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The Biological Limits of Overexploitation

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Abstract

We examine the fundamental limitations to withstand overexploitation imposed by the reproductive biology of marine and anadromous fish. We derive simple mathematical models based on the simplest possible age strucural model for fish populations in which the maximum sustainable fishing mortality can be estimated. The model is applied to estimate the biological limits of fishing for 146 fish populations.

Introduction

For many of the world's major fish stocks, exploitation rates have climbed well above the limits of economically optimal harvesting and are approaching or exceeding the biological limits of sustained harvest (e.g., Ludwig et al. 1993, Rosenberg et al. 1993, Hutchings and Myers 1994). Surpassing the biological limit for exploitation implies that the population growth rate is negative until fishing pressure is relaxed (Hutchings and Myers 1994). In this paper we will formulate, explicitly, the *fundamental limitations* of fish populations to withstand overexploitation.

Our approach is different from previous attempts to estimate biological reference points based on somatic growth (Beverton and Holt 1957, Gulland and Borema 1973) or from spawner recruitment data (Ricker 1954, Sissenwine and Shepherd 1987, Thompson 1993, Mace and Sissenwine 1993, Mace 1994, Myers et al. 1994) in that we seek to estimate the maximum possible biological limit. Brander (1981) has shown using methods similar to ours that overfishing probably caused the extinction of the common skate, *Raia batis*, from Irish Sea.

Many stocks can apparently withstand extreme harvest rates indefinitely, while others are observed to collapse to the point of commercial extinction. It is our intention to elucidate the reasons for these disparate responses to overfishing. The evident resilience of some fish populations is readily understood: for a species such as cod, at low population densities, each spawning produces 10 to 30 spawners (after a lag equal to the age at maturity) for each spawner in the population (Myers et al. 1995). Thus, if harvesting is confined to mature fish, survival after fishing and natural mortality need only be 3% to 10% in order to sustain the stock, albeit at an extremely reduced abundance.

It has long been appreciated that intense harvesting leads to a compression of the age structure of the stock (Larkin 1977), prompting a tendency to land younger, immature fish. We will demonstrate that much more stringent limits on fishing are necessary when juveniles of slowly maturing fish are harvested. The results of this simple analysis will be applied to the 146 fish populations described in Myers et al. (1995).

The 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 1992) for fish is displayed as a spawner-recruitment curve (Ricker 1954). From the reproduction curve we will estimate the slope of this curve near the origin (low population).

Juvenile fish become vulnerable to fishing gear, that is, they recruit, at an age designated as a_{rec}. We consider the Ricker spawner-recruitment models which describe the number of recruits at age j in year $t + a_{rec}$, $N_{t+a_{rec},a_{rec}}$, 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

$$E(N_{t+a_{rec},a_{rec}}) = \alpha S_t e^{-\beta S_t}, \tag{1}$$

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 $\mathrm{SPR}_{F=0}$, i.e.

$$\tilde{\alpha} = \alpha \cdot \mathrm{SPR}_{F=0} \tag{2}$$

where $\mathrm{SPR}_{F=0}$ 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_{mat} years later, where a_{mat} is the age at maturity.

We now consider a simple model that incorporates age-structure with overlapping generations introduced by Clark (1976), and extended by Botsford (1992) and Mertz and Myers (1995). The model makes the assumption that the proportion of spawners that survive each year in the absence of fishing is e^{-m} and it is reasonable to ignore somatic growth once maturity has been achieved. In this case the Clark model under the assumption of Ricker recruitment in the absence of fishing becomes

$$S_t = e^{-m} S_{t-1} + \tilde{\alpha} S_{t-a_{mat}} e^{-\beta S_{t-a_{mat}}}. \tag{3}$$

For low population sizes we can approximate the dynamics of a fish population with no exploitation as

$$S_t = e^{-m} S_{t-1} + \tilde{\alpha} S_{t-a_{mat}}. \tag{4}$$

We will consider various types of fishing mortality on the above dynamics.

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 (Fig. 1). 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 almost all the stocks have been reduced to very low levels.

Fig. 1 near here

Data

The data we used are estimates obtained from assessments of the populations complied by Myers et al. (1995). For marine fish we used population numbers and fishing mortality 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). The population dynamics model assumed for these methods once a fish has entered the fishery is

$$N_{t+1,a+1} = N_{t,a}e^{-M_a-F_{t,a}}, \tag{5}$$

where $N_{t,a}$ is the numbers at the beginning of year t at age a, M_a is natural mortality at age a and $F_{t,a}$ is the fishing mortality at age a in year t. 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 and fishing mortalities under the assumption that commercial catch at age is known without error and that natural mortality at age is known and constant.

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

Results

Estimation of the slope at the origin

The Ricker model and the robust median estimate of the slope at the origin was estimated for 146 spawner recruit time series (Table 1, Table 2). We first compare the results for the Ricker model with the robust procedure. The slope at the origin for the Ricker model is generally higher than that calculated for the median slope from the 6 observations with the lowest SSB (Fig. 2a,b). The alternative estimates for sockeye salmon are fairly similar for all stocks, with only a slight tendency for the robust method to produce lower slopes. The Ricker model estimates are almost always higher for the other Pacific salmons e.g., Pink salmon (Fig. 2a).

Table 1 near here

Table 2 near here

Fig. 2 near here

The iteroparous species show that the estimates are not as robust at higher $\tilde{\alpha}$ values (Fig. 2b). The hakes and pollocks approximately follow the one-to-one line, whereas some sole and cod stocks generally have lower estimates using the Ricker model that the median of the 6 observations with the lowest spawner abundance.

Semelparous Species

If the annual survival fraction for spawners (e^{-m}) was zero, the population of spawners, S_t, would obey the following equation at very low density:

$$S_{t+a_{mat}} = \tilde{\alpha} S_t \tag{6}$$

The maximum finite exploitation rate of a fishery that occurred just before spawning would simply be:

$$e^{-F_{lim}} = 1/\tilde{\alpha}. \ , \tag{7}$$

Thus, the maximum proportion of fish that can be harvested is $H_{\max} = 1 - e^{-F_{lim}}$.

The maximum harvest rate for the Pacific salmons is generally 80% using the Ricker model, except for Chinook, which is higher (Fig. 3a). The

Fig. 3 near here

estimated maximum harvest rate is reduced using the robust method (Fig. 3b). The reduction is small for Sockeye salmon, but significant for the other species.

Iteroparous Species

Exploitation for iteroparous reproduction can be divided into two components: fishing mortality that occurs before reproduction and mortality that occurs only on the sexually mature component of the population.

We first consider exploitation that only occurs on the sexually mature component of the fishery. The dynamics of such a population would be

$$S_t = e^{-F}(e^{-m}S_{t-1} + \tilde{\alpha}S_{t-a_{mat}}). \tag{8}$$

The traditional fishery on Atlantic cod off of Norway was a fishery of this type. In this case the maximum rate of exploitation F_{lim}, that occurred just before spawning would be:

$$e^{-F_{lim}} = \frac{1}{e^{-m} + \tilde{\alpha}} \approx \frac{1}{\tilde{\alpha}} \ ; \tag{9}$$

we have used the fact that $\tilde{\alpha}$ is generally large relative to e^{-m} to show that (8) is approximately equivalent to (6).

If a fishery on adults occurs only after spawning then the dynamics would be

$$S_t = e^{-F}e^{-m}S_{t-1} + \tilde{\alpha}S_{t-a_{mat}}. \tag{10}$$

The population would increase at very low population abundance as long as

$$S_t > e^{-F_{lim}}e^{-m}S_{t-1} + \tilde{\alpha}S_{t-a_{mat}}. \tag{11}$$

This condition would be met at very low population abundance if

$$1 - e^{-F_{lim}}e^{-m} > \tilde{\alpha}. \tag{12}$$

That is, the population could not be eliminated as long as $\tilde{\alpha}$ is greater than 1, which it would have to be.

A fishery on the juvenile component is assumed to begin at the age of recruitment to the fishery (a_{rec}) and the fishing mortality is assumed to apply to adults as well. The dynamics would be

$$S_t = e^{-(F+m)}S_{t-1} + e^{-(a_{mat}-a_{rec})F_j}\tilde{\alpha}S_{t-a_{mat}}, \tag{13}$$

where F_j is the fishing mortality on juveniles. We have assumed that the harvesting of adults occurs after spawning; if harvesting occurred before spawning, $\tilde{\alpha}$ would be reduced by a factor of e^{-F}. Because we are interested in the maximum possible value for F_j, we emphasize the latter case. With these stipulations, we find that F_j is given by

$$e^{-(a_{mat}-a_{rec})F_j} = \frac{1}{e^{-m}e^{F} + \tilde{\alpha}} \ . \tag{14}$$

If $e^{-m}e^{F} \ll \tilde{\alpha}$, then

$$e^{-(a_{mat}-a_{rec})F_{lim}} \approx \frac{1}{\tilde{\alpha}} \ , \tag{15}$$

where we have now written F_j as F_{lim} to emphasize that equation (14) defines the maximum possible fishing mortality on a stock which is subject to harvesting of juvenile fish.

How good of an approximation is Eq. (15) to Eq. (14)? There are two parameters that determine how good an approximation Eq. 15 is: natural mortality and the difference between the age of reproduction and age of recruitment ($a_{mat} - a_{rec}$). The second of these two factors is the dominant one (Fig. 4). If ($a_{mat} - a_{rec}$) > 1, then Eq. (14) will be a good approximation. **Fig. 4 near here** This is fortunate, because it is these populations that are most in danger of overexploitation. The natural mortality determines how much of an underestimate Eq. (14) is to Eq. (15) at a fixed level of ($a_{mat} - a_{rec}$); but m is only important for small ($a_{mat} - a_{rec}$) (Fig. 4).

Equation (14) should be compared to (8): when juveniles are exploited, the fishing mortality is compounded over the duration from age at recruitment to age at maturity, making the stock more vulnerable to overexploitation. It is clear enough that the susceptibility to overexploitation increases as the period between recruitment and maturity $a_{mat} - a_{rec}$ increases. Consider the following example: for a cod stock with a typical $\tilde{\alpha}$ of approximately 15, and for which the fish recruit at 3 and mature at 7, if only mature fish are harvested after spawning, a fishing mortality of about 3.0 (from (8)) can be sustained. In contrast, if juveniles are harvested, the maximum sustainable fishing mortality (from (14)) is about 0.75. The first case corresponds to a harvest rate of 95% (per annum), while the latter example gives a much lower maximum harvest rate of 53%. In the former case, overexploitation is likely to become self-limiting as the fishing fleet experience greater and greater difficulty in finding fish once the harvest rate exceeds (say) 80%. In contrast, a 53% harvest rate is easily achieved, and will see in the data to be presented that fishing mortalities well in excess of 0.75 are not unusual.

The ability of a population to withstand fishing is determined by both the number of years that a cohort can be exploited before reproduction ($a_{mat} - a_{rec}$) and the slope at the origin (Fig. 5 and 6).

Fig. 5 and 6 near here

We repeated the analysis of limits of fishing and found similar results to those using the Median model (Table 1, Fig. 6). We conclude that our results are robust to the method used to estimate $\tilde{\alpha}$.

We have limited our analysis to deterministic models. Real fish populations are subject to high levels of fluctuations in recruitment primarily because of environmental variability. Stochastic models of harvesting demonstrate that stochastic recruitments reduce the maximum expected harvest below the maximum sustained yield expected under a deterministic model (Beddington and May 1977, Reed 1974, Clark 1976). The same mechanism would reduce the deterministic biological limits we have calculated here. However, by examining the slope at the origin of the observations with the six lowest spawner abundance our approach should be conservative.

Prediction of the collapse of fish stocks

We can compare the estimated F_{lim} with the maximum observed fishing mortality for the iteroparous populations (Fig. 7). Except for those stocks in which the difference between the age of reproduction and age of recruitment ($a_{mat} - a_{rec}$) is one year, almost all populations have been fished at levels approximately equal to their biological limit.

Fig. 7 near here

The populations that appear to be most resistant to overfishing are the ones with ($a_{mat} - a_{rec}$) = 1. The sole and the plaice populations are prime examples of these. These stocks often have maintained high catch levels despite great overfishing.

Does this method correspond to the commercial extinction? For cod, the 8 most sensitive stocks have been overexploited to the extent that complete moratoriums have been imposed.

The most sensitive herring stock, the Icelandic spring spawning stock, is the only population that has been overexploited to the point of commercial extinction. It has not recovered from the high levels of fishing mortality in the 1970's.

Herring represents a special case. In the 1960's most of the exploitation of herring was for commercial meal reduction. In such cases, the exploitation was only any concentrations that could be detected, no matter how young. In the 1980's, some of the fisheries changed into fisheries for spawning adults, particularly in British Columbia.

Discussion

We have demonstrated that the biological limits of exploitation can be calculated from data that is readily available. The analysis emphasizes the hazards of harvesting juvenile fish, a practise which tends to arise when the age structure of a stock is compressed by fishing. The vulnerability of slowly maturing fish populations to overexploitation is underscored by the analysis presented. For example, the biological limits for exploitation for Atlantic cod range from a fishing mortality around 0.5 (age of maturity = 7) to 2 (age at maturity = 3). The populations that are predicted to have the lowest limits to overexploitation are the more northern populations, e.g. Iceland, Barents Sea, and the Canadian stocks. These populations all have relatively long periods between recruitment to the fishery and sexual maturity (at least 3 years with the single exception of 4X cod), although some have relatively large $\tilde{\alpha}$'s. Each of these populations have been exploited to the point that in the late 1980's or early 1990's there has been a partial or complete moratorium on fishing. Although the other cod populations have been overexploited, none has reached the very low stock levels the slow growing populations have. The late maturing rock fish of the genus *Sebastes*, which may not mature until age 15, and deep water species such as turbot, *Reinhardtius hippoglossoides*, which may not mature to age 12, are possibly the species which have the lowest limit to overexploitation. Such species should be managed with great care, and fishing mortality on juveniles eliminated.

Our analysis has revealed that for many fish stocks there are stringent biological limits to fishing mortality. If the limit is exceeded, the abundance will decline until fishing mortality is reduced. This invites the question of what limits fishing mortality at low stock sizes. Two important factors are discussed in the following two paragraphs.

Declining economic returns may promote withdrawal from the fishery before the biological threshold of overfishing is surpassed. However, as discussed by Caddy and Gulland (1983) and Ludwig et al. (1993), a ratchet effect in management policy may delay or prevent withdrawal from the fishery when abundance slumps. The deployment of additional catch capacity during good years is not matched by a reduction in poor years since direct or indirect subsidies are often provided by concerned governments. In consequence, when fishing mortality exceeds the biological limit, the decline in abundance with time does not necessarily lead to elimination of catch capacity, which could serve to reduce fishing mortality. Of course, even if fishing effort does not abate, limitations in availability may prevent a prolonged exceedance of the biological limit, a point dealt with in the next paragraph.

As a stock declines in abundance, the availability of fish must correspondingly fall. The extent to which this will limit fishing mortality at a given level of effort is easily evaluated. The instantaneous fishing mortality is $f = (dC/dt)/N$ where dC/dt is the catch per unit time and N represents abundance. It is now easily shown (see Hilborn and Walters 1992 Chapter 5) that $f = E(\text{CPUE}/N)$ where E represents fishing effort, and CPUE is the catch per unit effort, which is a convenient index of availability. In the simplest case, termed proportionality by Hilborn and Walters (1992), the ratio of CPUE to N does not change as N diminishes. Thus, at constant effort, there will be no reduction in fishing mortality as the abundance shrinks. A biologically unsustainable fishing mortality can be maintained even until the stock reaches commercial extinction. The condition of hyperdepletion (Hilborn and Walters 1992) is more forgiving since CPUE/N decreases as abundance declines. However, a condition of hyperstability (Hilborn and Walters 1992) may prevail in which case the CPUE/N increases as the stock shrinks, so that at a constant effort, the fishing mortality will actually increase as abundance declines. In summary, violation of the biological limits to fishing are likely to occur when effort is not reduced as abundance slumps (perhaps due to subsidization) and when the aggregation characteristics of the stock produce a condition of proportionality or hyperstability.

To conclude, the biological limits of of the exploitation of a fish stock are likely to be violated in populations which mature slowly, particularly when harvesting has removed the older fish in a population, so that catch quotas are met through the landing of immature fish. The biological limits to fishing mortality are surprisingly low in many cases, no doubt accounting for a number of recent stock collapses.

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TABLE 1. Summary statistics for each stock, listed in the standard order (i.e. sorted by order, family, scientific name, and ID). Id gives the id number of each stock shown in the figures. a_{mat} gives the age of maturity of each stock. a_{rec} gives the age of recruitment of each stock. m gives the natural mortality of each stock. $\tilde{\alpha}$(R) gives the slope at the origin for the Ricker Stock-Recruitment (SR) function. F_{lim}(R) gives the maximum rate of fishing mortality for the Ricker SR function. $\tilde{\alpha}$(M) gives the slope at the origin for the Median Stock-Recruitment (SR) function. F_{lim}(M) gives the maximum rate of fishing mortality for the Median SR function. $MaxF(obs)$ gives the maximum rate of observed fishing mortality.

Stock	Id	a_{mat}	a_{rec}	m	$\tilde{\alpha}$(R)	F_{lim}(R)	$\tilde{\alpha}$(M)	F_{lim}(M)	$MaxF(obs)$
CLUPEIFORMES									
Clupeidae									
Clupea harengus (Herring)									
Baltic areas 22 and 24	40	2.5	1.0	0.3	42.5	2.6	11.7	1.9	1.0
NAFO 4-5	41	3.5	1.0	0.2	27.7	1.4	34.0	1.4	1.5
Central Coast B.C.	42	4.0	2.0	0.4	14.3	1.4	9.5	1.2	
Gulf of Finland	43	2.0	1.0	0.2	27.7	5.0	6.2	3.5	0.5
Gulf of Maine	44	3.5	1.0	0.2	42.1	1.5	16.9	1.2	1.6
Gulf of Riga	45	2.0	1.0	0.2	9.9	4.0	3.9	3.1	1.1
Iceland (Spring spawners)	46	4.0	1.0	0.1	4.3	0.6	1.2	0.3	1.9
Iceland (Summer spawners)	47	3.5	2.0	0.1	8.6	1.8	10.2	1.9	1.5
Norway (Spring spawners)	48	4.5	3.0	0.1	9.0	1.8	10.1	1.8	1.7
North Strait of Georgia	49	4.0	3.0	0.7	9.4	2.9	7.2	2.7	
North West Coast Vancouver Island	50	4.0	3.0	0.7	7.4	2.7	7.3	2.7	
Prince Rupert District	51	4.0	3.0	0.4	23.4	4.3	16.6	4.0	
Queen Charlotte Islands	52	4.0	3.0	0.4	20.0	4.0	9.1	3.3	
Southern Strait of Georgia	53	4.0	3.0	0.7	8.7	2.9	4.8	2.3	
South West Coast Vancouver Island	54	4.0	3.0	0.3	22.0	4.5	29.0	4.7	
Sardinops sagax (Sardine)									
California	71	2.0	1.5	0.4	2.8		1.8		2.4
Sprattus sprattus (Sprat)									
Baltic Areas 22-32	82	2.0	1.0	0.3	47.6	5.3	16.3	4.2	0.4
Baltic Areas 26 and 28	83	2.0	1.0	0.4	8.3	3.3	7.9	3.2	0.8
Engraulidae									
Engraulis mordax (Northern anchovy)									
California	1	2.0	0.5	0.6	4.4	1.2	2.1	0.8	
GADIFORMES									
Gadidae									
Gadus morhua (Cod)									
NAFO 1	6	6.0	3.0	0.2	20.4	1.0	12.6	0.9	1.0
NAFO 2J3KL	7	7.0	3.0	0.2	11.4	0.6	18.1	0.8	2.4
NAFO 3NO	8	6.0	3.0	0.2	16.9	1.0	16.8	1.0	1.1
NAFO 3Pn4RS	9	7.0	3.0	0.2	14.5	0.7	6.4	0.5	1.4
NAFO 3Ps	10	6.0	3.0	0.2	22.9	1.1	16.6	1.0	1.2
NAFO 4TVn	11	7.0	3.0	0.2	9.3	0.6	12.9	0.7	1.1
NAFO 4VsW	12	6.0	1.0	0.2	48.7	0.8	25.9	0.7	1.4
NAFO 4X	13	3.5	1.0	0.2	12.4	1.1	5.7	0.8	1.4
NAFO 5Y	14	3.0	1.0	0.2	101.9	2.4	13.2	1.4	1.1
NAFO 5Z	15	2.0	1.0	0.2	10.7	4.1	5.8	3.5	0.8
Baltic Areas 22 and 24	16	3.0	1.0	0.2	40.9	1.9	21.4	1.6	1.7
Baltic Areas 25-32	17	3.0	2.0	0.2	15.3	4.4	14.8	4.4	1.4
Celtic Sea	18	3.0	1.0	0.2	25.5	1.7	18.2	1.6	1.0
Faroe Plateau	19	4.0	2.0	0.2	20.6	1.6	11.8	1.4	0.8
Iceland	20	7.0	3.0	0.2	21.6	0.8	15.8	0.7	1.0
Irish Sea	21	3.0	1.0	0.2	114.7	2.4	39.8	1.9	1.2
Kattegat	22	3.0	1.0	0.2	18.9	1.6	15.9	1.5	1.4
North East Arctic	23	8.0	3.0	0.2	51.3	0.8	30.8	0.7	1.0
North East Arctic	24	7.5	3.0	0.2	32.5	0.8	22.9	0.7	1.0
North Sea	25	4.0	1.0	0.2	44.7	1.3	24.6	1.1	1.0
Skagerrak	26	3.0	1.0	0.2	55.4	2.1	19.0	1.6	1.4
ICES VIId	27	3.0	1.0	0.1	19.5	1.6	7.6	1.2	2.8
ICES VIa	28	2.5	1.0	0.2	31.5	2.5	13.2	2.0	1.0

Stock	Id	a_{mat}	a_{rec}	m	$\tilde{\alpha}$(R)	F_{lim}(R)	$\tilde{\alpha}$(M)	F_{lim}(M)	$MaxF(ob$
Melanogrammus aeglefinus (Haddock)									
NAFO 4TVW	32	4.5	1.0	0.2	16.5	0.8	37.9	1.1	
NAFO 5Z	33	2.0	1.0	0.2	7.7	3.8	7.6	3.7	0.6
Faroe Plateau	34	3.5	2.0	0.2	12.6	1.9	3.5	1.2	1.0
Iceland	35	5.5	2.0	0.2	15.1	0.8	13.3	0.8	1.1
North East Arctic	36	6.0	3.0	0.2	13.8	0.9	12.8	0.9	0.9
North Sea	37	2.5	0.5	0.2	29.2	1.8	27.0	1.7	1.1
ICES VIa	38	3.0	0.5	0.2	18.7	1.2	8.0	0.9	1.1
Merlangius merlangus (Whiting)									
Celtic Sea	84	2.0	1.0	0.2	34.1	5.2	10.2	4.0	1.5
Irish Sea	85	2.0	0.5	0.2	90.0	3.1	33.6	2.5	1.6
North Sea	86	2.0	0.5	0.2	7.6	1.6	2.8	1.1	1.4
ICES VIId	87	3.0	1.0	0.2	9.6	1.3	6.4	1.1	1.4
ICES VIa	88	2.0	1.0	0.2	11.7	4.2	5.1	3.3	1.3
Micromesistius poutassou (Blue whiting)									
Northern ICES	3	3.0	0.5	0.2	11.7	1.1	3.5	0.7	0.4
Southern ICES	4	3.0	0.5	0.2	12.9	1.1	13.2	1.1	0.8
Pollachius virens (Pollock or saithe)									
Faroe	65	5.0	3.0	0.2	33.4	1.8	5.4	1.0	0.7
Iceland	66	5.0	3.0	0.2	23.1	1.6	12.0	1.4	0.5
North East Arctic	67	6.0	1.0	0.2	25.4	0.7	16.4	0.6	0.7
North Sea	68	4.5	1.0	0.2	17.0	0.8	12.8	0.8	0.9
ICES VI	69	5.0	1.0	0.2	16.4	0.7	5.7	0.5	0.7
Theragra chalcogramma (Walleye pollock)									
E. Bering Sea	89	6.0	3.0	0.3	6.2	0.7	2.9	0.5	0.5
Gulf of Alaska	90	5.0	3.0	0.3	6.7	1.1	3.8	0.8	
Merlucciidae									
Merluccius bilinearis (Silver hake)									
NAFO 4VWX	72	3.0	1.0	0.4	5.5	1.0	2.8	0.7	1.2
NAFO 5Ze	73	2.0	1.0	0.4	2.1	1.9	2.4	2.0	1.1
Mid Atlantic Bight	74	2.0	1.0	0.4	3.9	2.5	3.1	2.2	1.6
Merluccius capensis (S.A. Hake)									
South Africa 1.6	70	3.0	1.0	0.3	13.0	1.4	9.6	1.2	
Merluccius merluccius (Hake)									
ICES VIIIc and IXa	39	4.0	0.5	0.2	8.1	0.7	8.4	0.7	0.4
Merluccius productus (Pacific hake)									
W. US. + Canada	56	4.0	2.0	0.2	3.5	0.8	0.5	0.2	0.6
PERCIFORMES									
Scombridae									
Scomber japonicus (Chub mackerel)									
Southern California	5	2.0	1.0	0.5	6.2	2.8	8.7	3.1	
Scomber scombrus (Mackerel)									
NAFO 2 to 6	55	3.0	1.0	0.2	76.8	2.2	42.6	1.9	1.1
Thunnus thynnus (Atlantic bluefin tuna)									
West Atlantic	2	8.0	1.0	0.1	6.2	0.3	8.7	0.3	0.3
PLEURONECTIFORMES									
Pleuronectidae									
Pleuronectes platessa (Plaice)									
ICES VIId	57	3.0	1.0	0.1	35.5	1.9	14.9	1.5	0.6
ICES VIIe	58	3.0	1.0	0.1	21.1	1.6	10.6	1.3	0.8
Celtic Sea	59	3.0	1.0	0.1	34.3	1.8	17.5	1.5	0.9
ICES IIIa	60	3.0	2.0	0.1	47.0	6.2	10.4	4.7	1.1
Irish Sea	61	3.0	1.0	0.1	25.2	1.7	15.3	1.5	0.9
Kattegat	62	3.0	1.0	0.1	12.7	1.4	4.5	1.0	0.8
North Sea	63	3.0	1.0	0.1	31.9	1.8	6.4	1.1	0.5
Skagerrak	64	3.0	2.0	0.1	22.6	5.5	7.7	4.4	1.1
Reinhardtius hippoglossoides (Greenland halibut)									
North East Arctic	29	9.0	3.0	0.1	7.1	0.3	5.0	0.3	0.4
Northwest Atlantic	30	14.0	5.0	0.1	30.7	0.4	11.2	0.3	
ICES V and XIV	31	10.5	5.0	0.1	42.8	0.7	7.2	0.4	0.5
Soleidae									
Solea vulgaris (Sole)									
Celtic Sea	75	3.0	2.0	0.1	83.5	6.8	6.9	4.3	0.9
ICES IIIa	76	3.0	2.0	0.1	20.7	5.4			0.5
Irish Sea	77	3.0	2.0	0.1	73.1	6.6	7.3	4.3	0.8
North Sea	78	3.0	1.0	0.1	17.6	1.5	11.1	1.3	0.5
Bay of Biscay (VIII)	79	3.0	0.5	0.1	36.1	1.5	12.6	1.1	0.5
ICES VIId	80	3.0	1.0	0.1	16.1	1.5	5.1	1.0	0.6
ICES VIIe	81	3.0	1.0	0.1	5.5	1.0	3.6	0.9	0.5

TABLE 2. Summary statistics for each salmon stock, listed in the standard order (i.e. sorted by order, family, scientific name, and ID). $\tilde{\alpha}$(Ricker) gives the slope at the origin for the Ricker Stock-Recruitment (SR) function. F_{lim}(Ricker) gives the maximum rate of fishing mortality for the Ricker SR function $\tilde{\alpha}$(Median) gives the slope at the origin for the Median Stock-Recruitment (SR) function. F_{lim}(Median) gives the maximum rate of fishing mortality for the Median SR function.

Stock	$\tilde{\alpha}$(Ricker)	F_{lim}(Ricker)	$\tilde{\alpha}$(Median)	F_{lim}(Median)
SALMONIFORMES				
Salmonidae				
Oncorhynchus gorbuscha (Pink salmon)				
Prince William Sound, Alaska	5.2	1.64	5.6	1.72
Brown's Peak Creek, Lower Cook Inlet, Alaska	5.2	1.65	3.3	1.20
Bruin Bay, Lower Cook Inlet, Alaska	8.9	2.19	5.3	1.67
Central Alaska	5.2	1.65	3.0	1.10
Central B.C., Canada	7.7	2.05	4.7	1.55
Desire Lake, Lower Cook Inlet, Alaska	16.3	2.79	4.4	1.49
Fraser River, B.C., Canada	9.8	2.29	9.3	2.23
Humpy Creek, Lower Cook Inlet, Alaska	6.2	1.83	4.9	1.59
Island Creek, Lower Cook Inlet, Alaska	51.6	3.94	15.9	2.76
James Lagoon, Lower Cook Inlet, Alaska	9.6	2.26	3.6	1.28
Kodiak Area, Alaska	10.1	2.31	6.1	1.81
Northern section of Southeastern Alaska	4.3	1.45	3.0	1.11
Port Chatham, Lower Cook Inlet, Alaska	4.7	1.55	4.2	1.44
Port Dick, Lower Cook Inlet, Alaska	9.5	2.25	6.3	1.84
Port Graham, Lower Cook Inlet, Alaska	5.5	1.71	3.6	1.29
Rocky River, Lower Cook Inlet, Alaska	3.1	1.12	1.8	0.59
Seldovia, Lower Cook Inlet, Alaska	4.5	1.51	2.6	0.95
Southern section of Southeastern Alaska	4.6	1.53	3.0	1.11
Sunday Creek, Lower Cook Inlet, Alaska	9.2	2.22	2.0	0.69
Windy Left, Lower Cook Inlet, Alaska	3.9	1.37	1.8	0.57
Windy Right, Lower Cook Inlet, Alaska	2.7	1.00	1.8	0.56
Oncorhynchus keta (Chum salmon)				
Central Alaska	8.0	2.08	5.0	1.60
Central Coast, B.C., Canada	4.0	1.38	3.3	1.20
Fraser River, B.C., Canada	2.2	0.79	1.7	0.53
Johnstone Strait	2.2	0.80	2.3	0.84
North Coast, B.C., Canada	10.6	2.36	7.3	1.99
Queen Charlotte Islands, B.C., Canada	3.9	1.37	1.9	0.65
West Coast Vancouver Island, B.C., Canada	2.9	1.07	1.6	0.45
Oncorhynchus nerka (Sockeye salmon)				
Adams Complex,B.C., Canada	9.3	2.23	14.2	2.65
Birkenhead River, B.C., Canada	11.2	2.41	9.1	2.21
Black Lake, Alaska	6.0	1.80	4.7	1.54
Branch River, Alaska	3.3	1.20	2.9	1.05
Bristol Bay, Alaska	2.8	1.03	4.2	1.44
Chignik Lake, Alaska	5.0	1.61	2.7	1.00
Chilko River, B.C., Canada	8.8	2.17	4.4	1.49
Columbia River, Washington	16.8	2.82	11.3	2.43
Egegik, Alaska	2.7	0.98	2.6	0.97
Egegik River, Alaska	4.9	1.59	5.4	1.68
Horsefly River, B.C., Canada	10.3	2.33	9.9	2.29
Igushik River, Alaska	10.1	2.31	8.1	2.09
Karluk River, Alaska	4.6	1.52	5.2	1.65
Kvichak River, Alaska	2.6	0.95	2.5	0.90
Naknek-Kvichak, Alaska	6.0	1.79	5.5	1.70
Naknek River, Alaska	6.9	1.93	4.9	1.59
Nushagak, Alaska	6.4	1.86	5.3	1.67
Nuyakuk River, Alaska	4.9	1.59	3.8	1.34
Rivers Inlet, B.C., Canada	6.7	1.91	6.5	1.87
Skeena River, B.C., Canada	4.2	1.43	3.6	1.28
Skeena River, B.C., Canada	3.8	1.34	3.4	1.21
Stellako River, B.C., Canada	8.3	2.12	8.2	2.11
Early Stuart Complex, B.C., Canada	7.1	1.96	8.6	2.15
Togiak River, Alaska	4.7	1.54	4.3	1.46
Ugashik, Alaska	4.9	1.58	4.0	1.38
Ugashik River, Alaska	2.5	0.93	2.2	0.77
Wood River, Alaska	4.1	1.41	3.0	1.08
Oncorhynchus tshawytscha (Chinook salmon)				
Wild Canadian Coastwide	20.4	3.01	8.4	2.12

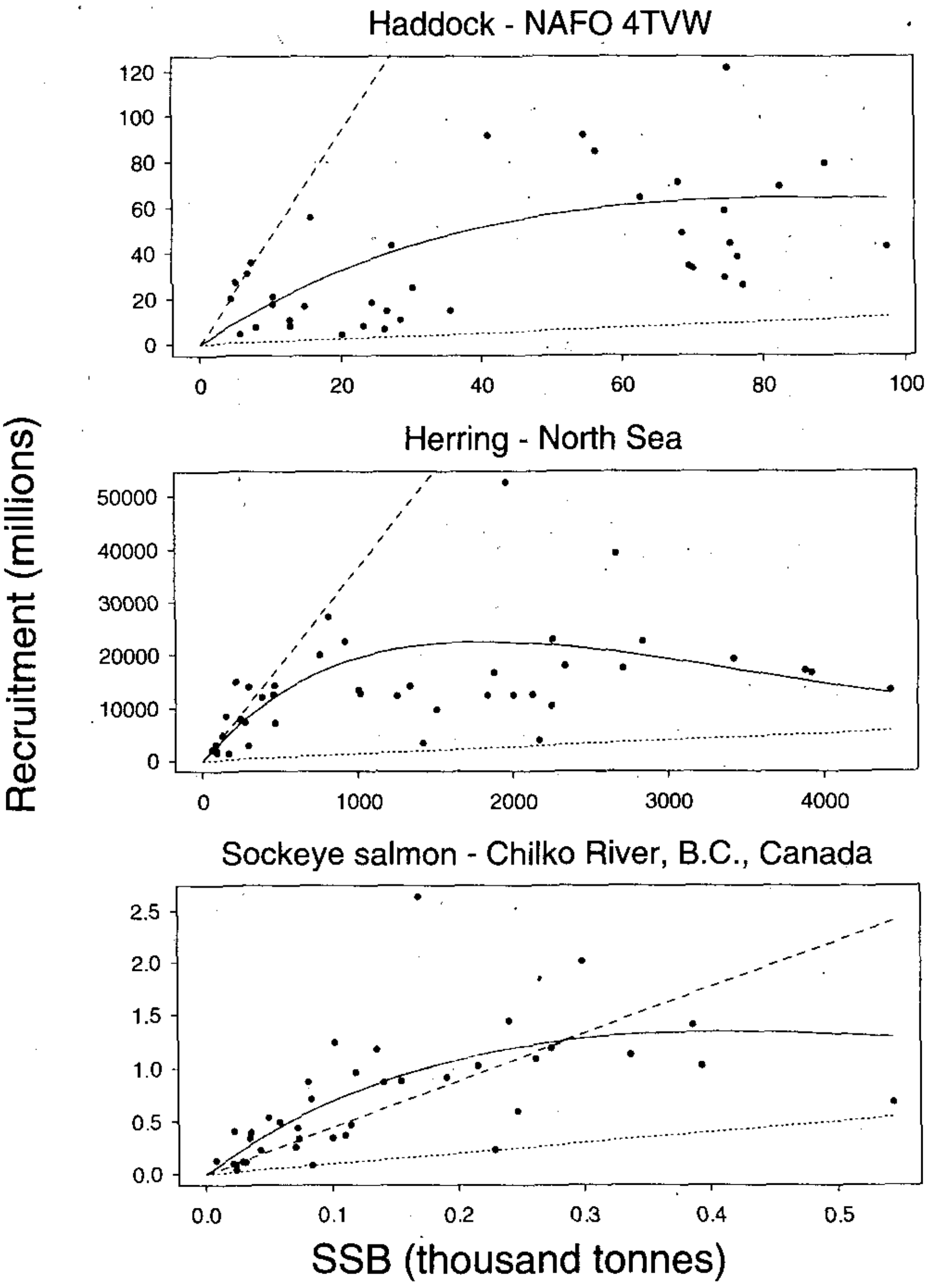
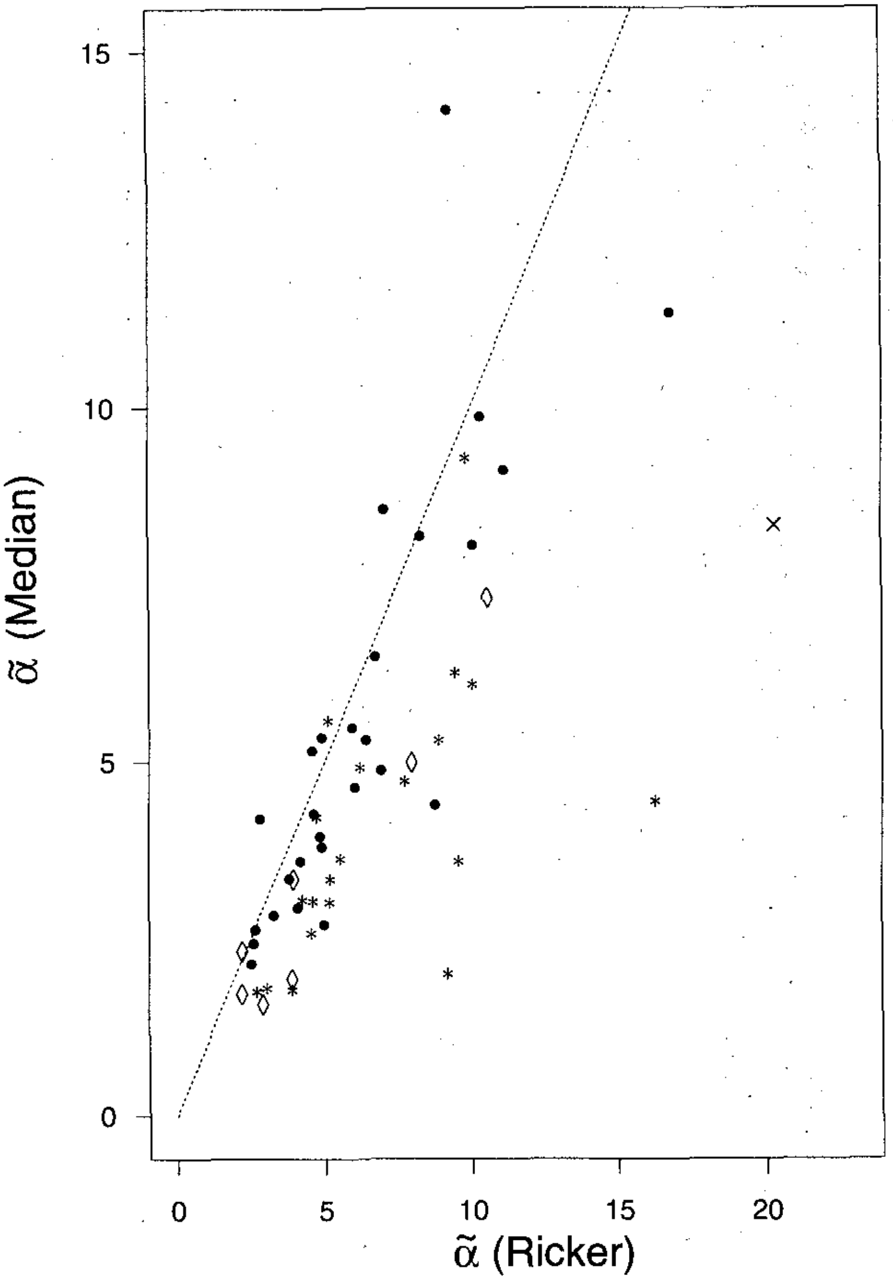
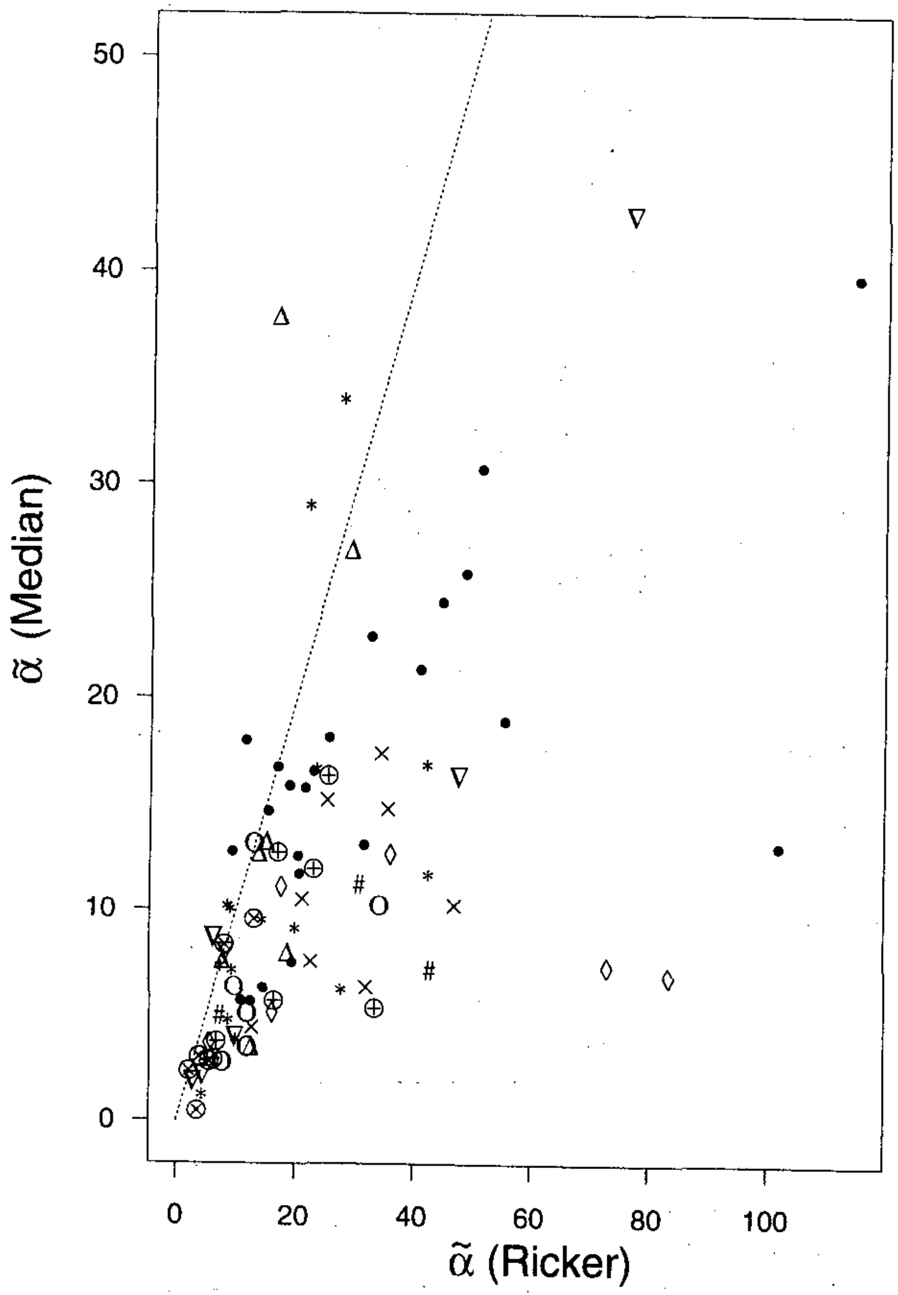


Fig. 1. Recruitment versus Spawning Stock Biomass (SSB) for several representative stocks. The solid line is the maximum likelihood estimate of the mean for Ricker spawner-recruitment functions under the assumption that the probability distribution for any SSB is given by a lognormal distribution. The 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.



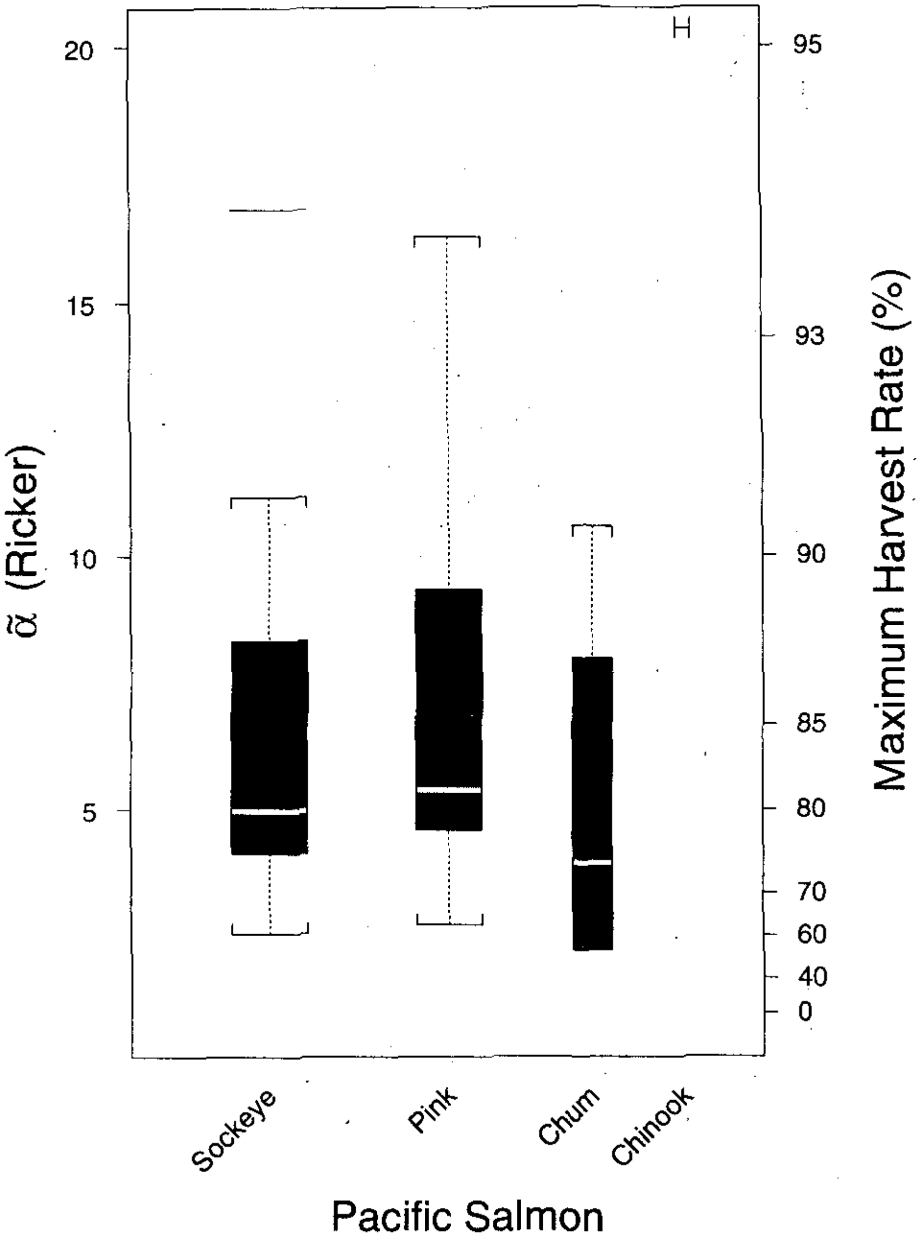
2A

Fig. 2. 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 a) for the Pacific salmon species: Chinook (×); Chum (◊); Pink (∗); Sockeye (•) and b) for all other species: cod (•); haddock (Δ); herring (∗); plaice (×); sole (◊); the hakes(hake, Pacific hake, South African hake, and Silver hake) (⊗); the pollocks(pollock and Walleye pollock) (⊕); the whitings (whiting and Blue whiting) (O); Greenland halibut (#); Northern anchovy, Chub mackerel, mackerel, sardine, Atlantic bluefin tuna, and the sprat (∇).


50
40
30
20
10
0
$\tilde{\alpha}$ (Median)
0
20
40
60
80
100
$\tilde{\alpha}$ (Ricker)

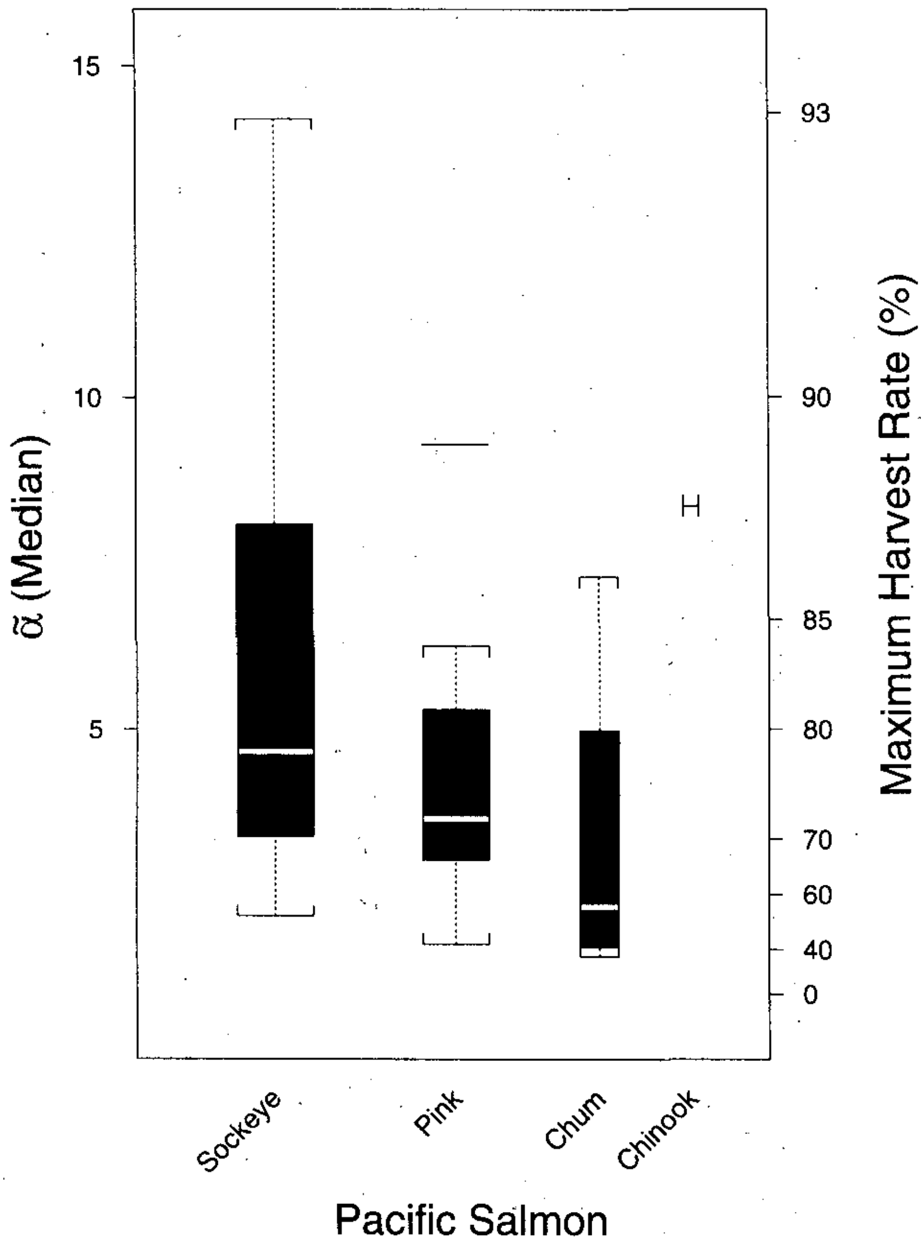
2 B

- fig2b -



- fig3a -

Fig. 3. Box plots of the slope at the origin ($\tilde{\alpha}$) at minimum population size the for Pacific salmon species for a) the Ricker model and b) for the Median model. The right hand side gives the biological limit of harvesting.


15
10
5
α̃ (Median)
93
90
85
80
70
60
40
0
Maximum Harvest Rate (%)
Sockeye
Pink
Chum
Chinook
Pacific Salmon

- fig3b -

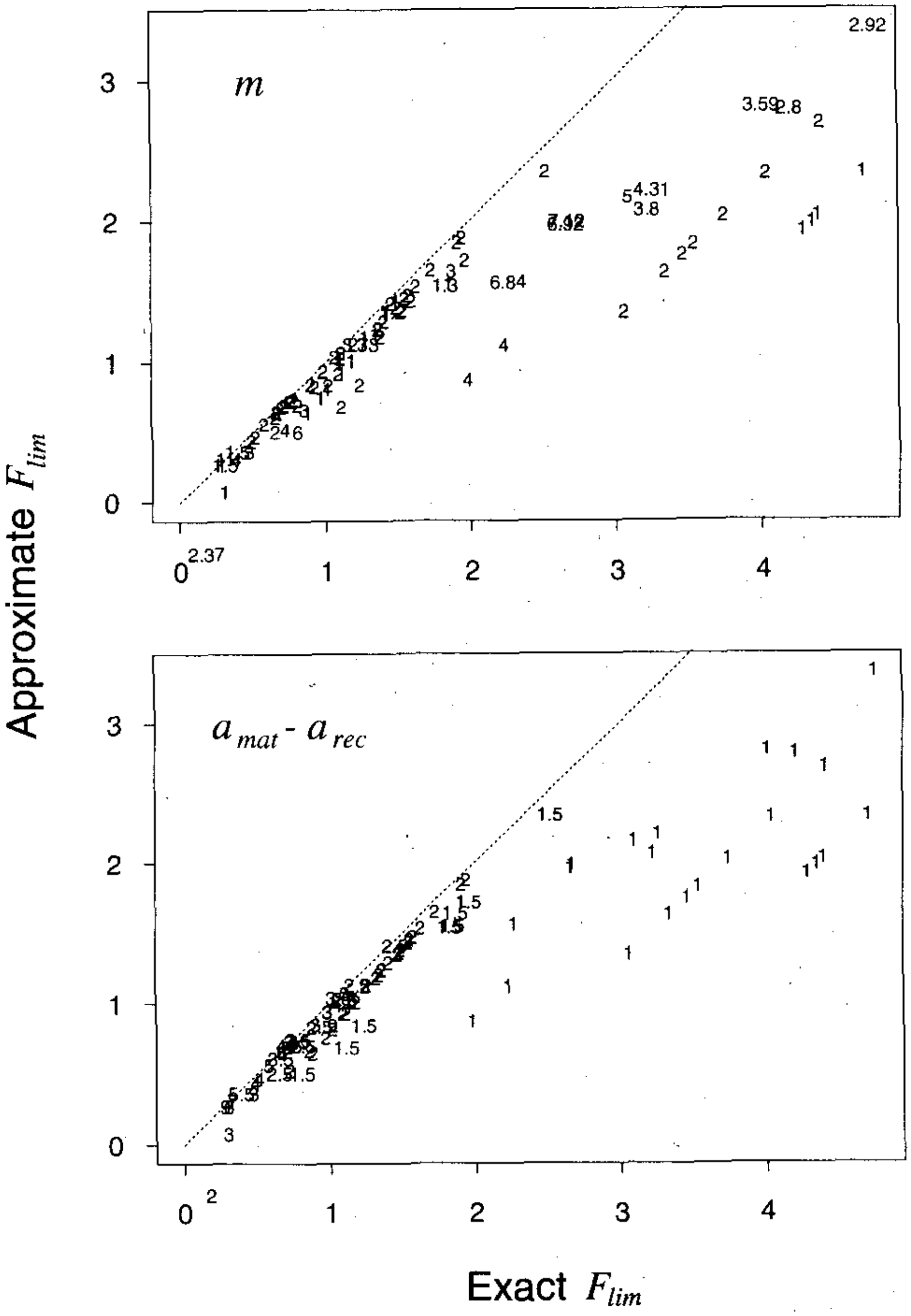
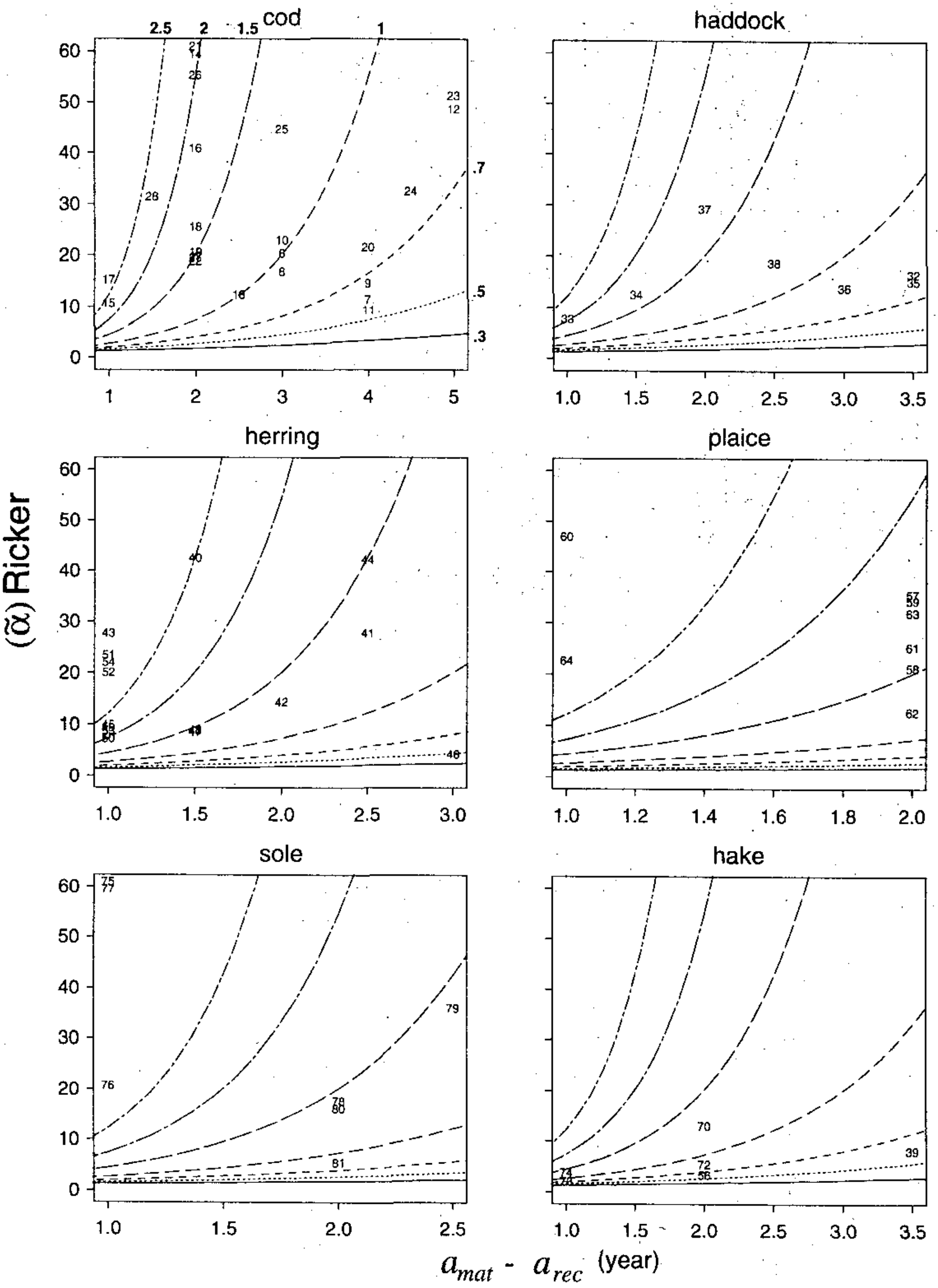


Fig. 4. The biological limit of fishing, F_{lim}, calculated using the exact solution Eq. 14 and the approximate solution Eq. 15 for the iteroparous species using our robust median estimates. In the upper panel, the populations are identified by the estimated natural mortality multiplied by 10, where in the lower panel the populations are identified by the difference between the age of reproduction and age of recruitment ($a_{mat} - a_{rec}$) The dotted line is the one-to-one line.


cod
2.5
2
1.5
1
.7
.5
.3
60
50
40
30
20
10
0
1
2
3
4
5
21
14
26
23
12
25
16
28
24
18
10
6
20
17
8
9
15
16
7
11
haddock
1.0
1.5
2.0
2.5
3.0
3.5
37
38
34
36
32
35
33
herring
1.0
1.5
2.0
2.5
3.0
40
44
43
41
51
54
52
42
46
plaice
1.0
1.2
1.4
1.6
1.8
2.0
60
57
59
63
64
61
58
62
sole
1.0
1.5
2.0
2.5
75
77
79
76
78
80
81
hake
1.0
1.5
2.0
2.5
3.0
3.5
70
39
72
56
74
($\tilde{\alpha}$) Ricker
a_{mat} - a_{rec} (year)

- fig5 -

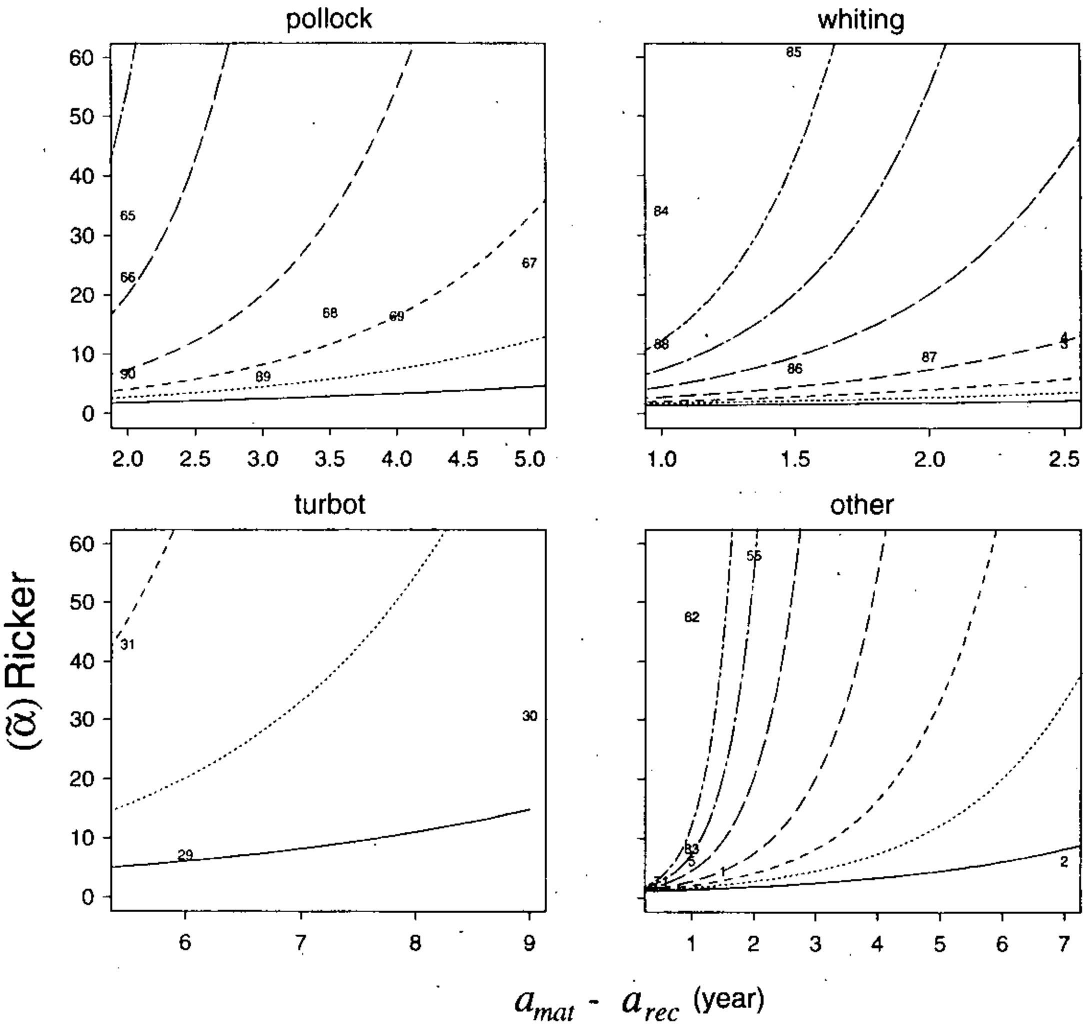
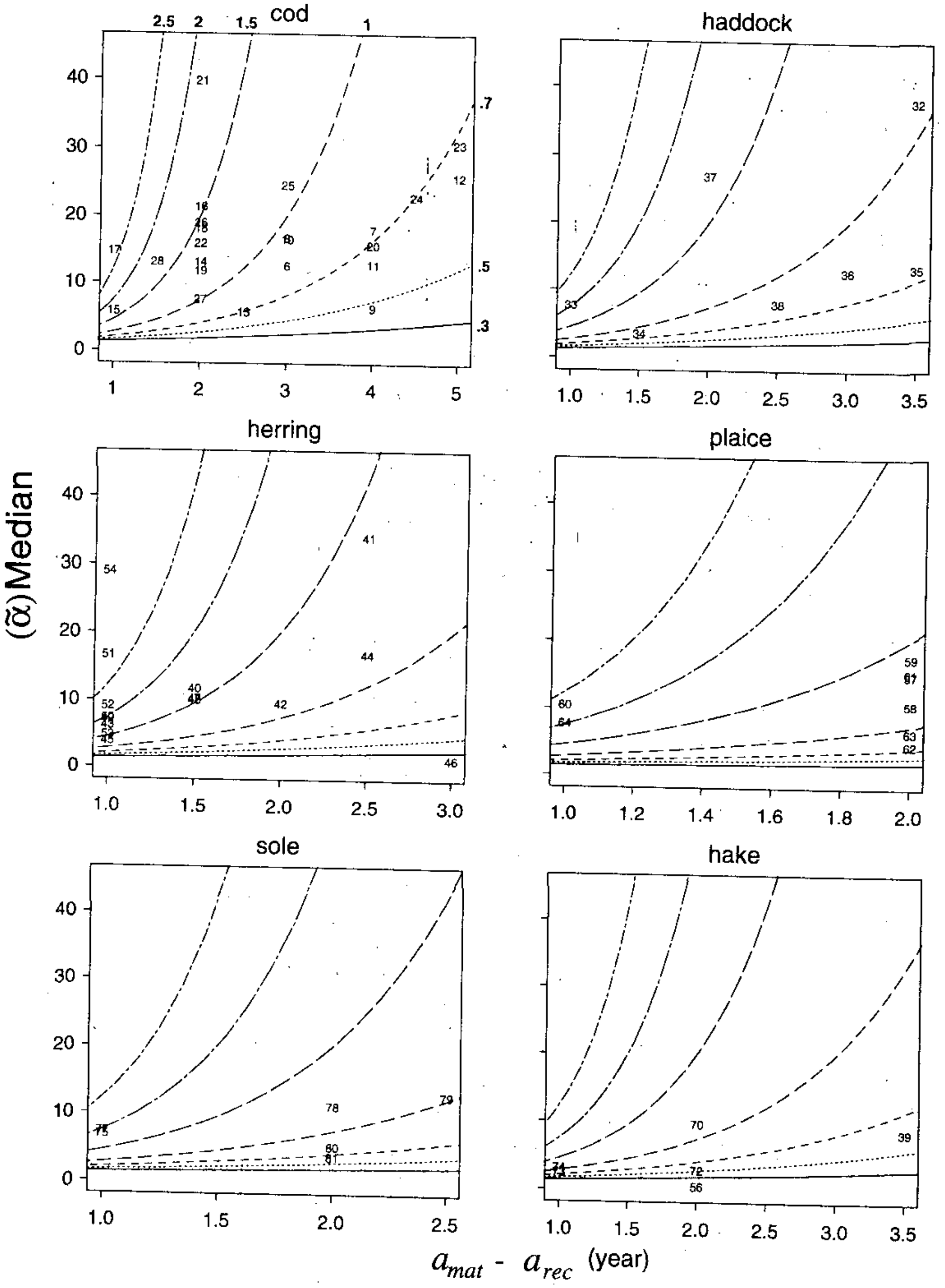


Fig. 5. Estimates of slope at the origin ($\tilde{\alpha}$) using the Ricker model at minimum population size and the approximate number of years before maturity ($a_{mat} - a_{rec}$) for iteroparous species. The numbers are stock IDs (See Table 1 for the corresponding stocks). The lines of equal levels of F_{lim}, the biological limit of fishing is given by Eq. 15. The levels of F_{lim} are: 0.3 (solid line), 0.5 (dotted line), 0.7 (short dashed line), 1.0 (medium dashed line), 1.5 (long dashed line), 2.0(short & long dashed line) and 2.5(short & medium dashed line). For illustrative purposes, the lines indicating the levels of F_{lim} for the cod stocks plot are labeled around the outside of the plot.


cod
2.5
2
1.5
1
.7
.5
.3
haddock
herring
plaice
sole
hake
(α̃) Median
0
10
20
30
40
1
2
3
4
5
1.0
1.5
2.0
2.5
3.0
3.5
1.2
1.4
1.6
1.8
21
25
23
12
24
16
26
18
22
14
19
10
6
7
20
11
17
28
15
27
13
9
32
37
36
35
33
38
34
54
51
52
40
41
44
42
46
60
64
59
61
58
63
62
78
79
75
80
81
70
39
74
72
56
a_{mat} - a_{rec} (year)

- fig6 -

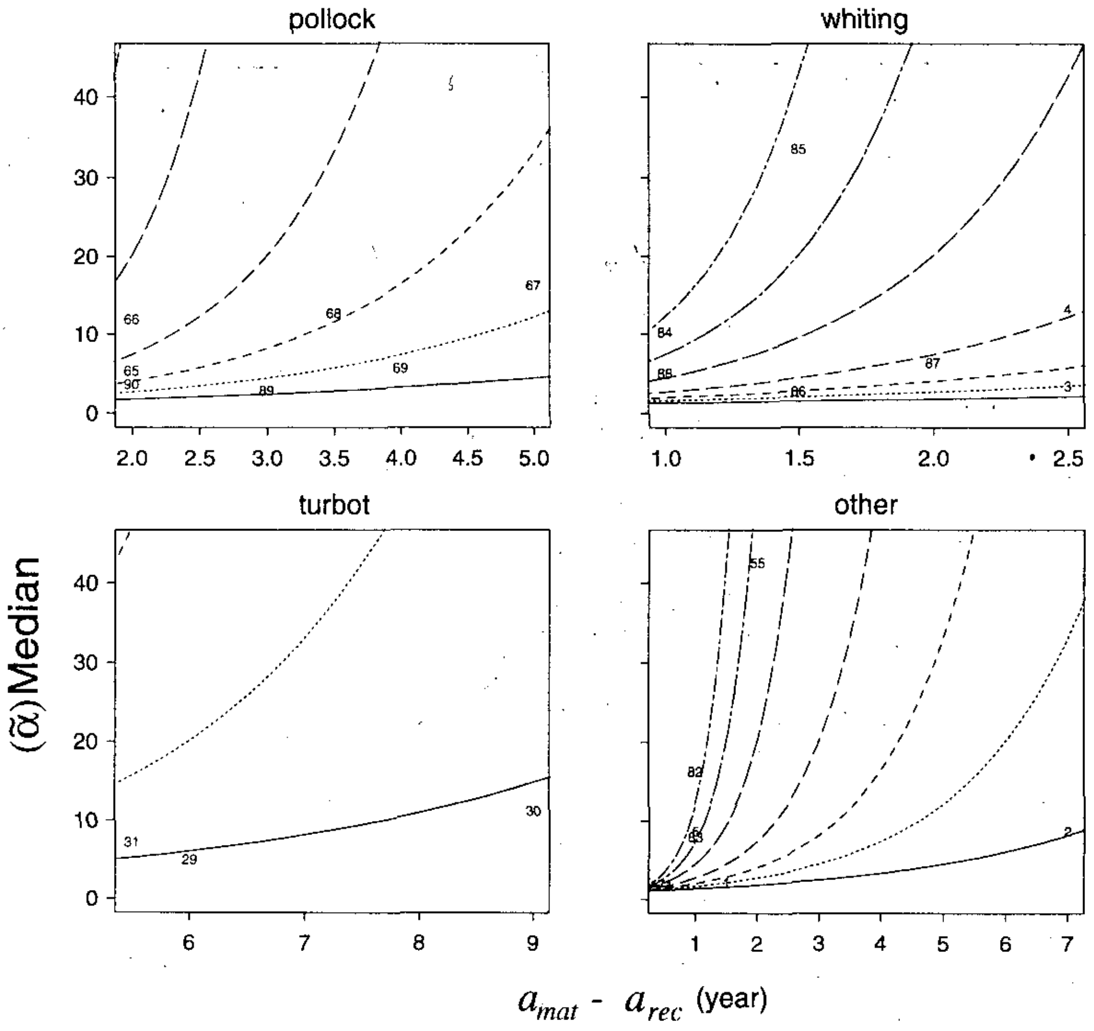


Fig. 6. Estimates of slope at the origin ($\tilde{\alpha}$) using the median method at minimum population size and the approximate number of years before maturity ($a_{mat} - a_{rec}$) for iteroparous species. The numbers are stock IDs (See Table 1 for the corresponding stocks). The lines of equal levels of F_{lim}, the biological limit of fishing is given by Eq. 15. The levels of F_{lim} are: 0.3 (solid line), 0.5 (dotted line), 0.7 (short dashed line), 1.0 (medium dashed line), 1.5 (long dashed line), 2.0(short & long dashed line) and 2.5(short & medium dashed line). For illustrative purposes, the lines indicating the levels of F_{lim} for the cod stocks plot are labeled around the outside of the plot.

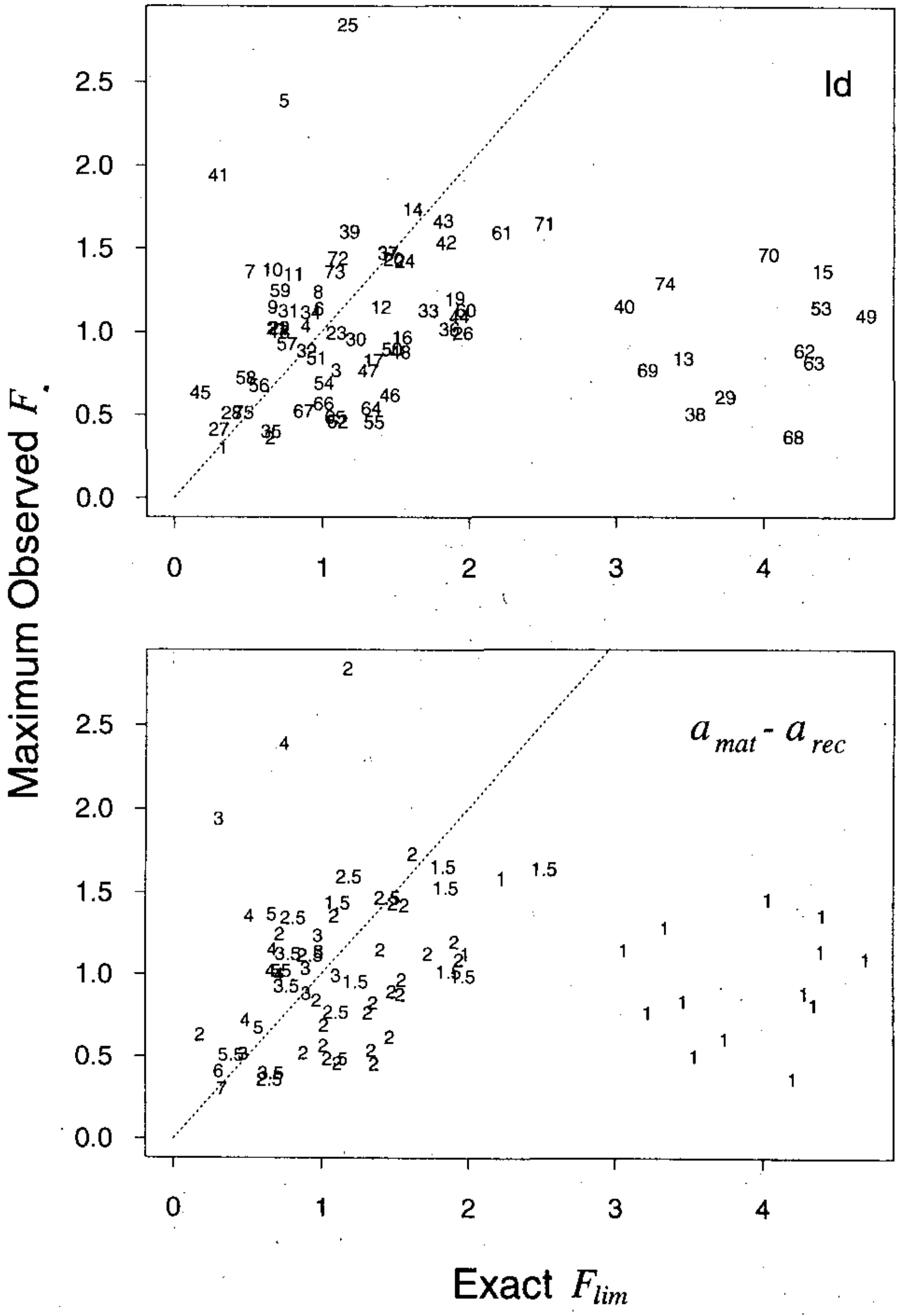


Fig. 7. Observed maximum level of fishing mortality with the estimated biological limit of fishing F_{lim} for the iteroparous species using our robust median estimates. In the upper panel, the populations are identified by their Id number (see Table 1), where in the lower panel the populations are identified by the difference between the age of reproduction and age of recruitment ($a_{mat} - a_{rec}$). The dotted line is the one-to-one line.