VADER Bottom-Up Feedback Data Exploration

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SEDAR 102-WP-09: VADER Bottom-Up Feedback Data Exploration

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Introduction

The concept of bottom-up feedback in ecosystem models emphasizes how prey abundance can influence predator growth and mortality. In contrast, the effects of top-down processes—namely predation—have been well studied, and various modeling approaches have been developed to capture this relationship (Curti et al., 2013; Lewy & Vinther, 2014; van Kirk et al., 2010). One such approach is the multispecies statistical catch-at-age model developed for the 2020 Ecological Reference Points (ERP) benchmark assessment, hereafter referred to as the *Virtual Assessment for the Description of Ecosystem Responses* (VADER), which serves as the focus of this working paper.

A key reviewer comment from the 2020 benchmark recommended to "continue development of the VADER model to include bottom-up effects of Atlantic menhaden abundance on key predator species." In response to this prompt—and given that VADER already incorporates top-down interactions—an effort was initiated to explore the development of bottom-up functionality within the VADER framework.

In the VADER model, predation dynamics are statistically estimated using various diet and consumption data (see Working Paper SEDAR 102-WP-08). To incorporate bottom-up processes in a similar manner, empirical information describing the effect of prey abundance on predator performance is required to parameterize these relationships. The present analysis investigates whether such relationships exist, particularly between prey availability and predator growth metrics (e.g., weight-at-age or length-at-age).

This working paper addresses the following key questions:

- Does prey biomass (e.g., menhaden alone or in combination with other prey species) influence predator weight-at-age (WAA)?
- Is this relationship detectable using existing data streams?

The following analyses explore these questions using multiple methodological approaches, with a primary focus on striped bass as a key predator species. Given that density-dependent growth and prey-dependent growth can produce similar patterns, both processes are evaluated in order to compare and distinguish their relative effects.

Methods

We used multiple empirical and model-derived datasets to evaluate density- and prey-dependent effects on striped bass growth. Key data sources included:
(1) time series of empirical mean weight-at-age for striped bass, which were standardized by

dividing each value by the long-term average for each age class to yield relative weight-at-age;
(2) spawning stock biomass (SSB) of striped bass through time, obtained from the most recent stock assessment report;
(3) biomass of Atlantic menhaden through time, also from the most recent stock assessment;
(4) an aggregated biomass index of major prey species of striped bass (menhaden, weakfish, and herring), derived from the output of the VADER ecosystem model; and
(5) a dataset of length-at-age for striped bass based on otolith-aged samples developed in Schiano et al. (2025), which was similarly converted to a standardized relative length-at-age, as was done for weight-at-age.

Using these data, we tested for evidence of (1) density-dependent and (2) prey-dependent effects on striped bass growth. Analyses were conducted using both weight-at-age and length-at-age as proxies for individual growth.

Two methodological approaches were applied:

1. Non-linear modeling approach

We fit the following non-linear models using the nls() function in R:

- **Density dependence model**:

$$RelWeight = \frac{\alpha}{\beta + SSB_{striped\ bass}}$$

- **Prey dependence model**:

$$RelWeight = \frac{\alpha * Biomass_{prey}}{\beta * Biomass_{prey} + SSB_{striped\ bass}}$$

Here, prey biomass was represented either by Atlantic menhaden alone or by the aggregated prey biomass from VADER. These models were repeated using relative length-at-age as the response variable in place of relative weight-at-age.

2. Consumption-based method following Rindorf et al. (2022)

We also applied a method based on the framework from Rindorf et al. (2022), which evaluates density dependence by analyzing the relationship between weight deviations and consumption. This approach assumes that intraspecific competition limits food availability and hence growth. The analysis was stratified by age group: age 2–4 (mid-aged) and age 5–15 (older individuals). Weight deviations were assessed relative to estimated consumption across time, providing an alternative metric of density dependence. Menhaden were the prey used in this part of the analysis.

Results

1. **Weight-at-Age Analyses**

An initial visual inspection of weight-at-age (WAA) for striped bass over time, relative to spawning stock biomass, is presented in Figure 1. This plot does not reveal a strong or obvious pattern indicative of density-dependent growth regulation.

A second-level exploration was conducted by examining deviations in WAA across years (Figure 2). This visualization suggests a temporal trend, with notably higher variance in the earlier years of the time series. However, these trends remain inconclusive based on visual inspection alone.

Density Dependence

As shown in Figure 3 and summarized in Table 1, there is some evidence of weak density dependence between striped bass biomass and WAA. This finding may indicate modest self-limiting growth mechanisms within the predator population.

Menhaden Biomass Effects

Adding Atlantic menhaden biomass as an explanatory variable did not reveal a significant relationship with striped bass WAA. As shown in Figure 4 and Table 2, this suggests that WAA is not notably influenced by variation in menhaden abundance, at least as captured in the current model framework with the data used for this part of the analysis.

Aggregated Prey Biomass Effects

Similarly, when aggregated prey biomass—derived from the VADER model—was used as a predictor, no evidence emerged of prey-dependent effects on striped bass WAA (Figure 5, Table 3). This further supports the conclusion that prey availability, as represented in this part of the analysis, may not be a key driver of predator growth variation based on changes in weight.

Consumption-based Analysis (Rindorf et al. 2022)

To explore prey limitation from a consumption-based perspective, we applied the method of Rindorf et al. (2022), which evaluates weight deviations across two striped bass age groups (ages 2–4 and 5–15) in relation to estimated prey (menhaden) consumption. This analysis also failed to detect a meaningful relationship between menhaden biomass and predator WAA (Figures 6 and 7; Tables 4 and 5).

2. Length-at-Age Analyses

Length-at-age (LAA) was used as an alternative indicator of individual growth. These data were derived from an otolith-aged sample covering the years 1998–2019. The same modeling framework applied to WAA was repeated here with adjustments for the length-based dataset.

Initial visual inspection of LAA through time relative to striped bass biomass (Figure 8) yielded no compelling pattern indicative of a density-dependent relationship.

Density Dependence

Figure 9 and Table 6 provide some evidence of a weak negative relationship between striped bass biomass and LAA, suggesting that density-dependent growth effects may be present.

Interestingly, this relationship appears stronger than that observed in the WAA analysis, though still relatively weak in absolute terms.

Menhaden Biomass Effects

When menhaden biomass was included as a predictor of LAA, results showed some evidence of a prey-dependent relationship (Figure 10, Table 7). This suggests that variation in menhaden biomass may influence length-based growth metrics in striped bass, providing preliminary support for prey availability affecting somatic growth in striped bass.

Aggregated Prey Biomass Effects

In contrast, substituting aggregated prey biomass for menhaden alone did not yield a detectable effect on LAA (Figure 11, Table 8). This mirrors the pattern seen in the WAA analysis and may indicate that menhaden has a more direct or stronger influence on striped bass growth than the broader prey base represented in the aggregated index.

Consumption-based Analysis (Rindorf et al. 2022)

As with the WAA analysis, the Rindorf et al. (2022) method showed no evidence of a relationship between menhaden biomass and LAA across the two age groups examined (Figures 12 and 13; Tables 9 and 10). This further supports the interpretation that prey biomass generally is not having a very strong influence on individual growth as the signal is not being picked up across methods.

Discussion

This analysis explored the roles of density dependence and prey availability in regulating striped bass growth, using both weight-at-age (WAA) and length-at-age (LAA) as indicators. While evidence for strong density-dependent growth was limited, one of the most important findings to emerge was a positive relationship between menhaden biomass and striped bass length-at-age. This relationship was not observed for weight-at-age or for the aggregated prey biomass metric, underscoring the potential value of length-based growth data in detecting biologically meaningful prey-dependent signals. The alternative Rindorf et al. method also did not indicate a strong statistically significant relationship between prey and growth. Additionally, it is of note that the LAA data was a newer dataset with ages that were derived from otoliths, as opposed to scales, therefore this may be an indication that there is a difference in the determination of age between these two aging methods.

Key Finding: Prey Dependence of Length-at-Age

The relationship between menhaden biomass and LAA represents a central result of this study. While striped bass WAA did not respond significantly to either menhaden or aggregated prey biomass, LAA increased with menhaden biomass in a manner suggestive of prey-mediated growth regulation. It is important to note that this signal was not a very strong one, but it was statistically significant. This pattern supports the ecological importance of Atlantic menhaden as a key forage species and highlights the potential for prey availability to influence striped bass somatic growth—particularly over longer time scales captured by otolith-derived length data.

Importantly, this finding provides empirical justification for a new feature developed in VADER for this assessment process: that growth in striped bass is dynamically linked to prey availability via natural mortality. The LAA-menhaden relationship is consistent with the conceptual and mechanistic approach used in Schiano et al. (2025), in which otolith-based growth trajectories were employed to inform and parameterize time-varying M1 in the predator-prey dynamics of striped bass. Thus, this result not only reinforces the biological relevance of menhaden to striped bass growth, but also lends credibility to the implementation of dynamic M1 calculations in the VADER model.

Density Dependence and Alternative Growth Metrics

Although some weak density-dependent effects were observed in both WAA and LAA analyses, the relationships were modest and not consistently significant. The LAA-based models suggested slightly stronger evidence for density dependence than WAA, potentially due to the fact that length integrates growth over a longer period and is less sensitive to short-term variation in energetic condition, reproduction, or feeding.

The contrast between WAA and LAA results underscores the value of using multiple metrics to assess growth. Weight can fluctuate due to recent foraging success or reproductive state, while length—particularly when derived from otolith-based age estimates—may better reflect cumulative growth processes and provide a more stable signal of environmental and ecological influences.

Aggregated Prey Biomass and Consumption-Based Approaches

Neither WAA nor LAA showed a relationship with aggregated prey biomass, whether assessed through non-linear modeling or the consumption-based method adapted from Rindorf et al. (2022). These results suggest that generalized indices of prey biomass may lack the specificity or resolution necessary to detect meaningful trophic linkages, especially in generalist predators like striped bass that exhibit dietary plasticity and spatial foraging flexibility.

The Rindorf et al. (2022) framework, while useful for exploring potential density-driven foraging limitations, did not identify significant weight or length deviations attributable to consumption patterns across age groups. These findings reinforce the importance of prey identity—rather than just total biomass—in shaping growth outcomes for predators.

Implications for Modeling and Management

The observed link between menhaden biomass and striped bass growth represented by length has important implications for ecosystem-based fisheries management and multispecies modeling. It provides empirical support for a prey-dependent growth pathway in an important estuarine predator, striped bass, thereby justifying the incorporation of dynamic M1 calculations in VADER and similar modeling efforts. This finding connects the empirical growth data available for striped bass and the ecosystem modeling methodology of VADER through the use of the methods developed by Schiano et al. (2025).

Moving forward, these results suggest several avenues for further refinement. Future work could build a truly dynamic model that uses the parameters generated from the non-linear model developed in this work that can dynamically influence striped bass growth based on the biomass trajectory of menhaden. Additionally, another avenue that can be explored is, instead of growth, links between various environmental drivers and mortality is another mechanism that can manifest bottom-up processes. These ideas can be further developed for the next ecological reference point benchmark process.

References

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Tables

Table 1. Weight-at-age analysis: Density dependence non-linear model parameter estimates

Parameter	Estimate	Standard error	T value	P value
α	2071.8	644.0	3.217	0.001
β	1977.6	643.3	3.074	0.002

Table 2. Weight-at-age analysis: Menhaden dependence non-linear model parameter estimates

Parameter	Estimate	Standard error	T value	P value
α	7.698	30.253	0.254	0.799
β	7.678	30.252	0.254	0.800

Table 3. Weight-at-age analysis: Aggregated prey dependence non-linear model parameter estimates

Parameter	Estimate	Standard error	T value	P value
α	2.209	1.539	1.435	0.152
β	2.168	1.538	1.410	0.159

Table 4. Weight-at-age analysis: Rindorf et al. method model parameter estimates striped bass ages 2 - 4

Parameter	Estimate	Standard error	T value	P value
α	0.011	0.075	0.142	0.890
β	-2.282	0.060	-38.322	2e-16

Table 5. Weight-at-age analysis: Rindorf et al. method model parameter estimates striped bass ages 5 - 15

Parameter	Estimate	Standard error	T value	P value
α	0.0002	0.018	0.011	0.991
β	-0.273	0.0280	-9.921	4.3e-12

Table 6. Length-at-age analysis: Density dependence non-linear model parameter estimates

Parameter	Estimate	Standard error	T value	P value
α	1436.2	289.4	4.962	1.20e-6
β	1316.3	289.2	4.552	7.89e-6

Table 7. Length -at-age analysis: Menhaden dependence non-linear model parameter estimates

Parameter	Estimate	Standard error	T value	P value
α	0.636	0.150	4.243	2.99e-5
β	0.612	0.150	4.084	5.76e-5

Table 8. Length -at-age analysis: Aggregated prey dependence non-linear model parameter estimates

Parameter	Estimate	Standard error	T value	P value
α	991.4	2828.7	0.350	0.728
β	-8039.2	9780.3	-0.822	0.417

Table 9. Length -at-age analysis: Rindorf et al. method model parameter estimates striped bass ages 2 - 4

Parameter	Estimate	Standard error	T value	P value
α	0.664	1.966	0.338	0.74
β	-35.547	3.001	-11.844	2.49e-9

Table 10. Length -at-age analysis: Rindorf et al. method model parameter estimates striped bass ages 5 - 15

Parameter	Estimate	Standard error	T value	P value
α	-0.854	1.750	-0.488	0.632
β	-0.728	4.925	-0.148	0.884

Figures

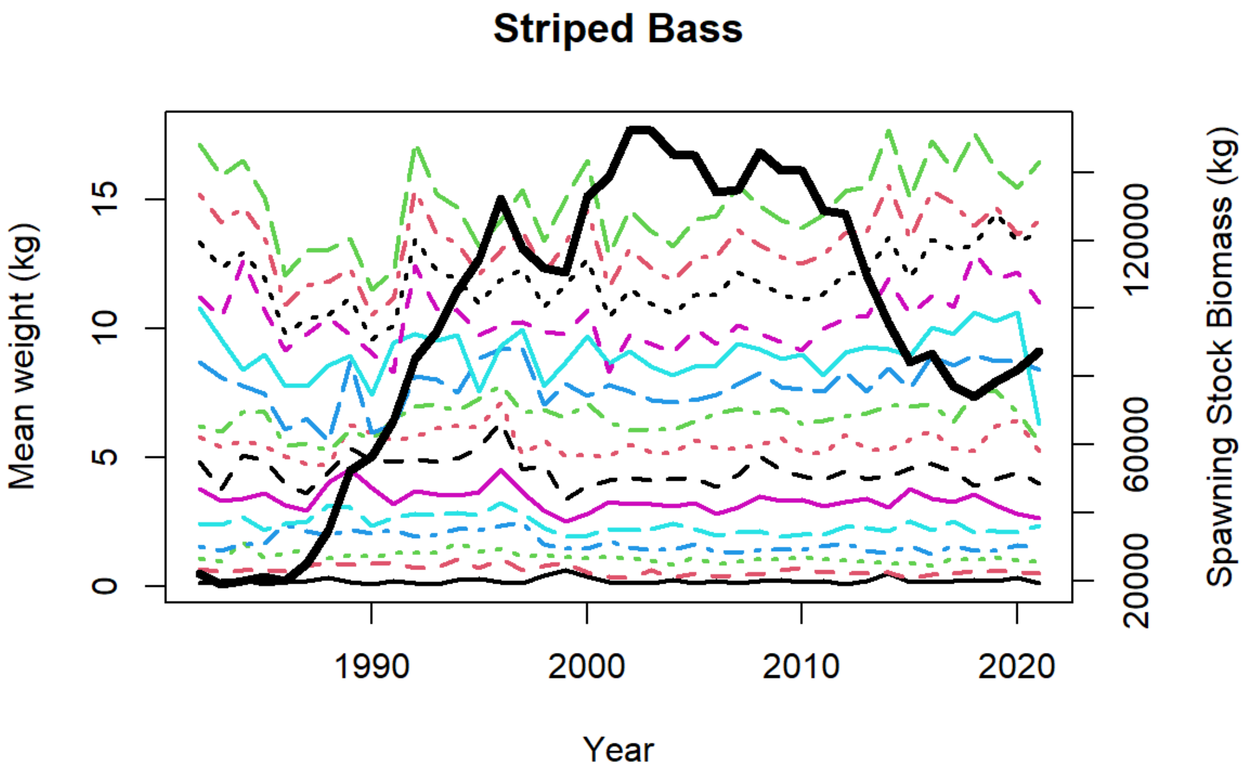

Figure 1. Striped bass empirical mean weight-at-age (colored lines) and model derived spawning stock biomass (bold black line) by year.

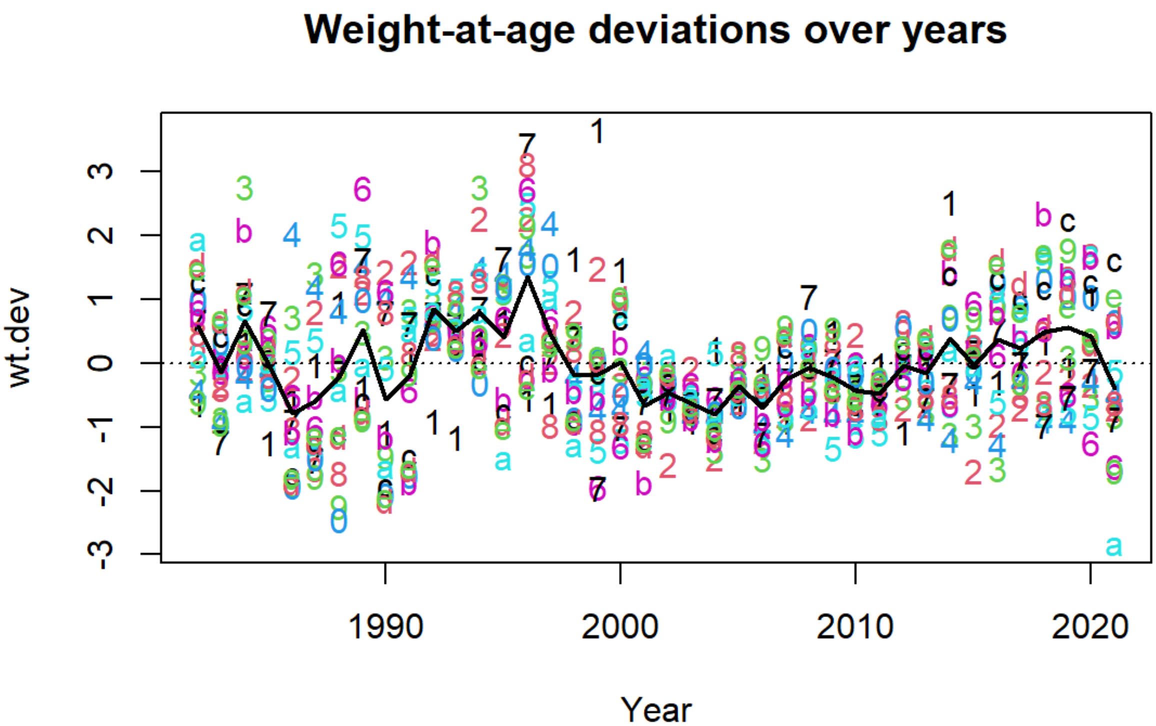

Figure 2. Striped bass weight-at-age deviations (points) and average trendline (black line) by year.

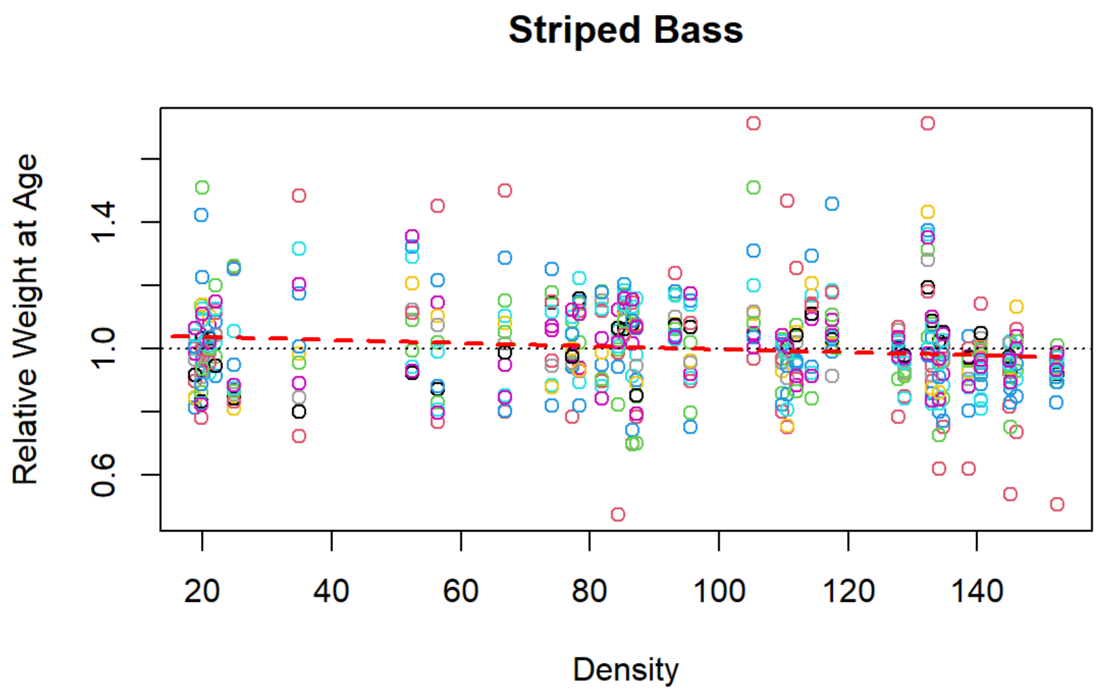

Figure 3. Striped bass relative weight-at-age (colored point) and non-linear model output for striped bass density dependence (red dashed line).

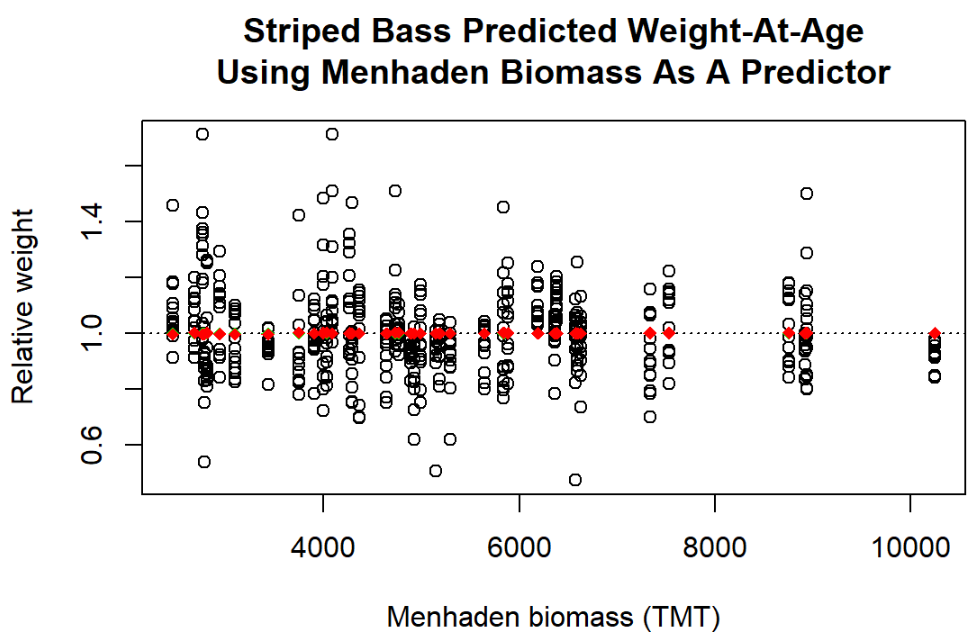

Figure 4. Striped bass relative weight-at-age (open points) and non-linear model output for menhaden dependence (red points).

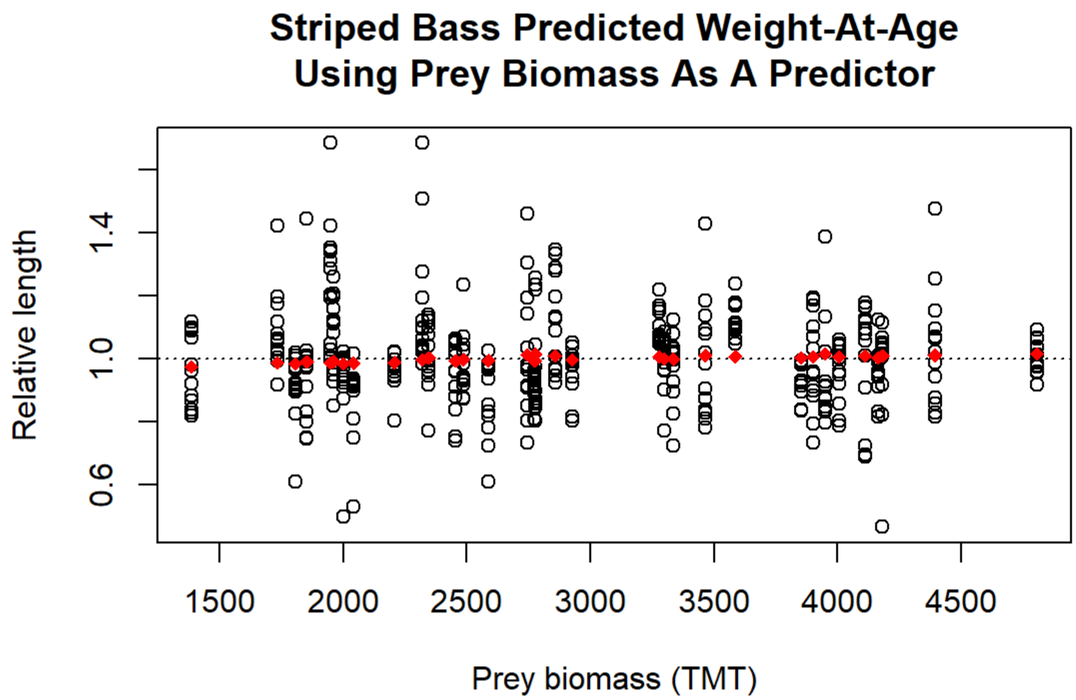

Figure 5. Striped bass relative weight-at-age (open points) and non-linear model output for aggregated prey dependence (red points).

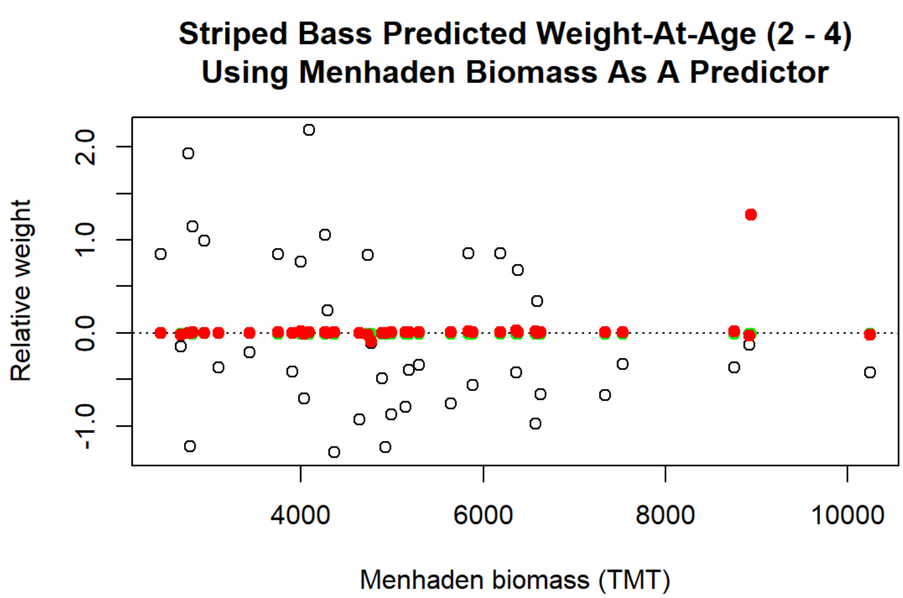

Figure 6. Striped bass relative weight-at-age ages 2 through 4 (open points) and Rindorf et al. method output for menhaden dependence (red points).

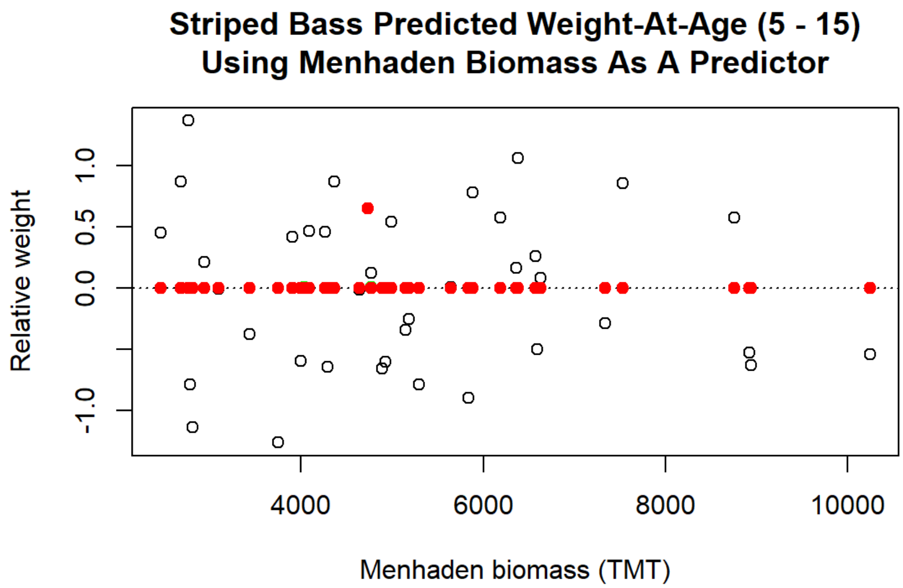

Figure 7. Striped bass relative weight-at-age ages 5 through 15 (open points) and Rindorf et al. method output for menhaden dependence (red points).

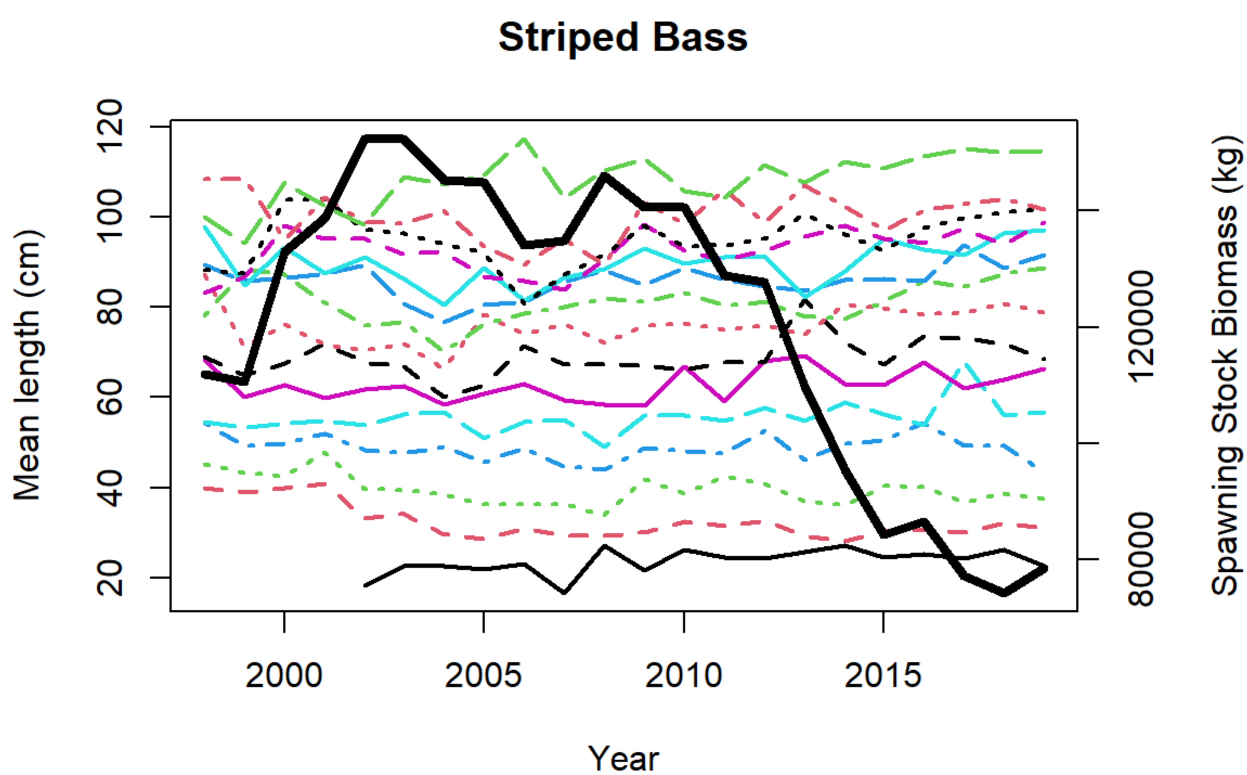

Figure 8. Striped bass empirical mean length-at-age from otoliths (colored lines) and model derived spawning stock biomass (bold black line) by year.

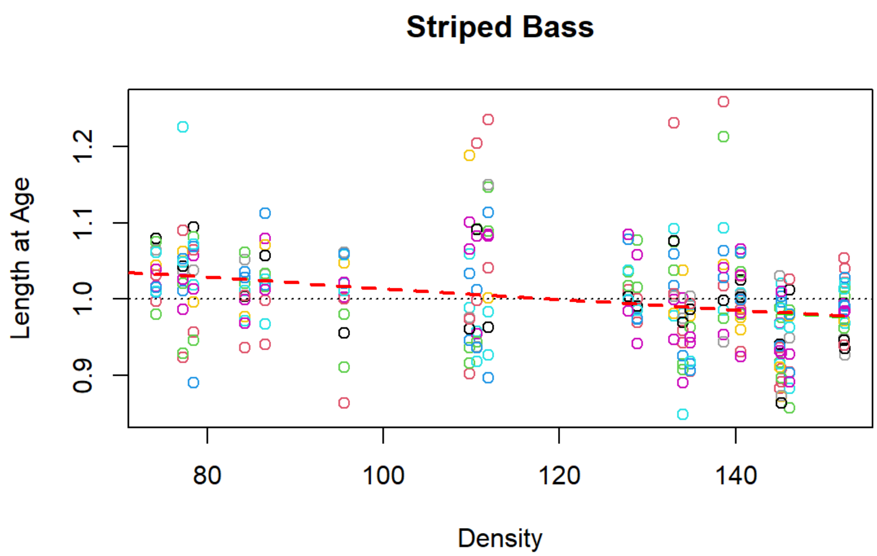

Figure 9. Striped bass relative length-at-age (colored point) and non-linear model output for striped bass density dependence (red dashed line).

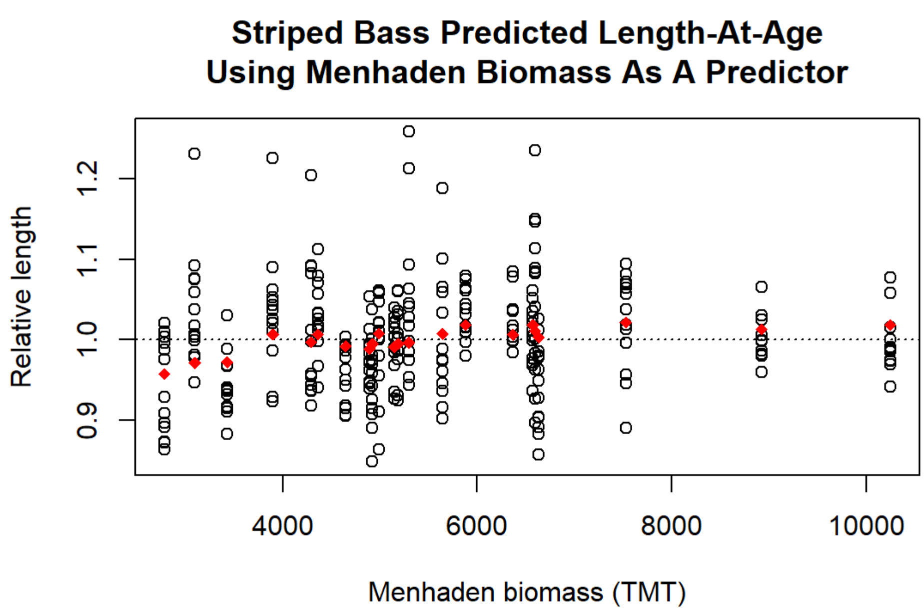

Figure 10. Striped bass relative length-at-age (open points) and non-linear model output for menhaden dependence (red points).

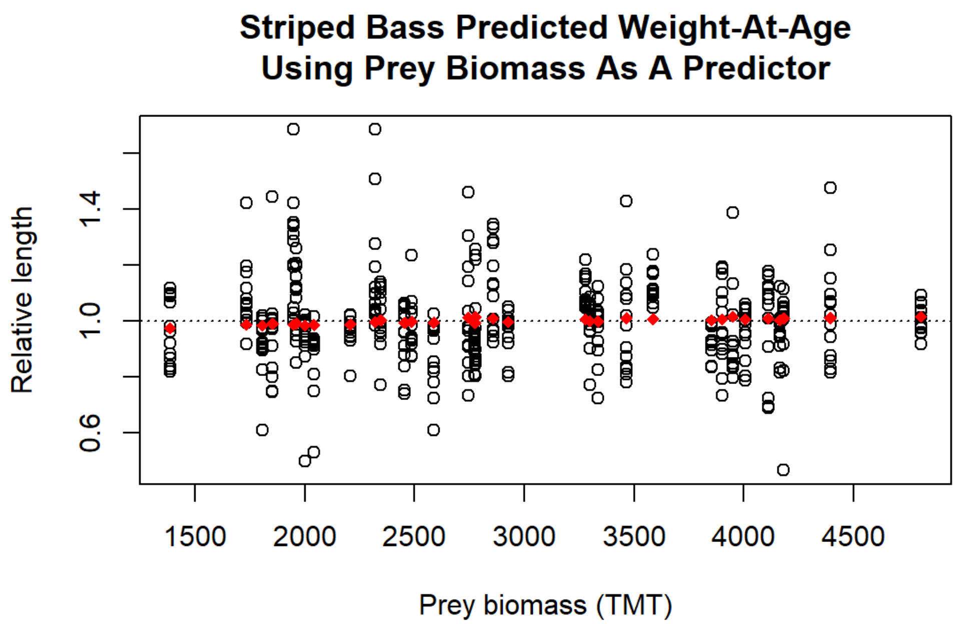

Figure 11. Striped bass relative weight-at-age (open points) and non-linear model output for aggregated prey dependence (red points).

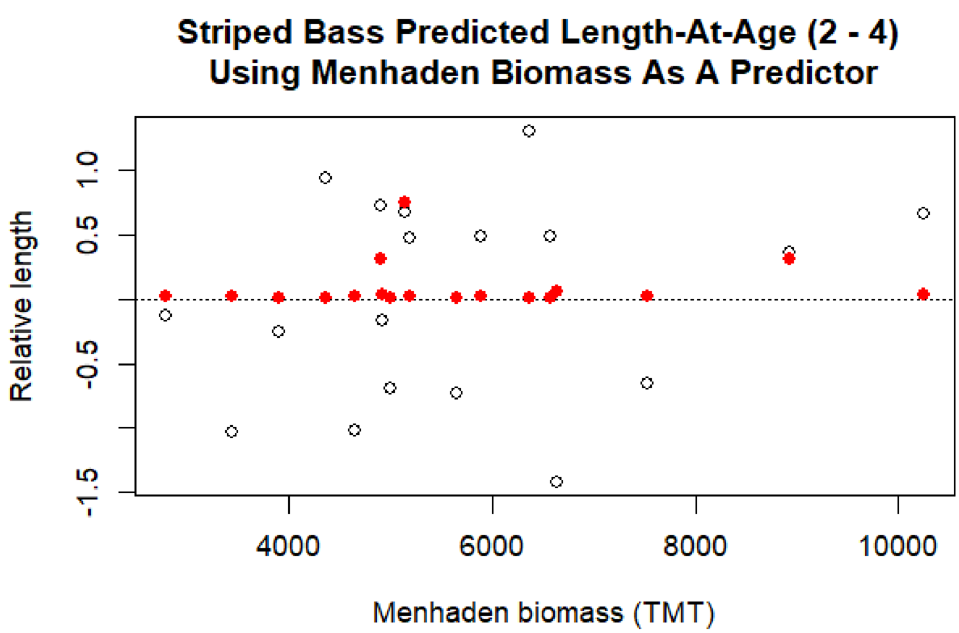

Figure 12. Striped bass relative length-at-age ages 2 through 4 (open points) and Rindorf et al. method output for menhaden dependence (red points).

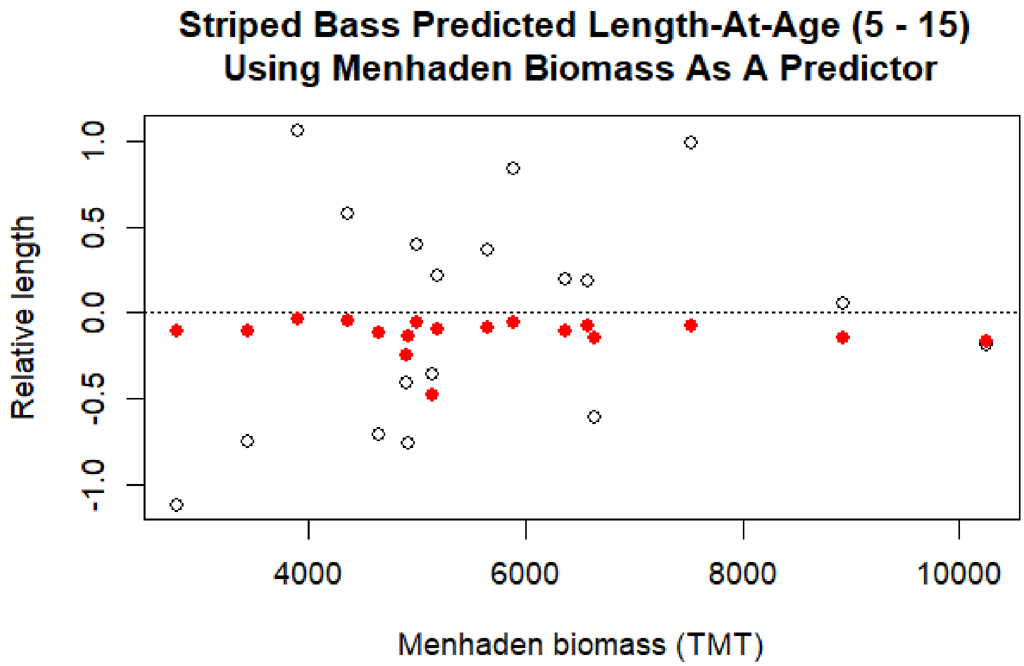

Figure 13. Striped bass relative length-at-age ages 5 through 15 (open points) and Rindorf et al. method output for menhaden dependence (red points).