NATURAL MORTALITY AND FISHING MORTALITY IN A COASTAL COD POPULATION: A RELEASE–RECAPTURE EXPERIMENT

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Abstract. As with most teleosts, the life cycle of the cod (*Gadus morhua*) is characterized by high productivity of eggs leading to high concentration of larvae. These stages are known to be associated with high mortality rates. Mortality of older stages (juveniles and adults) has been relatively poorly studied. We use capture–mark–recapture (CMR) methodology to estimate time and age variation of natural mortality and fishing mortality in a coastal cod population within the Norwegian Skagerrak coast. A total of 36 728 reared 6-mo-old, and 2415 wild-caught mostly 18-mo-old, individually tagged cod were released in four consecutive years, leading to 4155 recaptures by fishermen. Tag loss and mortality due to tagging appeared negligible for reared young fish, but up to 60% of the wild-caught tagged fish disappeared just after release. Tag return by fishermen was ~50–60%. Natural mortality was found to be high in the 6–12 mo range, but subsequently it decreased rapidly and was no longer age-dependent. Fishing mortality was negligible for fish younger than 1-yr-old, intermediate for 1-yr-old fish, and high for older fish. The seasonal pattern of fishing varied much between age classes, with 2-yr-old fish mostly taken by recreational fishermen in summer, and older fish mostly taken by professional fishermen in winter. Because it is directed toward relatively young fish, recreational fishing may have a strong impact on the population; we specifically point out the coincidence between the increase of tourism and the decrease of the cod stock in the Risør area during the last 20 yr. Total mortality varied little between years, except during ~5 mo after a major algae bloom in May 1988, when fish disappeared at a high rate whatever their age (no emigration was observed in connection with the algae bloom). We conclude that mortality of adult fish may be an important determinant of the stock size.

Key words: age classification; age- and time-dependent mortality; capture–mark–recapture; cod, Gadus morhua; *natural mortality and fishing mortality; Norwegian Skagerrak coast; statistical modeling; toxic algae bloom.*

INTRODUCTION

Due to the high variability in survival of eggs and fish larvae, it is generally assumed that the strength of a year class is mainly determined during early life stages (e.g., Hjort 1914, Ricker and Foerster 1948, Campana et al. 1989, Shepherd and Cushing 1990, Doherty and Fowler 1994). Many studies have therefore focused on these early stages, while the life history of older stages has been studied far less. Recent studies have, however, suggested that variation in survival among juvenile fishes may also contribute significantly to variations in recruitment (e.g., May 1974, Sundby et al. 1989, Myers and Cadigan 1993). This variation in survival seems mainly related to starvation (the match–mismatch hypothesis, e.g., Cushing and Horwood [1994]) and to predation varying among age classes (i.e., younger stages being more subject to predation; e.g., Wootton [1990]) as well as among habitats (Tupper and Boutilier 1995*a, b,* 1997). It is well known that fishing is often a major factor contributing to mortality of older individuals (Garrod and Schumacher 1994, Myers et al. 1996, Roughgarden and Smith 1996, Cook et al. 1997). Little is known, however, about variation in natural mortality of adult fish (for review, see Vetter [1988]).

Quantitative assessment of mortality and identification of the underlying processes are important if we want to improve our understanding of the demography of fish populations. Fish mortality has been studied for years, using a wide variety of approaches. Natural mortality is particularly difficult to quantify, and Vetter (1988) concluded that all methods commonly used to estimate mortality have serious limitations. As prerecruit and postrecruit stages of fish are usually caught by different gears, and analyzed using different methods, few studies of life history include the entire life span. Releasing individually tagged fish and recording
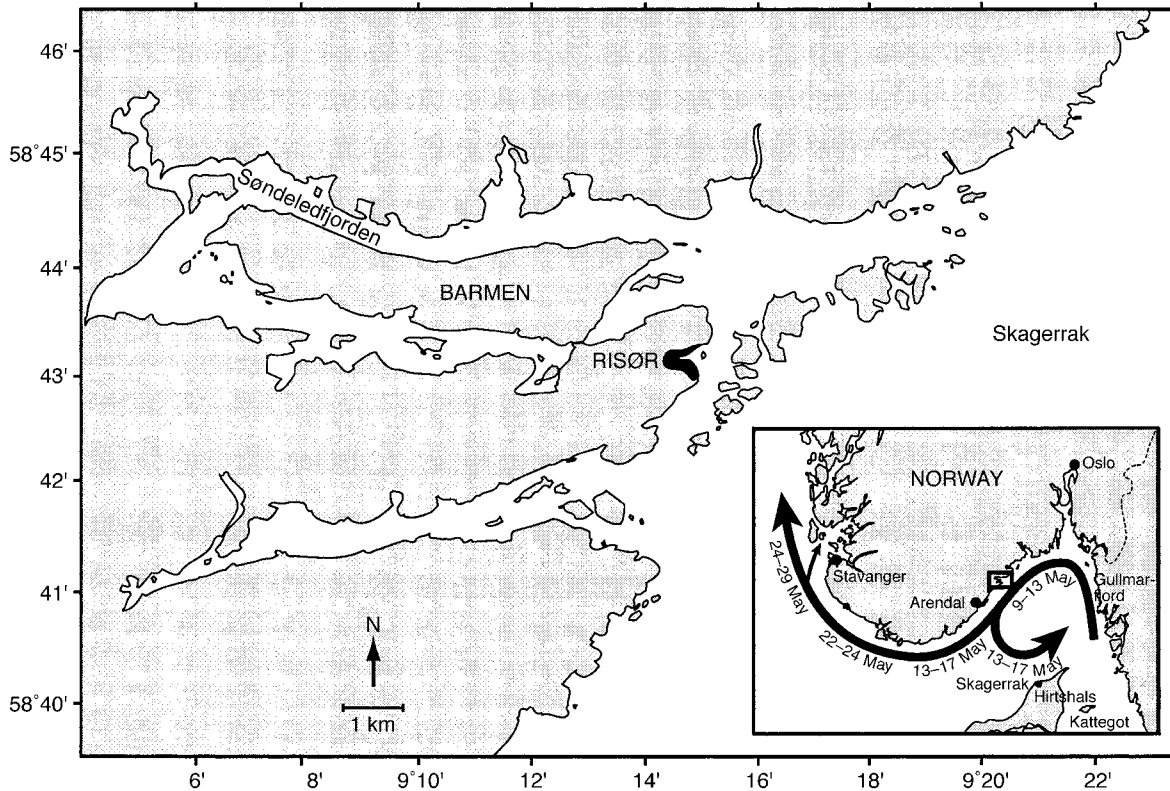
FIG. 1. Location of the Risør area (our study site) within the Norwegian Skagerrak coast. Individual fish were released in the fjords just inside Risør. Inset: the development of the algae bloom in May 1988 (modified from Dahl et al. [1989]), with the Risør area indicated. The bloom started 9 May in the Kattegat, reached the Risør area by 15 May, and the western coast of Norway by 24 May. In any given place, the bloom was visible for at most five days.

their subsequent recaptures by fishermen is one way of assessing the magnitude of various (age- and time-specific) mortality factors.

In order to assess the relative importance of natural mortality and fishing mortality in coastal cod populations (*Gadus morhua,* L.), we have analyzed release–recapture data on tagged cod within a fjord of the Norwegian Skagerrak coast (Danielssen and Gjøsæter 1994). Our study includes the year 1988, during which a toxic algae bloom (*Chrysochromulina polylepis*) occurred, affecting the entire Skagerrak–Kattegat ecosystem (Underdal et al. 1989, Johannessen and Gjøsæter 1990, Granéli et al. 1993).

We used "capture–mark–recapture methodology" (CMR; see Burnham et al. [1987] and Lebreton et al. [1992] for reviews) to investigate three sources of variability of the mortality probability of tagged fish: (1) variation in fishing probability (age and time specific), (2) variation in natural-mortality probability (age and time specific), and (3) variation in tagging mortality (i.e., mortality immediately following release). Specifically, this methodology allows us to estimate separately the age- and time-dependent capture probabilities (the probability that an individual being alive, is captured during a "capture occasion") and the age-

and time-dependent survival probabilities (the probability of surviving between two capture occasions). Recent analyses of fish populations have, to various degrees, incorporated several of the methodological features involved in CMR modeling (Hilborn 1990, Schweigert and Schwarz 1993, Myers et al. 1997). Much more common within the field of fish ecology is, however, the application of "cohort analysis" ("virtual population analysis" [VPA]); Fry 1949, Gulland 1965, Ulltang 1979), but VPA requires independent estimates of the natural mortality for all the stages and of the fishing mortality for the oldest stage. Here we demonstrate that CMR methodology provides an opportunity to assess mortality (and test hypotheses about) patterns, without making strong assumptions on any life history parameters.

MATERIAL

The release experiment

The release experiment was performed in the Søndeledfjord (i.e., the Risør area; see Gjøsæter and Danielssen [1990]), located along the Norwegian Skagerrak coast (Fig. 1). This fjord consists of a 180 m deep outer basin, separated from the Skagerrak by the Sker-

ROMAIN JULLIARD ET AL.

TABLE 1. Number of cod tagged and released in the Risør area during 1986–1989 (modified from Danielssen and Gjøsæter 1994).

Co-hort	Date	Type of fish released	No. fish released	Mean length (cm)	Percentage recovered
R 86	October 1986	reared	5894	15.9	3.5
R 87	October 1987	reared	6701	15.2	2.0
R 88	October 1988	reared	11 408	17.4	12.9
R 89	October 1989	reared	12 725	17.3	9.3
W 86	December 1986	wild-caught	791	34.6	28.4
W 88	December 1988	wild-caught	1387	35.1	26.8
W 89	December 1989	wild-caught	237	38.0	20.7

ries, which consist of many small islands, narrow inlets, and shallow archipelago. The depth of the threshold separating the fjord from the open sea is 15–20 m. The inner part is shallower and has several thresholds with depth varying from 20 m to 40 m.

Two categories of fish have been released (Table 1): (1) artificially reared, 6-mo-old fish released in October in 1986, 1987, 1988, and 1989; and (2) wild-caught fish, primarily ~18-mo-old, selected from commercial catches in the Risør area and released in December in 1986, 1988, and 1989.

All fish were tagged using FD-67 Floy individually numbered tag attached under the first dorsal fin (see Danielssen and Gjøsæter 1994). The artificially reared fish were raised on the western coast of Norway, just outside Bergen (at the Institute of Marine Research, Austevoll Aquaculture Station, and at the Lagoon Management and Construction), and brought to Risør by trucks or boats in large tanks. The fish were kept at the release site for some days to assure that they were not hurt during transportation. Wild fish were bought from commercial fishermen who had caught them in pots. Only fish not obviously hurt were used. They were further kept in a big net pen for at least a week to assure that they in fact were viable. After tagging (which occurred in the Risør area) all fish were kept in tanks onboard for a period lasting from 30 min to several hours. Thus, fish that appeared to have been hurt by tagging could be detected and excluded from the release experiment. Fish were released in groups of not more than a few hundred individuals to make sure that they spread over a large area.

The release experiments were announced in local newspapers, radio, and posters along the Norwegian Skagerrak coast, and a reward of NOK 25 (~US$4) for each reported tagged fish was offered. Fishermen were asked to record the length of the tagged fish they caught, as well as the location where the fish was caught and the gear being used. Eel fishermen, using traps, fished intensively in the area during the study period. In 1989, an agreement was made with eel fishermen to record tag number and length of caught individuals (with tags) and thereafter to release them. Altogether, eel fishermen have caught >1500 tagged fish (some fish being caught several times), of which more than half have been rereleased. Altogether, there have been 4382 recaptures of tagged fish up to the end of 1993 (of these 996 (23%) were released again).

Fish released in December were measured, but not aged. Using an age–length key based on 1400 cod caught in the Risør area during 1986–1996 (J. Gjøsæter, *unpublished data*), it was estimated that 58% of the tagged wild fish were one year old, 33% were two years old, and a few fishes belonged to age classes 0, 3, and 4. In addition, the size distribution of the wild-caught fish tagged and released in December was compared to the size distribution of artificially reared fish recaptured during the same period (November–January) one, two, three, and more years after being released. It was thus found that the size distribution of wild fish caught in December appeared to be very close to the size distribution of one-year-old reared fish recaptured at that time (Fig. 2).

Background life history

Fish larvae metamorphose into small fish around May–June in these coastal populations (Gjøsæter and Danielssen 1990). These young-of-the-year constitute the 0-group cod up to the first of January. They constitute the 1-group in the following calendar year, the 2-group the next calendar year, and so on (see Ricker 1958). The demarcation on the first of January is merely a convenient classification, and it is used by the International Council for the Exploration of the Sea (ICES). However, since hatching occurs in February–April (Dannevig 1933, 1966), we used another classification scheme, extending from April–April instead of January–January. In the following, we refer to the ICES-classification as 0-group, 1-group, etc., and to the other classification proposed as "0-age class" (for the period between hatching and April one year later), "1-age class" (for individuals 1–2 yr old), "2-age class" (for individuals 2–3 yr old) and "3$^+$-age class" (for individuals aged >3 yr).

Along the Skagerrak coast, 75% of the spawning stock is represented by 2- and 3-yr-old fish (Gjøsæter et al. 1996). The maximum age recorded in the Norwegian Skagerrak population is 12 yr; however, very few fish seem to reach such an old age (Gjøsæter et al. 1996).

Individuals of the studied cod population exhibit vertical migration related to temperature (Dannevig 1966,
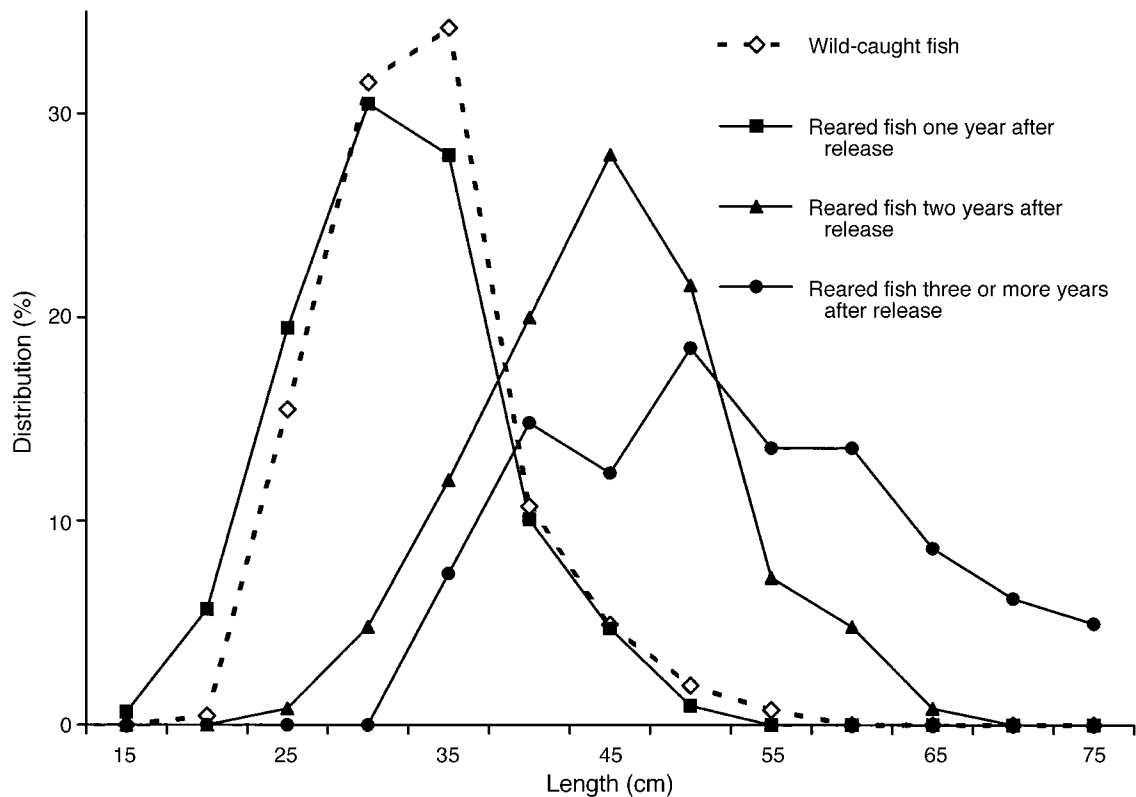
FIG. 2. Length distribution of wild fish caught in December compared with length distribution of reared fish recaptured during November–January on the first, second, and third (or more) years following release.

Danielssen and Gjøsæter 1994): they stay in shallow waters during autumn and spring and descend to deeper water during summer and winter. The 0-group and a fraction of the 1-group are generally found to occur in more shallow waters and closer to the shore than the older individuals (Dahl 1906, Dalley and Anderson 1997). Dahl (1906) and Løversen (1946) also suggested that spawning fish aggregated in the inner parts of the Risør fjords for spawning and moved outwards for feeding. Extensive release and recapture experiments have demonstrated that the coastal Norwegian Skagerrak cod consists of nonmigratory and semi-isolated local populations (Danielssen and Gjøsæter 1994; see also Ruud 1939, Løversen 1946, Moksness and Øiestad 1984). Indeed, 91.5% of the recaptures occurred <7 km from the release site, despite high fishing intensity throughout the Norwegian coast as well as in the open Skagerrak sea.

Fishing pattern

The Norwegian Skagerrak cod populations are exploited by professional fishermen, who use various nets and pots (i.e., traps). They generally catch large fish, and release the smaller fish whenever possible. Fish caught in nets are, however, generally dead. The most important season for this fishery is from late autumn until early spring (Fig. 3). Professional fishermen also use eel pots, often giving large by-catches of small cods, which are usually released; the main season for this eel fishery is spring–autumn (Fig. 3). Various types of leisure fishery are carried out by people using a wide variety of gears. The distribution of catches among the different gears used, was strongly dependent on fish size (Table 2) and on month of the year (Fig. 3).

The toxic algae bloom of 1988

The *Chrysochromulina* bloom (Fig. 1) killed most fish and several other organisms in the upper 20 m along extensive parts of the Skagerrak coast during May–June 1988 (Underdal et al. 1989, Johannessen and Gjøsæter 1990, Granéli et al. 1993). Cod belonging to the 0-group were almost completely exterminated (3-mo-old at the time of the algae bloom, thus mostly pelagic), while it is assumed that older cod survived better by descending into deeper waters and thus avoiding the toxic algae (e.g., Gjøsæter 1988). The plankton algae community in some areas was affected for two weeks (Nielsen et al. 1990), whereas the benthic community was affected for two years (Olsgard 1993).

ANALYSES

The basis of capture–mark–recapture (CMR) modeling

Comprehensive reviews of capture–mark–recapture (CMR) modeling are given by Burnham et al. (1987)
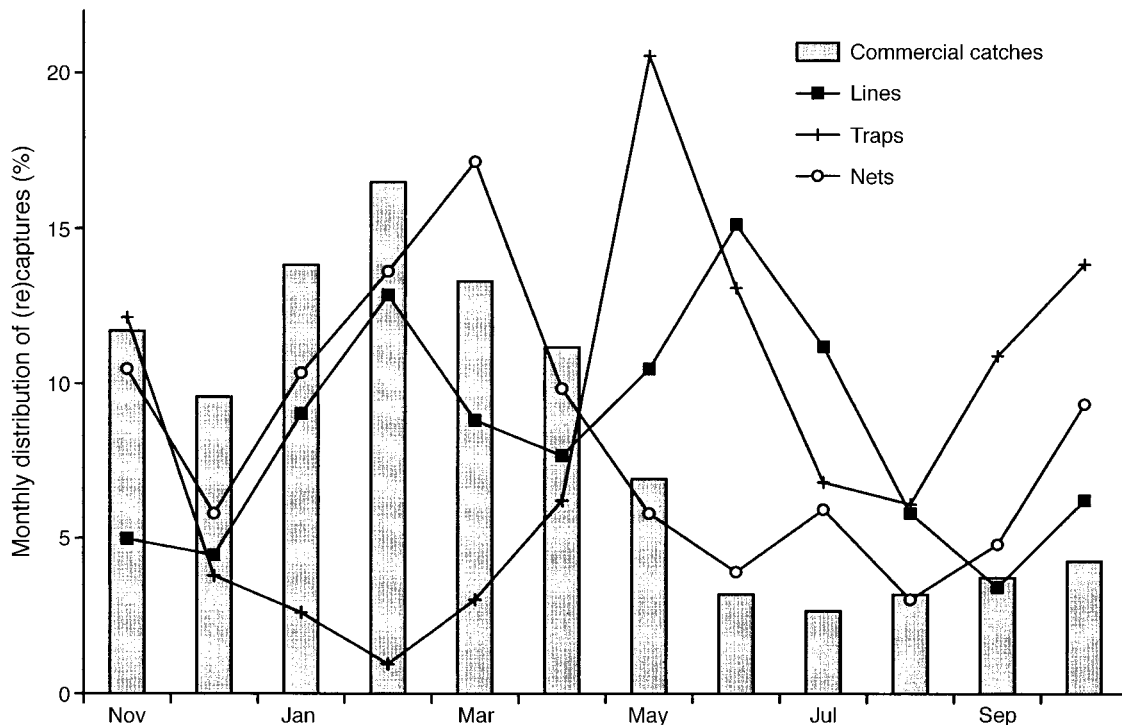
FIG. 3. Monthly distribution of recaptures of marked fish by the various gear, superimposed on commercial catches (monthly mean no. landings for 1986–1991 in the Risør area). The latter were obtained from the Norwegian Directorate of Fisheries (Fiskeridirektoratet, P.O. Box 185, N-5002 Bergen, Norway).

and Lebreton et al. (1992). In short, CMR modeling assumes that, after being released, tagged individuals may be recaptured at different capture occasions. At each capture occasion, only a proportion of individuals originally marked and released may still be alive, and only a proportion of them may be recaptured. Define p, the capture probability, as the probability of capture, conditional on the individual still being alive (in fact, conditional on being ''capturable''; i.e., present in the population and still having a tag). The capture probability may be both time and age dependent. Survival up to a given occasion may further be split into survival (ϕ) between consecutive occasions, which again may be both age and time dependent. Note that ϕ is a persistence probability between two occasions and includes the probability of not emigrating permanently from area of study and not loosing the tag between the two occasions.

A capture–recapture history is defined as a sequence of captures and noncaptures in successive capture occasions. To each capture–recapture history, a multinomial probability with the parameters p and ϕ may be assigned. Using the number of individuals having different capture histories, it is then possible to estimate the different parameters using the maximum likelihood method (software SURGE; Pradel and Lebreton 1991, Reboulet et al. 1998). A model assuming full age and time dependence of capture and survival probabilities may be denoted $\phi_{age \times time}$, $p_{age \times time}$.

A full time- and age-specific model would require a large number of parameters to be estimated, many of which will not be independently identifiable. Therefore, constraints must be introduced in order to reduce the number of parameters. We may make various assumptions and then constrain the parameters accordingly. For example, we may assume no variation with respect to age (or no variation with respect to time) of survival and capture probabilities. More subtly, we may assume additive effect of time (t) and age (a) (e.g., for capture probability, $p_{a,t} = \alpha_a + \beta_t$). Furthermore, we may assume a linear relation between parameters and some quantitative variable (such as temporal trend, age, or any environmental variables if available). Compar-

TABLE 2. Size specificity of the different gear.

Gear type	Size at recapture (cm)	Time in sea since release (d)
Reared fish		
Trap	31.0 ± 10.0	359 ± 241
Line	35.6 ± 9.1	511 ± 276
Net	39.0 ± 10.4	585 ± 312
Wild-caught fish		
Trap	43.5 ± 7.9	266 ± 211
Line	41.3 ± 6.7	216 ± 218
Net	45.2 ± 8.5	311 ± 271

Note: Entries represent means ± 1 SD.

ing nested models with different constraints allows testing of different hypotheses.

The first step is thus to specify a model with sensible constraints on the parameters. The specified parameters are then estimated (with standard errors, if parameter estimates are different from 0 or 1). The *deviance* of the model is calculated as $-2 \log(\text{likelihood})$. The number of parameters being separately identifiable is calculated from the rank of the variance–covariance matrix. The Akaike information-theoretic criterion (AIC) (our selection criterion; see, e.g., Burnham and Anderson [1998] for a review), is calculated as the deviance plus twice the number of identifiable parameters. The model with the lowest AIC is considered the best model. Nested models (i.e., simplified models) can be compared using likelihood-ratio tests (LRT; Lebreton et al. 1992).

The small proportion of individuals released after being recaptured induces many difficulties in parameter identification; in particular, for a given cohort, there is no way to separate time-specific survival probability from time-specific capture probabilities. Such a model would generally estimate $\phi = 1$ and p equal to the number of recaptures per number of initial releases. Therefore, CMR modeling requires at least one of the following properties of the data: (1) some individuals are released after being recaptured; (2) several cohorts of fish are released at different times (and we assumed some parameters to be equal between cohorts); and (3) survival and capture probabilities are assumed to be somewhat constant in time. In addition, when no re-release occurs at all, survival between release and the first capture occasion is not identifiable, whatever the constraint on other parameters (Anderson et al. 1985; R. Julliard, *unpublished results*).

When capture probability is low and highly variable as in our case (see *Results*), it is difficult to ascertain when mortality has occurred. Hence, if the parameters are not sufficiently constrained, survival estimates cannot be obtained without suffering a large uncertainty; in such cases, estimates may vary greatly from one model to another.

Building capture history

The CMR methodology requires the definition of "capture occasions." However, in our case, captures are continuous, and can occur essentially every day of the year. Therefore, we pool all the recaptures within a given month and thus assume each month to represent a capture occasion. Hence, survival (or mortality) estimates become estimates of monthly survival (or mortality). The first capture occasion was November 1986, and the last one December 1993; altogether, there were 86 captures occasions.

After being caught by fishermen, tagged individuals were either released (if healthy) or kept onboard. For the latter, capture histories were coded to indicate that these individuals were removed from the population after being caught, but considered alive until their final capture.

The panel model

A CMR analysis starts with the definition of a "panel model," being the most complicated model built under untested assumptions specific to our analysis:

1) For survival, we assumed four age classes. The second and third classes span 12 mo (i.e., monthly survival is constant during these 12 mo), while the last one is survival for older fish (assumed to be independent of age). A key step is the determination of the date of change from one age class to the next (see age classification in *Material: Background life history*). Hence, the first age class spans the period from November (date of first release) to the date of transition to the subsequent age class. In the panel model, we assumed an interactive effect of year (each year covering a full age class) and age (i.e., $\phi_{\text{year}\times\text{age}}$; 19 estimated parameters; Table 3a).

2) Capture probability is likely to be different in each month of each year (full time variation, denoted t). In addition, for a given month, it may vary according to age (i.e., the size of the fish). We assumed that after two years in the sea, reared fish have the same capture probability regardless of when they were released (e.g., in August 1990, reared fish released in October of 1986 and October of 1987 have the same capture probability, being different from fish released in October of 1988 [less than two years in the sea], which in turn have a different capture probability from fish released in October of 1989 [less than one year in the sea]). We thus considered three age classes for modeling capture probabilities (Table 3b). Wild fish released in December are assumed to have the same capture probability as reared fish released one year before. The full time variation may be split into a monthly component (indicating seasonal variation of capture probability) and a yearly component. This model is denoted $p_{\text{month}\times\text{age}\times\text{year}}$ or $p_{t\times\text{age}}$ (180 estimated parameters; Table 3b).

Here the panel model is assumed to be both time and age dependent, with respect to survival and capture probability. The aim of the further analysis is to constrain this model adequately in order to reduce the number of estimated parameters.

Correspondence between parameters used in fishery biology and CMR modeling

Standard parameters in the fishery literature (e.g., Beverton and Holt 1957, Gulland 1965, Rothschild 1986) include the survival probability defined as: $S_{a,t} = \exp(-M_{a,t} - F_{a,t})$, where $M_{a,t}$ is the instantaneous natural mortality (dependent both on age [a] and time [t]), and $F_{a,t}$ is the instantaneous fishing mortality (also dependent on age and time). Total mortality is often denoted as $Z_{a,t} = M_{a,t} + F_{a,t}$. Immediately after release, a proportion of fish may die or move to places where fishing probability is low. Therefore, not all released

TABLE 3. Structure of panel model for modeling survival and capture probabilities.

a) Panel model for modeling survival probabilities†

Cohort	N 1986– M 1987	A 1987– M 1988	A 1988– M 1989	A 1989– M 1990	A 1990– M 1991	A 1991– M 1992	A 1992– D 1993
R 86	$\phi_{1,86}$	$\phi_{2,87}$	$\phi_{3,88}$	$\phi_{4,89}$	$\phi_{4,90}$	$\phi_{4,91}$	$\phi_{4,92}$
W 86	$\phi_{2,86}$	$\phi_{3,87}$	$\phi_{4,88}$	$\phi_{4,89}$	$\phi_{4,90}$	$\phi_{4,91}$	$\phi_{4,92}$
R 87		$\phi_{1,87}$	$\phi_{2,88}$	$\phi_{3,89}$	$\phi_{4,90}$	$\phi_{4,91}$	$\phi_{4,92}$
R 88			$\phi_{1,88}$	$\phi_{2,89}$	$\phi_{3,90}$	$\phi_{4,91}$	$\phi_{4,92}$
W 88			$\phi_{2,88}$	$\phi_{3,89}$	$\phi_{4,90}$	$\phi_{4,91}$	$\phi_{4,92}$
R 89				$\phi_{1,89}$	$\phi_{2,90}$	$\phi_{3,91}$	$\phi_{4,92}$
W 89				$\phi_{2,89}$	$\phi_{3,90}$	$\phi_{4,91}$	$\phi_{4,92}$

b) Panel model for modeling capture probabilities‡

Cohort	N 1986– O 1987	N 1987– O 1988	N 1988– O 1989	N 1989– O 1990	N 1990– O 1991	N 1991– O 1992	N 1992– D 1993
R 86	$p_{1,87}$	$p_{2,88}$	$p_{3,89}$	$p_{3,90}$	$p_{3,91}$	$p_{3,92}$	$p_{3,93}$
W 86	$p_{2,87}$	$p_{3,88}$	$p_{3,89}$	$p_{3,90}$	$p_{3,91}$	$p_{3,92}$	$p_{3,93}$
R 87		$p_{1,88}$	$p_{2,89}$	$p_{3,90}$	$p_{3,91}$	$p_{3,92}$	$p_{3,93}$
R 88			$p_{1,89}$	$p_{3,90}$	$p_{3,91}$	$p_{3,92}$	$p_{3,93}$
W 88			$p_{2,89}$	$p_{2,90}$	$p_{3,91}$	$p_{3,92}$	$p_{3,93}$
R 89				$p_{1,90}$	$p_{2,91}$	$p_{3,92}$	$p_{3,93}$
W 89				$p_{2,90}$	$p_{3,91}$	$p_{3,92}$	$p_{3,93}$

Notes: See Table 1 for definition of cohorts. A = April, D = December, M = March, N = November, O = October.

† Four age classes are assumed, spanning one year each (5 mo for the first age class from release date of reared fish to following March). Survival is allowed to vary between years, a year being defined so as to match age classes (1992 and 1993 were pooled, due to the small number of capture in 1993). See Table 1 for definition of cohorts.

‡ Capture probabilities are further month-dependent. Hence, for each parameter here indicated, 12 parameters were actually estimated (10 for $p_{2,87}$ because wild-caught fish were released in December, and 14 for $p_{3,93}$). Capture probabilities in a given month were assumed to be equal for reared fish released more than two years previously. Hence, in a given month, at most three different capture probabilities may be estimated, corresponding to three age classes.

fish may enter the studied population. Fish may also lose their tag at a given instantaneous probability, generally assumed to be constant over age and time (Tag$_{loss}$). Fishermen (of any kind) recapturing a tagged fish will return the tag only with a certain probability (Tag$_{return}$).

Capture–recapture parameters and their correspondence with fishery parameters are: $p_{a,t}$, the capture probability, which is the fishing probability by fishermen (of any kind) who return tags, equals

$$1 - \text{Tag}_{return} \times \exp(-F_{a,t}).$$

The capture probability represents a probability of capture during a given occasion, conditional on being alive, and thus differs from the standard overall recovery rate (sometime called recapture rate), which is the cumulative proportion of released fish eventually recovered; $\phi_{a,t}$, the survival probability, which includes any source of mortality other than fishing by fishermen reporting tags, equals

$$(1 - \text{Tag}_{return}) \times \exp(-M_{a,t} - F_{a,t} - \text{Tag}_{loss}).$$

RESULTS

Before starting the capture–mark–recapture (CMR) analysis, an exploration of the data was done in order to evaluate whether there were any effects of size at release on the cumulative recovery rate.

Size effect on recovery rate

Artificially reared fish released in October.—It is a general observation that fish being released as small individuals are recovered at a lower rate than are larger ones (e.g., Svåsand and Kristiansen 1990), which is due, at least partly, to low fishing probability on small fish. Recovery rate increased significantly with size at release in all four cohorts of reared fish (Fig. 4). Despite the relatively short length span (12–20 cm), recovery rate is strongly affected by size at release. On a logistic scale, it appears that the slope of recovery rate regressed on the length at release did not differ for the 1986 and the 1987 cohorts, but was slightly flatter for the 1989 cohort ($P = 0.02$) and much flatter for the 1988 cohort (i.e., weaker selection on size at release). The goodness-of-fit test of the model with a separate linear slope for each cohort was acceptable ($\chi^2_{88} = 70.13$, $P > 0.5$), suggesting that the length at release has a linear effect on recovery rate, measured at a logistic scale.

Assuming that fishing rate is negligible for fish <25 cm (actually estimated as percent growth of ~0.2% mo^{-1}), the difference in recovery rates between fish of 25 cm (the maximum length at release) and smaller fish of length x may be assumed to result from natural mortality during the period it takes to grow from x to 25 cm. Hence, the recovery rate of x cm long fish when released (rec$_x$) may be written as rec$_x$ = rec$_{25}(\phi_{1\,cm})^{(25 - x)}$, with $\phi_{1\,cm}$ being the survival probability during the time it takes to grow one centimeter. These parameters can be estimated using a binomial error and a logarithmic link (implemented in S-PLUS; Venables and Ripley 1994). The mean slope obtained for the four cohorts is −0.225 (1 SE = 0.029). This corresponds to $\phi_{1\,cm}$ =
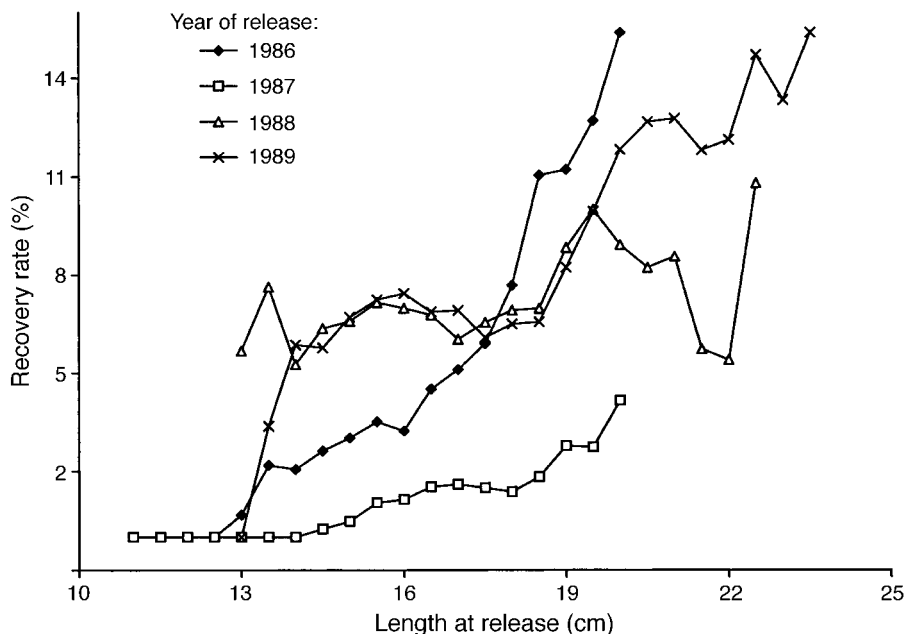
FIG. 4. Recovery rates (excluding recaptures by eel traps) as a function of length at release for the different cohorts of reared fish. Length was measured to the nearest half centimeter (thus constituting the different length classes). For the clarity of the illustration, adjacent length classes including fewer than 50 individuals were pooled, and data were further smoothed by calculating recovery rate over three consecutive length classes.

0.80. Growth rate for fish ranging 10–25 cm was found to be constant (independent of year of release and size at release) and equal to 0.049 cm/d (estimates based on length at recapture 50–200 d after release; $n = 125$). Hence, this allows us to estimate a monthly survival as $\phi_{1\,cm}^{(30\times0.049)} = 0.72$ (or instantaneous mortality $Z = 3.97$ yr^{-1}).

Wild-caught fish released in December.—There was a slight tendency for recovery rate to increase with increasing size at the time of release ($\chi_1^2 = 3.01$, $P = 0.08$). This tendency disappears if the smallest 3% of fishes (i.e., fish <26.5 cm) were removed ($\chi_1^2 = 1.47$, $P = 0.22$). Hence, fishing rate and mortality rates appeared to become approximately independent of size somewhere in the 25–30 cm range.

Fish released by eel-fishermen.—Eel fishermen measured the length of 1126 individuals ranging 14–59 cm. We studied the size-dependent recovery rate of these fish by gear other than eel pot. Since recaptures occurred approximately continuously in time, it was, however, impossible to separate data by date of recapture (because of the extreme complexity of the resulting model). For fish <22.5 cm (thus, comparable to artificially reared fish released in October), there was a significant slope relating size to recovery rate on a log scale (slope estimated as 0.217 ± 0.104; $n = 183$; $P = 0.03$), which thus appears to be similar to the slope found for reared fish. Considering only fish >29 cm, there was no relationship between size and recovery rate (slope estimated as 0.008 ± 0.010; $n = 599$; $P = 0.4$). The recovery rate for these large fish was esti-

mated to be 0.27 ± 0.02 (the recovery rate for fish 22–29 cm was estimated to be 0.18 ± 0.02; $n = 342$). These recovery rates may be compared to the recovery rate for wild-caught fish released in December being of similar size. Recovery rates (excluding recapture by eel fishermen) were estimated to be 0.26 ± 0.02, 0.21 ± 0.01 and 0.16 ± 0.02 for fish released in December 1986, 1988, and 1989, respectively; that is, the recovery rate is significantly lower (for 1988 and 1989, at least) than the recovery rate calculated for fish released by eel fishermen. This suggests that a significant proportion of fish released in December disappeared from the population. However, recovery rate of small fish is comparable to recovery rate of reared fish released in October (0.09 ± 0.02 for fish <20.5 cm; 0.15 ± 0.03 for fish 20.5–25 cm). This suggests that tagging mortality is low for artificially reared fish released in October.

Capture–mark–recapture (CMR) modeling of capture and survival probabilities

Different constraints may be incorporated simultaneously in the model. In practice, models with all combinations of constraints are fitted to the data, and the AIC criteria select the best model among them. However, for the sake of clarity, we will explore successively the different constraints.

Modeling capture probability.—Fishing pressure showed high variability between months as well as between years (e.g., number of recapture in March and June: 6 and 24, 55 and 153, and 164 and 170 in 1988,
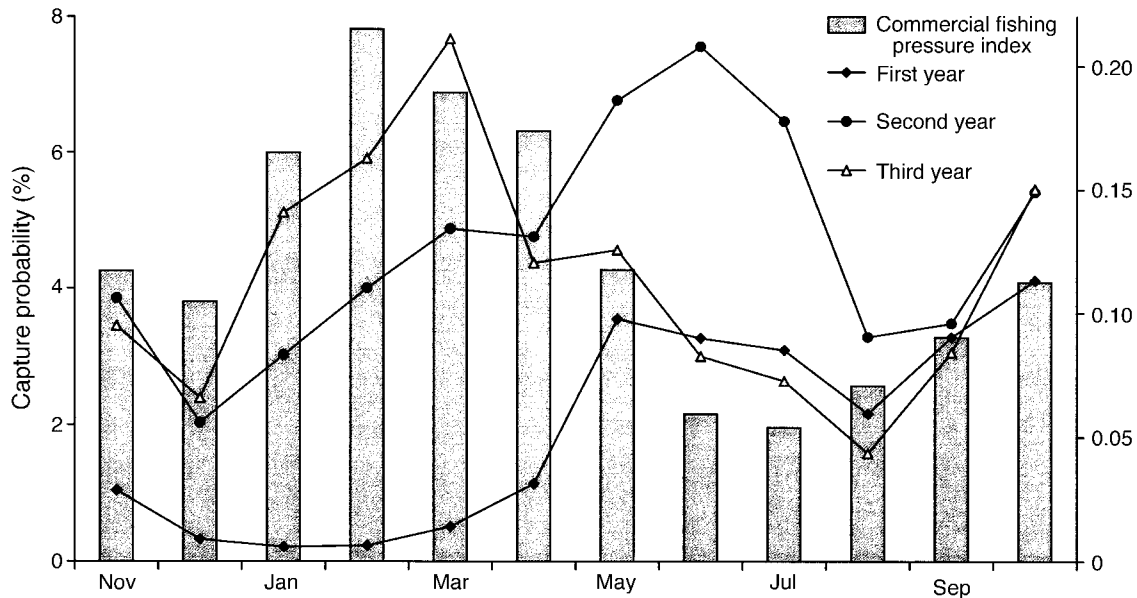
FIG. 5. Estimated seasonal variation of age-specific capture probabilities, superimposed on the inferred commercial fishing pressure index. This index was calculated from the monthly distribution of the commercial catches divided by the estimated survival probability from November to the given month (estimates from Table 4 [age class]), in order to take into account the fact that the number of fish of a given age class (here considered from November to November) decreased throughout the year. Hence, the same amount of fish caught by professional fishermen has a larger relative impact at the end than at the beginning of an age class.

1989, and 1990, respectively). We may, however, expect seasonal variation of size-dependent fishing pressure because of seasonal behavior of the fish, or because the type of fishermen (and thus the type of gear used) changes seasonally. This could be modeled as a month × year effect (each month of each year has its own level of capture probability) and an additive age × (month + year) effect. Whatever the constraints on survival probability, the AIC of a model with such constraints on capture probability was always lower (hence the model was better) than the AIC of the panel model (i.e., age × month × year). However, none of the residual interactions could be removed. In particular, the fishing pressure cannot be considered strictly seasonal (i.e., the difference in capture probability in different months was not consistent between years), and the seasonal pattern of capture probability variation was not the same for the three age classes considered (Fig. 5).

For 3-yr-old fish, monthly capture probability variation appears to be well correlated to variation of the commercial fishing pressure index (commercial fishing pressure index included in the model as a covariate ($F_{1,10} = 18.45$, $P = 0.002$); for the justification of the use of the F ratio test for modeling time dependence of survival probability, see Julliard et al. [1999]). The unexplained residual variation was, however, still significant ($\chi^2_{10} = 19.14$, $P = 0.04$). Hence, monthly variation in commercial catches determined most, but not all, variation of monthly capture probability of 3-yr-old fish. There was, in contrast, no correlation between

monthly commercial catches and monthly capture probability of 2-yr-old fish ($F_{1,10} = 0.36$, $P = 0.56$).

Tagging mortality.—Because the length at release varied between cohorts of artificially reared fish (Table 1), survival during the first months after release was expected to differ between cohorts. As capture probabilities were very low during these months, we expected that this could be entirely taken into account with a model with a cohort-specific survival, spanning one month immediately after release. These parameters would also take into account tagging mortality. We tested whether the apparent survival during this month differed from survival during later months, using likelihood ratio tests. However, for reared fish released in October 1986 and 1987, the low number of rereleased individuals affects the power of the test (see *Method*), and the test was deliberately not performed. For reared fish released in 1988 and 1989, apparent survival during the first month following release did not differ from survival in subsequent months ($\chi^2_2 = 2.15$; $P = 0.34$). For wild-caught fish released in December, there was a strong difference between apparent survival in the first month following release and survival during subsequent months ($\chi^2_3 = 55.49$; $P < 0.001$; mean estimates ± 1 SE, 0.52 ± 0.04 and 0.972 ± 0.010). This suggests that tagging mortality is not distinguishable from estimated mortality for artificially reared fish, but that ~47% ($1 - 0.52/0.972$) of the wild-caught fish released in December disappeared from the studied population. It furthermore appears that this proportion differs between cohorts; the survival estimates in the first month
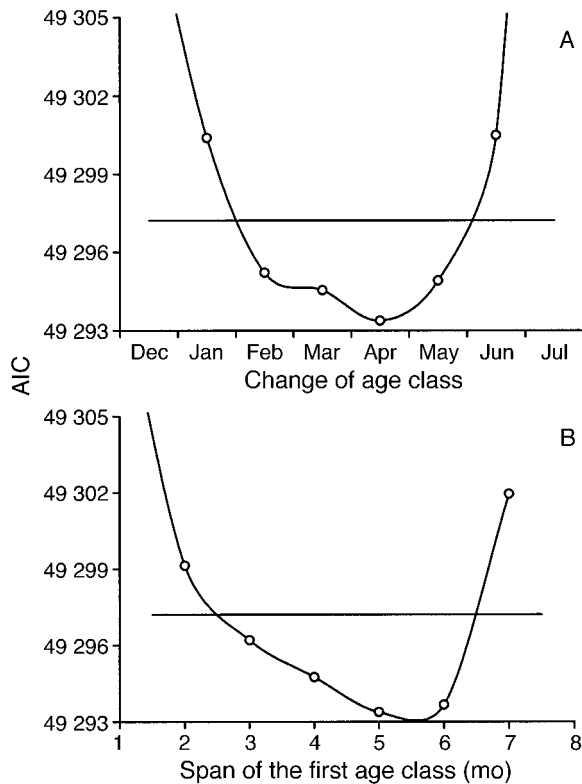
FIG. 6. Determining the month of transition between age classes by capture–mark–recapture (CMR) modeling. (A) Models were built with various dates of transition between age classes. The Akaike information-theoretic criterion (AIC) of each model was calculated. The model with the lowest AIC gives the best estimate for the transition date. From the minimum AIC + 3.84 (horizontal line), the 95% confidence interval of the estimate can be inferred. (B) The date of transition between the first two age classes was determined more precisely, holding the transition between later age classes equal to 1 April. AIC values for models with various lengths for the first age class were then calculated.

following release were 1.00 (SE not estimable), 0.56 ± 0.05, and 0.40 ± 0.06 for the 1986, 1988, and 1989 cohorts, respectively (LRT for equality between these probabilities, $\chi_2^2 = 9.44$; $P = 0.009$).

Age-specific survival probability.—One critical question, often difficult to answer, is when a fish changes age class. In our analysis, we have assumed four age classes, the three latter lasting 12 mo each. The temporal demarcation between age classes may be determined by building models for survival with different limits for the age class. According to AIC, the best time demarcation corresponds to a change of age class in approximately April, with a confidence interval covering February–May (Fig. 6a).

Since artificially reared fish were released in October, the first age class in our study spans from November to the subsequent March. Survival during this first age class was clearly lower than survival estimated during the subsequent age class. Therefore, we paid particular

attention to the span of this first age class. We compared several models for which the limit between the first and the second age class changed: the first 17 mo (5 + 12) were split in two parts of varying length. The AIC was again the lowest for a change in age class near April (Fig. 6b). Based on the profile of the AIC function, the change in age class occurred between mid-January and end of May (Fig. 6b).

The change in survival was rather abrupt, monthly estimates changing from 0.74 ± 0.01 (mean ± 1 SE) in March to 0.97 ± 0.01 in April. We built two models with gradual changes in survival during February–May and January–June, respectively. However, although these models have the same number of parameters as the previous one, AIC was increased (0.63 and 1.30, respectively). Hence, this suggested that change in mortality regime indeed occurs within a very short period. During the first five months after release, 78% of the reared fish disappeared.

Time-specific survival probability: the algae bloom effect.—Because of the toxic algae bloom during the end of May 1988, we suspected that survival in 1988 was lower than survival in other years. We therefore built the model $\phi_{age\times bloom}$, which constrained survival to be equal across age classes except in 1988 (assuming no impact on artificially reared individuals released in October 1988). This model was not rejected ($\chi_{12}^2 = 11.86$; $P = 0.46$), indicating no detectable time variation in survival in normal years; in particular, survival of the 0-age class did not differ between years ($\chi_3^2 = 1.76$; $P = 0.62$). The bloom–year effect was, however, extremely strong (test for equal survival in all years: ($\chi_3^2 = 107.45$; $P < 0.001$).

We further paid particular attention to the length of the algae bloom effect. In this model, we assumed that the algae bloom affected survival during a whole age class lasting April 1988–March 1989. We then built different models in which the algae bloom started and ended in different months. The model with the smallest AIC assumed an effect starting in June 1988 and ending in November 1988 (i.e., ~5 mo with an uncertainty of 4 mo; Fig. 7). Thus, the algae bloom effect lasted ≥2–3 mo after the end of the visible part of the algae bloom.

Survival estimates during the algae bloom were very similar for the different age classes (monthly survival estimates, 0.75 ± 0.02, 0.77 ± 0.03, and 0.69 ± 0.04 for age classes 1, 2, and 3, respectively; pooled estimate, 0.759 [0.726–0.789]), corresponding to an instantaneous mortality of 3.3 yr^{-1} [2.8–3.8], or to the disappearance of 75% of the stock during the period of high mortality.

An alternative hypothesis to explain the apparent high mortality probability during the algae bloom is that fish dispersed out of the study area to places less affected by the bloom. If so, the long-distance recovery rate should be higher for fish that experienced the algae bloom than fish that did not. Hence, we studied the distance-dependent recovery rate after the algae bloom
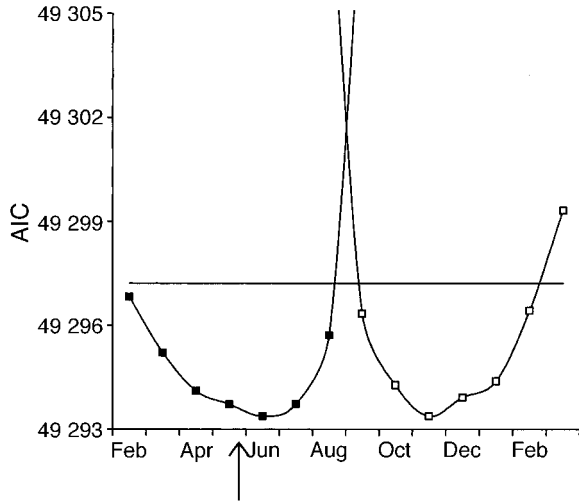
FIG. 7. Determining the span of the algae bloom effect on survival. A series of models with various dates of beginning and end of the algae bloom effect were fitted to the data. The best one according to Akaike information criterion (AIC) was for the beginning of the effect in June 1988 and the end of the effect in November 1988. The AIC of models assumed one limit being moved by up to three months (filled square, beginning; open square, end), with the other limit fixed. The horizontal line is for minimum of AIC + 3.84, and gives an idea of the 95% confidence interval of the estimated beginning and end. The arrow indicates the date of occurrence of the algae bloom.

of fish released before the algae bloom, as well as the recovery rate of fish of the same age released after the algae bloom. The recovery rate for fish >15 km away was not affected by the algae bloom: recovery rates after 225 d in the sea (i.e., for fish released in 1987, after the algae bloom occurred) and >15 km away were 0.30% and 0.33% for fish released in October 1987 and in October 1988 and 1989 pooled, respectively; recovery rates after 580 d in the sea (i.e., for fish released in 1986, after the algae bloom occurred) and >15 km away were 0.17% and 0.20% for fish released in October 1986 and in October 1988 and 1989 pooled, respectively. In contrast, the recovery rate for fish <5 km away was strongly reduced for fish experiencing the algae bloom. Recovery rates <5 km away after 225 d in the sea were 2.13% and 9.22% for fish released in October 1987 and October 1988 and 1989, respectively; recovery rates after 580 d in the sea <5 km away were 1.59% and 2.79% for fish released in October 1986 and October 1988 and 1989, respectively. The data for the 1987 and the 1988–1989 combined cohorts is shown in Fig. 8.

Altogether, this suggests that fish did not move further because of the algae bloom (the long-distance recovery rate did not increase), but that those remaining in the vicinity of release probably died at a higher rate (short-distance recovery rate strongly decreased). This again suggests that initial persistence of all cohorts of reared fish were the same (otherwise, all recovery rates would have been affected in the same way).

Estimating total mortality.—To estimate the total mortality affecting the different age classes, we calculated the yearly capture probability per age class as $1 - \Pi (1 - p_i)$, where the p_i are the monthly capture probability estimates. We also calculated the age-specific proportion of recaptured fish that were not released. The product of these two numbers equals the
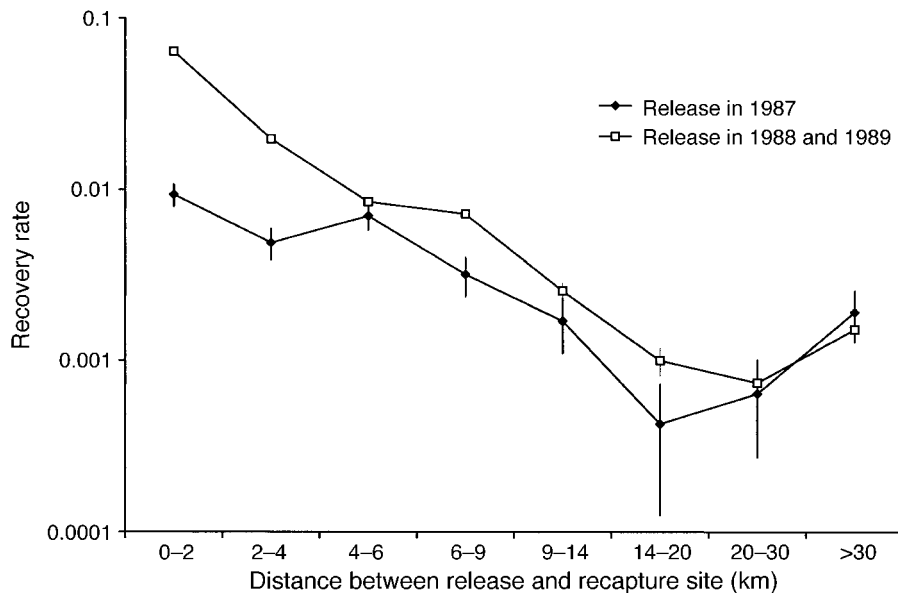

FIG. 8. Recovery rates (excluding recaptures by eel traps) as a function of distance from the site of release for artificially reared fish released in 1987, and in 1988–1989 combined. Vertical bars represent ± 1 SE. Note the logarithmic scale for the recovery rate.

TABLE 4. Age-specific mortality estimated by capture–mark–recapture (CMR) modeling or age classification scheme.

Age or group	$1 - \phi$†	p‡	$(1 - \phi) \times p$§
0-age class‖	0.259	0.0012	0.260
	(3.60)	(0.015)	(3.61)
1-age class	0.025	0.021	0.045
	(0.30)	(0.25)	(0.55)
2-age class	0.044	0.041	0.085
	(0.55)	(0.51)	(1.06)
≥3-age class	0.045	0.041	0.087
	(0.58)	(0.51)	(1.09)
0-group¶	0.455	0.0013	0.456
	(7.28)	(0.018)	(7.30)
1-group	0.048	0.015	0.062
	(0.59)	(0.18)	(0.77)
2-group	0.032	0.034	0.065
	(0.39)	(0.42)	(0.81)
≥3-group	0.050	0.041	0.090
	(0.62)	(0.51)	(1.13)

Notes: Number in parentheses is the instantaneous mortality rate per year. Mean estimates exclude the five months following the 1988 algae bloom.

† Definition: $1 - \phi = M + \text{Tag}_{\text{loss}} + F(1 - \text{Tag}_{\text{return}})$.
‡ Definition: $p = (F \times \text{Tag}_{\text{return}})$.
§ Definition: $(1 - \phi) \times p = Z + \text{Tag}_{\text{loss}}$.
‖ November–March.
¶ November–December.

fishing mortality multiplied by the tag return probability. The figures thus obtained are summarized in Table 4 (age class). Fishing mortality appears very low during the first five months after release (see Fig. 5) and was evenly distributed among gear (24% with traps, 21% with lines, 22% in nets, 33% with unknown gear; $n = 123$ individuals reported as killed).

Interestingly, for older fish, age-specific survival estimates appear to parallel capture estimates. Indeed, both estimates included mortality due to fishing (multiplied by tag return probability for capture probability, and multiplied by [1 − tag return probability] for survival; Table 4 [age class]). Hence, if we assumed that natural mortality (M), tag return probability ($\text{Tag}_{\text{return}}$) and tag loss probability (Tag_{loss}) are independent of age (from the 1-group), then $-\ln(\phi_a)$ and $-\ln(p_a)$ should be linearly related with the intercept equal to $M + \text{Tag}_{\text{loss}}$ and the slope equal to $(1 - \text{Tag}_{\text{return}})/\text{Tag}_{\text{return}}$. The regression line among the three age-specific points (Fig. 9) displayed an estimate of $M + \text{Tag}_{\text{loss}} = 0.04$, and $\text{Tag}_{\text{return}} = 0.50$. The literature usually refers to $M = 0.2$, $\text{Tag}_{\text{loss}} = 0.05$, and $\text{Tag}_{\text{return}}$ as high as 0.90. Assuming such values for M and Tag_{loss} would, in our case, lead to an estimate of $\text{Tag}_{\text{return}} = 0.65$. Assuming $\text{Tag}_{\text{return}} = 0.90$, we would obtain an estimate for $M + \text{Tag}_{\text{loss}} = 0.43$ (Fig. 9). Since the regression was based on three points, it should be interpreted with caution. However, our analysis suggests that the tag return probability is ≪90%, more likely ~50–60%.

For comparison, we also report in Table 4 (group) the estimates assuming the traditional age classification (i.e., 0-group, 1-group, 2-group . . . , with change between age classes occurring the 1 January). Notice the

very high instantaneous mortality then estimated for 0-group ($Z = 7.3$), as well as the lack of relation between capture and survival probabilities estimates for the 1-, 2-, and 3-groups. Assuming a constant tag return probability with age, we would thus infer a high natural mortality for the 1-group.

Mortality estimated by the catch–curve method.— During the mark–recapture experiment, and until 1996, regular sampling of the cod population was done with trammel nets (Gjøsæter et al. 1996; D. Danielssen, *unpublished data*). The exact ages of <2000 individuals were determined from otoliths. Assuming a stable age distribution in time, no sampling bias toward any size, and constant mortality with respect to age and time, it is possible to estimate the total mortality rate (Z) with the catch–curve method (e.g., Ricker 1975). Such an exercise provides an estimation of mortality independent of the CMR estimate. For fish older than one (long enough so that trammel net is not very selective, $N = 1410$), $Z = 0.96 \pm 0.07$. The fit of the regression was not very good, however (regression with binomial error and log link, residual deviance $\chi_5^2 = 32.33$, $P < 0.001$; Fig. 10). A closer inspection of the data shows an apparent change in mortality regime from 5 yr old (Fig. 10). Indeed, allowing for a change in mortality regime at an age of 5 yr considerably improved the fit of the model (residual deviance $\chi_4^2 = 1.54$, $P = 0.82$). Mortality estimates were then 1.08 ± 0.02 for fish of ages 2–5 yr and 0.53 ± 0.11 for fish >5 yr old. The total disappearance rate estimated by CMR includes the tag loss rate (i.e., $Z + \text{Tag}_{\text{loss}}$) and is 1.07 ± 0.02 for fish >1 yr old (Table 4 [age class]). Very few tagged fish reached the age of 5 yr before the experiment ended in 1993, in particular since fish released before 1988
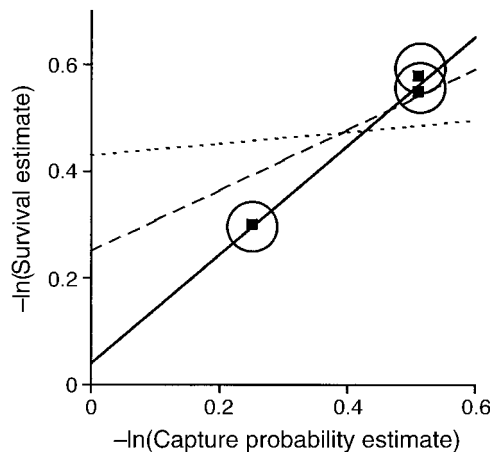

FIG. 9. Estimating total mortality. The three points derive from Table 4 (age class) and correspond to the three older age classes. The points are enclosed by circles approximately covering the 95% CI. Key: ——, unconstrained regression line through the three points; — — —, regression line with intercept being fixed at 0.25; – – –, regression line with slope being fixed at 0.1/0.9 (i.e., tag return probability corresponding to 0.9).
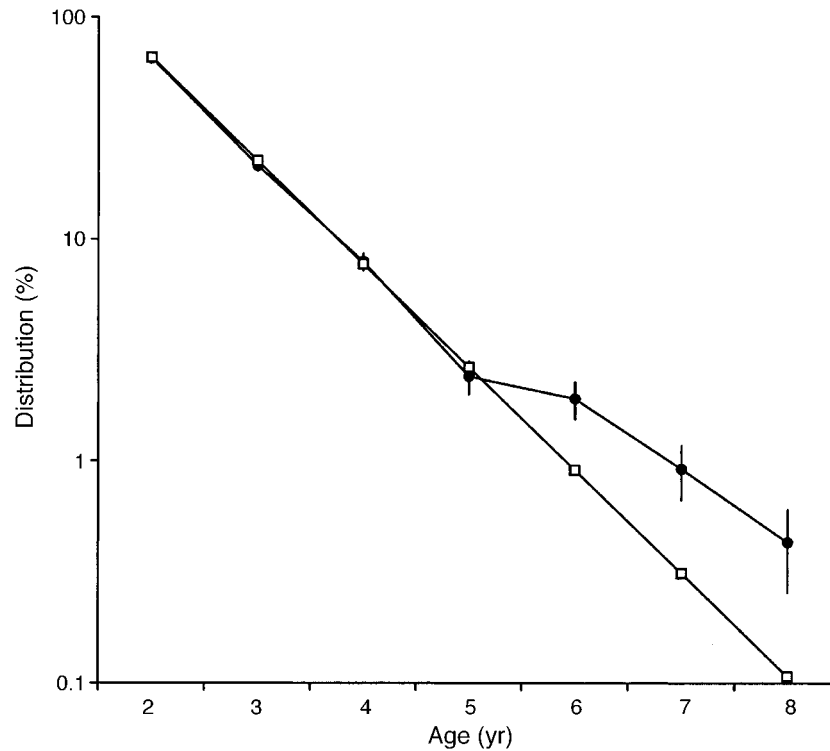
FIG. 10.   Age distribution of the cod population in the Risør area. Solid circles represent data from trammel net ($N =$ 1470); vertical bars represent $1 \pm$ SE. Open squares represent the predicted age distribution with constant mortality rate Z = 1.07 (i.e., the mean value obtained from Table 4 for 2- and ≥3-age classes).

suffered from the algae bloom. Hence, the CMR estimate can safely be compared to the mortality estimate from the catch–curve method for fish between ages 2–5 yr. The extreme closeness of the estimates suggests that the tag loss probability is negligible.

DISCUSSION

Synopsis of findings

Using data on released cod on the Norwegian Skagerrak coast we have found the following:

1) There was a low disappearance probability immediately after release for reared 6-mo-old fish, whereas ≤60% of older fish disappeared just after tagging.

2) The tag return was estimated to be ~50–60%.

3) The cumulative recovery rate was clearly dependent on the size of the fish at release.

4) A high natural-mortality rate was found during 6–12 mo of age (i.e., first 6 mo after release).

5) The natural mortality of the older age classes was low; most of the mortality was then due to fishing.

6) The seasonal pattern of fishing appeared to vary greatly between age classes.

7) During several months after the algae bloom of 1988, fish disappeared at a high rate, whatever their age. No emigration was detectable in relation to the algae bloom.

Here, we discuss these findings.

Tagging mortality, tag loss, and tag return probability

Tagging mortality has been reported to be negligible when using anchor tags (such as the Floy tag used in the present study; e.g., Svåsand and Kristianssen 1990, Kristianssen and Svåsand 1990, Wisniewolski and Nabialek 1993). This fits with our observations for 6-mo-old reared fish, for which tagging mortality was indistinguishable from natural mortality. However, as much as 60% of wild-caught fish that were tagged and released in December seemed to disappear immediately after tagging. There was no direct evidence for any immediate tagging mortality or tag loss (see also Fowler and Stobo [1991], Barrowman and Myers [1996]). Wild-caught fish may have been released quite far from the place were they were caught (see *Methods*). They may thus disperse after release and reach areas with lower fishing intensity or lower tag return probability. Indeed, the tag return probability may be higher in the vicinity of the release area, where people are more aware of the release experiment and generally more interested in its results (Kristiansen 1996). However, the dispersal pattern of the wild fish was not very different from that of artificially reared fish (Danielssen and Gjøsæter 1994).

Tag loss may be a serious problem in such analyses, since it will lead to overestimating the mortality prob-

ability. There have been several studies on tag loss. Svåsand (1991), who reviewed loss of Floy tags, gave yearly loss rates varying between 1% (for *Alosa aestivalis*) and 19–90% (for *Ictalurus punctatus*). Morgan and Walsh (1993), keeping tagged juvenile *Hippoglossoides platessoides* in captivity, found that 78% of the fish retained their tags after one year. Fowler and Stobo (1991) compared recovery rates of different types of tags on cod and found that ''spaghetti tags'' (an anchor tag) gave the best results. They did not however, separate the effects of tagging mortality from tag loss. In our study, assuming a constant tag return probability, we estimated the sum of tag loss probability and natural mortality to be very low. Moreover, the capture–mark–recapture (CMR) estimates of total mortality plus tag loss probability coincided with an independent estimate of total mortality. We may thus conclude that the tag loss is negligible in the present study.

The tag return probability during the present experiment was estimated to be ~50–60%. The values obtained are lower than previously assumed (Danielssen and Gjøsæter 1994). However, the tag return probability is difficult to compare between experiments, since it is a function of the announcement of the experiment and varies between the different types of fishermen. For instance, Svåsand and Kristiansen (1990) assumed that ~90% of the tags on caught fish were reported, whereas Otterå et al. (1999) estimated the percentage of tags being reported to be as low as 41% in an exposed coastal area in western Norway. Our results, however, are close to those of Kristiansen (1996), who reviewed >15 tagging experiments on cod from various parts of Norway and reported tag return probabilities to be ~50% or lower.

Reared fish came from coastal stocks from western Norway. These stocks are ecologically similar to the Norwegian Skagerrak cod (e.g., habitat preference, dispersal behavior; Godø et al. 1989, Smedstad et al. 1994, Gjøsæter 1990) and, although there are genetic differences (according to haemoglobin genotype), the differences are small (Nævdal 1994, Gjøsæter et al. 1992). On the other hand, released reared fishes enter into a completely unknown environment. In that sense, our results primarily referred to the demography of foreign reared cod released in a natural habitat, and their survival scheme may not be representative of the demography of wild fish (see also Nordeide et al. [1994], Steingrund and Fernø [1997]). We may expect that most of the excess of mortality attributable to a ''reared effect'' would show up soon after release and would therefore be similar to an apparent tag mortality. However, the mortality probability of reared fish did not increase immediately after release. The reared effect may last longer than a few weeks, which would induce a reduced survival of reared fish. Consequently, we may slightly overestimate the mortality during the first five months after release (i.e., period during which a strong selection for the most fit individuals may occur).

We are convinced, however, that this would not affect the validity of our other results.

Age-dependent mortality

Both the capture–recapture analysis and the study of size-dependent recovery rate consistently indicate that small fish (<25 cm) experience high natural mortality (instantaneous mortality probability = 3.8) during a period lasting ~5 mo (which corresponds to the time required to grow from 17 to 25 cm). Our results also suggest a sudden change in the mortality pattern around April. It is likely that this change corresponds to a shift in the feeding regime at the end of the winter period (Hop et al. 1992), which is crucial, and during which mortality is generally higher for most of the marine organisms (e.g, Colebrook 1985, Hawkins et al. 1985, Winters et al. 1993, Fromentin and Ibannez 1994).

High mortality in the youngest fish is probably related to the higher vulnerability to predation and/or starvation in the younger life stages (e.g., Cushing 1975, 1982). There are, however, very few reliable estimates of mortality of the earliest stages (Vetter 1988); data on these ages are generally lacking. Mostly for the same reason, variation of natural mortality with age is also poorly known. Tretyak (1984) estimated natural mortality in Arcto-Norwegian cod to be at a minimum for 7–10-yr-old fish, and higher for both younger and older fish. In this study, it was also found that natural mortality among young fish was dependent on fishing intensity, so that a high fishing mortality was partly compensated for by a lower natural mortality. Although our estimates of natural mortality were low (≤0.2, the value typically assumed), it is difficult to argue whether these estimates could be related to the high fishing pressure on the Norwegian Skagerrak cod.

Our natural-mortality estimate of fish of the ''1-age class'' was not higher than that of older fish. This suggests that the high mortality of the ''classical'' 1-group estimated in previous studies (e.g., Svåsand and Kristiansen 1990), may result from a heterogeneous pattern of mortality within 1-group. Therefore, the age classification during April–April, which allows a change in age class in early spring, is probably more appropriate from an ecological point of view.

In summary, out of 100 6-mo-old individuals released in October, 75 died during the first 5 mo, and at ≥20 of the remaining were taken by fishermen (mostly in the second and third year after release), of which 10 tags were reported. What happen to the remaining five individuals is a bit uncertain; they may have died of natural causes, or they may have lost their tags before being caught by fishermen.

Seasonal pattern of fishing intensity

No accurate information on the seasonal variation in fishing effort (e.g., number of fishermen) was available. However, fishing statistics tend to suggest that commercial fisheries in the fjords are most active during
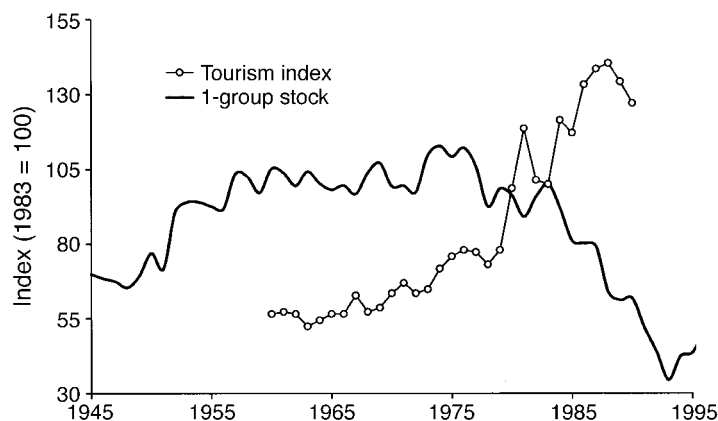
FIG. 11. Long-term trends of cod stock and of tourism along the coast of Aust-Agder. The cod stock is calculated from standard sampling by beach seines in 50 stations each October. The number of 1-yr-old cod was averaged over the 50 stations and log-transformed. The time series was then smoothed with a 5-yr window (see Fromentin et al. [1997, 1998] for further details). The tourism index is the number of nights sold by hotels in Aust-Agder (Lystad 1991).

winter (Fig. 3), whereas recreational fishing is most intense during spring and summer (i.e., May–July). The eel fishermen, mainly fishing during spring and autumn, caught a large proportion of the youngest fish that were recaptured (Table 2, Fig. 3). Therefore, the close resemblance between seasonal variation of estimated capture probability of first year and pattern of capture by traps is not surprising. The majority of small cod caught in eel pots were, however, released.

The monthly variation of capture probability between 2-yr-old and ≥3-yr-old fish are quite different, although there is no reason to suspect differences in behavior and/or habitat use between these two age groups. Catches by the different gear do appear to depend both on size and season (Table 2, Fig. 3). Hence, the distribution of catches by lines (which primarily catch medium-size fish) is close to the seasonal pattern of fishing probability of 2-yr-old fish, whereas capture probability of ≥3-yr-old fish appear to parallel distribution of capture by nets and commercial catches (Fig. 5). Hence, the difference in the seasonal pattern of fishing probability between 2-yr-old and older fish is most likely to be due to the seasonal variation of the (strongly size-specific) gear being used. Note that total fishing mortality for 2- and 3-yr-olds appear very similar (Table 4 [group]), which may rather be coincidental considering the seasonal variability of the capture probability of these two categories.

Our results suggest that recreational fishing, which is directed towards the younger fish, may be fairly high (for two years old fish, $F \approx 0.9$; Table 4). Tourism in the Aust-Agder county (which includes the Risør area) has markedly increased in the last 50 yr, with a strong increase occurring near 1980 (Fig. 11). We may expect that recreational fishing (primarily undertaken by tourists) has increased in the same way. Hence, the fishing pressure on young cod in the area is likely to have increased in recent years. The Flødevigen Marine Research Station has monitored the stock of 1-yr-old cod along the Norwegian Skagerrak coast since 1919 (e.g., Johannessen and Sollie 1994, Fromentin et al. 1997, Stenseth et al. 1999). During 1950–1980, the stock in

Aust-Agder did not show any strong temporal trend (neither increasing nor decreasing), but has continuously decreased from ~1980. Fromentin et al. (1998) have studied the long-term trend of these populations. They rejected the hypothesis of a large-scale climatic impact and put forward that trends in the sea grass bed during the last decades, as well as fishing effort in the recent years, could cause the observed trend in the cod stock. Our results support the importance of fishing, and as part of that, emphasize the strength of the impact of recreational fishing during spring and summer.

Effects of the toxic algae bloom in 1988

Our results suggest that ~75% of grown-up fish died as a result of the algae bloom. All three cohorts of tagged fish present in spring 1988 exhibited such a high mortality (notice that the three mortality estimates are almost entirely independent). There is, therefore, little doubt that mortality was extremely high during this period. The main period of high mortality spanned June–October 1988, whereas the visible part of the algae bloom was restricted to May–June. This suggests that fish did not only die due to direct effects (e.g., anoxia and/or poisoning), but also due to the resulting perturbation of the ecosystem. It is claimed that there may be some refuges away from the fjord or deep inside the fjord. However, our analysis suggests that fish did not actively move to these refuges. Although natural mortality was found to be low for grown-up fish, it can clearly rise to very high values for short periods.

We expected that fish released in 1988 after the algae bloom, would benefit from the virtual absence of competition from fish of the same age (suspected to have been decimated by the algae bloom), and therefore exhibit a lower natural mortality. However, the 1-age class survival was found to be very similar for the four cohorts. However, there was a much weaker size selection for reared fish released in 1988. A possible explanation for this could be a lower predation pressure, as many of the potential predators may have been eliminated, as well.
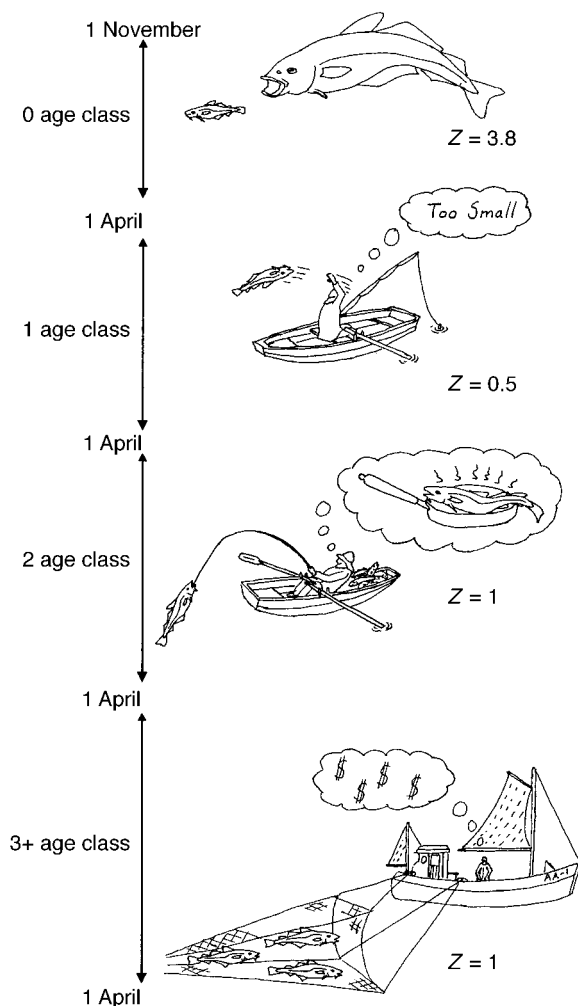
FIG. 12. Age-specific pattern of mortality in a coastal cod population in the Risør area.

CONCLUSION: THE DEMOGRAPHY OF COASTAL COD

Based on capture–mark–recapture (CMR) statistical modeling, we provide in this paper one of the first synthetic attempts of describing the demography of cods along the Norwegian Skagerrak coast. Our findings are summarized in Fig. 12.

1) During age 6–12 mo, natural mortality is very high ($M \approx 3.8$), possibly because of predation and cannibalism (Myers and Cadigan 1993, Folkvord 1993, Folkvord et al. 1994).

2) During the second year of life, mortality is significantly lower ($Z \approx 0.55$). Fishes are too small to be of interest for fishermen (recreational or commercial fishermen) and sufficiently large to avoid predation and cannibalism (Ricker and Foerster 1948, Folkvord 1993, Rice et al. 1993, Cushing and Horwood 1994; but see Campana [1996]).

3) From their third year of life, mortality is again high ($Z \approx 1.05$), due to high fishing mortality (by recreational fishing for 3-yr-old individuals and commer-

cial fishing for older fish). Natural mortality appears to be low for these older age classes. Hence, the recently increased fishing pressure (by recreational or commercial fishing) must have had a pronounced impact on the population.

4) Our experimental study also included the toxic algae bloom of May–June 1988. This was shown to affect mortality of all age classes during almost half a year. Because of the algae bloom, 1988 may be considered exceptional. Although events such as the this algae bloom are probably related to the general eutrophication of the Northeast Atlantic and adjacent seas, they may also be of natural origin and thus constitute a natural part of the marine ecosystems (e.g., Steele and Henderson 1994, Richardson 1997), and should be taken into account when attempting to describe the demography and the resulting population dynamics of marine fish populations.

Combining our findings with earlier findings on the Skagerrak coastal cod population, we are left with the following picture: year class strength may essentially be considered as a density-independent and highly stochastic process (e.g., Hjort 1914; see also Stenseth et al. [1999]). Intra- and intercohort density-dependent processes occur at the juvenile stages. These processes may arise from competition between juveniles of the 0-group and cannibalism by the 1-group onto the 0-group (Fromentin et al. 1997, 2000, Bjørnstad et al. 1999, Stenseth et al. 1999). The present study further suggests that fishing causes most of the mortality of fish that have attained more than one year in age. We also suggest that high fishing pressure may be responsible of the decrease of the stock in recent years.

Hence, the stock size of the Norwegian Skagerrak cod populations appears closely related to the fishing pressure; decreasing fishing intensity is the most likely way to increase the stock size. We have thus contributed to a long-lasting and well-known (see, e.g., Dahl 1906, Solemdal et al. 1984, Solemdal 1997) controversy involving Gunder Mathisen Dannevig (the father of Alf Nicholay Dannevig, to whom this paper is dedicated) and Johan Hjort. Our results provide some support in favor of Hjort, who regarded Dannevig's effort of releasing cod larvae in order to increase the coastal cod populations to be rather futile. This conclusion is in accordance with the conclusions drawn at a recent conference on Sea Ranching (Howell et al. 1999; see also Tveite [1971]). Paradoxically, we have been able to draw this conclusion on the basis of a long research tradition of the Flødevigen Marine Biological Station initiated by G. M. Dannevig and further developed by A. N. Dannevig in order to terminate the controversy between the late G. M. Dannevig and J. Hjort.

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