## FISHERIES

# Fish reproductive-energy output increases disproportionately with body size

Diego R. Barneche,[1]*† D. Ross Robertson,[2] Craig R. White,[1] Dustin J. Marshall[1]

Body size determines total reproductive-energy output. Most theories assume reproductive output is a fixed proportion of size, with respect to mass, but formal macroecological tests are lacking. Management based on that assumption risks underestimating the contribution of larger mothers to replenishment, hindering sustainable harvesting. We test this assumption in marine fishes with a phylogenetically controlled meta-analysis of the intraspecific mass scaling of reproductive-energy output. We show that larger mothers reproduce disproportionately more than smaller mothers in not only fecundity but also total reproductive energy. Our results reset much of the theory on how reproduction scales with size and suggest that larger mothers contribute disproportionately to population replenishment. Global change and overharvesting cause fish sizes to decline; our results provide quantitative estimates of how these declines affect fisheries and ecosystem-level productivity.

How does reproductive output scale with body size? Despite the august history of this question (1, 2), theoreticians, fisheries scientists, and field biologists still disagree about the answer (tables S1 and S2). Resolving this uncertainty is essential for understanding the forces driving the evolution of body size in general and for managing fish stocks sustainably. Most life-history models, mechanistic theories of growth, and fisheries models assume that reproductive output scales isometrically with female mass (table S1)—that is, for every increase in female somatic mass, there is a constant proportional increase in reproductive output (Fig. 1A, dashed line). Under such a model, the reproductive output of one 2-kg fish is equal to that of two 1-kg fish.

In contrast to most theoreticians and fisheries models, field biologists have repeatedly suggested that fish fecundity may increase disproportionately with body mass within species (that is, it scales hyperallometrically; table S2) (3, 4). Thus, two 1-kg fish would have less reproductive output than a single 2-kg fish (Fig. 1). This discrepancy between theory and empiricism takes on particular importance because reproductive output drives the replenishment of fisheries (3). Energy investment into individual offspring may also change with female size, such that larger mothers produce larger offspring, which survive better (4, 5). Many life-history models make explicit assumptions about the energy devoted to reproductive tissue (table S1). Therefore, understanding how reproductive output scales with female size requires not only fecundity estimates

but also estimates of how egg size and egg energy scale with female size. Such an understanding would (i) improve the management of exploited populations and protected areas by better estimating the relationship between standing biomass and egg production (3, 4, 6) and (ii) allow direct tests of energy-budget models that characterize changes in reproductive allocation over ontogeny (7).

Here we perform a meta-analysis of intraspecific mass scaling of total reproductive-energy output (fecundity × egg volume × egg energy), with controls for phylogenetic nonindependence, for 342 species of marine fishes from 15 orders (8). We collected data on how egg energy content scales with egg volume within and among a subset of species (n = 1366 clutches from 126 species). We estimated scaling of both egg characteristics and fecundity because these traits could trade off against each other, resulting in no net relationship between maternal size and reproductive output. For example, if larger mothers produce more, but smaller, offspring, net reproductive output might not change with maternal size.

Fish fecundity varied from 11 to 57,600,000 eggs per clutch, spanning about seven orders of magnitude. Fish fecundity scaled hyperallometrically (a power-function relationship with an exponent greater than 1) with body mass (8) (Fig. 2A). In this analysis, 140 (79.1%) of the 177 species presented hyperallometric mass scaling of fecundity.

The volume of individual eggs varied from 0.01 to 344.8 mm$^3$ and increased hypoallometrically with female body mass. A 1.2-fold increase in egg volume would be expected with an increase in body mass from 0.3 to 1.3 kg (Fig. 2B), hence strengthening the effect of female mass on total reproductive output. Considering only the species for which we had both fecundity and egg-volume data (n = 45), we find a hyperallometric

relationship between female mass and total reproductive volume (that is, fecundity × egg volume) [average scaling exponent = 1.21; 95% credible interval (CI) 1.07 to 1.37; table S6] (8).

Energy content of individual eggs varied from 0.07 to 299.41 J. Egg energy scaled hypoallometrically with egg volume (Fig. 2C). That is, larger eggs have slightly less energy content per unit volume than smaller eggs but still have a greater energy content in absolute terms. The combination of this relationship and the relationship between female mass and egg volume still yields a positive, hypoallometric relationship between female size and per-egg energy content (8).

By combining the posterior distributions of model parameters from the three models above (8), we were able to estimate how the average total reproductive-energy output changes with body size for marine fish. Total reproductive-energy output per spawning scales hyperallometrically with female body mass (mean scaling exponent = 1.29; 95% CI 1.20 to 1.38). An estimate of mass scaling of fecundity in the commercially important Atlantic cod (Gadus morhua) illustrates these scaling effects. If fecundity scaled isometrically with mass, then 15 2-kg female cod would produce the same number of eggs as 1 30-kg female. Instead, we find that a single 30-kg female produces more eggs than ~28 2-kg females (weighing a total of 56 kg). Further, because egg volume and egg energy content also increase with female size, a 30-kg female actually spawns a batch of eggs with a total energy content ~37 times as high as that of a batch of eggs from a single 2-kg female (Fig. 1B); assuming an isometric relationship would underestimate this difference by 147%.

Unsurprisingly, substantial variation in reproductive-energy output exists among species, and a small proportion of species (5.0%) show isometric or hypoallometric scaling (Fig. 3). Nevertheless, hyperallometric reproductive scaling holds for almost all species (95.0%) and is consistent for the subset of nine species for which we had data on all three relationships of interest (table S7) and for three studies in which all the data came from the same populations (table S8). Thus, larger females have disproportionately higher fecundity and produce offspring of greater size, content, and possibly quality. Assuming that larger mothers take part in at least as many reproductive bouts each reproductive season as smaller mothers [which seems likely (4)], these relationships may explain why larger fish are so important for the replenishment of marine fish populations (6, 9).

Marine protected areas (MPAs) increase the size of fish by 28% on average (7). Because the per-capita reproductive output of fish increases with size, the potential for MPAs to replenish populations has been underestimated. For example, for the widow rockfish, Sebastes entomelas, an MPA could enhance population replenishment by 60 and 74% for fecundity and reproductive-energy output, respectively—no such increase would be predicted if reproductive output was assumed to be isometric (8).

[1]Centre for Geometric Biology, School of Biological Sciences, Monash University, Clayton, VIC 3800, Australia. [2]Smithsonian Tropical Research Institute, Balboa, Panama. *Present address: School of Life and Environmental Sciences, The University of Sydney, Sydney, NSW 2006, Australia.
†Corresponding author. Email: barnechedr@gmail.com

Our results also reveal the insidious costs of global change. Fish sizes are predicted to decrease in some instances as temperatures rise with global warming. For example, a 1.5°C increase in sea surface temperature will decrease fish lengths by ~15% in the Mediterranean (10). On the basis of our estimates, such a size decrease would incur a 50% per-capita reduction in fecundity for Atlantic mackerel, *Scomber scombrus* (8). Such effects would exacerbate the impacts of predicted decreases in total fish biomass associated with warming—warmer oceans will likely have fewer fish and much lower reproductive output (11).

Here we show that hyperallometry of reproductive-energy output is not the exception but rather the rule for marine fishes, a relationship that fisheries models now need to incorporate. For example, balanced harvesting approaches to fishing, which are the subject of intense debate (12, 13), emphasize somatic productivity alone and assume isometric reproduction. Our results confirm the suspicion (3) that such assumptions severely underestimate the importance of larger females for population replenishment (6, 7, 9). Worryingly, many exploited species have declined in size as result of overharvesting, and our findings suggest that such declines will massively reduce reproductive output and recruitment (14).

Because our results formally establish a general hyperallometric body-mass scaling of reproductive output in marine fishes, they also have direct implications for fundamental theory. Most theories of growth and life history assume that reproductive output scales isometrically with size, hence underestimating the advantages of growing larger, although some branches of theory do anticipate our findings (table S1). However, even among studies that anticipate hyperallometric scaling, some assume that energy content of reproductive tissues stays constant with body size (table S1); our results contradict this core assumption for fishes, at least.

Future studies will establish whether our results are general across groups of organisms other than marine fishes, thus helping determine the generality of conclusions about the putative evolutionary advantages of large size to mothers. All
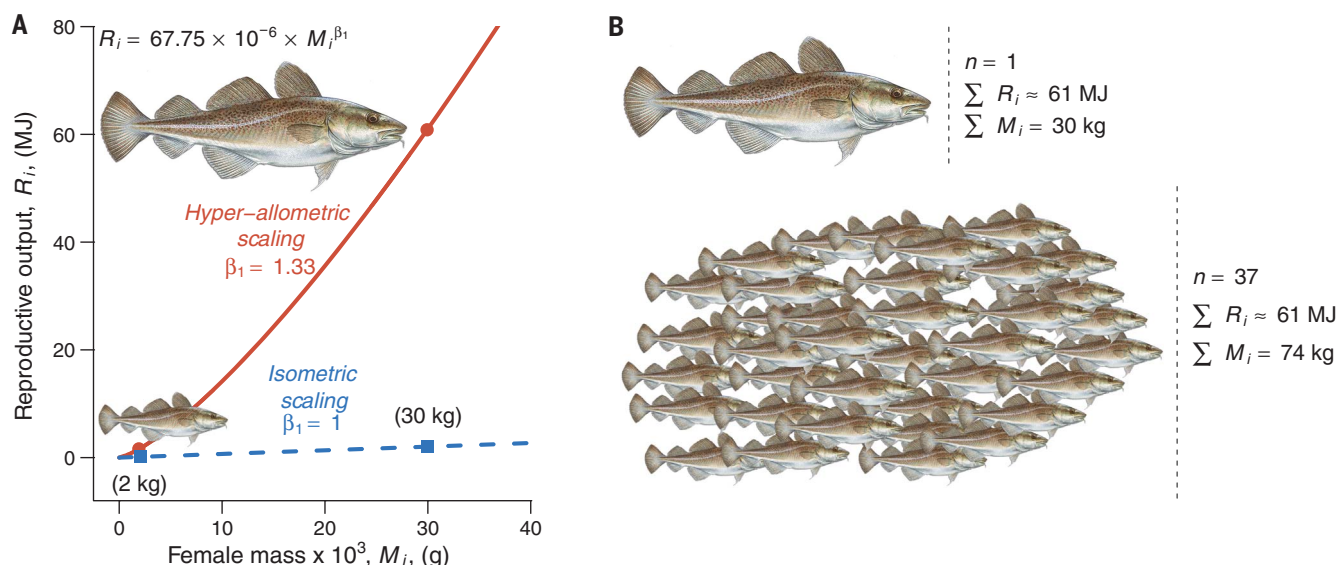


**Fig. 1. Hyperallometric scaling of reproductive-energy output.**
(**A**) Hyperallometric ($\beta_1$ = 1.33, solid red curve; see table S7) and isometric mass scaling ($\beta_1$ = 1, dashed blue curve) relationships for the Atlantic cod, *G. morhua*. Fish sizes span more than one order of magnitude in mass (2 versus 30 kg). (**B**) Total population-level biomass ($\sum M_i$) required to produce the same reproductive output ($\sum R_i$, in megajoules) for two populations of fish with hyperallometric scaling that differ in the mass of the individual fish, where *i* is individuals: The standing-biomass ratio differs by ~2.5-fold (that is, 74 versus 30 kg) from the larger individual to the population with smaller individuals. [Illustration credit: Diane Rome Peebles]
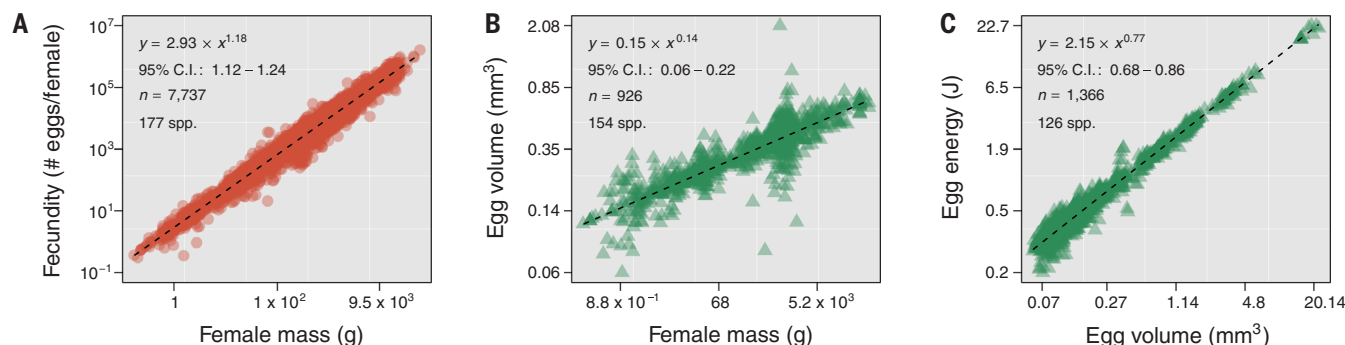


**Fig. 2. Scaling relationships of fish reproductive traits.** (**A**) Relationship between fecundity and female mass. Red circles represent individual clutches. (**B**) Mass scaling of egg volume. (**C**) Volume scaling of egg energy content. Green triangles represent independent observations [egg volume and egg energy content in (B) and (C), respectively]. The *y* axes were corrected for species-specific deviations on the intercept and scaling exponent, which were obtained using Bayesian phylogenetic hierarchical modeling. Equations in the top-left corners depict average fixed effects; 95% CI is Bayesian credible interval for the scaling exponent; *n* is the total number of observations. Dashed black lines depict average model fits. Species and family names and the data summary and contributions for the three models [shown in (A), (B), and (C)] (8) are provided in tables S3 to S5, respectively. Note both axes are logged.
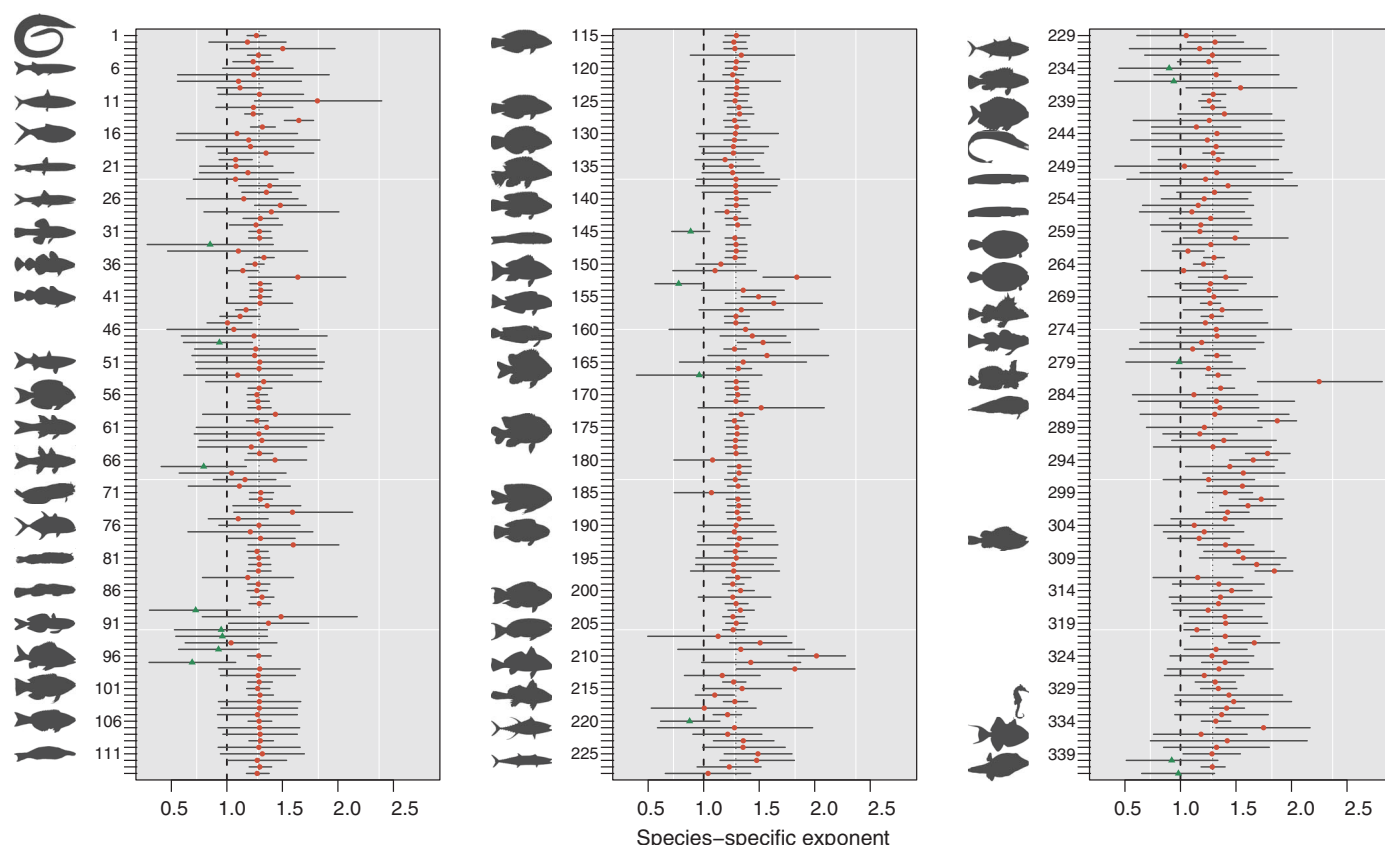
**Fig. 3. Species-specific reproductive-energy mass-scaling exponents.**
Average exponents and 95% CIs (shown by horizontal bars) for 342 species were obtained by combining species-specific (when available) posterior estimates from models in Fig. 2, A to C (8). If a species was not present in a given data set, we used the population-level fixed-effect posterior estimates for the model in question. The dashed line represents the reproductive isometry reference point; the dotted line represents the average fixed-effect exponent value. Red circles and green triangles represent species whose scaling exponents are greater than and less than 1, respectively. Fish silhouettes depict the major clades represented in this figure. See table S7 for species and family names and estimates of reproductive energy–output slopes.

else being equal, size declines reduce the capacity of marine fish populations to replenish, particularly if increased egg size increases recruitment success [but see (15)]. Our findings prove particularly relevant in light of body-size declines of major fishery species owing to overharvesting and climate change (10, 16, 17) and suggest that the reproductive consequences of these size declines will be dramatic.

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# Science

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**Big mamas matter for fish**
      The theoretical relationship between reproduction and body size has assumed that total mass relates directly to fecundity, regardless of the number of individuals involved. This assumption leads to fisheries management practices that suggest that one large female fish can be replaced by several smaller females. However, this assumption is incorrect. Barneche *et al.* show that larger females are far more productive than the same weight's worth of smaller females. Management practices that ignore the value of large females could contribute to unexplained declines seen in some fish stocks.
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