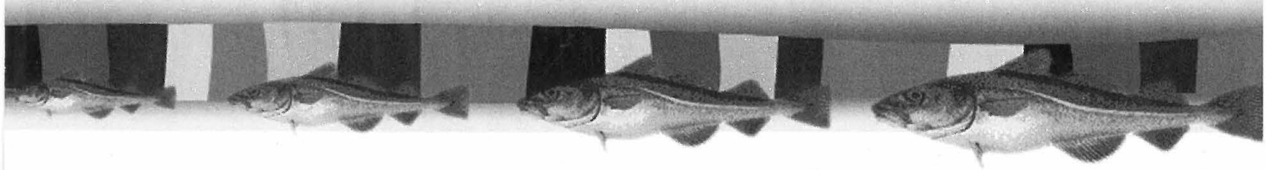

Enhancement studies of coastal cod in Norway

Stage- and size-dependent mortality of reared and wild cod (*Gadus morhua* L.)

Tore S. Kristiansen

Dr. scient. thesis

Department of Fisheries and Marine Biology, University of Bergen
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«That there had to be large quantities of cod fry close to shore, I later got the opportunity to convince myself of when I investigated the stomach contents of large fishes and especially the stomachs of what at this time were very large catches of large saithe. Almost all of the saithe studied were stuffed with fish fry, often partly digested and not easily identifiable to species, but just as often they could without any doubt be recognised as fry of saithe and cod, the last as often in as large numbers as the first; and what I especially noticed was that the cod fry that were studied in this way were a lot larger than those that I had observed in company with jellyfish.»

from G.O. Sars' report from Lofoten in 1867
(Sars 1879; Translated quotation)

I dedicate this thesis to my father, who died in 1991

CONTENTS

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Preface and acknowledgements

When we started the first large release experiments with reared cod in Austevoll in 1983, very little knowledge was available regarding the ecology of juvenile coastal cod, and the next few years showed us how little we really knew. We soon learnt that it was not easy to play God, and it sometimes seemed as though our offers of assistance were being directly rejected. However, in the course of fifteen years of rearing and release experiments and studies of the nursery areas of the coastal cod, we have become a littler wiser. This is the seventh Ph.D. thesis related to the Norwegian cod enhancement programmes and as well more than 60 related papers have been published in international journals. In this thesis I use data from several projects whose major source of finance has been the Norwegian Sea Ranching Programme (PUSH) and the Research Council of Norway.

Without extremely large inputs of work and enthusiasm on the part of very many people this thesis would not have been possible. First I would thank my supervisor, boss, co-author and good friend Terje Svåsand, for his unfailing co-operation, support, and great patience, and my supervisors Arne Johannessen and Anne Gro Vea Salvanes from Department of Fisheries and Marine Biology, University of Bergen, for their advice and support. Secondly I am grateful to my co-authors, Knut Jørstad, Håkon Otterå, Ole Ingar Paulsen, Mariann Nødtvedt and Asbjørn Borge, and technicians Leiv Aardal, Gunnar Bakke, Harald Næss, Jan P. Pedersen, Jon Kåre Stordal, Vidar Wennevik, and all others who have participated in the projects at the Institute of Marine Research. Thanks also to Ann Lisbeth Agnalt for comments to the synthesis and to Dr. Hugh Allen who revised the English. Thanks are also due to the Institute of Marine Research for making data available and for grants to finish the PhD thesis.

A special thanks goes to the Nord-Trøndelag team on the cod enhancement project in Ytre Namdal: Alf Albrigtsen, Trond Ivar Arnøy, Frode Kirkeby Garstad, Sissel Heimsvik, Lisbeth Ruud Kringstad, Anne Grete Nordalen, Gunnar, Lilleba and Odd Rauø, Aris Todal, Anita Wiborg and Tore Wiik, and all others who contributed to this project.

Finally, special thanks go to my wife Tone and my daughters Miriam and Felicia for all their love and support.

Bergen, 01.10.2000

Tore S Kristiansen

ABSTRACT

This thesis is based on a series of release experiments on reared cod in Hordaland, Western Norway and in Nord-Trøndelag, Mid-Norway. These experiments formed part of the Norwegian cod enhancement programmes in 1983-97. The main objectives of this thesis were to study how survival after release was related to size-at-release, release habitat, release season and release methods. Further objectives were to estimate mortality rates of genetically marked yolk-sac larvae during the first 40 days after release, and survival at one year of age. The thesis also includes a model study of the effects of size-selective fishing mortality on growth and yield estimates.

Eighteen million genetically marked yolk-sac larvae were released into a small, almost landlocked fjord in western Norway. The average rate of mortality was estimated to be 23% day^{-1} during the first ten days after release and 12% day^{-1} during the following month. Only about 0.15% survived the first 40 days after release, and less than 120 of the released larvae survived to one year of age.

Survival and recapture rates of individually tagged reared cod after release rose with increasing size-at-release, due to size-dependent natural mortality during the first few months after release. Size-selective fishing mortality of I-group cod also led to higher recapture rates with increasing size-at-release. Recapture rates and survival after release varied considerably between areas, due to variations in natural and fishing mortality. There seemed to be a negative relationship between the natural mortality of young fish and fishing mortality of larger fish. The density and size distribution of predators and distance from predator concentrations had also significant effects on mortality. Recapture rates and survival within areas also varied between release season and years, probably due to seasonal and annual variations in predation pressure. Releases in shallow sea-weed covered areas, preconditioning and predator training had no effects on survival after release.

The effects of size-dependent fishing mortality and individual growth variation on growth and yield estimates were evaluated using an individual-based model. The effects could be large when there were large individual variations in growth and high fishing mortality.

SAMMENDRAG

Denne avhandlingen bygger på en rekke eksperimenter med utsettinger av oppdrettet torskeyngel i Hordaland og i Nord-Trøndelag. Forsøkene har vært del i de norske havbeiteprogrammene med torsk som ble gjennomført i perioden 1983-97. Målet med avhandlingen var å undersøke hvordan overlevelsen etter utsetting var relatert til størrelse ved utsetting, utsettingsmetode, utsettingsområde og sesong. Videre var målet å måle dødelighet til genetisk merkede plommesekklarver fram til metamorfose og ett år etter utsetting. Avhandlingen omfatter også et modellstudium av effekter av størrelsesavhengig fiskedødelighet på vekst og utbytteberegninger.

Atten millioner genetisk merkede plommesekklarver ble satt ut i en liten nesten innelukket fjord, Heimarkspollen i Hordaland. Gjennomsnittlig dødelighet ble estimert til 23% per dag de første 10 dagene etter utsetting og 12% per dag de neste 30 dagene. Ca. 0.15% overlevde de første 40 dagene og mindre enn 120 overlevde til de var ett år gamle.

Overlevelse etter utsetting av individmerkede torsk økte med økende størrelse ved utsetting, på grunn av størrelsesavhengig naturlig dødelighet det første månedene etter utsetting. Selektivt fiske på de største individene den første sommeren etter utsetting bidro også til økende gjenfangsprosent med økende størrelse ved utsetting. Det var stor variasjon i naturlig dødelighet og fiskedødelighet mellom områder. Det så ut til å være en negativ sammenheng mellom fiskedødelighet på stor torsk og naturlig dødelighet på liten torsk. Tetthet og størrelse av predatorer og avstand fra predator konsentrasjoner hadde også betydelig effekt på overlevingen. Overleving innen samme område varierte både mellom årstider og mellom år, trolig på grunn av variasjoner i predatortetthet. Utsetting i tareskog på grunt vann, predator trening eller kondisjonering til utsettingsstedet hadde ingen effekt på overleving etter utsetting.

Effekter av størrelsesselektiv fiskedødelighet på vekst- og utbytteberegninger ble evaluert ved hjelp av en individbasert modell basert på individuelle vekstdata fra Heimarkspollen. Resultatene viste at dette kunne føre til store effekter på vekst og utbytteberegninger, og effektene økte med økt fiskedødelighet og økt vekstvariasjon.

LIST OF PAPERS

Paper I

Kristiansen, T. S., Jørstad, K. E., Otterå, H., Paulsen, O. I. & Svåsand, T. (1997). Estimates of larval survival of cod by releases of genetically marked yolk-sac larvae. *Journal of Fish Biology* **51** (Supplement A), 264-283.

Paper II

Kristiansen, T. S. (1999). Enhancement studies of coastal cod (*Gadus morhua* L.) in Nord-Trøndelag, Norway. In *Stock Enhancement and Sea Ranching* (Howell, B. R., Moksness, E., & Svåsand, T., eds.), pp 277-292. Fishing News Books, Blackwell Science. Oxford, U.K.

Paper III

Otterå, H., Kristiansen, T. S., Svåsand, T., Nødtvedt, M. & Borge, A. (1999). Sea-ranching of Atlantic cod (*Gadus morhua* L.): effects of release strategy on survival. In *Stock Enhancement and Sea Ranching* (Howell, B. R., Moksness, E., & Svåsand, T., eds.), pp. 293-305. Fishing News Books. Blackwell Science. Oxford, U.K.

Paper IV

Kristiansen, T. S., Otterå, H., & Svåsand, T. (2000). Size-dependent mortality of juvenile reared Atlantic cod, released in a small fjord. *Journal of Fish Biology* **56**, 792-801.

Paper V

Kristiansen, T. S., Otterå, H., & Svåsand, T. (2000) Size-dependent mortality of juvenile Atlantic cod, estimated from recaptures of released reared cod and tagged wild cod. *Journal of Fish Biology* **56**, 687-712.

Paper VI

Kristiansen, T. S. & Svåsand, T. (1998). Effect of size-selective mortality on growth of coastal cod illustrated by tagging data and an individual-based growth and mortality model. *Journal of Fish Biology* **52**, 688-705.

INTRODUCTION

Throughout history, variations in the abundance and availability of fish resources have produced both poverty and wealth in coastal societies. The discovery of methods for determining age and studies of age structure in fish landings demonstrated that the main reason for the variation in abundance was variable year-class abundance (Hjort 1914; Sinclair 1997). Theories that explain the causes of variation have been many (reviewed by Anderson 1988), but the existing evidence suggests that there is a coarse control of recruitment during the pre–juvenile stages and a fine control during later life stages (Sissenwine 1984; Rothschild 1986; Anderson 1988; Miller *et al.* 1988; Bradford 1992; Myers & Cadigan 1993; Leggett & Deblois 1994). Typical for many stocks are also occasional very high levels of recruitment, which often seems to be the result of large-scale environmental effects (Rothschild 1986).

The high survival of fish larvae in 'predator-free' marine enclosures, in contrast to the very high mortality of marine fish eggs and yolk-sac larvae in the sea, show that predation must be a major source of natural mortality (Øiestad 1985; 1990; Bailey & Houde 1989). In general, the numbers of potential predators and predation mortality decrease with increasing size (Peterson & Wroblewski 1984; McGurk 1986; Vetter 1988; Sogard 1997) and ontogenetic development (Balon 1984; Fuiman & Magurran 1994). By protecting the most vulnerable stages in a favourable environment it should intuitively be possible to increase recruitment via a relatively small broodstock.

Since hatching and rearing techniques began to be developed in the 19th century, hatchery-based stock enhancement has been an important technique used in attempts to restore or create new fisheries or to increase recruitment in areas in which the natural recruitment of juveniles is, or is believed to be, less than the body of water can sustain (Shelbourne 1964; Bowen 1970; Cowx 1994; White *et al.* 1995, Munro & Bell 1997; Blaxter 2000). In marine waters mass releases of yolk sack larvae began in many countries at the end of the 19th century. Thousands of millions of unmarked larvae were released for several decades, however, without any possibilities to estimate any effects of the releases (Shelbourne 1964; Solemdal *et al.* 1984; Kirk 1987). Techniques for mass production of juveniles of marine fish were not developed until after the 1960s, and during the past few decades a greater amount of effort has been put into mass releases of juveniles, with Japan playing a leading role (Bartley 1999; Imamura 1999). In most cases the benefits of the releases have not been properly evaluated, and the use of reared fish for stock enhancement is still a controversial issue (Cowx 1994; Blankenship & Leber 1995; White *et al.* 1995; Welcomme 1998). However, since 1980 more work has been put into documenting the effects of the releases (Howell *et al.* 1999; Kitada 1999), and during the Norwegian cod enhancement experiments in particular, a major effort has been put into evaluating the releases (Smedstad *et al.* 1994; Svåsand *et al.* 1998a)

The fundamental assumption underlying marine stock enhancement is recruitment limitation (Doherty 1999), i.e. that for various reasons too few recruits are being produced to exploit the available feeding resources in an area. Possible reasons for recruitment limitation include low spawning stock biomass, unfavourable climatic or oceanographic conditions (Sinclair 1988; Doherty 1999) and recruitment bottlenecks at certain developmental stages, e.g. limited spawning areas with acceptable hydrographic conditions for the Baltic cod (Wieland *et al.* 1994), limited spawning and nursery areas in rivers for anadromous fish, or high predation mortality of the juvenile stages of scallops. By removing the bottleneck or by releasing juveniles on the right side of the bottleneck one can increase the harvestable stock. Successful examples are the Japanese sea ranching of chum salmon (*Onchorhynchus keta*) (Kaeriyama 1999) and scallop (*Patinopecten yessoensis*) (Kitada 1999).

The Norwegian cod enhancement experiments

In Norway, the first releases of artificially hatched cod date back to the last half of the 19th century. Inspired by G.O Sars' discoveries of pelagic cod eggs and his hatching experiments and proposals (Sars 1879), G.M. Dannevig built a cod hatchery at Flødevigen outside Arendal in 1883, and from 1884 until 1971 an average of 200 million cod yolk-sac larvae per year were released in fjords along the Norwegian Skagerak coast (Dannevig 1932; Tveite 1971; Solemdal *et al.* 1984). Since the larvae were unmarked and relatively few in number in comparison with naturally hatched larvae, it was impossible to measure whether the releases had any effects (Dahl 1909; Tveite 1971). This long and controversial story is revisited in **Paper I**.

As early as 1886 G.M. Dannevig had produced a few thousand cod juveniles in an outdoor basin (Rognerud 1887), but further development of techniques for the production of cod juveniles did not take place until 1975-85, when successful methods for the production of juveniles in marine ponds were developed (Kvenseth & Øiestad, 1984, Øiestad 1985; Øiestad *et al.* 1985). These results, together with relatively high recapture rates obtained from small experimental releases of reared cod juveniles (Moksness & Øiestad 1984), opened up new perspectives for cod enhancement and a series of new release experiments was initiated. Between 1983 and 1986 more than 40,000 reared cod juveniles (15-20 cm total length) were tagged and released in the Austevoll archipelago in western Norway (Svåsand & Kristiansen, 1990a,b; Svåsand 1998). The reported recapture rates varied between 11 and 26% and in the release areas investigated the released fish made up between 21 and 61% of their own year-class (Kristiansen 1987, Kristiansen and Svåsand 1990, Svåsand & Kristiansen, 1990b). Most of the fish remained in the release areas (Svåsand and Kristiansen 1990a).

In 1985 Norway launched a national research programme on sea ranching of cod. The aims were to investigate whether cod production could be enhanced by releasing reared cod juveniles and elucidating the physical and biological factors which determine carrying capacity for cod (see references in Smedstad *et al.* 1994 and Svåsand *et al.* 1998a). Experiments were carried out in fjords in southern (Danielssen & Gjøsæter, 1994), western (Salvanes & Ulltang 1991, Smedstad *et al.* 1994) and northern Norway (Kanapathipillay *et al.* 1994; Svåsand *et al.* 1998a). The cod enhancement programme was further scaled up in 1990 when three new release projects in open, more productive, coastal areas were added: Øygarden in western Norway (Otterå *et al.* 1999; **Papers III** and **V**), Ytre-Namdal in Mid-Norway (**Paper II**) and Vestfjorden (Skreslet *et al.* 1999). The main results and references to most of the publications from the cod enhancement programme are found in Svåsand *et al.* (1998a).

Objectives

The following synthesis focuses on the relationship between developmental stage or size and mortality, and the implications of these results for cod enhancement. The six papers present the results of release experiments carried out in the main release areas in Hordaland (Papers I, III-VI); and Nord-Trøndelag (Papers II & V) (Fig. 1).

According to Leber (1999) the hypothesis that releases of reared fish can increase fish production has two corollaries that need to be tested:

1. *The released fish survive, grow and contribute to the recruitment to the fisheries or spawning stock.*
2. *The released fish increase overall abundance rather than displace parts of wild stocks.*

However, the effects of the releases will depend on the release strategies chosen and the ecological conditions under which the releases are carried out. As a cohort of cod grows from yolk-sac larvae to mature fish they will pass through the prey preference ranges of various predators, and the outcome of the interaction between prey and predators will depend on the abundance and size distribution of prey and predators, the predators' prey-size preference range, encounter, attack and escape probability, etc. (Bailey & Houde 1989). In order to optimise the release strategy in relation to release size and production costs, it is necessary to know how the mortality is distributed among the various developmental stages and how the results of the releases are affected by alternative release strategies. The main objectives of the studies presented here were to answer the following questions:

1. *How is survival after release affected by:*
    - i. *stage- or size-at-release? (Papers I – V)*
    - ii. *release location? (Papers II –V)*
    - iii. *release season? (Papers II-V)*
2. *Can predator training and improved release methods increase survival after release? (Paper III)*
3. *Does size-selective fishing mortality affect growth- and yield-per recruit estimates? (Paper VI)*

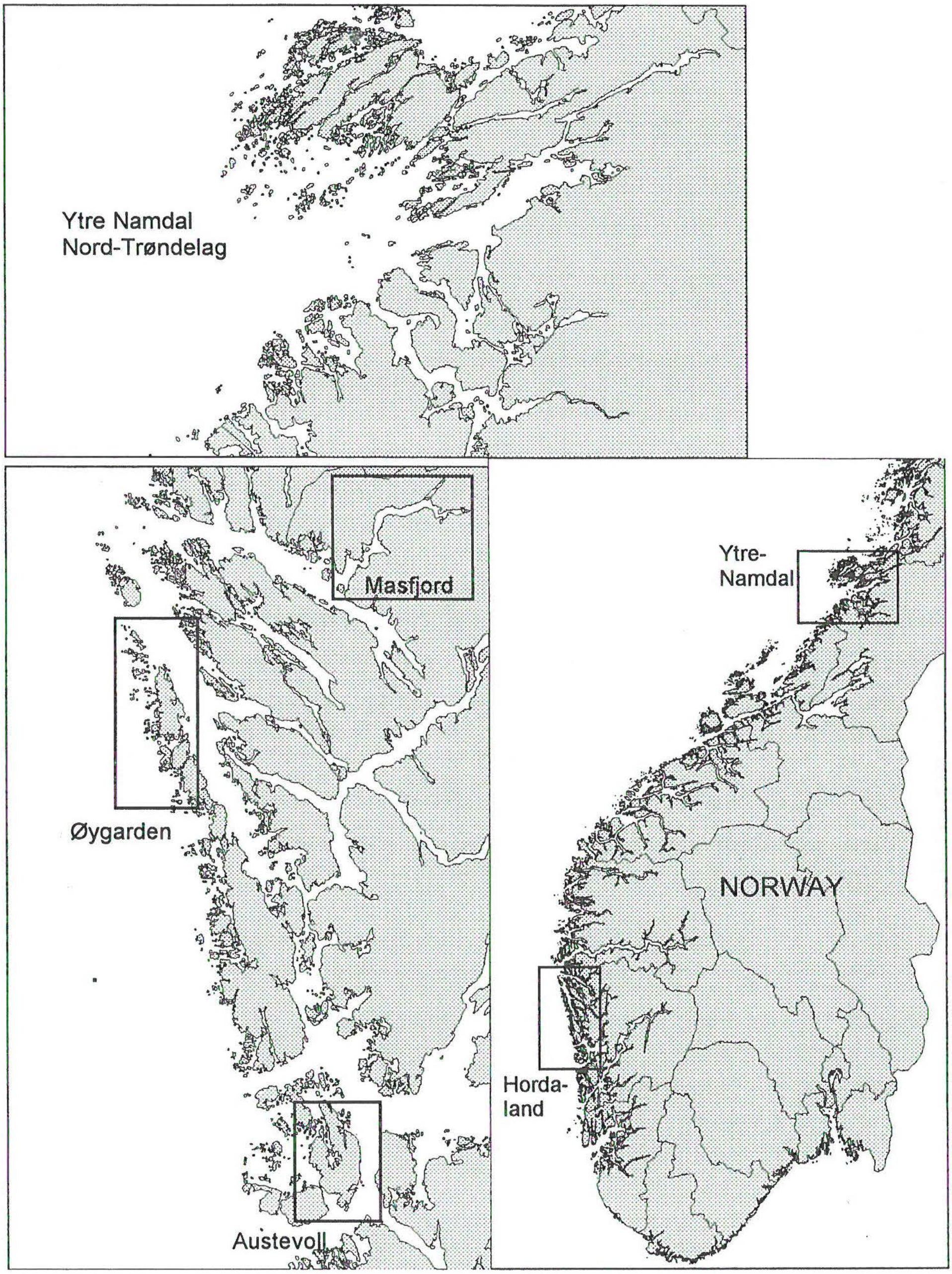

FIG 1. The release areas studied: Ytre-Namdal in Nord-Trøndelag, mid-Norway (top) and Masfjord, Øygarden and Austevoll in Hordaland, western Norway (left).

Stage-dependent mortality

Stage-dependent mortality is defined here as the cumulative mortality rate from the beginning to the end of a developmental stage, e.g. the egg-stage or a given size interval. Assuming an exponential decay model (Gulland 1969), survival in the pre-recruitment stages can be described by the equation:

$$\mathbf{S_R=e^{-\Sigma Mt}}, \tag{1}$$

where $\mathbf{S_R}$ is survival ratio and $\mathbf{-\Sigma Mt}$ is the sum of the cumulative instantaneous mortality rates in each stage or size interval. If we divide the recruitment period into e.g. four developmental stages: eggs (E), larvae (L; pre metamorphosis), early juveniles (EJ; post metamorphosis, pelagic stage) and juveniles (J; from benthic stage to recruitment to fishery), the survival to recruitment (at e.g. 40 cm length) will be the product of the survival ratios in each stage:

$$\mathbf{S_R = S_E S_L S_{EJ} S_J} \tag{2}$$

and correspondingly the cumulative instantaneous mortality will be:

$$\mathbf{\Sigma Mt = Mt_E+Mt_L+Mt_{EJ}+Mt_J} \tag{3}$$

$\mathbf{Mt_x}$ for a stage is the sum of the daily mortality rates of each day spent in the stage, and will depend both on the level of the daily mortality rates and the development or growth rate. The effect of releases of hatchery reared larvae or juveniles will depend on the difference in cumulative mortality from egg until recruitment between hatchery reared ($\mathbf{\Sigma Mt_h}$) and wild cod ($\mathbf{\Sigma Mt_w}$). The relative increase in survival of the reared cod compared to the wild will be:

$$\mathbf{s_h = S_h S_w^{-1} = e^{(-\Sigma Mth+\Sigma Mtw)}} \tag{4}$$

The expected contribution to recruitment also depends on the ratio of the spawned eggs incubated in the hatchery (e_h):

$$\mathbf{e_h=E_h E_w^{-1}}, \tag{5}$$

where $\mathbf{E_h}$ is the number incubated in the hatchery and $\mathbf{E_w}$ the total number spawned in the stock, including the eggs that would have been spawned by the broodstock used in the hatchery if they had been allowed to spawn in the sea. If we assume no density-dependent effects the expected relative effect of the releases ($\mathbf{r_h}$) can be written as:

$$\mathbf{r_h=[E_h S_h+(E_w-E_h)S_w](E_w S_w)^{-1} = s_h e_h+(1-e_h)} \tag{6}$$

The cumulative mortality $\mathbf{\Sigma Mt}$, for the entire pre-recruit stage is $\mathbf{-ln(R/E)}$, where $\mathbf{R}$ is the number of recruits and $\mathbf{E}$ is the number of eggs spawned. There exist no stock-recruitment statistics for Norwegian coastal cod, but for the large NE Arctic cod stock the median survival from egg to III-group (mean length 30-35 cm) is only about seven survivors per million spawned eggs (Fig. 2).

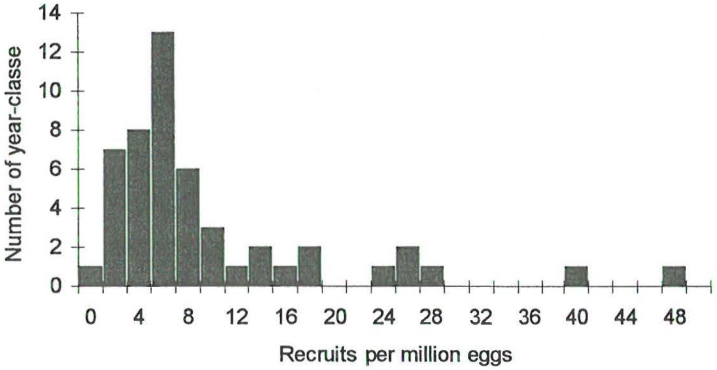

FIG. 2. Variation in survival from egg to III-group for year-classes 1946-1995 of NE Arctic cod stock. Survival is calculated using spawning stock biomass (SSB) and recruitment number (R) estimates given in ICES (1999), and the relationship between spawning stock biomass, SSB (kg), and egg production (numbers) given in Sundby *et al.* (1989): $E=0.37*10^6(0.4SSB)$; Recruits per million eggs=$R/E*10^6$). X-axis values: 0 includes values from 0-1.99, 4 includes values from 4.0-5.99, etc.

Except in a relatively few years with extraordinarily high survival the survival rates have been relatively stable (Fig. 2), and even subtle changes in the growth or mortality rates in the pre-recruitment stages are capable of explaining the observed variability in recruitment (Houde 1987, Beyer 1989).

The survival to recruitment of released juveniles will depend on the stage at which the fish is released and on how much of the cumulative mortality from egg to recruitment is expected to take place during the remaining stages. The costs of rearing fry increase with increasing size-at-release, and to find the optimal release size one needs to know the relationship between size-at-release and expected survival and yield. What do we know about mortality at the various stages?

Egg mortality

Each female coastal cod can spawn 0.5-1 million eggs per kilo body weight (Kjesbu *et al.* 1991) and the duration of the egg stage is 2-4 weeks, depending on the temperature (Ellertsen *et al.* 1987). Norwegian coastal cod spawn at a large number of small spawning locations close to the shore along the whole coastline, partly in the same areas as the NE Arctic cod (Dannevig 1954; Godø 1984; Reisegg & Jørstad, 1984). The main spawning season is from February to May, and the pelagic eggs and larvae become dispersed by ocean currents over large areas (Bjørke, 1984; Fossum, 1988). Field estimates of egg mortality of cod are few and relatively inaccurate due to the difficulties and huge costs of quantitative sampling. For Norwegian coastal cod the only published estimate of egg mortality comes from the small nearly landlocked fjord Heimarkspollen **(Paper I),** where egg mortality was estimated to be approximately M=0.18 day^{-1}, which gave approximately 5% survival to hatching (Table 1). Estimates obtained from other stocks show rates of survival to hatching that range from 0.1 - 58%, but with most estimates below 5% (Table 1).

Table I. Egg mortality (M day^{-1}) estimates from four areas (t = days to hatching; Mt_E cumulative mortality rate at the egg stage). Stage duration (t) is an approximation based on ambient sea temperatures in the spawning areas (Ellertsen *et al.* 1987).

Reference	Area	(day^{-1})	t(days)^1	Mt_E	Hatching %
Fossum 1988	Lofoten 1984	0.11	20	2.2	11.1
Heessen & Rijnsdorp 1989	North Sea 1970	0.03	18	0.5	58.3
Heessen & Rijnsdorp 1989	North Sea 1971	0.41	17	7.0	0.1
Heessen & Rijnsdorp 1989	North Sea 1972	0.28	17	4.8	0.9
Heessen & Rijnsdorp 1989	North Sea 1973	0.25	16	4.0	1.8
Heessen & Rijnsdorp 1989	North Sea 1974	0.30	18	5.4	0.5
Heessen & Rijnsdorp 1989	North Sea 1987	0.14	21	2.9	5.3
Rijnsdorp & Jaworski 1990	North Sea 1987	0.23	21	4.8	0.8
Heessen & Rijnsdorp 1989	North Sea 1988	0.22	16	3.5	3.0
Campana *et al.* 1989	SW Nova Scotia	0.27	24	6.5	0.2
Campana *et al.* 1989	SW Nova Scotia	0.16	24	3.8	2.1
Campana *et al.* 1989	SW Nova Scotia	0.14	24	3.4	3.5
PAPER I	Heimarkspollen	0.18	17	3.1	4.7
Average	All areas	0.20	19.6	4.0	1.8

The average egg mortality in the cod hatchery at the Institute of Marine Research has been around 50% (H. Otterå, Institute of Marine Research, personal communication). Furthermore, not all of the spawned eggs from the spawning stock used in the hatchery were incubated, an aspect that must be corrected for when Mt_E is calculated. The benefit of protecting the eggs in the hatchery is the positive effect of the greater numbers of larvae in the sea. By hatching the larvae in the hatchery these eggs will on average produce around 20 times more larvae than if the same number had hatched in the sea. However, since the number of eggs that it is possible to incubate in practice is relatively low in comparison with the huge numbers spawned in the sea (eq. 5), and given that the correlation between abundance of early larvae and recruitment is weak (Bradford 1992; Helle *et al.* 2000), the effects of releasing yolk-sack larvae can be expected to be variable and very small. This is also experimentally shown and further discussed in **Paper I**.

Mortality of larvae and early juveniles

The fragile, 4 mm-long yolk-sac larvae of cod are vulnerable to both predators and physical injury. About five days after hatching their eyes and jaws are developed and they start feeding, preferably on copepod nauplii (Ellertsen *et al.* 1980). Metamorphosis in cod is usually defined as the stage at which median finfold resorption is complete, around 12 mm total length (25 - 45 days after hatching), but the juvenile form is not fully developed before they reach a total length of around 40 mm (55 - 75 days after hatching) (Pedersen & Falk-Petersen 1992).

In **Paper I**, the mortality of genetically marked yolk-sac larvae during the first 10 days after release in a small fjord was estimated at $M=0.26$ day^{-1} and at $M=0.13$ day^{-1} in the following 30-day period. After 40 days in the sea only 0.15% were estimated to remain alive ($Mt_L=6.5$). These values are in the upper range of the few other reported mortality estimates of cod larvae (Table II). However, it is difficult to compare these results since different methods, models and age intervals have been used. For NE Arctic cod, Sundby *et al.* (1989) estimated the average mortality from hatching to early juvenile to be $M= 0.10$ day^{-1} (range 0.07-0.15 day^{-1}) in 1979-88, assuming 10% hatching. By using data derived from Sundby *et al.* (1989) and Fossum (1988), mortality rate from the large larval (>22 days) to early juvenile stage was calculated to $M=0.04$ day^{-1} (Table II: Stage L-EJ, mean value for year classes 1983 and 84), which indicates a strong reduction in mortality during the late larval stage. However, for NW Atlantic (Browns Bank) cod mortality estimates for the life history stages from egg to early juvenile varied from $M=0.11$ to 0.26 day^{-1}, but none of the stages were consistently associated with particularly high or low mortality rates (Campana *et al.* 1989).

In the cod-rearing ponds estimated mortality rates ranged from 0.026 to 0.077 day^{-1}, with no significant differences between the pre- and post-metamorphosis stages (Blom 1995). The relatively high mortality after metamorphosis in the ponds and basins is mainly caused by a small fraction of the largest juveniles that become cannibals due to the lack of live food and wide variations in size within the cohort (Blom *et al.* 1994; Folkvord 1997). While mortality at the larval stage is much lower in the ponds than in the sea, thanks to the previous removal of fish predators (Øiestad 1985, Øiestad *et al.* 1985), mortality after metamorphosis seems to be fairly similar (Table II: stage L-EJ).

Table II. Larvae mortality (M day^{-1}) estimates (mean values) from four areas (t = days after hatching; Mt cumulative stage-dependent mortality rate; S: survival through stage. Stages; E: egg Y: Yolk-sac larvae; L: Larvae; EJ: early juvenile; 0G: 0-group).

Reference	Area	Stage	t(days)	M(day^{-1})	Mt	S
Fossum 1988	Lofoten 1983-84	E-Y	-20-2	0.14	3.1	0.05
Fossum 1988	Lofoten 1983-84	Y-L	2-22	0.14	2.5	0.06
Sundby *et al.* 1989[1]	Northern Norway 1983-84	L-EJ	22-75	0.04	2,3	0.12
Sundby *et al.* 1989[1]	Northern Norway 1983-84	Y-EJ	2-75	0.07	5.1	0.007
Sundby *et al.* 1989	Northern Norway 1983-84	EJ-0G	75-128	0.025	1.3	0.27
Blom 1995	Rearing ponds	Y-L	1-42	0.04	1.8	0.18
Blom 1995	Rearing ponds	L-EJ	42-75	0.05	1.7	0.18
Blom 1995	Rearing ponds	Y-EJ	1-75	0.05	3.5	0.03
PAPER I	Heimarkspollen	Y-L	1-10	0.26	2.6	0.074
PAPER I	Heimarkspollen	L-L	11-40	0.13	3.9	0.02
PAPER I	Heimarkspollen	Y-L	1-40	0.16	6.5	0.0015

[1] Egg data from Sundby *et al.* (1989) and E-Y and Y-L survival estimates (rows 1-2) from Fossum (1988) were used to calculate numbers of 2 and 22 days old larvae.

Mortality of juvenile cod

The coastal cod settle at the early juvenile stage (30-40 mm; age 2-3 months) in shallow water, often in rocky and seaweed-covered habitats. Mortality estimates of coastal cod from the early juvenile to 0-group are few. In monthly beach seine hauls from May to October in Masfjorden, Western Norway the early juveniles were found in the hauls as early as the beginning of June at a total length of 30-60 mm (Fosså 1991; Nordeide *et al.* 1994; Salvanes *et al.* 1994), which was at the same time of the year and size as observed by Dahl (1909) in Søndeledfjord, Southern Norway. In two years with high densities of 0-group fish in Masfjorden the density fell rapidly from June to July (estimated M=0.08-0.09 day^{-1}, based on data from Salvanes *et al.* 1994). A similar rapid decline in numbers of 0-group cod from July to August was also found in beach seine hauls on the Skagerak coast (estimated M=0.03-0.07 day^{-1}; based on data from Krakstad 1999).

The decrease in abundance was probably caused by both mortality and size-dependent habitat change. Sars (1879) and Dahl (1909) observed small juveniles settling over a long period and larger individuals emigrating to deeper water. In Masfjorden, one beach seine haul in June 1988 produced 1167 individuals, while the average of the others was 22. This may indicate that the early juveniles in the settling phase are schooling, as observed by Olsen & Soldal (1989) and as I have observed in the rearing basins (Paper II). If the schools break up after settling and the fish spread out more evenly along the shore, the decrease in the average number of juveniles in the beach seine will overestimate mortality. The small mean size (6 g) of the 0-group cod caught in the beach seine hauls (<5 m depth) in October in Masfjorden compared to the size of the 0-group cod caught in the net samples (<30 m depth) in the same area (42g in September) also indicates migration of larger fish to deeper water (Salvanes *et al.* 1994).

The smallest cod released in the cod enhancement programme were a group with a mean length of 8 cm, four months old, released in Heimarkspollen in late July 1993 (**Paper IV**). This group had very high mortality soon after release and less than 2% were estimated to remain alive three months later. However, a group with a mean length of 12 cm released in August 1994 in the same area had an estimated survival of 75% after three months. In **Paper IV** we speculate that a good match between prey (the released cod) size and the sizes of the most abundant predators, in addition to a low abundance of alternative prey of preferred sizes, could have led to the high mortality in 1993. Most of the release experiments have been done with 0-I-group cod >10 cm at release, and the survival rates have been shown to be very variable, depending on size, release location and year and season-at-release (**Papers II-V**). These aspects will be discussed in more detail in the following sections.

For the oceanic stocks there seems to be a drop in the daily mortality rate at the early juvenile stage, and then a slow reduction in natural mortality from 0-group to recruitment (Table II, III; Fig. 3; Fossum 1988; Campana *et al.* 1989; Sundby *et al.* 1989). Various estimates of mortality from 0-III-group are given in Table III, together with some examples of estimates of mortality of released reared cod (**Papers IV & V**), which indicate higher mortality in reared cod. However, the results are not strictly comparable since methods, age intervals and areas are different.

Table III. Mortality estimates (M day^{-1}) of juvenile cod from five areas. (age: age since hatching; assumed birth date 1 April; Mt: cumulative stage-dependent mortality rate in age interval; Stage 0: 0-group; I: I-group; II: II-group; III: III-group. M_2 – predation mortality only).

Reference	Area	Stage	Age (days)	M(day^{-1})	M(yr^{-1})	Mt	S
Sundby *et al.* 1989	Northern Norway (min)	0-III	123-984	0.0008	0.3	0.7	0.51
Sundby *et al.* 1989	Northern Norway (max)	0-III	123-984	0.0028	1.0	2.4	0.09
Nilssen *et al.* 1994	Northern Norway (M_2 - min)	0-III	180-1005	0.0001	0.04	0.1	0.90
Nilssen *et al.* 1994	Northern Norway (M_2 - max)	0-III	180-1005	0.0013	0.5	1.1	0.33
Bogstad *et al.* 1994	Iceland (M_2 - min)	0-III	180-1005	0.0009	0.3	0.8	0.47
Bogstad *et al.* 1994	Iceland (M_2 - max)	0-III	180-1005	0.0018	0.7	1.5	0.22
Sparholt 1990	North Sea (M_2)	0-I	90-275	0.0073	2.7	1.3	0.26
Sparholt 1990	North Sea (M_2)	I-II	276-640	0.0020	0.7	0.7	0.50
Sparholt 1990	North Sea (M_2)	II-III	641-1005	0.0004	0.3	0.2	0.82
Sparholt 1990	North Sea (M_2)	0-III	90-1005	0.0025	0.9	2.2	0.11
PAPER IV	Heimarkspollen, (8 cm)	0-I	117-386	0.017	6.3	4.6	0.01
PAPER IV	Heimarkspollen, (12 cm)	0-I	126-384	0.003	1.1	0.8	0.45
PAPER IV	Heimarkspollen, (17 cm)	0-I	210-358	0.003	1.1	0.4	0.64
PAPER V	Øygarden, (spring - small)	I-I	335-517	0.011	3.9	1.9	0.13
PAPER V	Øygarden, (spring - large)	I-I	335-517	0.006	2.2	1.1	0.28

Cumulative mortality from egg to recruitment

If we sum up the cumulative mortality from egg to the early juvenile stage it seems that much less than 1% of the spawned individuals reach this stage (Tables I-II). The only area where we have abundance estimates for egg, larvae and juveniles of coastal cod is the small fjord Heimarkspollen. The cumulative mortality of the released genetically marked larvae came to $\Sigma Mt=6.5$ by 40 days after release and $\Sigma Mt>12.6$ at one year of age. (Table II, Fig 3; **Paper I**). If we assume the same survival rates to an age of 40 days in wild larvae and a 5% hatching rate (Table I) this will sum up to as much as $\Sigma Mt=9.6$ (S<0.01%; Fig. 3). These results indicate very high mortality of the early stages of coastal cod, but these results are based on few data and are from a small area, so they must be treated with care.

In Heimarkspollen approximately $2*10^9$ eggs were spawned in (or advected into) the fjord in 1995 (**Paper I**). If we assume that the same number of eggs is spawned every year and use abundance estimates of 0-group cod (Kristiansen & Svåsand 1990) and I-group cod ('Petersen estimates' (Seber 1982) based on data in Paper IV) to calculate mortality from egg to age 6-8 months and age one year, this gives ΣMt between 11.7 and 13.2 at the 0-group stage (age ≈ 6 months), and between 14.2 and 15.1 at one year (Fig. 3). Assuming $2*10^9$ eggs spawned and $\Sigma Mt=9.6$ at 40 d, this means that 3-12% of the early juveniles (age 40 d) survived until the 0-

group and 0.4-1% survived until one year of age. The estimates for 0-group and I-group cod are for two different periods, and cannot be used to calculate survival from 0-group to I-group.

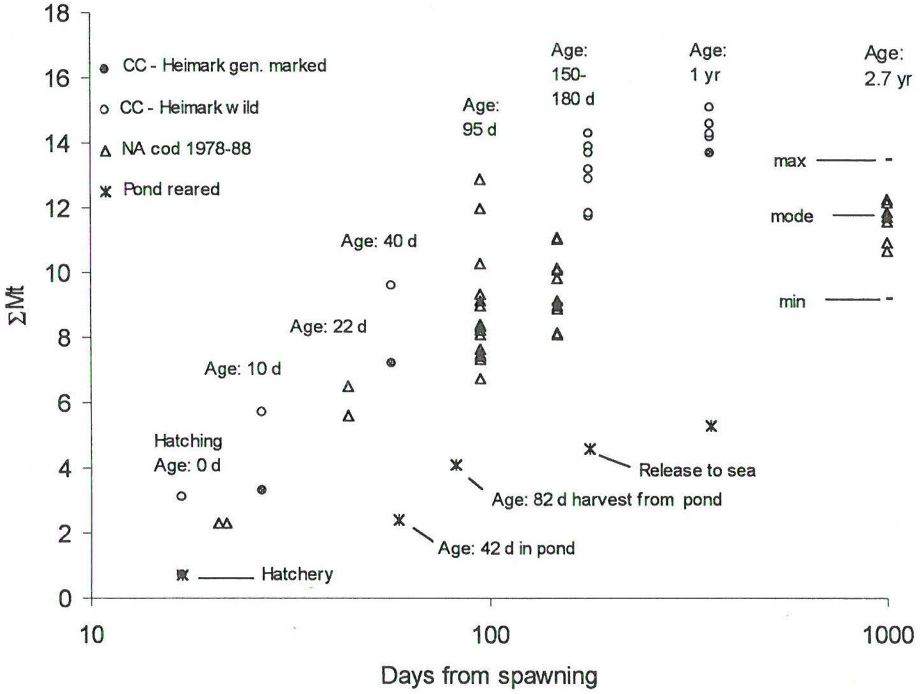

FIG. 3. Cumulative mortality (ΣMt) at various life stages in the small fjord Heimarkspollen (circles) NE Arctic cod (triangles), and pond reared cod (stars). Estimates from Heimarkspollen are based on data from Paper I (eggs and larvae), Kristiansen & Svåsand (1990) (0-group) and Paper IV (I-group). Estimates for NE Arctic cod are based on data from Sundby *et al.* (1989), Helle *et al.* (2000) and ICES 1999 (VPA III-group). Mode, and the max-min range shows the mode and range of mortality estimates for NE Arctic cod from egg to III-group from 1948-1998 based on data given ICES 1999. Average cumulative mortality for cod reared in ponds (stars) is given by Blom (1995), when egg mortality $Mt_E=0.7$ is added (50% survival to yolk-sac stage (H. Otterå, Institute of Marine Research, pers. com)). Average mortality from release as 0-group to one year of age is given in Paper IV.

The mortality estimates from Heimarkspollen are on average considerably higher than similar mortality estimates for NE Arctic cod (Fig. 3), where similar calculations give ΣMt in the range 6.7-12.9 at the early juvenile stage (30 mm), 8.1-9.2 at the 0-group stage (approx.10cm) and 9.2-12.3 at the III-group stage (Sundby *et al.* 1989). Survival estimates from early juvenile to 0-group (30mm to 100mm length) were as high as 6-46% (Sundby *et al.* 1989).
If the survival rates from egg to the 0-group stage in Heimarkspollen are compared with those of the pond-reared cod (Fig. 3), the mean survival of the pond-reared cod was (s_h=) 1,200-16,000 times better than in the sea (eq. 5). Alternatively, if we chose to release 40-day-old early juveniles (Fig 3), the survival from the egg stage to 40 days of age was about 1300 times better in the hatchery/pond than in the sea. However, with 0.4-1% survival from early juvenile to one year, we have to release more than 100 times as many early juveniles as one-year-old fish. The production costs of early-juveniles must then be <1% of the I-group cost, if we are to end up with the same number of one-year-old fish for the same total cost. However, as seen above the mortality pattern may vary greatly between areas and years, and we need more data and practical experiments to evaluate releases of early juveniles.

Size-dependent mortality of released reared cod

Within the various groups of individually tagged cod released in Hordaland and Nord-Trøndelag, the recapture rates increased with increasing size-at-release (**Paper V**). In Masfjorden and Øygarden the survival after release of fish belonging to small, medium and large size-fractions of groups released in the same season were estimated by virtual population analysis (**Paper V**). In all but one of the groups, survival rates six months after release increased with increasing size-at-release, and the survival rates of the large fractions were more than twice as high as those of the small ones (Fig 4a). The main reason for this was decreasing natural mortality in the first few months after release with increasing size-at-release. Yield per recruit also increased with increasing size-at-release, but net yield (recaptured biomass minus released biomass) was low or negative (Fig 4b).

Size-at-age was poorly correlated with size-at-release as early as 6-12 months after release, which showed that individuals that had good growth properties during the rearing period were not necessarily best fit for life at liberty (Fig. 8 in **Paper V**). The rapid changes in the size-distribution rankings also indicated that whatever incidents caused the effects of size-at-release they must have taken place relatively soon after release. Also, in Flatanger in Mid-Norway (**Paper II**) the survival of the large size fraction was more than twice as high as the smallest size fraction one year after release. On the Skagerak coast the natural mortality of small released cod was high and size-dependent for fish smaller than 25 cm (one year old), but not dependent on size in older cod (Julliard *et al.* in press).

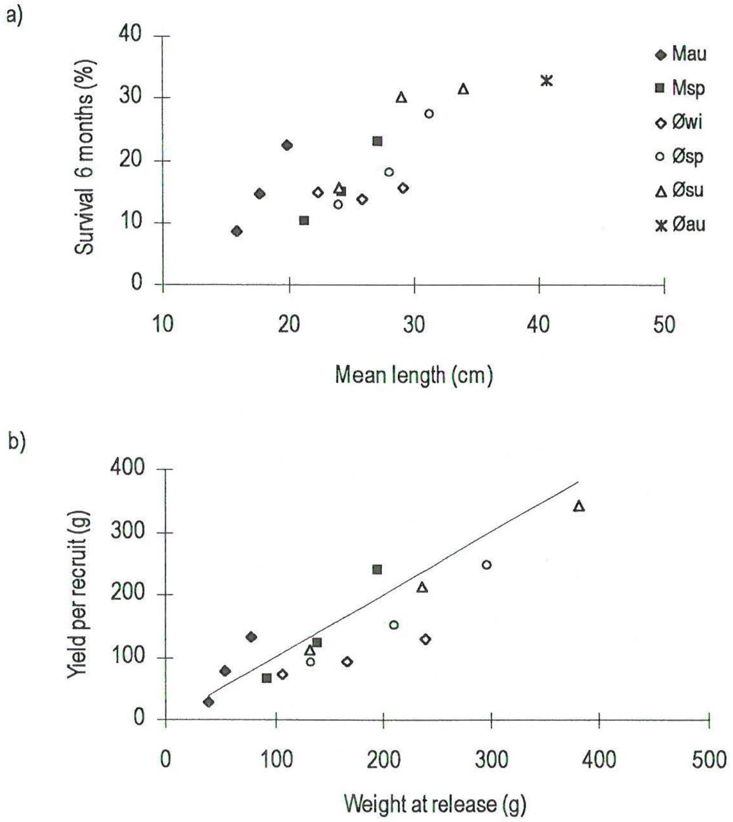

FIG. 4. a) Estimated survival (%) six months after release of the small, medium and large fractions of the release groups in Masfjorden and Øygarden. The small, medium and large fractions of the same release groups are plotted with the same symbol. b) Yield per recruit plotted against weight at release, corrected for tag loss and unreported tags. The straight line indicates where released biomass equals recaptured biomass. (redrawn from Paper V. Fig. 6)

Size-dependant natural mortality is probably caused by size-selective predation. Analysis of regurgitated tags from cormorants (*Phalacrocorax carbo carbo*) demonstrated that these birds preyed selectively on the smallest cod in the release groups (Paper III). By analysing regurgitated otoliths Johansen *et al.* (1999) showed that cormorants in a fjord in Northern Norway preyed on the smallest cod in each year-class I-V. Tank experiments with large cod as predators on juvenile cod showed that the large cod preferred the smallest individuals in a group of 15-25 cm cod (Otterå *et al.* 1998). Also analysis of stomach contents of large cod have shown a positive relationship between predator and prey size, and few cod larger than 40 cm were eaten by other cod (Daan 1981: Bogstad *et al.* 1994) In addition to a higher daily mortality rate for the small fish, the cumulative mortality rate will also increase because the smaller fish need longer on average to grow through the predators' prey preference range. Similarly, there will be growth-dependent mortality, but since there was no way of identifying slow or fast growing individuals in the sea before release, this question could not be evaluated.

Area-dependent mortality

The release experiments have shown very large variations in both natural mortality and fishing mortality at different locations. The level of natural mortality and the size at which the juveniles reach a size refuge from predators might be expected to depend on the abundance and size distribution of the potential predator species. In areas with high fishing mortality, relatively few old and large fish will be present, and we should therefore expect higher survival of small cod. Releases in such areas, e.g. fjords in western and southern Norway, have produced relatively high survival and recapture rates of small cod (<20 cm; **Papers V-VI**; Svåsand & Kristiansen 1990b; Danielssen & Gjøsæter 1994; Julliard *et al.* in press). In areas with low fishing mortality the numbers of large fish predators are expected to be higher, as found in **Paper V**, and the survival rates of small cod released in such areas were found to be lower (**Papers II-III, V**, Skreslet *et al.* 1999). Mortality also decreased with increased distance from predator concentrations; in **Paper III,** for example**,** it was shown that mortality fell as the distance from a cormorant roosting site rose.

In exposed coastal areas with low human populations the numbers of bird and mammal predators are often high, and releases in this type of areas have produced very low recapture and survival rates in small cod (<20 cm). Natural mortality of larger cod was also high in such areas and there seemed to be no size refuge from predators (**Paper II**, Skreslet *et al.* 1999). The bottom habitat probably also makes a difference. At the Faeroe Islands, for example, releases of cod on the 100 m deep Faeroe Bank with a sandy bottom gave very few recaptures, but releases in shallow, rocky areas in the sound between the Faeroe Islands produced recapture rates comparable to those in western Norway (Fjallstein & Jákupsstovu 1999)

Year- and season-dependent natural mortality

For various reasons the mortality after release may vary between seasons and years. The abundance and size of predators may vary between seasons and variable year-class abundance of predators and prey may change the mortality risk and food availability from one year to another. In Mid-Norway (**Paper II**) the mortality of small cod was almost 100% when released during winter, while survival was much higher when released in summer. This lower summer mortality was believed to be associated with the absence of cormorants and coastal seals (*Phoca vitulina* and *Halichoerus grypus*), as they bred in other areas. Similar, but weaker, effects of seasonal migrations of cormorants and shags (*Phalacrocorax aristotelis*) were also seen in Øygarden (**Papers III, V**). Environmental effects such as algal blooms (Julliard *et al.* in press) and wind-generated transport of zooplankton and early life stages of fish into or out off the nursery areas may affect the abundance of food organisms, survival rates, and local year-class abundance (Giske *et al.* 1991; Fosså *et al.* 1994; Salvanes & Baliño 1998; Asplin *et al.* 1999). The occurrence of large year-classes in the same or previous years may also affect survival, both directly through predation and indirectly through food competition (Salvanes & Baliño 1998).

Wild and reared cod – how do they compare?

Several studies of reared fish have showed that the rearing process may lead to morphological and behavioural changes that produce fish with relatively poor performance after release (reviews by Blaxter 1976; Howell 1994; Olla *et al.* 1998). However, rearing cod in marine ponds with an environment similar to the natural environment has been assumed to produce fish that resemble wild fish (Svåsand 1991). Several authors have compared wild and released cod (reviewed by Svåsand 1991; Nordeide 1993; Svåsand *et al.* 1998ab). Differences in food intake and food quality have been observed during the first weeks after release (Nordeide & Salvanes 1991), but the diet of the reared cod gradually changed to the same prey choice as wild cod after a few weeks (Kristiansen & Svåsand 1992). In most studies the growth rates of reared cod have been equal to or better than those of wild cod of the same age (Kristiansen 1987; Kristiansen & Svåsand 1990; Nordeide & Fosså 1992; Svåsand *et al.* 1998b; Otterå *et al.* 1999; **Paper II**). Small released cod suffered high mortality during their first months in the sea (Nordeide & Salvanes 1991; Svåsand & Kristiansen, 1990b, **Papers II-IV**; Julliard *et al.* in press), and we should assume that this mortality was higher than for similarly aged wild cod in the release areas. However, no comparable tag-recapture studies of wild and reared small cod (<25cm) to test this have been published, due to the difficulty of catching large numbers of 0-group wild cod. From I-group stage the ratio of reared cod of the same year-class in the release areas has been constant or slightly falling (Kristiansen & Svåsand 1990; Nordeide *et al.* 1994). The drop in this ratio, however, could, in addition to mortality, also have been caused by changes in the catchability of wild cod (Nordeide 1993) as well as different migration patterns of wild and reared cod (Nøstvik & Pedersen 1999).

Nordeide & Svåsand (1990) and Nødtvedt *et al.* (1999) demonstrated a differences in anti-predatory behaviour between predator-naive reared cod and wild cod. Reared cod went from a stage of excessively weak reactions to predators to a subsequent stage of excessively strong reactions, before developing the "balanced" response displayed by wild cod (Nødtvedt *et al.* 1999). However, in **Paper III**, no effects of predator training or acclimatisation in the release area were found. One explanation for this may be that the appropriate response to predators are learned within a short period of time, as indicated by Nødtvedt *et al.* (1999), and that the difference in mortality between trained and untrained fish is small in that short period. However, the high mortality of reared fish after release (**Paper V**) suggests that reared fish have behavioural weaknesses that make them more vulnerable to predators. Stengrund & Fernö (1997) showed that reared cod actively chased their prey, while wild cod utilised an ambush technique and spent much less energy on hunting prey, and were thus probably less likely to be spotted themselves by predators. There are also indications that the behavioural differences of reared cod increase with age and size before release. In both **Papers IV-V** the largest and oldest release groups showed different catchability from cod released at earlier ages. Large I-group cod released in Sørfjord in Troms migrated more than wild cod, stayed mainly in shallow water, and were more vulnerable to fishing than wild cod (Nøstvik & Pedersen 1999). In other species reduced behavioural quality with increasing rearing duration has also been reported (Tsukamoto *et al.* 1999).

Effects of fishing

In the study areas in southern and western Norway, released cod started to recruit to the fishery as I-group and were in most areas fully recruited as II-group. The recaptures came mainly from recreational fishermen and fishing mortality was very high (Svåsand & Kristiansen 1990b, Danielssen & Gjøsæter 1994; Julliard *et al.* in press; **Papers V-VI**.). In contrast, fishing mortality of young cod in mid-and northern-Norway was very low (Skreslet *et al.* 1999; Johansen *et al.* 1999; **Paper II**). Both the released cod and the wild cod that grew up in the nursery areas in mid-Norway had low recruitment to the fishery on spawning cod (**Paper II**) that concentrated on spawning concentrations of NE-Arctic cod and migrating offshore cod. Nor did the cod released in Masfjorden recruit to the spawning fishery to any significant degree (Jørstad *et al.* 1999).

In recruited cod, fishing mortality in most areas in western and southern Norway was much higher than natural mortality (Svåsand & Kristiansen 1990b, **Papers V, VI**). However, it is difficult to estimate the natural mortality of large cod, since unreported tags and tag losses are also included in total mortality estimates (**Paper V**). The recapture rate of 'large' tagged wild cod (>30 cm) showed no or only a slight increase with increasing size-at-release, indicating a minor effect of size on natural or fishing mortality (**Paper V**). Since very few predators can consume cod >40-50 cm in length (Daan 1981) it is reasonable to assume a low natural mortality rate, and since tag-loss rates have also been shown to be low (Otterå *et al.* 1998), the discrepancy between reported and expected recaptures must be caused by unreported tags (**Paper V**.) In most of the literature the natural mortality of large cod is assumed to be in the range 0.1-0.3, but few estimates are available. When assuming natural mortality $M=0.3$, the estimated reporting ratios lay between 0.38 - 0.72 (**Paper V**). In the release area on the Skagerak coast a similar reporting ratio was also found (0.5-0.6; Julliard *et al.* in press)

According to traditional single-species population models, juvenile cod in southern Norway are growth overfished (Ulltang 1984), and we should assume that there would be a larger yield from the releases if the cod were recaptured at a larger size. However, changing the fishing pattern would change the size distribution and biomass in the fish population, which in turn would affect predation mortality and prey and competitors. It is therefore uncertain what the results will be when cannibalism and multispecies effects are taken into account (Sparholt 1990).

In **Paper VI** the effects of individual growth variation and size selective fishing on growth and yield estimates are modelled and discussed using individual growth data from the experiments in Heimarkspollen. These data showed a large difference between mean population growth rate and mean individual growth rate. The modelled results showed that using mean lengths at age can lead to serious errors in growth and yield estimates when there is size-selective mortality and individual growth variation. The effects were caused by selective removal of the fastest-growing individuals, and the effects increased with increasing growth variation and increasing fishing mortality.

Both life history theory (e.g. Law & Grey, 1989), genetic models (e.g. Favro *et al.* 1979), and selection experiments (e.g. Gunnes & Gjerdrem, 1978, 1981; Gjerdrem 1983; Refstie & Steine 1978) show that selective removal of individuals with heritable traits, such as growth rate and age at maturity, will have effects on the traits of future generations. High mortality rates and age- and size-selective fishing mortality will select for early maturation and slower growth rate in the population. Compensatory phenotypic and ecological mechanisms, such as increased growth rate, fecundity and survival and earlier maturity, will obscure and make it difficult to quantify the heritable effects. However, in a period of several decades or centuries, this may lead to serious reduction in the future yield from the stock (Borisov 1978, Law and Grey 1989; Law and Rowell 1993; Policansky 1993). The size of the heritable effects will also depend on how large a part of the spawning population is influenced by the size-selective fisheries. In Heimarkspollen, for example, a large proportion of the eggs are advected in from outside the fjord (**Paper I**) from areas with a different fishing pattern (Kristiansen 1987).

Implications of the results for cod enhancement

The results from the enhancement programmes have shown that the net yield from the releases was low or negative in all areas and the values of the recaptures were far from covering the cost of release (Fig. 4b.; Svåsand *et al.* 1998a; **Paper V**). This was caused by high natural mortality before recruitment to the fishery (Svåsand & Kristiansen 1990b; **Papers II, IV-V**), excessive fishing mortality of small cod (growth overfishing; **Papers V-VI**) and/or insufficient weight increment between release and recapture (Svåsand *et al.* 1998a; **Papers II, V-VI**). If we also consider possible density-dependent effects on wild cod the situation becomes even worse.

The most complete cod enhancement project was carried out in Masfjorden between 1985 and 1992 (Nordeide *et al.* 1994; Smedstad *et al.* 1994). The fish populations in the fjord and in a control area outside the fjord were monitored before, during and after a period of releases of 0-group cod at the level of strong to medium natural year-class strength (23,000-82,000 individuals). The results showed that the high density of juvenile cod in the release area just after release fell to a density similar to that in the control area about a year after release (Nordeide *et al.* 1994). The results also indicated higher mortality and stronger density-dependent effects on the reared cod than on the same wild year-class (Fig. 4 in Nordeide *et al.* 1994). The releases happened in a period with relatively low production and following high natural recruitment of cod, pollack (*Pollachius pollachius*) and poor cod (*Trisopterus minutus*) in 1987-1998, which resulted in high competition and low carrying capacity (Fosså *et al.* 1994). By means of a dynamic ecosystem model, it was shown that the advection of plankton rich water to the fjord by south-westerly winds was the most important factor in determining the prey production and production potential for cod juveniles (Giske *et al.* 1991; Fosså; 1991; Salvanes *et al.* 1992; Salvanes & Baliño 1998). In addition to the advection of plankton, the growth and survival of 0-I group cod depended on density-dependent predation of older cod and pollack (Salvanes & Baliño 1998).

Giske & Salvanes (1999) explored the enhancement question using a simple stochastic age-structured model based on the results of the Masfjord project and a Leslie matrix life-history approach. By simulating the effects of releases in an environment with variable natural recruitment, variable carrying capacity (zooplankton advection) and frequency-dependent cannibalism, they found that 'perfect releases' that exactly matched current carrying capacity in years with natural recruitment below the carrying capacity tended to maintain the population at a higher level. However, releases of a fixed number in years with unknown but above-average carrying capacity did not enhance the population, but gave rise to unwanted frequency-dependent predation and mortality caused by limited carrying capacity. Since it is unlikely that the information necessary to perform 'perfect releases' can be obtained, the authors conclude that releases of additional recruits of stationary species in an area with variable carrying capacity will give very variable results and on average will not increase catches.

The results of the cod enhancement programmes offer no suggestion of recruitment bottlenecks at any developmental stage. The numbers of egg and larvae per km^2 nursery area seem to be higher than for the oceanic stocks (**Paper I**), so the recruitment does not seem to be limited by egg production or insufficient spawning stock biomass, even in areas with very high fishing mortality. Oceanographic conditions may limit transport of early juveniles to some available nursery areas, since the juveniles seem to be very stationary after settlement and will probably not colonise areas with low settlement. None of the areas investigated suggest that recruitment-limited areas exist, but few areas have in fact been studied. In areas with high predation mortality the catch per unit effort of juvenile cod was similar to or higher than in areas with low predator density, e.g. areas close to or far from cormorant breeding colonies (Kristiansen 1998; Otterå *et al.* 1999; **Paper II**). This indicates that the predators concentrate in areas with good recruitment of fish and that they prey on the surplus production of fish in these areas.

Concluding remarks

Returning to the objectives of this thesis, we can conclude that the release strategy selected had an important influence on the results.

The releases of genetically-marked yolk-sac larvae confirmed the assumption of very high mortality during the larval stage; only c. 0.15% survived the first 40 days after release, while less than 1% of these survivors survived to one year of age (**Paper I**).

Recapture rates of individually tagged reared cod and survival rates after release increased with increasing size-at-release, due to size-dependent natural mortality during the first few months after release (**Papers II-V**). However, the net yield was low or negative and increased only slightly or not at all with increasing size-at-release. Recapture rates and survival after release varied considerably between areas, due to variations in natural and fishing mortality (**Papers II-V**). There seemed to be a negative relationship between the natural mortality of young fish and the fishing mortality of larger fish, i.e. a positive effect of removing predators. The density and size distribution of predators and distance from predator concentrations had significant effects on mortality. Recapture rates and survival within areas also varied between season of release and years, probably due to seasonal and annual variations in predation pressure (**Papers II-V**). Releases in shallow seaweed-covered areas, preconditioning and predator training had no effects on survival after release (**Paper III**).

In western Norway the cod started to recruit to the fishery already as one-year-olds, and the fishing mortality of recruited cod was high. The local stocks were assumed to be growth overfished. On the other hand, in mid-Norway the fishing mortality of local cod was negligible (**Paper II**). Size-selective fishing mortality could have a major effect on growth and yield estimates in populations with individual growth variation and high fishing mortality (**Paper VI**).

The tests of Leber's (1999) two corollaries to the hypothesis that releases of reared fish can increase fish production were only partially passed.

1. The released fish survived, grew and contributed to the recruitment to the fisheries in most, but not all release areas. Their contributions to the spawning stock were small (Jørstad *et al.* 1999), due to high juvenile mortality (**Papers I-IV**). The ability of the released cod to find the local spawning areas was not demonstrated, except in a small release area in Austevoll (Svåsand *et al.* 1990).
2. At least in periods with limited feeding resources, the releases did not increase overall abundance (Nordeide *et al.* 1994), and the releases probably had negative effects on the wild cod stock, by reducing feeding resources and thereby wild cod production (Fosså *et al.* 1994).

Unlike the first "cod hatchery movement" (Solemdal *et al.* 1984), the second generation of cod enhancement experiments has given us a great deal of new scientific information and has made a significant contribution to our understanding of the ecology of juvenile coastal cod and their environment. Publications from these studies also make up a significant part of the world literature on marine enhancement experiments (see references in Svåsand *et al.* 1998; Howell *et al.* 1999; **Papers IV-V**).

Prospects for the future

The conclusion from the release areas studied was that there was no recruitment limitation, and that the available feeding resources limited production. To increase local cod production we therefore need to increase the feeding resources. Methods already tried include fjord ranching with released cod that have been trained to respond to a feeding signal (Midling *et al.* 1987) and feeding the wild cod stock (Björnson 1999). However, these methods may be less profitable than net pen farming, and they also need legal protection of the fish.

The high recapture rate and limited migration of released large cod in western and southern Norway make the cod a candidate for "put-and-take" fisheries in areas where fishing tourism is an important industry. The released fish should then have the same appearance as wild cod, or could be released some months before the tourist season in order to give them a "wild" quality. A combination with fjord-ranching would be another possibly profitable combination, if this kind of fish would be accepted by the fishing tourists.

Our ability to rear large numbers of cod (and other fish) of any size has given us the ability of carrying out large-scale ecosystem manipulations such as the Masfjord project (Smedstad *et al.* 1994), which can be used to test new hypotheses and model results and improve our understanding of population regulation mechanisms in coastal ecosystems. Experiments like the one described in **Paper I** can also be carried out to measure the mortality of larvae and early juveniles in natural environments. In particular, more precise estimates of mortality rates of early juvenile cod are lacking. If the wild stocks were to collapse, as happened in the western Atlantic at the end of the 1980s (Hutchings & Myers 1994; Myers *et al.* 1996), would it be possible to rear a new broodstock and allow them to spawn on the traditional spawning grounds? The possibilities are many, but expensive to realise or evaluate. Only the future will show if the cod enhancement story ends here, or if new chapters will be written.

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errata

Paper I, p. 280, line 33 and line 34: 10,000 should be corrected to 100,000.