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Evaluating a possible new paradigm for recruitment dynamics: predicting poor recruitment for striped bass (*Morone saxatilis*) from an environmental variable

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ABSTRACT

Understanding what causes large year classes and predicting them has been called the holy grail of fisheries science, one of the last great unanswered questions. Recruitment prediction, or forecasting, is an important component for setting fishery catch limits. We propose a new approach, called the "poor-recruitment paradigm", for predicting recruitment using environmental variables. This approach hypothesizes that it is easier to predict poor recruitment rather than good recruitment because an environmental variable affects recruitment only when its value is extreme (lethal); otherwise, the variable may be benign and not influence recruitment. Thus, good recruitment necessitates all environmental conditions not be harmful and for some to be especially favorable; poor recruitment, however, requires only one environmental variable to be extreme.

This idea was evaluated using recruitment and river discharge data for striped bass (*Morone saxatilis*) from seven major spawning tributaries of Chesapeake Bay. Low spring river discharge reliably resulted in poor recruitment of striped bass. Specifically, in all rivers, median recruitment and standard deviation of recruitment were lower when spring river discharge was low compared to when it was average or high; additionally, the proportion of years with poor recruitment was higher in years of low discharge than in years of average to high discharge. The consistent predictability of poor recruitment has the potential to improve stock projections, and therefore, has the potential to improve catch advice.

1. Introduction

Predicting recruitment is an important aspect of stock assessment as it affects our understanding of population dynamics and ecosystem function, is used for determining short term catch limits, and enables the industry to make rational decisions on capital investment. Despite major efforts to understand the factors driving recruitment success and to develop methods for forecasting recruitment, making reliable predictions is difficult. The relationship between spawning stock size and recruitment generally appears weak (but is demonstrably important, see Myers and Barrowman, 1996) indicating that spawning stock affects recruitment but not in a highly predictive way. Relationships between environmental variables and recruitment have been posited repeatedly, but these relationships tend to fall apart when additional data are collected and there are few instances of such relationships actually being used in stock assessments (Myers, 1998; Haltuch et al., 2019).

In this paper, we suggest a possible new paradigm for predicting recruitment, "the poor-recruitment paradigm". According to this paradigm, it is not possible, in general, to predict when above average or exceptionally good recruitment will occur, but it is possible in some cases to predict when poor recruitment will occur based on the value of an environmental condition. That is, recruitment cannot be predicted over the entire range of values of an environmental variable, however, poor recruitment is likely when a relevant environmental variable is at an extreme. Intuitively, in order for good recruitment to occur, it is necessary for all environmental variables to be at least benign. In contrast, one lethal environmental variable suffices for poor recruitment to occur. Hence, monitoring an environmental variable can indicate (some of the) years in which recruitment is likely to be poor, whereas predicting good recruitment requires a plethora of variables to be monitored. Of course, monitoring several relevant environmental variables could enable one to predict more of the years with poor recruitment.

To illustrate and evaluate the "poor-recruitment paradigm", we

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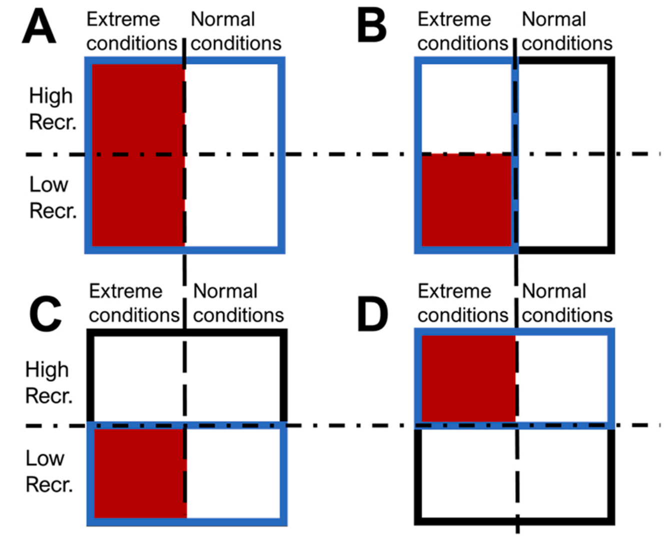

Fig. 1. The four key questions expressed diagrammatically. Probabilities are expressed as numerator (number of observations in the solid red box) divided by denominator (number of observations in the blue rectangle). For striped bass, the "extreme conditions" is low river discharge and "normal conditions" is average to high river discharge. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

examine recruitment of striped bass (*Morone saxatilis*), an anadromous fish that spawns in Chesapeake Bay during spring (April, May, early June), in relation to river discharge, and describe patterns of poor recruitment using simple metrics. Chesapeake Bay striped bass provide an informative case study, as their recruitment has been thoroughly studied in relation to environmental conditions, and the distinct spawning populations for each major tributary of Chesapeake Bay, each with over 35 years of data, provide replication in space and time. We hypothesize that low river discharge leads to poor recruitment (but the converse is not necessarily true – average or high river discharge can lead to good *or* poor recruitment).

A priori justification for choosing river discharge as a recruitment predictor comes from multiple studies in the Chesapeake Bay (Shielder and Houde, 2014; Martino and Houde, 2010; North and Houde, 2003; McGovern and Olney, 1996; Uphoff, 1989) as well as studies from other areas including North Carolina and California (Rulifson and Manooch, 1990; Stevens, 1977; Turner and Chadwick, 1972) which have shown that river discharge significantly affects juvenile striped bass survival, and therefore influences striped bass recruitment.

The exact mechanism driving the relationship between river discharge and recruitment (or juvenile mortality) is unclear, although it has been repeatedly suggested that river discharge influences the temporal and spatial abundance and availability of zooplankton as well as the availability of favorable nursery habitats (Shielder and Houde, 2014; Martino and Houde, 2010).

In our poor-recruitment paradigm, we offer an alleviation of the heavy focus on describing the underlying mechanisms of recruitment. Specifically, in terms of recruitment forecasting, the mechanisms governing environmental determinants of recruitment are superfluous; what matters is whether some range of an environmental variable is lethal to juveniles in a way that affords predictive power for poor recruitment, regardless of mechanism. Since over half of fished stocks are considered to be "data poor" (Berkson and Thorson, 2015), this approach's minimal data requirements make it a pragmatic choice for predicting future recruitment to a fishery. However, this is not to say that mechanistic studies are not important – they have significant value for furthering our understanding recruitment dynamics and provide the basis for *a priori* selection of predictive environmental variables, thus guarding against the adoption of spurious relationships.

Table 1
River discharge data sources for Maryland and Virginia rivers in the Chesapeake Bay. Note that the York River's discharge rate estimated as the combined discharge of its two major tributaries that occur at its headwaters, as there is no discharge monitoring station for York River itself.

River		Station ID	Latitude	Longitude
Choptank		USGS 01491000	38°59'49.9"	75°47'08.9"
James		USGS 02037500	37°33'47"	77°32'50"
Patuxent		USGS 01594440	38°57'21.3"	76°41'37.3"
Potomac		USGS 01646500	38°56'59.2"	77°07'39.5"
Rappahannock		USGS 01668000	38°18'30"	77°31'46"
Susquehanna		USGS 01578310	39°39'28.4"	76°10'28.0"
York	Mattaponi	USGS 01674500	37°53'02"	77°09'55"
	Pamunkey	USGS 01673000	37°46'03"	77°19'57"

To evaluate the poor-recruitment paradigm for forecasting recruitment, we characterized the ability to predict recruitment from river discharge by examining four key questions (Fig. 1):

A. How often can we make a prediction of poor recruitment based on an extreme environmental condition? (e.g., how often is river discharge low?) (Fig. 1A)
B. What is the probability we can correctly predict poor recruitment when we make a prediction (e.g., when river discharge is low) (Fig. 1B)?
C. What percentage of the poor recruitment events can we predict (Fig. 1C)?
D. What is the probability of falsely predicting poor recruitment given that recruitment is good (Fig. 1D)?

2. Methods

Recruitment indices and river discharge rates were obtained for seven spawning populations of striped bass in the Chesapeake Bay corresponding to seven major tributaries. Recruitment data (annual index of age-0 abundance) for striped bass were provided by the Virginia Institute of Marine Science Juvenile Striped Bass Seine Survey (Buchanan et al., 2021) for rivers in Virginia and by the Maryland Department of Natural Resources Juvenile Striped Bass Seine Survey for rivers in Maryland (Horne, 2019). River discharge data were gathered from United States Geological Survey (USGS) National Water Information System monitoring stations (Table 1).

Daily river discharges measured from 30 March – 15 May were averaged for each year from 1985 to 2018, to obtain annual values of mean spring river discharge, a measure that has been routinely used in previous studies of river discharge and recruitment (North and Houde, 2003; Rulifson and Manooch, 1990; Stevens, 1977). The time frame of 1985–2018 was initially chosen to maintain the same temporal structure of the data by avoiding gaps in river discharge and juvenile index data. However, additional data were obtained for three Virginia rivers for earlier years (1967–1973; 1980–1984) to further examine the hypothesis's replicability over time.

In order to make consistent comparisons across rivers, the annual mean spring river discharges were standardized to Z scores. To specify a threshold for extreme conditions, the standardized data for annual mean spring river discharge were combined across all rivers for all years; then the value delineating the lower one-third of the data was chosen as the threshold between extreme (low river discharge) and normal (average to high river discharge) environmental conditions. For a given river, this resulted in approximately one-third of its observations being characterized as exhibiting extreme conditions and two-thirds being normal conditions. In an actual stock assessment application, one could search for the optimal threshold between extreme and non-extreme conditions. However, in this study one-third was chosen as the dividing threshold in order to be objective and to ensure that there would be adequate sample sizes for both categories (extreme and non-extreme).

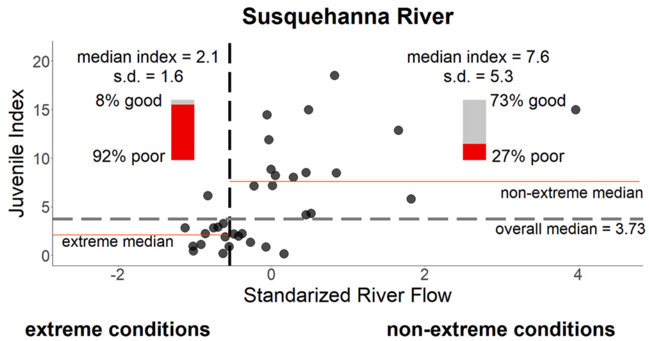

Fig. 2. Recruitment of striped bass in the Susquehanna River as a function of standardized river discharge. The vertical dashed line divides river discharge data into extreme and normal (non-extreme) river discharges. The horizontal dashed line divides the juvenile indices into below- and above-median recruitment, while the horizontal red lines indicate median recruitment for extreme and normal river discharge conditions.

To describe patterns of recruitment, we calculated three metrics for each of the seven rivers for both extreme and normal conditions: the median recruitment, the standard deviation of recruitment, and the proportion of years with poor vs. good recruitment. Recruitment was classified as "good" if it was above median recruitment for a given river, and "poor" if below median. Median recruitment (rather than mean recruitment) was used since recruitment data are not normally distributed.

For the analysis of the additional years of data for the three Virginia rivers, all of the data (old and recent) were combined, and the river discharges were standardized to Z scores. The overall median recruitment defining poor vs. good recruitment was recalculated including the new data. The cutoff between extreme and non-extreme conditions was left unchanged for consistency, however. Then, the three recruitment metrics (median, standard deviation, and proportion of poor vs. good recruitment) were recalculated including the additional data.

Under our application of the poor-recruitment paradigm, low river discharge is associated with poor recruitment. Four probabilities were estimated to examine the possible predictive power of extreme (low discharge) environmental conditions.

A. Prob(low discharge)
B. Prob(poor recruitment | low discharge)
C. Prob(predict poor recruitment | poor recruitment)
D. Prob(predict poor recruitment | good recruitment)

These four probabilities correspond to the four questions associated with Fig. 1. To estimate these probabilities for the entire Chesapeake Bay system, recruitment data were standardized to Z scores. Standardized river discharge and recruitment data for the seven rivers were then combined before computing probabilities. Note that, because extreme conditions were defined to be the lowest third of the river discharges, the probability of low discharge (Fig. 1A) was a fixed design parameter equal to 0.33. However, in a stock assessment application, one could estimate the optimum threshold to define conditions that predict poor recruitment. Then, the probability of extreme conditions (e.g. low discharge) would be a random variable. Additional data for the three Virginia rivers were not included in the estimation of these probabilities.

3. Results and discussion

For all seven stocks of striped bass in the Chesapeake Bay, median recruitment was lower during extreme environmental conditions than non-extreme conditions, and also had a higher proportion of years with poor recruitment compared to normal conditions. The variability (standard deviation) of recruitment during extreme conditions was lower than that of normal conditions (with one exception in the York River due to a single very large year class). These results indicate that extreme environmental conditions (low river discharge) consistently lead to poor recruitment; in contrast, recruitment is highly

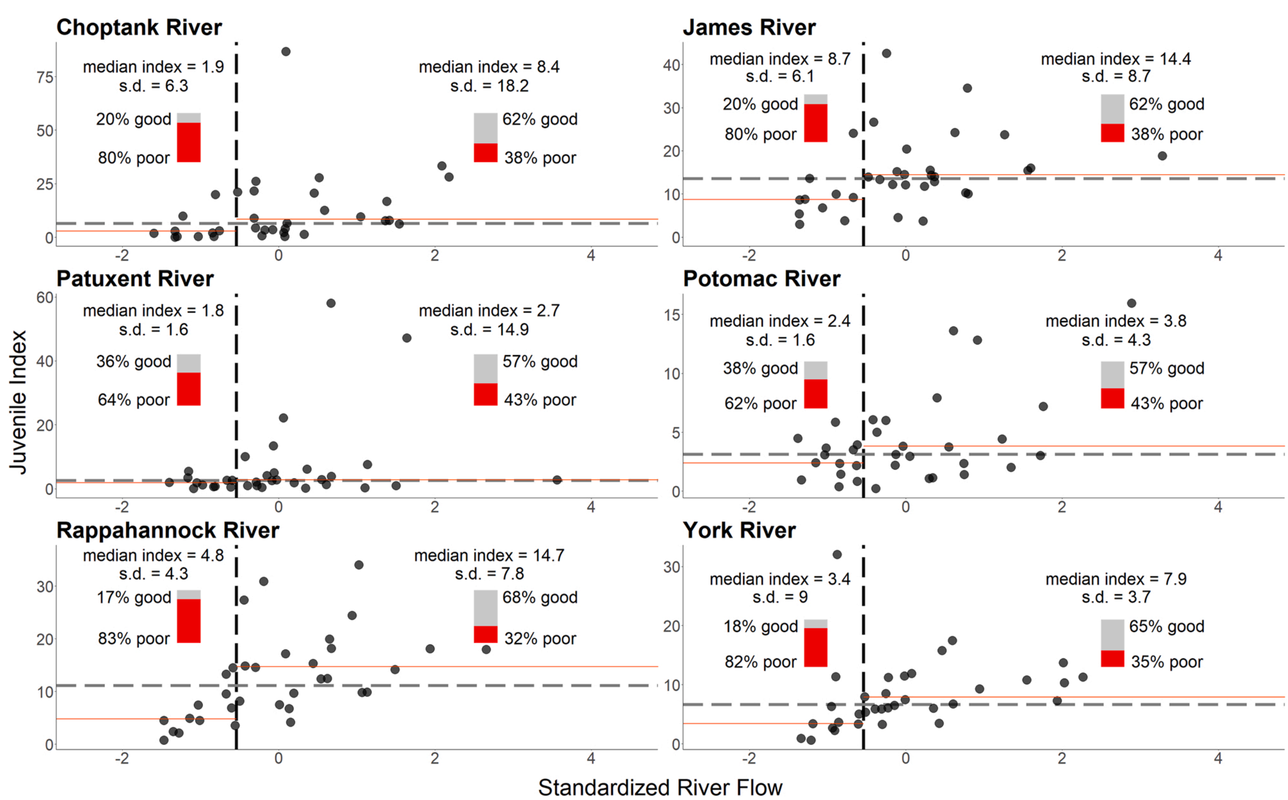

Fig. 3. Same type of diagram as Fig. 2, but for the other six tributaries of Chesapeake Bay.

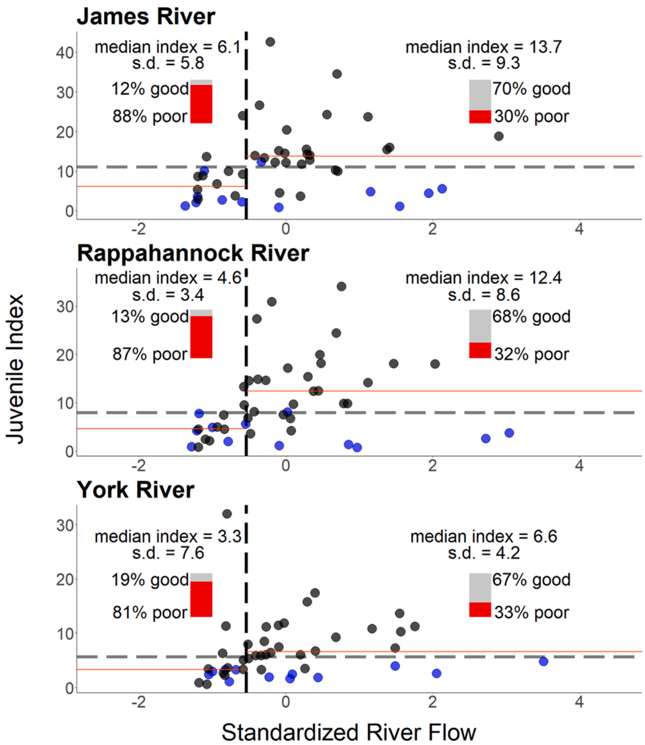

Fig. 4. Same type of diagram as Fig. 2, but including additional data (shown in blue) from earlier years (1967–1973; 1980–1984) that was used as an additional evaluation of the poor-recruitment paradigm. The cutoff between low and not-low river discharge is the same as in Fig. 2; the medians, standard deviations and proportions have been recalculated. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

unpredictable during non-extreme conditions (Figs. 2 and 3).

The Susquehanna River exemplifies these patterns of poor recruitment (Fig. 2). During extreme conditions, median recruitment (2.1) was approximately one third of the median recruitment during normal conditions (7.6). Similarly, the variability of recruitment was lower in extreme conditions (1.6) than during normal conditions (5.3), and the proportion of poor recruitment years was 92% whereas during non-extreme conditions it was lower, 27%.

The same qualitative results were observed in the remaining six stocks with one exception (Fig. 3). For these six rivers, the median recruitment was lower when river discharge was extreme than when it was non-extreme, and the percentage of years with poor recruitment was higher during extreme conditions than during non-extreme conditions. For five of the six other rivers, the standard deviation during extreme conditions was lower than it was during normal conditions. The exception was the York River, which had one very large recruitment year when river discharge was low (extreme) and, consequently, a higher standard deviation than that of the normal conditions. (However, if this large year class is ignored, the variability of recruitment in the York River would follow the pattern seen in all other rivers). While it is known that residuals for poor year classes tend to be small in models predicting recruitment it remains to be seen that this accrued information is utilized in recruitment forecasting for stock assessments. This, in essence, is part of the justification for adopting the “poor-recruitment paradigm” in stock assessments.

In the analysis of the additional data, it should be noted that this data pertains to a period when the striped bass stock underwent a precipitous decline (NEFSC, 2019). During this period, recruitment was consistently poor in Virginia rivers (Fig. 4). Nonetheless, the same qualitative results continue to hold. In particular, the difference between the proportion of years with poor recruitment during extreme conditions and during non-extreme conditions is higher when the additional data are included. For the James River’s recent data (1985 onwards), the difference in proportions of poor recruitment is 80–38% which is a 42% difference; including the additional years of data the difference is 58% (88–30%), suggesting that in the combined dataset the ability to predict poor recruitment is enhanced. Similarly, for the Rappahannock River, the difference in proportions is 51% for the recent data vs. 55% for the combined data; for the York River, the differences in proportions are 47% and 48%. These results support the idea that the poor-recruitment hypothesis can withstand regime changes in stock dynamics or environmental conditions. Thus, during the period of stock collapse, other factors (such as spawning stock biomass and habitat degradation) may have kept recruitment low, but there is evidence that river discharge continued to affect recruitment.

In terms of forecasting, the opportunity to make a recruitment prediction, i.e., Prob(low discharge), occurs 33% of the time (Question 1, Fig. 1A), which results directly from our definition of “extreme conditions”. Across the populations examined, and when river discharge is low, the prediction of poor recruitment is correct 78% of the time (Question 2, Fig. 1B). Out of all poor recruitments, we can predict 52% of them (Question 3, Fig. 1C) because 52% of them occur in extreme conditions. The chance of falsely predicting poor recruitment, when recruitment is actually good, is 14% (Question 4, Fig. 1D). Note that the probabilities will change as the percentage of years with low discharge changes. For example, when river discharge is low, we can confidently predict that recruitment will be poor. Consequently, when there is an extended period of years with low river discharges, we would expect to correctly predict poor recruitment most of the time (Question 3). Similarly, if there is an extended period where river discharges are low, the chances of falsely predicting poor recruitment are low (Question 4).

The relevance to stock assessments of being able to forecast poor recruitment depends on several factors, including how often the extreme conditions occur (i.e., how extreme is defined), the degree to which recruitment is reduced by extreme conditions, and the frequency of poor recruitment when environmental conditions are extreme. If poor recruitment could be reliably predicted from an extreme environmental variable, that information could be utilized in short-term stock projections, which are used when providing advice and setting catch limits. In projections of stock dynamics under various management actions, short-term recruitment is often assumed to be a recent average recruitment. However, this assumption could be replaced (in part) with predictions of poor recruitment during extreme environmental conditions, and therefore could improve the accuracy of short-term projections and, thus, catch advice. Furthermore, poor recruitment forecasts can be made without any direct observations (e.g. surveys) of fish recruitment strength itself; an additional benefit of this approach.

For Chesapeake Bay striped bass, the young-of-the-year abundance indices provide a clear demonstration of the “poor-recruitment” concept. However, the indices are river-specific and not a measure of recruitment for the entire Chesapeake Bay complex. The separate indices are combined into an overall bay-wide index, but this requires assumptions on the weighting of the components, a task which is difficult to address because it involves assessing the importance of each river and the correlation of the recruitment patterns among stocks. In general, a (single) stock’s recruitment history is measured directly through surveys or a catch-at-age analysis, which is then related to an environmental variable, to produce a procedure that can be used to forecast recruitment for the coming years. In the case of the Chesapeake Bay, however, we have related the environmental variable to river-specific young-of-the-year abundance indices, rather than relating the environmental variable to the overall recruitment to the fishery (age-3) for the spatially-diverse striped bass stock complex. This (likely) creates a disconnect between the poor recruitment patterns described for young-of-the-year fish in the various rivers, and recruitment to the fishery in the stock assessment of the (lumped) stock complex. However, if the poor-recruitment paradigm holds generally for all species, then forecasting recruitment to a fishery for any species, by considering whether environmental conditions are extreme, should reduce uncertainty in resulting catch advice.

The question of how often extreme conditions occur depends on how the category "extreme" is defined. The wider the range of conditions included in the extreme category, the more often one can make a prediction and the greater the percentage of poor recruitments that will be predicted. However, a wider range of conditions defining extreme comes at the expense of less reliable predictions, i.e., a greater number of false predictions of poor recruitment. Here, no attempt was made to optimize the accuracy of the prediction-making process with respect to the threshold used to define extreme conditions. We chose to use the lower 1/3 of observed river discharges as the definition of extreme as a practical matter so as to have at least 10 observations in the extreme category for each river. For stock assessment purposes, the choice of threshold and the accuracy of predictions relative to the threshold value could be evaluated. However, choosing the best fit to the data will exaggerate the estimated performance of the prediction procedure for future observations.

In this study, the environmental variable was chosen *a priori* based on scientific literature. Furthermore, preliminary findings from one river were tested by examining six other rivers. However, if an environmental variable is chosen by screening a suite of variables, then the statistical significance will be inflated. Therefore, there should be *a priori* justification for investigating a variable. For example, Myers (1991) showed that recruitment variability tends to be greater at the latitudinal extremes of a species' geographical range. Thus, one might expect that stocks at the southern limit of a species' range (in the northern hemisphere) might have poor recruitment when temperatures are extremely high while stocks at the northern limit have poor recruitment when temperatures are extremely low. *A priori* justification for a hypothesis offers a measure of protection against an apparent recruitment-environment relationship falling apart as more data are collected (as demonstrated by Myers, 1998).

We offer a new paradigm, called the "poor-recruitment paradigm," a universal approach for predicting recruitment from environmental variables for any given species. Under the conventional paradigm, recruitment is assumed to be linearly (or at least functionally) related to a suggested environmental predictor over the predictor's entire range of values, with interest centered on predicting strong year classes. We suggest that an environmental predictor can be both controlling *and* unimportant for recruitment depending on its value in a given year, allowing us to predict only some recruitment. When an environmental variable is within a species' lethal (extreme) limit there is noticeable egg, larval, or juvenile mortality, which consistently leads to poor recruitment (that can be predicted). But once an environmental variable is within a species' tolerable range, it no longer controls early life mortality, and therefore becomes unimportant as a predictor. For example, in the case of striped bass, when river discharge is extremely low, there is higher juvenile mortality, resulting in poor recruitment. And when river discharge is not extreme, mortality is no longer influenced by river discharge, so recruitment can either be good because conditions are favorable, or recruitment could be poor due to some other unknown factor. (To be clear, if river discharge were to be extreme in the other direction, i.e., unusually high, recruitment may also be reduced. This was suggested by Rulifson and Manooch, 1990 for striped bass in one locale.)

Through this lens, it becomes apparent that the focus for stock assessment should be on forecasting what is feasible (poor recruitment arising from one, or a few, lethal environmental variables) rather than predicting extremely good recruitment which requires detailed knowledge about a suite of variables, none of which can be lethal and some of which are especially favorable. By focusing on predicting poor recruitment, notable improvements could be made to stock assessment projections and, more importantly, management actions. The ability to predict a series of poor recruitment events is arguably of greater benefit to management than predicting good recruitment because of asymmetric risks: predicting poor recruitment may allow managers to avoid a stock collapse through risk averse policies whereas predicting good recruitment may allow an increase in quota earlier.

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CRediT authorship contribution statement

Julie M. Gross: Conceptualization, Data curation, Data analysis, Visualization, Writing – original draft, Writing – review & editing. **Philip Sadler:** Conceptualization, Data curation. **John M. Hoenig:** Conceptualization, Writing – original draft, Writing – review & editing, Validation of Data analysis, Visualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Recruitment data (annual juvenile abundance indices) for striped bass are made available for the Virginia portion of Chesapeake Bay through annual reports produced by the Virginia Institute of Marine Science (https://www.vims.edu/research/departments/fisheries/programs/juvenile_striped_bass/publications/index.php) and for the for the Maryland portion of Chesapeake Bay through the annual stock assessments produced by the Maryland Department of Natural Resources (https://dnr.maryland.gov/fisheries/pages/striped-bass/reports.aspx). All river discharge data for the USGS stations listed are publicly available through the USGS Water Information System: Web Interface (https://waterdata.usgs.gov/nwis)

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