Scientific and Technical Advisory Committee:
A Proposed Framework for Analyzing Water Quality and Habitat Effects on the Living Resources of Chesapeake Bay

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ABSTRACT. —A challenge for most large-scale ecosystem restoration efforts is to quantify the effects of multiple management actions on living resources. While there has been effort and analyses in the Chesapeake Bay to quantify the response of water quality and habitat to management actions related to the restoration of the Chesapeake Bay, analyses designed to quantify the responses of living resources are limited. This is partly due to the lack of requirement for such analyses. There is also the inherent challenge for such analyses to be able to detect responses and attribute them to specific management actions. There are many links between water quality and habitat. These challenges are not unique to the Chesapeake Bay, but rather are common to many ecosystems, especially when the response variable is mobile higher trophic level organisms, such as fish. In the situation of the well-studied and modeled Chesapeake Bay, the pieces exist to do analyses that relate water quality and habitat to fish and other organisms at biological scales relevant to management. The challenge is to put these pieces together so that a cohesive set of analyses can be done that allows for analyses to be tailored for specific situations, while also ensuring enough consistency to "roll-up" the results across analyses. There are many links between water quality and living resources imbedded in the water quality criteria and other goals of the 2014 Chesapeake Bay Watershed Agreement (CBWA). The water quality criteria used with the total maximum daily load (TMDL) were originally defined to support the Bay's aquatic living resources and designated uses. There are also examples of qualitative, numerical, and implied (e.g., sustainable population) living resource targets for each major component in the CBWA. With the upcoming 2025 assessment, there is an opportunity for a programmatic-level determination on how to assess living resource responses. In support of a broader STAC (Science and Technical Advisory Committee) activity looking at the responsiveness of the watershed and estuarine environments to the TMDL and other management actions, we present an initial framework for how to perform statistical and ecological modeling analyses to examine the *in-situ* responses of living resources. The proposed framework, if implemented, will enable a coordinated effort that uses existing and new analyses to provide a broad view of how Chesapeake Bay's living resources are responding to the broad set of restoration actions related to the goals of the CBWA. We propose a series of management questions and then outline four possible pathways for analyses that range from continuing the status-quo, to a comprehensive analysis that examines population and food-web level responses to restoration actions at system-wide scales. The ability to answer the management questions, and the degree of confidence in the answers, progresses going from the status-quo to a comprehensive pathway. The questions and challenges relating living resource responses to restoration are not unique to the Chesapeake Bay, but rather are common to many other large-scale restoration programs. The proposed framework would use the results of the water quality and habitat analyses to inform what types, timing, and magnitude of changes in water quality and habitat are expected from the TMDLs. Our proposed framework uses 12 ecological concepts and principles as the foundation, and then includes the steps involved in developing a strategic plan for statistical and modeling analyses. The framework is intended to aid in the decision-making about how to assess living resources' responses and provides guidance in developing an analytic plan. If it is determined

that analyses should proceed beyond the status-quo approach and the framework is implemented, resulting analyses will then attempt to translate these changes (observed and expected) to higher-order level responses of living resources (e.g., recruitment, population, sub-populations in subregions). Our proposed analyses would also provide information on realistic expectations for species responses to changes in water quality and habitat when species are long-lived, have complex life cycles, and are affected by multiple non-TMDL factors. The framework we describe has a series of linked modules: foundational concepts, available data and tools, logical workflow, illustrative examples, likely results and their interpretation, and suggestions for implementation. A strategic analysis based on the framework would provide a quantitative assessment of restoration progress based on *in-situ* responses and can also be used to provide feedback on the restoration goals, help design sensitive indicators, and inform adaptive management.

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1   Introduction

In this document, we present a framework for evaluating the responses of living resources[1] to improvements in water quality and habitat expected with the achievement of the Total Maximum Daily Loads (TMDL), and the implementation of management actions to achieve the relevant goals and targets under the 2014 Watershed Agreement (Chesapeake Bay Watershed Agreement (CBWA) 2014). This document was developed by a subset of members of the scientific action committee (STAC) and is a resource document to the STAC Report, "Comprehensive Evaluation of System Response (CESR)." This document is a companion to the other resource documents (Watershed, Estuary); all of which are the basis for the CESR report, but not all information in the resource documents is used in CESR. Additional information outside of the resource documents has also been added to CESR.

Water quality is evaluated through a broad set of variables, such as total suspended solids (TSS), temperature, pH, biological oxygen demand (BOD), nitrogen, phosphorus, as well as the specific variables for the water quality criteria, which are dissolved oxygen (DO), chlorophyll-a, and water clarity and submerged aquatic vegetation (SAV). Habitat is defined (CBP 1988) as the abiotic and biotic conditions upon which the living resources of the Chesapeake Bay depend. Abiotic conditions include factors such as water quality, substrate, circulation patterns, bathymetry, and weather; while three dominant factors are temperature, salinity, and depth. Biotic conditions are governed by variables such as biogenic cover (i.e., vegetative refuge or that made by living organisms like Eastern Oyster (*Crassostrea virginica*), quality and quantity of prey and competitive species, species composition, population density, and primary productivity (see CBP 1988).

To date, a major focus of evaluating the Chesapeake Bay Program's (CBP) actions has been on the effectiveness of the TMDL in achieving water quality standards. This approach is reasonable given the requirements of the CBWA and the feasibility of using monitoring data to assess progress. While the emphasis to date has been on water quality, the responses of living resources have been considered in several ways. One way is the use of species tolerances and habitat affinities in the initial design of the water quality numerical criteria and designated uses for regions throughout the Bay (Funderburk et al. 1991; Monaco et al. 1998; EPA 2003a and b; Tango and Batiuk 2013). This approach ensures that good conditions are present but does not necessarily translate into actual population and/or food web responses because of the many confounding factors that also affect species' abundances. A second way living resource responses are assessed are through metrics. Although limited in scope, the long-term trends of species that are tightly linked to water quality goals have been examined. Submerged aquatic

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[1] Living resources refers to fish, shellfish (e.g., oysters, crabs), benthos, zooplankton, birds, and waterfowl, SAV, wetlands, and high-level (mega-fauna) vertebrate species (e.g., turtles). (see CBP 1988)

vegetation (SAV)[2] is an excellent example as it is directly related to water clarity (i.e., one of water quality standards), and has a goal of 130,000 acres of SAV by 2025 (CBWA 2014). Assessing the variability of the relationship between SAV and water clarity facilitates attribution of management-influenced changes in water quality to the positive response of an ecologically important and iconic living resource. Such analyses require detailed monitoring and understanding of indicator species population demographics that are closely related to water quality criteria that are included in the TMDL.

The CBWA further expanded the consideration of the responses of living resources by adding goals and targets specific to actions of CBP that were designed to enhance habitat and ensure healthy (sustainable) abundances of specific living resources. These goals and targets include the use of habitat as the response variable (e.g., acres created), measures of the abundances of the living resources (e.g., total number of spawning-age female Blue Crabs (*Callinectes sapidus*), and qualitative metrics (e.g., understand the role of forage fish species and to develop indicators). Refinement of indicators continues, such as the ongoing activities developing quantitative indicators for forage fish in general and for menhaden in particular (*Brevortia* spp and *Ethmidium* spp.) (CBP 2020). There is also focused effort on assessing the degree of progress of restoration of oysters (Oysters - Chesapeake Progress) and related ecosystem impacts (Knoche et al. 2020; Bruce et al. 2021).

Several of CBWA's goals and targets pertaining to living resources provide progress status indices of CBP restoration based on their *in-situ* status, which are highly relevant because that is what is realized in the Bay. Examples are 196 million adult female Blue Crabs, an 8% increase in occupied habitat by Brook Trout (*Salvelinus fontinalis*), and sustainable oyster populations in 10 tributaries. An ongoing challenge related to using *in-situ* responses is that the populations are affected by many factors that are out of the control of the CBP (e.g., fisheries management) and, in many cases, out of management control in general (e.g., temperature). This multi-factor, multi-stressor situation therefore makes attributing the detected responses to the TMDL, specific habitat improvements, and other CBP-influenced actions challenging. This is an issue for even well-documented species that are tightly linked to water quality influenced by the CBP. For example, the recent increases in SAV over the long-term (Lefcheck et al. 2018) are strong evidence for responses to improving water clarity; however, areal extent decreased by 38% in 2019, a trend researchers link to higher than usual river flows that year. The 2020 survey showed SAV coverage similar to the low value in 2019[3]. The situation with attributing responses to specific actions becomes more complicated when living resources such as fish and shellfish are considered that have complex life cycles and are influenced by many factors and often whose dynamics are dominated by different factors across years.

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[2]"SAV" in the Chesapeake includes a range of different species of aquatic vegetation from deeply rooted eelgrass (*Zostera marina*) to more shallowly-rooted species (e.g., widgeongrass [*Rupia maritima*], wild celery [*Vallisneria americana*], or the invasive hydrilla [*Hydrilla verticillate*], among others).
[3] https://www.vims.edu/research/units/programs/sav/index.php

The Chesapeake Bay is often touted as one of the world's most studied estuaries and there are many examples of data collection, statistical analyses, and modeling that includes the effects of water quality and habitat on living resources. Most of these studies were done semi-independently, for specific time periods, used different methods and data, and were not focused on isolating the effects of the restoration actions designed to achieve the goals of the CBWA. The lack of consistency and standardization of time periods, spatial scales, and data examined across these studies hinders general assessment of living resources responses to changes in water quality and habitat, especially attribution to specific restoration actions. The many studies on Chesapeake Bay's living resource requirements for water quality and habitat have been synthesized in several instances (e.g., defining water quality criteria) and summarized in reports (e.g., CBP 1987; Funderburk et al. 1991; STAC 2009; Tetra Tech 2020).

The challenge of how to relate living resources' responses to specific management and restoration actions is not limited to the Chesapeake Bay and is common to many large-scale ecosystem restoration efforts (e.g., DeAngelis et al. 1998; Alymov et al. 2017). In most cases, how to assess program success based on the *in-situ* observed or predicted responses of living resources, including mobile higher trophic level organisms such as fish, has been discussed and, in some cases, performed. The strategy used varies across ecosystems to accommodate the goals of the restoration and the site-specific environmental drivers and ecology. Large-scale restoration projects cover the spectrum of using assessment of meeting water quality and habitat goals as the end-result, using a mix of indicator species, and, for a few restoration programs, almost complete reliance for judging success based on the responses of many living resources (population to food web) using a mix of data, ecological models, and expert opinions.

For the Chesapeake Bay, there are many opportunities and challenges to performing an assessment of living resources' responses to the TMDL and to the other restoration actions related to CBWA goals. There is an opportunity to embark on a new analysis effort specifically designed to assess the responses of living resources to water quality and habitat. This is possible because there are field data and well-tested watershed-estuary models that can generate and isolate the effects of specific actions on the water quality and lower trophic levels, as well as extensive data and existing modeling of living resources available for use for the Chesapeake Bay. A major challenge is that not only do analyses have to detect living resources' responses, but analyses must also facilitate attribution of responses to changes in water quality and habitat. This is especially challenging in a large and complex estuarine system like the Chesapeake Bay, because the importance of many factors affecting living resources vary spatially and temporally within the Bay. Further, the new analyses should be capable of partitioning detected responses attributed to water quality and habitat to those changes in water quality and habitat that result from the TMDL and other actions related to CBWA's goals. Without attribution to specific causative factors, documented changes in living resources (positive and negative trends) become difficult to interpret as the result of restoration efforts. Without information on the causes, if the restoration program gets credit for positive changes,

then should the program be considered unsuccessful with negative changes? In reality, these changes may be due to restoration actions, other factors, or an unknown combination of both.

The upcoming 2025 assessment and beyond provides a timely opportunity for the CBP to consider how to assess living resources' responses beyond the approach taken to date. Expanding the current approach for considering living resources' responses would provide information for a more complete assessment of the ecological benefits of the investment in restoration and enable expressing responses in units (e.g., SAV, fishes, crabs) highly valued by stakeholders and others. Such an assessment, however, requires substantial effort, although small compared to the very large effort invested in the CBP's modeling system over decades. Depending on how an assessment is done, results could allow for quantification of changes in living resources (e.g., condition of individuals, trends) and may be able estimate the role played by specific restoration actions.

There are four major pathways for assessing living resource responses as the 2025 assessment approaches, and for further consideration beyond 2025. These pathways include:

- Status-quo: Continue with reliance on the design of the water quality standards, the examination of habitat improvements (e.g., acres of wetlands), and selected temporal trends (without attribution to water quality or habitat variables) in a relatively limited number of indicator species;

- Moderate expansion: Expand on the status-quo habitat construction and indicator species approach in terms of adding Bay-wide assessments of habitat changes and additional species, and perform, when feasible, analyses linking detected responses to specific aspects of water quality and habitat (although not necessarily to CBP's actions);

- Major expansion: Expand on the habitat construction and indicator-species approach but start at the beginning and design a systematic approach with the purpose of making statements at the levels of population and food web, and attempt to attribute responses to specific water quality and habitat variables and CBP-related actions or other causative factors;

- New approach: Continue with the status-quo, but also design and implement a comprehensive living resources' assessment that examines population and food web level responses that is wide-ranging enough to enable statements about specific responses of species to CBP's actions and other factors, while also assessing the health and status of the whole Bay's ecosystem.

These pathways are presented as discrete options for clarity. Actual pathways can be a combination of the approaches and intermediate versions of these four options.

In this document, we offer a framework for guiding how one could proceed to quantify living resources' responses to changes in water quality and habitat. Important to note is that this document does not answer the management-relevant questions about the actual effects of

the TMDL and other CBWA-related actions on living resources. If the recommended approach and analyses are determined to be pursued, then the implementation of the framework would then facilitate answers to the management questions. This document provides guidance for determining how to proceed in deciding how to assess living resource responses to CBP's management actions and offers a framework for structuring and planning for such analyses going forward.

2   Why now for an evaluation of how to assess living resource responses?

The important role of assessing the responses of living resources to the water quality and habitat actions as part of the CBWA is not new and has long been recognized within the CBP (STAC 2005; STAC 2006). The commitment statement of the CBP includes tracking progress towards the goals and outcomes of the CBWA to achieve a Bay with "abundant life, clean water, conserved lands and a diverse range of citizens and stakeholders who will steward an environmentally and economically sustainable watershed." The upcoming 2025 assessment and beyond offers a timely opportunity to consider how the responses of the living resources should best be assessed. An analysis scheme for a focused effort to assess living resources' responses begins where the watershed and estuary modeling presently ends (Hood et al. 2021) and would provide empirical evidence on the progress and enhance effective implementation of adaptive management[4].

To date, progress of the restoration has been determined by achievement of the water quality standards (which were informed by living resource information) and status and trends indicators as part of the CBWA (Zhang et al. 2018; www.chesapeakeprogress.com). Extensions of this status quo (to the moderate, major, or new pathways) would enable broader conclusions and more refined statements about the role of the TMDL and the other restoration actions in the CBWA. Analyses could determine the influence of water quality (e.g., DO, chlorophyll, and water clarity) and enhanced habitat on the abundance and ecology of living resources. The analyses would also provide information on realistic expectations to managers and the public about species' responses to changes in water quality and habitat. Grounding expectations is especially important when the responding species (like many in the Chesapeake Bay) are long-lived, have complex life cycles, and are affected by multiple factors. Further analyses would also be useful as a guide for interpretation of living resources' responses to the TMDL and habitat actions, and future design of indicators, informing adaptive management, and possibly refining restoration goals.

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[4] https://www.chesapeakebay.net/what/adaptive_management

3   Management Questions that Could Be Answered

The pathway going forward dictates to what extent and confidence management questions can be answered. Examples of management questions related to living resources' responses include:

- To what extent are the water quality, habitat, and living resources' goals and targets in the CBWA (e.g., TMDL, acres of wetlands, etc.) being met?

- How have changes over multiple decades in water quality and habitat (due to both natural variation and restoration actions) affected living resources' populations and food webs in the Bay?

- What is the expected (projected) response of living resources to water quality and habitat conditions in the Bay: (a) without the TMDL and habitat and sustainable fisheries targets, (b) if present conditions of attainment and partial achievement of the habitat and fisheries goals continued, and (c) if the water quality under the TMDL and/or the vital habitat and sustainable fisheries targets were fully achieved?

- Given the current state or condition, how can the analyses inform what types and magnitude of changes in water quality and habitat are needed to evoke an agreed-upon target set of the desired living resources' responses? That is, start from desired responses in living resources (i.e., desired targets) and back-calculate, given the influences of other variables and factors, the changes in water quality and habitat needed, on-average, to generate such responses.

- What are the certainties and critical uncertainties of the analyses and how can they help guide future monitoring and modeling efforts? This information could be used to inform natural resources' managers about research needs into the future, and what are quantitatively defensible indicators and measures for tracking living resources' responses.

Analyses to address these management questions can be used to identify the tradeoffs among species for alternative combinations of restoration actions, provide an assessment of progress for species of interest and the food web, and can inform what magnitude of changes in water quality and habitat are needed for certain sets of responses. This approach differs from the present approach by using predicted *in-situ* responses of populations and food webs, rather than tolerances and preferences of individual organisms, to inform water quality and habitat targets.

The present approach (status-quo) offers valuable information on progress towards goals and targets, but is mostly limited to answering the first question about whether goals are being met. The status-quo approach is based on measures of whether the water quality standards are achieved and the degree to which the specific set of habitat goals and the temporal trends of a few indicator species have changed without attribution to causes. In contrast, the new (most comprehensive) pathway may, in principle, address all these questions. The movement from

the status-quo to the comprehensive allows for the strategic selection of species, data, and models so that the analyses are designed for specific questions (e.g., role of restoration actions in responses) and for broader conclusions about the Bay-wide condition of living resources' populations. The same progression of status-quo to moderate to major to new however, involves substantially more effort and while cause-and-effect is possible, increasing uncertainty in analyses can limit their usefulness in contributing to living resources' management decisions.

4   Existing Links Between Water Quality/Habitat and Living Resources

4.1   Assessing Progress of Restoring Living Resources of the Chesapeake Bay

There are many links between water quality and living resources imbedded in the water quality standards and the CBWA. The water quality standards were originally defined using water quality criteria designed to support the Bay's aquatic living resources' designated uses (Tango and Batiuk 2013). Dissolved oxygen, chlorophyll-a, and water clarity/SAV are used to capture the physical conditions required by biota to ensure that minimally survivable conditions are present throughout the Bay. The conceptual basis is that achievement of the water quality conditions throughout the Bay would benefit the living resources. The designated uses (DUs) do not reflect the *in-situ* status of living resources, but rather measure the availability of specific habitats. The choice of water quality criteria and designated uses was based on extensive information about living resources, but modeling of population and food web responses (analogous to the watershed and estuary models for water quality) was not used.

The Biennial Strategy Review (www.chesapeakebay.net/decisions/srs) includes descriptions of the living resource-related indicators used, degree of progress, and lessons learned, and factors that may affect progress going forward. There are examples of qualitative, numerical, and implied (e.g., sustainable population) living resources' targets for each major component in the CBWA: wetlands, healthy streams, fish passage, SAV, Brook Trout, Eastern Oysters, Blue Crabs, and Black Ducks (*Anas rubripes*). The degree of progress (including lack of progress) is documented every two years for each of the major habitat and living resources' goals and targets.

There are also annual report cards (ecoreportcard.org/report-cards/Chesapeake-bay) and biennial state-of-the-bay reports (CBF 2020) that include habitat and living resources' indicators, as well as water quality metrics. The report card and State-of-the-Bay use goals from the CBWA (e.g., wetlands, SAV, Blue Crabs, Eastern Oysters) and the status of other species. The report card also includes the status and trends in benthos, Bay Anchovy (*Anchoa mitchilli*), Striped Bass (*Morone saxatilis*), and shad species (*Alosa* sp.), and examines these by watershed. The state-of-the-bay adds striped bass and shad to the indicators specified in the CBWA. The assessments are generally a relatively simple examination of the trends in these indicators to form qualitative overall grading (A, B, C, D, F) of progress. Each reporting mechanism also includes water quality measures and other indicators.

4.2　Example of Analyses for Chesapeake Bay Living Resources

There are many examples of scientific studies that document how water quality affects vegetation (e.g., water clarity affecting seagrass), lower trophic levels (eutrophication affecting phytoplankton, zooplankton, and benthos), and upper trophic levels (fish growth, spatial distributions). Similarly, there is a long history of assessing habitat quality and quantity on organisms of the Chesapeake Bay (Funderburk et al. 1991; Tetra Tech 2020; Fabrizio et al. 2020), predicated on either laboratory-derived information or monitoring data, delineating the aspects of habitat (e.g., substrate type, temperature) that consistently have organisms present. We briefly summarize several of the many examples below. The examples were selected because they were closely aligned with the types of analyses we consider promising for future analyses. Many of the analyses and models continue to be actively used and further developed, and others can be easily reactivated.

The degree to which specific aspects of water quality and habitat (e.g., DO, wetlands) are identified as the causes of detected changes in the living resources vary widely among these analyses. The limitations of the present information based on the extensive studies of Chesapeake Bay include: (1) many independently completed analyses that resulted in results that hinder easy synthesis, (2) the species, statistical and modeling methods, and spatial coverage (e.g., regions of the Bay) and temporal coverage (e.g., which years) used vary greatly across analyses, (3) existing analyses addressed study-specific questions and hypotheses but application of results to assess specific restoration actions have been mostly, at best, suggestive (i.e., speculative), and (4) *in situ* analyses specific to water quality and habitat rarely are specifically designed to advance the understanding of the role of the TMDL and other CBWA-related restoration actions in affecting the living resources response. To date, there has not been a comprehensive examination of living resources responses *in-situ* that also attempts to relate the responses to CBP actions.

4.2.1　Examples of Habitat-based Assessment

Schlender et al. (2021) used output from a DO model coupled to a 3-D hydrodynamics model (temperature, salinity) for the Chesapeake Bay to determine the volume of required and optimal habitat for a suite of species. The temperature, salinity, and DO levels needed to avoid mortality (required) and the value outside of which would lead to physiological stress (e.g., reduced growth) were defined for combinations of egg, larval, juvenile, and adult life history stages for 10 species comprised of fishes, Blue Crab, and Eastern Oysters. Daily volumes of habitat were generated for 1996-2005 and annual values were determined using the daily values for specific seasons. The importance of each explanatory variable (i.e., temperature, salinity, DO) was assessed by repeating the analysis but without each of the variables. Large differences among analyses with all three variables included compared to analyses with one variable removed indicate the removed variable had a large effect on habitat volume. Optimal habitat showed greater variability and more complicated patterns than required habitat and DO was important in determining required habitat while salinity dominated for optimal habitat.

Niklitschek and Secor (2005) also analyzed habitat suitability and they focused on the nursery habitat for Atlantic Sturgeon (*Acipenser oxyrinchus*). They combined potential energy gain (growth) with mortality rate to define habitat quality at a location in terms of potential juvenile sturgeon production. Growth and mortality (and therefore production) depended on temperature, DO saturation, salinity, and weight. Water quality data for time periods within 1990 to 2002 were obtained and interpolated from the CBP Water Quality Monitoring Program. The mainstem was divided into 1 km^2 cells and tributaries divided into 0.0025 to 0.25 km^2 cells. Total suitable habitat was the summed areas of the cells in January, April, July, and October that supported positive production. Sensitivity of total suitable habitat was mapped under historical conditions, and then assuming DO levels were set to the water quality standards for the designated uses and assuming a 1°C increase in temperature. A 1°C warming had much larger negative effect on habitat than the positive effect of achieving the DO values.

4.2.2   Examples of Statistical Analysis of Living Resource Monitoring Data

Seitz et al. (2009) analyzed the CBP benthic monitoring data (2,250 samples) collected July to September in tributaries and mainstem for 1996-2004. Density and biomass of each species, and species diversity, were analyzed using the explanatory variables of depth, DO, salinity, temperature, TOC, and sediment silt-clay fraction. Dissolved Oxygen was consistently important for determining summertime benthos variables when benthos was analyzed by depth intervals.

Woodland et al. (2021) analyzed spatial and temporal trends in forage fishes and benthic invertebrates in the Chesapeake Bay from multiple monitoring programs. These included the Maryland and Virginia uvenile surveys of Striped Bass, the Trophic Interactions in Estuarine Systems (TIES) study, the Chesapeake Bay Fisheries Independent Motoring survey, and the Chesapeake Bay Benthic Survey. The environmental and water quality explanatory variables were from the CBP Water Quality Monitoring Program, as well as from other sources. Chlorophyll concentrations, temperature, salinity, and DO were included. Annual indices by species or functional group for 1995 to 2015 were estimated. Statistical analyses of the indices for the upper, middle, and lower mainstem, and the tributaries showed spatial and temporal trends and a mix of relationships to the explanatory variables. Temperature showed a positive relationship to all species and groups, while other explanatory variables showed complicated (positive, neutral, negative) relationships across species and groups.

4.2.3   Examples of Living Resource Models

Adamack et al. (2017) examined the population response of Bay Anchovy to reduced nutrient loadings using an agent-based approach and imbedding the individuals within the 3-D CH3D-WES hydrodynamics model coupled to the CE-QUAL-ICM water quality model for the Chesapeake Bay. Individual Bay Anchovy (Anchoa mitchilli) were followed within the 3-D grid and experienced the temperature and zooplankton generated from the water quality model. Early juveniles were injected into the grid as weekly cohorts, and individuals use bioenergetics (temperature, zooplankton, DO) to generate growth and incur length-dependent mortality.

Individuals were moved within the cells of the hydrodynamics model using temperature and zooplankton for horizontal movement and temperature, and DO for vertical movement. Ten-year simulations that used a sequence of 1984, 1985, and 1986 matched to water-year types observed during 1984-1994 were performed for baseline, and a 50% increase and 50% decrease in nutrient loadings. By simulating a range of assumed initial juveniles to represent hypoxia effects in earlier (egg and larval) life stages not represented in the model, Adamack et al. (2017) determined that relatively small negative effects of increased hypoxia under increased nutrients under low recruitment years would offset the reduced food effect, while larger negative effects (albeit still within the realm of possibility) of hypoxia were needed to offset the food effect under high recruitment years. A similar pattern was predicted with increased predation pressure due to habitat constriction; offsetting occurred with small effects under low recruitment and higher effects under high recruitment. Daylander and Cerco (2010) used a very similar modeling approach for Atlantic Menhaden (*Brevoortia tyrannus*) in the Bay.

Fulford et al. (2010) developed and applied a multi-species simulation model separately to the Patuxent and to the mainstem Bay, and compared the responses of key species of the food web to restoration of Eastern Oyster with reduced nutrient loading. Both model configurations yielded similar results. The model represented sizes classes of phytoplankton; multiple functional groups of zooplankton and benthos; larvae of Eastern Oyster, Bay Anchovy, and ctenophores; pelagic fish as zooplanktivores (e.g., Bay Anchovy); and suspension feeding herbivores (menhaden). The link to the upper food web was captured by summing biomasses of forage species above specific thresholds as an index of the energy (food) available to higher trophic levels. One-year simulations were performed under current conditions, Eastern Oysters increased 10, 25, and 50 times, and under reduced nutrient loading phytoplankton reduced by 50% and there was an assumed increase in benthic habitat due to less hypoxia. The direction and magnitude of species or functional groups responses differed between increased Eastern Oysters and reduced nutrients. For example, zooplankton and bay anchovy decreased with increased numbers of Eastern Oysters, while they showed little response to reduced nutrients. Reduced nutrients generally lowered the biomasses of the responsive groups in the spring, while increased numbers of Eastern Oysters reduced biomasses of most all consumers (except benthic fishes that increased) during the summer.

Network Analysis and Ecopath with Ecosim (EwE) models have been developed for the Chesapeake Bay (Monaco and Ulanowicz 1997; Christensen et al. 2009, Ma et al. 2010, Townsend 2014). Ecopath with Ecosim is the most applied trophic ecosystem model in the world and used in other locations to assess responses to restoration (Vasslides et al. 2017). The Ecosim (time-dependent) version for the Chesapeake Bay (CBFEM) represented 45 trophic groups representing fishes of interest to the Bay, as well as their prey and predators. The CBFEM Ecosim model simulated the annual mean biomass values of the species and groups for 53-years (1950–2002) to provide an assessment of the recent decadal dynamics of the Bay's fish species (Townsend 2014). The CBFEM Ecosim simulations have been loosely coupled to the CBP water quality model (ICM) by forcing it with time-dependent chlorophyll-a (Townsend

2014) and SAV (Ma et al. 2010) generated by the ICM. The model was used to simulate the impacts of a 40% reduction of nutrient inputs on upper-trophic-level species (e.g., the biomass of Striped Bass and Blue Crabs), and other commercially important harvested species (e.g., menhaden, Eastern Oysters). These simulations allowed connections to be made between water quality and commercially and recreationally important species, and they can be used to assess the benefits and trade-offs between water quality restoration goals and fisheries management goals.

A coupled biogeochemical-food web model for the Chesapeake Bay is the Chesapeake Atlantis Model (CAM). Like EwE, predator-prey interactions are a core function, and the Atlantis model is used around the world (Fulton et al. 2011). Unlike EwE, the Atlantis modeling approach includes physical forcing for water, salt, and heat, and is a three-dimensional spatial approach that accounts for animal movement and the availability of habitat refuge. The CAM model domain is 97 irregular polygons and includes the brackish waters and sediments of the mainstem Chesapeake Bay and nine of its largest tributaries. Water movement in CAM is driven by the Navy Coastal Ocean Model (NCOM) Relocatable Model. Nutrient and sediment loads to the model are derived from the CBP dynamic watershed Phase 5.3.2 model. CAM includes 26 invertebrate functional groups, including primary producers and multiple bacterial groups, and 29 vertebrate groups. Most invertebrates are modeled as single state variables (mg N m^{-3}); Blue Crab and Brief Squid are modeled as linked juvenile and adult state variables. All vertebrate groups are divided into 10 age classes, each tracked by abundance and weight-at-age. CAM uses nitrogen as the currency for all state variables. Habitat types in CAM include both static physical factors, such as mud, sand, rock, and woody debris, and dynamic biogenic functional groups, such as marsh, SAV, and reefs of Eastern Oyster, that provide refuge for prey from predator groups. The CAM has been used to estimate the higher trophic level impacts of fully achieving the goals of the TMDL requirements for nitrogen and sediment under present day climate conditions, as well as under warmer water temperatures, and simulations were also combined with habitat loss and gain (restoration) scenarios (Ihde et al. 2016; Ihde and Townsend 2017).

5 Living Resources and Other Large-scale Restoration Efforts

Other large-scale ecosystem restoration programs have included analyses to assess the responses of living resources to restoration actions. The Everglades' restoration program explored using simulation models to examine how water routing and other actions would affect fishes, birds, and other wildlife (e.g., Gaff et al. 2000). Presently, the CERP (Comprehensive Everglades Restoration Program) uses the principle that by addressing the quantity, quality, timing, and distribution (QQTD) of water, the ecosystem will respond. This can be viewed as analogous to the status-quo approach of the CBP of assuming that creating the proper water quality and habitat conditions will lead to the desired ecosystem responses.

The Gulf of Mexico offers two examples of large-scale ecosystem restoration, both of which have progressed to directly assessing living resource responses. The "dead zone" issue of the Gulf is similar to the Chesapeake Bay in that managers are attempting to reduce nutrient loads from the watershed (via the Mississippi River) to reduce the summertime hypoxic zone in the receiving shelf waters. The US Congress established the Hypoxia Task Force that is comprised of 7 Federal agencies, 12 states, and one tribal member. An Action Plan was developed to reduce nutrient loadings (Task Force 2008) and is updated periodically with assessments. The 2013 Assessment (Task Force 2013, page 28) states:

> *Development of the quantitative relationship between nutrients, hypoxia, and living resource populations represents an important milestone that will allow for improved goal setting and nutrient reduction targets. During the scientific reassessment that preceded the 2008 Action Plan, understanding of the living resource impacts of hypoxia in the Gulf of Mexico was relatively limited, and quantification of population level impacts proved elusive….*

NOAA initiated the NGOMEX program that had as its third of 3 objectives, "Develop quantitative models to determine the impacts of the hypoxic zone on ecologically and economically important living resources." These analyses of living resources' responses are ongoing.

The second Gulf of Mexico restoration program is the Louisiana Coastal Master Plan, which is a 50 billion dollar 50-year program that is designed to build and maintain land in the coastal zone, reduce flood risk to coastal communities, and provide habitats to support ecosystems. The focus on habitat has led the program to use extensive modeling that is centered on coupled sets of models (hydrodynamics, wetland, vegetation, ecosystem outcomes), analogous to the CBP modeling system, but that goes further and includes habitat-based models for many living resources' species and an extensive, spatially explicit food web model (Alymov et al. 2017). The responses of living resources (mostly as habitat suitability) are a major consideration for the design (optimization of the mix of management actions) and performance evaluation of the program.

Undoing the eutrophication of the Baltic Sea due to excess nutrient loadings has been an ongoing restoration program for decades. The Baltic Sea Action Plan (BSAP) was adopted by the HELCOM member countries (Denmark, Estonia, Finland, Germany, Latvia, Lithuania, Poland, Russia and Sweden) in 2007, with the aim to restore the good ecological status of the Baltic marine environment by 2021. Because of the large reductions in nutrient loadings achieved to date, many view the Baltic Sea experience as providing a glimpse of how other similar systems will respond (Reusch et al. 2018). A recent evaluation (BSAP 2021) stated:

> *The overall objective of the Baltic Sea Action Plan (BSAP) to reach good environmental status of the Baltic Sea by 2021 will most likely not be reached.*

Nevertheless, the BSAP has shown promising results towards improving the state of the sea.

The eutrophication issue is one of multiple restoration components in the Baltic plan and progress was assessed mostly using water quality variables (nutrients, oxygen, clarity, chlorophyll), with some use of benthos and macrophytes. Interestingly, habitat-based (e.g., seabed area) and living resource (e.g., fish and fisheries) indicators were used to track the progress of other components of the restoration program, similar to the habitat and living resource goals and targets of the CBWA. While the decline in key species (e.g., cod, *Gadus* spp.) is well documented, the cause-and-effect role played by nutrient loadings on this indicator species has been debated in the scientific literature (see Rose et al. 2019).

Other large-scale restoration efforts also fall within the bounds of assessing living resources' responses illustrated above. For example, the Great Lakes Restoration Initiative (GLRI) uses similar metrics as the CBP water quality and CBWA habitat and living resources' goals and targets (GLRI 2019), while the long-term efforts on the Columbia River focus on how changes in habitat due to hydropower operations influence salmon and therefore use habitat-based metrics and extensive population dynamics modeling to evaluate program effectiveness. Restoration of Tampa Bay via nutrient management and its focus on responses of specific water quality variables (Greening et al. 2014) has many parallels to the CBP.

These examples illustrate how large-scale ecosystem restoration programs vary in their emphasis and approaches for using living resources responses to assess restoration performance. The Everglades restoration modeling initially focused on population-level responses and then retreated to habitat-based measures that used the approach that "if the water is done correctly, the rest will follow." A good analogue for the CBP, the Baltic Sea, is using a mix of metrics, including water quality like the CBP. Others, such as the Gulf of Mexico examples, relied more heavily on habitat-based and population and food web responses. At the other extreme, the Columbia River uses habitat-based and extensive monitoring and modeling of salmonid population dynamics in response to changes in habitat related to hydropower. Such variations in approach reflect the site-specific aspects of each program and also indicate that such decisions are complicated and deserve careful planning to evaluate the tradeoffs between easily measurable metrics (water quality and habitat) and highly ecologically and management relevant metrics (e.g., long-term population and food web responses).

6   Going Forward

A major advantage with the Chesapeake Bay is that the ingredients (e.g., physical and biological information) needed to expand upon the status-quo approach, which are usually limiting in other systems, are available, well established, and vetted. The long-term monitoring and the CBP's watershed-estuary modeling system can provide the water quality as drivers to assessing living resources' responses, both historically and projected. Such a modeling system can further provide an assessment of the water quality of the Bay with and without specific

management actions. Habitat suitability (quality) and quantity within the Chesapeake Bay has been studied and mapped in various ways. Many living resources, especially mid to high trophic level consumers, have sufficient information about their life history, vital rates (growth, mortality, reproduction), diets, movement patterns, inter-specific interactions (competition and predation), and harvest to support statistical and ecological modeling of their responses to water quality and habitat. Many examples of statistical analyses of monitoring data, habitat analyses, and population and food web models already exist.

How to proceed to address the management questions about living resource responses can be unclear because of its very wide scope and because the available information (data, models) is both extensive and fragmented. One approach, and the one used to date (status-quo), is to focus on the achievement of water quality and habitat goals, with indicators of a few key species that are tightly tied to the CBWA goals and targets. The Biennial Strategy Review is the adaptive management mechanism for this approach, supplemented by annual or biennial assessments like report cards and state-of-the-bay reports. Achieving water quality, habitat, and status-based indicators, all directly tied to the CBWA, is necessary (but may not be sufficient) to evaluate the CBP's actions.

If obtaining more comprehensive and robust answers to the management questions is determined to be needed, such an effort will involve moderate to large changes from the status quo approach. Such an approach requires a concerted and coordinated effort and the framework (described below) provides a way to guide such an analysis. Practical questions, such as which species, data availability, and what models to use in new analyses, and how to leverage the extensive analyses already done, should be systematically examined. The challenge is how can existing and new analyses be combined in a cohesive way that allows for analyses to be tailored for specific situations while also ensuring enough consistency to "roll-up" the results across analyses and species. Another challenge will be to see if we can integrate field monitoring and laboratory data with coupled bio-physical modeling to enable separation and quantification of the contribution of the changes in water quality and habitat to overall responses and express these at the population and food web levels. The pieces exist for performing such analyses on a subset of species; the information and data need to be synthesized and the appropriate models further developed (if already existing) for these specific analyses and some models may need to be newly developed. We offer a framework for guiding the decision about how to assess living resources' responses that can also be used to formulate a strategic analysis plan and interpret results.

7 Proposed Framework

The proposed framework is intended to aid in decision-making about how to assess living resources' responses (Figure 1). The framework is guide to performing the analyses in a systematic manner so that the results of different analyses can be viewed as part of general strategy and common conceptual model and results can therefore be easily be synthesized. The framework applies to all of the pathways going forward (status quo, moderate and major expansions, and new approach); it can be used to help interpret the status quo results and can

be used to both design and interpret the analyses for the other pathways. Results of the analyses from implementation of the framework could provide a quantitative assessment of restoration progress based on *in-situ* responses and can also be used to provide feedback on the restoration goals, help design sensitive indicators, refine ongoing monitoring to reduce uncertainties, and inform adaptive management.

The logic of the framework begins with the blue circles located in the center of Figure 1. These are the observations *in situ* of water quality, habitat, and living resources. The challenge is to use this information to determine how changes in water quality and habitat have affected living resources, given all three are affected by many additional factors (e.g., fishing) and stressors (e.g., pollution) (grey shapes in Figure 1) than just the TMDL and the subset of habitat restoration actions specifically implemented under the CBWA (orange boxes in Figure 1). Many of the species of interest spend some portion of life outside of the Bay (in rivers or on the shelf; green life cycle in Figure 1), where they are exposed to conditions there that are unrelated to conditions within the Bay. Further, the effects of the TMDL and habitat restoration on living resources within the Bay are themselves modulated by the environmental conditions and other factors in the Bay (e.g., temperature, river flows; large grey rectangle in Figure 1). Thus, the realized DO, chlorophyll-a, water clarity/SAV and other water quality variables in response to the TMDL and other actions may not be a simple response and can vary spatially and temporally around the Bay. Estuaries are complex environments and realized responses of living resources to simultaneous factors are expected to be distinctly non-linear under these conditions, and in such systems, the properties of the whole are not expected to be the same as the sum of its parts (Fogarty 2014). Consequently, the response of zooplankton, benthos, and higher trophic organisms to water quality and habitat conditions within the Bay will also not be simple responses. The flow of information provides feedback on progress to goals and explanatory information on the underlying reasons for observed responses. The results can then be used to inform adaptive management (red box in Figure 1).

A core aspect of the framework includes a process on how to isolate the responses of living resources to changes in water quality and habitat when there are many other factors and stressors that affect the living resources. Past analyses and the availability of monitoring data and models for the Bay indicate that documenting spatial patterns and trends in living resources is feasible. The next step of attributing those patterns and trends to specific causal mechanisms, such as responses to changes in water quality and habitat, is challenging but appears feasible for a candidate set of species. In general, the more specific the causal reasons, the greater the challenge. Results documenting the portion of a response to the effects of a variety of measured water quality variables (relatively general) is easier than determining the portion of the response attributable to the TMDL. Thus, the final step of trying to isolate the proportion of the documented responses to specific management actions (e.g., TMDL, more wetlands) is uncertain, but possible for a smaller subset of species and would involve a heavy reliance on simulation modeling rather than pure analyses of monitoring data. This final step can be viewed as the analogue to how simulation modeling is used to isolate how the TMDL can achieve water quality criteria, so while consistent with the general use of modeling in the CBP's system, the models for living resources entail a much higher degree of uncertainty than the predictions from the watershed and estuarine water quality models.

Analyses relating water quality and habitat to living resources rely heavily on principles of population ecology and ecosystem science. We describe 12 major concepts; many of these principles and concepts have appeared in textbooks and reviews and best practice papers. We used the presentation in Rose et al. (2015), which synthesized ideas from other papers, as the source here and borrow heavily from that paper. These principles and concepts are widely accepted and subsets of them are very frequently incorporated into individual analyses; we present them here in one place as a type of check list to aid in determining how to assess living resource responses. For convenience, we discuss these in terms of fish, but they apply to most living resources, especially as one moves up the trophic levels, and to rivers and other aquatic habitat as well as the Bay proper.

7.1 Complex Life cycles and life history strategies

A life cycle diagram follows individuals as they progress through the life stages from birth to death (Caswell, 2001). There are many examples; we show diagrams for generalized species in how they use the estuary during their life cycles (Figure 2), and the egg to adult progression of life stages (Figure 3). Other useful schemes of grouping species by habitat use in the estuary are available (Pihl et al. 2002; Elliott et al. 2007; Cowan et al. 2013; Whitfield 2020). A life history strategy is determined by the combination of vital rates with the life cycle, and this combination of rates determines how quickly individuals progress through their life cycle. Life history strategy has been used to categorize species in a variety of different ways, such as how they respond to environmental changes and use habitats. A coarse view of fish life history strategies that is in commonly used for fish is how most species fall on the surface defined by juvenile survival, fecundity, and maturity (Figure 4, Winemiller and Rose 1992). Expressing life cycles and strategies quantitatively is often accomplished using life tables and space-time plots by life stage. These plots often show which stages and vital rates are influenced by water quality and habitat. Identification of bottlenecks in the life cycle helps understand *in-situ* responses to stage-specific manipulations of vital rates resulting from restoration actions.

7.2 Variability, uncertainty, and stochasticity

There are different sources of variability in data and models that require proper interpretation for the analysis results to be used effectively in detecting responses to water quality and habitat (Regan et al. 2002; Link et al. 2012). In general, if more measurements reduce variability, then one is dealing with uncertainty, whereas when more measurements do not reduce the variability, one is dealing with stochasticity (Ferson and Ginzburg 1996). For example, specification of how mortality rate for the juveniles of a species of fish change when they are located in sea grass (habitat effect) becomes more confident with additional measurements. River flows delivering nutrients to an estuary, however will vary based on precipitation timing and other factors and that stochasticity in river flows is not reduced with more measurements.

Link et al. (2012) discussed sources of variability in the use of models for managing living resources. They reviewed the extensive literature on uncertainty and delineated six types when using models to inform management: (1) natural variability (same as stochasticity above), (2) observation error that arises from finite sampling (frequency, specific locations) of the complex ecosystem such that the data differ from truth (Figure 5), (3) inability to determine the optimal structural complexity of models (discussed below), (4) inadequate communication of results to various audiences, (5) unclear management objectives and vaguely stated questions to answer, and (6) outcome uncertainty due to responses to the actual implementation of the management differ from the *a priori* management goals.

All modeling related to assessing the responses of living resources to management actions must carefully consider all these sources. Dealing with lumped and vague terms like "variability" or "uncertainty" reduces our ability to interpret and communicate the results.

7.3   Model complexity

A long-standing issue in analyses in what is the optimal level of complexity. While this applies to all (statistical and simulation) models, it is especially important for simulation approaches because there is not one standard way to develop simulation models for living resources. Decisions about the temporal, spatial, and biological scales represented in the model depend on the decisions of the models' developer(s). Defining the biological scale in a model involves what is tracked (e.g., biomass by cell, population abundance, individuals), at what biological organizational level (e.g., single-species, food web), and how the processes for the vital rates are represented. An example of the many possibilities of how environmental variables can affect vital rates, which are then evaluated and sifted through as part of model development, are shown in Figure 6 for fish.

Levins (1966) proposed that the development of a model involved the trade-offs among generality, realism (accuracy), and precision. While his idea is still being debated (Orzack 2005), the concept of trade-offs among these three features is useful when developing or selecting a simulation model. For example, to have a very general model (highly portable) necessarily means that it cannot simultaneously be very realistic and be very precise (quantitative predictions) for a specific location. The key concept is that a single model cannot be formulated that meets arbitrarily defined standards of generality, realism, and precision; decisions about model formulation requires trade-offs. A highly precise (site-specific) model has little precedent for being applied and tested elsewhere, and similarly, an off-the-shelf (highly generalized) model used in many places can be criticized for restricting users to a set of built-in options for representations that lack site-specificity. For the CBP, the questions to be answered can and must be formulated with a high degree of specificity (e.g., TMDL effects, create and enhance wetlands) and are intended to inform restoration of the Bay and thus modeling emphasizes accuracy and precision at the sacrifice of generality. The key is to find the "sweet spot" in model complexity (Collie et al. 2016).

7.4   Vital rates

Four fundamental processes affect the abundances of living resources: 1) growth affects size of individuals, 2) mortality, 3)reproduction affects the number of individuals, and 4) movement affects the locations of individuals. Growth is important to abundance because mortality and reproduction are often based on size. Movement is important because many species have at least one life stage that involves transport or movement, which in turn, affects the habitat, predators, and prey experienced by the individuals and hence their growth, mortality, and reproductive rates.

Discussions about living resources' responses to restoration actions related to abundances should be grounded in vital rates. Restoration actions will have multiple effects on vital rates for many species. For example, reduced nutrients can lower food availability, increase seagrass habitat (growth and mortality), and reduce hypoxia (expand space and reduce predation), and these can vary temporally (seasonally), spatially (subregions of the Bay), and by life stage. Use of conceptual models that depict factors affecting vital rates, coupled with framing responses as to how water quality and habitat affect these vital rates, provide a sound basis for tracking responses (Ogden et al. 2005; DiGennaro et al. 2012). An example of a conceptual model developed for the restoration program for the California Delta is shown in Figure 7. Such diagrams help organize and put into context how various restoration actions could affect species and food webs.

7.5   Habitat suitability and capacity

The term "habitat" is often used in a vague way without explicit definition (Bamford and Calver 2014). Whenever the term "habitat" is used, its link to the affected vital rates should be specified to ensure effective communication. Habitat suitability is used to assess the capacity of the environment for organisms; habitat capacity may or may not be related to realized abundance depending on whether the habitat of interest is limiting and whether other habitat is already limiting in other life stages. Habitat-based analyses (often statistical) avoids many of the confounding issues associated with relating water quality and habitat to the abundance of living resources that must rely on simulation of vital rates. The predictions of habitat suitability, however, are constrained to changes in capacity or opportunity rather than expected changes in abundance. Situations occur where large changes in habitat can result in small responses because the affected habitat is not limiting or has a weak relationship to the vital rates of the life stage that uses the habitat.

7.6   Biological organization

The level of biological organization for analyses of living resources are typically individuals (e.g., from a sample), life stages (e.g., recruitment), population, community, multi-species, guild (functionality), and food web. Most collected data provide information on water quality and habitat effects on groups of individuals; the role of the statistical and simulation modeling is to express those effects at one or more of the higher levels of biological organization. Responses can include many variables, such as Bay-wide estimates of life stage

abundance, long-term population dynamics, energetic structure of food webs, and biodiversity. The key is that these responses represent responses on a biological scale higher than just the localized or short-term effects measured on a subset of individuals.

In general, there is a tradeoff in which confidence in analysis (statistical and simulation) results decrease, while relevance to management increases, with increasing biological, temporal, and spatial scales of the response variable (Figure 8). We can have high confidence in predicted changes in habitat and individuals at the price of lowered relevance. At the other extreme, predicting how the response of the entire Bay ecosystem is highly relevant but also highly uncertain. One needs to find the sweet spot, which will change for different questions and response variables.

7.7   Nonequilibrium theory and baseline

While changes in abundance of a population are often described as a simple shift from one long-term equilibrium level to another, populations in nature show more complicated dynamics (Figure 9). Most populations do not show deterministic equilibrium, but rather show different types of stability (Bjørnstad and Grenfell 2001; Turchin 2003). Some typical forms are the very rare classical stability where the population goes to a steady state (Figure 9a); bounded stability, in which abundances vary year to year but within a range (Figure 9b); episodic stability (Figure 9c), typical of many fish species that have highly variable recruitment; regime shifts (deYoung et al. 2008) that shift the population up or down at certain times (Figure 9d); and shifting baselines (Duarte et al. 2009) that can add a slow trend to the interannual variation (Figure 9e). Fisheries stock assessment relies on a traditional view of equilibrium, although steps are taken in interpreting the results to account for deviations from the steady-state dynamics (Hilborn and Walters 2013).

Another aspect of the long-term dynamics of a complex ecosystem that has undergone major environmental changes is defining baseline conditions (Duarte et al. 2009). Defining baseline conditions is critical because it provides the basis for then defining goals and targets and for assessing the success of the restoration actions. Defining baseline in realistic cases (i.e., anything but deterministic equilibrium) is challenging because it requires agreement on what is the desired state of the ecosystem (e.g., now, 50 years ago, pre-settlement) and also because restoration of complex systems do not typically result in ecosystems simply reversing their state (i.e., hysteresis) by following the historical trajectory from now to the past condition. Models used to assess living resource responses to restoration should be evaluated for how well they resemble the baseline pattern, and evaluated based on whether they include species (e.g., invasives) and processes (e.g., pelagic-benthic decoupling) that were not important in the past but could be anticipated to be important in the future. For example, accounting for changing baselines due to global climate change is necessary for accurate assessment of living resources' responses to restoration (STAC 2012; Sheaves et al. 2021). Climate change will affect many aspects of the Chesapeake Bay ecosystem (Wood et al. 2002; Najjar et al. 2010), including defining baseline, vital rates of many taxa, and formulating habitat suitability relationships.

Models developed based only on historical and present-day information will be limited in their capabilities for assessing the responses to restoration actions into the future.

7.8   Multiple Influencing Factors

The dynamics of living resources are influenced by multiple factors (promoters and stressors), and some are purposely manipulated by management (e.g., adding habitat, increasing oxygen, harvest limits). Factors generally include environmental variables (e.g., water quality) and other organisms (e.g., predators, invasive species). Stressors are factors that act negatively on individuals and can be natural (e.g., drought or warm year) or anthropogenic (e.g., contaminants). Three major complicating aspects of multiple factors is that they often operate on different spatial and temporal scales making representation in analyses difficult, they have interactive effects (the response to one depends on the value of another), and they covary together to various degrees hindering separation of their individual effects (Teichert et al. 2016). The relationships between these factors and fish-indices from monitoring data can be difficult to interpret and pinpoint causes (e.g., Chesney et al. 2000). The restoration of the Bay increases a select set of promoters and reduces a select set of stressors; *in-situ* responses are the results of the cumulative effects of these selected actions combined with the effects of all other important factors. There are methods and models for untangling individual factors effects and assessing cumulative effects, and many have been previously applied to various aspects of the living resources of the Chesapeake Bay.

7.9   Tradeoffs (win-lose), Win-win, and Lose-lose

Changes in water quality and habitat will have positive and/or negative effects on living resources when one considers the complicated mix of factors that are affected and the diversity of species that form the system-level response. The phenomena of "winners-and-losers" occur under most all types of environmental changes (Mumby et al. 2017; Filguerias et al. 2021). A key is to consider these throughout the analyses so that decisions about responses can be fully informed and accurate information is conveyed to stakeholders and managers.

A tradeoff common to most all nutrient loading reductions is between the improved water quality versus the possibility of lowered primary and lower trophic level productivity affecting food web energetics. Reduced nutrients and sediments will improve dissolved oxygen conditions and other aspects of water quality (e.g., increased clarity) and benefit specific species (e.g., SAV, certain fish species). Reduced nutrients can also reduce primary production that fuels the energy transfer for certain other living resources (e.g., planktivores such as menhaden). This issue has been examined for decades, and one approach has been to compare the relationship of chlorophyll and primary production to measures of fish production across systems (e.g. Figure 10; Breitburg et al. 2009; Marshak and Link 2021). The idea is that with low to moderate nutrients, there is a positive relationship until hypoxia and other negative consequences of over-enrichment occur that cause the relationship to then decline. Going the next step however, and substituting time for space to say that a specific system will respond this way over time to changes in primary production requires additional analyses. Other

analyses have more appropriately included processes pertaining to how the fish in a specific system of interest will respond over time using historical data or modeling (e.g., de Mutsert et al. 2016; Capuzzo et al. 2018; Rose et al. 2018a and b). In those, there is generally a mix of positive, neutral, and negative species-specific responses to reduced nutrient loadings within a system.

A second contributing factor that causes trade-offs is that living resources effectively occupy a wide range of habitats in estuaries (Pihl et al. 2002). Except for perhaps the actual deep hypoxia zone, species have different tolerances and preferences to the same habitat and most habitats are, to various degrees, occupied. Thus, restoring certain types of habitats will clearly benefit specific species, but also not all species will respond favorably to the new availability of certain habitat types. In some cases, species can even respond negatively (often locally) if the habitat restoration involves significant conversion of some of their preferred habitat types to other habitat (e.g., open water to structured habitat), or alters the food web (e.g., increased shunt of energy to jellyfish or from pelagic to benthic dominance). Responses can occur differently within subregions of a large ecosystem (Luo et al. 2001; Niklischek and Secor 2005; Murphy et al. 2022), and regional-scale changes in climate can led to invasions of new species to an area who can also inhabit various habitat types (Rahel et al. 2008). Consideration of a wide range of species with different life histories and preferences and sensitivities to water quality and habitat will ensure that an assessment encompasses the full range of possible responses.

7.10 Power to detect responses

The power of many analyses to connect responses of living resources to specific water quality and habitat changes will generally be low (although this might be offset by strategic use of the weight-of-evidence approach), with false negatives much more common than false positives. A false negative is when no effect is detected when there is an effect present. Considering the magnitude of the effects estimated from the analyses, rather than just statistical significance, is important for all analyses (Smith 2020). Responses of groups of individuals in specific locations should be documented with field data and modeling. As those are extrapolated to broader time and space scales and expressed at higher levels of biological organization, they become more ecologically- and management-relevant but also can delay, dampen, amplify, override, or cover-up the signal detected at the local level.

A challenge is to manage expectations of managers, politicians, and stakeholders under these conditions of low power. Not detecting a response at the population or food web levels and Bay-wide can be wrongly interpreted to imply ineffective management actions, especially when looking at short time periods. Analyses over a range of temporal and spatial scales is needed to show localized effects that have higher power of detectability to establish some degree of in-situ responses, and then analyses can be done to see if these localized effects get expressed at the higher levels of biological organization and broader time and space scales.

Statistical analyses of field data are useful for establishing the localized effects, while simulation modeling is needed to isolate potential responses at higher levels of biological organization.

7.11 Explicit and implicit representations

Expressing the effects of water quality and habitat on organisms is often through their vital rates and simulation models, and these effects can be represented explicitly or implicitly. Explicit representation means the specific effect is an actual term (or "knob") in the model. Many water quality and habitat effects not stated in a model can still be assessed by first determining how these effects influence variables already in the model and then vary those variables. For example, consider a model that has growth rate as a parameter and we want to assess the effects of improving water quality (e.g., clarity) or adding more of a habitat type (e.g., marsh, SAV). We think the improvements will affect feeding success or food availability, so we first determine (outside of the model) how the more opportunities for feeding will change growth of the species of interest. We then impose these changes in growth rates in the model. While there was no explicit representation of habitat in the model, we can still use the model to assess the effects of adding habitat (Lipcius et al. 2019). Caution is needed with both explicit and implicit representations of effects to ensure they are imposed realistically. But analyses for the CBP do not need to include (and should not include) explicit variables or parameters for every possible effect of all water quality and habitat changes (see Model complexity).

7.12 Relative versus absolute predictions

Assessment of the responses of living resources is more certain for relative changes, but absolute results are more management relevant. Many analyses (especially from simulation modeling) are best viewed as relative predictions of the responses of living resources to changes in water quality and habitat. This is because changes between two model simulations will only differ by the inclusion/exclusion of the effects of interest. To move to absolute predictions requires that the representation of baseline closely mimics the time sequence and spatial aspects of the actual populations and accurate representation of the effects of the management actions, and further, that the predictions realistically describe conditions in the future. Therefore, models would need to include the many factors that can affect the results in nature. Relative predictions (e.g., percent change from baseline) relax these requirements and are effective if the model is sufficiently realistic. Model predictions of how different restoration combinations (e.g., TMDL, habitat enhancements) under alternative system conditions (e.g., low and high river inflows) affect the relative changes in populations and food webs offers a powerful strategic approach to evaluating the responses of living resources (Gruss et al. 2017; Kaplan et al. 2021). Care is needed labeling and defining the prediction-type of modeling results to ensure clarity; common terms that should be carefully defined when they are used to label results are projections, predictions, forecasts, hindcasts, and scenarios (Luo et al. 2011). As part of scenarios, global climate change will need to be accounted for in most all predictions or projections that go decades into the future.

8   Strategic determination of an analysis plan

Evaluating the merits and feasibility of the different options (i.e., pathways) for assessing living resources' responses involves systematically proceeding through a series of steps or considerations. The process (framework) is to consider the management questions, along with the foundational concepts and principles, to determine the confidence (uncertainties), technical and practical feasibility, and usefulness (ability to answer questions) of different analysis-related decisions at each step. Figure 1 provides an initial conceptual basis to guide the formation of an analysis plan and to help in the implementation of the analyses.

8.1   Selecting species

An important step is the selection of the species to analyze. The selection should be done strategically to enable broad general statements to be made. Criteria to consider include: (1) the life history of species and their role in the food web, (2) their life cycle and dependence on habitats by life stage, (3) their sensitivity to changes in water quality and habitat, (4) what information and data are available about the species, and (6) the scope and results from previous analyses. Development of conceptual models about candidate species, as was done in other large-scale restoration programs, is an effective way to proceed. Including the species that are specifically targeted by management actions is a good start; however, there should be a general evaluation of the other species as well (e.g., to capture indirect effects) whose responses would add to the generality and robustness of the assessment. There are a variety of ways of grouping species to examine general responses (Pla et al. 2012; Harrison and Whitfield 2021).

8.2   Available Data

Another consideration is the evaluation and inventory of the available data. The term "data" is used here in the broad sense as the information available about a species and food web. In addition to the monitoring data on the status and trends of the species, data also includes information on life history cycles and strategies, laboratory results on environmental tolerances and preferences (such as used to define the water quality criteria), and outputs from other models (e.g., dissolved oxygen and chlorophyll from the CBP modeling system). There have been multiple STAC workshops on water quality modeling and data, reviews of the habitat tolerances and preferences of many species found in the Chesapeake Bay, and published analyses of the fish-related monitoring data (e.g., Tetra Tech 2020). In many cases, the available data for living resources (SAV being an exception) were not collected, simulated, or analyzed for the specific purpose being considered here. While much of the preparatory work on availability of data and information is done, there should be a specific effort to synthesize (i.e., refine and tailor) the information for its use in the assessment of living resource responses to management changes in water quality and habitat.

8.3   Response and explanatory variables

The selection of the response variables is based on a balance between the ecological and management relevance of the variable and how well the response variable can be

predicted (Figure 8). A major dichotomy in response variables is between habitat-based variables and variables that are the actual density or abundance of organisms. The extensive work done on developing indicators for the CBP (STAC 2007; see Status and Trends Workgroup[5]), the species targeted in the CBWA and named in related documents, the Goal Implementation Teams (GITs), and the lessons learned from other large-scale restoration projects (e.g., Doren et al. 2009) provide a solid basis for selecting response variables for analyses of living resource responses.

Habitat suitability is widely used in analyses to inform management to assess changes in fish habitat under varying or altered environmental conditions (e.g., STAC 2009; O'Connell et al. 2017). There is a long history of habitat-based analyses often estimated from monitoring data. While the approach is still fundamentally species and life stage specific, recent advancements include more reliance on statistical estimation to determine the suitability functions and formulation of functions that are rooted in physiology and ecological theory (Robinson et al. 2017; Guillera-Arroita 2017). These new methods for habitat suitability include species distribution models, niche modelling, and bioclimatic models, all of which use the framework of mapping spatial information on environmental conditions and species presence or densities to habitat metrics of quality-adjusted area.

Using habitat as the response variable has advantages as it avoids dealing with the population and food web dynamics (which can be challenging and uncertain), uses monitoring data (extensive for the Bay) to define the quality of habitat (organisms are present in good habitat), and, for the water column, can directly use the outputs from the CBP modeling system (Hood et al. 2021). Using the modeling system allows for the simulation of the specific effects of the TMDLs on water quality expected under future conditions to be expressed as changes in the habitat of key species. The interpretation of habitat quality depends on how suitability is defined; avoiding lethal conditions leads to a broad definition of suitable while identifying specific ranges and combination of conditions can be interpreted as limiting the definition of suitable to be only when conditions are near-optimal. Disadvantages include the results being specific to life stages (no link between life stages), limited to average or snapshot conditions whereas habitat is dynamic, little consideration of trophic interactions, and the interpretation of habitat suitability as capacity for species that may or may not be manifested in the actual in-situ responses in terms of abundances. Habitat suitability analyses would be evaluated for their use under climate change conditions to ensure their fits to historical data are valid for the future conditions.

Assessing habitat as part of the CBP has been explored (STAC 2000, 2009, 2018). Adding habitat suitability to the CBP modeling system would be relatively easy in comparison to predicting abundance-based response variables that shift to simulating the vital rates that form the basis of population and food web models. An example of a habitat analysis using merged

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[5] https://www.chesapeakebay.net/who/group/status_trends_workgroup

data from multiple monitoring programs is the analyses done for the Gulf of Mexico to assess habitat suitability and in support of food web modeling (Gruss et al. 2018, 2020).

Response variables at the levels of population abundances and food web dynamics are more challenging to predict, but the benefit is that they are more closely aligned with the scales of management and what is of primary interest to stakeholders and the goal of Bay restoration. Such response variables move from the potential for more high-quality habitat to groups of individuals (e.g., juveniles in marshes) benefitting to the responses at the population, community (e.g., diversity), and food web levels. A general tradeoff is between the increasing relevance of the results and decreasing feasibility and confidence as one goes from habitat to food web (Figure 8). A multi-model approach is likely useful to address certain questions to develop results with quantifiable and acceptable levels of confidence (STAC 2014; Rose et al. 2015).

As part of selecting the response variables, there is a parallel activity of ensuring the important explanatory variables are estimable with sufficient confidence at the appropriate temporal and spatial scales. While some explanatory variables, such as water temperature, salinity, dissolved oxygen, turbidity, and chlorophyll can be estimated based on their extensive monitoring and modeling, other explanatory variables (e.g., prey, predators) will involve significant effort. Including explanatory variables besides the TMDL-targeted variables is critical since these other variables will account for some (even most in some instances) of the variability ("noise") in the living resources responses, and thereby increases the chances of detecting responses attributable to the restoration-induced changes in water quality and habitat variables. The approach that would most likely generate robust and generalizable results to beyond the species analyzed would use a mix of the habitat and abundance-based response variables.

8.4   Biological, temporal, and spatial scales

An important consideration is the determination of the biological, temporal, and spatial scales of the analyses. The biological scale was partially considered with the specification of the response variable, such as habitat, species abundance index, population-level, community, or food web. Strong inference at a chosen biological scale dictates the temporal and spatial scale of the analyses, which in turn, requires that the data for the response and explanatory variables be usable at those scales. For example, using the population abundance of a species implies certain spatial and temporal scales that are dictated by the life cycle and movement patterns of the species. If the scales used are too fine (e.g., small subregions of the Bay), then one cannot interpret the dynamics as being on the population-level. On the other hand, response variables like community structure (e.g., diversity) can be compared on relatively fine spatial and temporal scales but are difficult to interpret on broad scales like Bay-wide.

Once the scales of the analyses via the specification of the response variable (e.g., Bay-wide adult abundance of Blue Crabs) are determined, this then determines the scales needed for the explanatory variables. While a seasonal to annual temporal scale for a location,

subregion, or Bay-wide are typical for examining trends for many living resources, how to represent the different explanatory variables on the same scales requires careful analyses. For example, how should one aggregate fine-scale variation in temperature and episodic hypoxia events to relate to a population-level response variable? The frequency and spatial distribution of sampling dictates the finest spatial and temporal scales of water quality responses possible from the monitoring data. The model-generated data also has constraints on what types of variability can be captured. Both were well designed to operate on scales to characterize patterns and trends in water quality. Their use as inputs to quantitative analyses of living resources' responses requires additional considerations and scrutiny. The best time and space scales for trend analysis (either from data or models) in water quality are not necessarily the same as the temporal and spatial scales required for modeling water quality relationships with long-lived, mobile organisms. For example, one can envision a situation where the fine-scale variation in water quality (such as extremes, episodic events) is important to the organisms, but such estimation was not the goal of the monitoring or modeling that focused on estimating averaged values. Post-processing of the monitoring or modeling data then requires another model (with its attendant assumptions) to resolve (aggregate and disaggregate) the data to the temporal and spatial scales needed for the response and explanatory variables.

8.5   Analytical approaches

Identifying the analytical methods to be used is important to ensure compatibility between the formulation of response and explanatory variables and how analysis of these will answer the posed management questions. We offer brief comments on the available methods, categorized as statistical and simulation, focusing on how they play a role in working through deciding how to assess living resource responses. Both categories of methods have long and extensive histories and are scientific disciplines unto themselves.

There are many possible statistical methods and simulation models that can be used, and each has its own set of advantages and limitations when used to relate living resources' responses to changes in water quality and habitat. When *in-situ* responses are the focus of response variables, both are fundamentally limited by only having a single Chesapeake Bay that is observed over time while many factors that influence the response variables are varying (independently to correlated) in time and space. Statistical approaches have a major advantage of a well-established methodology and protocols when they are used to analyze data. They also have compact presentation (e.g., regression model), clearly stated and testable assumptions, and interpretable measures of how well the model agrees with the empirical data. A major limitation of many statistical methods, which leads to using simulation approaches, is that the identified relationships are not cause-and-effect and are highly uncertain when used for conditions outside the domain covered by the data (e.g., models estimated with historical data can struggle to predict responses under novel conditions).

The theory behind simulation approaches is to shift the analysis from analyzing densities and abundances to represent rates of changes of processes that affect rates (e.g., how feeding

and temperature affect growth, predators affect mortality) that when solved, generate the densities and abundances. In theory, this should enable better extrapolation to novel conditions (expected under restoration) and easier identification of cause and effect (see Sugihara et al. 2012). Simulation approaches, however, do not have a standardized method for development and testing (validation) and thus are more difficult to quantify their uncertainties and to communicate the results of their predictions. While statistical analyses, when properly documented, are transparent, simulation modeling is often more difficult to document. Historical trends with correlative partitioning favors statistical methods, while novel conditions and highly specific attribution favors simulation modeling. The available data and models for use with Chesapeake Bay is extensive and the many examples provide a sound basis for adapting models for a coordinated assessment. Sifting through the many available approaches requires a targeted and deliberate effort. Some key considerations are the specific questions to be addressed, the degree of attribution to specific causative factors needed, the biological organization and temporal and spatial scales of the response variable, and the availability of data and information.

8.6   Coordination and combining results

Any assessment that involves multiple analyses needs a plan for how to integrate the results so that synthesized information can be leveraged beyond a simple collection of independent analyses. Given the effort and diverse analyses and data involved, several data synthesis and analysis teams would enable efficient and timely reporting of results. Conceptually, this is analogous to a multi-model analysis that involves different teams using different models (STAC 2014; Fulton et al. 2015), which is used in other fields, ranging from medicine, harmful algal bloom forecasts, to hurricane predictions, to climate change. In the case of the CBP, there should be some shared information across teams and analyses to ensure results can be smoothly combined. Likely candidates are a set of shared scenarios, overlapping time periods, and common inputs when possible. The long-term monitoring data and CBP modeling system are likely good sources for generating sharing water quality inputs; assessing habitat actions would require a group-effort to develop a template for doing this. The success of the CBP's monitoring and modeling systems and the activities of the working groups and GITs show the CBP is well suited to pursue a coordinated analysis of living resources' responses. Sufficient coordination across teams and analyses is needed to ensure useful synthesis, but without too much coordination that then forces some analyses to sacrifice realism in order to conform with other analyses.

Also important is a scheme for the actual synthesis to ensure the results lead to robust conclusions and transparency. Schemes have been proposed, including approaches tailored to large-scale ecosystem restoration (Swannack et al. 2012; Rose et al. 2015). Figure 11 is one example of a way to organize the evidence (Diefenderfer et al. 2016, 2021); the CBP could develop their own that is tailored to the management questions and the types and uncertainties generated by the various analyses. The other considerations, such as species' life

cycles, conceptual models, types of predators, biological scales of the different analyses, possible trade-offs, the sensitivity of the species, and power of analyses would be incorporated and inform the details of the scheme.

9   Final comments

We have outlined a path forward (a framework) for evaluation of the responses of living resources to the TMDL and other restoration actions of the CBWA. We started with the statement of management questions for 2025 and beyond and provided background information on the various ways water quality and habitat are presently linked to living resources and how progress is being assessed in the Chesapeake Bay. For context, we included examples of statistical and modeling analyses for the Chesapeake Bay and how responses of living resources are being assessed at other large-scale restoration programs. Concepts and principles from ecological and ecosystem theory were discussed, which when combined with a series of decisions (steps), would lead to the development of strategic analysis plan for assessing the responses of the living resources.

Development of an analysis plan using this framework would provide a transparent basis for subsequent assessments. The decision by the CBP going forward can be from continuing the status-quo to adding analyses to the status-quo to a comprehensive assessment. The framework documents the rationale for such decisions and ensures clear understanding of why analyses were done and why other analyses were not done. In practical terms, a next step could be to form a Living Resource Modeling and Assessment Workgroup that would parallel the other workgroups (STAC 2019; Hood et al. 2021). Such an organizational model has proven very effective for the Chesapeake Bay Program.

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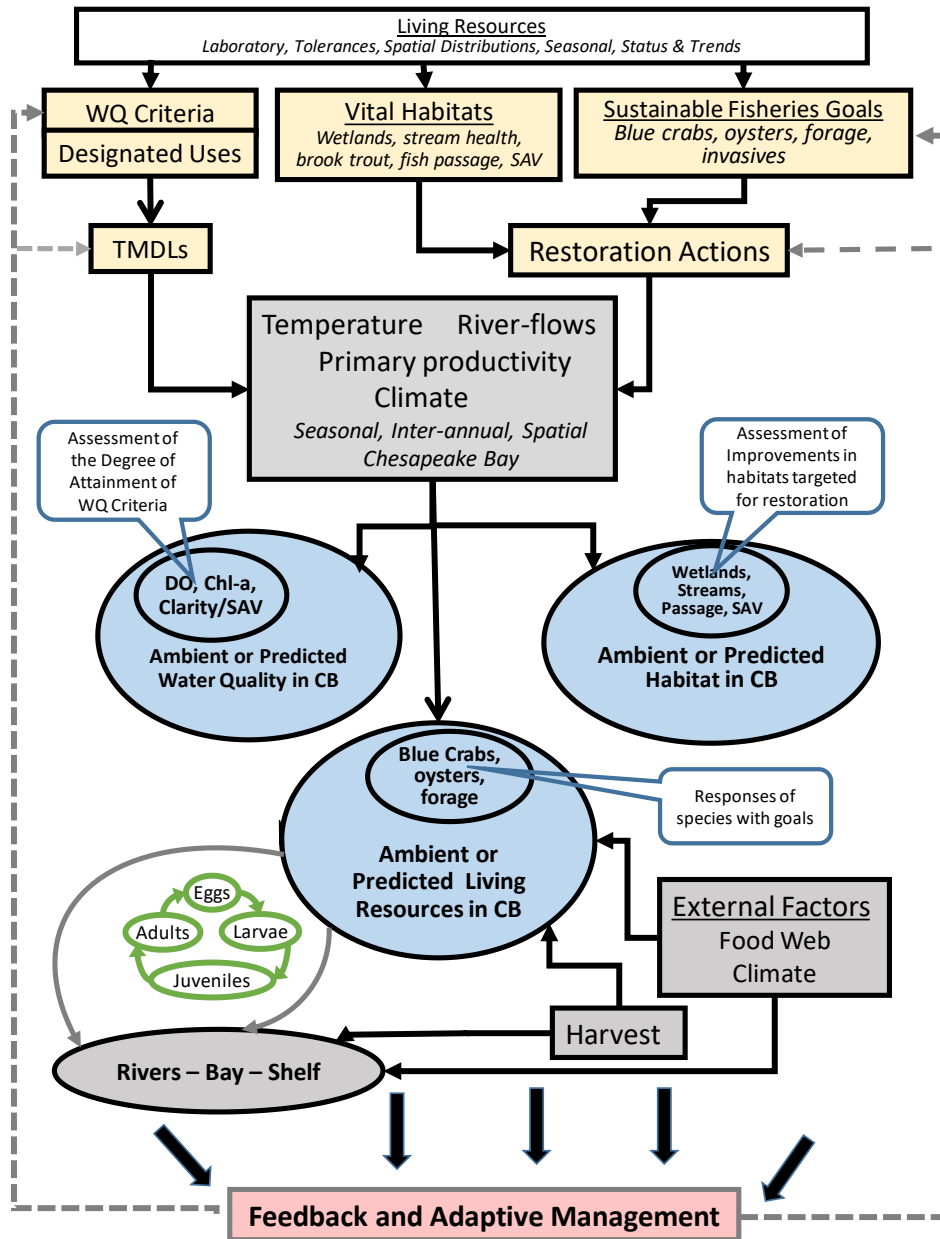
Figure 1. Schematic flowchart of how information on living resources are presently incorporated into water quality and habitat within the CBP (top box) and how their effects can be traced through to the in-situ responses of the living resources. Yellow boxes denote restoration and management actions of the CBP. Grey denotes factors outside of the CBP that affect the response to actions within the Bay and outside of the Bay (grey). Blue are the fundamental observations of ambient or predicted water quality, habitat, and living resources within the Bay. The green life cycle represents how most species have complex life cycles that use multiple habitats both within and outside of the Bay. The red box is how feedback from the analysis results can inform Adaptive Management.
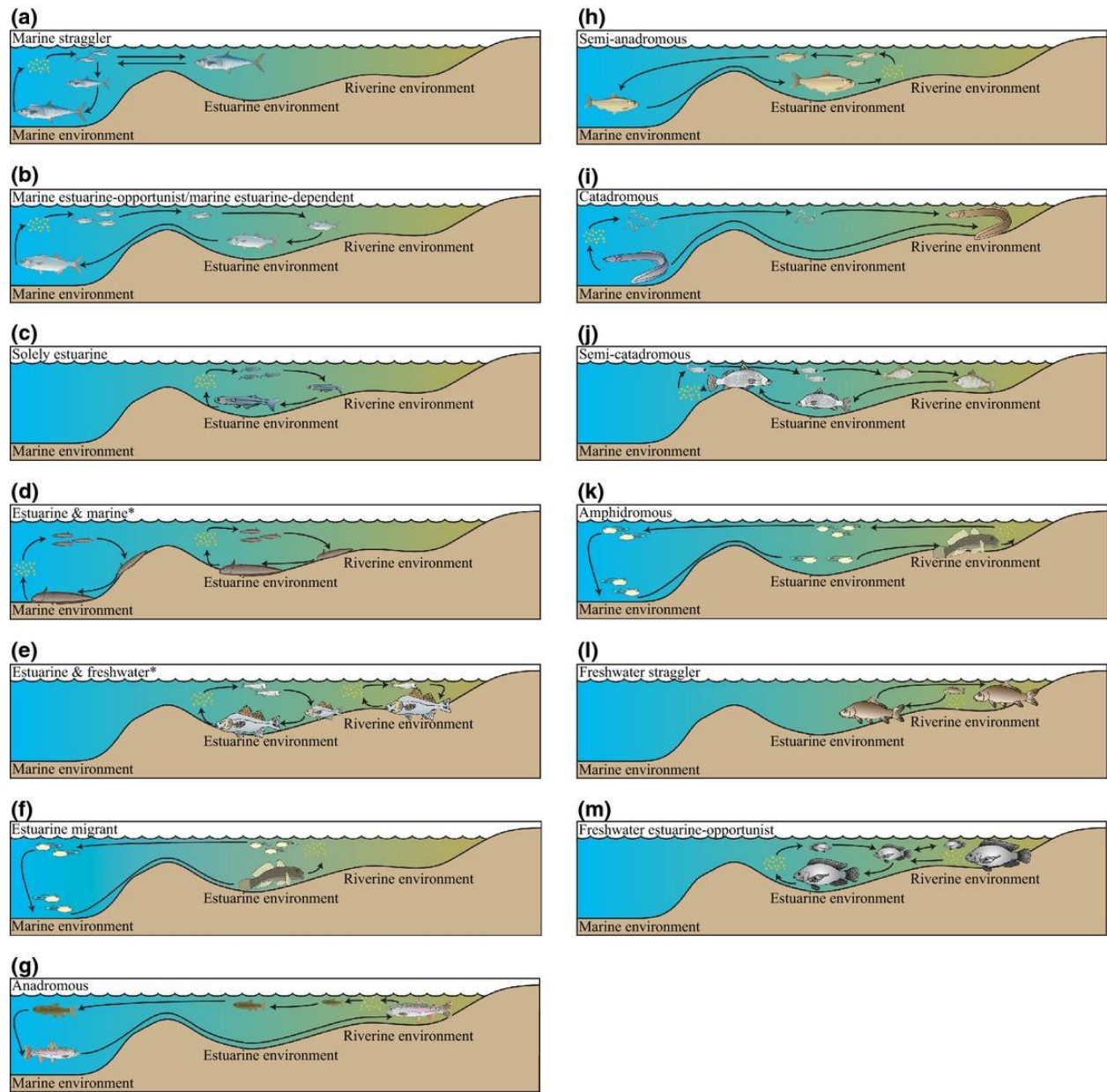
Figure 2. Common fish life cycles that use the marine, estuarine, and freshwater habitats. (from Potter et al. 2015)
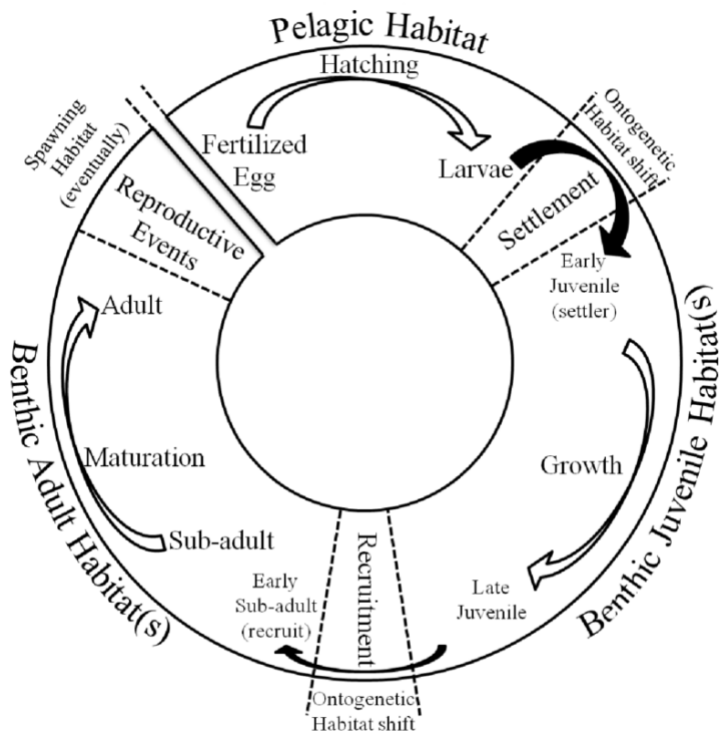
Figure 3. Life cycle of a hypothetical fish species with a bipartite life cycle (pelagic and benthic) and segregation between juvenile and adult habitats. (from Thiriet 2014)
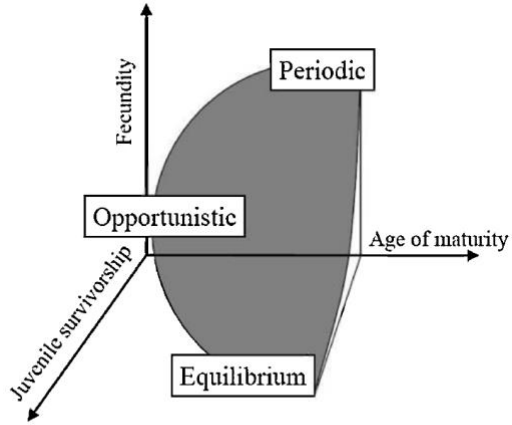
Figure 4. Life history strategies for fish species based on age of maturity, juvenile survivorship, and fecundity defined by Winemiller and Rose (1992).
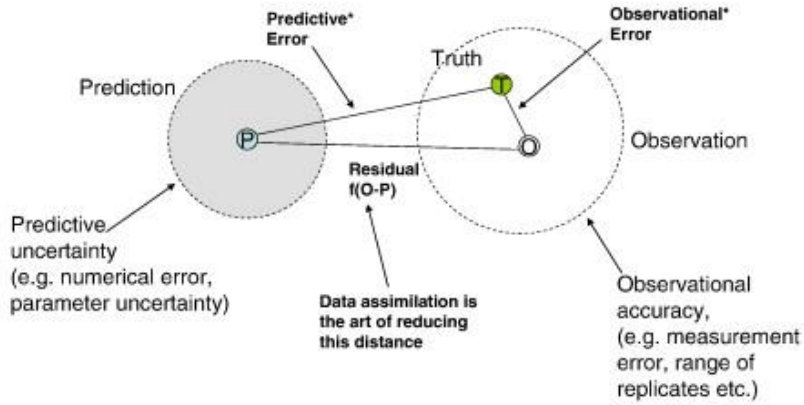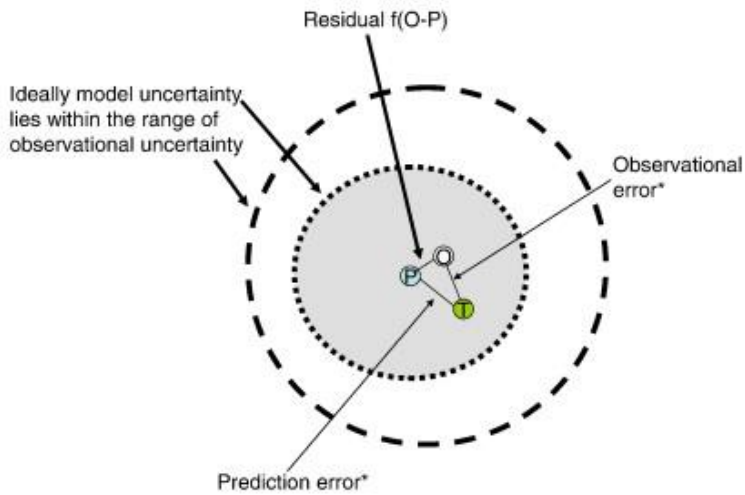
Figure 5. The relationships between model prediction (P), observations (O), and the truth (T). Both P and O have halos of uncertainty; gray circles for prediction and open circles for observations. (a) example of a model with low skill, (b) example of a model with ideal skill. (from Stow et al. 2009)
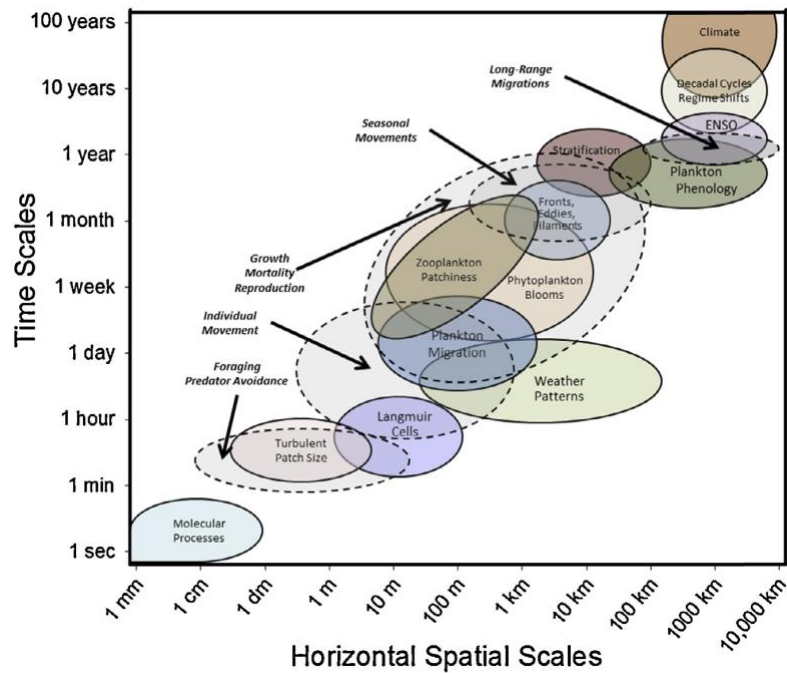
Figure 6. The spatial and temporal scales of some of the physical and biological factors that could influence how growth, mortality, reproduction, and movement of fish are represented in models. The solid line ellipses show some of the physical and biological factors, while the dotted ellipses show the fish processes of growth, mortality, reproduction, and movement. (from Rose et al. 2015)
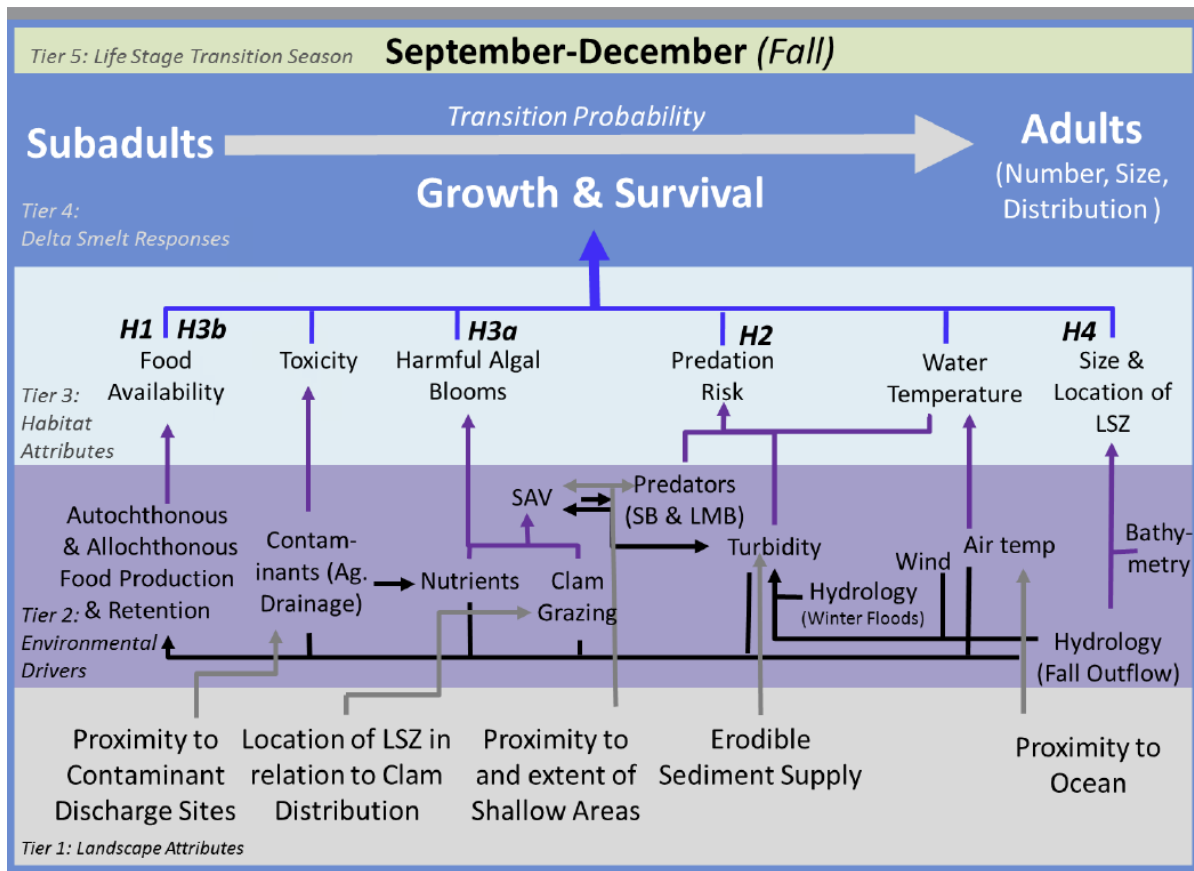
Figure 7. Example of a conceptual model used for understanding possible effects of factors and restoration actions on the transition (growth and survival) from subadults to adults for Delta smelt. H1, H2, H3, and H4 refer to hypotheses proposed to explain how certain factors would affect the transition (growth and survival). (from MAST 2015)
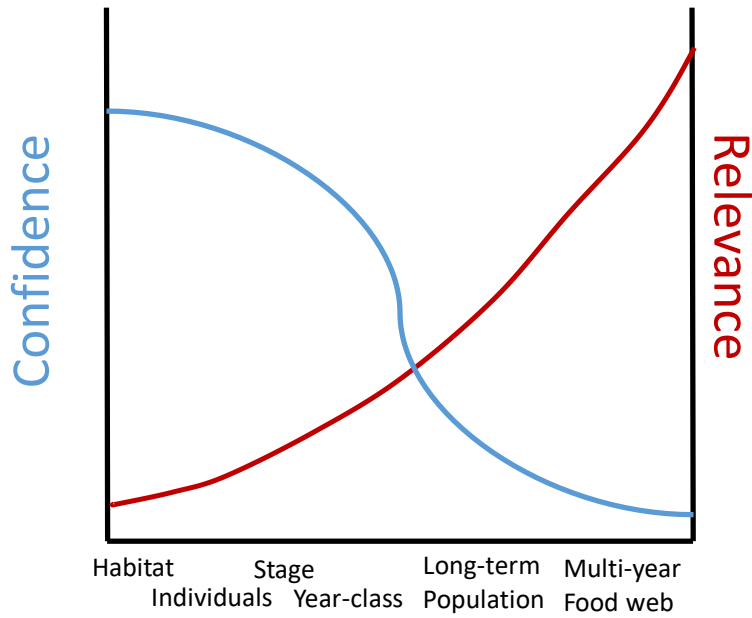
Figure 8. The tradeoff between confidence and relevance with increasing level of biological organization of analyses. The two lines are constructed for a particular question to be addressed and how the results will be used in decision-making. One then weighs the confidence versus relevance for the series of alternative analyses that can be done at different levels of biological organization. How the predictions of the model are used to assess responses to management actions can be either in absolute terms or as relative changes at the selected level of biological organization.
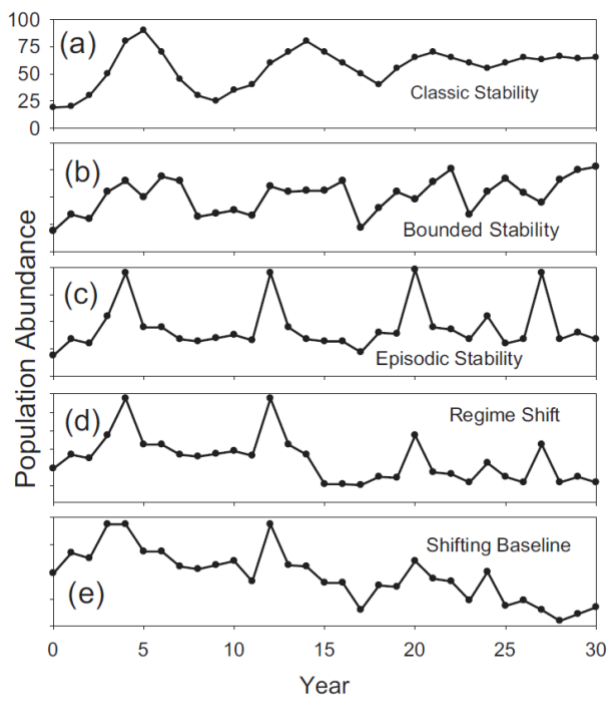
Figure 9. Various types of equilibrium stability exhibited by many populations. (From Rose et al. 2015)
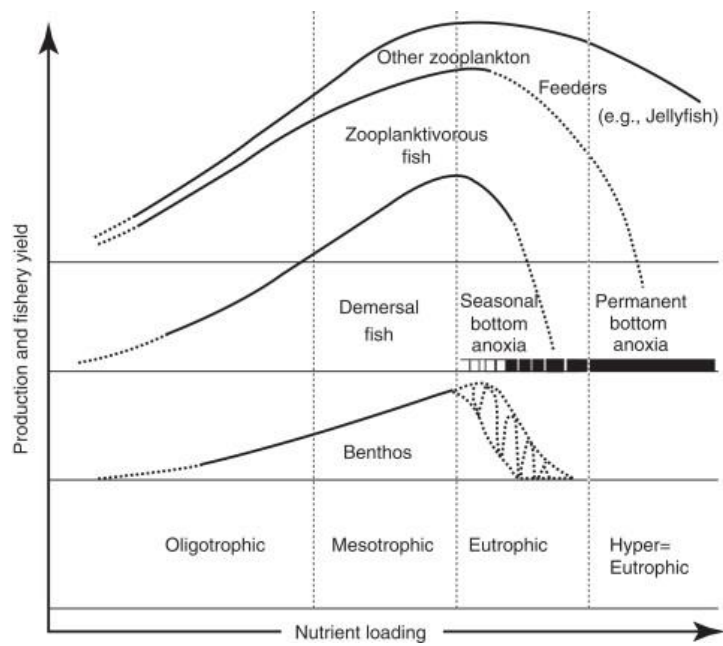
Figure 10. Schematic showing the dependence of fish production and fishery yield on nutrient loading. (from Burkholder and Glibert 2013).
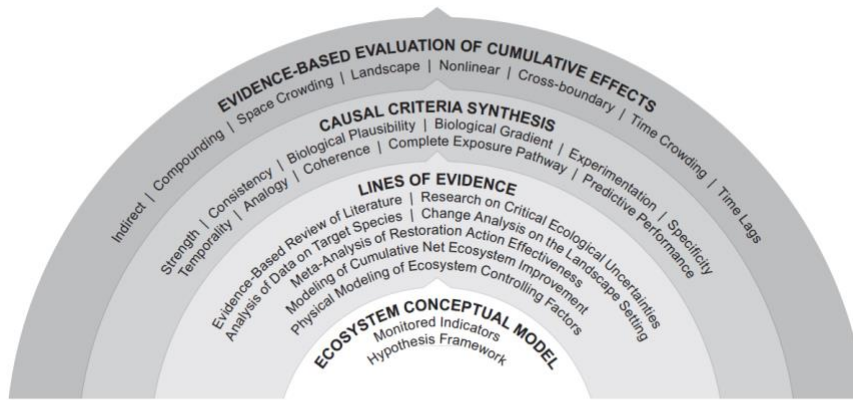
Fig. 1.   The process of evidence-based evaluation includes developing a hypothesis framework and monitored indicators from an ecosystem conceptual model, multiple analyses within lines of evidence, synthesis of the evidence using causal criteria, and evaluation of cumulative effects.

Figure 11. Example of a formal process for integrating and synthesizing information analysis results to assess the responses of the ecosystem to restoration. (from Diefenderfer et al. 2016).