

## NO RELATIONSHIP BETWEEN FECUNDITY AND ANNUAL REPRODUCTIVE RATE IN BONY FISH

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**Background.** There is still a widespread notion that bony fishes with high fecundities are more productive and therefore more resistant to overexploitation. The purpose of this study was to formally explore the relationship between fecundity and reproductive success expressed as maximum annual reproductive rate, i.e. the number of new spawners produced by existing spawners at low population densities.

**Material and methods.** We used maximum annual reproductive rate from a recent study covering 49 species of bony fish; we used fecundity estimates from the published literature.

**Results.** We found no significant relationship between fecundity (ranging from 368 to 10 million eggs) and maximum annual reproductive rate (ranging from 0.4 to 13.5 replacement spawners).

**Conclusion.** Fecundity in oviparous bony fish without parental care has no relation with reproductive success. Apparently high fecundity in bony fish has evolved to counterbalance pre-adult mortality, as indicated by the fact that variance in fecundity is 3 orders of magnitude larger than variance in annual reproductive rate.

**Key words:** fish, fecundity, annual reproductive rate, pre-adult mortality.

### INTRODUCTION

The widespread notion that the high fecundity of fish protects them against overexploitation is rather old, and can be traced at least to Jean-Baptiste de Monet de Lamarck, who thought that: “*animals living in the waters, especially the sea waters are protected from the destruction of their species by man. Their multiplication is so rapid and their means of evading pursuit or traps are so great that there is no likelihood of his being able to destroy the entire species of these animals*” (Lamarck 1809). The ‘rapid multiplication’ mentioned here was probably inferred from the well-known high fecundity of most commercial fish. However, if such relationship existed then the

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oceans of the world should be packed with ocean sunfish, *Mola mola* (Linnaeus, 1758), which made it into the Guinness Book of World Records (Foot 2000) as the most fecund fish with up to 300 million eggs per female. In reality, however, the ocean sunfish is less abundant than some sharks with very low fecundity. Indeed, this paradox was noted by Charles Darwin, who observed that: “[t]he *picked dog-fish* (*Squalus acanthias*) *actually swarms on many coasts & yet is said to lay only six \*eggs; whereas the cod-fish sometimes lays above three million & a half*” (Stauffer 1975). Similarly, Hjort (1914) at the dawn of fishery research observed that: “...it is difficult to avoid the conclusion that the actual quantity of eggs spawned is not a factor in itself sufficient to determine the numerical value of a [resulting] year class.”

The reproductive rate of animals is defined as the average number of offspring per parent that survive to a certain age. If such age is taken as age at first maturity, then we obtain the number of replacement spawners per spawner. Population theory suggests that this rate will be near its maximum at low population densities far from the carrying capacity of the respective ecosystem (Baranov 1918, Ricker 1975, Myers and Mertz 1997, Myers 2001). Myers et al. (1999) provided estimates of maximum annual reproductive rate at low population densities for 57 species of bony fish based on analyses of spawner-recruitment series for 700 stocks. They reviewed various methods that have been used to estimate reproductive rate in fishes and concluded that the standardized slope at the origin of the spawner-recruitment function was most appropriate, being relatively constant within species and with relatively little variance among species. Here we use these data to explore the relationship between annual reproductive rate and annual mean and minimum fecundity.

## MATERIAL AND METHODS

Maximum annual reproductive rates ( $\alpha$ ) at low population densities were taken from Myers et al. (1999). For annual fecundity we used two independent data sets: The first set is from Mertz and Myers (1996) who provided “mean fecundity per year for reproductive individuals” for twenty-three species.

The second set consists of fecundity estimates from the literature as compiled in FishBase (Froese and Pauly 2000). For the purpose of this study we assumed that the lower end of fecundity ranges given in the literature was a reasonable proxy for fecundity at first maturity. No fecundity estimates were found for *Pennahia argentata* and *Pleurogrammus monopterygius*. Table 1 shows the maximum annual reproductive rates of Myers et al. (1999), mean fecundity estimates by Mertz and Myers (1996), and fecundity at first maturity estimates, together with the respective references.

**Table 1**

Maximum annual reproductive rate ( $\alpha$ ), mean and minimum annual fecundity with references for 49 species used in this study

Species	$\alpha^*$	Annual Fecundity (mean)**	Annual Fecundity (min.)	References
<i>Alosa aestivalis</i>	13.5		52 300	Jessop 1993
<i>Alosa pseudoharengus</i>	3.63		68 400	Jessop 1993
<i>Alosa sapidissima</i>	5.21		70 000	Melvin et al. 1985
<i>Brevoortia patronus</i>	3.49	335 000	5000	Lewis and Roithmayr 1981
<i>Brevoortia tyrannus</i>	9.02	335 000	38 000	Higham and Nicholson 1964
<i>Clupea harengus</i>	2.08	142 000	20 000	Muus and Nielsen 1999
<i>Engraulis encrasicolus</i>	2.01		13 000	Muus and Nielsen 1999
<i>Engraulis mordax</i>	1.39	25 000	20 000	Hart 1973
<i>Esox lucius</i>	1.66		25 000	Koli 1990
<i>Gadus morhua</i>	3.94	2 000 000	500 000	Muus and Nielsen 1999
<i>Harpodon nehereus</i>	1.36		89 600	Fernandez and Devaraj 1996
<i>Lophius budegassa</i>	0.93		46 320	Tsimenidis 1980
<i>Lutjanus campechanus</i>	6.68		11 613	Collins et al. 1996
<i>Melanogrammus aeglefinus</i>	2.05	700 000	55 000	Cohen et al. 1990
<i>Merlangius merlangus</i>	3.13	400 000	109 358	Christiansen et al. 1997
<i>Merluccius bilinearis</i>	0.84	700 000		
<i>Merluccius hubbsi</i>	3.25		267 400	Ehrlich 1998
<i>Merluccius productus</i>	0.39	79 000	33 000	MacGregor 1966
<i>Micromesistius poutassou</i>	1.8	200 000	122 000	Christiansen et al. 1997
<i>Morone saxatilis</i>	2.58		14 000	Scott and Crossman 1973
<i>Oncorhynchus gorbuscha</i>	3.39	1500	800	Scott and Crossman 1973
<i>Oncorhynchus keta</i>	3.71	3600	2400	Scott and Crossman 1973
<i>Oncorhynchus nerka</i>	4.81	3600	368	Scott and Crossman 1973
<i>Oncorhynchus tshawytscha</i>	7.32		4242	Scott and Crossman 1973
<i>Pagrus auratus</i>	3.82		150 000	Hayes 1994
<i>Platichthys flesus</i>	0.97		400 000	Spratte and Hartmann 1997
<i>Limanda ferruginea</i>	2.2	1 500 000		
<i>Pleuronectes platessa</i>	2.51	80 000	50 000	Muus and Nielsen 1999
<i>Pollachius virens</i>	3.19	225 000	220 000	Christiansen et al. 1997
<i>Reinhardtius hippoglossoides</i>	2.12	165 000	15 000	Junquera et al. 1999
<i>Salmo salar</i>	4.31	8300	8000	Muus and Dahlström 1974
<i>Salvelinus fontinalis</i>	4.71		1000	Scott and Crossman 1973
<i>Salvelinus namaycush</i>	2.51		5000	Spillman 1961
<i>Sardina pilchardus</i>	0.57		50 000	Muus and Nielsen 1999
<i>Sardinops sagax</i>	1.93	200 000	10 000	Fletcher 1990
<i>Scomber japonicus</i>	0.95	1 000 000	101 859	Ciechowski and Capezzani 1969
<i>Scomber scombrus</i>	3.03	400 000	200 000	Muus and Nielsen 1999
<i>Sebastes goodie</i>	0.43		29 000	Hart 1973
<i>Solea solea</i>	1.93	350 000	100 000	Muus and Nielsen 1999
<i>Sprattus sprattus</i>	2.39		242 800	Torstensen 1985
<i>Stenotomus chrysops</i>	13.5		3860	Gray 1990
<i>Stizostedion vitreum</i>	2.48		46 524	Sakamoto and White 1974
<i>Theragra chalcogramma</i>	1.32	600 000	60 000	Witherell 1996
<i>Thunnus albacares</i>	4.18		200 000	McPherson 1991
<i>Thunnus obesus</i>	2.08		2 900 000	Collette and Nauen 1983
<i>Thunnus thynnus</i>	0.67		10 000 000	Muus and Nielsen 1999
<i>Trachurus mediterraneus</i>	1.28		425 061	Anon. 2001
<i>Trachurus trachurus</i>	1.68	364 000	77 090	Deniel 1989
<i>Xiphias gladius</i>	5.47		2 000 000	Nakamura 1985

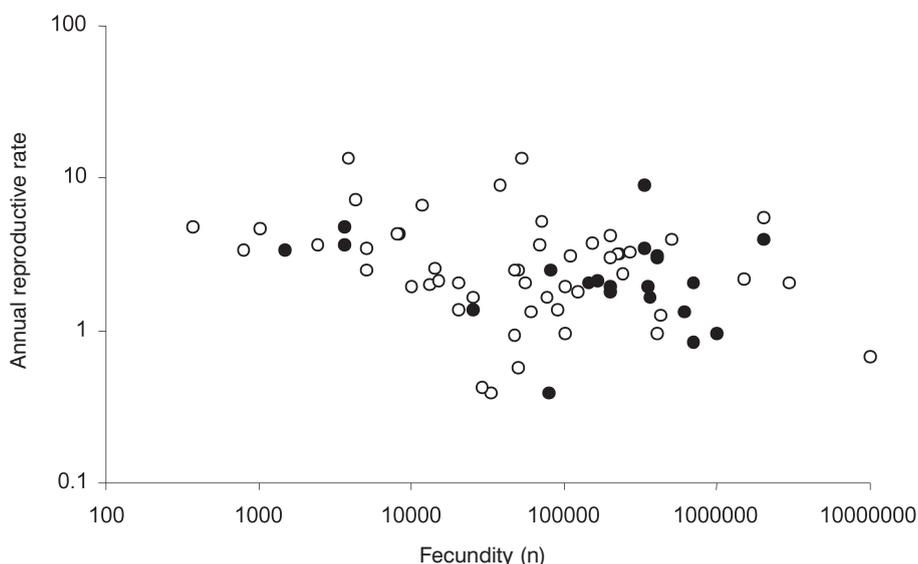
\* Values taken from Myers et al. 1999, \*\*Values taken from Mertz and Myers 1996.

## RESULTS AND DISCUSSION

Fecundity in number of eggs spawned annually per female is mainly a function of female body weight, and thus population fecundity depends foremost on the size composition of females in a given spawning stock. For the purpose of this study we considered two scenarios: 1) that spawning stocks at low densities consists mainly of first-time spawners (Ballara and Livingston 2001, Murphy and Crabtree 2001, Walsh et al. 2003) and therefore fecundity at age of first maturity is taken as proxy for population fecundity; and 2) that spawning stocks have some age structure and therefore mean fecundity is taken as proxy of population fecundity (Mertz and Myers 1996).

Myers et al. (1999) suggested that the maximum annual reproductive rate ( $\alpha$ ) is log-normally distributed, “usually ranging from 1 to 7 for species for which we have several populations in our analysis.” We re-examined their data and found the annual reproductive rates of *Anoplopoma fimbria* ( $\alpha = 0.10$ ), *Coilia dussumieri* ( $\alpha = 15.3$ ), *Plecoglossus altivelis* ( $\alpha = 113$ ), *Sebastes alutus* ( $\alpha = 0.15$ ), *Sebastes mentella* ( $\alpha = 0.34$ ), and *Thunnus maccoyii* ( $\alpha = 0.22$ ) to be outliers (distance from mean much larger than two standard deviations) if log-normal distribution of  $\alpha$  is assumed. After removal of these species the dataset passed normality tests (Skewness Test: Value =  $-0.19$ ,  $Z = -0.62$ , Prob. = 0.5342; Kurtosis Test: Value = 3.07,  $Z = 0.52$ , Prob. = 0.6002; Omnibus Test:  $K_2 = 0.66$ , Prob. = 0.7186).

Mertz and Myers (1996) found no significant relationship between recruitment variability and fecundity. In the present paper we explored the relationship between reproductive rate and fecundity. Fig. 1 shows a plot of maximum annual reproductive rates versus mean fecundity (solid dots) and minimum fecundity (open dots). Analysis of variance results in acceptance of the null hypothesis for minimum fecundity estimates ( $F_{43, 0.05} = 1.99$ ;  $P = 0.266$ ) as well as for mean fecundity ( $F_{17, 0.05} = 2.91$ ;  $P = 0.121$ ), i.e. there is no significant correlation between fecundity and reproductive success as expressed by the maximum annual reproductive rate. Myers and Barrowman (1996) and Myers (1997) demonstrated that especially at low population sizes “recruitment is a function of spawner abundance.” Sadovy (2001) presents evidence of depensation, i.e. less than expected reproductive success at very low population densities. Combining these findings with our results suggests that the number of spawners is more important for recruitment than the number of eggs produced. We hypothesise that a high number of spawners will cover a larger area and a wider time window in sufficient densities and thus increase the chances that at least some batches of eggs and larvae encounter conditions in their highly variable aquatic environment that favour survival and growth.



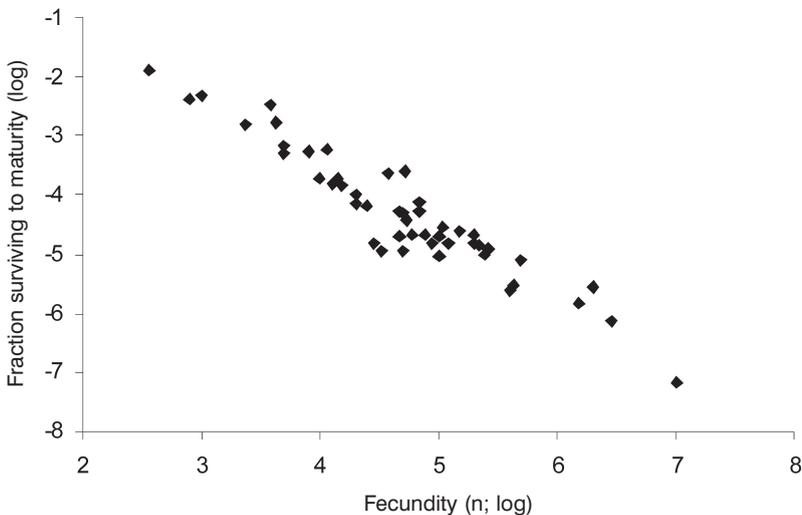
**Fig. 1.** Maximum annual reproductive rate versus mean (solid dots) and minimum (open dots) annual fecundity

Our results confirm a study by Denney et al. (2002) who found no relationship between annual reproductive rate (which they term 'adult production') and fecundity in 20 fish species of the Northeast Atlantic. They found a negative correlation between 'recruit production' and fecundity, but this may be biased by the artificial nature of the age at recruitment, i.e. the age when fish are first caught, compared to the age at first maturity. Our analysis of a larger data set confirms the conclusion of Denney et al. (2002) that there is no basis for assuming that high fecundity confers high resilience to exploitation; such misconceptions actually pose a threat to highly fecund fishes (Sadovy 2001). Note that our study refers strictly to highly fecund bony fish, not to species with very low fecundities such as most elasmobranchs which have annual reproductive rates an order of magnitude below bony fish (Smith et al. 1998) and thus appear unsuitable to withstand commercial fishing pressure.

Serge Garcia (FAO, pers. comm.) pointed out that an un-fished population reduced by natural events such as a sequence of recruitment failures will consist mostly of large, old fishes with higher fecundity, larger eggs and larvae, and more 'spawning experience', all of which should contribute to increased reproductive success per spawner in addition to density-related effects enhancing pre-adult survival. In contrast, a population reduced by fishing will consist mostly of first-time spawners with lower fecundity, less viable eggs and larvae, and no spawning experience (Longhurst 2002). Thus, the maximum annual reproductive rate can be expected to be different depending whether it was estimated from a population reduced by fishing or

by natural events. We agree with this reasoning, which would suggest that the  $\alpha$ -estimates of Myers et al. (1999)—which were derived from heavily fished stocks—should be lower than those derived from populations reduced by natural events. Such bias should, however, have no bearing on the missing relationship between fecundity and maximum annual reproductive rate explored in this study.

The variance of the maximum annual reproductive rate ( $\alpha$ ) is considerably smaller than that of fecundity, which spans 5 orders of magnitude in oviparous bony fish without parental care (Fig. 1). Given that  $\alpha$ —which was derived here without consideration of fecundity—can be viewed as the product of annual fecundity ( $F$ ) and the fraction surviving to maturity ( $S$ ) and given that there is no relationship between  $\alpha$  and  $F$ , it follows that there is also no relationship between  $\alpha$  and pre-adult survival ( $S$ ). Thus, it seems that high fecundity has evolved primarily to counter-balance pre-adult mortality typically suffered by offspring, resulting on average in a maximum annual reproductive rate that is high enough to ensure replacement of spawners and population growth, and small enough to avoid over-investment in reproductive effort. This is highlighted by Fig. 2 where we plot  $S$  over  $F$ . Note, however, that we derived  $S$  from  $S = \alpha / F$  and thus while the graph is useful to visualize how variance of both variables is reduced from 5 to about 1 order of magnitude, it can not be used to predict  $S$  or  $\alpha$  from fecundity.



**Fig. 2.** Relationship between pre-adult survival ( $S$ ) and fecundity ( $F$ ) (note, however, that  $S = \alpha / F$  and thus not independent of  $F$ )

The lack of a relationship between fecundity and maximum annual reproductive rate should not be surprising given that the life-time reproductive rate at steady population sizes near the carrying capacity of the respective environment is unity, i.e.

every spawner is replaced by one spawner, independent from fecundity and reproductive strategies.

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