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

Ontogenetic deepening not driven by fishing

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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 optimise growth and reproduction (3). In their recent publication, Frank et al. (4) suggest an alternative explanation. They examined age-structured data from the eastern Scotian Shelf cod (*Gadus morhua*), 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 concluded that higher abundances of large fish in deeper waters was an artefact of greater fishing intensity at shallower depths and questioned whether ontogenetic deepening is a real ecological phenomenon.

Frank et al. (4)'s analysis was 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[*], and the average fishing mortality of each stock (F) 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. (4)'s findings and challenges their conclusion that the deepening of marine species may not be an adequate indicator of warming seas (8, 9) 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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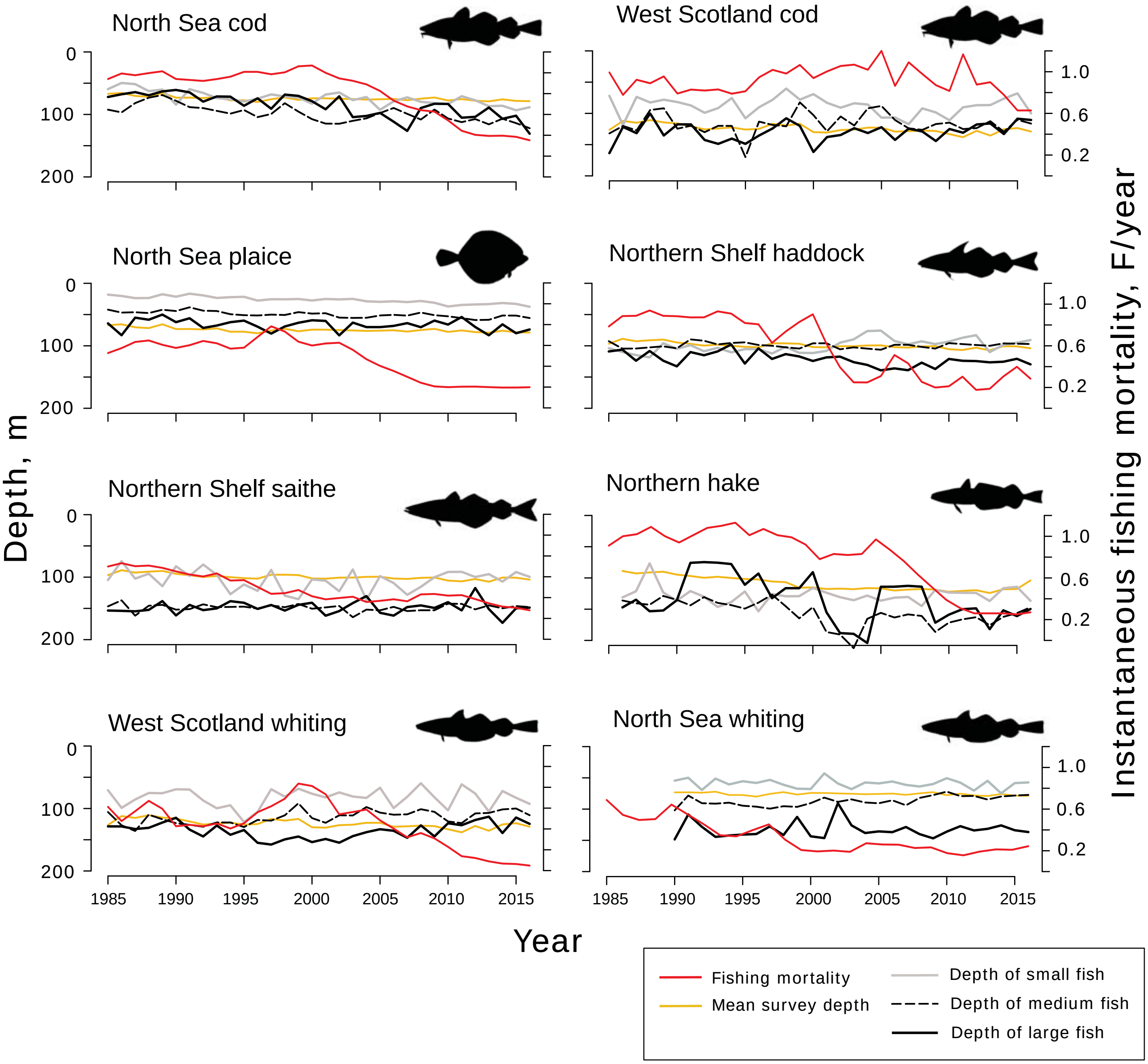
Figure legends

Figure 1. Mean depth distribution of small, medium and large fish in bottom trawl surveys for eight Northeast Atlantic stocks (North Sea cod *Gadus morhua*, west Scotland cod, North Sea plaice *Pleuronectes platessa*, Northern Shelf haddock *Melanogrammus aeglefinus*, Northern Shelf saithe *Pollachius virens*, Northern hake *Merluccius merluccius*, west Scotland whiting *Merlangius merlangus*, North Sea whiting) 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 (http://ices.dk/marine-data/data-portals/Pages/DATRAS.aspx).



North Sea cod
West Scotland cod
North Sea plaice
Northern Shelf haddock
Northern Shelf saithe
Northern hake
West Scotland whiting
North Sea whiting
0
100
200
1.0
0.6
0.2
1985
1990
1995
2000
2005
2010
2015
Depth, m
Instantaneous fishing mortality, F/year
Year
Fishing mortality
Mean survey depth
Depth of small fish
Depth of medium fish
Depth of large fish

Table 1. Details of model selection in mixed effect model analyses. 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 χ2 test and 0.05 significance cut-off and Akaike information criterion (AIC). *No.* shows the model number for each response variable, R_m^2 indicates variation explained by fixed effects (marginal R^2), R^2 – variation explained by the entire model (fixed and random effects), *test* – shows the model pair compared using a χ2 test, where *p* shows the corresponding *p* value and *df* indicates the degrees of freedom in the model. *p* values larger than 0.05 suggest that the first model in the pair is not significantly better than the second one. For each model the slope of fixed effects is given in the last three columns: ***F*** – effect of fishing mortality, ***MSD*** – effect of mean survey depth, ***year*** – effect of year transformed to values form 0 (corresponding to 1985) to 31 (corresponding to 2016).

No.	Response	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%	3-4	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)	23%	89%	1-2	2e-6	1942.8	5	-13.7	0.64	
3	Depth medium	~ year + MSD + (1|stock)	38%	91%	2-3	5e-5	1937.1	5	-	1.05	-0.26
4	Depth medium	~ year + F + (1|stock)	2%	90%	3-4	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**	**0.350**	**2001.7**	**4**	**-**	**0.35**	**-**
4	Depth small	~ F + (1|stock)	0%	85%	3-4	0.007	2008.6	4	-2.53	-	-