent to grow trough the predation phase probably affect the survival of released cod, and may explain the observed size-dependent mortality (paper V). For earlier life stages of coastal cod, no survival data has up to now been available, primarily due to problems with effective tagging methods for cod smaller than $10-15 \mathrm{~cm}$ (Svåsand 1990).

Intrinsic density-dependent mechanisms are important in fish population dynamics (Beverton 1984), and may also influence the benefit from commercial enhancement programmes (Peterman 1991). The results given in paper V suggest a negative relationship between 0 -group density and pre-recruit survival. Sundby et al. (1989) suggested density-dependent mortality between early juvenile and 0 -group stage of northeast Arctic cod. Moreover, density-dependent mortality was found for 0-group plaice, Pleuronectes platessa (Lockwood 1980; Veer 1986), and Vetter (1988) sites several additional papers discussing density-dependent changes in natural mortality.

Juvenile cod in inshore waters off eastern Newfoundland were strongly associated with macrophyte beds serving as refuges from predators (Keats et. al 1987). Thus, a densitydependent pre-recruit mortality of cod in Heimarkspollen might be attributed to the number of hiding places, and interactions between juvenile cod and potential predators. An alternative explanation is that increased 0 -group abundance might reduce the growth potential and thereby increase the mortality. However, in a population with size-dependent mortality and large individual heterogeneity in growth rates (paper V), density-dependent growth may not necessarily be observed as reduced mean population growth rate but more likely as increased mortality of the slowest growing individuals that would spend a longer time in growing through the predation field.

In summary, the mortality of juvenile cod decreases with increased size, and there are circumstantial evidences that the pre-recruit mortality is density-dependent, probably connected to density-dependent effects on growth rates of individual cod. For a future large scale cod enhancement programme, it will be very important to maximize the survival in the pre-recruit period. Thus, further effort should be made to investigate the mechanisms determining the prerecruit survival.

## Consequences of today's fishing pattern

The exploitation pattern of the natural cod populations has significance both for the management of wild populations and for cod enhancement (Ulltang 1984). The coastal cod are heavily exploited (mean $\mathrm{F}=0.6$ year $^{-1}$ ) already from the 2 -group stage at a size of about 30 cm , while also younger cod are being captured to some extent (paper V, Table 1). In addition, large variations in size of equally aged fish are found (paper II\&V, Fig. 1).

Table 1. Survival (S) and mean instantaneous coefficients of natural (M), fishing (F), and total (Z) mortality (year ${ }^{-1}$ ) during two periods for different groups of 0 -group cod released in Heimarkspollen between 1983 and 1985 (calculated from data in paper V).

| RELEASE <br> GROUP | PRE-RECRUIT ${ }^{\text {a }}$ |  |  |  | POST-RECRUIT ${ }^{\text {b,c }}$ |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | S(\%) | $\mathrm{M}_{0,1}$ | $F_{0,1}$ | $\mathrm{Z}_{0,1}$ | S(\%) | $\mathrm{M}_{2,3}$ | $F_{2,3}$ | $\mathrm{Z}_{2,3}$ |
| 83 | 28.4 | 0.95 | 0.12 | 1.07 | 17.9 | 0.22 | 0.64 | 0.86 |
| 84-2 | 14.4 | 1.59 | 0.07 | 1.66 | 17.6 | 0.22 | 0.65 | 0.87 |
| 84-3 | 18.6 | 1.32 | 0.12 | 1.44 | 14.6 | 0.22 | 0.74 | 0.96 |
| 84-4 | 26.6 | 1.00 | 0.14 | 1.14 | 20.9 | 0.22 | 0.56 | 0.78 |
| 85 | 12.8 | 1.57 | 0.19 | 1.76 | $45.4{ }^{\text {c }}$ | $0.22^{\text {c }}$ | $0.57^{\circ}$ | $0.79{ }^{\circ}$ |

a Period from release to the end of the 1-group stage (Set to 14 months for all groups)
$b$ Period from entering the 2 -group to the end of the 3 -group stage
c For the 85 -yearclass survival and mortality estimates are given from beginning to the end of the 2-group stage

Fishing imposes a mortality on a population that is usually size-selective (Ricker 1969). Sizeselective harvesting in combination with large variations in growth rates may give as a result that observed increase in mean fish size with age of a cohort is lower than the actual mean growth rate of individual fish. Indication of this is actually found in a group of cod at one of the investigated areas (Heimarkspollen, Svåsand, unpubl.) However, this is very difficult to prove statistically, and further data are needed before any conclusion can be drawn.

However, it can be concluded that growth rates of cod can not be interpreted in linear terms. It should rather be stressed that efforts should be made to model the mixture of endogenous and exogenous growth variability for use in population models. Such models will enable us to
evaluate todays's exploitation pattern, and effects of changing the fishing pattern can be computed as suggested by Ulltang (1984).


Figure 1. Length at recapture. All tag returns from the five groups referred to in Table 1 are pooled.

In addition to the effects discussed above, size- and age-specific cropping may reduce the total yield that the population is able to sustain (Silliman 1975; Law and Grey 1989; Sutherland 1990). Law and Grey (1989) calculated the consequences of managing the northeast Arctic cod stock under different managing regimes and found a considerable increase in the equilibrium yield when changing the fishing intensity from young cod in the Barents Sea to mature cod on the spawning ground. Thus, before starting full scale enhancement programmes, effort should be made to optimize the management of the indigenous populations. It is quite clear that the released fish will be exploited the same way as the wild cod, and if today's harvesting is not
optimal, the exploitation of enhanced populations will also be less good. A better approach would be to develop a good management strategy before starting cod enhancement.

## Are reared cod suited for a life in the wild?

The main question that has to be raised when planning to enhance natural fish populations is whether reared fish are suited for a life in the wild, or more specific, if there are differences between reared and indigenous fish. There are many published examples of observed differences between reared and wild individuals (e.g. see reviews by Blaxter 1975; Browman 1989). In contrast, only minor differences have been revealed in this thesis.

Paper I shows that two rare alleles, $P G M(150)$ and $P G M(70)$, found in the wild population were lacking in the broodstock. This can, however, be attributed to the low number of spawners used ( 74 fish) and may be avoided in future release experiments by using a higher number of spawners. Moreover, differences in median time in the sea were found for two groups of reared and wild cod (paper III). This my indicate different behaviour between the two groups, although a more probable reason is unequal number of wild (946) and reared (121) cod released in this experiment. In addition to these minor differences it has been shown that migration (paper III), growth (papers I\&IV) and recruitment to a local spawning ground (paper I) were similar for wild and reared cod.

This is in accordance with other investigations comparing wild and reared cod. Similar feeding preferences (Svåsand and Kristiansen 1985; Kristiansen 1987) and weight of the stomach contents between wild and reared cod (Kristiansen 1987) have been reported, based on stomach content analyses of I+ cod. However, 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 acclimatize to the new environment. Also with regard to predation, Nordeide and Salvanes (1991) found that densely stocked 0-group cod were heavily preyed upon just after release, and Nordeide and Svåsand (1990) reported differences in behaviour of juvenile reared and wild cod towards a potential predator. The first period after transition from the production unit to the release area might, therefore, be critical.

These differences are, however, small compared to what is reported for other species. What may 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 are. The reared cod fed on natural zooplankton from startfeeding to past metamorphosis, and were only offered artificial feed from about one month past metamorphosis. The production pond has also 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. In addition, the production environment is often tanks with little or no resemblance to the natural environment.

Browman (1989) focused on critical periods and suggested that spatial and temporal overlap between the developing organism and specific environmental input is essential. From this viewpoint, the production environment should be as natural as possible to ensure that the fish get the necessary stimulus at the right time (critical window). All rearing of fish will to some extent be artificial, but application of a semi-natural production regime and the use of live prey may be an important explanation to why successful results were obtained in these cod release experiments.

To summarize, none of the observed differences between reared and wild cod is critical for a further development of the cod enhancement programme. On the other hand, it is important not to ignore these observations, and necessary precautions (e.g. use of larger spawning stocks) and training of reared cod prior to release should be tried out. Especially, development of methods giving a more rapid acclimatization to and dispersal within the release environment should be investigated in future enhancement programmes. Thus, effect of training is supported by several authors. Learning is suggested as an important mechanism providing behavioural flexibility (Dill 1983), and may increase the ability to avoid predators in salmonids (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 modified by early experience (Magurran 1990).

## The potential of using early life stages to enhance natural populations

At what stage in the life cycle the level of recruitment is determined, has been a main question concerning the recruitment processes in marine ecosystems (e.g. Jones 1989). Sundby et al. (1989) suggested that the yearclass strength of northeast Arctic cod is determined before early juvenile stage, and Campana et al. (1989) found that both pelagic and settled juveniles of the cod population off Southwest Nova Scotia appeared to reflect yearclass strength. If this is the
case also for coastal cod in Norway, releases of early juveniles ( $12-80 \mathrm{~mm}$ ) might be an effective way to augment local populations. The main part of this thesis deals with releases of 0 -groups larger than about 15 cm (papers I-V). However, the cost of rearing increases with size, and although the survival after release also increases with fish size (paper V ), there will be a breaking point between size at release and economic outcome. Today we do not know the optimal fish size for release, and further data on survival and growth, especially of early juvenile stages are therefore needed.

A bottleneck for using larvae and early juveniles in enhancement studies has until recently been the lack of appropriate tagging methods (paper VI). Almost 100 years of mass releases of artificially hatched cod larvae in Norway and USA have been carried out without any proven beneficial results (Shelbourne 1964; Solemdal et al. 1984). This clearly illustrates that large scale stocking programmes without tagging or marking can be waste of resources. Paper VI describes the first release of genetically marked yolk-sac larvae, and was the first documentation of survival to metamorphosis of artificially hatched cod larvae liberated in the sea. Thus, releases of genetically marked cod, as proposed in paper VI, will be an excellent means of testing the benefit of releases of early life stages of cod.

## Concluding remarks

The Norwegian coast consists of a variety of fjords and coastal areas with varying hydrographic conditions (Braaten and Sætre 1973; Aure 1990). Attributed to differences in sill depths and other topographical parameters, different fjord ecosystems exhibit large variations both within and between regions (Lie 1985). One might therefore question how far it is possible to generalize the results obtained in this thesis. Furthermore, results from the cod enhancement programme show conformity between areas in some parameters but dissimilarity in others (Svåsand 1990). This suggests that several of the results put forward in thesis might not be valid for other regions without further investigations. Nevertheless, the conclusions will be important as hypotheses for such investigations.

In 1990, the Norwegian government decided to grant 300 millions NOK for large scale enhancement experiments with Atlantic cod, Atlantic salmon, Arctic charr, and lobster during a 5-7 years period (Anon. 1990). This new grant has secured a continuation of the cod enhancement research, and the final conclusions from the programme will probably be reached within the next five years. In this period emphasis will be laid on describing the carrying
capacity of different areas for production of cod (Giske et al. 1991), optimizing the release and recapture strategies (Fosså and Nordeide 1991) and to carry out large scale releases of reared cod in cooperation with the fishermen's organizations.

However, even if the conclusion of this research should be that it is possible to increase the output from the inshore cod fisheries through releases of reared cod, some important questions remain to be answered before this kind of extensive aquaculture can be a reality. A full scale enhancement programme will demand a continuous supply of low cost cod fry. Today, this seems to be a problem, but great effort is put into optimizing the rearing techniques (e.g. Blom et al. 1991). Legal aspects involving ownership of the released fish will have to be solved (Ørebech 1988), and a final question will be whether a cod enhancement programme will be economically feasible (Sandberg 1988; Sandberg and Flåm 1988).

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[^0]:    ${ }^{1}$ In this thesis $I$ have followed the general definition of fish migration given by Baker (1978): 'the act of moving from one spatial unit to another'
    ${ }^{2}$ Hatching and release of yolk-sac larvae was terminated in 1952 in USA, but continued to 1971 in Norway (Solemdal et al. 1984).

[^1]:    ${ }^{3}$ The Floy tags were obtainted from the Floy Tag Manufacturing Company, Seattle, Washington.

