Abstract.—We examine the population to population variability of intrinsic rate of natural increase, r_m, of Atlantic cod, *Gadus morhua*. The intrinsic rate of increase is positively related to temperature, contrary to the expectation that r_m might increase as the high and low temperature limits of habitability for cod are approached. For the parameter regime considered, r_m has a simple dependence on age-at-maturity and the number of replacements each spawner can produce at low population densities ($\tilde{\alpha}$). It is shown that $\tilde{\alpha}$ has no significant temperature dependence, and thus the covariation of r_m and temperature arises from the influence of temperature on age-at-maturity. We demonstrate that our estimates of r_m are robust and thus may be of use in estimating the recovery time of depleted populations.

Maximum population growth rates and recovery times for Atlantic cod, *Gadus morhua*

Ransom A. Myers*
Gordon Mertz

Science Branch
Department of Fisheries and Oceans
P.O. Box 5667
St John's, Newfoundland, Canada A1C 5X1
*Present address: Department of Biology
                   Dalhousie University
                   Halifax, Nova Scotia, Canada B3H 4J1

E-mail address (for R. Myers):Ransom.Myers@Dal.Ca

P. Stacey Fowlow

Seaborne Ltd.
P.O. Box 2035
Station C, 200 White Hills Road
St. John's, Newfoundland, Canada A1C 5R6

Perhaps the most fundamental of all ecological parameters is the intrinsic rate of natural increase, r_m (Cole, 1954; Pimm, 1991). High r_m will be selected for in populations that experience frequent excursions to low density (Charlesworth, 1994). Populations subjected to strong environmental variability should evolve toward high r_m (MacArthur and Wilson, 1967), which will impart resilience to the population. However, allometric (cross species) comparisons (Fenchel, 1974; Hennemann. 1983; Charnov, 1993) suggest that r_m chiefly depends on metabolic rate or somatic growth rate. Perhaps, the influence of environmental variability on r_m can be more readily discerned in cross population comparisons for a single species. In this paper we examine 20 populations of Atlantic cod, *Gadus morhua*, to determine their maximum growth rates. We also discuss how these estimates help predict the recovery times of severely overfished populations.

Atlantic cod lends itself to a study of this nature because there is a wealth of good quality biological data collected for stock management purposes. Moreover, these cod populations occupy a broad span of latitudes, including regions that are thought to represent the northern and southern limits of habitability for cod, and there is evidence that population variability increases as these extremes are approached (Myers, 1991). The increase in population variability at the limits of the range of cod could impose constraints on r_m that would mask the simple dependence of r_m on metabolic rate or somatic growth rate apparent in cross species comparisons. In fact, we will show, in what we believe is an unanticipated result, that even for a within-species comparison, there is strong coupling between r_m and metabolic rate or somatic growth rate (as represented by age at maturity or temperature). Our results have implications for the recovery rates of a number of

Methods

Model

For fish populations, reproduction is generally expressed as recruitment, the number of juvenile fish reaching, in a given year, the age of vulnerability to fishing gear. Thus, the reproduction curve (Royama, 1993) for fish is displayed as a spawner-recruitment curve (Ricker, 1954), and r_m must be derived from the slope of this curve near the origin (low population). This derivation will be presented immediately following a brief discussion of the standard population-recruitment curves.

Juvenile fish become vulnerable to fishing gear, that is, they recruit at an age designated as j'. We consider the Ricker spawner-recruitment model which describes the number of recruits at age j' in year $t+j'$, $N_{t+j', j'}$, resulting from a spawning stock biomass (SSB) of S_t. We follow the usual convention in fisheries science of assuming that the number of eggs produced is proportional to the biomass of spawners.

The Ricker model has the form

$$E(N_{t+j',j'}) = \alpha S_t e^{-\beta S_t},\qquad(1)$$

where α = the slope at the origin (measured perhaps in recruits per kilogram of spawners). Density-dependent mortality is assumed to be the product of β multiplied by the spawning biomass (S_t).

For the forthcoming calculations the slope at origin, α, must be standardized. First consider

$$\hat{\alpha} = \alpha \cdot \text{SPR}_{F=0},$$

where $SPR_{F=0}$ is the spawning biomass resulting from each recruit (perhaps in units of kg of spawning fish per recruit) in the limit of no fishing mortality ($F=0$). This quantity, $\hat{\alpha}$, represents, on a lifetime basis, the number of recruits per recruit at very low spawner abundance or, equivalently, the number of spawners produced per spawner (assuming that there is constant survival from recruit to spawner).

The quantity, $\tilde{\alpha}$, required for our calculations is the number of spawners produced by each spawner per year (after a lag of a years, where a is age-at-maturity).

If adult survival is p_s then $\hat{\alpha} = \Sigma_j p_s^j \tilde{\alpha}$, or summing the geometric series

$$\tilde{\alpha} = \hat{\alpha}(1 - p_s) = \alpha \cdot \text{SPR}_{F=0}(1 - p_s).\qquad(2)$$

If the annual survival fraction for spawners was zero, the population of spawners, N_t, would obey the following equation:

$$N_{t+a} = \tilde{\alpha} N_t.\qquad(3)$$

Equation 3 has the solution $N_{t=na} = \tilde{\alpha}^n N_0$, where N_0 is the number of spawners at $t = 0$. It follows that the natural growth rate, per annum, of the population is

$$r_m = (1/a)\log\tilde{\alpha},\qquad(4)$$

for the limit of small p_s. The analogous result for the case of overlapping generations is derived below.

When adult survival in not zero ($p_s \neq 0$), one has an age-structured spawning population, and r_m cannot be derived in the simple manner presented above. Rather, one must solve the Euler-Lotka equation (Charlesworth, 1994) to obtain r_m in this situation.

The Euler-Lotka equation is

$$\sum_j l_j m_j e^{-r_m j} = 1,\qquad(5)$$

where l_j = the fraction of animals surviving to age j; and

m_j = the number of offspring per animal produced at age j.

We now assume that $m_j = m_0$ for fish of age a and older, and also, for $j \geq a$, $l_j = l_a p_s^{j-a}$, where l_a is the fraction of juveniles that survive from age zero to age a, and, again, p_s is the annual survival fraction of spawners. It follows from Equation 5 that

$$l_a m_0 \sum_{j=a}^{j=\infty} p_s^{j-a} e^{-r_m j} = 1.\qquad(6)$$

A little manipulation, and the summing of a geometric series, allows Equation 6 to be written as

$$\frac{l_a m_0 e^{-r_m a}}{1 - p_s e^{-r_m}} = 1.\qquad(7)$$

Since m_0 is the number of age-zero fish produced by each spawner, and since l_a is the fraction of age-zero fish surviving through the juvenile stage to maturity, it follows that $m_0 l_a = \tilde{\alpha}$, and thus Equation 7 can be expressed as

$$(e^{r_m})^a - p_s(e^{r_m})^{a-1} - \tilde{\alpha} = 0.\qquad(8)$$

We have bracketed the e^{r_m} term to emphasize that Equation 8 is a simple algebraic equation for $\chi = e^{r_m}$. Note that in the limit $p_s = 0$, we recover Equation 4 from Equation 8. Equation 8 is very similar to Equation 1 of Goodman (1984), amounting to a translation into parameters available for fish populations. Equation 8 may also be obtained as the low density limit of the simplified age-structured model of Clark (1976), as modified by Mertz and Myers (1996).
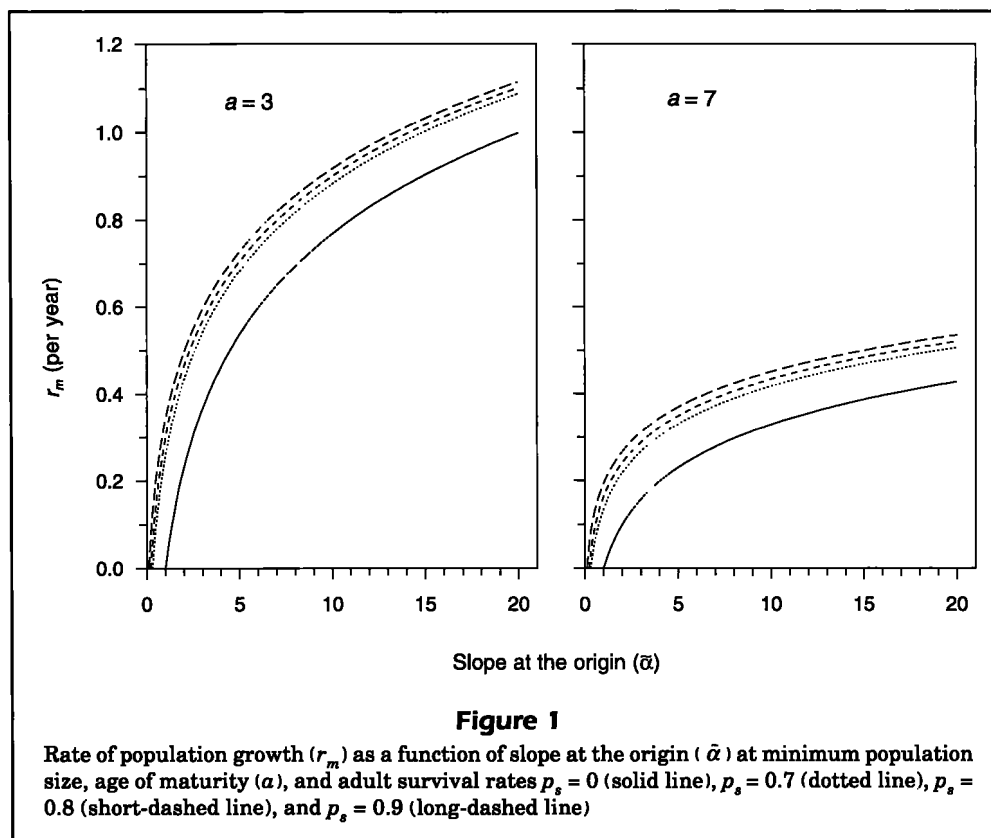
It is clear for a moderately large slope at the origin ($\tilde{\alpha}$) that age of maturity (a) is the most important factor in determining r_m (Fig. 1). The solid line in Figure 1 shows, for reference, the case $p_s = 0$, for which r_m may be calculated from Equation 4. The three broken lines in Figure 1 represent $p_s = 0.7$, 0.8, 0.9, a range that should encompass all North Atlantic cod stocks (see next section). For this range, survival after reproduction (p_s) has only a minor effect on r_m.

Data sources and treatment

The data we used are estimates obtained from assessments compiled by Myers et al. (1995b). Population numbers and fishing mortality were estimated by using sequential population analysis (SPA) of commercial catch-at-age data for most marine populations. Sequential population analysis techniques include virtual population analysis (VPA), cohort analysis, and related methods that reconstruct population size from catch-at-age data (see Hilborn and Walters, 1992) chapters 10 and 11, for description of the methods used to reconstruct the population history). Briefly, the commercial catch-at-age is combined with estimates from research surveys and commercial catch rates to estimate numbers-at-age in the final year and to reconstruct previous numbers-at-age under the assumption that commercial catch-at-age is known without error and that natural mortality-at- age is known and constant.

The population boundaries in the North Atlantic generally follow those of the Northwest Atlantic Fisheries Organization (NAFO) or the International Council for the Exploration of the Sea (ICES) (Fig. 2). Many populations cover more than one NAFO or ICES unit area, e.g. the cod population off Labrador and Northeast Newfoundland, known as "northern" cod, inhabits three NAFO divisions (2J, 3K, and 3L) and is designated as 2J3KL cod. There are three minor populations that are not included in the comparative analysis: Flemish Cap, Gulf of Maine, and the English Channel. There are no reliable catch data for the Flemish Cap population (NAFO 3M) or the English Channel population (ICES VIId), and the

Figure 1

Rate of population growth (r_m) as a function of slope at the origin ($\tilde{\alpha}$) at minimum population size, age of maturity (a), and adult survival rates $p_s = 0$ (solid line), $p_s = 0.7$ (dotted line), $p_s = 0.8$ (short-dashed line), and $p_s = 0.9$ (long-dashed line)

time series of data for the Gulf of Maine (NAFO 5Y) is not included in the comparative analysis because the time series is too short (less than 10 years) (Myers et al., 1995b).

Maturity and weight-at-age were estimated from research surveys carried out for each population. Typically hundreds of fish are measured from a stratified random or systematic design each year. Adult natural mortality (M) has been investigated by a variety of methods; for each of the 20 populations, the value of $M=0.2$ was accepted by the researchers studying each population. This natural mortality corresponds to adult survival of $p_s = e^{-M} \approx 0.8$ (which will be our working value). The uniformity (across populations) of acceptable values for p_s suggests that one can safely assume that the true p_s lies in the range 0.7 to 0.9, as shown in Figure 1.

Bottom temperature was estimated by Brander (1994) for all the populations except the Baltic populations. We used data in Dickson et. al. (1992) to make estimates for the Baltic populations. We estimated independent temperatures for the Northwest Atlantic from deYoung et. al. (1994). These changes were small (less than 2°C) and did not have an important effect on our findings.

Estimation

The slope at the origin, $\tilde{\alpha}$, and other parameters of the Ricker model were fitted by using maximum-likelihood estimation and by assuming lognormal variability in the residuals (Hilborn and Walters, 1992); the assumption of gamma variability in model residuals resulted in only minor changes in the esti-
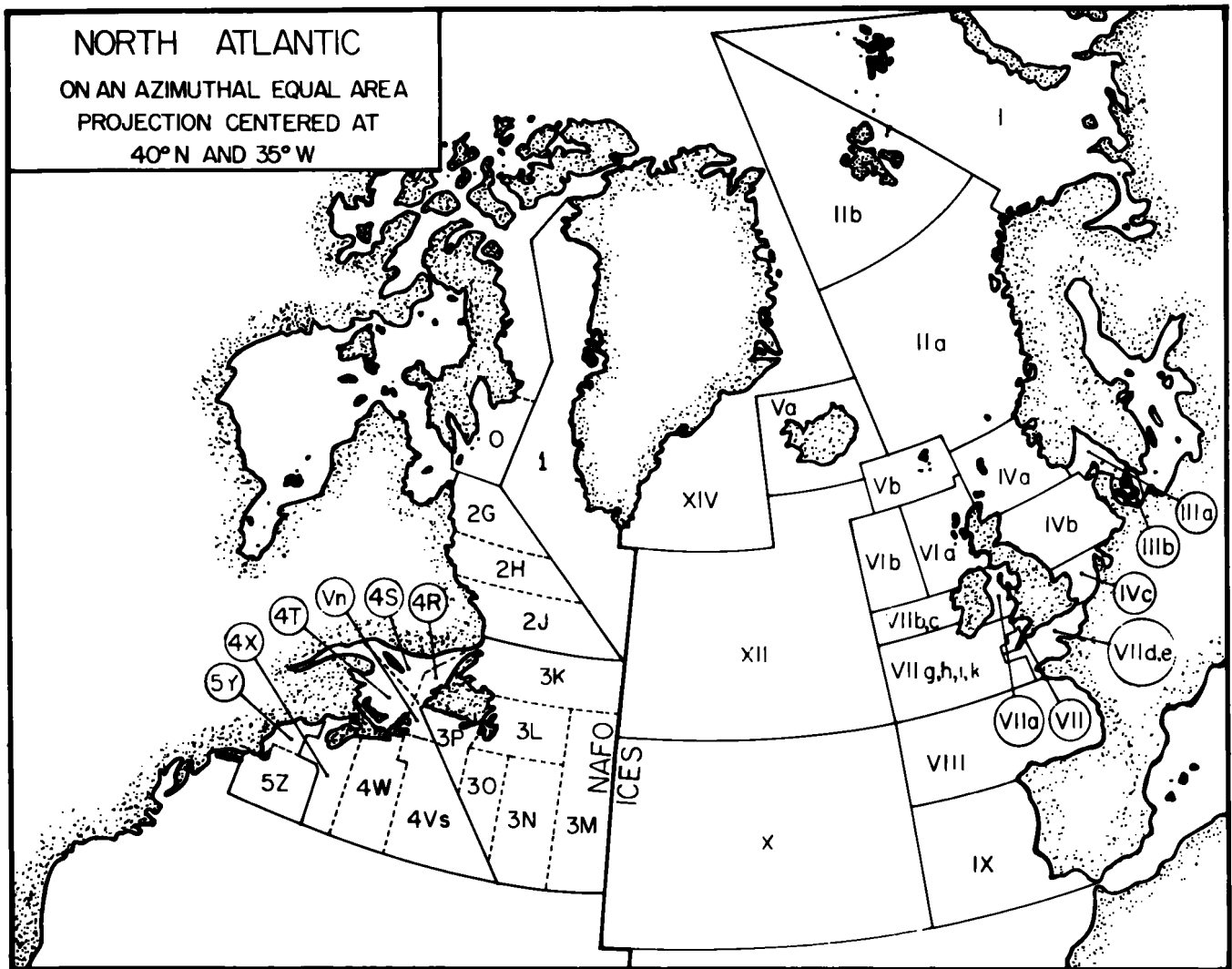

Figure 2

Map of the North Atlantic showing the regions used to define fish populations for fisheries management.

mated parameters (Myers et al., 1995b). Difficulties in estimating density-dependent model parameters are well known for insect and bird populations (Holyoak, 1993; Wolda and Dennis, 1993) and have been extensivly studied for exploited fish populations (Hilborn and Walters, 1992). The most important source of statistical bias for exploited fish populations is the nonindependence of spawners and recruitment, i.e. large recruitment usually leads to large spawner abundance (Walters, 1985). Bias in the parameter estimates of the spawner recruit function has been extensively studied with simulations for cod populations by Myers and Barrowman (1995) who found minimal bias in the estimates of the α parameter.

The slope at the origin can be well estimated for cod populations, in spite of the large variability in recruitment, because each population has been reduced to very low levels by overexploitation (Myers et al., 1994). Furthermore, there is no evidence that mortality increases at low population size, i.e. depensation or the Allee effect, that would invalidate the assumption of our spawner recruitment model (Myers et al., 1995).

The disadvantage of using the Ricker model, or any other parametric spawner recruitment model, is that the slope at the origin is influenced by observations far from the origin. We investigated an alternative approach: we regressed recruitment versus spawner biomass with only six observations with the lowest spawner biomass, forcing the regression line through the origin. This simple procedure should be reasonable because all the populations have been reduced to very low levels.

Results

The Ricker model estimates of the slope at the origin and of the population growth rate were estimated for the 20 spawner recruit data sets (Table 1; Fig. 3). The slope at the origin, $\tilde{\alpha}$, did not vary enormously
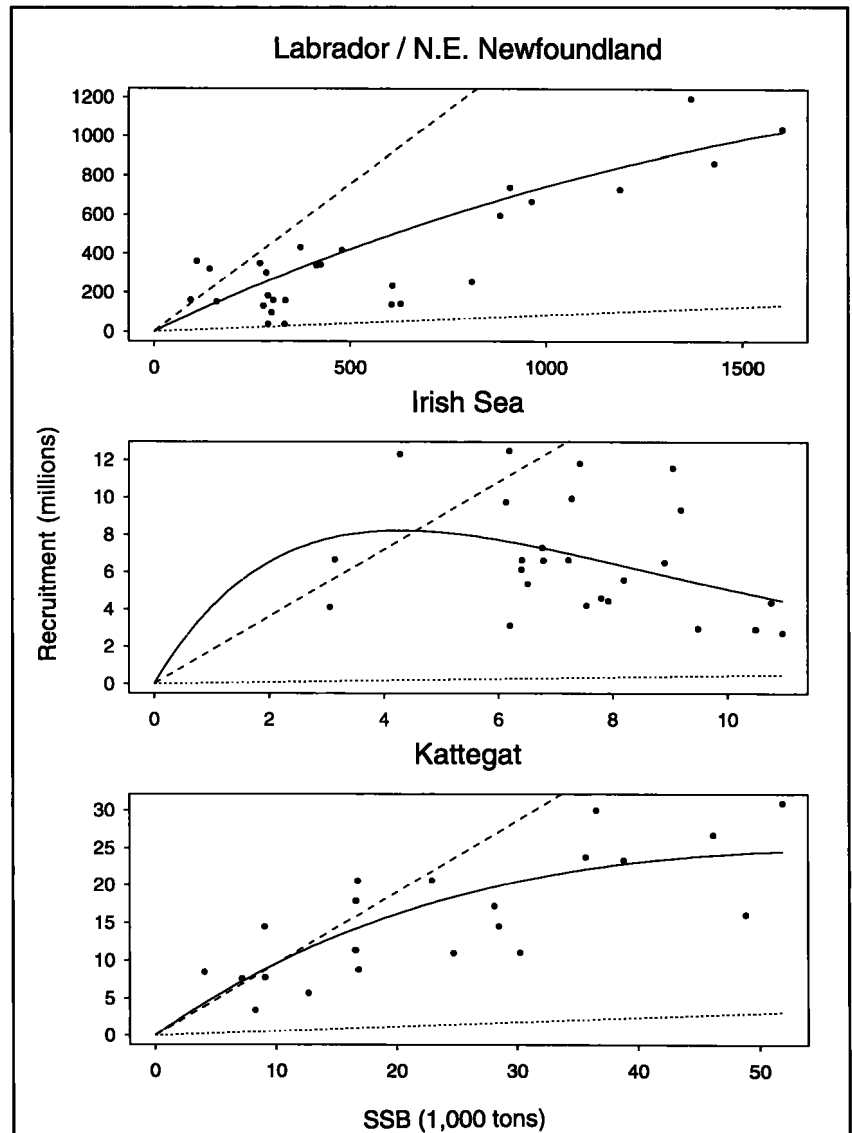

Figure 3

Recruitment versus spawning stock biomass (SSB) for the three representative cod populations. The solid line is the maximum likelihood estimate of the mean for Ricker spawner-recruitment functions under the assumption that the probability distribution for any SSB is given by a lognormal distribution. The dashed line is the median slope at the origin estimated from the six points with the lowest SSB. The straight dotted line is the replacement line with no fishing mortality.

among populations (Fig. 4). There is one population, Irish Sea, for which the $\tilde{\alpha}$ is much larger; we believe that this large $\tilde{\alpha}$ is an overestimate (this will be discussed later).

It is evident that r_m strongly covaries with temperature (Fig. 5; Table 2). It is also clear that this behavior does not arise from any dependence of $\tilde{\alpha}$ on temperature, because $\tilde{\alpha}$ is not correlated with temperature (Fig. 5; Table 2). There is a strong de-

Table 1

Estimates of rate of population growth (r_m), slope at the origin $(\tilde{\alpha})$ estimated from the Ricker model, age of maturity (a), bottom temperature, and NAFO/ICES management units for 20 cod populations in the North Atlantic.

ID no.	Stock location	NAFO/ICES management unit	r_m	$\tilde{\alpha}$	a	Temperature
1	West Greenland	1	0.23	2.4	6	1.75
2	Labrador/N.E. Newfoundland	2J3KL	0.17	2.3	7	0.00
3	S. Grand Bank	3NO	0.27	3.5	6	1.75
4	N. Gulf of St. Lawrence	3Pn4RS	0.20	3.0	7	1.00
5	St. Pierre Bank	3Ps	0.31	4.6	6	2.50
6	S. Gulf of St. Lawrence	4TVn	0.15	1.9	7	1.75
7	E. Scotian Shelf	4VsW	0.36	9.8	6	3.75
8	S.W. Scotian Shelf	4X	0.36	2.5	3.5	6.75
9	Georges Bank	5Z	0.60	2.2	2	8.00
10	S.E. Baltic	22–24	0.74	8.4	3	7.00
11	Central Baltic	25–32	0.53	3.1	3	5.00
12	Celtic Sea	VIIg,f	0.62	5.3	3	11.00
13	Faroe Plateau	Vb	0.44	4.2	4	7.40
14	Iceland	Va	0.24	4.3	7	5.80
15	Irish Sea	VIIa	1.03	23.1	3	10.00
16	Kattegat	South IIIa	0.53	3.8	3	6.50
17	Barents Sea	I	0.26	6.6	7.5	4.00
18	North Sea	IV	0.56	9.0	4	8.60
19	Skagerrak	North IIIa	0.82	11.2	3	6.50
20	West of Scotland	VIa	0.80	6.4	2.5	10.00

pendence of r_m on age-at-maturity, but there is no corresponding significant relation between $\tilde{\alpha}$ and age-at-maturity (Fig. 6). Consistency demands that there be a relation between age-at-maturity and temperature, and, indeed, Table 2 and Figure 7 show that there is a significant correlation between these two variables.

We repeated the above analysis with $\tilde{\alpha}$ calculated at the median slope of the six observations with the lowest spawner abundance. The estimates calculated with this robust procedure were generally comparable with those estimated from the Ricker model, although the Ricker values were generally higher (Fig. 8). The larger discrepancies in the two methods occurred for the populations in which there were low estimates of recruitment at the largest population sizes, e.g. Irish Sea cod (Fig. 3). These points, although they are farthest from the origin, resulted in a higher estimate of the slope at the origin because the Ricker model assumes a linear relation between egg-to-recruit mortality and SSB.

We repeated the regression analysis of rate of population growth and slope at the origin $(\tilde{\alpha})$ at minimum population size versus bottom temperature with the robust estimate of the slope, and found simi-

Table 2

For each of the three variables r_m (population growth rate), $\tilde{\alpha}$ (standardized slope of the spawner-recruit curve at the origin), and a (age-at-maturity), the estimated slope parameter of the regression on temperature (T) (e.g. $r_m = a + bT$) is presented, labeled b. For r_m and $\tilde{\alpha}$, there are two b values based respectively on the Ricker fit to each spawner-recruit data set and the median of the first six points of each spawner-recruit data set. Also shown are the significance levels of the regressions on temperature and the corresponding r^2. The results are presented for the Northwest, Northeast, and entire Atlantic.

Variable	Ricker b	Ricker $P(b=0)$	Ricker r^2	Median b	Median $P(b+0)$	Median r^2
r_m						
West	0.04	0.001	0.63	0.02	0.03	0.51
East	0.09	0.003	0.64	0.04	0.06	0.35
All	0.06	0.00008	0.59	0.04	0.00003	0.62
$\tilde{\alpha}$						
West	0.32	0.5	0.06	−0.16	0.3	0.15
East	0.83	0.2	0.16	0.09	0.7	0.02
All	0.67	0.04	0.21	0.13	0.2	0.08
a						
West	−0.62	0.00005	0.92	—	—	—
East	−0.45	0.06	0.34	—	—	—
All	−0.47	0.00002	0.65	—	—	—

lar results to those using the Ricker model (Table 2; Fig. 9). We conclude that our results are robust in relation to the method used to estimate $\tilde{\alpha}$.

Discussion

Perhaps remarkably, our study has revealed that the allometric (cross species) approximate inverse proportionality between r_m and age-at-maturity holds within the species Atlantic cod. Despite the much narrower range of r_m used in our single-species comparison (in contrast to the wide variation in r_m found in cross-species studies), the relation between r_m and age-at-maturity prevails over other influences. The expectation t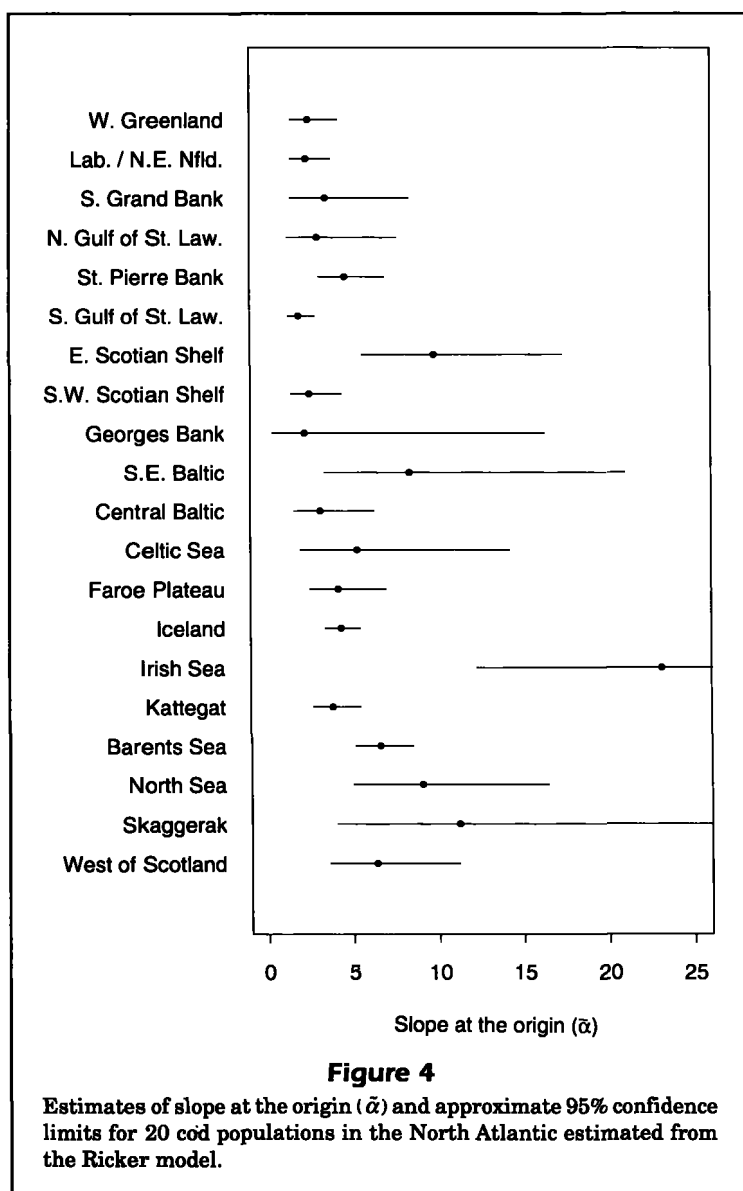hat cod populations at the northern and southern extremes of their range should show higher resilience (r_m), because of greater susceptibility to environmental change (Myers, 1991), is not realized.
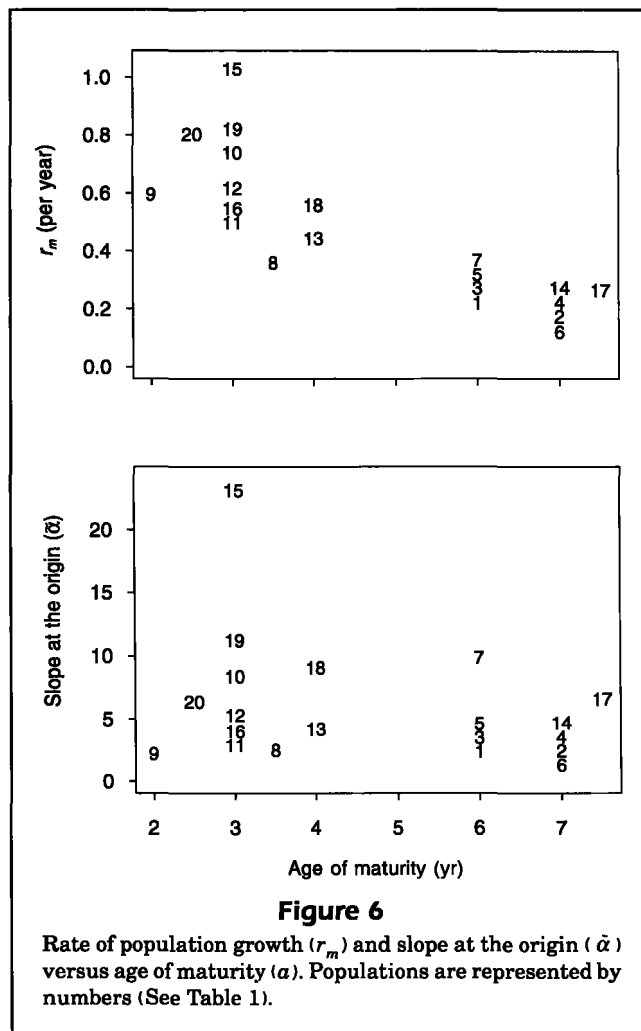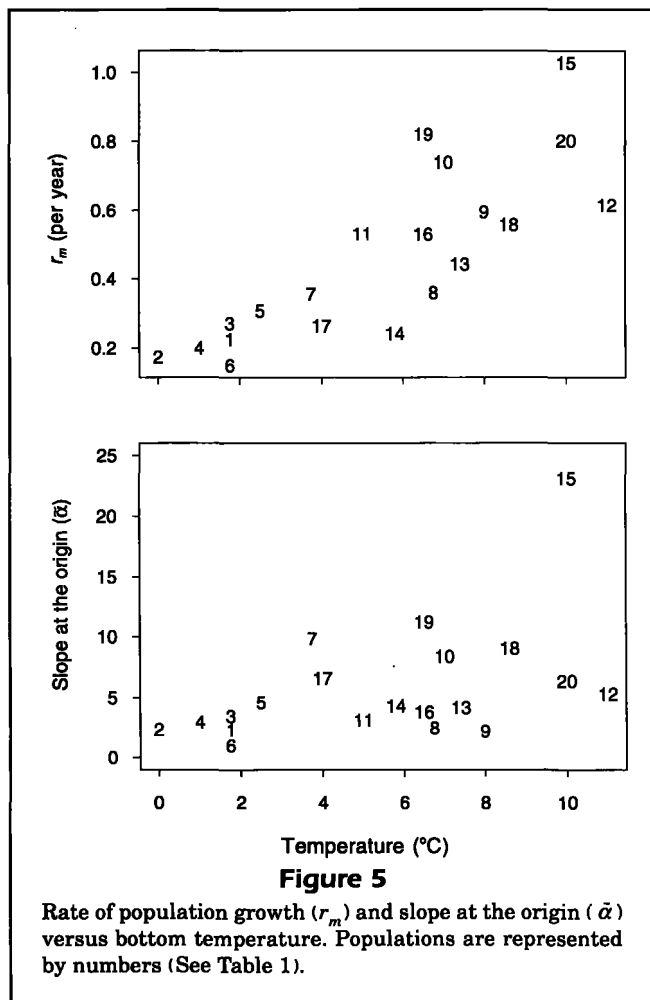
In a similar vein, Roff (1984) suggested that early maturity in fish species may arise through r-selection (in response to extreme environmental variability); our findings show that age-at-maturity appears to be chiefly explained by ambient temperature.

Although we have found a clear relation between r_m and temperature, this was not necessarily expected a priori because mortality is positively related to temperature in comparative studies (Pauly, 1980). That temperature dependent (egg to adult) mortality can offset the effect of temperature-dependent growth is emphasized by the temperature independence of $\tilde{\alpha}$. More specifically, $\tilde{\alpha}$ depends on both fecundity and mortality. Fecundity, being growth dependent (Roff, 1984) increases with temperature; however, mortality also increases with temperature and counteracts the influence of temperature-dependent growth, leaving $\tilde{\alpha}$ temperature independent. (Note that many empirical studies of life histories of fish have found that somatic growth rate and survival covary [Beverton and Holt, 1959; Pauly, 1980; Myers and Doyle, 1983; Hutchings, 1993]).

The relation between r_m and temperature is presumably a metabolic effect, in that fish growth is strongly influenced by temperature (Taylor, 1958; Pauly, 1980), and implies that a fish in a warm environment will reach the required size for maturity at an early age, which tends to increase r_m. Although Birch (1948) has noted, for insect populations, that higher r_m values do not necessarily correspond to higher temperatures, investigators such as Hennemann (1983) and McNab (1980) have suggested that r_m should be closely related to metabolic rate, which is closely linked to temperature. Certainly our presentation corroborates this proposed parallel between metabolism and r_m.

The importance of the determination of r_m has long been known (Lewontin, 1965); however, it is certainly not always the case that age-at-maturity is the dominant factor. For species for which the production of replacement adults at low population density, $\tilde{\alpha}$, is relatively low (e.g. for many mammals and birds), then changes in $\tilde{\alpha}$ or adult survival will have large effects on r_m (Fig. 1). However, for cod, and perhaps many fish, $\tilde{\alpha}$ is relatively large (e.g. around 4). In this case, the effects of reasonable changes in adult

Figure 4

Estimates of slope at the origin ($\tilde{\alpha}$) and approximate 95% confidence limits for 20 cod populations in the North Atlantic estimated from the Ricker model.

Figure 5

Rate of population growth (r_m) and slope at the origin $(\tilde{\alpha})$ versus bottom temperature. Populations are represented by numbers (See Table 1).

Figure 6

Rate of population growth (r_m) and slope at the origin $(\tilde{\alpha})$ versus age of maturity (a). Populations are represented by numbers (See Table 1).

survival (between 0.7 to 0.9) or $\tilde{\alpha}$ have a relatively small effect compared with age-at-maturity (Fig. 1).
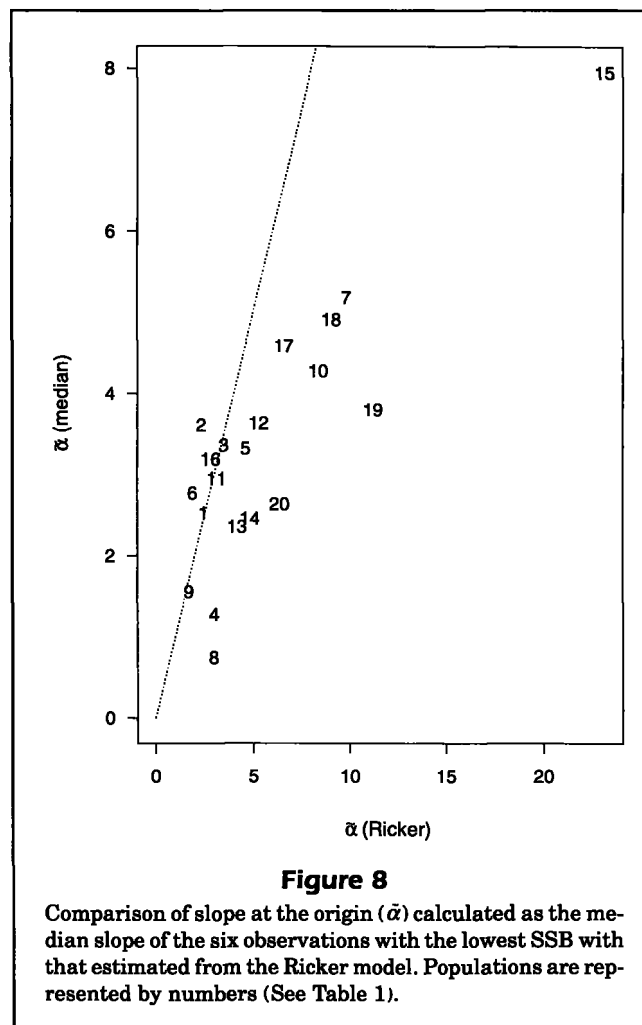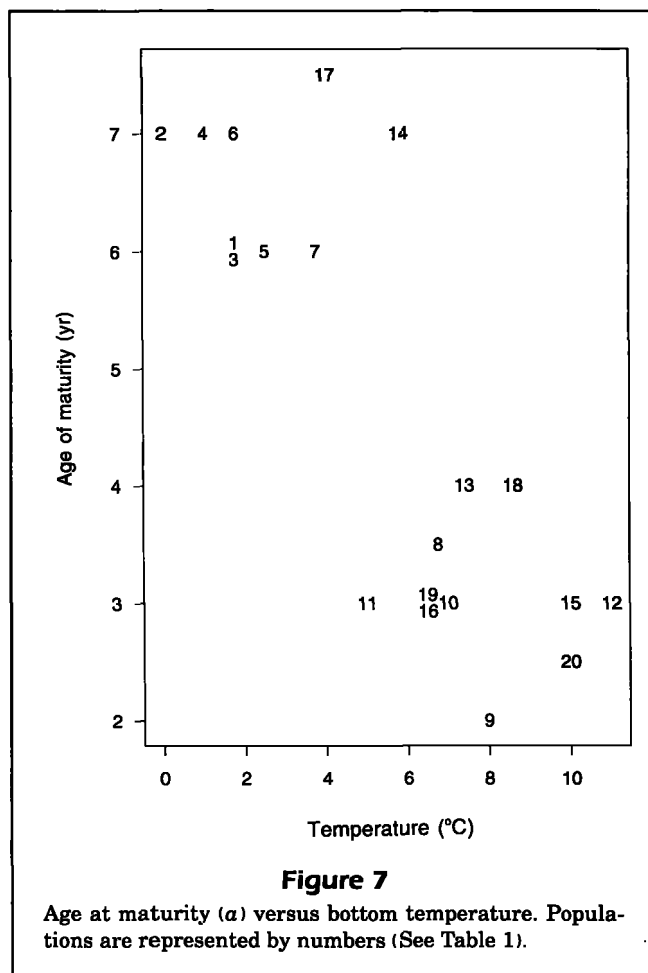
Our study has presented robust estimates (see Fig. 8) of r_m for a variety of Atlantic cod populations, thus establishing recovery times for overfished populations relieved from fishing pressure. At colder temperatures, r_m is around 18% a year for all populations, independent of how we calculate r_m.

A major source of uncertainty in the SPA estimates of recruitment and SSB used in our analysis is that catches are assumed to be known without error. This assumption is particularly important when estimates of discarding and misreporting are not included in the catch-at-age data used in the SPA.These errors are clearly important for some periods of time for some of the cod stocks (Myers et al., 1997), and these errors will affect our estimates of the number of replacements each spawner can produce at low population densities ($\tilde{\alpha}$). However, we have shown that the estimates of r_m are not very sensitive to reasonable changes in this parameter.

We have carried our estimation of the model parameters separately for each stock. An alternative approach is to analyze simultaneously all stocks in models that include separate estimation error for each stock and a parameter describing the variation among stocks. Myers et al.[1] carried out such an analysis using variance components models for the data analyzed in this study and found that the optimal estimates of the variation in $\tilde{\alpha}$ was much less than that estimated, e.g. the very high estimate for Irish Sea cod was found to be overestimated.

The parameters estimated in this study have management implications that go beyond the estimation of population growth rate. In particular, the number of replacements each spawner can produce at low population densities ($\tilde{\alpha}$), is critical for determining

[1] Myers, R., G. Mertz, and N. Barrowman. 1996. Invariants of spawner-recruitment relationships for marine, anadromous, and freshwater species. ICES Council Meeting 1996 /D:11, 17 p.

Figure 7

Age at maturity (a) versus bottom temperature. Populations are represented by numbers (See Table 1).

Figure 8

Comparison of slope at the origin ($\tilde{\alpha}$) calculated as the median slope of the six observations with the lowest SSB with that estimated from the Ricker model. Populations are represented by numbers (See Table 1).
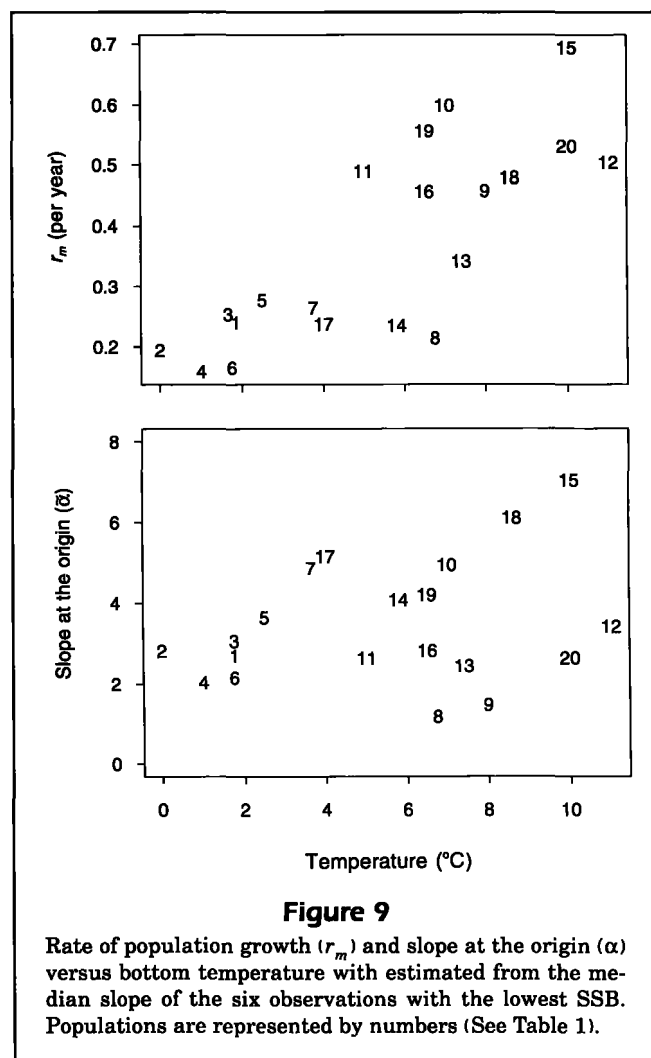
the limits of exploitation (Cook et al., 1997; Myers and Mertz, in press). A comparative approach, such as the one used here, should help refine our understanding of the rational exploitation of fisheries.

We have used as simple a model as possible to estimate r_m. This has the very great advantage that the we can compare the crucial demographic parameters (i.e. the replacements each spawner can produce at low population densities ($\tilde{\alpha}$), age-at-maturity (a), and adult survival (p_s) among populations) and can easily study the sensitivity of r_m to errors in each of these parameters (Fig. 1). Furthermore, Hutchings and Myers (1994) found similar estimates of r_m when they used a fully age-structured model for "northern" cod, i.e. cod in NAFO Division 2J3KL.

Previous estimates of the recovery time for depleted cod stocks that have not included a detailed analysis of population growth rate have yielded widely different results. For example, it was initially projected that northern cod would recover close to historic levels of spawning biomass after a two-year fishing moratorium (Lear and Parsons, 1993). This projection has since been shown to be incorrect

(Myers et al., 1996; Hutchings et al., 1997). Roughgarden and Smith (1996) estimated r_m for northern cod to be ≈1 by simply taking the greatest difference between adjacent estimates of total population abundance from annual research vessel surveys. That is, they assumed that any change in the estimates represented an increase in population abundance.

However, this change in estimated abundance was almost entirely estimation error (Myers and Cadigan 1995, a and b) and had nothing to do with an increase in abundance. At present (March 1997) there are six Canadian cod populations (2 to 7 in Table 1) that are currently protected by a fishing moratorium because the populations have been greatly reduced by overfishing (Myers et al., 1997). Unfortunately, our results indicate that recovery could require a long period. Under average environmental conditions, our results suggest a doubling time of about 4 years. Given the severe depletion of these populations (some are less than 5% of their maximum observed levels (Myers et al., 1996) recovery to

Figure 9

Rate of population growth (r_m) and slope at the origin (α) versus bottom temperature with estimated from the median slope of the six observations with the lowest SSB. Populations are represented by numbers (See Table 1).

desired levels of spawning biomass should not be expected for at least a decade of minimal mortality caused be fishing.

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