

Evidence for harvest-induced maternal influences on the reproductive rates of fish populations

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Knowledge of the relationship between the number of offspring produced (recruitment) and adult abundance is fundamental to forecasting the dynamics of an exploited population. Although small-scale experiments have documented the importance of maternal quality to offspring survival in plants and animals, the effects of this association on the recruitment dynamics of exploited populations are largely unknown. Here, we present results from both a simple population model and a meta-analysis of time-series data from 25 species of exploited marine fishes that suggest that a population of older, larger individuals has a higher maximum reproductive rate than an equivalent population of younger, smaller individuals, and that this difference increases with the reproductive lifespan of the population. These findings (i) establish an empirical link between population age structure and reproductive rate that is consistent with strong effects of maternal quality on population dynamics and (ii) provide further evidence that extended age structure is essential to the sustainability of many exploited fish stocks.

Keywords: maternal effects; fisheries-induced demographic shift; population dynamics; reproductive rate; stock recruitment; relative fecundity

1. INTRODUCTION

The importance of parental quality (both genotypic and phenotypic) to offspring survival has been documented extensively in plants and animals (Bernardo 1996; Rossiter 1996; Mousseau & Fox 1998), and these parental influences on survival are believed to contribute to the dynamics of natural populations (Ginzburg 1998; Fowler 2005). Such an effect of parental quality on population dynamics has been demonstrated convincingly in soil mites (Benton *et al.* 2005), but empirical evidence from other taxa is both limited and inconsistent (e.g. Erelli & Elkinton 2000; Banks & Powell 2004).

Experiments with fishes suggest that offspring survival varies positively with the age, size and condition of parents, as well as the size and content of gametes (Heath & Blouw 1998; Berkeley *et al.* 2004; Rideout *et al.* 2004; Kamler 2005 and references therein), and recent evidence has suggested that these relationships are relatively consistent across years (Seamons *et al.* 2007). When parental influences are incorporated into population models, total offspring production (i.e. recruitment) is sensitive to fisheries-induced demographic changes that alter the distribution of ages or sizes within a population (e.g. Forbes & Peterman 1994; Murawski *et al.* 2001; but see O'Farrell & Botsford 2006). These results are at odds with both prevailing fisheries

theory—which assumes that parental quality plays a negligible role in shaping population dynamics—and current management strategies—which largely either ignore population age structure or promote the harvest of larger individuals (e.g. Myers & Mertz 1998).

The extrapolation of results from experiments to entire populations can be problematic because parental influences might be expressed differently in the wild than in captivity (Bernardo 1996; Chambers & Leggett 1996), or might affect the relative fitness of individual adults (Einum & Fleming 2000) without affecting the reproductive rate of a population (Charlesworth 1980). While the dynamics of exploited fish stocks can behave in ways that are consistent with effects of parental influences on offspring survival (Martensdottir & Thorarinsson 1998; Marshall & Frank 1999; Marshall *et al.* 1999; Hsieh *et al.* 2006, 2008), direct evidence of this phenomenon is limited to one study of a population of Atlantic cod (*Gadus morhua*) in which recruitment varied positively with the proportion of eggs spawned by older fish (Vallin & Nissling 2000). Indeed, a recent comparison of 29 exploited and unexploited populations of coastal California fish has yielded little support for the hypothesis that parental influences drive boom-and-bust cycles at low abundance (Anderson *et al.* 2008).

In this study, we use both a population model and a meta-analysis of data from 25 exploited marine fish species to show that maternal quality can have strong effects on a population's maximum reproductive rate. We refer to these effects as maternal influences (MI), which acknowledge potential effects of both maternal phenotype (i.e. maternal effects) and genotype. Because maximum reproductive rate is an estimate of the maximum rate of

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Table 1. Abbreviations and symbols.

abbreviation or symbol	description
A	maternal age in years
$\bar{A}$	the mean age of spawners in years (an index of age structure)
b	the exponent of maternal age-specific fecundity
d	the exponent of maternal age-specific egg viability
f	fecundity (the number of eggs)
f'	relative fecundity (the number of eggs per unit mass of female)
RLS	reproductive lifespan in years ($=L-T+1$)
L	maximum age in years
MI	maternal influences; the effects of maternal quality (both phenotypic and genetic) on offspring survival
$m[\bar{A}]$	the body mass of a spawner of average age
N	abundance in numbers (subscripts specify age(s) and time)
SSB	spawning stock biomass (the total mass of all spawning adults)
t	time in years
T	age-at-maturity in years
v	egg viability
α	the slope at any point along the stock–recruitment relationship ($=$ age 1 abundance at time $t+1$ divided by a measure of spawning population size such as abundance, SSB, or egg production at time t)
α_0	the slope at the origin of the stock–recruitment relationship (an estimate of the maximum reproductive rate that occurs when spawning population size is very small)
α_0^g/α_0^d	the ratio of α_0 during the period of population growth to α_0 during the period of population decline (an estimate of the difference in reproductive rate between periods of growth and decline)

exploitation that a population can sustain (Myers *et al.* 1999), our findings provide insight into failures of past management strategies, and offer a practical remedy by demonstrating that fisheries that promote or protect extended age structure in a stock can be both sustainable and productive.

2. THE LOGIC OF MI ON REPRODUCTIVE RATE

In fisheries science, stock–recruitment relationships (i.e. relationships that link offspring abundance to adult abundance, adult biomass or egg production) are fundamental to determining the dynamics of exploited populations and the sustainability of fisheries (Hilborn & Walters 1992). In this section, we introduce a population model that illustrates how MI on survival can affect the slope at the origin of a stock–recruitment relationship (α_0). The symbols and abbreviations used here and throughout the text are summarized in table 1. A complete description of this model is available as electronic supplementary material.

Consider an age-structured population in which (i) maturity and survival are fixed for ages 1 to L , where L is maximum age, (ii) individuals reproduce once annually from the start of their T th year of life until they die at the end of their L th year, where T is the age-at-maturity, (iii) all age groups exhibit a 1 : 1 sex ratio and (iv) demographic effects of density are limited to a linear, positive relationship between larval mortality and density that results in a Beverton–Holt (i.e. concave down, positive asymptotic) recruitment relationship (Hilborn & Walters 1992) between larval abundance in year t and the abundance of age-1 fish in year $t+1$. As population abundance declines, larval mortality becomes increasingly density independent, and the slope (α) of the stock–recruitment relationship approaches a maximum value (α_0). Finally, assume that egg production per female increases with maternal age (A) according to the equation

$f \cdot A^b$ (e.g. Quince *et al.* 2008a,b), and the density-independent component of egg viability (i.e. MI) increases with A according to the equation $v \cdot A^d$ where f and v are >0 and the exponents b and d are ≥ 0 . Because $v \cdot A^d$ often arises from an increase in egg size with A (Heath & Blouw 1998), either (or both) of these expressions is consistent with theoretical and empirical evidence that the ratio of gonadal mass to somatic mass (i.e. reproductive investment) often increases with maternal age (e.g. Quince *et al.* 2008a,b).

Given these assumptions, it follows that, when population abundance is low,

$$N_{1,t+1} \approx f \cdot \bar{A}^d \cdot v \cdot \bar{A}^d \cdot N_{T:L,t}^F = f \cdot \bar{A}^d \cdot v \cdot \bar{A}^d \cdot 1/2 \cdot N_{T:L,t}, \quad (2.1)$$

where $N_{1,t+1}$ is the number of age-1 individuals at the start of year $t+1$; $N_{T:L,t}^F$ is the number of spawning females (i.e. females aged T to L) at the start of year t ; $N_{T:L,t}$ is the number of spawning adults at the start of year t ; and $\bar{A}$ is the mean age of spawners, sexes combined (see the electronic supplementary material). According to this equation, α_0 will only depend on $\bar{A}$ if egg production or viability increase with A (i.e. b or $d > 0$). For example, if exponents b and $d = 0$ (i.e. both egg production and viability are independent of A) then α_0 is independent of $\bar{A}$, regardless of whether the spawning population is measured as abundance ($\alpha_0 \approx N_{1,t+1}/N_{T:L,t} \approx 1/2 \cdot f \cdot v$) or total egg production [$\alpha_0 \approx N_{1,t+1}/(f \cdot 1/2 \cdot N_{T:L,t}) \approx v$]. If $b > 0$ and $d = 0$ (i.e. egg production increases with A while egg viability remains constant), then α_0 is independent of $\bar{A}$ only if the spawning population is measured as total egg production $\alpha_0 \approx N_{1,t+1}/(f \cdot \bar{A}^b \cdot 1/2 \cdot N_{T:L,t}) \approx v$. However, if relative fecundity (the number of eggs per unit female body mass, f') does not vary with A or size, then spawning stock biomass (SSB) can also be used to express α_0 , so that it is independent of $\bar{A}$: $\alpha_0 \approx N_{1,t+1}/(m[\bar{A}] \cdot N_{T:L,t}) \approx 1/2 \cdot f' \cdot v$, where $m[\bar{A}]$ is the body mass of an age- $\bar{A}$

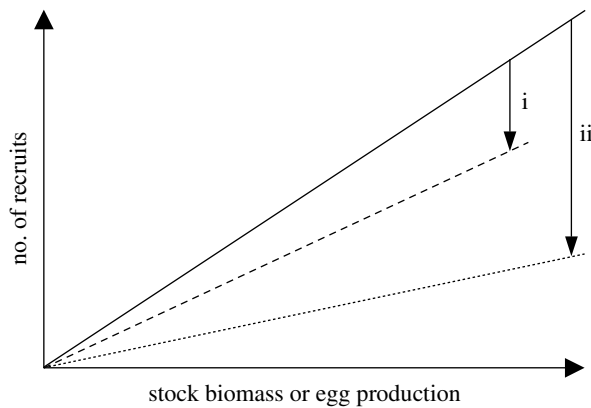


Figure 1. Hypothetical stock–recruitment relationships showing how MI on survival can affect the slope at the origin (α_0), and how this affect increases with RLS. When MI are absent, α_0 is independent of the mean age of spawners ($\bar{A}$) and describes a single (solid) line. When MI are present, α_0 decreases with a decrease in $\bar{A}$. Because the decrease in $\bar{A}$ for a fixed reduction in adult survival rate depends directly on RLS (figure 1 in the electronic supplementary material), the decrease in α_0 for a species that has a short RLS will be small (i, dashed line) relative to the decrease in α_0 for a species that has a long RLS (ii, dotted line). See text and the electronic supplementary material for details.

spawner. See §3c for further discussion of the age- or size dependence of relative fecundity. Finally, if both b and $d > 0$ (i.e. both egg production and viability increase with A), then α_0 depends on $\bar{A}$, even when the spawning population is measured as total egg production [$\alpha_0 \approx N_{1,t+1}/(f \cdot \bar{A}^b \cdot 1/2 \cdot N_{T,L,t}) \approx v \cdot \bar{A}^d$].

Another property of this model is that $\bar{A}$ varies directly with both adult survival rate and reproductive lifespan (RLS = $L - T + 1$) such that the absolute reduction in $\bar{A}$ that results from a fixed reduction in adult survival rate (e.g. as a result of exploitation) is effectively 0 if RLS = 1, but increases rapidly as RLS increases from 1 (see the electronic supplementary material and figure 1 in the electronic supplementary material). Therefore, in an exploited, age-structured population in which f' and (or) egg viability increase with A , we expect α_0 for a stock–recruitment relationship based on SSB to exhibit the following dynamics: (i) α_0 during periods of high adult survival is greater than α_0 during periods of low adult survival, because the former is associated with higher values of $\bar{A}$ and (ii) this difference in values of α_0 increases with RLS because the reduction in $\bar{A}$ for a given reduction in survival rate increases with RLS (figure 1).

3. EVIDENCE FOR MI ON REPRODUCTIVE RATE

(a) Meta-analysis of marine fisheries data

Although our model predicts MI on maximum reproductive rate that increases with RLS (figure 1), population dynamics in the wild are shaped by a suite of interacting physical and biological factors (Hilborn & Walters 1992; Trippel 1995; Mueter *et al.* 2007) that could overwhelm MI and limit their relevance to management.

To test for this mechanism in wild populations, we conducted a within-population meta-analysis of published marine stock–recruitment data. We restricted this meta-analysis to populations in which fishing mortality was likely to have contributed to large and consistent changes in SSB by applying the following selection

criteria: (i) minimum SSB 40 per cent or less of maximum SSB over the duration of the time series, (ii) SSB exhibiting distinct periods of both growth and decline that each span 10 years or more, (iii) periods of both growth and decline spanning a similar range of SSB, and (iv) fishing mortality (or exploitation rate) significantly higher during the period of SSB decline than during the period of SSB growth (tables 1 and 2 in the electronic supplementary material). Because fishing mortality in these time series was typically estimated by analysing the age distribution of a catch, high and low fishing mortalities sustained for periods of 10 years or longer were reliable indicators of adult survival and, by extension, the mean age of spawners. Criterion (ii) also ensured a reasonable sample size with which to estimate the stock–recruitment relationship for each period and criterion (iii) controlled for possible confounding effects of density by ensuring that differences in population dynamics did not simply reflect differences in the intensity of density-dependent processes (e.g. life-history changes, Allee effects). To avoid confounding effects of viviparity, parental care and associated characteristics of life history, we limited our analysis to broadcast spawners that did not change sex with age.

For each population (or region if population-specific data were unavailable), we estimated RLS from published data by subtracting age-at-maturity from maximum age and then adding 1 (tables 1 and 2 in the electronic supplementary material). For the periods of both growth and decline in a population, we then calculated the slope at the origin of the stock–recruitment relationship (α_0) by linear analysis of covariance of log recruitment on log SSB with period as a categorical variable. Sample sizes were generally too small (10–39 per period) to assess the normality of residuals via statistic tests, but visual inspection of the distribution of residuals indicated no serious departures from normality. We detected one influential observation in 7 of 39 populations, but the removal of these observations had a negligible effect on the overall result (i.e. figure 2). Following diagnostics, we used the ratio of α_0 during the period of population growth to α_0 during the period of population decline α_0^g/α_0^d as a measure of the difference in maximum reproductive rate between periods. Values of α_0^g/α_0^d were then regressed on values of RLS at both the species and family level (table 2 in the electronic supplementary material).

(b) Meta-analysis results and discussion

We identified 39 marine populations (25 species) in which SSB showed distinct periods of growth and decline that were associated with periods of low and high fishing mortality (i.e. extended and truncated age structure), respectively. All of these populations were located in the north temperate and Arctic climatic zones. Consistent with our population model, our meta-analysis of these data suggested that the ratio of α_0 during growth to α_0 during decline α_0^g/α_0^d varied positively and significantly with RLS across both species (figure 2a) and families (figure 2b). This result suggests that MI on reproductive rate is a general phenomenon among populations of long-lived, marine fishes; independent of SSB, populations that have an extended age structure have higher reproductive rates—and therefore support a higher rate of exploitation—when that structure is preserved.

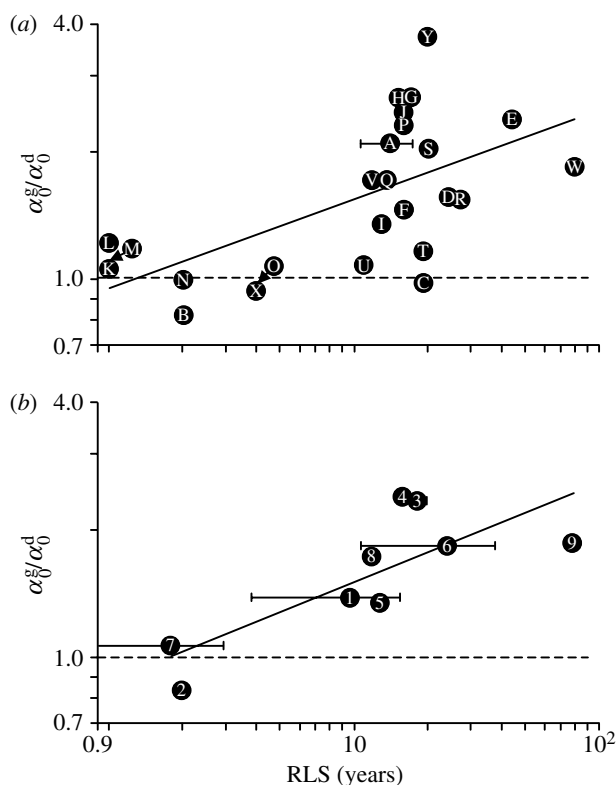


Figure 2. Results of a meta-analysis showing the ratio of α_0 during growth to α_0 during decline (α_0^g/α_0^d) versus RLS for (a) species ($\alpha_0^g/\alpha_0^d = 0.950 \cdot \text{RLS}^{0.209}$, $r^2 = 0.38$, $n = 25$, $P = 0.001$) and (b) families ($\alpha_0^g/\alpha_0^d = 0.878 \cdot \text{RLS}^{0.232}$, $r^2 = 0.61$, $n = 9$, $P = 0.006$). Solid lines were fit by regression analysis. Dashed lines indicate no difference between α_0 s (i.e. $\alpha_0^g/\alpha_0^d = 1$). Horizontal error bars are 95% CI; vertical error bars were not calculated because of the statistical properties of ratios (Atchley *et al.* 1976). Note that both axes are logarithmic. Letters and numbers refer to species and families, respectively: (a) A, *Clupea harengus* (Atlantic herring); B, *Engraulis encrasicolus* (European anchovy); C, *Gadus macrocephalus* (Pacific cod); D, *Gadus morhua* (Atlantic cod); E, *Hippoglossus stenolepis* (Pacific halibut); F, *Limanda aspera* (yellowfin sole); G, *Merlangius merlangus* (whiting); H, *Melanogrammus aeglefinus* (haddock); I, *Merluccius productus* (North Pacific hake); J, *Micromesistius poutassou* (blue whiting); K, *Oncorhynchus gorbuscha* (pink salmon); L, *Oncorhynchus keta* (chum salmon); M, *Oncorhynchus kisutch* (coho salmon); N, *Oncorhynchus nerka* (sockeye salmon); O, *Oncorhynchus tshawytscha* (chinook salmon); P, *Ophiodon elongatus* (lingcod); Q, *Parophrys vetulus* (English sole); R, *Pleuronectes platessa* (European plaice); S, *Pleuronectes quadrituberculatus* (Alaska plaice); T, *Pollachius virens* (saithe); U, *Sardinops sagax* (South American pilchard); V, *Scomber japonicus* (chub mackerel); W, *Sebastes alutus* (Pacific Ocean perch); X, *Sprattus sprattus* (European sprat); Y, *Theragra chalcogramma* (Alaska Pollock) and (b) 1, Clupeidae (herring-like fishes); 2, Engraulidae (anchovies); 3, Gadidae (cods and haddocks); 4, Hexagrammidae (greenlings); 5, Merlucciidae (merluccid hakes); 6, Pleuronectidae (righteye flounders); 7, Salmonidae (salmonids); 8, Scombridae (mackerels); 9, Scorpaenidae (rockfishes).

This result is also consistent with evidence that recruitment can vary with indices of maternal energy reserves (Marshall & Frank 1999; Marshall *et al.* 1999) or positive effects of maternal age on egg size (Vallin & Nissling 2000). Conversely, the absence of this phenomenon among salmonids (data points K–O and 7 in figure 2) is

inconsistent with the overwhelming evidence for MI on survival in this taxon (reviewed in Seamons *et al.* 2007). We propose two mechanisms to explain this discrepancy. First, because the age and size ranges of adults in these populations are relatively narrow, it is unlikely that fisheries differentially selected for reproductively valuable adults (although selection can be strong if these adults are spatially or temporally distributed). Second, our population model predicts relatively small differences in α_0 at low values of RLS, even when exploitation is age- or size selective (see above).

(c) Alternative explanations

A comprehensive evaluation of the importance of MI on survival, relative to other factors that affect the dynamics of individual populations, requires thorough, population-specific analyses that are beyond the scope of this paper. However, we can assess whether alternative explanations are plausible.

First, exploitation often triggers density-dependent life-history responses (e.g. early maturation, more eggs per mass of female) that can accelerate population growth rate (Rochet 1998). Results of our meta-analysis are largely independent of these and other density-dependent processes (e.g. cannibalism, Allee effects) because we explicitly controlled for effects of density by ensuring that, for each population, periods of growth and decline spanned a similar range of population densities (i.e. SSB values).

Second, a history of intense exploitation in most of the populations that we included in our analysis might have affected our estimates of both α_0^g/α_0^d and RLS. For example, we probably underestimated RLS in populations where exploitation limited longevity. In addition, lower than expected α_0^g/α_0^d values for some intensely exploited species (e.g. Atlantic cod) might reflect either a shift in age structure from truncated to extremely truncated, or slow rates of population growth as a result of fisheries-induced evolutionary changes in life history (Law 2007 and references therein). Given that these ‘ghosts of exploitation past’ tend to underestimate α_0^g/α_0^d , it seems unlikely to us that they generated a spurious relationship with RLS.

Third, long-term climatic conditions (regimes) can dominate the recruitment dynamics of many marine fish stocks by causing persistent and geographically pervasive changes in the carrying capacity of a marine environment (Mueter *et al.* 2007). However, for climate regimes to explain the positive relationship between α_0^g/α_0^d and RLS, they must have closely coincided with periods of relatively high and low fishing mortality, and affected long-lived species more strongly than short-lived ones. We argue that such coincidences are highly unlikely, and instead suggest that the extent to which climate regimes influence population dynamics in ways that are consistent with MI on reproductive rate is more likely to depend on the extent of fisheries-induced age or size truncation. Specifically, if individuals that could contribute the most to recruitment are absent from a population, then that population will be less likely to produce strong year classes when environmental conditions are favourable, and more likely to experience recruitment failure when environmental conditions are poor. Whereas climate regimes determine maximum reproductive rate (α_0), MI determine, via a fisheries-induced demographic shift, the extent to which this maximum is realized.

Finally, our model predicts that if egg production increases disproportionately with female size or age, such that older females produce more eggs per unit body mass (i.e. have a higher relative fecundity; f') than younger females, then egg production alone might explain the positive relationship between α_0^g/α_0^d and RLS (note that differences in f' among ages are not to be confused with a density-dependent change in f' across all ages, which was largely controlled for in our study; see above). An increase in f' with age is consistent with both a trade-off between egg size and number (Roff 1992)—provided that this trade-off affects older females more than it does younger females—and an increase in reproductive investment with age (Quince *et al.* 2008a,b). To estimate the extent to which maternal age and size affects f' in exploited, north temperate and arctic marine fish populations, we conducted a meta-analysis of published results and data (table 3 in the electronic supplementary material). Of the 25 species examined, 15 (60%) showed a significant ($P > 0.05$) increase in f' with age or size in at least 1 year or population (table 3 in the electronic supplementary material); 9 of 16 (56%) among long-lived species ($RLS \geq 10$ according to figure 2). Across all populations, species, families and orders, these significant relationships explained, on average, $31\% \pm 11$, 95% CI of the variation in f' and predicted a doubling of f' (2.2 ± 1.1) between observed extremes of age or size (table 3 in the electronic supplementary material). Including the non-significant regressions, maternal age or size explained 17 ± 7 per cent of the variation in f' and predicted a 1.7 ± 0.4 fold increase in f' (table 3 in the electronic supplementary material). Therefore, population-specific analyses should consider the importance of age- or size-specific f' to recruitment, and use total egg production, rather than SSB, to develop stock–recruitment relationships (Rothschild & Fogarty 1989). However, given that (i) predicted increases in f' were based on the unlikely assumption that populations were composed of extremes of age or size and (ii) relationships between f' and age or size can be absent in many years, populations and species (table 3 in the electronic supplementary material), these MI on egg production, while potentially influential, are insufficient to explain the observed relationship between α_0^g/α_0^d and RLS.

4. MANAGEMENT IMPLICATIONS

Given that MI on survival (and relative fecundity) can affect the maximum reproductive rates of long-lived marine fishes, management strategies must recognize that stock–recruitment relationships can vary in the absence of meta-population structure and environmental variability (Hilborn & Walters 1992); non-stationarity can also result from fisheries-induced demographic changes in long-lived species. In effect, the shape of any stock–recruitment relationship is user defined; it depends upon the age- or size classes that a fishery targets, as well as those that it protects. Our evidence for MI on maximum reproductive rate contributes to a growing body of literature that illustrates the complexity of stock–recruitment relationships (e.g. Sakuramoto 2005; Minto *et al.* 2008), and cautions strongly against the continued use of these relationships without considering explicitly fisheries-induced demographic changes over time (Marteinsdottir & Thorarinsson 1998).

Management strategies must also recognize that older, larger females are essential to the sustainability of a fishery. Age structure exists, in part, because the strategy of maturing late and spawning over multiple years (i.e. having a relatively long RLS) confers—on older, larger females—an advantage when competing in variable environments for resources that support successful reproduction (Winemiller & Rose 1992; Hsieh *et al.* 2006); MI on offspring survival stem directly from this advantage. Existing management strategies typically operate to reduce age structure, which undermines the advantages of an extended RLS (Hsieh *et al.* 2006). In short, forcing an iteroparous species to spawn as if it was semelparous is unsustainable.

We acknowledge that there are conditions (e.g. reproductive senescence) and species (e.g. sex-changing fishes) for which parental age does not equate to parental quality. However, our study shows that, over a broad range of densities and species of exploited fishes, maximum reproductive rate tends to increase with the mean age or size of spawning adults, a result that stems, in part, from the tendency of older, larger females to produce offspring that are more likely to survive. This result argues strongly for management strategies that not only regulate total mortality, but do so in ways that restore and protect age- or size structure—e.g. by adopting appropriate size regulations, changing the design and use of fishing gear, or implementing spatially explicit conservation measures (e.g. marine protected areas). These and other structure-based management strategies are necessary in the face of strong evidence that fisheries-induced demographic changes to age- and size structure affect the reproductive rate (this study), stability (Anderson *et al.* 2008) and evolutionary trajectory (Law 2007 and references therein) of exploited fish stocks. These strategies also provide practical and effective ways of ensuring the sustainability of a fishery in the face of uncontrollable environmental variability (Trippel *et al.* 1997; Berkeley *et al.* 2004; Law 2007; Secor 2007; Hsieh *et al.* 2008).

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