Ontogenetic deepening of Northeast Atlantic fish stocks is not driven by fishing exploitation

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For many marine fish species, the average size of individuals increases with depth. This phenomenon, first described a century ago, is known as ontogenetic deepening (1, 2). Several mechanisms have been proposed to explain it: optimal foraging; predation avoidance; and different optimal growth temperature for larger individuals, causing them to seek deeper and cooler waters to optimize growth and reproduction (3). In their recent paper in PNAS, Frank et al. (4) suggest an alternative explanation. They examined age-structured data from Atlantic cod (*Gadus morhua*) on the eastern Scotian Shelf, a stock that has experienced successive periods of intense, and absence of, fishing. In their study, fishing explained 72% of the variation in the observed age-related deepening, with the remaining variability attributed to ontogenetic deepening. They conclude that higher abundances of large fish in deeper waters is an artifact of greater fishing intensity at shallower depths and question whether ontogenetic deepening is a real ecological phenomenon.

Frank et al. (4)'s analysis is based on a single stock. If their 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. To test this hypothesis, we used length-structured fisheries-independent data from bottom trawl surveys for eight Northeast Atlantic stocks which experienced substantial changes in fishing mortality (5–7). Fishing mortality trends were similar across age classes (8), and the average fishing mortality (F) of each stock was used as a proxy for fishing intensity. Despite F decreasing over the past two decades for all but one stock, the depth at which medium and large fish were found either remained stable or deepened for most stocks (Fig. 1). The depth of small individuals showed mixed trends. Linear mixed-effect models with F, mean survey depth (MSD), and year as explanatory variables and stock as a random effect confirmed that while the depths of large and medium fish were positively correlated to MSD, they were negatively correlated to F, meaning that depth increased as F decreased (Table 1). The depth of medium fish was also negatively correlated to year, suggesting a long-term temporal trend, while no significant correlations were observed for small fish, except for MSD.

In summary, we found no evidence that declining fishing intensity resulted in relatively more medium and large fish in shallower waters. Our brief analysis does not diminish the fact that different fishing intensities at different depths may influence the size structure at depth. But it does suggest that, in Northeast Atlantic stocks at least, ontogenetic deepening is unlikely to be driven mainly by fishing. This questions the universality of Frank et al.'s (4) findings and challenges their conclusion that the deepening of marine species may not be an adequate indicator of warming seas (9, 10) due to the confounding and possibly overarching impact of fishing. We do acknowledge, however, that Frank et al. (4) highlight a crucial point: Fishing must be accounted for when assessing the impact of climate change on commercially exploited fish stocks.

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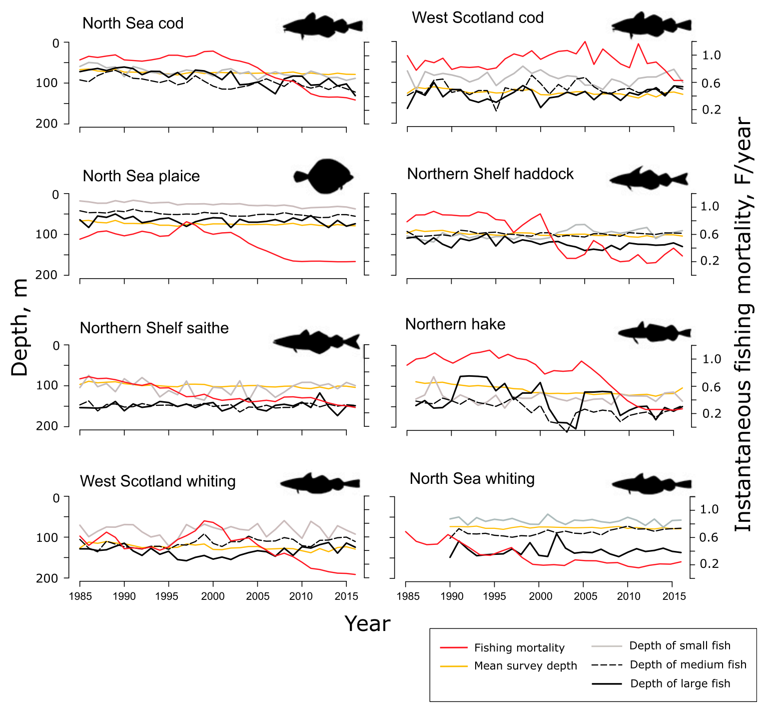

Fig. 1. Mean depth distribution of small, medium, and large fish in bottom trawl surveys for eight Northeast Atlantic stocks [cod (*Gadus morhua*) in the North Sea and west of Scotland, plaice (*Pleuronectes platessa*) in the North Sea, haddock (*Melanogrammus aeglefinus*) and saithe (*Pollachius virens*) in the Northern Shelf, hake (*Merluccius merluccius)* in the Northeast Atlantic, and whiting (*Merlangius merlangus*) in the west of Scotland and the North Sea] together with the mean depth of the survey covering each stock area and the average fishing mortality experienced by each stock. Survey data were obtained from the DATRAS database available from ICES (ices.dk/marine-data/data-portals/Pages/DATRAS.aspx).

Table 1. Details of model selection in mixed-effect model analyses

No.*	Response variable	Model	R_m^2,† %	R^2,‡ %	Test§	P¶	AIC	df	F#	MSD#	Year#
1	Depth large	~ Year + F + MSD + (1|stock)	28	69			2154.2	6	−20.1	0.78	−0.26
2	**Depth large**	**~ F + MSD + (1|stock)**	**21**	**68**	**1-2**	**0.190**	**2153.9**	**5**	**−13.7**	**0.64**	**—‖**
3	Depth large	~ MSD + (1|stock)	29	71	2-3	0.009	2158.7	4	—	0.82	—
4	Depth large	~ F + (1|stock)	4	73	2-4	0.001	2164.1	4	−21.4	—	—
1	**Depth medium**	**~ Year + F + MSD + (1|stock)**	**37**	**92**			**1922.7**	**6**	**−18.2**	**1.09**	**−0.59**
2	Depth medium	~ F + MSD + (1|stock)	22	89	1-2	2e-6	1942.8	5	−4.2	0.72	—
3	Depth medium	~ Year + MSD + (1|stock)	38	91	1-3	5e-5	1937.1	5	—	1.05	−0.26
4	Depth medium	~ Year + F + (1|stock)	2	90	1-4	4e-13	1973.2	5	−16.1	—	−0.09
1	Depth small	~ Year + F + MSD + (1|stock)	5	82			2004.3	6	5.85	0.29	0.15
2	Depth small	~ F + MSD + (1|stock)	8	82	1-2	0.310	2003.3	5	2.36	0.39	—
3	**Depth small**	**~ MSD + (1|stock)**	**6**	**82**	**2-3**	**0.550**	**2001.7**	**4**	**—**	**0.35**	**—**
4	Depth small	~ F + (1|stock)	0	85	2-4	0.007	2008.6	4	−2.53	—	—

Highlighted in bold are the best mixed-effect models explaining the depth distributions of large, medium, and small fish in eight Northeast Atlantic fish stocks. For each response variable, the best model was selected using the χ^2 test, a 0.05 significance cutoff, and Akaike information criterion (AIC).

*Model number for each response variable.

†Marginal R^2, indicating variation explained by fixed effects.

‡Variation explained by the entire model (fixed and random effects).

§Analyses were started with the full model and insignificant terms were dropped progressively using a χ^2 test.

¶*P* values corresponding to the Test column. Values larger than 0.05 suggest that the first model in the pair is not significantly better than the second one, i.e., a term from the first model can be dropped.

#For each model, the slope of fixed effects (F, MSD, and Year) is given in the last three columns, where the effect of Year is transformed to values from 0 (corresponding to 1985) to 31 (corresponding to 2016). Negative slope values suggest an increasing mean depth with the decreasing explanatory variable.

‖Dashes indicate absence of values, i.e., the corresponding explanatory variable is not present in the model tested.

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