



REPLY TO BAUDRON ET AL.:

Fishing matters: Age-specific deepening is driven by exploitation

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In their response to our paper “Exploitation drives an ontogenetic-like deepening in marine fish” (1), Baudron et al. (2) unfairly characterize our result as an alternative explanation. Throughout our paper, and in the closing remark, we explicitly state that additional factors must be considered: “Ontogenetic factors, fisheries exploitation, and climate variability must be considered before deepening or any other spatial adjustment of populations/assemblages can be attributed to any of these mechanisms.” Recent research on a wide variety of species supports this contention (3–5).

Baudron et al. (2) claim that we attribute 72% of the observed deepening to size-selective fishing and that we question “whether ontogenetic deepening is a real ecological phenomenon.” In fact, we stated that ~28% of the observed deepening of cod was due to this cause.

Baudron et al. (2) draw upon an unpublished analysis of six Northeast Atlantic fish species to challenge our findings. They state, “If [our] findings are widely applicable, the depth at which large fish are observed should correlate positively with fishing intensity across stocks, assuming that fishing depth remains relatively stable.” This is not necessarily true because the effect of fishing and the resultant distribution with age depends on (i) the initial depth (z) distribution of fish with age, (ii) the overall fishing mortality (F), and (iii) its depth distribution, $F(z)$. If F were constant across the full depth range inhabited, the center of mass of fish would not deepen with age.

Baudron et al. (2) do not provide the initial depth distributions of any species; there is no information of

the depth distribution of F , which is both species and gear specific; their metric quantifying the depth of a species (mean) was not defined; and, variance estimates were not provided; nor were aging data (fish were categorized as small, medium, and large). Such use of size data assumes no temporal variation in growth, which has been repeatedly shown not to be the case for exploited stocks. Further, their “small fish” category probably includes prerecruits that are not harvested; this could explain why “the depth of small individuals showed mixed trends” (2).

Moreover, we have concerns regarding their modeling approach, particularly since it has not been sufficiently explained or peer reviewed (see table 1 in ref. 2). The models do not account for temporal (or spatial) dependence in the response, which is well known to bias model inference, leading to inflated type I errors. The mixed models only include a random intercept but should also have tested for randomly varying slopes, different effects of F , survey depth, and year within individual surveys. Their approach allows for the mean depth to vary by stock but assumes that the remaining effects are constant. It is unclear why mean survey depth, which would be highly correlated with the depth of capture, is included as a predictor. No P values for the individual predictors are reported.

We welcome Baudron et al.’s (1) discussion of this timely and important topic; however, the concerns we raise cast serious doubt on the validity of their conclusions.

1 Frank KT, Petrie B, Leggett WC, Boyce DG (2018) Exploitation drives an ontogenetic-like deepening in marine fish. *Proc Natl Acad Sci USA* 115:6422–6427.

2 Baudron AR, Pecl G, Gardner C, Fernandes PG, Audzijonyte ADG (2019) Ontogenetic deepening of Northeast Atlantic fish stocks is not driven by fishing exploitation. *Proc Natl Acad Sci USA* 116:2390–2392.

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Author contributions: K.T.F. and B.P. designed research; K.T.F., B.P., W.C.L., and D.G.B. performed research; K.T.F., B.P., and D.G.B. analyzed data; and K.T.F., B.P., W.C.L., and D.G.B. wrote the paper.

The authors declare no conflict of interest.

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Published online January 23, 2019.

- 3 Engelhard GH, Pinnegar JK, Kell LT, Rijnsdorp AD (2011) Nine decades of North Sea sole and plaice distribution. *ICES J Mar Sci* 68:1090–1104.
- 4 Bell RJ, Richardson DE, Hare JA, Lynch PD, Fratantoni PS (2015) Disentangling the effects of climate, abundance, and size distribution of marine fish: an example based on four stocks from the Northeast US shelf. *ICES J Mar Sci* 72:1311–1322.
- 5 Adams CF, et al. (2018) Relative importance of population size, fishing pressure and temperature on the spatial distribution of nine Northwest Atlantic groundfish stocks. *PLoS One* 13:e0196583.