DTU Library

Limited impact of big fish mothers for population replenishment

Andersen, Ken Haste; Jacobsen, Nis Sand; van Denderen, P. Daniël

Published in:
Canadian Journal of Fisheries and Aquatic Sciences

Link to article, DOI:
10.1139/cjfas-2018-0354

Publication date:
2019

Document Version
Peer reviewed version

Limited impact of big fish mothers for population replenishment

Ken H. Andersen[1*], Nis Sand Jacobsen[2], P. Daniël van Denderen[1]

[1] Centre for Ocean Life, DTU Aqua, Technical University of Denmark, Building 202, 2800 Kgs. Lyngby, Denmark
[2] National Research Council Postdoctoral Research Associate, Washington, DC, USA
* kha@aqua.dtu.dk

A recent meta-analysis by Barneche et al. (Science 360(6389): 642) show that fish reproductive output scales hypergeometrically with female weight. This result challenges the common assumption that reproductive output is proportional to weight. The implication made is that current theory and practice severely underestimates the importance of larger females for population replenishment. Their example for cod shows that current practice makes an error of 149%. By properly accounting for fish demography we show that the error is maximally on the order of 10%, and in most other fish stocks likely much less.

Fisheries advice and management relies on stock assessments and impact analyses that are based on demographic calculations on fish populations. In general, such calculations assume that the egg production is proportional to the weight of fish mother (isometric scaling). However, examples have been found where egg production is not proportional to reproductive output: Atlantic cod (*Gadus morhua*) (Kjesbu et al. 1996; Trippel 1998; Marteinsdóttir and Steinarsson 1998), haddock (*Melanogrammus aeglefinus*) (Hislop 1988), black rockfish (*Sebastes melanops*) (Berkeley et al. 2004), and winter flounder (*Pseudopleuronectes americanus*) (Buckley et al. 1991). Such examples have resulted in the theory that the "BOFFs" (the Big Old Fecund Females) are crucial to the replenishment of a fish stock, and that management actions should focus more on preserving the largest individuals in stock (Hixon et al 2013; Birkeland and Dayton 2005). While there is evidence that BOFFs have higher weight-specific reproductive output in some stocks, so far, no general pattern has been demonstrated.

To fill this knowledge gap, a recent study by Barneche et al (2018) created and analysed a large database of reproductive output from fish as a function of size. The analysis showed that fish reproductive output increases with the weight of the mother roughly to the power 1.29. This analysis is relevant and timely and challenges the current assumption that reproductive output is proportional to fish weight.

The question is whether the difference between an isometric and hypergeometric scaling matters for practical fisheries advice and management. Based on simple demographic calculations, Barneche et al (2018) conclude that current fisheries science and management severely underestimate the importance of large mothers for fish populations. Here we show that the estimates by Barneche et al (2018) are incorrect because they fail to account for demography and density dependence. For the cod example highlighted in their study we show that the bias from using isometric scaling is not 149% but maximally on the order of 10%, and most likely much less, also for other fish.

Individual-level differences

Figure 1A in the Barneche et al (2018) compares the isometric and hypergeometric scalings of reproductive output for cod and shows a large difference. Redrawing the figure with the cod data added (Figure 1) clearly shows that the isometric line from the Barneche et al. (2018) study (blue line) does not represent the actual data points for cod. A reasonable representation of the isometric assumption for cod (magenta line) shows a much smaller difference between isometric and hypergeometric scalings. The error is due to Barneche et al. (2018) using a general coefficient for the coefficient of proportionality, and not the specific one for cod. Because of this error, the graphical representation of the results in Barneche et al (2018) therefore grossly inflates the difference between the isometric and hypergeometric assumptions.

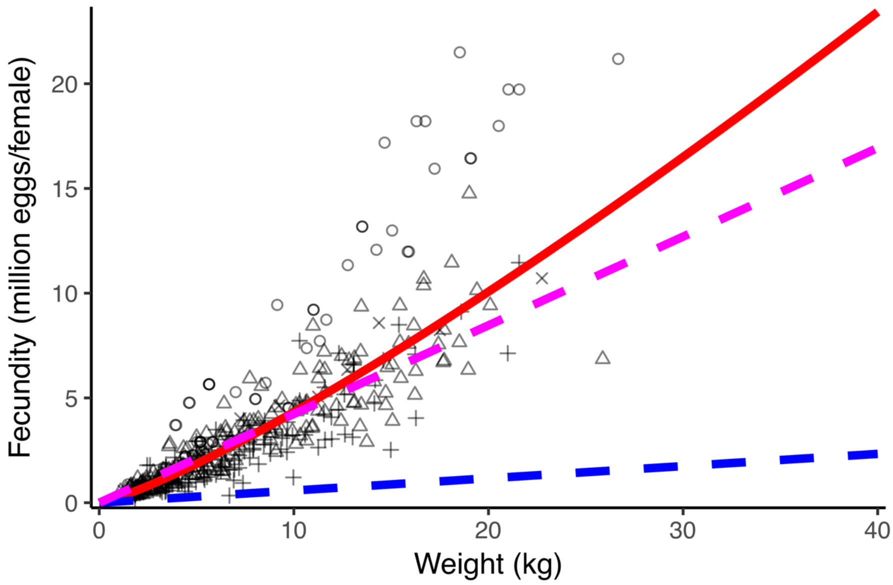

Figure 1. A partial reconstruction of figure 1A from Barneche et al. (2018) with data from cod added with different symbols for each stock. The red line is a fit to the data with exponent 1.22. The dashed blue line is similar to the line drawn in Barneche et al. (2018). The thick magenta line is a mean of the egg numbers/weight. A reasonable comparison is between the magenta and red lines, not between the blue and red lines. Note that in the figure we only look at number of eggs, and therefore ignore the effect of egg size and energy content, which counteract one another.

Demography

For fisheries applications, the main concern is whether population-level calculations are systematically wrong when an isometric instead of a hypergeometric assumption is used. The assessment of population-level consequences in Barneche et al (2018) uses a demographic calculation that compares the reproductive output of very small mature individuals with very large ones. This procedure does not account for two well-known demographic effects: 1) most of the smaller individuals are immature, and 2) there are very few large individuals. Here we account for these two effects.

The average weight of maturation of fish is roughly 0.6 times the average maximum length of individuals (Beverton, 1992), or $0.6^3 = 0.23$ in weight. Comparing the very smallest mature individuals with the very largest individuals, both of which are rare in the population, will overestimate the relative importance of small vs large individuals for population reproduction. Barneche et al. (2018) compare the reproductive output of a 2 and 30 kg cod leading to an underestimation of reproductive output of $(30/2)^{1.33-1} - 1 = 145\%$ under the isometric assumption. Using the 0.23 ratio of average maturation and maximum size the underestimation becomes $0.23^{0.33} = 62\%$. Even when correcting for the typical size range of mature fish, the common isometric assumption substantially underestimates the reproductive output of large mothers.

The above calculation does not account for there being fewer older than younger mothers. This demographic effect is well described in the literature (Hixon et al 2013, Berkeley, et al 2004, Field et al 2008, O'Farrell and Botsford 2006, Spencer et al 2014, Calduch-Verdiell et al 2014). Here we demonstrate the contribution of large fish to reproduction with a simple example based on cod; see Calduch-Verdiell et al (2014) for a general calculation.

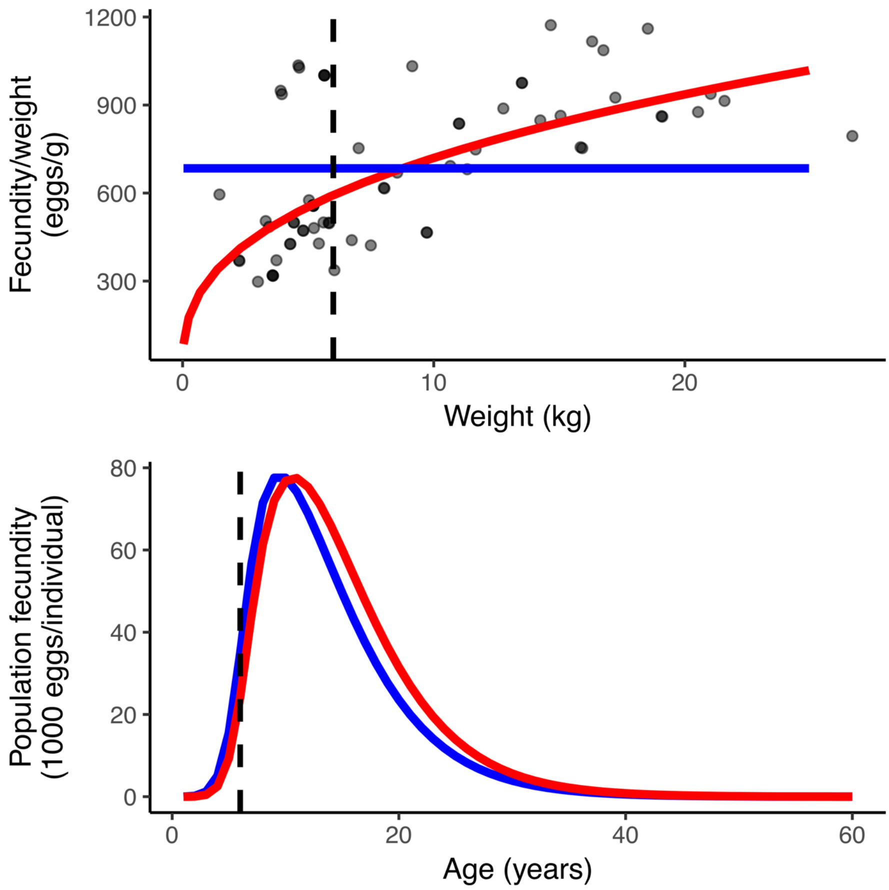

Figure 2. Weight-specific reproductive output (A) and population level reproductive output (B) for Icelandic cod with asymptotic weight 25 kg, growth parameter $K = 0.12$ yr^{-1}, 50% age of maturation around 7 years (Marteinsdottir and Begg, 2002), and mortality $Z = 0.2$ yr^{-1}. The red lines show how reproductive output scales as weight$^{1.42}$; the blue lines show isometric reproductive output. Size and age of 50 % maturity are indicated with the vertical dashed lines.

The number of fish at age, N_a, at age a is:

$$N_a = N_0\, e^{-Z\, a},$$

where Z is the adult mortality. The weight of individuals w_a is described by a standard von Bertalanffy growth curve:

$$w_a = W_\infty\, (1 - e^{-K\, a})^3,$$

where K is the von Bertalanffy growth constant and W_∞ the average maximum weight. The total population-level reproductive output is $\propto \sum N_a\, w_a^\beta$, where β is the exponent and the summation is over all ages of mature fish.

As an example, we compare the population-level reproductive output made with hypergeometric and isometric assumptions for the cod data set with the largest exponent (Icelandic cod, $\beta = 1.42$, Figure 2). With a mortality of 0.2 yr^{-1}, only about 6% of newly mature Icelandic cod of age 6 (around 3 kg) survive to age 22 (20 kg). In this case, the isometric assumption will underestimate the populations' reproductive output by 10%. With a fishing mortality at 0.3 yr^{-1}, only 0.1% survives and the isometric assumption will overestimate population reproductive output by 20%. Both errors are a far cry from 145%.

Icelandic cod is an extreme example with high exponent and high ratio between size at maturation and maximum size. For the Icelandic cod, the estimated high exponent is an artefact of converting from length to weight and the original analysis found an isometric scaling with weight (Marteinsdottir et al 2002). Yet, we do not believe that this is a general error in the analysis. The other cod stocks have smaller exponents (1.11-1.21) and the differences between a hypergeometric and isometric scaling will be smaller for those stocks. In the other examples presented in Barneche et al. (2018; rockfish and mackerel), demography is also not accounted for. Since ignoring hypergeometric scaling of reproductive output in a case with high exponent (1.42) makes an error on the order of 10%, the error in other cases (e.g. rockfish and mackerel) is expected to be much less. Therefore, using the isometric assumption does not "…severely underestimate the importance of larger females for *population replenishment*" (our emphasis).

Density dependence

In fisheries science and management, the renewal of a population is described by the number of recruits entering the population. In some cases, recruitment is almost independent of the reproductive output, for example in many cod stocks. In such cases, the calculation of reproductive output is immaterial and using isometric or hypergeometric scaling makes no difference to recruitment. In other cases, typically for smaller-bodied species, the recruitment is a saturating or unimodal function of reproductive output. In both cases, the density dependence implied by the recruitment function will reduce the importance of the population-level reproductive output and therefore reduce the difference between isometric or hypergeometric descriptions.

There are relevant usage cases where density dependence should not be accounted for. One example is when egg surveys are used to estimate spawning stock biomass. Normally, the spawning stock biomass is assumed to be proportional to the egg survey index. However, if the stock has hypergeometric scaling of egg production, larger individuals will contribute more eggs than smaller one per biomass. In such cases, the error will be on the same order of magnitude as calculated in the cod example above, about 10%.

Conclusion

Barneche et al. (2018) conclude in their abstract "Global change and over-harvesting cause fish sizes to decline; our results provide quantitative estimates of how these declines impact fisheries and ecosystem-level productivity.". We show that these quantitative estimates do not account for well-known effects of demography and density dependence, and therefore do not properly address population-level reproductive output. The calculations hence fail to estimate impacts on fisheries and productivity. We show that the underestimation that current practice risks is maximally on the order of 10% due to demography and most likely even lower due to density dependence.

Nevertheless, accounting for hypergeometric scaling in stocks where it is clearly evident demonstrates judicious practice. Further, it remains to be explored whether there are some stocks and some circumstances where accounting for hypergeometric scaling of reproductive output needs to be accounted for. However, in general, the finding by Barneche et al (2018) does not invalidate current advice and management practice and management does not risk substantially "…underestimating the contribution of larger mothers to replenishment, hindering sustainable harvesting".

Acknowledgements
This work was supported by The Centre for Ocean Life, a Villum Kahn Rasmussen Centre of Excellence funded by the Villum Foundation.

References

Barneche, D.R., Robertson, D.R, White, C.R., and Marshall D.J. 2018. Fish reproductive-energy output increases disproportionately with body size. Science **360**(6389): 642 doi: 10.1126/science.aao6868

Berkeley, S.A., Hixon, M.A., Larson, R.J., and Love, M.S. 2004. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. Fisheries, **29**(8): 23–32. doi:10.1577/1548-8446(2004)29.

Beverton, R.J.H. 1992. Patterns of reproductive strategy parameters in some marine teleost fishes. Journal Fish Biology **41**: 137–160.

Birkeland, C., and Dayton, P.K. 2005. The importance in fishery management of leaving the big ones. Trends Ecol. Evol. **20**(7): 356–358. doi:10.1016/j.tree.2005.03.015..

Buckley, L.J., Smigielski, A.S., Halavik, T.A., Caldarone, E.M., Burns, B.R., and Laurence, G.C. 1991. Winter flounder *Pseudopleuronectes americanus* reproductive success. II. Effects of spawning time and female size on size, composition and viability of eggs and larvae. Mar. Ecol. Prog. Ser. **74**: 125–135. doi:10.3354/ meps074125.

Calduch-Verdiell, N., MacKenzie, B.R., Vaupel, J.W., and Andersen, K.H. 2014. A life-history evaluation of the impact of maternal effects on recruitment and fisheries reference points. Canadian Journal of Fisheries and Aquatic Science **71**: 1113–1120.

Field, J.G., Moloney, C.L., du Buisson, L., Jarre, A., Strømme, T., Lipinski, M.R., and Kainge, P. 2008. Exploring the BOFFFF hypothesis using a model of Southern African deepwater hake (*Merluccius paradoxus*). *In* Fisheries for Global Welfare and Environment, 5th World Fisheries Congress. *Edited by* K. Tsukamoto, T. Kawamura, T. Takeuchi, T.D. Beard, Jr., and M.J. Kaiser. pp. 17–26.

Hixon, M., Johnson, D., and Sogard, S. 2013. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. ICES J. Mar. Sci. **71**(8): 2171-2185. doi:10.1093/icesjms/fst200.

Hislop, J. 1988. The influence of maternal length and age on the size and weight of the eggs and the relative fecundity of the haddock, *Melanogrammus aeglefinus*, in British waters. J. Fish Biol. **32**(6): 923–930. doi:10.1111/j.1095-8649. 1988.tb05435.x.

Kjesbu, O.S., Solemdal, P., Bratland, P., and Fonn, M. 1996. Variation in annual egg production in individual captive Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **53**(3): 610–620. doi:10.1139/f95-215.

Marteinsdóttir, G., and G. A. Begg. 2002. Essential relationships incorporating the influence of age, size and condition on variables required for estimation of reproductive potential in Atlantic cod *Gadus morhua*." Marine Ecology Progress Series **235**: 235-256.

Marteinsdóttir, G., and Steinarsson, A. 1998. Maternal influence on the size and viability of Iceland cod *Gadus morhua* eggs and larvae. J. Fish Biol. **52**(6): 1241–1258. doi:10.1111/j.1095-8649.1998.tb00969.x.

O'Farrell, M.R., and Botsford, L.W. 2006. The fisheries management implications of maternal-age-dependent larval survival. Can. J. Fish. Aquat. Sci. **63**(10): 2249–2258. doi:10.1139/f06-130.

Spencer, P.D., Kraak, S.B.M., and Trippel, E.A. 2014. The influence of maternal effects in larval survival on fishery harvest reference points for two life-history patterns. Can. J. Fish. Aquat. Sci. **71**(1): 151–161. doi:10.1139/cjfas-2013- 0253.

Trippel, E.A. 1998. Egg size and viability and seasonal offspring production of young Atlantic cod. Trans. Am. Fish. Soc. **127**(3): 339–359. doi:10.1577/1548 8659(1998)127.