TECHNICAL RESPONSE

CLIMATE CHANGE

Response to Comments on "Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery"

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Palmer *et al*. and Swain *et al*. suggest that our "extra mortality" time series is spurious. In response, we show that including temperature-dependent mortality improves abundance estimates and that warming waters reduce growth rates in Gulf of Maine cod. Far from being spurious, temperature effects on this stock are clear, and continuing to ignore them puts the stock in jeopardy.

In their Comments on our Report (*1*), Palmer *et al.* (*2*) and Swain *et al.* (*3*) both expressed concerns about our "extra mortality" calculation. Although they raise important issues about the role of simultaneous estimation of parameters within stock assessment models, their critiques miss the key point of our analysis.

The goal of our "extra mortality" calculation was not to consider how changing natural mortality assumptions would alter the model output. Rather, it was meant to evaluate how well the assessment model could predict the future state of the cod population, assuming a constant natural mortality of 0.2 and observed landings. Our analysis clearly shows that including a temperature effect would have improved the catch advice for Gulf of Maine cod. Although, as suggested in both Comments, post hoc analysis of stock assessments may push analytical limits, neither Comment addresses the critical question of why there is a strong correlation between model residuals and temperature. It is worth noting that Palmer *et al.*'s suggestion to remove outliers via a jackknife procedure finds the same temperature correlations, including one for older fish reported in our supplementary materials, as our procedure using a continuous, consistent section of the time series.

Our interpretation of the projection skill presumes an accurate estimate of abundance; however, a major challenge for the management of this stock has been the presence of a large retrospective pattern in the stock assessment. A retrospective pattern means that the abundance estimated for a given year changes as additional years of data are added. For Gulf of Maine cod, adding another year of data has consistently led to a downward adjustment of biomass in previous years (Fig. 1A). Thus, the projections for this stock started from an erroneous assumption that there were more fish and then were projected assuming that more would survive.

To further evaluate the assertions in our original Report, we investigated whether including temperature-dependent natural mortality would improve the performance of the Gulf of Maine cod assessment. We built a scenario for natural mortality (M) that depends on temperature (T)

$$M_j (T_j, T_{j-3}) = \max(a\, T_j + b\, T_{j-3} + c, 0.05)$$

where the subscript j indicates the year, a = 0.0828, b = 0.0695, and c = 0.1204 [see (*1*)]. We then used this scenario to reconstruct the stock status using the same model, catch, survey indices, and model parameters used in the most recent assessment (*4*).

Using temperature-dependent mortality reduces the retrospective pattern (Fig. 1B). The value of Mohn's ρ, a statistic developed to quantify the magnitude of a retrospective pattern (*5*), declines from 0.54 to 0.19. Therefore, incorporating temperature would have reduced the positive bias in the stock assessment, allowed for better projections of future survival, and, thus, would have supported improved management of Gulf of Maine cod. We agree with both Palmer *et al.* and Swain *et al.* that it would be preferable to fit environmental relationships within the assessment. The success of our scenario using natural mortality linked to temperature strongly suggests that further exploration of temperature effects in this stock is warranted.

The remaining question is whether there are mechanisms that can explain increased natural mortality during warm years. Although we did not attempt to identify a specific cause, we articulated several hypotheses. We considered how temperature effects on metabolism and predation could lead to higher mortality, and it is likely that a combination of these mechanisms act together to increase natural mortality.

Elevated temperature leads to higher metabolic rate (*6*, *7*) and, when coupled with the fact that oxygen levels decrease in warmer waters, helps determine the equatorward limit of fish distributions, including cod (*8*, *9*). The effect of increased metabolic rate is complex and depends on size, age, and reproductive status. If caloric intake does

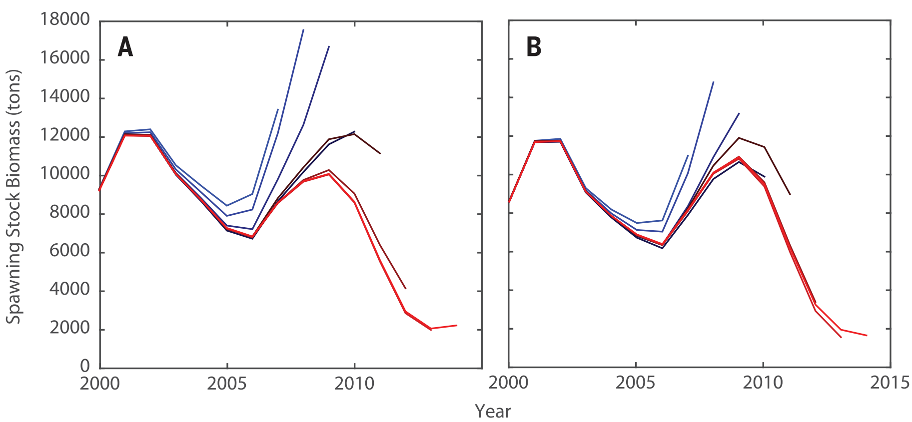

Fig. 1. Spawning stock biomass estimates for Gulf of Maine cod. (**A**) Spawning stock biomass estimated using a constant natural mortality of M = 0.2. The model was run seven times, each time adding another year of data. (**B**) Same as (A) but using a natural mortality scenario that incorporates summer temperatures.

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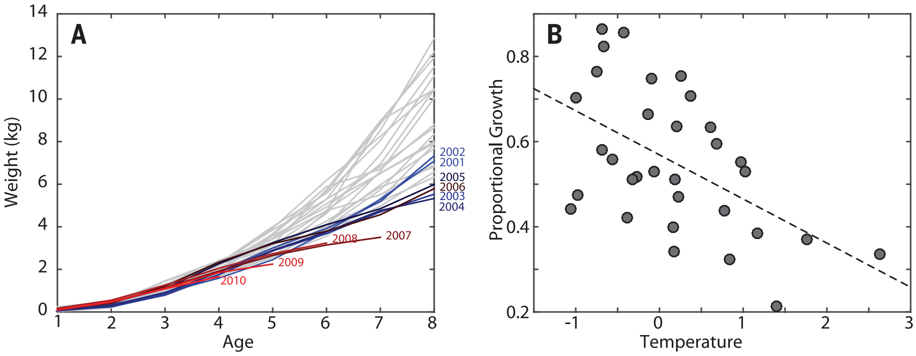

Fig. 2. Relationships between Gulf of Maine cod weight and temperature. (**A**) Growth of different cohorts. Year classes before 2001 are plotted in gray. The final 10-year classes are plotted starting with 2001 in blue and grading to 2010 in red. (**B**) Relationship between the change in weight between ages 5 and 6, expressed as a proportion of the age-5 weight and the summer temperature (R^2 = 0.283, P < 0.1).

Table 1. Linear models relating quarterly and annual temperatures to annual proportional growth increments. If $w_{j,k}$ is the weight of age j fish in year k, then the proportional growth increment $g_{j,k}$ is defined as $(w_{j+1,k+1} - w_{j,k})/w_{j,k}$. For each relationship, we report the coefficient m of the linear model $g_{j,k}\ (T_k) = m\ T_k + b$, the coefficient of determination (R^2), the P value of the relationship, and the P value after accounting for autocorrelation (P_{acf}). Relationships significant at the 95% level are in bold. Those that are also significant at the 90% level when accounting for autocorrelation are in bold and italic.

Age (years)	Statistic	Winter	Spring	Summer	Fall	Year
1 to 2	m	4.8×10^{-6}	8.3×10^{-6}	**$1.0 \times ^{-5}$**	**1.1×10^{-5}**	**1.2×10^{-5}**
	R^2	0.028	0.099	**0.184**	**0.134**	**0.144**
	P	0.36	0.08	**0.01**	**0.04**	**0.03**
	P_{acf}	0.31	0.19	**0.12**	**0.15**	**0.14**
2 to 3	m	$1.9 \times 10^{+00}$	$1.1 \times 10^{+00}$	4.1×10^{-2}	-3.8×10^{-1}	8.7×10^{-1}
	R^2	0.046	0.021	0.000	0.002	0.009
	P	0.24	0.43	0.97	0.82	0.62
	P_{acf}	0.25	0.33	0.49	0.45	0.39
3 to 4	m	***-6×10^{-1}***	-3.5×10^{-1}	-1.7×10^{-1}	**-5.5×10^{-1}**	**-5.3×10^{-1}**
	R^2	***0.222***	0.093	0.027	**0.181**	**0.149**
	P	***0.01***	0.09	0.37	**0.02**	**0.03**
	P_{acf}	***0.08***	0.22	0.35	**0.13**	**0.17**
4 to 5	m	-2.0×10^{-2}	-5.4×10^{-2}	-3.1×10^{-2}	-2.2×10^{-2}	-4.5×10^{-2}
	R^2	0.003	0.028	0.012	0.004	0.014
	P	0.76	0.36	0.55	0.74	0.52
	P_{acf}	0.44	0.32	0.38	0.43	0.37
5 to 6	m	-4.8×10^{-2}	***-1.1×10^{-1}***	***-1×10^{-1}***	**-1×10^{-1}**	***-1.3×10^{-1}***
	R^2	0.038	***0.233***	***0.283***	**0.174**	***0.236***
	P	0.28	***0.01***	***0.00***	**0.02**	***0.00***
	P_{acf}	0.29	***0.10***	***0.08***	**0.14**	***0.10***
6 to 7	m	-7.0×10^{-2}	**-8.4×10^{-2}**	**-7.8×10^{-2}**	**-1.1×10^{-1}**	**-1.2×10^{-1}**
	R^2	0.079	**0.136**	**0.151**	**0.196**	**0.188**
	P	0.12	**0.04**	**0.03**	**0.01**	**0.01**
	P_{acf}	0.21	**0.16**	**0.16**	**0.12**	**0.13**

not increae in proportion with metabolism, then we would expect to see fish that are either poorly conditioned or undersized (low weight for a given age). In our Report, we highlighted the former, based on the report that condition factor had been at or below the long-term mean since 2002 (*10*). However, condition factor has recovered in recent years (*2*, *11*), but this recovery has come at the expense of growth.

Young cod are now larger than in the past, whereas fish age 5 and older are smaller (Fig. 2A). Growth from age 1 to 2 is positively related to temperature, whereas warmer waters produce smaller growth increments in older fish (Table 1). The strongest negative relationships are for age 5 fish (Fig. 2B and Table 1). Because of the strong trend in the temperature data, several of the relationships are not significant when corrected for autocorrelation. However, the overall relationship of increased growth in young fish and decreased growth in older fish is a classic response to warming (*12*). Given the general relationship between body size and mortality in the ocean (*13*), we would expect higher mortality in the current population of smaller fish.

Our Report did not claim to have a definite answer to what is causing cod mortality to increase. Rather, we claimed that this increase is real, that it is likely related to temperature, and that failing to account for it led to catch advice that allowed for overfishing. There have been more than 900 studies describing temperature effects on cod and more than 8000 on fish (*14*). Given the importance of temperature on fish behavior, growth, and ecology, any model that does not consider temperature effects should be viewed with suspicion, especially for stocks near the edge of their range. In particular, any model used to make projections for a commercially important species should reflect current and likely future conditions in the ocean. In contrast to the assertion that stock assessment outputs should not be subjected to post hoc analyses (*15*), we feel that it is vital to evaluate the implications of these models and to strive to improve their ability to accurately represent the state of nature.

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