

Northwest Atlantic



Fisheries Organization

Serial No. N2715

NAFO SCR Doc. 96/40

SCIENTIFIC COUNCIL MEETING - JUNE 1996

The Population Growth Rate of Atlantic Cod (*Gadus Morhua*) at Low Abundance

by

R. A. Myers and G. Mertz

Science Branch, Department of Fisheries and Oceans
P. O. Box 5667, St. John's, Newfoundland, Canada A1C 5X1

and

P. S. Fowlow

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

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 ($\bar{\alpha}$). It is shown that $\bar{\alpha}$ is not temperature dependent, 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 stocks.

Key Words: Atlantic cod, *Gadus morhua*, population growth rate, spawner, temperature, stock, recruitment, resilience, mortality, age of maturity.

Key Phrases: intrinsic rate of natural increase (r_m), population growth rate versus age of maturity, temperature, and net reproductive rate.

Introduction

Perhaps the most fundamental of all ecological parameters is the intrinsic rate of natural increase, r_m , (Cole 1954). High r_m will be selected for in populations which experience frequent excursions to low density (e.g., Charlesworth 1980). Populations subjected to strong environmental variability should evolve toward high r_m (MacArthur and Wilson 1967), which will impart resilience to the population. However, cross species, allometric, 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 will carry out such an examination for 20 stocks of Atlantic cod (*Gadus morhua*).

Atlantic cod lends itself to a study of this nature since in that there is a wealth of good quality biological data collected for stock management purposes. Moreover, these cod stocks occupy a broad span of latitudes, including regions which 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 northern 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 recently collapsed Atlantic cod stocks (Hutchings and Myers 1994).

Methods and data

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 will be presented immediately following a brief discussion of the standard stock-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 of assuming the number of eggs produced is proportional to the biomass of spawners. The Ricker model has the form

$$E(N_{t+j,j}) = \alpha S_t e^{-\beta S_t}, \quad (1)$$

where α is the slope at the origin (measured perhaps in recruits per kilogram of spawners). Density-dependent mortality is assumed to be the product of β times the recruitment. The parameters were fit using maximum likelihood estimation assuming lognormal variability (Hilborn and Walters 1992, Myers et al. 1995).

The *standardized* initial slope, $\tilde{\alpha}$, is obtained by scaling the initial slope α by $SPR_{F=0}$, i.e.

$$\tilde{\alpha} = \alpha \cdot SPR_{F=0} \quad (2)$$

where $SPR_{F=0}$ is the spawning biomass resulting from each recruit in the limit of no fishing mortality ($F = 0$). This quantity $\tilde{\alpha}$ may be interpreted as follows: at low population density each spawner will produce $\tilde{\alpha}$ spawners a years later, where a is the age at maturity. If the annual survival fraction for spawners (p_s) was zero, the population of spawners, N_t , would obey the following equation:

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

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

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

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

Overlapping generations

The overlapping generations case is conveniently treated by solving for r_m in the Euler-Lotka equation,

$$\sum_t l_t m_t e^{r_m t} = 1 \quad (5)$$

where l_t is the fraction of animals surviving to age t and m_t is the number of offspring per animal produced at age t . We now specify that $m_t = m_0$

for fish of age a and older, and also, for $t \geq a$, $l_t = l_j p_s^{t-a}$, where l_j 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 (5) that

$$l_j m_0 \sum_{t=a}^{t=\infty} p_s^{t-a} e^{-r_m t} = 1 \quad (6)$$

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

$$\frac{l_j m_0 e^{-r_m a}}{1 - p_s e^{-r_m}} = 1 \quad (7)$$

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

$$(e^{r_m})^a - p_s (e^{r_m})^{a-1} - \bar{\alpha} = 0 \quad (8)$$

We have bracketed the e^{r_m} term to emphasize that (8) is a simple algebraic equation for $\chi = e^{r_m}$. Note that in the limit $p_s = 0$, we recover (4) from (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 (1995).

It is clear for a moderately large slope at the origin ($\bar{\alpha}$) that the age of maturity (a) is the most important factor in determining r_m (Fig. 1). The survival after reproduction (p_s) has only a minor effect on r_m except when $\bar{\alpha}$ is close to one, and over much of the range of $\bar{\alpha}$, equation (4) (which is valid for $p_s = 0$) provides a good approximation to the true r_m . The r_m values used will be calculated from (8) using the fisheries data described in the next subsection.

Fig. 1 near here

Data sources and treatment

The data we used are estimates obtained from assessments compiled by Myers et al. (1995). Population numbers and fishing mortality were estimated using sequential population analysis (SPA) of commercial catch at age data for most marine stocks. SPA techniques include virtual population analysis (VPA; Gulland 1965), cohort analysis (Pope 1972); and related methods which reconstruct population size from catch at age data (Hilborn and Walters (1992). See Hilborn and Walters (1992, chapters 10 and 11) for a 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 the 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 stock 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 stock 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 stocks 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 stock (NAFO 3M) or the English Channel stock (ICES VIIId) and the 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 1995).

Fig. 2 near here

The Ricker model was fit using a transformation recommended by Hilborn and Walters (1992): $\log(N_{t+j}/S_t) = \log \bar{\alpha} - \beta S_t + \epsilon$, where ϵ is normally distributed with mean zero and variance σ^2 . The estimate of $\bar{\alpha}$ from the above equation is $\exp(\log \bar{\alpha} + \frac{1}{2}\sigma^2)$, $\frac{1}{2}\sigma^2$ is a bias correction term that occurs because the nonlinear transformation that was used after estimation (Cox and Hinkley 1974). Another source of bias is caused by the non-independence

of spawners and recruitment, i.e., large recruitment usually leads to large spawner abundance (Walters 1985); however, this bias is relatively small in the estimates for cod stocks (Myers and Barrowman 1995).

The disadvantage of using the Ricker model, or any other stock 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 using only the 6 observations with the lowest spawner biomass, forcing the regression line through the origin. This simple procedure should be reasonable because all the stocks have been reduced to very low levels.

Bottom temperature was estimated by Brander (1994) for all the stocks except the Baltic stocks. We used data in Dickson et al. (1992) to make estimates for the Baltic stocks. 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.

Results

The Ricker model estimates of the slope at the origin and the population growth rate was estimated for the 20 spawner recruit data sets (Table 1, Fig. 3). The slope at the origin, $\hat{\alpha}$, did not vary enormously among populations (Fig. 4). There is one stock, Irish Sea, for which the $\hat{\alpha}$ is much larger; we believe that this large $\hat{\alpha}$ is not real and is caused by errors in the data.

Table 1 near here
Fig. 3 near here
Fig. 4 near here
Table 2 near here
Fig. 5 near here

It is evident from Fig. 5 and Table 2 that r_m strongly covaries with temperature. It is clear from Fig. 5 and Table 2 that this behavior does not arise from any dependence of $\hat{\alpha}$ on temperature, since $\hat{\alpha}$ is not correlated with temperature. Table 2 and Fig. 6 reveal a strong dependence of r_m on age at maturity; there is no corresponding significant relationship between $\hat{\alpha}$ and age at maturity. Consistency demands that there be a relationship between age at maturity and temperature, and indeed, Table 2 and Fig. 7 show that there is a significant correlation between these two variables. Since equation (4) (which is an adequate approximation) specifies an inverse relationship between r_m and a , it is reasonable to assert that the temperature dependence of a drives the temperature dependence of r_m .

Fig. 6 near here
Fig. 7 near here

We repeated the above analysis using $\hat{\alpha}$ calculated at the median slope of the 6 observations with the lowest spawner abundance. The estimates calculated using this robust procedure were generally comparable with those estimated from the Ricker model, though 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 stock 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 relationship between egg to recruit mortality and SSB.

Fig. 8 near here

We repeated the regression analysis of rate of population growth and slope at the origin ($\hat{\alpha}$) at minimum population size versus bottom temperature using the robust estimate of the slope, and found similar results to those using the Ricker model (Table 2, Fig. 9). We conclude that our results are robust to the method used to estimate $\hat{\alpha}$.

Fig. 9 near here

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 for the single species comparison, the relation between r_m and age at maturity prevails over other influences. The expectation that cod stocks 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 determined by ambient temperature.

Although we have found a clear relationship between r_m and temperature, this was not necessarily expected *a priori* because mortality is also strongly influenced by temperature (Pauly 1980). That temperature dependent (egg to adult) mortality can offset the effect of temperature dependent growth is emphasized by the temperature independence of $\bar{\alpha}$. More specifically, $\bar{\alpha}$ 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 $\bar{\alpha}$ temperature independent. (Note that many empirical studies of life-histories of fish have found that growth rate and survival covary; e.g., 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 (Pauly 1980, Taylor 1958), implying 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 Henne-mann (1983) and McNab (1980) have suggested that r_m should be closely related to metabolic rate, establishing a link with 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 where age at maturity is the dominant factor. For species for which the production of replacement adults at low population density, $\bar{\alpha}$, is relatively low, e.g. many mammals and birds, then changes in $\bar{\alpha}$ or adult survival will have large effects on r_m (Fig. 1). However, for cod, and perhaps many fish, $\bar{\alpha}$ is relatively large, e.g., around 15. In this case, the effects of changes in adult survival or $\bar{\alpha}$ have a relatively small effect compared to age at maturity (Fig. 1).

Our study has presented robust estimates (see Fig. 8) of r_m for a variety of Atlantic cod stocks, thus establishing recovery times for overfished stocks relieved from fishing pressure. The rapid rebound of Barents Sea cod (circa two years; Jakobsen 1994) after a stock collapse is consistent with our results. For the Labrador/N.E. Newfoundland cod stock, currently protected by a fishing moratorium, recovery could require a long period, given the doubling time of about two years and the severe depletion (compared to the Barents Sea) of the spawning stock (Hutchings and Myers 1994).

Acknowledgments

We thank the Northern Cod Science program for financial assistance. We thank J. Hutchings, J. Morgan, and S. Walde for helpful suggestions, and Nick Barrowman for programming.

References

- Beverton, R.J.H., and S.J. Holt. 1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. Pages 142-174 in G.E.W. Wolstenholme and M. O'Connor, editors. CIBA Foundation Colloquia on Ageing 5.
- Birch, L.C. 1948. The intrinsic rate of increase of an insect populations. *Journal of Animal Ecology* 17:15-26.
- Brander, K. 1994. Patterns of distribution, spawning, and growth in North Atlantic cod: the utility of inter-regional comparisons. *International Council for the Exploration of the Sea Marine Science Symposia* 198: 406-413.

- Charlesworth, B. 1980. Evolution in age-structured populations. Cambridge University Press, Cambridge.
- Charnov, E.L. 1993. Life history invariants: some explorations of symmetry in evolutionary ecology. Oxford University Press, Oxford.
- Clark, C.W. 1976. A delayed-recruitment model of population dynamics, with an application to baleen whale populations, *Journal of Mathematical Biology* 3:381-391.
- Cole, L.C. 1954. The population consequences of life history phenomena. *Quarterly Review of Biology* 29:103-137.
- Cox, D.R., and D.V. Hinkley. 1974. Theoretical statistics. Chapman and Hall, London.
- deYoung, B., F. Perry, and R. Greatbach. 1994. Objective analysis of hydrographic data in the Northwest Atlantic. Canadian Data Report of Hydrography and Ocean Sciences 130:v + 1-93.
- Dickson, R.R., P. Mälkki, G. Radach, R. Sætre, and M.P. Sissenwine. 1992. Hydrobiological variability in the ICES area, 1980-1989. International Council for the Exploration of the Sea, Marine Science Symposia 195
- Fenchel, T. 1974. Intrinsic rate of natural increase: the relationship with body size. *Oecologia* 14: 317-326.
- Goodman, D. 1984. Statistics of reproductive rate estimates, and their implications for population projection. Reports of the International Whaling Commission Special Issue 6:161-173.
- Gulland, J.A. 1965. Estimation of mortality rates. Annex to Rep. Arctic Fish. Working Group, ICES C.M. 3: 1-9.
- Hennemann, W.W. 1983. Relationship among body mass, metabolic rate and the intrinsic rate of natural increase in mammals. *Oecologia* 56:104-108.
- Hilborn, R., and C.J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York.
- Hutchings, J.A. 1993. Adaptive life histories effected by age-specific survival and growth rate. *Ecology* 74:673-684.
- Hutchings, J.A., and R.A. Myers. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Canadian Journal of Fisheries and Aquatic Sciences*, 51:2126-2146.
- Jakobsen, T. 1994. Management of the northeast Arctic cod - past, present, and future. Pages 321-338 in G. Kruse, D.M. Eggers, R.J. Marasco, C. Pautzke, T.J. Quinn, editors. International symposium of management strategies for exploited fish populations. Alaska Sea Grant College Program.
- Lewontin, R.C. 1965. Selection for colonizing ability. Pages 77-91 in H.G. Baker and G.L. Stebbins, editors. The genetics of colonizing species. Academic Press, New York.
- MacArthur, R.H., and E.O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton.
- McNab, B.K. 1980. Food habits, energetics, and the population biology of mammals. *American Naturalist* 116:106-124.
- Mertz, G. and R.A. Myers. 1995. An augmented Clark model for stability of populations. *Mathematical Biosciences* in press.

- Myers, R.A. 1991. Recruitment variability and range of three fish species. Northwest Atlantic Fisheries Organization Scientific Council Studies 16:21-24.
- Myers, R. A., and N. J. Barrowman. 1995. Time series bias in the estimation of density-dependent mortality in stock-recruitment models. Canadian Technical Report of Fisheries and Aquatic Sciences in press.
- Myers, R.A., J. Bridson, N.J. Barrowman. 1995. Summary of worldwide stock and recruitment data. Canadian Technical Report of Fisheries and Aquatic Sciences 2024:iv + 327.
- Myers, R.A., and R.W. Doyle. 1983. Predicting natural mortality rates and reproduction-mortality trade-offs from fish life history data. Canadian Journal of Fisheries and Aquatic Science 40:612-620.
- Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. Journal du Conseil International pour L'Exploration de la Mer 39: 175-193.
- Pope, J.G. 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. International Commission for the Northwest Atlantic Fisheries Research Bulletin 9:65-74.
- Ricker, W.E. 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada 11:559-623.
- Roff, D.A. 1984. The evolution of life history parameters in teleosts. Canadian Journal of Fisheries and Aquatic Sciences 41:989-1000.
- Royama, T. 1993. Analytical population dynamics. Chapman and Hall, London.
- Taylor, C.C. 1958. Cod growth and temperature. Journal du Conseil, Conseil Permanent International Pour L'Exploration de la Mer 23:366-370.
- Walters, C. J. 1985. Bias in the estimation of function relationships from time series data. Canadian Technical Report of Fisheries and Aquatic Sciences 42: 147-149.

TABLE 1. Estimates of rate of population growth (r_m), slope at the origin ($\tilde{\alpha}$) at minimum population size 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	Stock	NAFO/ICES	r_m	$\tilde{\alpha}$	a	temp
1	West Greenland	1	0.44	12	6	1.75
2	Labrador/N.E. Nfld.	2J3KL	0.36	12	7	0.00
3	S. Grand Bank	3NO	0.49	17	6	1.75
4	N. Gulf of St. Lawrence	3Pn4RS	0.39	15	7	1.00
5	St. Pierre Bank	3Ps	0.53	23	6	2.50
6	S. Gulf of St. Lawrence	4TVn	0.33	9	7	1.75
7	E. Scotian Shelf	4VsW	0.58	49	6	3.75
8	S.W. Scotian Shelf	4X	0.72	12	3.5	6.75
9	Georges Bank	5Z	1.24	11	2	8.00
10	S.E. Baltic	22-24	1.20	42	3	7.00
11	Central Baltic	25-32	0.97	16	3	5.00
12	Celtic Sea	VIIg,f	1.07	26	3	11.00
13	Faroe Plateau	Vb	0.78	21	4	7.40
14	Iceland	Va	0.43	22	7	5.80
15	Irish Sea	VIIb,c,h-k	1.52	116	3	10.00
16	Kattegat	south IIIa	0.97	19	3	6.50
17	Barents Sea	I	0.44	33	7.5	4.00
18	North Sea	IV	0.90	45	4	8.60
19	Skagerrak	north IIIa	1.29	56	3	6.50
20	West of Scotland	VIa	1.36	32	2.5	10.00

TABLE 2. For each of the three variables r_m (population growth rate), $\tilde{\alpha}$ (slope of the stock-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 \hat{b} . For r_m and $\tilde{\alpha}$ there are two b values based respectively on the Ricker fit to each stock-recruit data set and the median of the first six points of each stock-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.

	Ricker \hat{b}	Ricker $P(b=0)$	Ricker R^2	Median \hat{b}	Median $P(b=0)$	Median R^2
r_m						
West	0.07	0.002	0.78	0.07	0.005	0.70
East	0.15	0.003	0.64	0.07	0.05	0.36
All	0.09	0.00009	0.58	0.07	0.00001	0.67
$\tilde{\alpha}$						
West	1.58	0.5	0.06	-0.82	0.3	0.15
East	4.15	0.2	0.16	0.45	0.7	0.02
All	3.33	0.04	0.21	0.67	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			

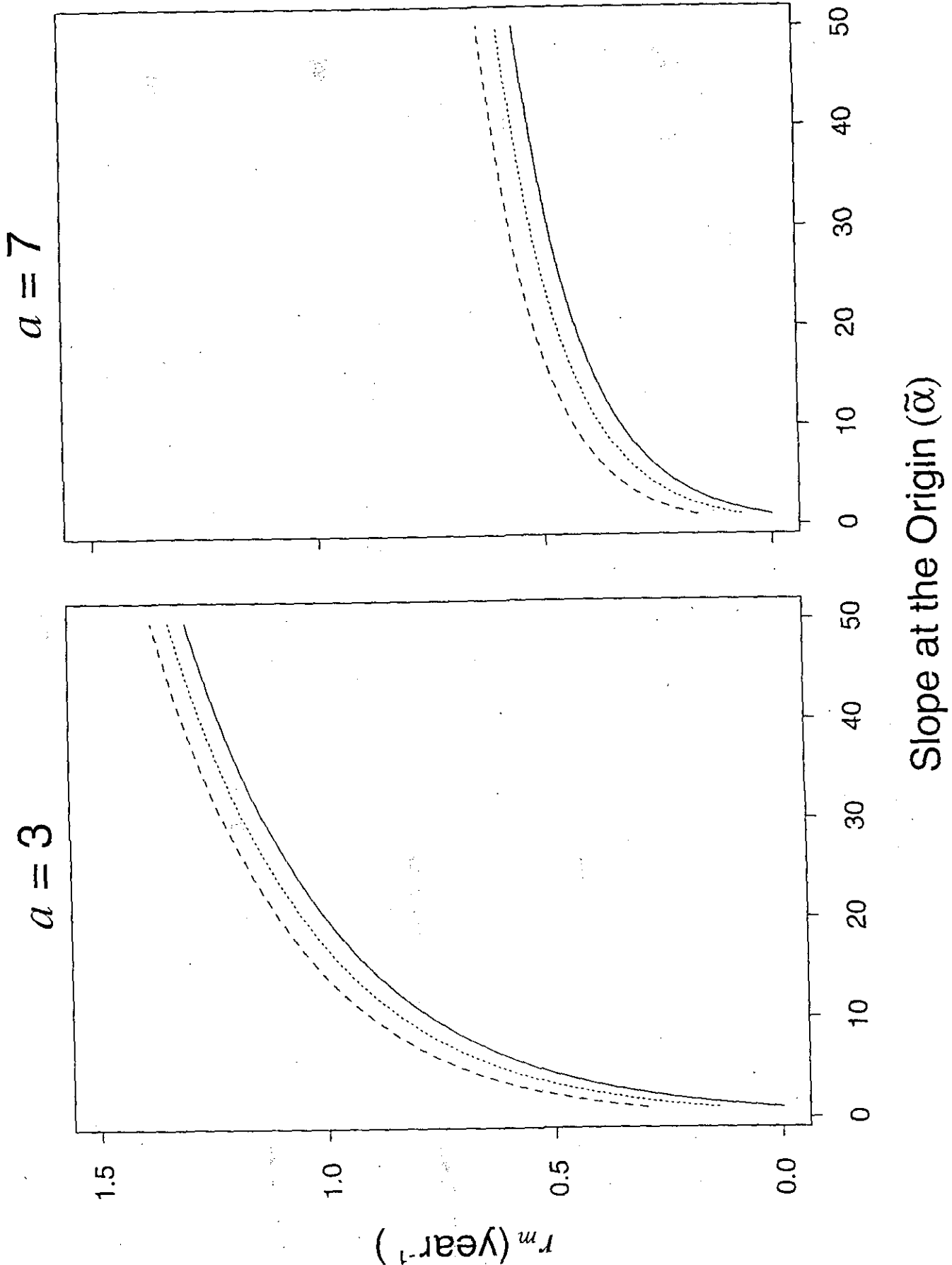


Fig. 1. Rate of population growth (r_m) as a function of slope at the origin ($\tilde{\alpha}$) at minimum population size, age of maturity (a), and adult survival rates $p_s = 0$ (solid line), $p_s = 0.4$ (dotted line) and $p_s = 0.8$ (dashed line).

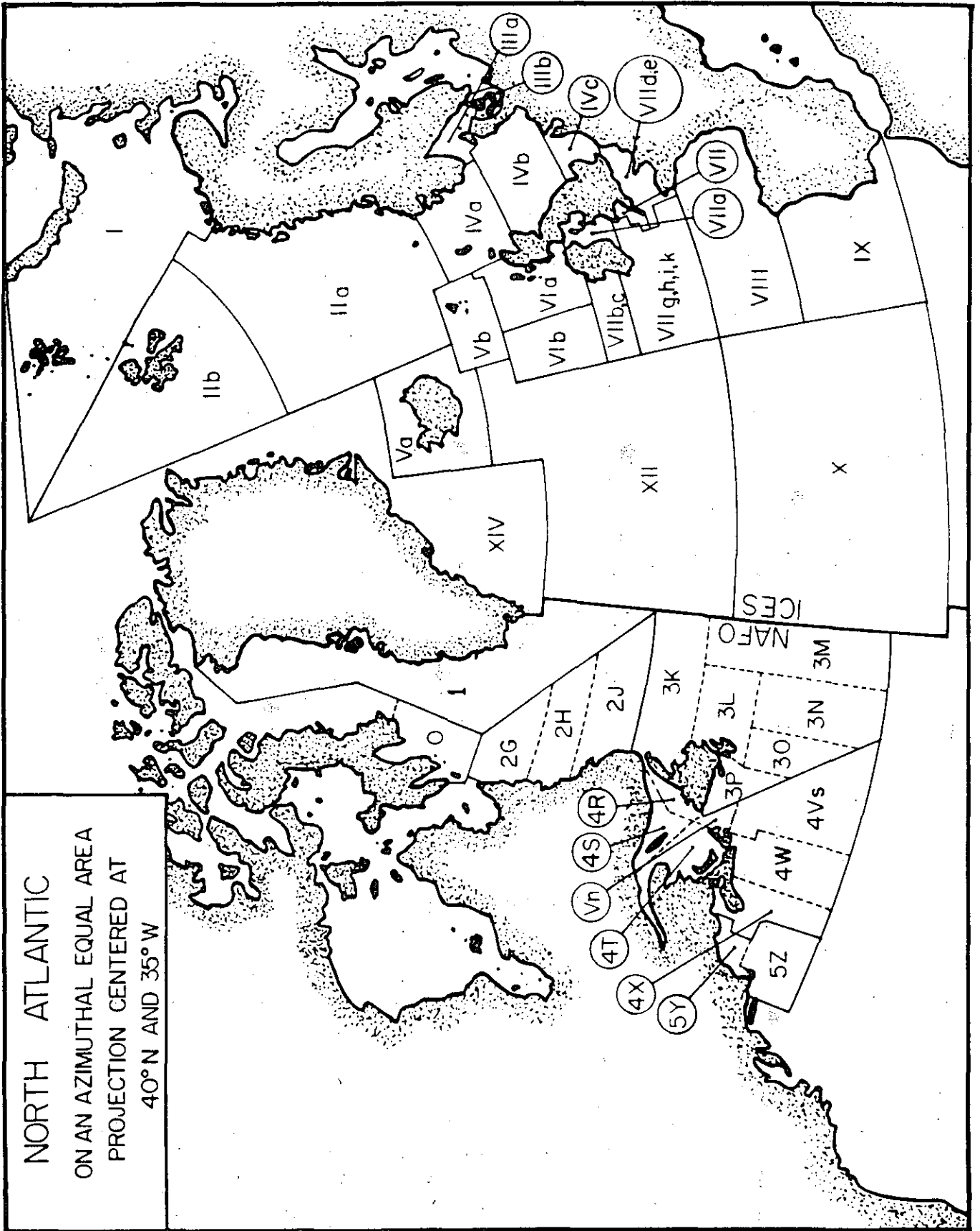
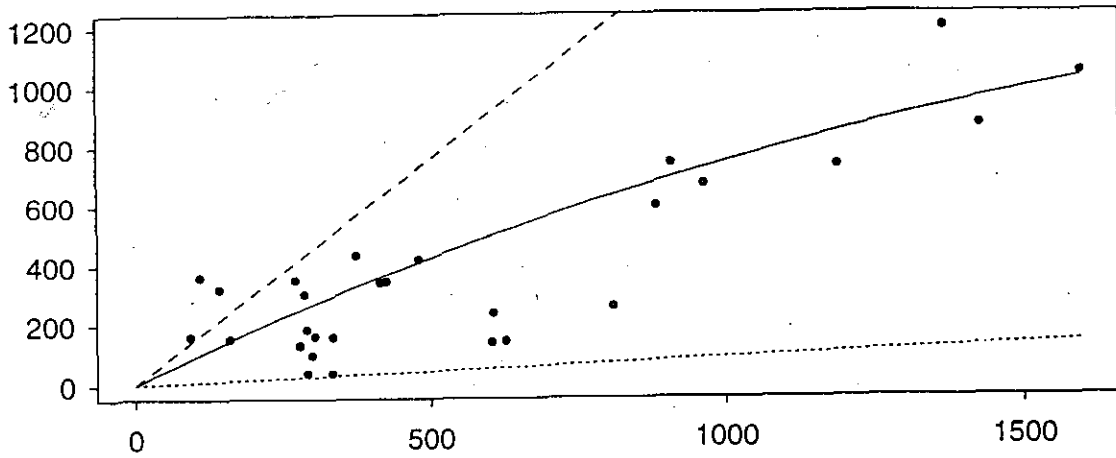


Fig. 2

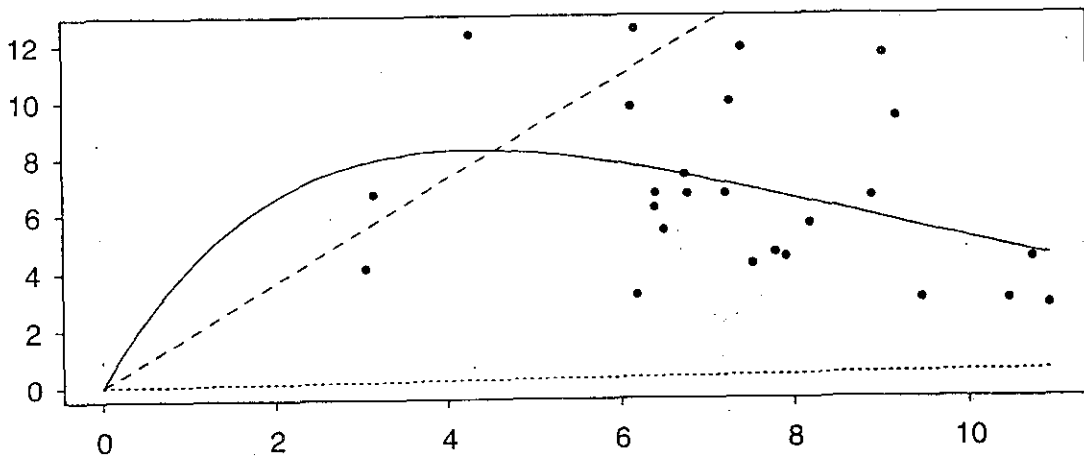
Fig. 2. Map of the North Atlantic showing the regions used to define populations for management.

Labrador / N.E. Newfoundland

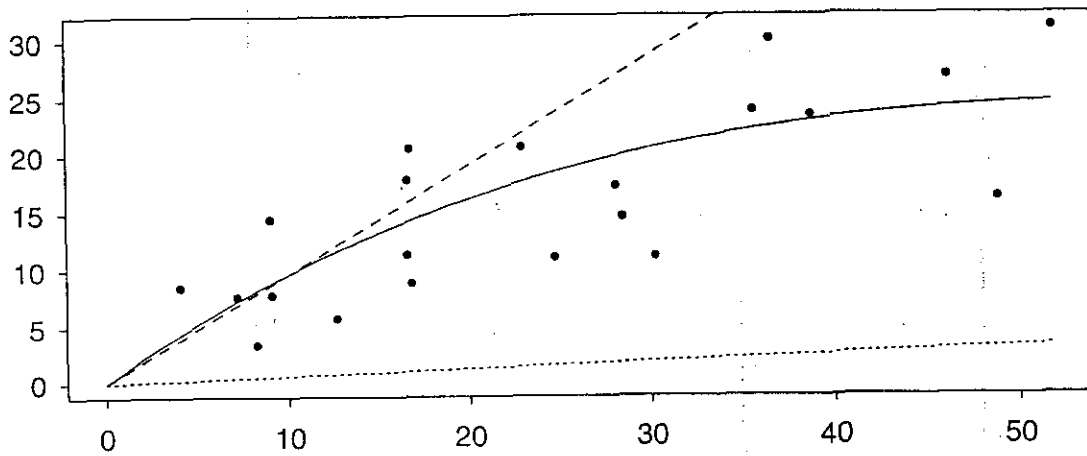


Irish Sea

Recruitment (millions)



Kattegat



SSB (thousand tonnes)

Fig. 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 6 points with the lowest SSB. The straight dotted line is the replacement line.

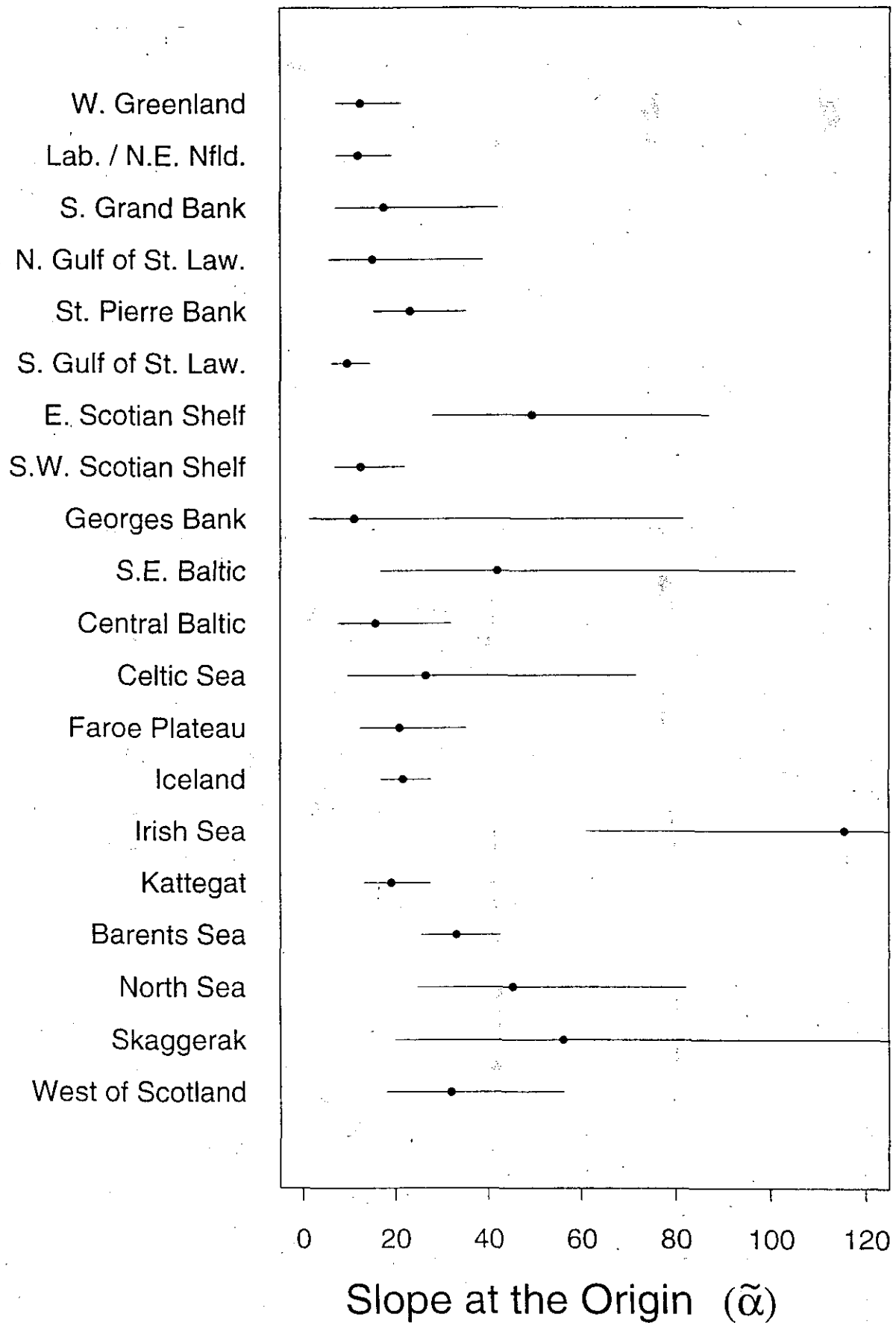


Fig. 4. Estimates of slope at the origin ($\hat{\alpha}$) at minimum population size and approximate 95% confidence limits for 20 cod populations in the North Atlantic estimated from the Ricker model.

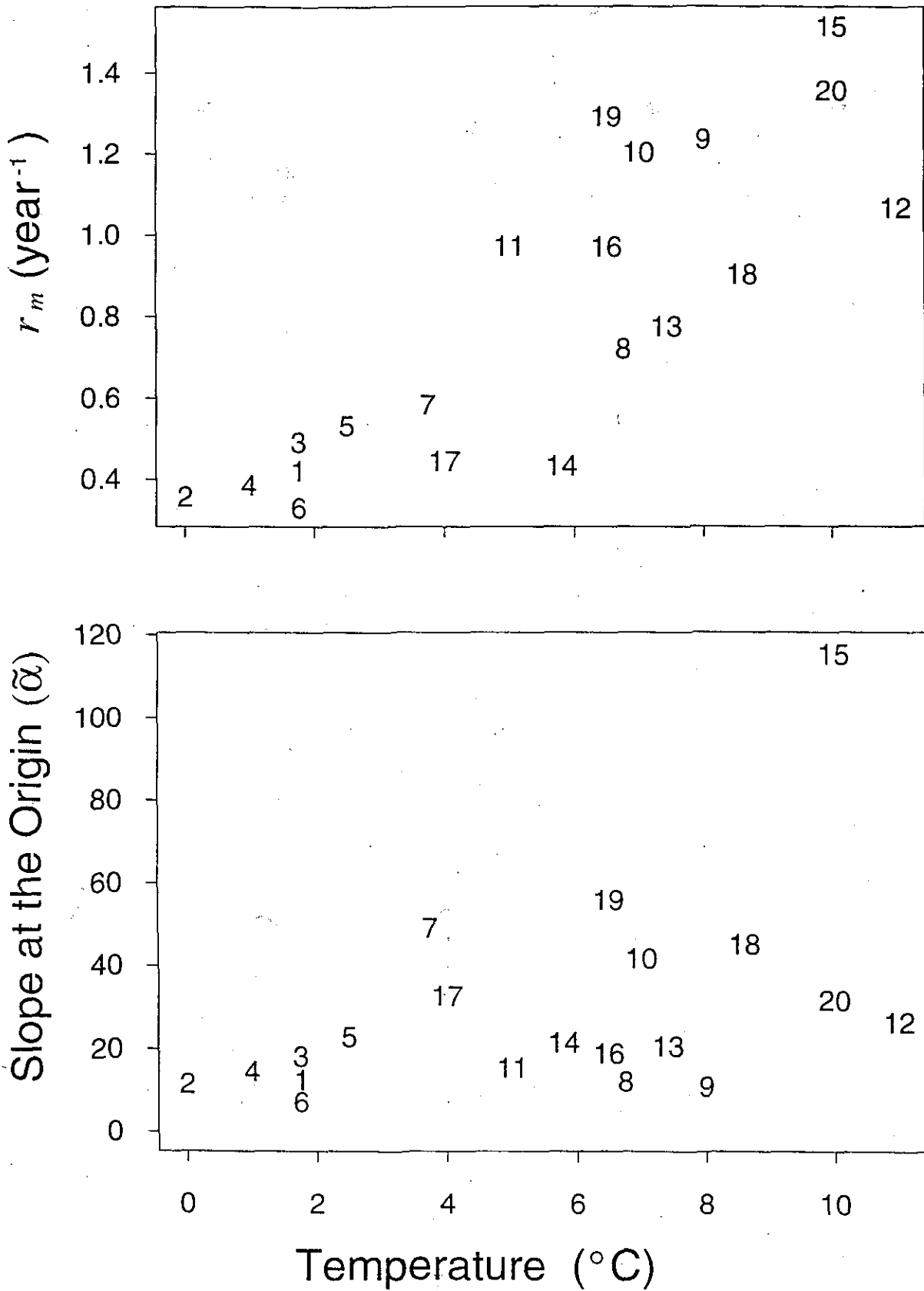


Fig. -5. Rate of population growth (r_m) and slope at the origin ($\tilde{\alpha}$) at minimum population size versus bottom temperature. Populations are represented by numbers (See Table 1).

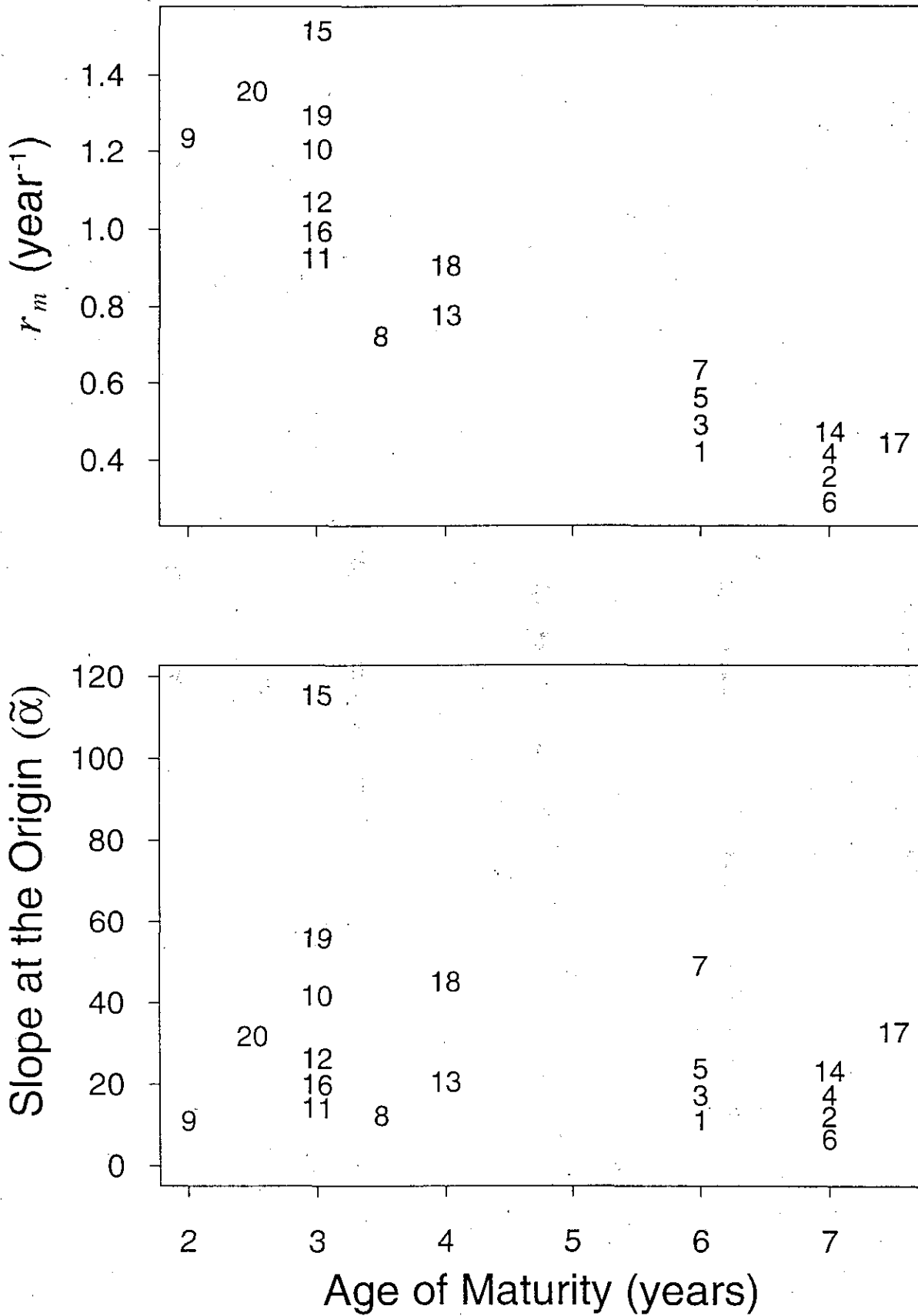


Fig. 6. Rate of population growth (r_m) and slope at the origin ($\tilde{\alpha}$) at minimum population size versus age of maturity (a). Populations are represented by numbers (See Table 1).

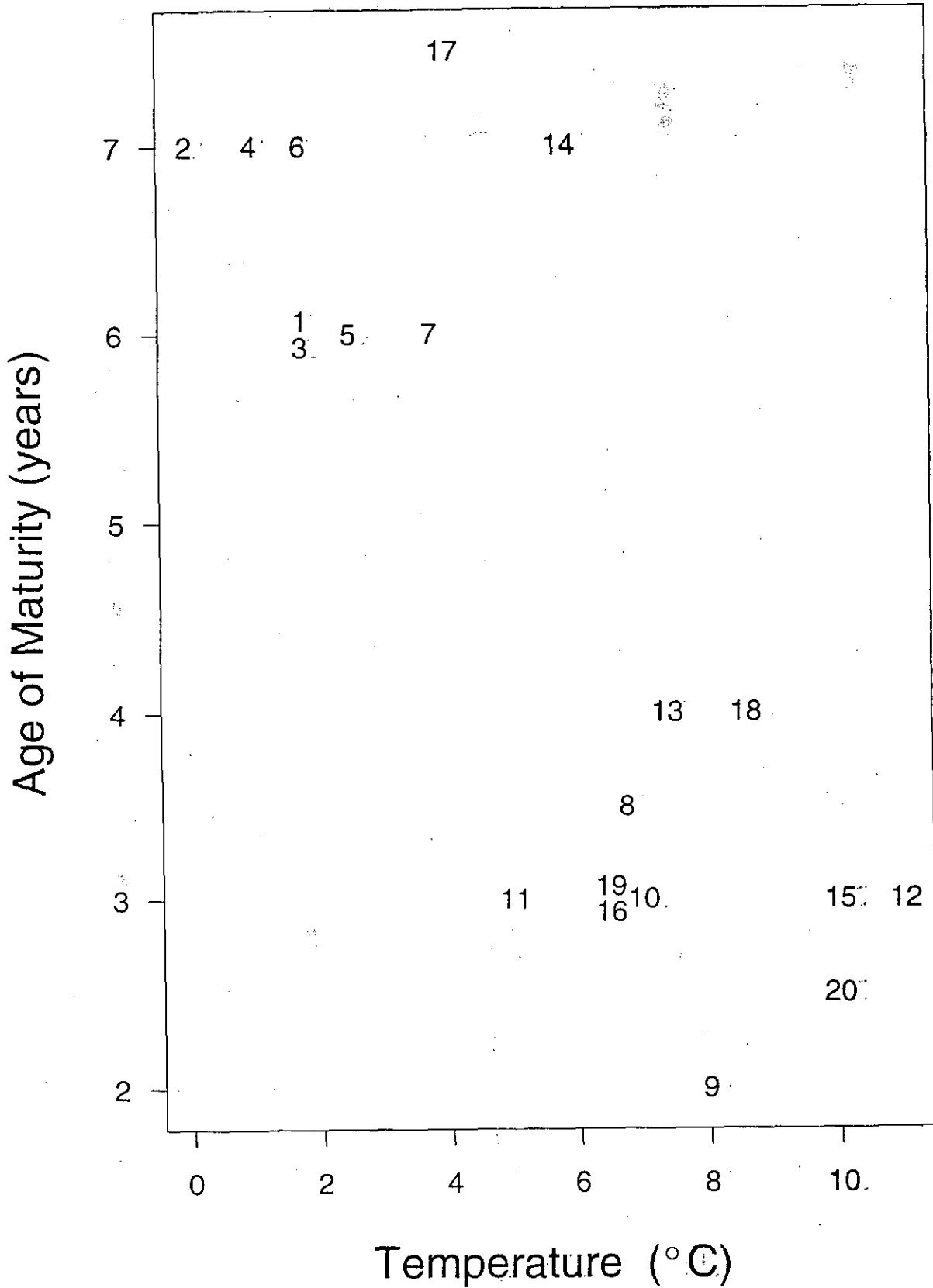


Fig. 7. Age of maturity (*a*) versus bottom temperature. Populations are represented by numbers (See Table 1).

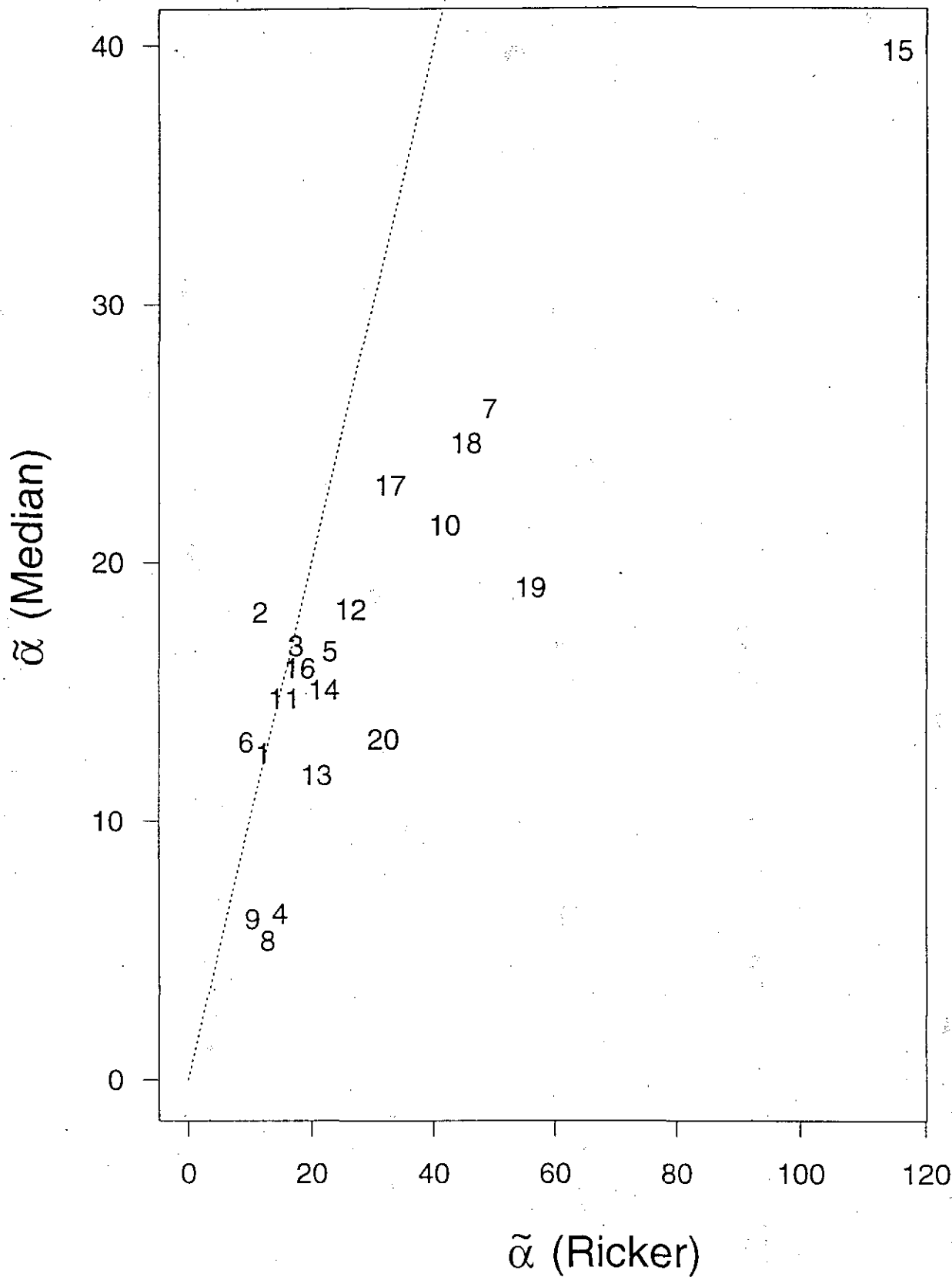


Fig. 8. Comparison of slope at the origin ($\tilde{\alpha}$) calculated as the median slope of the 6 observations with the lowest SSB with that estimated from the Ricker model. Populations are represented by numbers (See Table 1).

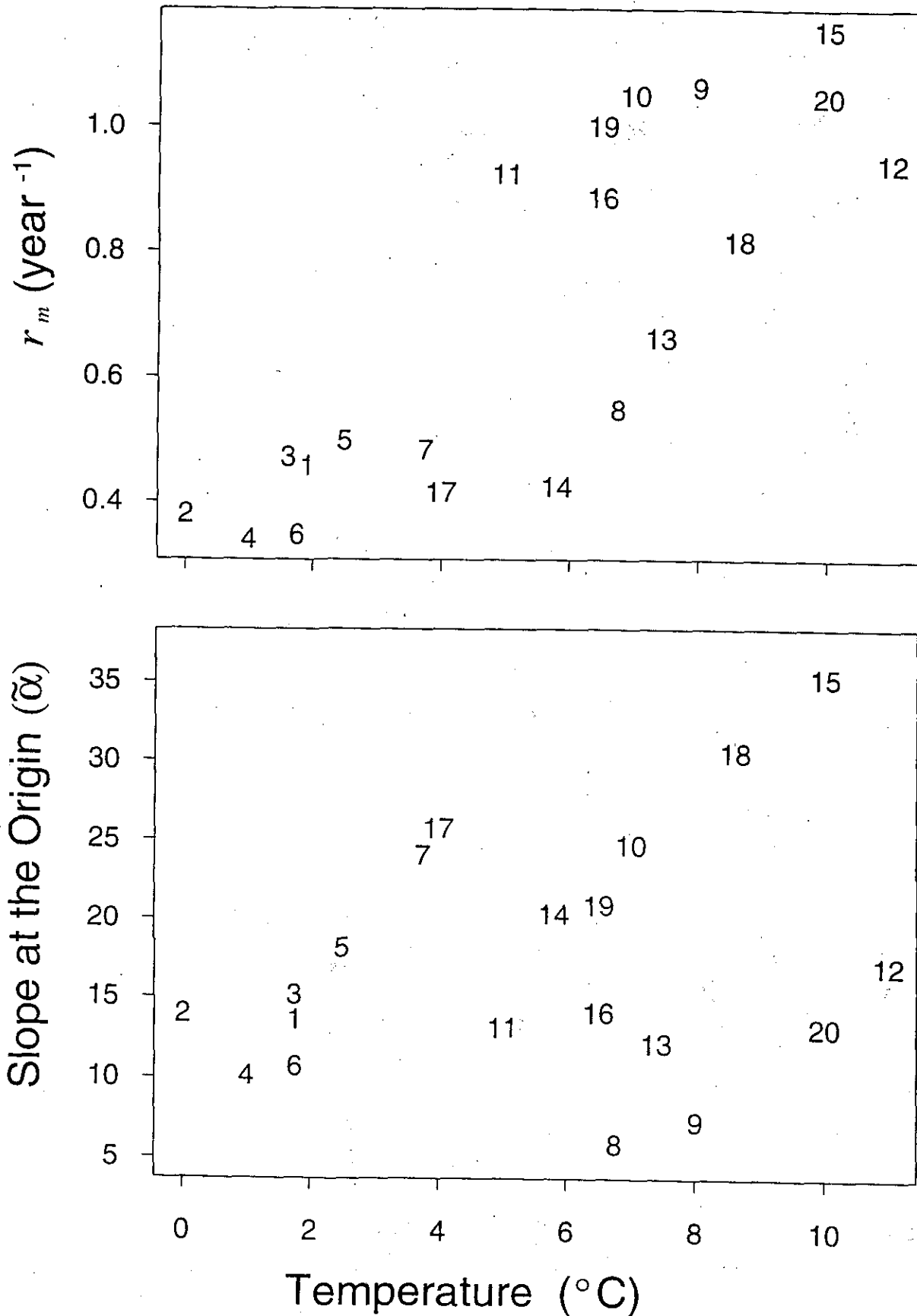


Fig. 9. Rate of population growth (r_m) and slope at the origin ($\tilde{\alpha}$) at minimum population size versus bottom temperature with $\tilde{\alpha}$ estimated from the median slope of the 6 observations with the lowest SSB. Populations are represented by numbers (See Table 1).