
#### Abstract

Over 22,000 Atlantic cod, Gadus morhua, were tagged with T-bar tags and released in the Gulf of Maine area in 1984-97 and 2400 recovered tags were used to interpret movement of tagged fish. M ost of the rel eases were of adult fish made during the winter cod spawning season from aggregations found on known spawning banks. Recaptures by NAFO divisions were weighted with an annual index of fishing effort to account for probability of recapture. At the division level, very little exchange between the area east of $4 X$ and the Gulf of Maine was evident. However, within the Gulf of Maine an exchange of about $15 \%$ between 4 X and $5 Z$ and somewhat higher between 4 X and 5 Y was apparent. Cod tagged on Browns Bank and Georges Bank during the spawning season showed widespread dispersal both within their respective division and to adjacent divisions. The seasonal distribution of recaptures in 4X indicates aggregation for spawning followed by postspawning dispersal. The seasonal pattern for Georges Bank is less clear but there are indications of net loss to the 4 X area. Distribution of recaptures from Georges Bank releases in 1994 was similar to those observed for releases made in 1984-85. Results of the study were consistent with results from earlier tagging experiments and demonstrate substantial interaction of cod from different management areas. These findings may have implications for stock assessment models and management objectives.


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# Movement of Atlantic cod, G adus morhua, tagged in the Gulf of Maine area 

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TheAtlantic cod (Gadus morhua) is a demersal species with a wide Northwest Atlantic geographic range extending from the Gulf of Maine in the south to the Davis Strait in the north (Scott and Scott, 1988). It is one of the most important commercially exploited groundfish species in Atlantic waters off Canada and the eastern U.S. region, and cod stocks havesupported fisheries in the Gulf of Maine since the 1700s (Serchuk and Wigley, 1992).

The Gulf of Maine area, as defined in this study, includes waters of the Bay of Fundy, Georges Bank to $71^{\circ} 41^{\prime}$ W, and the Scotian Shelf west of $63^{\circ} 20^{\prime} \mathrm{W}$, an area of approximately $150,000 \mathrm{~km}^{2}$. There are four fisheries management units identified for Atlantic cod in this area, based on known areas of spawning aggregation and commercial fisheries (Halliday et al., 1986). Geographic boundaries of North Atlantic Fisheries Organisation (NAFO) divisions and the U.S. National Marine Fisheries Service (NMFS) and Canadian Department of Fisheries and Oceans (DFO) unit areas (Fig. 1) are used to approximate the distribution of the stocks. The
present management units are division 4X, subdivision 5Ze in unit areasj and $m$ (Canada), subdivision 5Zw+SA6 (USA) and division 5Y. The area is also divided by the International Maritime Boundary (IMB) between Canada and the United States, established in 1984. Halliday and Pinhorn (1990) have provided an extensive review of the basis for existing statistical areas used to report fisheries activities and note that unit areas were established in the early 1970s.

Population characteristics of the four cod stocks have been reported by Canada (Clark 1996; Hunt and Buzeta 1996) and by the United States (NEFSC, 1994). Stock abundance has shown substantial variation in the last fifteen years and a broad range of recruitment. In general, all the stocks have declined from the long-term average abundance and, with the exception of the 4X stock, appear to be at low levels of spawning stock biomass.

Numerous tagging studies have been undertaken to examine movement of cod in the Gulf of Maine area. Hunt and Neilson (1993) provided a synopsis of tag-recapture
results from experiments conducted between 1923 and 1960. An earlier summary of cod tagging studies is given in Wise (1963). Templeman (1962) provided a comprehensive summary of the basis for separating cod stocks in the northwest Atlantic using meristic and results of tagging experiments and concluded "there are Browns Bank and eastern Georges Bank stocks, probably essentially separate as spawning stocks but with some intermigration in both directions across the Fundian Channel and some intermingling of both these stocks with those of southwestern Nova Scotia." In general, results of these early experiments indicate substantial movement of cod within the 4 X area and to a lesser extent to and from the adjacent 5Y and 5Ze areas. The pattern of recapture locations shows a general dispersal from the area of release and some increase in the number of cod moving with elapsed time. However, it is difficult to interpret these studies as proportional movements because landings and effort are generally not available for weighting probability of recapture by area.

Canada has conducted a number of tagging studies on cod in the Browns Bank, Georges Bank, and Bay of Fundy areas since the 1970s. Studies conducted between 1994 and 1996 were part of a co-operative research study involving Canada and the United States. This report provides an interpretation of cod movements in the Gulf of Maine area based on results of recaptures of cod tagged in the 1979-97 time period.

## Methods

Canada has conducted stratified random bottom trawl surveys in the Gulf of Maine since 1970 and on Georges Bank since 1986. The United States has also conducted similar surveys in the spring (1968) and fall (1963) of each year. Indices of abundance derived from these surveys are routinely used in stock assessment models to estimate popuIation abundance (Hunt and Buzeta, 1996), and they provide a synoptic view of cod distributions in the Gulf of Maine area during both spawning and postspawning seasons. The mean catch per tow, aggregated by ten-min latitude and longitude squares, was calculated for the U.S. spring and fall research-vessel timeseries. Thesesurveys cover most of the Gulf of Maine area, compared with the Canadian summer survey (4X only) and Canadian winter survey (5Ze only), and therefore provide a distribution pattern for cod in the entire study area.

Tagging locations were determined from areas of high catch rates in research vessel surveys, as well


Figure 1
North Atlantic Fisheries Organization (NAFO) division (4X, 5Y, 5Z) and unit areas (eg. 5Zj) boundaries in the Gulf of Maine area and cod tag release locations. The dashed lines indicates the International Maritime Boundary line between Canada and the United States.
as the location and timing of historical cod spawning activity. Additional tagging was completed during other times in areas of fishing activity or special interest locations. Fishing trials were used to identify sites with high catch rates and at least $50 \%$ cod composition, and new sites were selected when catch rates or cod composition declined. Typically, once an aggregation of cod was located, fishing and tagging continued at that site for 1-2 days. Areas with high
catches of skates (Raja spp.) and dogfish (Squalus acanthias) were avoi ded because their abrasive skin resulted in damageto cod and poor quality specimens for tagging.

Fisheries research stern trawlers, 50-70 m in length, equipped with a research Western II a otter trawl and with wet laboratory facilities below the trawl deck, were used for large-scale tagging operations. Fishing operations consisted of 5-20 min tows at depths ranging from 40 to 70 fathoms. At the end of each tow, cod were rel eased into a sluice way leading to the bel ow-deck wet laboratory area and transferred into 1500-L holding tanks with recirculating ambient sea water. Viability of each cod was assessed prior to tagging and fish in poor condition or that had apparent external injuries were discarded. Control experiments to assess tag or stress induced mortality were not conducted, but observation showed that even fish that were initially inverted or dormant on the bottom of the tank returned to an apparent active and normal behavior within 15-30 minutes. Tagged fish were released through a sluice way exiting about one to two meters above the water line. Approximately 100 to 250 cod could be held, tagged, and released from each tow, depending on average fish size in a tow.

Fish to betagged were removed from hol ding tanks by hand with dip nets and placed on a measuring board to obtain length. A tag was inserted near the leading edge of the first dorsal fin and the fish was released. Total elapsed time from start to end of the tagging operation was in most cases less than 30 seconds for each fish. An ad hoc representative sample was examined to verify the spawning state of reproductive development (Hunt, 1996) but results were not recorded.

Several small-scale cooperative studies were carried out with commercial fishing vessels. Thefirst of theseopportunistictagging operations was conducted aboard the U.S. FV Mary V, a longline vessel fishing out of Gloucester, MA. During routine fishing operations on the northern edge of Georges Bank, cod caught that were less than the U.S. minimum legal size ( 49 cm 19 inches) were tagged by the vessel's crew and released. Tags were also supplied to staff of the Massachusetts Division of Marine Fisheries (MA-DMF) and the Maine Department of Marine Resources (ME-DMR) to use during trips when onboard fishery observers were present on commercial longliners fishing in the N antucket Shoals (MADMF) and on commercial charter boats fishing the inshore waters of the Gulf of Maine (ME-DMR). During these trips, undersize cod were also tagged and released. A small number of cod, taken as bycatch in lobster traps during the winter lobster fishing sea-
son (4Xq inshore), were tagged and released by Canadian fishermen.
All tags were of the T-bar type (FD-67 and FD-94 in 1994) applied with the Mark-II tag insertion gun and were supplied by Floy Tag and Manufacturing, Inc (4616 Union Bay Place NE, Seattle, WA 98105). Overall length of the tag was about 6.5 cm and each tag had a $3.5-\mathrm{cm}$ bright yellow address sleeve and a $1.0-\mathrm{cm}$ attachment T-bar. Each tag was imprinted with a unique identification number and Canadian return mail address on the vinyl sleeve. Tags used in the 1994 experiment included a second mailing address for the National Marine Fisheries Service (NMFS), N ortheast Fisheries Science Center, Woods Hole, MA. Tags were provided in clips of fifty with consecutive numbering to facilitate record keeping.
An extensive advertising campaign, targeting Canadian and U.S. fishing enterprises and communities, was completed prior to and after each of the large-scale tagging experiments. This included notices in local newspapers and other industry publications, all-weather bilingual posters located at major fish landing and processing facilities, personal contact with industry representatives, and follow-up with individuals submitting tags. A representative of the fishing sector participated in the 1994 experiment to obtain firsthand knowledge of operations and, as was hoped, to convey the importance of returning tags to colleagues.
In Canada, a nominal reward of seven dollars was offered for each tag returned. In the United States, a reward of five dollars was paid for tags returned with recapture information and two dollars for tag only returns. In addition to the reward, the finder was provided with a summary of release and recapture information for each tag returned.
All release and recapture data were loaded to a database to facilitate analysis. Tag-recapture information was edited to eliminate obvious errors such as onshore recoveries, substantial decreases in fish length, unrealistic travel and elapsed time factors, etc. Quality of recapture data was variable, ranging from no information to a detailed record of how, when, and where (latitude and longitude) fish were caught, fish size at recapture, age determination material, and other anecdotal information. About $80 \%$ of recaptures included detailed information on location and about $20 \%$ had length-at-recapture measurements.
Analysis of recapture data was completed first at the divisional level, then at the unit area level for the Gulf of Maine and finally at 10-min latitude and longitude squares. Results were compiled to show movement from area of rel ease to adjacent areas and, conversely, movement to an area from adjacent sites. Analysis of recapture patterns at the divisional level
was used to assess exchange between management areas. Observed numbers of returns were used for this purpose because exploitation rates and commercial fishery landings, required for weighting, were not as readily available for areas outside of the Gulf of Maine area. All releases and recaptures in divisions $4 \mathrm{~W}, 4 \mathrm{~V}, 4 \mathrm{~T}, 4 \mathrm{R}, 4 \mathrm{~S}$, and subarea 3 , which were geographically east of the division 4X-4W boundary, were grouped for this part of the analysis; we refer to this combined geographic area as "east of 4 X ."

Because recaptures from tagging studies are usually dependent on commercial fisheries, the distribution and abundance of recaptures is a function of the distribution of fishing effort as well as of fish movements. In an attempt to account for the effect of fishing effort, we weighted recaptures using the commercial fishery exploitation rates for cod stocks in the area. Landings, effort, and exploitation rates of cod by unit area were obtained from the published literature (NEFSC, 1994; Clark, 1996; Hunt and Buzeta, 1996). No provision was made for potential discarding, misreporting of catches, or allocation to unit area. The extent of these problems in landing statistics are thought to be substantial in someyears and areas but have not been quantified (Clark, 1996; Hunt and Buzeta, 1996). A review of both the quality and quantity of effort data indicated that a low proportion of landings, particularly for fixed gear components, were represented. Therefore, direct measures of effort could not be used to make adjustments to returns on the basis of distribution of effort. However, trends in landings by unit area and fleet composition showed a relatively stable spatial and seasonal pattern. In some years a considerable proportion of total Canadian landings from division 4 X was not allocated to a specific unit area. On the basis of preliminary work by Clark (1996), an algorithm was applied to allocate this unspecified proportion to unit area. The reported annual exploitation rate for each stock was then partitioned according to annual percent of unit area landings and used as a year- and area-specific index of the probability of recapture:

$$
A_{a, y}=\sum C_{y} /\left(C_{a, y} \times E_{y}\right),
$$

where $A=$ adjustment factor;
$C=$ percent of annual reported landings by management area;
$E=$ reported annual exploitation rate by management area;
a = unit area; and
$y=$ year.
Within a year, tag recaptures from areas with low landings werethereforegiven higher relative weight-
ing than those from areas of high landings. Annual differences in exploitation rate were used to weight for between-year effects. The derived adjustment factors were standardized to the unit area and year with the lowest landings and exploitation rate.

Summaries of tag recaptures within an area by area of release required standardisation to reduce the impact of large numbers of releases from some areas. F or example, the large number of releases from the Browns Bank area and subsequent number of recaptures would tend to overshadow recaptures from small-scale releases. Therefore all recaptures for this part of the analysis were standardized to the equivalent number of recaptures from 1000 releases.

Seasonal effects of cod movements were evaluated for the two Browns Bank and Georges Bank rel ease sites. Recaptures from these sites were aggregated by quarter with recaptures in the first month after release excluded. Results were summarized by unit area within the release division.

To evaluate temporal effects, data were partitioned into groups representing recaptures from 0-12 months, $>12$ months after release, and total recaptures. The influence of size at release was also investigated but initial examination showed no substantial difference in either direction or distance among size groups. This may be due to the fact that most fish were greater than the $\mathrm{L}_{50}$ mature reported by Hunt (1996) for Georges Bank cod at the time of release and would be expected to diminish the potential impact of size on movement.

Recapture information that included latitude and longitude was used to summarize the tag recoveries by $10-\mathrm{min}$ latitude and longitude squares for the Browns and Georges Bank release sites. Recaptures in each square were weighted by the adjustment factor index associated with the unit area in which the square was located. The Browns Bank and Georges Bank areas support substantial commercial fisheries and are thought to be centers of spawning activity. Tag releases were made during the spawning season and therefore recoveries should represent movement of postspawning fish.

The minimum, maximum, and average time at large after tagging was calculated for releases from each unit area. For recaptures with latitude and Iongitude location, the straight line distance between release and recapture site was calculated to determinetheminimum, maximum. and average distance travelled.

A small proportion of recaptures included size at the time of recapture and these were used to estimate individual specific growth rates. The increase in length between release and recapture was adjusted to an annual value ((increment $\times 365$ )/days at Iarge)
for each fish and averaged by $10-\mathrm{cm}$ intervals of release length to give an annual growth rate.

## Results

Average cod catches per tow, derived from U.S. spring and fall research surveys for 1982-91, are shown in Figure 2, A and B, and indicate widespread distribution throughout the area with some apparent centers of aggregation associated with banks. Densities and distributions show seasonal variation between the spring and fall. In the spring, distribution (with localized areas of high density) appears to be contiguous from Cape Cod, across Georges Bank, to Browns Bank and then farther east and west to the Bay of Fundy. In the fall, densities are lower and thereis moreapparent geographic isolation. Gavaris et al. (1993) found similar results when comparing seasonal distributions in relation to the IMB line in the Georges Bank area. The central part of the Gulf of Maine area has relatively low densities for both spring and fall seasons.

Over 58,000 releases were included in our study of which about 22,300 were in the Gulf of Maine primary study area. The release sites in the Gulf of Maine area, aggregated by ten-min latitude and Iongitude squares, are shown in Figure 1 and summarized by date and unit area in Table 1. Releases by area ranged from about 11,000 in 4Xp (Browns Bank) to only seven in 5 Yd . Total recaptures were more than 6300 with over 2400 from the Gulf of Maine. Return rate by area varied between $0 \%$ and $34 \%$ with an average of $9 \%$. Release length ranged from about 15 cm to about 140 cm . A relatively high proportion of released fish were $>80 \mathrm{~cm}$ in the 5 Zj area. The majority of released cod were larger than the $\mathrm{L}_{50}$ maturity ( $\sim 43 \mathrm{~cm}$; see Hunt 1996), with the exception of unit areas 4 Xm and 4 Xo .

Observed numbers of recaptures by division of release and recapture for each of "east of 4 X, " $4 \mathrm{X}, 5 \mathrm{Y}$, and $5 Z$ areas are shown in Figure 3. Over $97 \%$ of cod recaptured from releases east of 4X were also recovered east of $4 X$ and, conversely, $74 \%$ of fish recaptured in this area originated from releases east of 4X. Further analysis of information on the area east of 4 X is required but, in general, movement between this area and the Gulf of Maine appears to be limited. For division $4 \mathrm{X}, 80 \%$ of recaptures from releases in 4 X occurred in 4 X , with $8 \%$ moving east of 4 X and $12 \%$ west to 5 Z and 5 Y . Of the total recaptures taken in 4X, 50\% were from 4X releases, 42\% from 5Y releases, and 8\% from division $5 Z$ releases. In division $5 \mathrm{Y}, 63 \%$ of recaptures from releases in 5 Y occurred in 4 X and of these only $21 \%$ occurred in 5 Y and $2 \%$


Figure 2
Mean catch per tow of cod derived from 1982-91 U.S. research surveys in the Gulf of Maine area: (A) spring and (B) fall.
from $5 Z$. However, of the total recaptures in 5 Y , over $80 \%$ were from $5 Y$ releases and $17 \%$ from $4 X$. The high proportion of recaptures in 5 Y from division 4X is probably influenced by the small numbers of releases and recaptures as well as the distribution of commercial fishing in the vicinity of the 4 X and 5 Y boundary. Clark (1996) noted that Canadian Iand-


Figure 3
Percent of cod tag recoveries by NAFO Division of release (solid bar) and Division of recapture (pattern bar, based on 1000 releases) for divisions 4X, $5 Y, 5 Z$, and the area east of $4 X$.
ings from the 5 Y area near the $4 \mathrm{X}-5 \mathrm{Y}$ boundary are considered part of the $4 X$ fishery and therefore were included in our $4 X$ stock assessment. In division 5Z, $77 \%$ of cod rel eased in $5 Z$ were recaptured in $5 Z$ and $21 \%$ were recaptured in 4 X . Of the total recaptures in division $5 Z, 81 \%$ were from $5 Z$ releases and most of the movement out of the area occurred to the northeast ( $15 \%$ ), towards division 4 X .

The annual percent exploitation rate of cod by management area ( $4 \mathrm{X}, 5 \mathrm{Y}, 5 \mathrm{Z}$ ) is summarized in Figure 4 for the 1980-97 time period. Reported Iandings by unit area showed considerable variation but proportions were relatively stable over time. In division 4 X , unit area 4 Xo accounted for about $38 \%$ of the 1980-97 total landings and unit area 5Yd for about $40 \%$ of the $5 Y$ total. In subdivision $5 Z e$, unit areas $5 Z g$ ( $30 \%$ ) and 5Zj (40\%) dominated, representing theU.S. and Canadian fisheries, respectively. The derived recapture adjustment factors, standardized to a maximum of 1.00, are given in Table 2 for each year and unit area. Annual factors ranged from 0.02 to 1.00 , meaning that about 100 recaptures from a unit area with high landings and exploitation were proportionally equivalent to about two recaptures from a unit area with low landings and exploitation rate.

The effect of weighting tag recoveries to account for fishing effort is shown in Figure 5 for releases in the Browns Bank area. Weighted recoveries decrease the apparent extent of movement to 4 Xo and 5 Z j, because of their relatively high landings and exploita-


Figure 4
Reported percent exploitation rate of cod by the commercial fishery in management areas 4X, 5Y, and 5Z for 1980-97.
tion rates, and increases the contribution of 4Xp recoveries. Similar effects are seen for other unit areas.
Table 3 provides a detailed summary of recaptures by unit area of release and recapture partitioned into $<12$ months elapsed time from release and the total number of recaptures. The observed number of tag returns, the number adjusted by unit area landings, and the percent of total adjusted number are shown. The percent of recaptures reported is based on only those released and recaptured in the Gulf of Maine
area. Table 3 summarizes results by area of release and shows the pattern of movement away from the release site (or no movement when the area of release=area recapture). Table 3 shows the pattern of movement into an area from standardized releases in adjacent areas and is organized so that the two aspects of tag recoveries appear on the same horizontal line. F or example, in the second row of data, results show $31.4 \%$ of cod released in 4Xm were recaptured in 4Xo, whereas only $15.5 \%$ of cod recaptured in 4Xm originated from 4Xo releases.

About 63\% of the cod tagged in 4Xm appeared to remain in the area although there was some movement to the west into adjacent areas. Over $76 \%$ of
cod recaptured in 4Xm originated from 4Xm releases. At the divisional level, movement in relation to the division 4X/4W boundary is small (Fig. 3); however, exchange between divisions does occur and is concentrated in the $4 \mathrm{Xm}, 4 \mathrm{Xn}$, and 4Xo areas.
No rel eases were made in 4Xn but about 80 recaptures were taken in the area. Most of these recaptures were from the Browns Bank (46\%) and Georges Bank (27\%) releases. Additional recaptures originated in the Bay of F undy area and about 4\% from the area east of 4 X .
Results for the 4Xo area indicate a contrast between the two analyses of recaptures. Close to 100\% of recaptures of cod released in the 4Xo area were

Table 1
Summary of cod tag releases and recaptures in NAFO divisions by release date. * indicates release from commercial fishing vessels.

| Area released | East of 4X | 4Xm | 4Xo | 4Xp | 4Xq | 4Xr | 4Xs | 5 Yb | 5Yc | 5Yd | 5Zj | 5Zm | 5Zo |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Date | 1978-81 | Feb 80 | May 79 | Feb 84 | Dec 94* | J un 79 | Aug 84 | Jul 85 | J un 94* | Jul 94* | Feb 84 | Mar 94 | Jul 94* |
| N | 36,338 | 808 | 694 | 3,980 | 50 | 141 | 67 | 350 | 27 | 7 | 1988 | 843 | 100 |
| Length range (cm) | 15-135 | 13-92 | 21-87 | 33-140 | 36-64 | 22-75 | 38-100 | 33-112 | 34-47 | 36-43 | 16-136 | 31-130 | 35-48 |
| Mean length (cm) | 48.8 | 47.9 | 41.9 | 71.9 | 47.4 | 36.7 | 57.1 | 59.9 | 41.1 | 40.3 | 61.2 | 69.9 | 42.4 |
| Date |  |  |  | Mar 84 | May 94* | J ul 85 | Dec 85 |  |  |  | Mar 85 | J un 94* |  |
| N |  |  |  | 786 | 4 | 216 | 73 |  |  |  | 500 | 266 |  |
| Length range |  |  |  | 40-126 | 38-57 | 28-103 | 26-64 |  |  |  | 33-139 | 30-50 |  |
| Mean length |  |  |  | 66.3 | 43.5 | 52.9 | 42 |  |  |  | 72.1 | 44.4 |  |
| Date |  |  |  | Feb 85 | Dec 95* |  | J ul 85 |  |  |  | Mar 94 |  |  |
| N |  |  |  | 1,621 | 9 |  | 1399 |  |  |  | 3608 |  |  |
| Length range |  |  |  | 38-142 | 38-72 |  | 26-94 |  |  |  | 30-144 |  |  |
| Mean length |  |  |  | 79.8 | 48.1 |  | 52.6 |  |  |  | 73.8 |  |  |
| Date |  |  |  | Mar 85 | May 96* |  | Nov 85 |  |  |  |  |  |  |
| N |  |  |  | 4363 | 58 |  | 281 |  |  |  |  |  |  |
| Length range |  |  |  | 32-140 | 39-85 |  | 28-87 |  |  |  |  |  |  |
| Mean length |  |  |  | 72.9 | 58.8 |  | 48.9 |  |  |  |  |  |  |
| Date |  |  |  |  | Nov 96* |  | J an 85 |  |  |  |  |  |  |
| N |  |  |  |  | 17 |  | 4 |  |  |  |  |  |  |
| Length range |  |  |  |  | 39-72 |  | 36-56 |  |  |  |  |  |  |
| Mean length |  |  |  |  | 53.8 |  | 42.3 |  |  |  |  |  |  |
| Date |  |  |  |  |  |  | J ul 94* |  |  |  |  |  |  |
| N |  |  |  |  |  |  | 21 |  |  |  |  |  |  |
| Length range |  |  |  |  |  |  | 36-47 |  |  |  |  |  |  |
| Mean length |  |  |  |  |  |  | 40.3 |  |  |  |  |  |  |
| Total released | 36,338 | 808 | 694 | 10,750 | 138 | 357 | 1845 | 350 | 27 | 7 | 6096 | 1109 | 100 |
| Total recaptures | 3883 | 100 | 237 | 1346 | 1 | 57 | 139 | 49 | 0 | 0 | 476 | 29 | 0 |
| Percent recaptures | 10.7 | 12.4 | 34.1 | 12.5 | 0.7 | 16.0 | 7.5 | 14.0 | 0.0 | 0.0 | 7.8 | 2.6 | 0.0 |

recaptured in 4Xo. Cod tagged in 4Xo were from an inshore area and may have been part of a local resident population. About $90 \%$ of tags recovered in 4Xo were from fish released in 4Xo and additional small contributions werefrom other Gulf of Mainelocations.

Thelargest number of releases was from theBrowns Bank area and results indi catea widespread di spersal within the Gulf of Maine. The majority of recaptures were from division 4X; substantial numbers of cod moved to the inner Bay of Fundy and smaller numbers moved east to 4 Xn and 4 Xo . About $33 \%$ of cod released in 4Xp were recaptured in the same area. Movement into Divisions 5Y and $5 Z$ accounted for about $15 \%$ of the total releases. Of cod recaptured in $4 \times$ p, about $50 \%$ originated from the same area, $27 \%$ from 5 Yb , and about $11 \%$ originated from the Georges Bank area. Differences between immigration and emigration distributions may be dueto seasonal patterns and commercial fishing operations. TheBrowns Bank area has been closed to commercial fishing during the winter spawning season and there is a low probability of capture during this time. Cod recaptured during the summer-fall fishing season may represent postspawning dispersal patterns.

In 4Xq, all three of the recaptures were taken in 4Xo. However, cod caught in 4Xq appeared to originate from diverse locations including $39 \%$ from 5 Yb , 28\% from Browns Bank, 20\% from the inner Bay of Fundy, and 10\% from Georges Bank.


Figure 5
Comparison of percent recaptures by unit areas for Browns Bank releases using observed and effort-adjusted tag recoveries.

Unit area 4Xs and 4Xr represent the inner Bay of Fundy region. M ovement of cod appears to occur into and out of the region as well as across the Bay from the Nova Scotia to New Brunswick sides. Over 75\% of recaptured cod released in these areas were re-

Table 2
Annual adjustment factors by year and area used to prorate recoveries for probability of recapture, standardized to 1.00 for the area and year ( $5 \mathrm{Zn}, 1987$ ) with the lowest landings and exploitation rate.

| Area | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | Mean |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| 4 Xm | 0.13 | 0.13 | 0.10 | 0.16 | 0.20 | 0.10 | 0.10 | 0.10 | 0.13 | 0.24 | 0.17 | 0.14 | 0.14 | 0.14 | 0.19 | 0.71 | 0.84 | 0.67 | 0.24 |
| 4 Xn | 0.21 | 0.28 | 0.18 | 0.32 | 0.20 | 0.25 | 0.17 | 0.17 | 0.18 | 0.32 | 0.41 | 0.22 | 0.12 | 0.12 | 0.28 | 0.30 | 0.47 | 0.36 | 0.25 |
| 4 Xo | 0.07 | 0.05 | 0.05 | 0.06 | 0.07 | 0.06 | 0.06 | 0.06 | 0.04 | 0.06 | 0.04 | 0.04 | 0.02 | 0.04 | 0.04 | 0.12 | 0.14 | 0.14 | 0.06 |
| 4 Xp | 0.44 | 0.33 | 0.25 | 0.22 | 0.27 | 0.29 | 0.54 | 0.24 | 0.15 | 0.12 | 0.18 | 0.14 | 0.15 | 0.14 | 0.14 | 0.13 | 0.25 | 0.23 | 0.23 |
| 4 Xq | 0.19 | 0.24 | 0.14 | 0.16 | 0.15 | 0.12 | 0.11 | 0.12 | 0.12 | 0.17 | 0.12 | 0.13 | 0.08 | 0.10 | 0.11 | 0.16 | 0.24 | 0.17 | 0.15 |
| 4 Xr | 0.15 | 0.12 | 0.11 | 0.13 | 0.12 | 0.11 | 0.13 | 0.23 | 0.21 | 0.24 | 0.16 | 0.09 | 0.07 | 0.08 | 0.10 | 0.21 | 0.24 | 0.14 | 0.15 |
| 4 Xs | 0.30 | 0.30 | 0.27 | 0.34 | 0.36 | 0.23 | 0.23 | 0.28 | 0.28 | 0.46 | 0.23 | 0.15 | 0.16 | 0.15 | 0.21 | 0.50 | 0.43 | 0.28 | 0.29 |
| 5 gg | 0.04 | 0.05 | 0.04 | 0.05 | 0.05 | 0.04 | 0.07 | 0.08 | 0.05 | 0.05 | 0.05 | 0.04 | 0.06 | 0.04 | 0.03 | 0.06 | 0.11 | 0.08 | 0.06 |
| 5Zh | 0.14 | 0.16 | 0.16 | 0.12 | 0.13 | 0.12 | 0.25 | 0.16 | 0.10 | 0.15 | 0.20 | 0.13 | 0.14 | 0.08 | 0.08 | 0.17 | 0.33 | 0.24 | 0.16 |
| $5 Z \mathrm{Z}$ | 0.08 | 0.06 | 0.04 | 0.04 | 0.05 | 0.04 | 0.05 | 0.04 | 0.03 | 0.05 | 0.04 | 0.03 | 0.02 | 0.02 | 0.03 | 0.20 | 0.23 | 0.12 | 0.06 |
| $5 Z m$ | 0.33 | 0.26 | 0.23 | 0.23 | 0.10 | 0.10 | 0.13 | 0.22 | 0.10 | 0.13 | 0.15 | 0.11 | 0.12 | 0.08 | 0.11 | 0.32 | 0.55 | 0.62 | 0.22 |
| $5 Z n$ | 0.39 | 0.40 | 0.71 | 0.97 | 0.28 | 0.38 | 0.79 | 1.00 | 0.57 | 0.53 | 0.32 | 0.21 | 0.34 | 0.19 | 0.15 | 0.33 | 0.64 | 0.46 | 0.48 |
| $5 Z 0$ | 0.49 | 0.76 | 0.44 | 0.38 | 0.29 | 0.22 | 0.32 | 0.78 | 0.34 | 0.40 | 0.32 | 0.27 | 0.46 | 0.33 | 0.18 | 0.41 | 0.79 | 0.57 | 0.43 |
| 5 Yb | 0.61 | 0.76 | 0.41 | 0.31 | 0.30 | 0.15 | 0.19 | 0.13 | 0.33 | 0.44 | 0.28 | 0.06 | 0.06 | 0.07 | 0.07 | 0.07 | 0.07 | 0.07 | 0.24 |
| 5 Yc | 0.15 | 0.15 | 0.10 | 0.11 | 0.10 | 0.08 | 0.06 | 0.06 | 0.13 | 0.07 | 0.07 | 0.08 | 0.08 | 0.09 | 0.09 | 0.09 | 0.09 | 0.09 | 0.09 |
| 5 Yd | 0.02 | 0.02 | 0.03 | 0.03 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 |
| 5 Ye | 0.02 | 0.02 | 0.02 | 0.02 | 0.03 | 0.03 | 0.04 | 0.05 | 0.04 | 0.05 | 0.05 | 0.04 | 0.04 | 0.04 | 0.04 | 0.04 | 0.04 | 0.04 | 0.04 |
| 5 Yf | 0.12 | 0.09 | 0.07 | 0.09 | 0.08 | 0.05 | 0.06 | 0.05 | 0.12 | 0.09 | 0.07 | 0.07 | 0.07 | 0.08 | 0.08 | 0.08 | 0.08 | 0.08 | 0.08 |

Table 3



covered there and between $15 \%$ and $20 \%$ of recaptures were from releases in the 5Yb area. Cod tagged in unit area 4Xs show more widespread dispersal than those from 4Xr.

The small number of releases from division 5 Y precluded detailed interpretation of movement. However, there is an indication of association with the $4 X$ area, as well as movement from the Browns Bank area into 5 Y , both of which were not unexpected because the majority of releases were near the northeastern border of 5Y. Results, therefore, probably do not reflect those for the remainder of the 5 Y area.

The pattern observed for Georges Bank is similar to that seen on Browns Bank. Dispersal of postspawning cod appears to be substantial in both a north and south direction. Interaction between the Browns Bank and inshore area and Georges Bank accounted for most of the movement of tagged cod. The interchange was bidirectional, but more cod appeared to move from Georges Bank to Browns Bank (about $30 \%$ ) compared with about $3 \%$ of Browns Bank cod moving to Georges Bank. Relatively small numbers of cod released in the 5Zj and 5Zm area were recaptured in areas further to the south or west. However, Hunt and Buzeta (1996) noted that the U.S. commercial fishery, and therefore the prob-


Figure 6
Summary of adjusted cod tag recoveries for the Browns Bank (4Xp) and Georges Bank (5Zj) areas, aggregated by unit area. ability of recovering tags from the 1994 and later releases in the area west of the IMB, has been substantially reduced with the introduction of closed areas in 1995.

Information for the Browns Bank and Georges Bank areas is shown in Figure 6 for adjusted recaptures in the area and from the area. Preliminary comparison of recoveries in the first twelve months and total recoveries showed little variation in the distribution or proportions (Table 3) and therefore total recoveries were used. Dispersal from the area of release appears to be substantial for both the 4Xp and 5Zj areas. However, a high proportion of fish recaptured in the two areas was released from the same area. The two patterns may represent postspawning dispersal (top panel for each area) and summer distribution or year-round residents (bottom panel for each area).

The seasonal distribution of recaptures from the Browns Bank and Georges Bank areas is shown in Figure 7. Recaptures were combined by quarter and
unit area (by division for recaptures outside the division of release). In the Browns Bank area, seasonal distribution appears to be consistent with aggregation in the spawning season (first quarter) and with progressive dispersal to adjacent areas in the remainder of the year. This pattern may be repeated on an annual basis with return of migrants during the spawning season. Seasonal trends in the Georges Bank area are more difficult to interpret and the influence of fishing season may be a factor, compared with trends for Browns Bank, because closure to commercial groundfishing in the first half of the year limits potential recoveries during the spawning season. However, the recapture pattern for cod recovered in division 4 X suggests that the migrants do not return to Georges Bank because the proportion remains relatively constant over the first to third quarters and increases in the fourth quarter.

Figures 8 and 9 provide information on the spatial dispersal of cod tagged in the Browns Bank and Georges Bank areas with adjusted recoveries aggregated by $10-\mathrm{min}$ squares and expressed on a per thousand basis. Most recoveries were made near the respective release site. When movement occurred, a general pattern of dispersal from the releasesite with a gradient from the tagging site to the edges of the distribution was evident. Intermediate areas of aggregation were consistent with the geographic distribution of fisheries effort and associated probability of recapture. Interchange occurred between release site areas, but the main vector of movement from both sites was towards the northeast. As a result, most long distance recoveries were made in the


Figure 7
Quarterly distribution of cod tag recoveries from the Browns Bank (4Xp) and Georges Bank (5Zj) release areas, aggregated by unit area.
southwestern Nova Scotia and Bay of F undy inshore areas, although there was limited movement intothe northwestern Gulf of Maineor western Georges Bank areas.
The two time periods associated with Georges Bank tagging are compared in Figure 10 for the 1994 and 1984-85 experiments. Thetwo distributions are similar and both show the majority of cod remaining near the release area; more of the long distance dispersion occurred into the 4 X area than to the west into the inner Gulf of Maine. Similarity in theresults from the two time periods indicates some consistency in the northeast vector of movement. However, a higher proportion of cod were recaptured in 4X from the 1994 experiment (55\%) compared with the earlier releases (42\%). As noted above, the reduced U.S. commercial fishery in the area west of the IMB since 1995 also reduced the probability of tag recaptures from the 1994 experiment in this area.
The distribution of recaptures and elapsed time for the February and March releases for unit areas 4Xp (Browns Bank) and 5Zj (Georges Bank) are shown in Figure 11. The majority of returns in both areas occurred in the first 24 months after rel ease, and the maximum time at large was 87 months (Table 4), but the overall average of time at large was less than 8 months. Many fish were recaptured in the first month after release, probably before postspawning dispersion had occurred. Maximum distance travelled was over 620 km and the mean distanced travelled was 60 km . Substantial numbers of cod moved hundreds of kilometres, indicating that cod can survive the stress of tagging and are capable of long distance movements. A strong seasonal pattern, consistent with the seasonal nature of the commercial fishery, is evident. The fishery on Browns Bank is typically year round, with peaks late spring and summer (Clark, 1996), and on Georges Bank, the fishery typically opens in J une (Hunt and Buzeta 1996). The seasonal peaks in recaptures (4-6, 16-18, etc. months after February releases) coincides with the commercial fishing activity.
Length at the time of recapture was available for a relatively small proportion of recaptures. For these samples, the net increase in length and elapsed time was used to calculate a specific growth rate, expressed as annual rate, for each unit area. Results are given in Table 5 for $10-\mathrm{cm}$ length-at-release intervals but sample size was small for all but the $4 X p$, 4Xs, and 5Zj areas. The calculated annual growth rates indicate differences between areas and follow an expected pattern of decrease as the length at release increases. Of these three areas, the Georges Bank area had the fastest growth with an annual increase of about 19 cm for cod released as $40-\mathrm{cm}$
individuals. Estimates of growth rates from this study are consistent with the more extensive study on cod growth completed by Shackell et al. (1997).

## Discussion

Fisheries management objectives for either conservation or yield from a defined management unit are usually based on a closed system approach that requires that emigration and immigration of fish from adjacent stocks be sufficiently low so as to avoid confounding stock-status evaluations. Gulland's (1983) operational definition of a stock also considered interchange between stocks and he suggested that it can be ignored if conclusions on the population dynamics of the stock remain valid. Therefore, two problems require evaluation in assessing stock definitions: 1) Is there evidence of interchange of fish at a geographic scale larger than the one used to define a stock boundary? and 2) If interchange does occur, what are the impacts on population dynamics and on the assumptions used in models to estimate population parameters?

Tagging experiments can address the first of the two questions provided that the study logistics have not compromised the results and that both ongoing fisheries removals and management activities during the recapture period do not invalidate interpretation of the results. Capture, tagging, and release of cod with bottom trawl methods and T-bar tags can generate a large number of releases and, according to a relatively high recapture rate and extended time at large, appear to result in nominal tag- or stress-induced mortality. During the 1994 experiment, cod tagged from one tow were recaptured in a subsequent tow, either the same day or several days later and thus may indicate that tagged cod resumea normal schooling pattern shortly after release. Efficiency of the tagging operation is al so a contributing factor as is the time of year, depth, and condition of tagged fish. Clay et al. (1989) reported on tagging experiments under winter conditions and concluded that cod at this time of year have a better chance of survi ving the tagging process. Tag loss was not examined in our study but Saunders et al. (1990), in a study of sablefish tagged with tags similar to those used in our study, concluded that tag loss could be as high as $10 \%$ in the first year and $2 \%$ per year thereafter. Less than $10 \%$ of cod tagged with T-bar tags for identification in a live-fish holding facility experienced tag loss in the first week, al-


Figure 8
Distribution of adjusted cod tag recoveries from releases in the Browns Bank (4Xp) area, aggregated by 10-min latitude and longitude squares.
though losses were higher after biweekly netting and sampling for length and weight observation (Nelson ${ }^{1}$ ).

In the present study, the influence of high annual mortality rates ( $Z$ ), failure to report recaptures, and theeffectiveness of advertisements and rewards, the impact of fishery controls, and the potential bias between Canada and U.S. reporting rates may be more substantial than factors such as tag loss. However, these variables are difficult to quantify.

All cod stocks in the study area have been subjected to very high exploitation rates in the last decade. F or example, Hunt and Buzeta (1996) reported rates of over $40 \%$ in the 1990s for the Georges Bank cod stock. A similar capture rate applied to the tagged population [ N ] could result in an apparent rate [R] of over 20\% returns after accounting for tagging mortality ( $\sim 20 \%$ ) and tag loss ( $\sim 10 \%$ ) and assuming full reporting $[\mathrm{R}=0.4(\mathrm{~N}-\mathrm{N}(0.2+0.1)=0.28 \mathrm{~N}]$. Observed return rates were less than half those for the Georges Bank and Browns Bank areas and a lack of reporting could be a contributing factor. Anecdotal information from field staff working in fishing ports

[^0]indicates that some fishermen with tags did not return them because of resistance to identifying fishing locations and because of preconcei ved ideas and concerns about the significance of the release and recapture site. The extent of a lack of reporting is difficult to quantify and its effect may not introduce bias if nonreported tags have the same geographic distribution as reported tags.
Advertizing campaigns for the 1994 experiment were much more extensive than those used in the early 1980s. Printed notices covered a larger audience, the experiment was discussed with industry representatives and conducted with their support, interim results were presented, and a more active role was taken by field staff to collect recovered tags. However, the return rate was higher in the 1980s. F or example, the return rate in the first 24 months for the 1984-85 Georges Bank experiments was about $12.2 \%$ compared with $5.5 \%$ for the 1994 experiment.

Fisheries management controls may play a more substantial role in determining the number of recaptures. Controls may include area closures, restricted seasons, and catch limitations. The Browns Bank area has been closed to fishing during the winter


Figure 9
Distribution of adjusted cod tag recoveries from releases in the Georges Bank (5Zj) area, aggregated by 10-min latitude and longitude squares.
spawning season for many years. Canadian commercial fishing on Georges Bank has been closed between J anuary and May since 1994, and the United States has an extensive closed area covering most of the northeast part of the Bank. These restrictions substantially reduce the possibility of recaptures during the spawning season.
The establishment of the International Maritime Boundary in 1984 between the United States and Canada and the associated opinions and concerns of the fishing industry have undoubtedly introduced bias in the tag return rate and perhaps in the reported recovery location. It might be assumed that the direction of the bias would tend to support the concept of national ownership of the resource by the fishing industry and that tags recovered at times or locations that appeared to contradict this opinion would be withheld or discarded. Comparison of tag recoveries from the 1984-85 releases with those from the 1994 releases does not show substantial differences in distribution of fish. Thefirst period includes the time when response to international boundary change would have been most sensitive and pronounced. The second period, more than ten years after the change, might be expected to have reduced concerns by fishermen on tag location. However, the impact of nonreporting bias would be of most concern in evaluating the proportional spatial distribution of tag recoveries. Bias in reported recapture location is of less concern because fishing activities are monitored and there is limited opportunity to misreport the area of operations.

Total allowable catches and landings of cod from the Georges Bank area in 1994 declined to less than $50 \%$ of the recent ten-yr average and are expected to remain at low levels for a number of years (Hunt and Buzeta, 1996). The impact of reduced catches is accounted for, to some extent, by reduced annual exploitation and its impact on tag-recapture adjustment. However, other changes in the fishery, such as shifts in gear sectors and spatial redirection of effort, may offset this adjustment.

Even with the need, discussed above, to qualify the interpretation of tagging data, we believe the results of the present study clearly indicate that interchange between the $5 \mathrm{Zj}, \mathrm{m}$ and $4 X$ cod management units occurs with a net movement from $5 \mathrm{Zj}, \mathrm{m}$ to 4 X . Cod released on Georges Bank exhibited movement outside the $5 Z$ management area onto Browns Bank and the inshore areas of Nova Scotia and the Bay of Fundy. Cod released on Browns Bank also moved to the inshore area of Nova Scotia
as well as onto Georges Bank. These results correspond to those of historical studies, although conclusions from the earlier studies may be more limited in scope owing to the smaller number of released fish and the lower intensity of commercial fisheries at the time. In his review of tagging results from the late 1890s to the 1960s in the Gulf of Maine, Wise (1963) concluded that cod of the offshore areas of Browns and Georges Banks were closely related to fish of the southwestern Nova Scotia area. Wise and J ensen (1960) had earlier concluded that the eastern Georges Bank cod population mixed little with the more western or southern components and interacted primarily with the southwestern Nova Scotia area. Templeman (1962) in summarizing cod tagging information for the northwest Atlantic concluded that there were discrete spawning stocks on the eastern part of Georges Bank and Browns Bank and mixing in both directions across the Fundian Channel as well as to inshore areas. Results of tagging studies completed in 1969 on Browns Bank and in 1972 from inshore areas of Nova Scotia were reported by Halliday (1973) and he concluded that there was a separation of inshore and offshore stocks. McKenzie (1956) and McCracken (1956) tagged cod in the inshore area of southwest Nova Scotia and observed limited interchange with the offshore banks and the Bay of Fundy. They concluded that the resident inshore cod stocks in the Bay of Fundy and southwestern Nova Scotia were relatively stationary. They also explained the offshore re captures of cod tagged in the inshore area as evidence that cod from more migratory stocks could be present in inshore areas at certain times of the year.

Hunt and Buzeta (1989) provide details of the basis for partitioning the northeast part of Georges Bank ( $5 \mathrm{Zj}, \mathrm{m}$ ) as a separate Canadian management unit distinct from the remainder of the $5 Z w+S A 6$ area. They concluded that spatial distribution from tagging studies and other biological characteristics were sufficiently distinct to define the 5Zj,m area as a management unit that could be expected to benefit from management controls. H owever, the $5 \mathrm{Zj}, \mathrm{m}$ area is partitioned by the IMB so that commercial fisheries by Canada and the United States are limited to their respective sides. Gavaris et al. (1993) conducted an analysis of cod movement in relation to the IMB using commercial catches and research sur-


Figure 10
Distribution of adjusted cod tag recoveries from releases in the Georges Bank (5Zj) area, aggregated by $10-\mathrm{min}$ latitude and longitude squares: (A) 1994 releases; (B) 1984-85 rel eases

Table 4
Summary by unit area of release of months after release to recapture and distance travelled (km).

| Area of release | Months after release |  |  | Distance travelled |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Minimum | Maximum | Average | Minimum | Maximum | Average |
| 4Xm | 0 | 87 | 12.0 | 1.12 | 385 | 64.5 |
| 4Xo | 0 | 25 | 2.4 | 0 | 448 | 7.2 |
| 4Xp | 0 | 62 | 12.2 | 2 | 626 | 128.6 |
| 4Xq | 7 | 7 | 7 | 24 | 24 | 24.0 |
| 4Xr | 0 | 28 | 4.4 | 0 | 235 | 25.4 |
| 4Xs | 0 | 38 | 8.5 | 0 | 385 | 75.8 |
| 5 Yb | 0 | 31 | 7.0 | 2 | 221 | 66.5 |
| 5Zj | 0 | 65 | 10.1 | 2 | 367 | 62.3 |
| 5 Zm | 3 | 16 | 5.3 | 22 | 265 | 93.4 |
| Average | 0 | 39.9 | 7.6 | 5.9 | 328.6 | 61.0 |



Figure 11
Summary of adjusted cod tag recoveries for releases in the Browns Bank (4Xp) and Georges Bank (5Zj) areas by elapsed time from release to recovery, in months.
vey indices. They concluded that extensive movement does occur with a strong seasonal pattern in which almost $100 \%$ of the biomass is on the Canadian side in the fall-winter period and about 65\% in the spring-summer period. Results of the present study support the occurrence of seasonal movement but al so indi cate that it is not a closed system. There is evidence of immigration and emigration and an apparent net loss from the Georges Bank area to the Browns Bank and division 4 X area.
In division 4X, two substocks (Bay of Fundy and Scotian Shelf) are already assumed (Clark, 1996) with distinct growth characteristics. However, tagging results show interchange between the Bay of Fundy, the inshore areas of southern Nova Scotia, and Browns and Georges Banks. The greatest exchange occurs between the offshore Browns Bank area and the inshore areas and the Bay of Fundy. Our results indicate that the extent of movement by cod in the Gulf of Maine area is substantial and that it crosses the present stock boundaries between $4 \mathrm{X}, 5 \mathrm{Y}$, and 5 Z . The interchange appears to be primarily between the eastern part of Georges Bank (theCanadian management unit) and $4 X$. Although movement between 4 X and 5 Y was observed, the number of releases and recaptures was small and the tagging location was close to the boundary between these areas. Exchange between 5 Z and 5 Y also occurs but at a relatively low rate.

Investigation of the potential impact of cod movement between stocks on models used for population estimates will require further work. Interpretation of diagnostics for population models such asADAPT (Gavaris, 1988) from a stock concept might give

Table 5
Growth rate of cod estimated from net increase in length and elapsed time, expressed as an annual rate. Number of observations are shown in parentheses.

| Release <br> length (cm) | 4 Xm | 4 Xo | 4 Xp | 4 Xr | 4 Xs | 5 Yb | 5 Cj |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $20-29$ | $12.5(2)$ | $12.0(4)$ |  |  |  |  |  |
| $30-39$ | $13.4(7)$ | $14.9(6)$ |  | $17.7(8)$ | $26.6(4)$ |  |  |
| $40-49$ | $7.9(7)$ | $8.9(8)$ | $12.4(7)$ |  | $15.8(15)$ | $33.8(5)$ | $18.9(16)$ |
| $50-59$ | $10.7(22)$ | $8.0(4)$ | $9.2(28)$ | $2.6(3)$ | $15.8(16)$ | $30.7(3)$ | $16.9(12)$ |
| $60-69$ | $5.1(4)$ |  | $7.5(66)$ | $18.0(2)$ | $10.8(18)$ | $18.9(9)$ | $12.2(45)$ |
| $70-79$ |  |  | $6.7(88)$ | $6.0(1)$ | $4.8(7)$ | $21.0(2)$ | $11.9(26)$ |
| $80-89$ |  |  | $5.7(46)$ |  |  | $4.0(1)$ | $7.2(18)$ |
| $90-99$ |  |  | $3.7(14)$ |  |  | $5.8(11)$ |  |
| $100-109$ |  |  | $3.1(3)$ |  |  | $6.9(2)$ |  |

some indication of the need for revising model formulations. For example, changes in apparent natural mortality or unexplained changes in fishing mortality could be evaluated as the result of losses due to emi gration or increases due to immigration. However, stock definition may be further confounded if cod movements have a temporal element and shifts in distribution occur without permanent loss or gain.

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