

How does spawning frequency scale with body size in marine fishes?

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Abstract

How does fecundity scale with female size? Female size not only affects the number and size of offspring released in any one reproductive bout (i.e. batch fecundity) but also affects frequency of bouts that occur within a given spawning season (i.e. spawning frequency). Previous studies have noted contrasting effects of female size on spawning frequency such that the effect of female size on reproductive output and total egg production of a population remains unclear. If smaller females spawn more frequently, this could effectively nullify hyperallometry—the disproportionate contribution of larger females to batch fecundity. Here, we explore the relationship between female size and spawning frequency in marine fishes and test this relationship while controlling for phylogeny. Within all of the species considered, spawning frequency scaled positively with body size. Comparing across species, the smallest species showed steeper scaling than the largest. Considering only batch fecundity scaling probably underestimates the relationship between body size and absolute fecundity for many species; reproduction is likely to be more hyperallometric than is currently appreciated based on batch fecundity estimates. Second, an understanding of fecundity scaling depends on estimates of batch fecundity, spawning frequency and spawning duration—we have far more estimates of the first parameter than we do the others, and more studies are required.

KEYWORDS

allometry, fecundity, fisheries, scaling, spawning duration, total egg production



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Etymology of Ghoti

George Bernard Shaw (1856–1950), polymath, playwright, Nobel prize winner, and the most prolific letter writer in history, was an advocate of English spelling reform. He was reportedly fond of pointing out its absurdities by proving that 'fish' could be spelt 'ghoti'. That is: 'gh' as in 'rough', 'o' as in 'women' and 'ti' as in palatal.

1 | INTRODUCTION

Larger females of marine fishes tend to produce disproportionately more eggs and larger eggs, such that they invest disproportionately more reproductive energy in a given spawning event compared with smaller females of the same species (Barneche et al., 2018; Berkeley et al., 2004). To date, the effect of size on reproduction has been quantified only at the scale of a single reproductive event (Barneche et al., 2018 considered only the number and size of offspring released in any one reproductive bout within a season). The absolute fecundity of fish (total number of eggs released per individual per spawning season; Murua et al., 2003) depends on (at least) three components: batch fecundity, spawning frequency (the number of spawning events per season) and the duration of the spawning season (Figure 1; Brown-Peterson et al., 2011). Depending on how the frequency and duration of spawning covaries with body size, estimates of the scaling of absolute reproductive output based on batch fecundity could be wrong (Armstrong & Witthames, 2012). Most models that seek to estimate the total egg production of fished populations assume that batch fecundity scales isometrically—i.e. proportionally—with body size, and that spawning frequency and spawning duration are size-independent (Marshall et al., 2021, but see Fitzhugh et al., 2012; Figure 1).

The most recent qualitative assessments of how female size affects spawning frequency are inconclusive—larger fish spawned more frequently in most cases, but the reverse was true in other cases (Fitzhugh et al., 2012). Here, we compile quantitative estimates of the intraspecific relationship between body size and spawning frequency and analyse them in a phylogenetically controlled framework. We then combine the estimates of the scaling of spawning frequency with those of batch fecundity to estimate of the scaling of absolute fecundity for those species for which data are available. Note that, like most other studies, we assume that spawning duration is size-independent but we do explore how different scaling relationships between size and duration would affect our predictions.

1.1 | Spawning frequency data

We define spawning frequency specifically as the number of spawning events within a given spawning season. We relied on earlier reviews (Fitzhugh et al., 2012; Hixon et al., 2014) exploring how female size affects reproduction to source the original data for some species as well as literature searches using various combinations of synonyms for size and “spawning frequency” to find any additional papers that were missed or published more recently. We searched the literature for studies that estimated the relationship between fish size (either length or mass) and the frequency with which they spawned. While many studies estimated spawning frequency (over 5,000 on “spawning frequency” and “fish” in Google Scholar in April 2019), very few examined the covariance between spawning frequency and size. We did not do a search of how fish age affected spawning frequency (c.f. Fitzhugh et al., 2012) because we were interested in linking estimates of the size scaling of spawning frequency with estimates of the size scaling of batch fecundity. Spawning frequency was quantified by direct observation of spawning in the laboratory (Kjesbu et al., 1996), histological and statistical approaches (Kraus & Koster, 2004) or combinations of both (Claramunt et al., 2007). See Lowerre-Barbieri et al., (2011) for a comprehensive discussion of the methods used to make these estimates. We included only quantitative estimates of the relationship between size and spawning frequency in our compilation. As such, there were many studies (some of which are included in qualitative reviews ([Fitzhugh et al., 2012; Hixon et al., 2014]) that could not be included.

Once we identified studies that quantitatively estimated the relationship between size and spawning frequency, we retrieved the data either directly from tables and text or used image capture software to extract the data from figures (<https://automeris.io/WebPlotDigitizer/>). In some instances, only data for 2 or 3 size classes were presented because studies presented only categories of greater than or less than a certain value. We fit a power function to the data because a linear function would have automatically imposed an

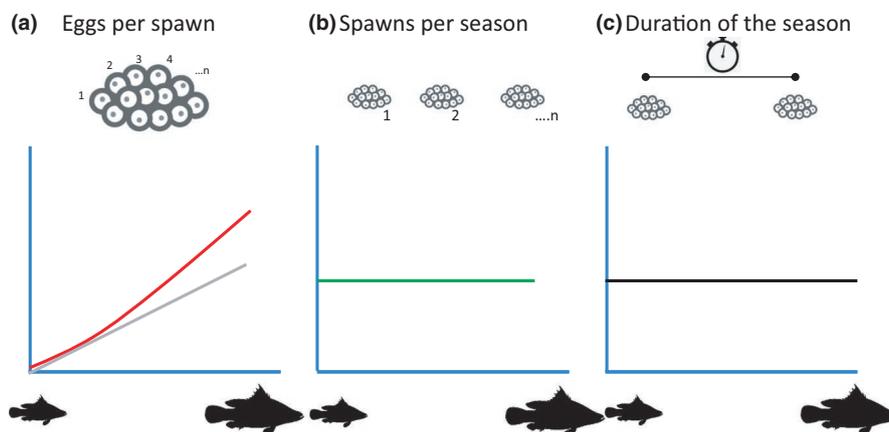


FIGURE 1 Schematic showing the relationships between size various components of reproduction as assumed by the vast majority of fishery models. Panel (a) shows the traditionally assumed linear relationship between fish mass and batch fecundity (in grey) and the updated hyperallometric relationship (in red), Panels (b) and (c) show the size-independent of spawning frequency and spawning duration traditionally assumed by most fishery models

exponent of 1 onto the spawning frequency, and thus risked overestimating the contribution of larger females. Given that for many species spawning frequency scaled at less than 1, we therefore only fit sublinear power functions (i.e. exponents <1) for those species for which there were few size classes. Our estimates of spawning frequency scaling tended to be smaller for those species for which there were fewer body mass classes, so our scaling estimates here should be regarded as representative of lower bounds for those species.

2 | ABSOLUTE FECUNDITY ESTIMATES

Absolute (sometimes termed “annual” or “total”) fecundity (eggs season⁻¹ or eggs year⁻¹ if one season = one year) at the individual level is the key factor of interest when considering the replenishment of populations. Absolute fecundity determines egg production per capita and therefore Total Egg Production.

Our approach makes a number of assumptions and oversimplifications (see Kjesbu, 1989) because of limitations of the available data. We assume that batch fecundity across multiple spawning events in a season shows a consistent relationship with female size. Such consistency is unlikely in the real world because egg number and size change with each successive spawning within a season (Fitzhugh et al., 2012; Pettersen et al., 2019). In this regard, our explorations represent a first approximation of how absolute fecundity scales with size but as more detailed data comes to hand, these estimates should be refined further.

In some instances, both batch fecundity and spawning frequency were reported, while in others absolute fecundity was reported along with either batch fecundity or spawning frequency such that the other parameter needed could be calculated indirectly (assuming spawning duration was size-independent).

3 | PHYLOGENETIC ANALYSES

We first tested whether the variation in mass scaling exponent of spawning frequency could be explained by phylogenetic relationships using an intercept-only model of phylogenetic generalised least squares (PGLS). We then tested separately whether the magnitude of the mass scaling of spawning frequency with size was related to any other life-history variables. To that end, we employed a PGLS regression between the mass scaling of spawning frequency (response) and the von Bertalanffy growth parameters L_{∞} and κ (predictors, where L_{∞} is the asymptotic length (cm) and κ is the von Bertalanffy growth parameter (year⁻¹)). Because κ and L_{∞} are strongly correlated, we restricted our predictor to L_{∞} alone on the natural log scale. However, κ should also be considered in our all discussions of this regression.

Data on the mass scaling exponent of spawning frequency were analysed using phylogenetic generalised least squares (Garland & Ives, 2000; Grafen, 1989) using the “ape” v3.1-1 (Paradis et al., 2004) and “caper” v1.0.1 (Orme et al., 2013) packages of R v3.5.3 (R Core Team, 2019). The

tree was taken from the Open Tree of Life (Hinchliff et al., 2015), downloaded using “rotl” v3.0.7 (Michonneau et al., 2016). The degree of phylogenetic signal in the residuals from each model was quantified using the maximum likelihood estimate of Pagel's λ (Revell, 2010). Where $\lambda = 0$, there is no effect of phylogeny on the observed trait whereas values approaching 1 indicate almost all the variance, conditioned on the fixed effects, is attributed to phylogenetic effects.

4 | HOW DOES SPAWNING FREQUENCY SCALE WITH SIZE?

In total, we found size-specific spawning frequency data for 26 species from 13 families (Table 1). On average, spawning frequency scaled with fish body mass with an exponent of 0.70 and ranged from 0.07 to 3.46 (Figure 2). For the 26 species considered here, incorporating spawning frequency scaling into our estimates of absolute fecundity scaling raises the average across-species reproductive output exponent from 1.20 to 1.90 (mean increase = 0.70 ± 0.15 [SE]). An increase in individual mass of 50% therefore yields an increase in spawning frequency of ~33% and an increase in absolute fecundity of ~119% on average. Note, our results assume that spawning duration (length of the spawning season) is size-independent.

5 | PHYLOGENETIC EFFECTS

Our intercept-only PGLS suggests an average mass scaling exponent of spawning frequency of 0.76 ± 0.28 (95% C.I.), which is significantly different from 0 ($t_{25} = 2.71$, p -value = 0.01). There was a significant phylogenetic signal in spawning frequency ($\lambda = 0.45$, p -value = 0.008), indicating that closely related species were more similar in this trait than distantly related species.

Our PGLS regression revealed that the mass scaling exponent of spawning frequency correlated negatively with asymptotic size across species ($\ln(L_{\infty})$ $t_{24} = 2.417$; p -value = 0.024) but did not detect a phylogenetic effect (i.e. $\lambda = 0$). We thus re-ran the same regression using ordinary least squares (slope = -0.46 , p -value = 0.0088; $R^2 = 0.25$; Figure 3). The negative relationship between the mass scaling exponent of spawning frequency and asymptotic size was not driven by the inclusion of the species with the steepest spawning frequency scaling exponent. Thus, for a smaller species, increase in size yield much higher increase in the frequency with which they spawn in a season.

6 | SIZE, SPAWNING FREQUENCY AND BATCH FECUNDITY

We find that larger fish tend to have higher batch fecundities and spawn more frequently on average. The scaling of fecundity with female size is therefore more hyperallometric than previously reported

TABLE 1 Summary of the mass scaling of spawning frequency, batch fecundity and absolute fecundity with body mass for 26 species of fishes

Species	Spawning Frequency Scaling	Batch Fecundity Scaling	Absolute Fecundity Scaling	Reference
Ballyhoo halfbeak (<i>Hemiramphus brasiliensis</i> , Hemiramphidae)	0.37	0.62 ^a	0.99	McBride & Thurman (2003)
Spotted weakfish (<i>Cynoscion nebulosus</i> , Sciaenidae)	0.13	0.98 ^a	1.11	Roumillat & Brouwer (2004)
Yellowfin sole (<i>Limanda aspera</i> , Pleuronectidae)	0.15	1.06 ^a	1.21	Nichol & Acuna (2001)
Atlantic cod (<i>Gadus morhua</i> , Gadidae)	0.08	1.14	2.22	Kjesbu et al. (1996)
Hogfish (<i>Lachnolaimus maximus</i> , Labridae) ^a	0.07	1.21 ^a	1.28	Collins & McBride (2015)
Queen croaker (<i>Seriphys politus</i> , Sciaenidae)	0.11	1.30 ^a	1.41	Demartini & Fountain (1981)
Northern red snapper (<i>Lutjanus campechanus</i> , Lutjanidae)	0.08	1.35 ^a	1.43	Collins et al. (2001)
Argentine hake (<i>Merluccius hubbsi</i> , Merlucciidae)	0.19	1.29 ^a	1.48	Macchi et al. (2018)
Southern blue whiting (<i>Micromesistius australis</i> , Gadidae)	0.36	1.17 ^a	1.53	Macchi et al. (2005)
Southern bluefin tuna (<i>Thunnus maccoyii</i> , Scombridae)	0.12	1.41 ^a	1.53	Farley et al. (2015)
Blackspotted rockfish (<i>Sebastes melanostictus</i> , Sebastidae)	0.10	1.43 ^a	1.53	Conrath (2017)
Anchoveta (<i>Engraulis ringens</i> , Engraulidae)	0.31	1.35	1.66	Claramunt et al. (2007)
Tautog (<i>Tautoga onitus</i> , Labridae)	0.37	1.29 ^a	1.66	LaPlante & Schultz (2007)
Pacific sanddab (<i>Citharichthys sordidus</i> , Paralichthyidae)	0.45	1.33	1.78	Lefebvre et al. (2016)
Chilipepper rockfish (<i>Sebastes goodei</i> , Sebastidae)	0.57	1.24	1.81	Lefebvre et al. (2018)
European spratt (<i>Sprattus sprattus</i> , Clupeidae)	0.88	0.96 ^a	1.84	Kraus & Koster (2004)
Rougheye rockfish (<i>Sebastes aleutianus</i> , Sebastidae)	0.69	1.43 ^a	2.12	Conrath (2017)
Argentine anchovy (<i>Engraulis anchoita</i> , Engraulidae)	0.88	1.24 ^a	2.12	Claramunt et al. (2007)
Californian anchovy (<i>Engraulis mordax</i> , Engraulidae)	1.03	1.13 ^a	2.16	Parrish et al. (1986)
Yellowfin tuna (<i>Thunnus albacares</i> , Scombridae)	0.80	1.43 ^a	2.23	McPherson (1991)
Balao halfbeak (<i>Hemiramphus balao</i> , Hemiramphidae)	1.05	1.29 ^a	2.34	McBride & Thurman (2003)
Bannerfin shiner (<i>Cyprinella leedsii</i> , Leuciscidae)	1.64	0.73	2.37	Heins & Rabito (1986)
Shorthead rockfish (<i>Sebastes borealis</i> , Sebastidae)	1.04	1.43 ^a	2.47	Conrath (2017)
European pilchard (<i>Sardinus pilchardus</i> , Clupeidae)	1.24	1.23 ^a	2.47	Ganias et al. (2003)
Southern African anchovy (<i>Engraulis capensis</i> , Engraulidae)	2.19	1.18 ^a	3.37	Melo (1994)
South American pilchard (<i>Sardinops sagax</i> , Clupeidae)	3.46	0.88 ^a	4.34	Leclus (1989)

Notes: The scaling of batch fecundity was taken from the study in which spawning frequency scaling was estimated or from Table S3 in Barneche et al. (2018).

^aBatch fecundity was estimated via histology rather than spawned eggs

^bLargest size classes were omitted because females undergo sex change to male function with increasing size.

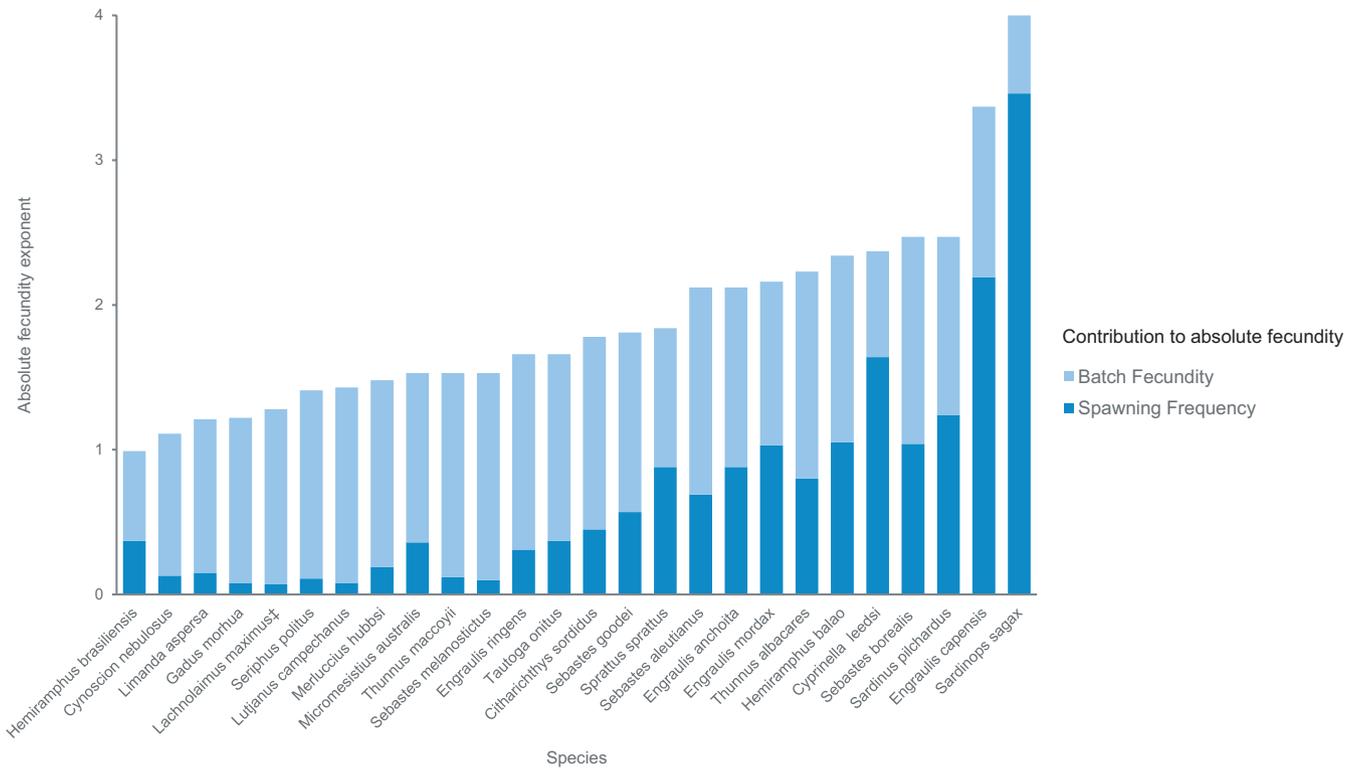


FIGURE 2 The scaling of absolute fecundity and the relative contribution of batch fecundity (light blue) and spawning frequency (dark blue) to absolute reproductive scaling across 26 species of fish

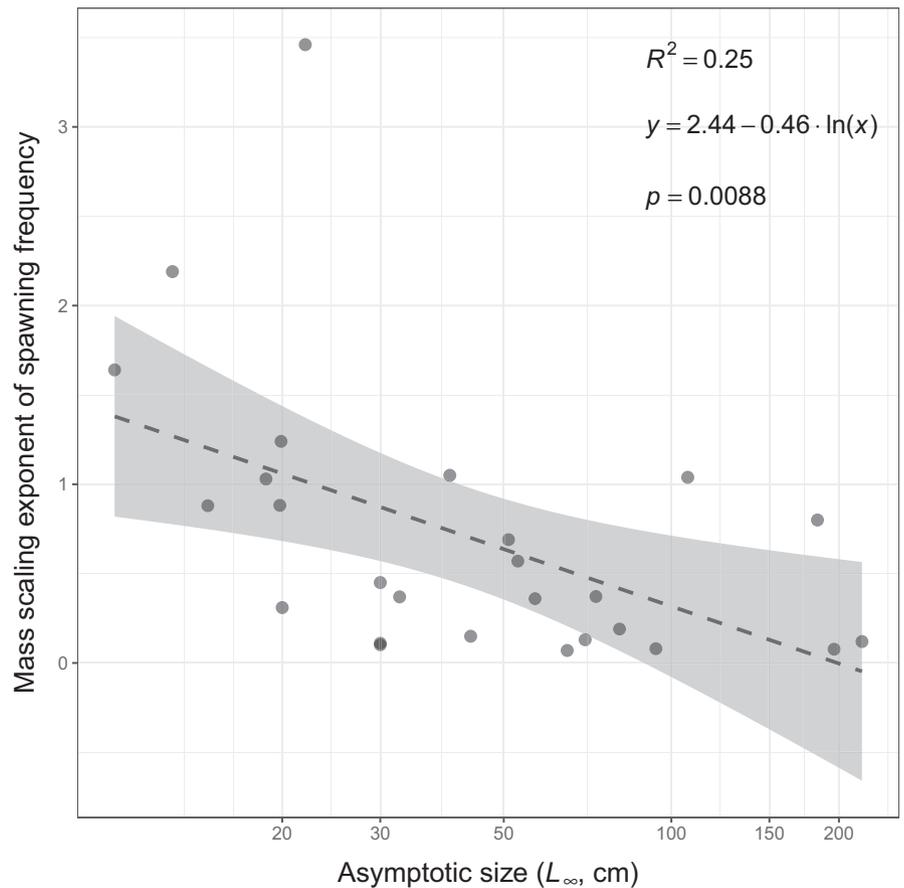


FIGURE 3 The relationship between asymptotic size (L_{∞}) (cm) and the scaling spawning frequency for 26 species of fish. Coefficients, p -value (slope) and R^2 are reported from a simple ordinary least squares regression given that our PGLS revealed $\lambda = 0$ (see Results)

based on studies of batch fecundity. Our sample of species is biased towards species that show repeated spawning within a season because these are the species in which spawning frequency can be studied. As such, we do not suggest that all species have absolute fecundity scaling exponents that are greater than those derived from measurements of batch fecundity (e.g. as reported in Barneche et al., 2018), but instead note that in some species, those reported exponents are likely to represent an underestimate.

We observed systematic patterns in the steepness of scaling of spawning frequency with size—scaling was steeper in species of shorter asymptotic lengths. When species are smaller, relatively larger individuals within that species spawn much more often. Thus, some smaller species that show isometric or even hypoallometric batch fecundity have hyperallometric absolute fecundity scaling because of the steep relationship between female size and spawning frequency. If larger individuals within a species have access to or allocate more resources for reproduction (and some models indicate they should; Audzijonyte & Richards, 2018; Marshall & White, 2019), then larger individuals must either become exceptionally gravid or spawn more frequently. The finding that small-bodied species tend to reproduce more often, rather than become more gravid as they grow makes sense from a biomechanical perspective. One can easily imagine that smaller fishes are under increased selection to maintain fineness (essentially a streamlined shape) relative to larger fishes. We are unaware of any existing life-history models that have anticipated the relationship between spawning frequency and body size, but future theory should explore this.

Within all of the species for which there were quantitative estimates, we found no evidence of negative relationships between size and spawning frequency. Note however that our results contrast with the qualitative analysis of Fitzhugh et al. (2012)—four species included in both showed conflicting patterns. Specifically, Fitzhugh et al. (2012) find studies that include all three possible outcomes between size and spawning frequency for Anchoveta (*Engraulis ringens*, Engraulidae), (positive, negative and no relationship) and find two different patterns for Atlantic cod (*Gadus morhua*, Gadidae), (negative and no relationship). Clearly, these relationships can vary from study to study and stock to stock. Whether this variation is a product of statistical power, sampling or biology remains unclear as there are still too few studies to generalize. Thus, based on our analyses here and the compilation of batch fecundity scaling (Barneche et al., 2018), it seems prudent to assume that, in most instances, larger fish produce disproportionately more offspring in a season than smaller fish of the same species, though exceptions must exist.

7 | SPAWNING DURATION

We do not consider the duration of the spawning season. Data on size-specific patterns in spawning season duration are hard to find but, for some species at least, there appears to be a strong effect of size on the duration of the spawning season, with larger individuals staying reproductively active for longer (Fitzhugh et al., 2012;

Hixon et al., 2014; Wright & Trippel, 2009). For example, larger Queen croaker (*Seriphus politus*, Sciaenidae) reproduce more often and release more eggs per reproductive bout than smaller individuals, such that reproductive output scales at 1.41 (Demartini & Fountain, 1981). But the duration of the spawning season is much longer for larger individuals in this species; where we to include spawning duration, absolute annual fecundity would scale at 2.46 (Demartini & Fountain, 1981). We also use a hypothetical negative scaling relationship between size and spawning duration to ask; what relationship between spawning duration and size would effectively nullify the positive scaling relationship between size and spawning frequency? For species with very shallow scaling between spawning frequency and body size (e.g. Atlantic cod), a subtle negative relationship between body size and spawning duration could offset the relationship between size and spawning frequency. However, for species with steep scaling (e.g. the South American pilchard (*Sardinops sagax*, Clupeidae)) the relationship between size and spawning duration would have to be unrealistically steep to offset the effect of size on spawning frequency for absolute fecundity. An important next step therefore is to estimate the relationship between body size and spawning duration for more species but for now, it seems safest to assume that our estimates of absolute fecundity scaling are an underestimate because larger females are more likely to spawn for longer (Wright & Trippel, 2009).

Overall, we find that larger mothers spawn more often in a season than smaller mothers of the same species, particularly for smaller species. The combination of batch fecundity scaling with spawning frequency scaling means that larger females play a disproportionate role in population replenishment, even after accounting for demography. We caution against assuming reproductive isometry for species with steep hyperallometric scaling as it results in the systematic *underestimation* of the role of larger females in population replenishment, and the *overestimation* of overall population replenishment in fished populations in particular (Marshall et al., 2021).

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created in this study.

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How to cite this article: Marshall, D. J., Barneche, D. R., & White, C. R. (2021). How does spawning frequency scale with body size in marine fishes? *Fish and Fisheries*, 00, 1–8. <https://doi.org/10.1111/faf.12617>