TROPHIC CHANGES IN A FRESHWATER TIDAL FOOD WEB AFTER WATER QUALITY IMPROVEMENTS AND INVASIVE SPECIES (ICTALURUS FURCATUS) INTRODUCTION

by

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DEDICATION

This is dedicated to my dear friend, the late Adrian Dahood-Fritz, Ph.D. You continue to be an inspiration to humans, and women in STEM everywhere. We will always tell your story.

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Gunston Cove, a freshwater tidal tributary to the Potomac River in Virginia, USA, underwent a stable state shift in 2005 from a phytoplankton-dominated state to a macrophyte-dominated state. Blue Catfish were observed as an invasive in the tributary in 2001 and a local population has since been established. An ecosystem modeling approach is used to evaluate the impacts of water quality improvement and invasive species introduction on ecosystem structure and function in Gunston Cove. Two trophic models are constructed in Ecopath with Ecosim using long-term survey data, and used to compare aquatic communities before and after the ecosystem underwent a stable state shift in which the primary production shifted from phytoplankton-dominated to submerged aquatic vegetation-dominated. Additionally, invasive Blue Catfish were introduced to Gunston Cove in 2001. Trophic changes accompanying water quality improvement and the subsequent stable state shift are evaluated, in addition to the trophic impacts of invasive species introduction. The comparative approach allows evaluation of

the effects of both events on trophic dynamics and ecosystem maturity and function. The comparison of Mixed Trophic Impact analyses shows that the invasive Blue Catfish is correlated with functional displacement of native catfishes in the Gunston Cove food web and reduced trophic impacts of the native catfishes on the greater food web. The comparison of system metrics showed evidence of a maturing system following water quality improvements. The food web model representing Gunston Cove in the current submerged aquatic vegetation stable state provides a foundation for future research and evaluation of management and policy decisions.

CHAPTER ONE: ANTHROPOGENIC IMPACTS ON AQUATIC ECOSYSTEMS AT THE ECOSYSTEM AND COMMUNITY LEVEL

1.1 Introduction

Increases in human population inevitably result in increased pressures on surrounding ecosystems, particularly aquatic ecosystems with many resources and services to humans (McLusky and Elliot 2004). Such anthropogenic impacts on aquatic ecosystems, both direct and indirect, result in changes observable at various scales from individual to the ecosystem level (Halpern et al. 2008). Impacts at the ecosystem level are particularly strong in estuarine habitats with relatively lower biodiversity and high productivity when compared to other aquatic habitats (McLusky and Elliot 2004). Threats to these ecosystems include overexploitation, water pollution, habitat degradation and destruction and nonnative species invasions (Dudgeon et al. 2006). These influences can be more difficult to predict and manage, particularly in such connected estuarine systems, due to the geographic breadth of the impact's origins: watershed and drainage, localized impacts, and downstream reaches (Dudgeon et al. 2006). The consequences of anthropogenic actions and introduction of nonnative species can include community level changes, such as those to the food web structure and energy flows, as well as those at the ecosystem level including changes to system function, cycles and pathways (McLusky and Elliot 2004, Crooks 2002).

Trophic structure, also referred to as the structure of a food web, describes how populations in the community relate to each other to obtain the energy needed for growth and reproduction (Christensen and MacLean 2011). Natural physical and chemical factors, climate, fishing, and other anthropogenic activities pressure and drive the dynamics between trophic groups in a given aquatic system (Christensen and MacLean 2011). Nutrient enrichment is a common bottom-up effect which fuels increased primary production, often of algae, that may outcompete submerged aquatic vegetation (SAV). While increased primary productivity may fuel production through higher trophic levels, algae blooms die off and the associated decomposition respiration may lead to hypoxia and subsequent reduced production. Events such as predation or fishing activity are considered top-down effects that can lead to trophic cascades that have a ripple effect throughout the food web (Matson and Hunter 1992).

Bottom-up drivers can be strong in urbanized areas where excess nutrient input leads to excessive primary production and eutrophication (Heath et al. 2014). Excess primary production puts more energy and production into the food web (Heath et al. 2014). Ecosystems experiencing eutrophication may undergo a stable state shift, in which the changes in primary producer composition and water quality are likely to result in altered trophic structure (Heath et al. 2014, Olin et al. 2002). Fish community structure is influenced by the consequences of eutrophication and therefore, stable state shifts also occur in the fish community. Stable state shifts can include changes to the physical environment such as vegetation structure or lack thereof, or increased turbidity from algal

populations, which may favor different species (e.g. increased turbidity does not favor predators that rely on sight, Olin et al. 2002).

Alternatively, higher trophic level predators can apply top-down pressures, resulting in trophic cascades which are often less predictable, though cascades are typically expected to result in inverse changes proceeding through each lower trophic level (Heath et al. 2014). Trophic cascades, put simply, are "indirect species interactions that originate with predators and spread downward through food webs" (Ripple et al. 2016). Further, there may be "knock-on effects" that ripple out from these initial indirect effects of trophic cascades; the complexity of the trophic cascade and these knock-on effects contributes to the likelihood that such an event to a food web is difficult to predict (Ripple et al. 2016). An example of a top-down driver is the introduction of an invasive predator, which may be particularly unpredictable (Heath et al. 2014). Invasive predators, such as the Blue Catfish in the Chesapeake Bay, are expected to strongly influence local trophic structures, but how they do so is not yet definitively understood (Schloesser et al. 2011).

The trophic impacts of perturbations on ecosystems that are experiencing both significant simultaneous bottom-up and top-down events are difficult to predict, though this is typical in reality and evaluation requires a holistic approach (Heath et al. 2014). Ecosystems are constantly influenced by both top-down and bottom-up effects, for example, an estuary receiving fluctuating levels of nutrient input from its watershed (bottom-up) is likely also experiencing top-down effects from fisheries and potentially introduced species from global shipping traffic. These events cannot be isolated in reality

in order to study their effects, which highlights the need for an ecosystem-based

modeling approach to evaluation, as well as ecosystem-level management.

1.1.1   Impacts of Eutrophication

Increases in human population and the associated urbanization and infrastructure

development in watersheds inevitably results in increased nutrient input from both direct

sources such as point source wastewater effluent, and indirect sources such as agricultural

runoff (McLusky and Elliot 2004). Eutrophication, the excess loading of the nutrients

nitrogen and phosphorus, is associated with an increase in algal biomass, followed by the

reduction of submerged aquatic vegetation, increased turbidity, and reduced dissolved

oxygen (Smith 2003). The increase in primary production can result in a shift towards an

algal-dominated ecosystem, which when sudden and drastic is referred to as a change in

stable state, which leads to direct and indirect changes at the community and ecosystem

level (McClelland and Valiela 1998, Smith 2003). The theory of alternative stable states

in ecological systems asserts that an underlying range of environmental drivers can hold

the system in a somewhat stable condition, but once the threshold of a particular driver is

exceeded, the ecosystem may abruptly transition to a different stable state (Beisner et al.

2003). Essentially, there are multiple equilibria in which an ecological system can exist

(Beisner et al. 2003). The nonlinear response of an abrupt state shift follows a delay

between surpassing critical condition levels and the switch to an alternative stable state, a

time lag referred to as hysteresis, which makes state shifts appear stochastic (Scheffer et

al. 2001). Hysteresis creates challenges to management as it distorts the true thresholds

of stable states, further so by its natural variance from system to system. Differences in

hysteresis, even in similar ecosystems, result from differences in resilience (Scheffer et al. 2001).

Some community level impacts of eutrophication are well understood and expected. For example, the shift in stable state towards algal-dominated ecosystems as nutrient levels increase resulting in eutrophic ecosystems whose food webs are dominated by planktivorous fishes that benefit from increased zooplankton populations (McClelland and Valiela 1998, Jeppesen et al. 1997). However, the bottom-up effects of increased primary productivity, such as increased food sources for a large zooplankton population to support piscivorous fishes, occur concurrently with conflicting or synegistic trophic cascade impacts (Heath et al. 2014, Jeppesen et al. 1997). Multiple combined events make community level impacts difficult to predict, especially in singularity, but utilizing the ecosystem approach facilitates such research.

Ecosystem-level impacts of eutrophication are well-documented in the literature, and are known to affect ecosystem function (Belgrano et al. 2005). Patrício and Marques (2006) found that more eutrophic estuaries exhibited higher total biomass, consumption, production, exports, respiration, flows into detritus, system throughput, and net primary productivity. Additionally, higher ratios of total primary production to total respiration have been observed in eutrophic ecosystems (Patrício and Marques 2006). Total system throughput, an information theory metric, represents "the size of the entire system in terms of flow", making it useful for comparisons (Christensen et al. 2005, Odum 1985). Patrício and Marques (2006) also observed a higher omnivory index (OI) in a strongly eutrophic ecosystem. Christensen et al. (2005) define the OI as "the variance of the

trophic level of a consumer's prey groups;" omnivory is expected to decrease as specialization increases in maturing ecosystems.

It is expected that ecosystem resilience is impacted by agitations such as nutrient loading and the subsequent increased primary production, and once resilience is lowered even minute changes can result in an abrupt stable state shift (Scheffer et al. 2001, Scheffer and Carpenter 2003). If resilience is lowered, the ecosystem may outwardly appear unchanged prior to shifting, but is "brittle" and vulnerable to being pushed into an alternative stable state (Scheffer and Carpenter 2003).

1.1.2 Impacts of Invasive Species

Invasive species are considered a threat to both biodiversity and ecosystem function. At the community level, invasive fishes alter trophic structure through predation, competition for resources, and indirectly through trophic cascades (Tumolo and Flinn 2017, Cucherousset and Olden 2011). Invasive fish species impacts can range from behavioral adaptations in native fishes to food web structure alterations including extirpation of native species (Cucherousset and Olden 2011). Kaufman (1992) asserted that Nile Perch, an invasive fish introduced in Lake Victoria, was responsible for the most radical vertebrate extinction in recent history. There are however competing theories, and conflicting evidence regarding the impacts of invasive omnivores: omnivores can broadly influence trophic structure both directly and indirectly through their varied consumption, altering trophic linkages that result in changes to the trophic structure (Tumolo and Flinn 2017, Cucherousset and Olden 2011). Alternatively, omnivores can differ from a standard trophic cascade due to their varied, non-specialized

diet compared to a localized impact on a specific trophic level with predictable outcomes (Carvalho et al. 2016). The variety of omnivore behaviors makes the outcome of their introduction on the food web difficult to predict.

The definitive ecosystem-level impacts of invasive species are poorly understood in aquatic ecosystems, particularly those from mobile and omnivorous species (Tumolo and Flinn 2017). Consumption, competition, and other indirect effects can interrupt, transform, or even simplify the trophic structure and result in an ecosystem less resilient to further stressors or events (Tumolo and Flinn 2017). Invasive species introductions can compound with other anthropogenic impacts providing further management issues.

1.1.3 Evaluating community and ecosystem level impacts using the ecosystem approach

While community- and ecosystem-level responses to stress are often difficult to predict, utilization of trophic network models and their associated network metrics provides useful insight into these responses (Odum 1985). Trophic networks in their most basic definition quantify the predator-prey interactions in an ecosystem (Ulanowicz 2004). The creation of programs such as Ecopath with Ecosim (EwE) to represent ecosystems as trophic networks facilitates the quantification of predator-prey impacts and further ecological network analysis (ENA, Christensen et al. 2005). This approach represents the ecosystem as a trophic model, enabling the investigation of the extensive web of direct and indirect effects from perturbations to the ecosystem. Further, trophic models enable the clarification of individual impacts of simultaneous perturbations to an ecosystem. Additionally, ENA provides understanding of ecosystem function, providing context for future events and the strength of the ecosystem response to such events.

EwE enables the ecosystem approach by facilitating the recreation of an ecosystem, and further, allowing both evaluation and manipulation. When inputs are equal to outputs to maintain mass-balance, Ecopath simulates biomass pools and the energy flows between them based on trophic networks, and this gradually leads to a non-static equilibrium (Christensen and Walters 2004). Biomass pools represent the organisms in the ecosystem, either as single species or as multiple species pooled together (such as functional groups), determined by similar niches in terms of habitat or diet preferences (Christensen et al. 2005, Chea et al. 2016).

Ecopath models are parameterized based on the following inputs for each model group: Biomass (B) represents the initial biomass (in tonnes per square kilometer) of a population or functional group (Christensen and Walters 2004). This comes from the time period the model is based on for any given model, which becomes the baseline for the population, e.g. a year or the average of five years that represent a certain period well. The ratio of production to biomass (P/B) is the net growth in biomass of a population or functional group, or what is added in a year (Christensen and Walters 2004). The ratio of consumption to biomass (Q/B) represents the consumption per year divided by the total initial biomass of a population (Christensen and Walters 2004). Q/B gives an idea of the food base required to sustain a population relative to the size of the population itself (Christensen and Walters 2004). Diet contribution (DC) is the fraction of a particular prey item in the diet of a predator (Christensen and Walters 2004). In opportunistic feeding situations, DC is expected to simply be a function of the proportion of biomass of the

prey items in the foraging arena, but if a predator is selective, DC represents the importance of the prey item to the success of the predator.

Ecotrophic efficiency (EE) represents the percentage of yearly production consumed by the ecosystem, whether through predation or harvest from fishing (Christensen and Walters 2004). In an energy efficient ecosystem, most lower trophic level species are consumed by the ecosystem rather than dying from other factors such as disease and natural death. When other parameters are entered in EwE, EE is calculated by the model (Christensen and Walters 2004). Heymans et al (2016) outlines general rules for a balanced Ecopath model. Ecotrophic efficiency must always be less than one (Christensen et al. 2005), as values greater than one indicate that more than the biomass produced is being consumed by the ecosystem (Heymans et al. 2016). However, apex predators that are not preyed upon or harvested have an EE near zero, whereas lower trophic levels that are utilized by the ecosystem have EE closer to one (Heymans et al. 2016). EE values above one can indicate overconsumption (in DC), which can be confirmed by utilizing the Mortality coefficient matrix within EwE, which is an important resource for balancing a model (Christensen et al. 2005).

The input parameters are organized per functional group into the two master equations of EwE, the first describing mass balance, the second the energy flow (Christensen and Walters 2004). Once balanced, EwE trophic model outputs include the Mixed Trophic Impacts (MTI) feature, which identifies both the direct and indirect effects to the ecosystem of predator-prey relationships (Christensen et al. 2005). The MTI feature makes the indirect relationships within trophic networks more tangible, and

provides valuable insights into trophic changes that accompany ecological impacts such as eutrophication and the introduction of invasive species. Chea et al. (2016), Chen et al. (2015), Lobry et al. (2008), and Lin et al. (2007) utilize MTI to investigate the indirect effects, including trophic cascades of fisheries on large lakes, bays, and estuaries under other simultaneous anthropogenic impacts such as power plant and sewage effluent. Pannikar and Khan (2007) utilizes the feature in conjunction with EE values to compare the short-term effect on ecosystems before and after the implementation of fishery policies to introduce a closed season. Lercari and Bergamino (2011) uses MTI in conjunction with niche overlap analyses to untangle the effects of two invasive species in an estuarine and nearshore habitat. As opposed to these reactive approaches to the ecosystem approach, Ortiz et al. (2015) utilizes the MTI to perform a preliminary evaluation of the impacts that changes in major functional groups (e.g. simulating fishery pressures) have on the remainder of the food web. Out of these studies, some explicitly state that the study purpose is to inform fishery management and policy decisions (Chea et al. 2016, Pannikar and Khan 2007, Lobry et al. 2008, Ortiz et al. 2015, and Lin et al. 2007).

Aside from the ecological insight gained by modeling trophic networks, ecosystem properties and network analysis provide perspective for ecosystem status as a whole (Ulanowicz 2004). Ecosystem disturbances such as nutrient input, pollution, or stochastic events interrupt the expected patterns that an unaltered ecosystem follows through its maturation (Odum 1985). Responses to such stressors have been defined through observed patterns (Odum 1985). These observed patterns have been used to

create a system of ecological network analysis metrics that are useful in classifying

ecosystem function. For example, the ratio of respiration to biomass (R/B) increases as

the energy required to maintain the current state increases (Odum 1985). Therefore, the

energy used in the ecosystem increases (respiration), but the biomass remains the same

(no growth, Odum 1985). The ratio of production to respiration (P/R) is greater than or

less than one in a stressed ecosystem, whereas in an unaffected ecosystem P/R equals 1,

representing efficient use of the energy within an ecosystem (Odum 1985). Alterations in

both R/B and P/R represent a decrease in the efficiency of assimilation and often an

increase in unused primary production, which may be a symptom of eutrophication

(Odum 1985). Reduced food chain length (path lengths) is expected when R/B and P/R

indicate less efficient energy use.

Ecosystem properties are used in several studies to quantify ecosystem health in

terms of maturity as defined by Odum (1969, 1971) (Costanza and Mageau 1999, Chea et

al. 2016, Belgrano et al. 2005, Patricio and Marques 2006). Commonly, studies

characterize these ecosystems in the context of the metrics proposed by Odum (1969),

including the following: primary production/respiration ratio (TPP/TR), primary

production/biomass ratio (TPP/TB), ascendency/capacity (A/C or A%), Finn's cycling

index (FCI), system omnivory index (OI), and total system throughput (TST). The ratio

of TPP/TR characterizes the amount of primary production available to fuel the

respiration in the ecosystem, and Odum (1971) asserted that in mature, balanced

ecosystems this value approaches 1 as primary production is uniformly utilized by

ecosystem respiration. Odum (1971) additionally asserts that as systems mature, the

amount of primary production would gradually decrease relative to the biomass of the ecosystem as shown by TPP/TB.

Many studies initially characterize ecosystems and compare them in the context of similar ecosystems, such as a large lake ecosystem, bays, reservoirs, etc. (Chea et al. 2016, Chen et al. 2015, Lin et al. 2007). Other studies utilize these metrics to compare ecosystems at two different points in time, such as before and after fishing bans (Pannikar and Khan 2007). Ortiz et al. (2015) compared two adjacent bays experiencing different anthropogenic impacts to understand the difference in maturity and function. Lobry et al. (2008) conducted ENA on an estuarine ecosystem impacted by both fisheries and the influx of power plant industrial pumping, comparing metrics to less impacted estuaries to better understand the extent of anthropogenic impacts on ecosystem function and maturity.

Additionally, Constanza and Mageau (1999) propose the use of these metrics to classify ecosystems in terms of their vulnerability by creating a conceptual model from them. Costanza and Mageau (1999) assert overall health can be determined from three properties that comprehensively represent the ecosystem: vigor, organization, and resilience. Vigor is simply the primary production activity of an ecosystem, and can be represented by gross primary productivity (GPP, Costanza and Mageau 1999). It is hypothesized that there is a relationship between an ecosystem's vigor and its resilience, or ability to recover from disturbance to its stable state (Odum and Barrett 1971). If GPP represents vigor, high GPP indicates energy available for use to return to the previous state after a disturbance.

Organization is the number of utilized links between taxa in a trophic network, and the diversity of those linkages (Costanza and Mageau 1999). Therefore, organization is thought to increase with diversity. Since the diversity of links is considered, an ecosystem of generalists will have less specialized organization than an ecosystem with more specialized taxa feeding on few specific prey (Costanza and Mageau 1999). Organization can be represented using network ascendency, a metric developed by Ulanowicz (1986) that quantifies the potential pathways of energy flows in an ecosystem that are defined and utilized in trophic interactions; vigor is included in the calculation (Samson and Knopf 1996). Ascendency is typically scaled to the entire ecosystem capacity (C) for comparison between ecosystems, and is therefore displayed as A/C or A(%). As ecosystems mature through succession, earlier stages of development are associated with lower ascendency that increases as efficiency and total system throughput increase. However, the support for this pattern is inconsistent (Mageau et al. 1995).

Resilience is less directly quantified. (Holling 1986) defines resilience as "the magnitude of stress beyond which the system never recovers," or the ecosystem's ability to return to its stable state. Scheffer et al. (2001) defines it as the maximum threshold of agitations that an ecosystem can take before being abruptly shifted into an alternative stable state. Resilience can be quantified by measuring the time it takes for an ecosystem to return to a reference stable state after disturbance or stress (Costanza and Mageau 1999). The dynamic nature of shifts into an alternative stable state is often difficult to predict in terms of resilience (McClelland and Valiela 1998).

Costanza and Mageau (1999) establish two representative proxies for the quantification of resilience. The first is the gross primary production to respiration ratio (GPP/R), as excess GPP represents energy available to the ecosystem to recover from stressors (Costanza and Mageau 1999). The second proxy is the weighted systems overhead, another metric developed by Ulanowicz (1986). Overhead also represents excess resources that can be used to recover from stress, in the form of quantifying the redundancy of pathways of material and energy exchange discussed during the definition of ascendancy (Costanza and Mageau 1999). If there are redundant pathways, the ecosystem will be better able to "absorb stress" by utilizing redundant pathways, without loss of function (Mageau et al. 1995). Ulanowicz (2004) asserts that to be truly healthy, an ecosystem must have a balance of both ascendancy and overhead, representing efficiency and resilience in the form of stress response. Accordingly, resilience in this form is thought to be higher in immature ecosystems and declines as the ecosystems mature due to the increase in efficiency by the elimination of alternate pathways (Mageau et al. 1995). The tradeoffs between ascendancy and resilience at different stages of succession or maturity in an ecosystem are the rationale behind the argument of Costanza and Mageau (1999) in including both in their definition of ecosystem health. The two metrics of ascendancy and resilience in these terms allow for the quantification of changes in an ecosystem, making them particularly useful in the face of anthropogenic stressors (Mageau et al. 1995).

1.1.4 Case Study: Gunston Cove

Gunston Cove is a shallow freshwater tidal estuary, providing a large sediment surface to water column ratio, mixing potential, and relatively high residence time (over 1 year, Jones et al. 2008, Neilson and Cronin 2012). Historic accounts of Gunston Cove describe lush beds of submerged aquatic vegetation (SAV) that were lost in the 1930s after urbanization fueled nutrient loading that lead to eutrophication (Carter and Rybicki 1986, Donabaum et al. 2004, Jones et al. 2008). Surveys in 1980 found that SAV was absent in Gunston Cove, despite construction of the Noman M. Cole Jr. Pollution Control Plant in 1971 (Carter and Rybicki 1986, Jones et al. 2008, Cerco et al. 2013, Jones and de Mutsert 2013). Increases in human population density and altered land use are strongly associated with increased point and nonpoint source nutrient loading of nitrogen and phosphorus into watersheds (Smith 2003). The eutrophication of Gunston Cove led to a stable state shift from an SAV-dominated regime to one dominated by phytoplankton, a well-documented occurrence in shallow lakes (Jones 2020).

The upstream Noman Cole wastewater treatment plant (WWTP) facilitated dramatic reductions in point source nutrient loading, but phosphorus remained a concern due to residence time in Gunston Cove, known to be as long as a year (Jones et al. 2008, Cerco et al. 2013). In 2005, 20 years after nutrient load reduction began, the ecosystem abruptly transitioned from a phytoplankton-dominated regime to an SAV-dominated regime (Jones et al. 2008). Water quality, fish, and zooplankton sampling have monitored ecological effects of efforts to increase water quality, producing long-term data sets for Gunston Cove.

The wealth of data available from the long-term monitoring of Gunston Cove fauna and water quality changes in response to nutrient load reductions provide an opportunity to investigate the trophic network to evaluate ecosystem recovery and progression (Jones and de Mutsert 2013). Gunston Cove provides a novel case study of recovery from eutrophication by means of phosphorus reduction in wastewater treatment, which is known to have positive impacts on eutrophication recovery as discussed by Schindler (1981). Human population density growth is associated with eutrophication: increased loading of nitrogen and phosphorus to surface waters, resulting in increased biomass of algae and macrophytes (Smith 2003). Therefore, eutrophication is associated with increased turbidity from algae reaching nuisance levels (Rothenberger et al. 2009). Changes in the composition of primary producers are an implication of eutrophication; the reduction in light availability plays a role in stable state shifts from SAV- to phytoplankton-dominated regimes (Smith 2003, Rothenberger et al. 2009). The reversal of such extensive SAV losses, as observed in Gunston Cove, is rare (Burkholder et al. 2007). The return and expansion of SAV can create positive feedback loops into recovery, through physical and chemical mechanisms such as sediment retention and nutrient uptake (Jones 2020). Such mechanisms can contribute to reduced turbidity and increased water quality, further supporting the expansion of SAV. Changes in fauna composition are expected to accompany such changes in water quality and flora composition (De Mutsert et al. 2017, Jones 2020).

Although reductions in phytoplankton and increases in water clarity have occurred in Gunston Cove since 1989, evidence suggests that the second stable state shift

did not occur until 2005, when SAV drastically increased in surface area (Jones 2020).

Hysteresis in the state shift in Gunston Cove can be partially attributed to changes in

nutrient loadings, particularly phosphorus residing in the sediment (Søndergaard et al.

2003, Jones 2020). Søndergaard et al. (2003) determined that following the

eutrophication of shallow lakes, there is an increased likelihood of phosphorus pooling in

the sediment. The residence time of phosphorus in sediments will result in a delayed

stable state shift (Søndergaard et al. 2003). A similar trend is described in Gunston Cove,

as it shares several hydrological characteristics with shallow lakes, including a high

sediment surface to water column ratio and relatively high residence time (De Mutsert et

al. 2017, Neilson and Cronin 2012).

The 2005 alternative stable state shift in Gunston Cove was characterized by an

abrupt shift from phytoplankton to SAV-dominated regime (Jones 2020). Natural and

anthropogenic changes in factors, such as nutrient abundances in Gunston Cove, can

iteratively and interactively lower a given ecosystem's resilience, wherein the ecosystem

will undergo a large-scale shift to an alternative state (Scheffer et al. 2001). State shifts

observed in seagrass have been associated with direct and indirect mechanisms resulting

from nutrient enrichment, such as light availability and physiological nutrient dynamics

(Burkholder et al. 2007).

De Mutsert et al. (2017) determined that the resurgence of SAV in Gunston Cove

was correlated with a shift in the fish community. Shifts in fish communities can be

attributed to increased SAV, which can provide benefits such as increased spawning

habitat, increased macroinvertebrate food availability, or increased availability of

predation refuges (De Mutsert et al. 2017). In Gunston Cove, banded killifish (*Fundulus diaphanus*) and sunfishes (*Lepomis sp.*) have particularly benefitted from the transition to an SAV-dominated state, evidenced by increases in relative abundance (De Mutsert et al. 2017). White perch (*Morone americana*), which utilize open water habitats, have remained a common species present in Gunston Cove, but have decreased in biomass and displaced into reduced open water areas (De Mutsert et al. 2017).

Nearly 30 years after Blue Catfish was introduced as game fish in the James, Rappahannock, and York River System in 1974, a single Blue Catfish was observed in Gunston Cove in 2001 under George Mason's monitoring survey (Schloesser et al. 2011, Jones et al. 2018). Due to their omnivorous diet, high growth rate, and large size at maturity they successfully self-sustained populations in stocked rivers, and within 15 years have rapidly expanded and invaded additional Chesapeake Bay tributaries, such as the Potomac River (Schloesser et al. 2011). Observed numbers of individuals in Gunston Cove grew as they replaced native catfishes, but appear to have stabilized as of the most recent confirmed data from 2018 (Jones et al. 2019).

1.2 Study Overview

1.2.1 Chapter Two: Trophic Changes in a Freshwater Tidal Food Web After Water Quality Improvements and Invasive Species (Ictalurus furcatus) Introduction.

This study investigates the trophic impacts of two key events in Gunston Cove, a freshwater tidal embayment of the Potomac River in Virginia, USA: (1) A stable state shift from a phytoplankton-dominated regime to a submerged aquatic vegetation regime resulting from reduced nutrient input and recovery from hypereutrophication, and (2) the

introduction of the invasive predator Blue Catfish (*Ictalurus furcatus*). This study utilizes

the long-term fish, phytoplankton, and zooplankton monitoring data for Gunston Cove to

create mass-balanced trophic models using EwE representing the regimes before

(phytoplankton-dominated) and after (SAV-dominated) the stable state shift and invasive

species introduction in order to explore the trophic impacts and changes to ecosystem

maturity and function resulting from these events, as well as placing the recovery into the

context of existing similar case studies. These results contextualize the adaptive

management of Gunston Cove and also provide consideration for continuing ecosystem-

based management.

1.2.1.1 Study rationale

There are no currently published EwE models of freshwater tidal embayments,

and as such, these models represent the apparent first of their kind. The creation of two

models, representing snapshots in time, facilitates the comparison and evaluation of the

changes and impacts on ecosystem structure and function. The identification of trophic

impacts and ecosystem metrics in this ecosystem further provides useful information for

management of Gunston Cove. These evaluations facilitate the identification of key

species for management in the current, SAV-dominated ecosystem. Herein, the trophic

model of Gunston Cove in the current SAV-dominant state is referred to as the After

model; the model of Gunston Cove in the previous state, phytoplankton-dominant, is

referred to as the Before model. Since the After model represents the current state of

Gunston Cove, it acts as a baseline for adaptive management moving forward. The After

model act as an important baseline for the current stable state of Gunston Cove and

illustrate how the recent stable state shift and invasive species introduction impacts trophic relationships.

The changes to ecosystem health properties that I evaluate in this work are broadly applicable in characterizing the trends in ecosystem function and health in the wake of water quality improvement in Gunston Cove. This evaluation of the ecosystem in terms of ENA allows for a better understanding of net ecosystem impacts of two factors that have the potential to affect the food web in Gunston Cove between the two snapshots provided by these models: hypereutrophication recovery and invasive predator introduction.

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CHAPTER TWO: TROPHIC CHANGES IN A FRESHWATER TIDAL FOOD WEB AFTER WATER QUALITY IMPROVEMENTS AND INVASIVE SPECIES (ICTALURUS FURCATUS) INTRODUCTION

2.1 Introduction

Aquatic ecosystems face increasing pressure as urbanization of the watershed continues, as does natural resource and service exploitation, resulting in a wide scale of changes up to the ecosystem level (McLusky and Elliot 2004, Halpern et al. 2008). Estuarine habitats are relatively more complex and interconnected than other aquatic ecosystems, making influences far-reaching, difficult to predict, and difficult to manage (Dudgeon et al. 2006). Estuarine stressors include overexploitation, water pollution, habitat degradation and destruction and nonnative species invasions that can originate locally, from the greater watershed, or downstream (Dudgeon et al. 2006). The consequences of anthropogenic pressures and stressors include community level changes, such as those to the food web structure and energy flows, as well as those at the ecosystem level including changes to ecosystem cycles and pathways (McLusky and Elliot 2004, Crooks 2002).

2.2 Background

Gunston Cove is a freshwater tidal estuarine embayment of the Potomac River, situated in the Washington, D.C. metropolitan area. Urbanization resulted in hypereutrophication and consequential loss of submerged aquatic vegetation (SAV) to

algal blooms as far back as the 1930s, suggesting the cove entered a new phytoplankton-dominated stable state around that time (Carter and Rybicki 1986, Donabaum et al. 2004, Jones et al. 2008, De Mutsert et al. 2017). Improved wastewater treatment policies were implemented in the 1980s to reduce phosphorus and nitrogen load in an effort to manage algal blooms and encourage SAV resurgence, which occurred abruptly in 2005 as a a second stable state shift (Jones 2020). Additionally, the Chesapeake Bay invasive Blue Catfish (*Ictalurus furcatus*) was identified in Gunston Cove in 2001 and has since appeared to replace native catfishes (Jones et al. 2019). Water quality, fish, and zooplankton monitoring accompanied policies to improve water quality, providing long-term data sets for Gunston Cove; the wealth of data available from monitoring in response to ecosystem-based water quality restoration provided an opportunity to investigate the trophic network to evaluate ecosystem recovery and progression in tandem with invasive species introduction (Jones and de Mutsert 2013). This work investigates the impacts to the trophic structure of Gunston Cove resulting from changes to water quality and invasive species introduction.

2.3 Study objectives

With this project, I aim to investigate the impacts of the 2005 stable state shift and invasive species introduction on trophic relationships and ecosystem function in Gunston Cove. My objectives are: (1) investigate the shift in trophic structure accompanying the stable state shift and invasive species introduction, and (2) evaluate the maturity and ecosystem function of Gunston Cove accompanying these two events. I hypothesize that the trophic impact of the before model is different from the trophic impact of the after

models (De Mutsert et al. 2017, Jones 2020), and differences in the ecosystem metrics reflect a recovery from hypereutrophication including increased ecosystem maturity.

2.4 Materials and Methods

Two mass-balanced trophic models representing Gunston Cove, a freshwater tidal embayment before and after a stable state shift and the introduction of an invasive predator, the Blue Catfish are created using Ecopath with Ecosim (EwE) software (Christensen et al. 2005). The EwE package has been developed to create balanced models of ecosystems for the purpose of investigating trophic interactions and flows of biomass and energy within the ecosystem (Christensen and Pauly 1992). For both models I utilize George Mason University's Potomac Environmental Research and Education Center long-term fish, zooplankton, and phytoplankton survey data to calculate biomasses and construct each trophic model. The Before model, representing a phytoplankton-dominated regime, utilizes survey data from Gunston Cove from the years preceding the stable state shift that occurred in 2005 and the invasion of Blue Catfish. This model is created using data from the years 1990-1994. The After model, representing the SAV-dominated regime, utilizes survey data from the years 2013-2017, collected after the stable state shift and Blue Catfish invasion. This allows for the exploration of differences in food web structure between two regimes representing different stable states and an invasion event. The two described Ecopath models are used to compare trophic structure impacts from the stable state shift and invasive species occurrences using MTI, and compare ecosystem function using ENA.

2.4.1 Study Site - Gunston Cove

Gunston Cove (Fig. 1) is a freshwater tidal embayment and tributary of the mainstem of

the Potomac River in Fairfax County, Virginia. It receives freshwater inflow from Pohick

and Accotink creeks, draining southern Fairfax County (Jones et al. 2008). Aside from

two channels (depth <5 m) the embayment is flat-bottomed and ranges 1.5-2 m in depth,

allowing for mixing (Jones et al. 2008). It is within the upper reaches of tidal influence

from the Chesapeake Bay with a tidal range average of 0.6 m (Jones et al. 2008). The

embayment is approximately 19 km south of Washington, D.C, therefore inflow comes

from within the Washington, D.C. metropolitan area (Jones et al. 2008). The watershed,

which is greater than 22,000 ha, is dominated by suburban development, with an average

population density of 10.68/ha in Fairfax County in 2015 (Jones et al., 2008, Fairfax

County, 2015). Water residence times in the tidal freshwater portions of the Potomac

River have been observed as long as a year under low flow conditions (Cerco et al. 2013).

Improved nutrient removal from treated wastewater effluent led to a hysteretic stable

state shift in Gunston Cove in 2005, and the ecosystem became once again SAV-

dominated (Jones 2020). The urbanized watershed implies the influence of nonpoint

source pollution (Smith 2003, Jones et al. 2008).

George Mason University has conducted fish, plankton, and water quality surveys

of Gunston Cove since 1984. Surveys are conducted semimonthly from April through

September. Fish surveys include three shore seines for littoral species, two stationary

fyke nets for vegetation-associated species, and two otter trawls for open water species

(Fig. 1). The trawl site in the main stem of the Potomac River falls outside of Gunston

Cove, and as such I did not include those data in these models (Fig. 1). Collected fishes are identified to species whenever possible and measured in standard length to nearest mm. Zooplankton samples are returned to R.C. Jones' Water Quality lab at the Potomac Environmental Research and Education Center (PEREC) and identified to genus (or closest taxonomic level possible) and converted to number per liter (microzooplankton) or per cubic meter (macrozooplankton).
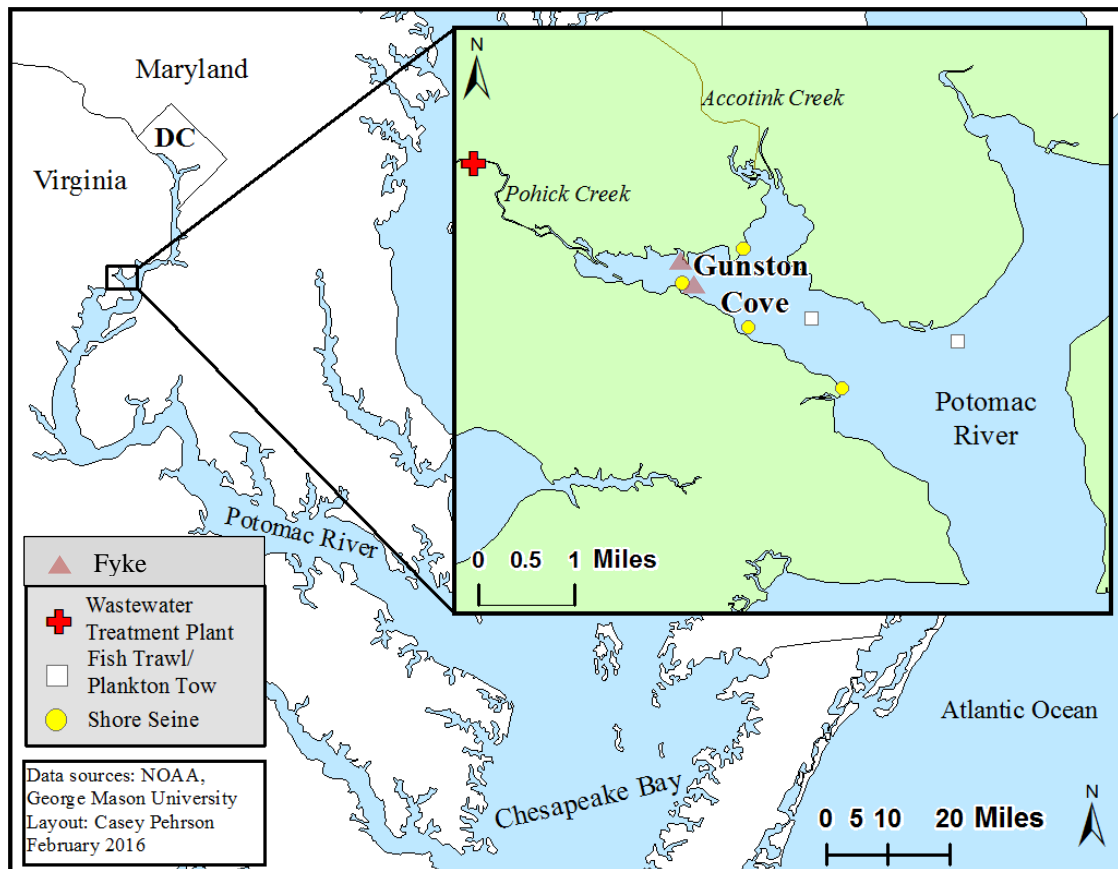
Figure 1 Map: Study site, Gunston Cove, on the Potomac River in Virginia, USA. Sample sites are identified as per legend. Fish Trawl and Plankton Tow within mainstem of the Potomac River data were excluded from models.

2.4.2. Ecopath Model Parameterization

Christensen et al. (2005) advise to group species with similar physical characteristics (growth, etc.) and diet preferences. This strategy is also useful when parameters are unavailable for each individual species in the model (Christensen et al. 2005). Species are aggregated into functional groups or kept as individual species for species of interest (e.g. associated with SAV, or most abundant species) (Tables 1 and 2).

Table 1. Model groups in the 'Before' model.

No.	Model Group Name	Scientific Name	Common Name
1	Channel nativecat	*Ictalurus punctatus*	Channel Catfish
2	bass	*Micropterus salmoides*	Largemouth Bass
		Pomoxis nigromaculatus	Black Crappie
3	smallmouthbass	*Micropterus dolomieu*	Smallmouth Bass
4	yellowperch	*Perca flavescens*	Yellow Perch
5	americaneel	*Anguilla rostrata*	American Eel
6	whiteperch	*Morone americana*	White Perch
7	*Ameiurus* nativecat	*Ameiurus catus*	White Bullhead
		Ameiurus nebulosus	Brown Bullhead
8	carp	*Cyprinus carpio*	Carp
9	croaker	*Micropogonias undulatus*	Atlantic Croaker
		Leiostomus xanthurus	Spot
10	hogchoker	*Trinectes maculatus*	Hogchoker
11	herringorshad	*Alosa mediocris*	Hickory Shad
		Alosa sapidissima	American Shad
		Alosa species	unk. Alosa species
		Brevoortia tyrannus	Atlantic Menhaden

No.	Model Group Name	Scientific Name	Common Name
		Dorosoma cepedianum	Gizzard Shad
12	riverherring	*Alosa aestivalis*	Blueback Herring
		Alosa pseudoharengus	Alewife
13	mosquitofish	*Gambusia holbrooki*	Mosquitofish
14	killifish	*Fundulus heteroclitus*	Mummichog
		Fundulus diaphanus	Banded Killifish
15	sucker	*Catostomus commersonii*	White Sucker
		Erimyzon oblongus	Creek Chubsucker
16	sunfish	*Enneacanthus gloriosus*	Bluespotted Sunfish
		Lepomis auritus	Redbreast Sunfish
		Lepomis cyanellus	Green Sunfish
		Lepomis gibbosus	Pumpkinseed
		Lepomis macrochirus	Bluegill
		Lepomis microlophus	Redear Sunfish
		Lepomis species	unk. sunfish
17	smallforagefish	*Anchoa mitchilli*	Bay anchovy
		Menidia beryllina	Inland Silverside
18	darter	*Etheostoma olmstedi*	Tessellated Darter
19	minnow	*Cyprinella analostana*	Satinfin Shiner
		Hybognathus regius	Eastern Silvery Minnow
		Notemigonus crysoleucas	Golden Shiner
		Notropis hudsonius	Spottail Shiner
20	goldfish	*Carassius auratus*	Goldfish
21	zoobenthos	All	
22	macrozooplankton	All	Copepods and Cladocerans (except Bosmina)
23	microzooplankton	All	Bosmina, all nauplii, Rotifers
24	SAV and benthic algae	All	
25	phytoplankton	All	
26	detritus	-	-

Table 2. Model groups in the 'After' model.

No.	Model Group Name	Scientific Name	Common Name
1	**invasivebluecat***	*Ictalurus furcatus*	Blue Catfish
2	Channel nativecat	*Ictalurus punctatus*	Channel Catfish
3	bass	*Micropterus salmoides*	Largemouth Bass
		Pomoxis nigromaculatus	Black Crappie
4	smallmouthbass	*Micropterus dolomieu*	Smallmouth Bass
5	yellowperch	*Perca flavescens*	Yellow Perch
6	americaneel	*Anguilla rostrata*	American Eel
7	whiteperch	*Morone americana*	White Perch
8	*Ameiurus* nativecat	*Ameiurus catus*	White Bullhead
		Ameiurus nebulosus	Brown Bullhead
9	**atlanticneedlefish***	*Strongylura marina*	Atlantic Needlefish
10	carp	*Cyprinus carpio*	Carp
11	croaker	*Micropogonias undulatus*	Atlantic Croaker
		Leiostomus xanthurus	Spot
12	hogchoker	*Trinectes maculatus*	Hogchoker
13	herringorshad	*Alosa mediocris*	Hickory Shad
		Alosa sapidissima	American Shad
		Alosa species	unk. Alosa species
		Brevoortia tyrannus	Atlantic Menhaden
		Dorosoma cepedianum	Gizzard Shad
14	riverherring	*Alosa aestivalis*	Blueback Herring
		Alosa pseudoharengus	Alewife
15	mosquitofish	*Gambusia holbrooki*	Mosquitofish
16	killifish	*Fundulus heteroclitus*	Mummichog
		Fundulus diaphanus	Banded Killifish
17	sucker	*Catostomus commersonii*	White Sucker
		Erimyzon oblongus	Creek Chubsucker
18	sunfish	*Enneacanthus gloriosus*	Bluespotted Sunfish
		Lepomis auritus	Redbreast Sunfish
		Lepomis cyanellus	Green Sunfish
		Lepomis gibbosus	Pumpkinseed
		Lepomis macrochirus	Bluegill
		Lepomis microlophus	Redear Sunfish
		Lepomis species	unk. sunfish

No.	Model Group Name	Scientific Name	Common Name
19	**quillback***	*Carpiodes cyprinus*	Quillback
20	smallforagefish	*Anchoa mitchilli*	Bay anchovy
		Menidia beryllina	Inland Silverside
21	darter	*Etheostoma olmstedi*	Tessellated Darter
22	minnow	*Cyprinella analostana*	Satinfin Shiner
		Hybognathus regius	Eastern Silvery Minnow
		Notemigonus crysoleucas	Golden Shiner
		Notropis hudsonius	Spottail Shiner
23	goldfish	*Carassius auratus*	Goldfish
24	zoobenthos	All	
25	macrozooplankton	All	Copepods and Cladocerans (except Bosmina)
26	microzooplankton	All	Bosmina, all nauplii, Rotifers
27	SAV	All	
28	phytoplankton	All	
29	detritus	-	-

*Bolded groups do not appear in the 'Before' model.

Biomass (B) values for each model group are calculated using long-term survey data collected by PEREC for fishes, phytoplankton, and zooplankton. All data must converted to biomass in grams per square meter to be included in the model. Fishes collected are identified and measured for SL in mm, therefore I use length-weight relationships gathered from the literature (per species where possible, if not, per genus) to calculate estimated weight per individual. Fish biomasses (g/m^2) are calculated by summing the total weight per species of collected fishes divided by the sum area swept of

all trips per year. I then take the average of the five years that the models represent (1990-1994 and 2013-2017 respectively).

Biomass of SAV is extrapolated from aerial imaging data collected by the United States Geological Survey in collaboration with the Virginia Institute of Marine Science. The SAV aerial imaging data categorizes vegetation patches into 4 buckets of percentage SAV coverage, and I accordingly scale the wet weight of 1064.8 g/m_2 that I extrapolated from dry weights in Burton et al.'s (1979) study to these density categories. I divide the sum weight of all SAV by the total area (m_2) of Gunston Cove for each year included in the given model, and the average of all years in the model (1990-1994 for the "Before" model and 2013-2017 for the "After" model) is used as final SAV biomass in grams per square meter. The zooplankton data are recorded in density: individuals per liter (microzooplankton) or per cubic meter (macrozooplankton). I use representative weights for each family of zooplankton from the literature to calculate biomass (g/m_2) using multiplication, and take the average biomass over all trips included in each model. I convert chlorophyll a values to biomass (g/m_2) using the assumption that chlorophyll a makes up an average of 0.88% of phytoplankton wet weight (Löffler 2012). Zoobenthos biomass data are not available, and are therefore estimated by EwE assuming an ecotrophic efficiency of 0.9, similar to what is seen in the literature (Chea et al. 2016, Chen et al. 2015). Parameter values for production to biomass ratio (P/B) and consumption to biomass ratio (Q/B) were gathered through a literature search with emphasis on proximity to local site and similar ecosystems.

2.4.2.1 Diet composition

Diet matrices summarize the proportion each prey group makes up in a predator's diet and explain the relationships between all groups. To construct a diet matrix of diet composition data, the most abundant species in Gunston Cove were selected and a diet study based on stomach content analysis and DNA barcoding was included in this study. Remaining supplemental diet composition information was obtained from literature searches, with emphasis on comparable or local study sites. Common species in Gunston Cove were collected in late summer of 2016 to provide local diet information required to build Ecopath models. Selected species included White Perch, Banded Killifish, Pumpkinseed, Bluegill, and Blue Catfish. A total of 111 specimens were collected and identified, and labeled with species, standard length (mm), collection site, date, and gear type (Table 3). Collection methods included seining the littoral zone, pulling open water trawls, and setting fyke nets within the submerged aquatic vegetation of Gunston Cove.

Fish were humanely euthanized by anesthetic overdose of tricaine methanesulfanate (MS-222) as per IACUC protocol # 0351, and then stored on ice until dissection upon arrival in the laboratory. Stomachs were removed by opening the coelom and severing the esophagus and intestine, then removing intact stomach (Murphy and Willis 1996). Stomach and label were then transferred into individual petri dishes and kept at -80°C until contents were identified.

For content identification, workspace and all tools were sanitized with a 10% household bleach solution. Stomachs were thawed one at a time immediately prior to content identification. Stomachs were weighed to the nearest tenth of a gram, then contents were washed out with chilled deionized (DI) water, and the empty stomach was

weighed. Under a dissecting scope, stomach contents were sorted to remove identifiable

pieces that were classified to the lowest taxonomic level (Murphy and Willis 1996,

D'Aguillo et al. 2014).

Contents were ranked according to the method described by Lima-Junior and

Goitein (2001). The weight of entire contents was used to calculate a standard weight,

and stomachs with comparable weights were assigned four points, to be divided

proportionally among contents (Lima-Junior and Goitein 2001). Stomachs that were

twice the standard weight received eight points, those that were half received two points

(Lima-Junior and Goitein 2001). This allows for comparison between stomachs of

different weights (Lima-Junior and Goitein 2001). This method proved useful in

developing relative quantification of visually identifiable prey items. Unfortunately, in

many cases stomach contents are moderately to highly digested, often leaving them

unidentifiable. In these cases, DNA barcoding was used to identify (but not quantify)

prey items as it has become an excellent supplemental tool in diet studies (Moran et al.

2016). For contents to be analyzed with DNA barcoding, unidentifiable stomach contents

were individually sorted into sterile well plates. DNA extraction, amplification, and

sequencing were carried out at the Smithsonian Environmental Research Center.

Stomach content data were used to construct diet composition (DC) matrices in

both the Before and After Ecopath models. Since SAV was absent under the

phytoplankton-dominated regime in the Before model, fish sampled from open water

areas (Table 3) were used as a proxy for that model. Fish sampled from SAV (Table 3)

were used in the After Ecopath model. The diets of fish sampled in littoral areas (Table 3)

were used in both models due to their sampling nature; seining is not carried out in heavily vegetated areas. Therefore, while sampling was done in 2016, under the SAV regime, the diet data used were selected to be as representative of the phytoplankton regime as possible.

Table 3. Samples collected for diet determination of selected species.

Species	No. Caught in Littoral Zone	No. Caught in Open water	No. Caught in SAV	Grand Total Caught
Banded Killifish	24			24
Blue Catfish		11		11
Bluegill	1	15	4	20
Pumpkinseed	2	10	15	27
Redear	2			2

The remaining diet contribution information was gathered through literature searches with emphasis on geographic and ecological similarities (Blumenshine 1992, Lohr 1992, Jearld and Brown 1971, Kline and Wood 1996, Saylor et al. 2012, Clady 1974, Facey and Labar 1981, Couture and Watzin 2008, Manooch 1973, Talde et al. 2004, Blanco et al. 2004, Johnson and Dropkin 1993, Huckins 1997, Mittelbach et al. 1992, García-Berthou and Moreno-Amich 2000, Christensen 2009, Layzer and Reed 1978, Schloesser et al. 2011, Parker 1987, Morgan and Beatty 2007, Carr and Adams 1973).

2.4.3 Model Balancing

The model balancing approach is initiated with attention to model groups with the highest ecotrophic efficiencies (EEs). The most reliable data, which are biomasses derived from samples collected in a long-term data set for the study site, are unaltered when making model adjustments during the balancing process, which begins with iterative changes to diet compositions, a lower confidence parameter. The small sample size for the selected species (see *2.4.2.1 Diet determination of selected species*) reduces the reliability of these data. Diet data were gathered in large part via literature search, making it less reliable than biomasses gathered at the study site.

Ecotrophic efficiencies above 1 indicate insufficient production to meet the demands of a group as a prey item, and in this case further literature research is carried out and diets are iteratively adjusted accordingly within the range of reported plausible diet choices. When this did not sufficiently reduce the EE values, the P/B and Q/B ratios are reevaluated and adjustments were made per further literature review. During iterative changes, the reevaluation of Q/B are compared to production to biomass ratios to ensure ecological validity, referencing Christensen and Pauly's (1993) work and comparing to a general rule of thumb of 1:3 for (P/B):(Q/B) (expert opinion, Dr. Kristy Lewis).

2.4.4 Evaluation of Model Outputs

2.4.4.1 Trophic impacts

Exploring changes in trophic structure provides insight into changes that accompanied the altering events in Gunston Cove. This is done using the Network Analysis plugin in EwE (Christensen et al. 2005). Changes are investigated using the Mixed Trophic Impact (MTI) analysis to understand the relative impacts of functional

groups on each other, either positive or negative (Christensen et al. 2005). MTI plots a

grid of predators (impacting group) on the y-axis against prey (impacted group) on the x-

axis. The grid box where two groups intersect is filled from a gradient of strong negative

impacts (dark red) to strong positive impacts (dark blue), representing the impacting

predator group's trophic impacts on the impacted prey group. In addition to direct

impacts such as predator-prey interactions, MTI analyses illustrate indirect interactions

such as competition or trophic cascades that may be unexpected (Christensen et al. 2005).

For example, a predator with a strong selectivity for a prey group would likely be

represented with dark red, and this same trophic interaction could indirectly positively

impact the prey's competitor, and the predator's trophic interaction with said competitor

would be a variant of blue. Comparison of MTI plots for both the algal (Before) and SAV

(After) dominated ecosystems allows for the description of changes in trophic dynamics

that accompanied the stable state shift and invasion of Blue Catfish.

2.4.4.2 Ecosystem metrics and network analysis
Overall ecosystem function changes between the two states are also examined

using Ecological Network Analysis (ENA) with the Network Analysis plugin in EwE

(Christensen et al. 2005). These metrics evaluate model ascendency, throughput (both

TST and in terms of consumption, respiration, export, and flows to detritus), total

pathways (representing all potential paths of energy implied by the food web), Finn's

cycling index (FCI) and mean path length (FMPL), and trophic aggregation. The outputs

of Finn's cycling index are evaluated to understand cycling within the ecosystem, and

Finn's mean path length is reviewed for indication of a stressed ecosystem with a

shortened food chain (Christensen et al. 2005, Chea et al. 2016). To compare the

efficiency of biomass assimilation and respiration between the two ecosystems, ratios of

total primary production to respiration (TPP/TR) as well as of respiration to total biomass

(TR/TB) from EwE are examined (Odum 1985, Heymans et al. 2016). These ratios

indicate the energy necessary to maintain the current ecosystem state, and can reflect an

ecosystem under stress when excess respiration is occurring to maintain the same

biomass (Odum 1985, Heymans et al. 2016).

Additionally, properties of vigor, organization, and resilience are compared to

ascertain approximate health of each ecosystem within the conceptual model developed

by Costanza and Mageau (1999). Total net primary productivity (TNPP) is used as a

proxy for vigor to estimate the energy available

to the ecosystem (Costanza and Mageau 1999).

When the surplus of vigor is estimated using the

total primary productivity to respiration

(TPP/TR) ratio, resilience is quantified

(Costanza and Mageau 1999). Finally,

organization is estimated using ascendancy
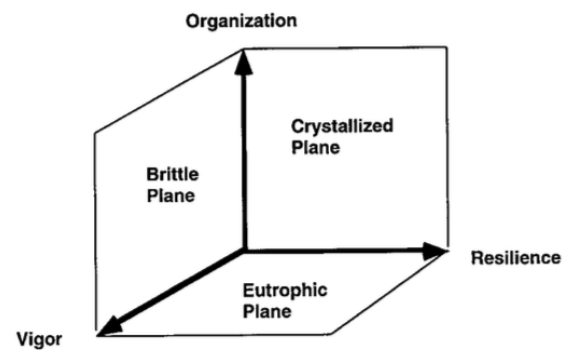
Figure 2. The three components of ecosystem health and their relationship as proposed by Costanza & Mageau (1999).

values from EwE to quantify the diversity and utilization of links within the trophic

network (Costanza and Mageau 1999, Patrício et al. 2006). In addition to comparisons of

those properties individually between the models, each ecosystem is plotted as in

Costanza and Mageau (1999) using vigor, organization, and resilience as x, y, and z axes,

respectively (Fig. 2). Theoretically healthy ecosystems are balanced in vigor,

organization, and resilience, those that are not fall into a plane characterized by function

problems including being brittle, crystallized, or eutrophic (Fig. 2; Costanza and Mageau 1999). Eutrophic ecosystems are driven by vigor and resilience but have insufficient organization (Costanza and Mageau 1999). Crystallized ecosystems are characterized by relatively higher organization and resilience, but with insufficient vigor whereas brittle ecosystems have relatively higher vigor and organization, but insufficient resilience (Costanza and Mageau 1999). Characterizing ecosystems in this context allows for a conceptual comparison between the two trophic states represented by Before and After models and other studied estuaries, and highlights any imbalances between the three metrics for vigor (TNPP), resilience (TPP/TR), and organization (A/C).

2.5 Results

A balanced EwE model has been created for each stable state which visualizes the biomass of and flows between model groups and their calculated trophic levels (Fig. 3 and 4). The Before model flow diagram shows Channel Catfish at the highest trophic level, above TL4. Bass were also above TL4 in the Before Model (Fig. 3). The remaining model groups of fishes in the Before Model were at or between TL3 and TL4, except Carp, sucker, and minnow, which were between TL2 and TL3 (Fig. 3).

The After model flow diagram shows the decrease in Channel Catfish biomass compared to Blue Catfish biomass (Fig. 4). Channel Catfish are above TL4, at a higher trophic level than Blue Catfish, which are closer in trophic level to bass and Yellow Perch (Fig. 4). Below Channel Catfish, remaining fish model groups were between TL3 and TL4, except Carp, sucker, minnow, and Quillback (Fig. 4).
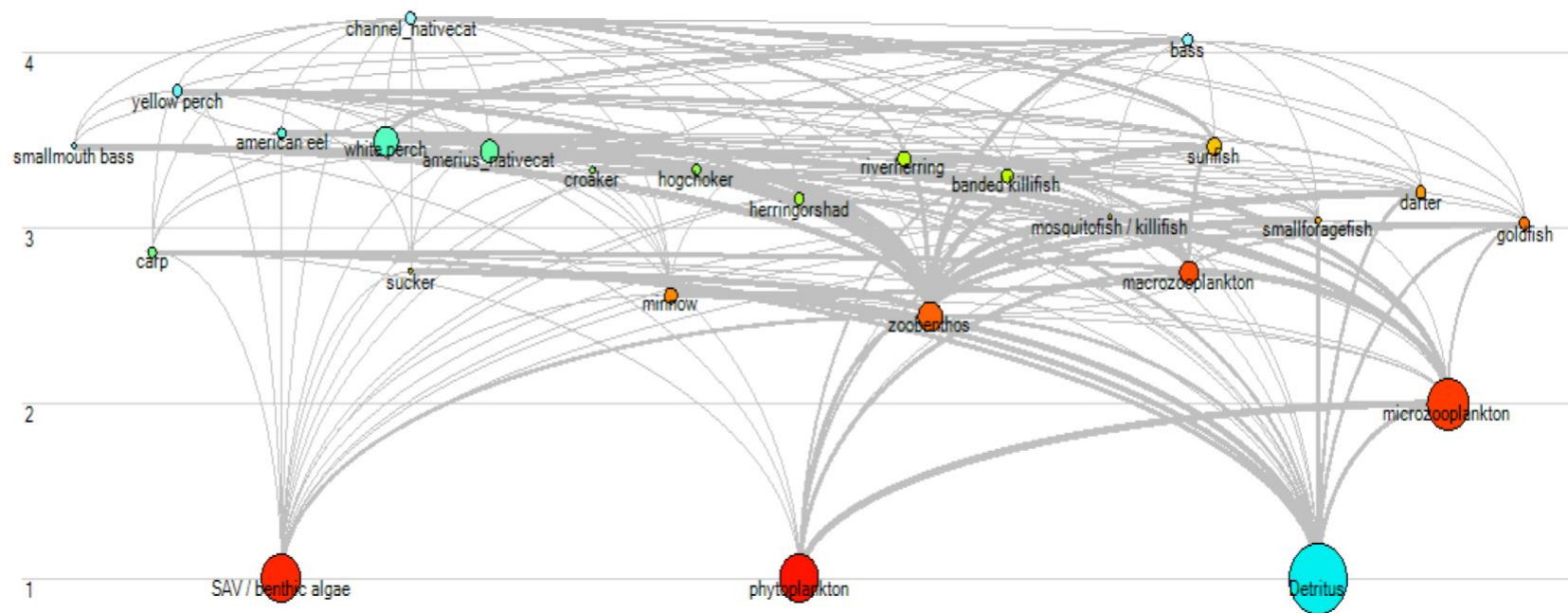
Figure 3. Ecopath flow diagram, Before model. Nodes represent relative biomass (scaled to square root). Lines represent biomass flow through predator-prey interactions. Y axis represents trophic level.
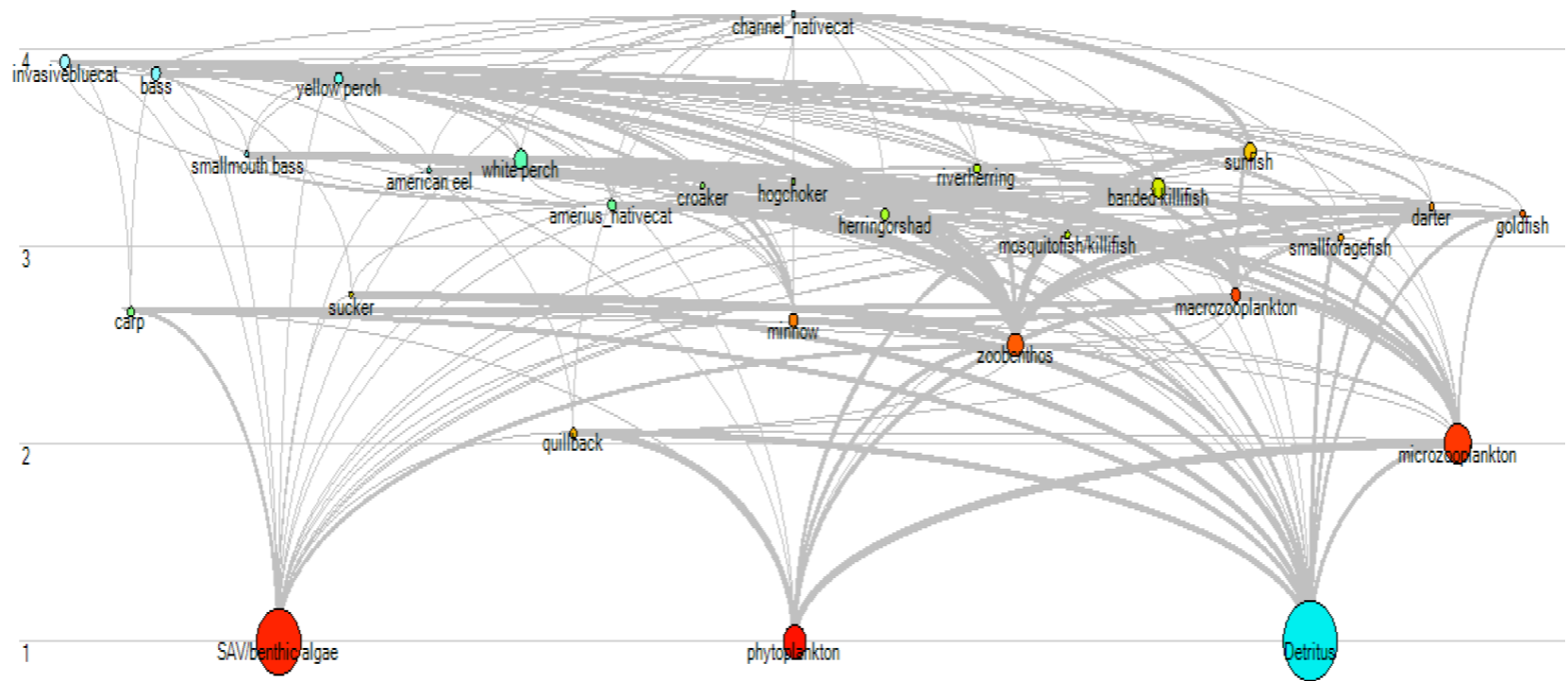
Figure 4. Ecopath flow diagram, After model. Nodes represent relative biomass (scaled to square root). Y axis represents trophic level. Lines represent biomass flow through predator-prey interactions.

2.5.1 Basic Estimates

        The final basic inputs of the balanced models include biomass, P/B, and Q/B (Tables 4 and 5). The basic inputs in addition to DC (see Appendix) allow EwE to calculate estimates of EE and P/Q (Tables 4 and 5). The composition of catfish notably changes with the introduction of Blue Catfish in the After model and biomass decreases in Channel Catfish and *Ameiurus* catfishes (Table 5). The biomass of bass, Smallmouth Bass, and Banded Killifish model groups has increased quite markedly in the After model, while the biomass of White Perch and river herring notably decreased. In lower trophic levels, the biomass of phytoplankton, microzooplankton, and macrozooplankton decrease in the After model by nearly half.

Table 4. Basic estimates, Before model. Biomass estimates were based on local collections from years 1990-1994, sources of production to biomass (P/B) ratios and consumption to biomass (Q/B) ratios are provided in the footnotes, italicized numbers were calculated by the model. Production to consumption (P/Q) ratios were calculated with the provided P/B and Q/B values.

No.	Group	Biomass (g/m2)	P/B	Q/B	EE	P/Q
1	Channel_Nativecat	0.0233	0.173[a]	3.466[e]	*0.005*	*0.05*
2	Bass	0.0236	0.39[b]	6.2[e]	*0.137*	*0.063*
3	Smallmouth Bass	0.0001	0.33[b]	3[e]	*0.479*	*0.11*
4	Yellow Perch	0.0229	0.53[b]	2.79[e]	*0.507*	*0.19*
5	American Eel	0.0208	0.31[b]	2.9[e]	*0.786*	*0.107*
6	White Perch	1.011	0.32[b]	4.2[d]	*0.536*	*0.076*
7	Ameiurus_Nativecat	0.344	0.468[b]	3.507[e]	*0.165*	*0.133*
8	Carp	0.0166	1.97[c]	8.3[c]	*0.315*	*0.237*
9	Croaker	0.00404	0.958[d]	5.6[d]	*0.939*	*0.171*
10	Hogchoker	0.018	0.46[d]	4.9[d]	*0.531*	*0.094*
11	Herring or Shad	0.0365	0.677[b]	8.6[d]	*0.75*	*0.079*
12	River Herring	0.0707	0.75[d]	9.4[d]	*0.604*	*0.08*
13	Banded Killifish	0.0401	0.802[d]	4.007[d]	*0.97*	*0.2*
14	Mosquitofish/Killifish	0.00094	0.802[e]	3.999[e]	*0.964*	*0.201*
15	Sucker	0.00079	0.715[b]	3.532[e]	*0.823*	*0.202*
16	Sunfish	0.119	0.703[f]	3.48[f]	*0.689*	*0.202*
17	Small Forage Fish	0.00437	1.75[g]	7.45[d]	*0.813*	*0.235*
18	Darter	0.0255	2.22[b]	3.487[e]	*0.886*	*0.637*
19	Minnow	0.0621	2[h]	3.487[h]	*0.767*	*0.574*
20	Goldfish	0.0322	1.06e	14.2[e]	*0.802*	*0.075*
21	Zoobenthos	*1.039*	5.939[j]	9.716[i]	0.9	*0.611*
22	Macrozooplankton	0.334	25[d]	83.33[d]	*0.338*	*0.3*
23	Microzooplankton	7.982	38[d]	138[d]	*0.076*	*0.275*
24	SAV_Benthic Algae	5.86	5.11[d]	-	*0.071*	-
25	Phytoplankton	5.898	245[d]	-	*0.54*	-
26	Detritus	30	-	-	*0.275*	-

[a]Colvin et al. 2015, [b]Randall and Minns 2000, [c]Ruddle and Christensen 1993, [d]Christensen 2009, [e]*FishBase estimate*, [f]De Mutsert et al. 2012, [g]Peterson et al. 2003, [h]Rogers and Allen 2011, [i]Kinter 2010

Table 5. Basic estimates, After model. Biomass estimates were based on local collections from years 2013-2017, sources of production to biomass (P/B) ratios and consumption to biomass (Q/B) ratios are provided in the footnotes, italicized numbers were calculated by the model. Production to consumption (P/Q) ratios were calculated with the provided P/B and Q/B values.

No.	Group	Biomass (t/km^2)	P/B	Q/B	EE	P/Q
1	Blue Catfish	0.0565	0.199[a, k]	3.489[f, i]	0.442	0.057
2	Channel_Nativecat	0.00085	0.173[b]	3.466[d]	0.643	0.05
3	Bass	0.0679	0.39[c]	6.2[d]	0.439	0.063
4	Smallmouth Bass	0.00051	0.33[c]	3[d]	*0.681*	*0.11*
5	Yellow Perch	0.0342	0.53[c]	2.79[d]	*0.403*	*0.19*
6	American Eel	6.8E-05	0.31[c]	2.9[d]	*0.472*	*0.107*
7	White Perch	0.244	0.32[c]	4.2[f]	*0.595*	*0.076*
8	Ameiurus_Nativecat	0.0296	0.468[c]	3.507[d]	*0.453*	*0.133*
9	Carp	0.0138	1.97[d]	8.3[e]	*0.366*	*0.237*
10	Croaker	0.00017	0.958[e]	5.6[f]	*0.822*	*0.171*
11	Hogchoker	7.5E-05	0.46[f]	4.9[f]	*0.741*	*0.094*
12	Herring or Shad	0.0359	0.677[c]	8.6[f]	*0.714*	*0.079*
13	River Herring	0.0217	0.75[f]	9.4[f]	*0.934*	*0.08*
14	Mosquitofish/Killifish	0.00614	0.802[d]	3.999[d]	*0.733*	*0.201*
15	Banded Killifish	0.24	0.802[f]	3.999[f]	*0.643*	*0.201*
16	Sucker	0.00016	0.715[c]	3.532[f]	*0.69*	*0.202*
17	Sunfish	0.175	0.703[g]	3.48[g]	*0.645*	*0.202*
18	Quillback	0.0119	0.17[c]	8.4[d]	*0.79*	*0.02*
19	Small Forage Fish	0.00702	1.75[h]	7.45[f]	*0.79*	*0.235*
20	Darter	0.00575	2.22[c]	3.487[d]	*0.95*	*0.637*
21	Minnow	0.0606	2[i]	3.487[i]	*0.728*	*0.574*
22	Goldfish	0.00854	1.06[d]	14.2[d]	*0.975*	*0.075*
23	Zoobenthos	*0.535*	5.939[j]	9.716[j]	0.9	*0.611*
24	Macrozooplankton	0.0658	25[f]	83.33[f]	*0.853*	*0.3*
25	Microzooplankton	3.75	38[f]	138[f]	*0.036*	*0.275*
26	SAV_Benthic Algae	27.21	5.11[f]	-	*0.008*	-
27	Phytoplankton	2.135	245[f]	-	*0.698*	-
28	Detritus	60	-	-	*0.29*	-

[a]Graham 1999, [b]Colvin et al. 2015, [c]Randall and Minns 2000, [d]*Fishbase estimate*, [e]Ruddle and Christensen 1993, [f]Christensen 2009, [g]De Mutsert et al. 2012, [h]Peterson et al. 2003, [i]Rogers and Allen 2011, [j]Kinter 2010, [k]K. Lewis expert opinion

2.5.2 Trophic impacts

The Mixed Trophic Impact (MTI) plots for the Before and After models are interpreted such that red coloration represents a negative impact (i.e. predation) and blue represents a positive impact (for example, acting as a food source, or indirectly relieving predation pressure by consuming a prey's predator); darker colors represent stronger impacts (Fig. 7 and 8, Christensen et al. 2005). The y-axis represents the impacting groups and x-axis represents impacted groups. The Before MTI (Fig. 7) shows that Channel Catfish has a strong negative impact on various populations: itself, bass (including Largemouth Bass and Black Crappie), Smallmouth Bass, Hogchoker, herring or shad (including Hickory Shad, American Shad, Atlantic Menhaden, Gizzard Shad, and unidentified Alosines), river herring (including Blueback Herring and Alewife), suckers (including White Sucker and Creek Chubsucker), sunfish (including Bluespotted Sunfish, Redbreast Sunfish, Green Sunfish, Pumpkinseed, Bluegill, Redear Sunfish, and unknown sunfish sp.), and small forage fish (including Bay Anchovy and Inland Silverside). Bass have a strong negative impact on certain populations including: itself, Smallmouth Bass, and Yellow Perch. Zoobenthos have a strong negative impact on SAV and benthic algae, macrozooplankton, zoobenthos (themselves), and minnows (including Eastern Silvery Minnow, Golden Shiner, and Spottail Shiner), but a positive impact on almost the entirety of the remaining food web. Macrozooplankton have a negative impact on both macrozooplankton (themselves) and microzooplankton, but have a positive impact on almost the entire remaining food web. Microzooplankton have a negative impact on detritus, phytoplankton, microzooplankton (themselves) and some mid-trophic level

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groups: minnows, darters, small forage fishes, suckers, and hogchokers. Smallmouth

Bass, Yellow Perch, American Eel, Carp, croaker (including Atlantic Croaker and Spot),

Hogchoker, herring or shad, river herring, Banded Killifish, suckers, small forage fish,

darters, minnows, and Goldfish do not strongly impact the food web in a positive or

negative way.

In the Before model, represented by years 1990 through 1994, native channel

catfish show moderate to strong trophic impacts on much of the mid to higher trophic

level consumer groups, and native *Ameiurus* catfishes show strong trophic impacts on

most mid trophic level consumers groups that were less impacted by Channel Catfish

(Fig. 7). However, the After model, representing the 2013 through 2017 community in

Gunston Cove, shows that the introduction of the Blue Catfish is correlated with the near

elimination of trophic impacts of both native catfish groups (Channel and *Ameiurus*

groups) (Fig. 8).
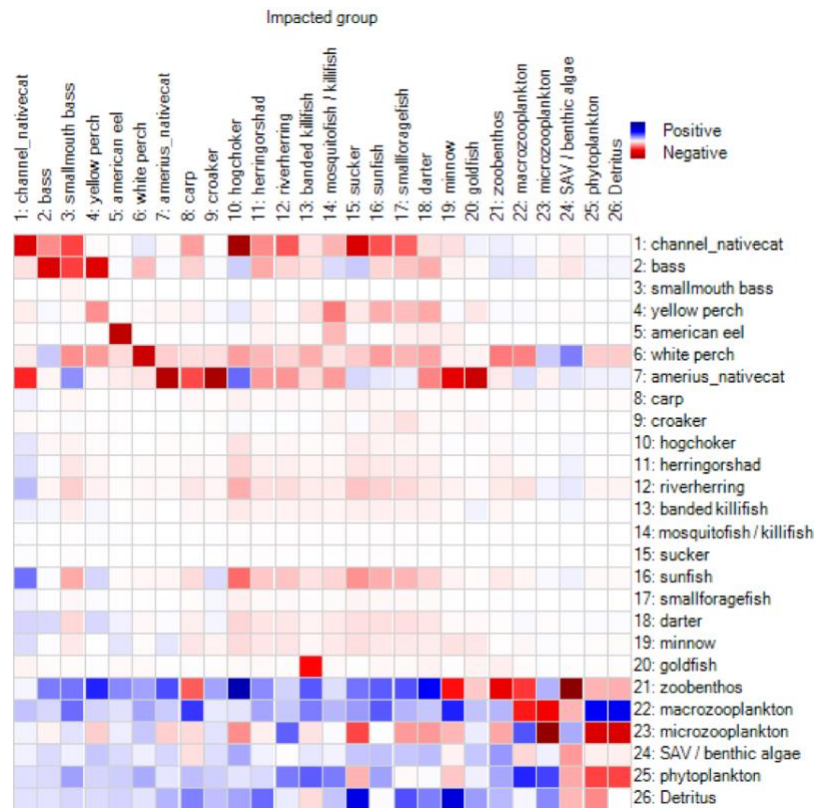
Figure 5. Mixed trophic impacts plot, Before model.
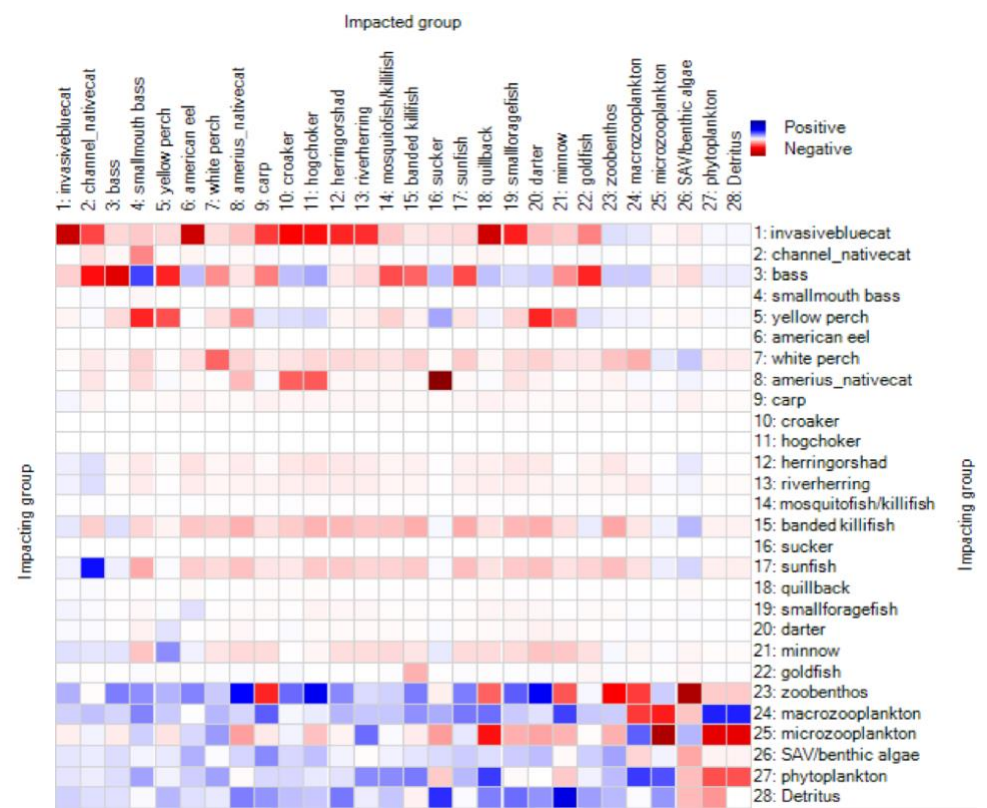
Figure 6. Mixed trophic impacts plot, After model.

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In the After model, Blue Catfish appear to have replaced both native catfish groups in terms of trophic impact, having a strong negative impact on the majority of consumer groups of fishes, leaving almost no impact from either native catfish functional group (Fig. 8). Blue Catfish appear to be exerting strong top-down control on the remainder of the ecosystem. The MTI output of the After model (Fig. 8) shows that Blue Catfish negatively impacts all fish groups to varying degrees, with the strongest negative impacts being felt by populations of Blue Catfish (themselves), Channel Catfish, American Eel, Carp, croaker, Hogchoker, herring or shad, river herring, Quillback, and small forage fish. Channel Catfish have no strong trophic impacts, positive or negative, on other populations. Bass have strong negative impacts on Channel Catfish, bass (themselves), Yellow Perch, Mosquitofish and killifish, Banded Killifish, sunfish, and zoobenthos, but a strong positive impact on Smallmouth Bass and a moderate positive impact on American Eel, croaker, Hogchoker, sucker, Quillback, small forage fishes, darter, and invertebrates. Yellow Perch exert strong negative pressure on Smallmouth Bass, Yellow Perch (themselves), *Ameiurus* catfish, darter, and minnows, and have a slight positive impact on Carp, croaker, Hogchoker, and sucker. White Perch exerts lower amounts of negative pressure on the majority of fish groups, and slightly benefit microzooplankton and zooplankton. *Ameiurus* catfish exert moderate negative pressure on themselves, croaker, Hogchoker, and the strongest negative pressure on suckers, but otherwise exert no other detectable trophic impacts on other groups. Most mid-trophic level model group including Carp, croaker, Hogchoker, herring or shad, river herring, Mosquitofish or killifish, sucker, Quillback, small forage fish, darter, and Goldfish exert

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no notable trophic impacts on other groups. Banded Killifish exert minute to moderate

negative impacts on the majority of the food web except for Blue Catfish, bass, and

Goldfish, and SAV and benthic algae groups, on which they exert some degree of

positive impact. Sunfish similarly exert minor to moderate negative impacts on the

majority of the food web, except Blue Catfish, Channel Catfish, bass, microzooplankton,

and SAV and benthic algae groups on which they exert a positive impact; sunfish appear

to have a particularly strong positive impact on Channel Catfish. Minnows have minor

negative impacts on the majority of fishes in the food web, except Blue Catfish, Channel

Catfish, bass, and Yellow Perch which they have minor positive impacts on. Zoobenthos

have a moderate to strong positive impact on the majority of the food web, but a

moderate to strong negative impact on Carp, sucker, Quillback, minnow, Goldfish,

zoobenthos (themselves), macrozooplankton, and phytoplankton. Macrozooplankton also

have a strong or moderate positive impact on all groups in the food web except for

microzooplankton and macrozooplankton (themselves), which they have a moderate

negative impact on. Microzooplankton have moderate positive impacts on groups

including White Perch, river herring, and macrozooplankton, and had negative impacts

on *Ameiurus* catfish, sucker, Quillback, small forage fish, darters, Goldfish,

microzooplankton (themselves), phytoplankton, and detritus.

2.5.3 Ecosystem metrics and network analysis

EwE calculated ecosystem statistics for both models (Table 6). The sum of all

production is greater in the Before model, 1794 t/km$_2$/yr, as opposed to 810.1 t/km$_2$/yr in

the After model; the After model produces 983.8 t/km2/yr less biomass than the Before

model. The calculated Total Net Primary Productivity (TNPP) is also higher in the

Before model, 1475 t/km2/yr, compared to 662.1 t/km2/yr in the After model. The ratio of

TPP over total respiration, TPP/TR, is slightly higher in the Before model at 2.461, and

2.380 in the After model. The sum of all consumption is 1147 t/km2/yr in the Before

model, higher than the After model whose sum was 532.8 t/km2/yr. The sum of all

exports is 875.8 t/km2/yr in the Before model, higher than the 383.9 t/km2/yr calculated

for the After model. The sum of all respiratory flows is 599.4 t/km2/yr in the Before

model, and a lower 278.2 t/km2/yr in the After model. The sum of all flows into detritus

is 1209 t/km2/yr in the Before model, higher than the After model that had 540.5 t/km2/yr

flowing into detritus. The total system throughput in the Before model is 3832 t/km2/yr,

higher than 1735 t/km2/yr in the After model.

The net system production was also higher in the Before model, 875.7 t/km2/yr,

and lower in the After model at 383.9 t/km2/yr. The total biomass (not including detritus)

is lower in the Before model, at 22.99 t/km2 and higher in the After model at 34.72 t/km2.

The ratio of total primary productivity over total biomass (TPP/TB) is higher in the

Before model as well at 64.16, and 19.07 in the After model. When the total biomass to

total throughput (TB/TT) is calculated, the Before model ratio is lower at 0.006 t/km2/yr

compared to 0.020 in the After model. The System Omnivory Index is slightly higher in

the Before model, 0.294, then the 0.293 in the After model. However, the difference

between Before and After omnivory indices is quite small.

Table 6. System statistics, output from Ecopath with Ecosim.

Statistic	Before model	After model	Units
Sum of all consumption	1147	533.8	$t/km^2/yr$
Sum of all exports	875.8	383.9	$t/km^2/yr$
Sum of all respiratory flows	599.4	278.2	$t/km^2/yr$
Sum of all flows into detritus	1209	540.5	$t/km^2/yr$
Total system throughput	3832	1735	$t/km^2/yr$
Sum of all production	1794	810.1	$t/km^2/yr$
Calculated $TNPP_1$	1475	662.1	$t/km^2/yr$
TPP_2/TR_3	2.461	2.380	-
Net system production	875.7	383.9	$t/km^2/yr$
TPP_2/TB_4	64.16	19.07	-
TB_4/TT_5	0.006	0.020	$t/km^2/yr$
Total biomass (excluding detritus)	22.99	34.72	t/km^2
System omnivory index	0.294	0.293	-

[1]TNPP: Total Net Primary Production, [2]TPP: Total Primary Production, [3]TR: Total Respiration, [4]TB: Total Biomass, [5]TT: Total (System) Throughput

The total flows including consumption by predators, respiration, flows to detritus, and throughput are all higher in the Before model than the After (Table 7). Ascendency is higher in the Before model at 3925 flowbits than the After model with 1925 flowbits, however when scaled to capacity (A/C), the After model is higher at 39.46% than the Before model: 37.26%. The overhead, and capacity are higher in the Before model than the After model (Table 8).

Table 7. Flows and biomasses from PP and D for each model.

Flow	PP Before	PP After	D Before	D After	Total (PP + D) Before	Total (PP+D) After
Consumption by predators	804.1	372.7	341.8	159.2	1146	531.9
Export	0	0	875.8	383.9	875.8	383.9
Flow to detritus	1055	467.2	154.1	73.33	1209	540.5
Respiration	420.6	194.9	178.8	83.27	599.4	278.2
Throughput	2279	1035	1551	699.8	3830	1735

Table 8. Ascendency metrics for each model.

Metric	Before	After
Ascendency (flowbits)	3925	1951
Ascendency (%, A_1/C_2)	37.26	39.46
Overhead (flowbits)	6610	2993
Overhead (% O_3/C)	62.74	60.54
Capacity (flowbits)	10534	4944

[1]Ascendency, [2]Capacity, [3]Overhead

EwE provides metrics of model cycles and pathways for each model (Table 9). The total pathways are higher in the After model, 19,879 compared to 4,338 pathways in the Before model. The throughput cycled is higher in the Before model than After, both excluding and including detritus: 1.651 t/km^2/yr versus 0.805 t/km^2/yr, and 295.4 t/km^2/yr versus 143.9 t/km^2/yr, respectively.

Finn's Cycling Index is higher in the After model than the Before model: 8.291% versus 7.711% of TT. Finn's mean path length is also slightly higher in the After model at 2.621, compared to 2.597 in the Before model.

Table 9. Cycles and pathways metrics for each model.

Metric	Model	
	Before	After
Total no. all pathways	4338	19879
Throughput cycled (excluding D_1) t/km^2/yr	1.651	0.805
Throughput cycled (including D_1) t/km^2/yr	295.4	143.9
Finn's Cycling Index (% of TT_2)	7.711	8.291
Finn's Mean Path Length	2.597	2.621
Finn's Straight-through Path Length (excluding D_1)	2.357	2.349
Finn's Straight-through Path Length (including D_1)	2.397	2.404

$_1$Detritus, $_2$Total (System) Throughput

Lindeman Spine plots have been constructed for Before and After models using EwE (Fig. 9 and 10). The flows from primary productivity and detritus into TL2 are 782.7 and 332.9 flowbits respectively in the Before model (Fig. 9). The After model flows from primary productivity and detritus into TL2 are 366.3 and 156.6, respectively (Fig. 10). The primary production, including that from SAV, is lower in the After model.
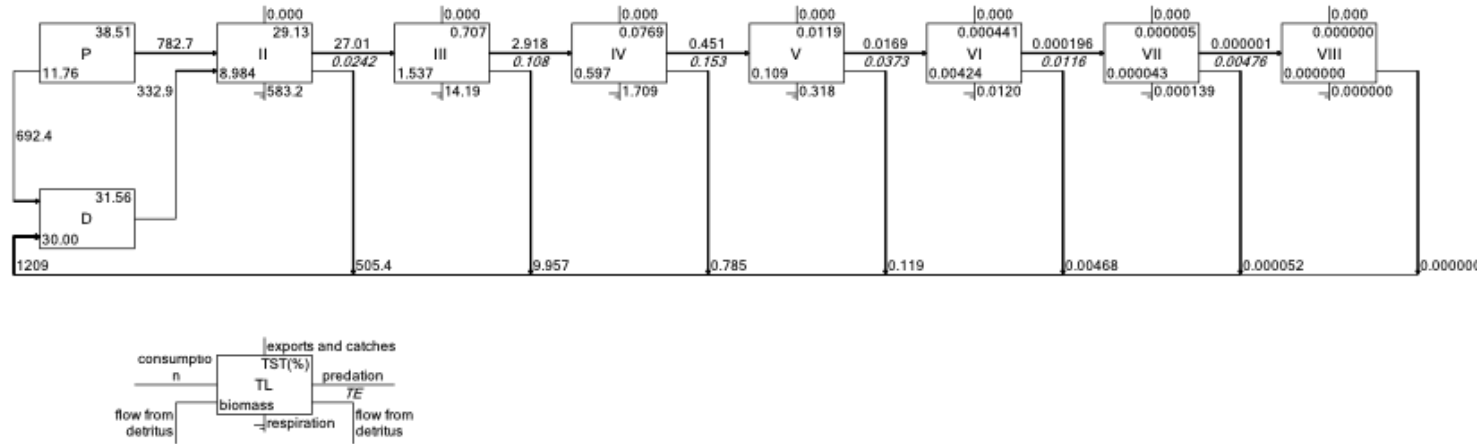
Figure 7. Lindeman spine, Before model.
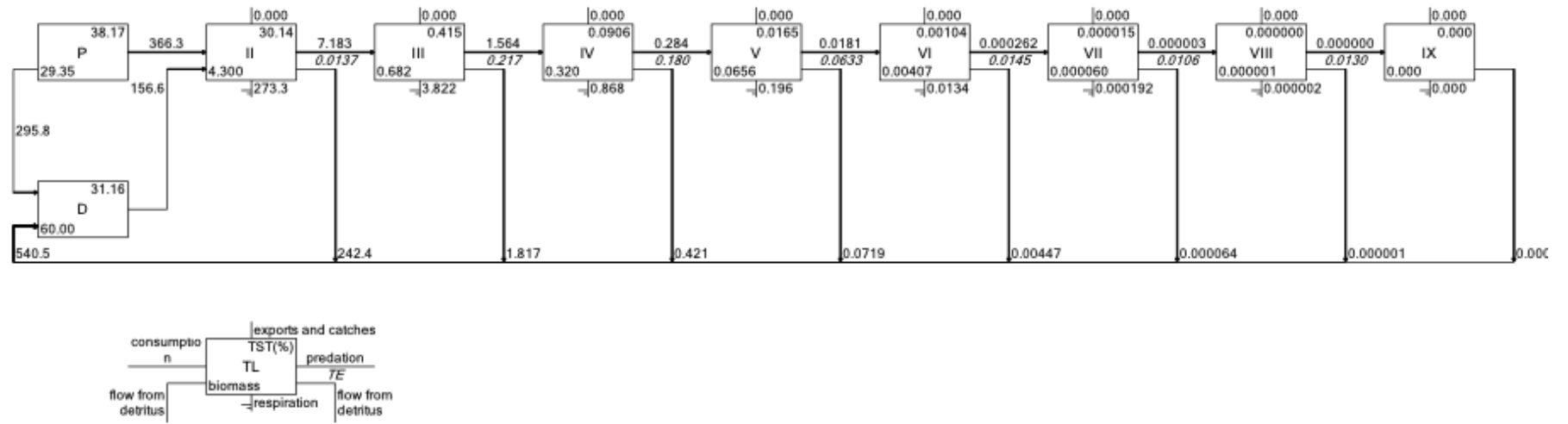
Figure 8. Lindeman spine, After model.

The TNPP in Gunston Cove Before is higher than either low maturity estuary used for comparison, though there is a relatively notable decrease in Gunston Cove After when viewed in context of selected published ENA metric values of other ecosystems (Table 10). The magnitude of decrease in TNPP in Gunston Cove can be considered ecologically significant in this context, although Gunston Cove After still has TNPP comparable to the selected low maturity estuaries, the Seine and Somme (Table 10). There does not appear to be an ecologically significant change in the TPP/TR in Gunston Cove, though when Gunston Cove (Before and After) is compared to the high anthropogenic impacted St. Michel estuary, TPP/TR is considerably more mature as defined by TPP/TR closer to one (Table 10). However, the low maturity Seine estuary is the lowest of the selected estuaries TPP/TR, and the low anthropogenic impacted Canche estuary is nearly the highest TPP/TR included herein (Table 10). While there is not a defined trend for TPP/TB in the selected comparable estuaries, the range of values suggests that the decrease in this ratio in Gunston Cove is ecologically significant. However, TPP/TB in the After model of Gunston Cove is most comparable to the high anthropogenically impacted St. Michel and low maturity Seine estuaries (Table 10). The small range of TB/TST among compared estuaries suggests that this is an ecologically significant change (Table 10). However, the highly impacted St. Michel estuary has the same TB/TST as Gunston Cove After, and the two low maturity estuaries Seine and Somme have lower TB/TST than Gunston Cove, making it difficult to conclude on the ecologically significance of this change (Table 10).

The high OI in context of other published estuaries does not suggest that the minute change in Gunston Cove OI is ecologically significant. The ascendency of Gunston Cove is closest to that of the low anthropogenically impacted estuary. The range of A/C in published values (Table 10) suggests that the small change in Gunston Cove is ecologically significant. Gunston Cove A/C values fall between low and highly impacted ecosystems. Further, when the FCI of Gunston Cove is compared to the estuary with high anthropogenic impacts and the presence of an invasive species, the St. Michel estuary (Table 10).

Table 10. Comparison of Gunston Cove and published estuarine ENA.

Metric	Gunston Cove, Before[A]	Gunston Cove, After[A]	Canche, Low Anthropogenic Impact Estuary[B]	Somme, Low Maturity Estuary[B,C]	Seine, Low Maturity Estuary[B,D]	St. Michel, High Anthropogenic Impact and Invasive Species Estuary[B,E]
$TNPP_1$	1475	662.1	450.9	598.6	853.4	177.2
TPP_1/TR_2	2.461	2.38	22.1	15.5	1.4	6.1
TPP_1/TB_2	64.16	19.07	100.6	21.8	38.3	24.6
TB_2/TST_4 (t/km$_2$/yr)	0.006	0.02	0.003	0.01	0.01	0.02
OI_5	0.294	0.293	0.04	0.01	0.11	0.06
A_6 (total flowbits)	3925	1951	1440	400.2	3944.3	451.6
A_6/C_7 (%)	37.26	39.46	53.6	35	34.8	44
FCI_8	7.711	8.291	0.8	12.2	16.1	0.6

[1]Total (Net) Primary Production, [2]Total Respiration, [3]Total Biomass, [4]Total System Throughput, [5]Omnivory Index, [6]Ascendency, [7]Capacity, [8]Finn's Cycling Index.
Sources: [A]This study, [B]Selleslagh et al. 2012, [C]Rybarczyk et al. 2003, [D]Rybarczyk and Bernard 2003, [E]Leloup et al. 2008

The proxies for vigor, resilience, and organization, which are total net primary productivity, total primary productivity over respiration, and ascendency over capacity, respectively, are shown in Figure 11 as per Costanza and Mageau's (1999) theory and corresponding conceptual model. Plotting these metrics places both Gunston Cove models in the brittle plane as defined by Costanza and Mageau (1999), similar to the Seine estuary modeled by Sellaslagh et al. (2012). The remainder of the selected estuaries from Sellaslagh et al. (2012), including the Canche, Somme, and St. Michel, fall into the crystallized plane.
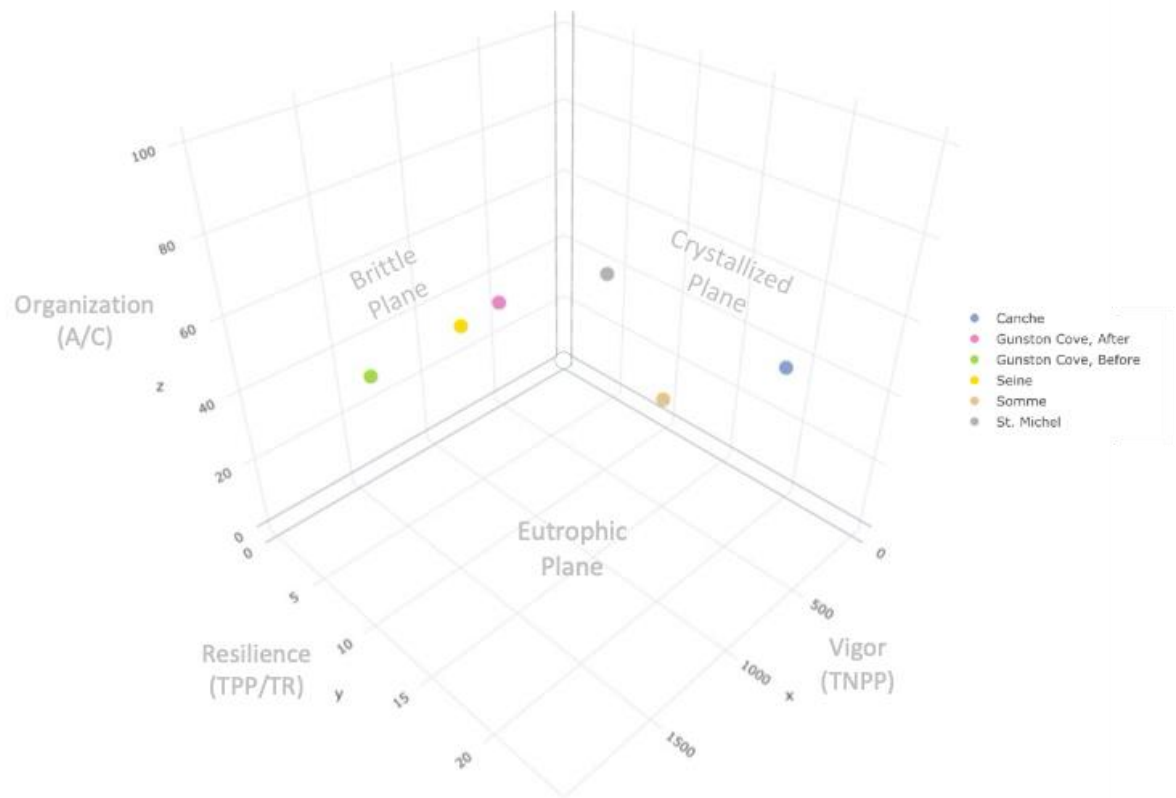
Figure 9. Plot of vigor (TNPP, x-axis), resilience (TPP/TR, y-axis), and organization (A/C, z-axis) per Costanza and Mageau (1999), comparing Gunston Cove to estuarine ecosystems modeled by Sellaslagh et al. (2012).

2.6 Discussion

2.6.1 Ecosystem Level Impacts

The reduction of the metrics describing consumption, production, exports, and flows in the After model when compared to the Before model supports the hypothesis that reduced nutrient input results in a less productive ecosystem, specifically evidenced by the sum of all production wherein the After model produces 983.8 t/km2/yr less

biomass than the Before model. The primary production, including that from SAV, is lower in the After model following nutrient reductions.

Results from ENA aditionally provide supporting evidence of recovery from Gunston Cove's historical hypereutrophication documented by Jones et al. (2008). While the After model has a higher total biomass, it has lower flow from primary productivity than the before model (366.3 vs. 782.7). The higher biomass in the After model is due to the expansive resurgence of SAV in Gunston Cove, which accounted for 27.21 g/m2 in the After model. Primary production in the After model is largely composed of SAV, which is directly consumed much less than phytoplankton, and therefore fuels much less production in the ecosystem. These findings both agree with and support the sustained recovery identified by Jones et al. (2018) that examined Gunston Cove's expansive SAV coverage in combination with sustained chlorophyll *a* concentrations below 30 μg/L (above which is typically considered eutrophic). By these standards, Gunston Cove can be considered nearly mesotrophic, falling only slightly below the 30 μg/L eutrophic benchmark (Jones et al. 2018).

Network indices provide insight into the overall ecosystem functioning and maturity indices, many of which were defined by Odum (1969) and further discussed in Christensen (1995). Odum's (1969) work asserted that as ecosystems develop and mature, they exhibit "greater internalization, feedback, cycling, specialization and information" (Ulanowicz 1980). The TPP/TR of both ecosystems is greater than 1, defining them as being earlier in development and maturity. Primary productivity continues to exceed respiration, however the ratio appears to be moving towards 1:1 as

the ecosystem recovers, indicating it is moving towards unity and maturity, though it is still considered immature per the After model (Odum 1969, Christensen 1995). The reduced TPP/TB provides further evidence that the ecosystem is moving towards maturity since it is understood that the ratio is highest in immature ecosystems due to excess primary production that is not efficiently assimilated into biomass (Christensen 1995). This increased ecosystem efficiency is further reflected in the increased TB/TT ratio in the After model, also indicative of a maturing ecosystem (Christensen 1995). Gunston Cove appears to be maturing as it recovers from hypereutrophication, despite the introduction of an invasive predator that can cause unanticipated effects, when evaluated using the indices of maturity defined by Odum (1969) and Christensen (1995). The OI for these models, which represent a shift from straight food chains towards a web-like trophic structure per Odum (1971), are only nominally different and therefore are considered inconclusive for determining maturation or stress of Gunston Cove.

While a shift in food chain or web complexity can not be detected via the proxy of omnivory indices, which are virtually unchanged, the increase in Finn's Cycling Index between the two periods indicates that the ecosystem is cycling more of the throughput internally, which is associated with increased stability and resilience. Another index developed by Finn (1980), mean path length, also increased, representing an increased diversity of flows as the ecosystem is developing and maturing towards a web-like structure. The shift towards a web-like structure provides a buffer of sorts to absorb stress from perturbations, such as an invasive species introduction as Gunston Cove have experienced; if a link in the food chain within a web is broken, it can be compensated for

by the larger number of pathways as opposed to a more simple ecosystem. While there is a minute decrease in the measure of resilience TPP/TR sensu Constanza and Mageau (1999), both measures of FCI and FMPL indicate increasing resilience in Gunston Cove. This implies that it is conceivable that the introduction of Blue Catfish to Gunston Cove prior to the 2005 stable state shift would have had more drastic effects on the food web than the most notable impact of seemingly replacing the trophic impact of native catfishes.

Odum (1969) theorized that all ecosystems mature towards the most optimal efficiency, that is to say that they will increase in efficiency and organization as they develop. Increased A/C indicates redundant pathways, providing a buffer of resilience to perturbations; this is also associated with an increase in: speciation, specialization, retention, or cycling (which are associated with maturity) per Odum (1969). Additionally, this is associated with a maturing ecosystem as defined by Odum (1969), and agrees with the previously described metrics that indicate that Gunston Cove is maturing in tandem with water quality improvements.

However, while many of the matrices discussed suggest that Gunston Cove is a maturing ecosystem, such ecosystems are expected to increasingly utilize detritus, and no increase in relative importance of detritus was observed using ratios of detrital flows to primary producer flows (Odum 2014). It is conceivable that this hasn't been observed in Gunston Cove because the phytoplankton levels are still high, but slightly below what is expected in a eutrophic ecosystem, as discussed in Jones et al. (2018), and despite recovery, the ecosystem is not yet mature enough to shift towards relatively larger detrital

flows. It should also be noted that the flows through primary producers as displayed in the Lindeman Spine plots include both SAV and phytoplankton. Knowing that SAV is less used as a directly utilized food item and more after it has been decomposed into detritus (Laney 1997), it is likely that the ecosystem is actually increasing utilization of detritus, but by describing SAV as the food source this is not shown in the model as it is currently configured. This could be addressed through adjustments in the diet matrix in future research. This would require further research into the form in which SAV is consumed, and the amount of detritus present and utilized in the ecosystem. The detrital dynamics are not currently studied or understood in Gunston Cove, but further research could improve the quality of the model for making these predictions and provide understanding the role of detritus in the food web.

The increased pathlength as shown by the higher FCI of Gunston Cove that was observed in the comparative ecosystem analyses and in context of published estuarine ENA metrics supports the hypothesis that the recovery in water quality in Gunston Cove and subsequent 2005 stable state shift provided sufficient resilience in the face of the impact of Blue Catfish invasion, else major changes to the trophic structure would be observed herein. The reduction of TNPP in Gunston Cove suggests that the ecosystem is increasing in maturity and becoming less eutrophic. Further evidence of maturation includes the decrease in TPP/TB and increase in TB/TST and A/C. The OI value in the context of published estuarine ENA suggests that Gunston Cove is relatively less organized. Additionally, the resilience of the ecosystem as expressed by TPP/TR sensu Costanza and Mageau (1999) showed that Gunston Cove was categorized as relatively

brittle both Before and After, which is characterized by relatively low resilience compared to high vigor and organization. This categorization of Gunston Cove is relative to published estuarine ENA metrics, where three of the four published estuaries are characterized as crystallized, with higher resilience and organization, but relatively lacking in vigor. It is however important to understand that plotting vigor, organization, and resilience allows for relative comparisons and as such, the context and purpose of this comparison should be kept in mind; this analysis cannot singly classify a particular ecosystem. While comparisons to similar published estuarine ENA metrics provide context for the function of Gunston Cove, such comparisons are relative and do not explicitly define any included ecosystem. Gunston Cove is certainly considered eutrophic, which impacts the classification of the ecosystem in this comparison through the metric of TNPP as a proxy for vigor. For the purpose of this study, the comparison highlighted the importance of resilience (in the form of A/C) as it drove the ecosystems classification of the functioning of Gunston Cove both Before and After. Though recovered, in a new stable state where SAV is present, and while it appears that Gunston Cove had sufficient resilience in the face of the Blue Catfish invasion, the ecosystem remains unbalanced per this evaluation, lacking sufficient resilience relative to the ecosystem's vigor and organization, which should be taken into consideration in any adaptive management.

2.6.2 Community Level (Trophic) Impacts

The most prominent trophic impact of Blue Catfish introduction and their success is the apparent niche replacement of the native catfishes: Channel Catfish, White

Bullhead and Brown Bullhead, that was observed when comparing the Before and After MTI. The success of Blue Catfish in Gunston Cove can likely be attributed to their life history: they are the largest of the ictalurids and also display rapid growth (Graham 1999). This trophic replacement of native catfishes, particularly White and Brown Bullhead, has been observed by Orth et al. (2017) in other Atlantic watersheds where Blue Catfish has been introduced and is unfortunately not unexpected. The establishment of Blue Catfish is correlated with drastically dulled trophic impacts of native catfishes in Gunston Cove.

There are implications felt throughout the food web by this replacement of native predators with one that is significantly more voracious (Schloesser et al. 2011). As seen in the MTI analysis of this study, Blue Catfish has a strong negative effect on both herring groups: herring and shad, and river herring; the extent of the negative impact that Blue Catfish exerts on both herring groups exceeds that of native catfishes in the Before model, confirming the increased difficulty that will continue to be faced in efforts to increase the local population of those species. The Blue Catfish's apparent trophic replacement of native catfishes correlates with the native catfishes becoming extremely minimal within the After model both in terms of biomass and impacts on the greater food web. The trophic impacts of the majority of the fishes in the After model are in fact weaker when compared to the Before model, and it is conceivable that this is due to the relatively larger population of Blue Catfish as a predator in comparison to the reduced populations native catfishes (Channel and *Ameiurus* Catfishes) when comparing the biomasses of the Before and the After model. Blue Catfish has not only replaced native

catfishes in trophic position, but has indirectly dampened many of the remaining trophic interactions.

Historically, American Shad was at one point one of the most abundant and economically important fisheries of the U.S. Atlantic Coast, it was valued for eating and would supply fish to Virginia, Pennsylvania, Maryland, and as far as Ohio when in season (Cummins 2011). The added pressure of pollution and habitat degradation to over-harvesting led to an American Shad moratorium in 1982 that did not result in improved stocks until nearly 2016 (Cummins 2011, Cummins 2016). Cummins (2016) confirmed improvement and establishment of a small stock of American Shad returning to the Potomac River. Gunston Cove will likely continue to act as an important nursery ground if water quality is maintained, however the strong pressure on this species from Blue Catfish could prove counterproductive should the predator's population increase.

The remainder of the herring and shad group also includes some of the most important and largest commercial fisheries of the West Atlantic coast, though those fisheries have dramatically declined and overall management efforts have been largely unsuccessful (ASMFC 2010).The highly migratory herring and shad fishes utilize estuaries such as Gunston Cove and its respective tributaries as nursery grounds, spawning grounds, or juvenile habitat (Greene et al. 2009). The drastic expansion and population growth of Blue Catfish in the majority of Chesapeake Bay tributaries that act as spawning sites for these species, translate to implications that reach further than Gunston Cove (Schloesser et al. 2011). As a predator, Blue Catfish is known to preferentially prey upon anadromous shads and herrings, and Atlantic menhaden

(Schloesser et al. 2011). These groups are already precarious, with historically low populations and are now subject to selective predation by the introduced Blue Catfish in addition to pre-existing habitat destruction and degradation (Schloesser et al. 2011, ASMFC 2010). The loss of these populations has the potential to destabilize the food web not only in Gunston Cove, but in the greater Chesapeake Bay where they critically link lower and higher trophic levels by filter-feeding.

While no longer of commercial importance, river herring are listed as a species of concern and are currently under moratorium in the Chesapeake Bay, as of December 2011 in Maryland, and January 2012 in Virginia (ASMFC 2012). This policy prioritized the return of river herring in the Chesapeake Bay and its tributaries, which includes Gunston Cove (ASMFC 2012). Growth in river herring spawning populations has been observed in Gunston Cove tributaries since 2015 despite lower biomasses seen within the Cove in the After model (De Mutsert 2019). Growth of river herring populations in the greater Chesapeake watershed within Virginia has not been sufficient to end the moratorium on river herring, which still remains in place (Pertaining to River Herring). The pressure from the established Blue Catfish is likely providing an impingement on their recovery due the strong negative pressure the predator puts on juveniles, which are the cohorts most frequently observed in Gunston Cove. The voracity of Blue Catfish and their preference for river herring has potentially bleak implications for the fragile, slowly recovering spawning population and young-of-the-year river herring in Gunston Cove. The reach of Blue Catfish impacts has the potential to destabilize the amount of work done under the policy to support the return of river herring to the Potomac River and its

tributaries (MacAvoy et al. 2009, Schmitt et al. 2017). Orth et al. (2017) found that in the James, Rappahannock, and York Rivers some depleted native species, including river herring and shad, make up a small diet proportion (around 10% each) for Blue Catfish, but the high consumption rates (Q/B) of Blue Catfish result in a larger impact seen in this study of Gunston Cove. As such, a growth in the Blue Catfish population is likely to have a magnified effect on at-risk populations, particularly river herring. This fate is not necessarily limited to Gunston Cove and the Potomac River. The trophic impacts observed in Gunston Cove provide potential foresight for the greater Chesapeake Bay tidal rivers under similar anthropogenic pressure (Orth et al. 2017).

2.7 Conclusions and Future Directions

This study provides a retrospective evaluation of improved water quality on the trophic structure of Gunston Cove through comparison of the ecosystem before and after the resulting stable state shift. I found that Gunston Cove shows signs of a maturing ecosystem based on ENA. Additionally, this study explains the response of the food web to the introduction of an invasive omnivorous predator, the Blue Catfish, which has effectively replaced the role of native catfishes according to MTI analysis. The ecosystem-based approach taken through trophic modeling allows me to evaluate the two events impacting Gunston Cove in context of each other as they have happened in reality, as opposed to evaluating each incident in isolation. This approach provides a realistic comparison that will be more useful to management of this ecosystem in the early stages of hypereutrophication recovery and the establishment of an invasive predator.

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The implications of this recovery, contextualized using ENA, in a previously hypereutrophic ecosystem, in addition to an introduced higher trophic level predator, provide important context for continued ecosystem-based management in Gunston Cove. While water quality has improved and the ecosystem shows a measured increase in resilience and maturity, EBM efforts should prioritize the management of invasive Blue Catfish to further support recovery and increase the resilience of the ecosystem by further reducing eutrophication where possible. As the research around the life history and trophic dynamics of Blue Catfish as an invasive species in the Chesapeake region continues to develop, this work can and should be further developed to better advise the suggested EMB of Gunston Cove.

Additionally, the After model is a starting point for use in Ecosim for the development of temporally dynamic simulations useful to proposed policy and management. Such simulations of future perturbations to the ecosystem are particularly useful to understand the risks of potential new nuisance species invasions, invasive species management, or future extirpations due to human activities, though such simulations were outside the scope of this work.

APPENDIX

EwE Input: Before Model Diet Matrix

#	Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Prey																								
1	channel_nativecat	0.01	0.033	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	bass	0.1	0.025	0	0.027	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	smallmouth bass	0.08	0	0.01	0.027	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	yellow perch	0.01	0	0	0.03	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	american eel	0	0	0	0	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	white perch	0.01	0.1	0	0.05	0	0.1	0.02	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	amerius_nativecat	0.01	0.033	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	carp	0	0.005	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	croaker	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	hogchoker	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	herringorshad	0.17	0.05	0	0.01	.	0.25	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	riverherring	0.164	0.05	0	0.01	0.01	0.25	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	mosquitofish	0.01	0.06	0.01	0.0725	0.02	0.07	0.02	0	0.01	0	0	0	0	0	0	0	0	0	0	0.05	0	0	0
14	killfish	0.01	0.06	0.01	0.0725	0.02	0.07	0.059	0	0.05	0	0	0	0	0	0	0	0	0	0	0.15	0	0	0
15	sucker	0		0	0	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	sunfish	0.29	0.091	0.01	0.08	0.01	0.01	0.08	0	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17	smallforagefish	0.01	0.033	0.01	0.01	0.08	0.05	0.02	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18	darter	0.01	0.02	0.01	0.1	0.02	0	0.001	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	minnow	0.01	0.06	0.01	0.01	0.09	0.08	0.02	0	0.02	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	goldfish	0	0.025	0	0	0	0	0.01	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21	zoobenthos	0.05	0.355	0.6	0.5	0.21	0.1	0.6	0.1	0.5	0.87	0.6	0.35	0	0.59	0.5	0.65	0.6	0.8	0.06	0.3	0.15	0	0
22	macrozooplankton	0.01	0	0.2	0	0.15	0	0	0.27	0.05	0.02	0.1	0.3	0.11	0.2	0	0.28	0.045	0	0.25	0.1	0.1	0	0
23	microzooplankton	0.01	0	0.05	0	0.15	0	0	0.05	0.15	0.02	0.1	0.35	0.29	0.05	0	0	0.045	0	0.1	0.1	0.1	0.7	0
24	SAVbenthicalgae	0.01	0	0	0	0	0	0	0.01	0.02	0.01	0	0	0	0.02	0	0.05	0	0	0	0.07	0.05	0	0
25	phytoplankton	0.001	0	0.01	0.001	0.18	0	0	0.1	0.05	0.01	0.01	0	0.25	0.13	0	0.02	0.01	0	0	0	0.4	0.25	0.7
26	detritus	0.02	0	0.03	0	0	0.01	0.05	0.25	0.05	0.05	0.18	0	0.2	0	0.5	0	0.28	0.2	0.6	0.15	0.2	0.05	0.3
27	import	0.005	0	0.04	0	0.05	0	0.01	0.22	0.02	0.02	0.01	0	0.15	0.01	0	0	0.02	0	0	0.08	0	0	0
	Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	(1 - Sum)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

EwE Input: After Model Diet Matrix

#	Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Prey																											
1	Blue Catfish	0.01	0	0.033	0	0.015	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	channel_nativecat	0.03	0.01	0.033	0	0.015	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	bass	0.01	0.1	0.025	0	0.027	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	smallmouth bass	0.01	0.08	0	0.01	0.027	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	yellow perch	0.01	0.01	0	0	0.02	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	american eel	0.0005	0	0	0	0	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	white perch	0.05	0.01	0.1	0	0.05	0	0.1	0.02	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	amerius_nativecat	0.07	0.01	0.033	0	0.015	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	atlanticneedlefish	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	carp	0.02	0	0.005	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	croaker	0.01	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	hogchoker	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	herringorshad	0.048	0.17	0.05	0	0.01	.	0.25	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	riverherring	0.0475	0.164	0.05	0	0.01	0.01	0.25	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	mosquitofish	0.05	0.01	0.06	0.01	0.04	0.02	0.07	0.02	0.05	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0.05	0	0	0
16	killfish	0.05	0.01	0.06	0.01	0.07	0.02	0.07	0.059	0.05	0	0.05	0	0	0	0	0	0	0	0	0	0	0	0.15	0	0	0
17	sucker	0.01	0	0	0	0	0	0	0.01	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18	sunfish	0.1	0.285	0.091	0.01	0.08	0.01	0.01	0.08	0	0	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	quillback	0.01	0.005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	smallforagefish	0.05	0.01	0	0.01	0.01	0.08	0.05	0.02	0.15	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21	darter	0.02	0.01	0.02	0.01	0.1	0.02	0	0.001	0.01	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	minnow	0.05	0.01	0.06	0.01	0.01	0.09	0.08	0.02	0.209	0	0.02	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	goldfish	0.01	0	0.025	0	0	0	0	0.01	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	zoobenthos	0.3	0.05	0.355	0.6	0.5	0.21	0.1	0.6	0.03	0.1	0.5	0.87	0.6	0.35	0	0.588	0.5	0.65	0.02	0.6	0.8	0.055	0.3	0.15	0	0
25	macrozooplankton	0.001	0.01	0	0.2	0	0.15	0	0	0.25	0.27	0.05	0.02	0.1	0.3	0.11	0.2	0	0.28	0.01	0.045	0	0.25	0.1	0.1	0	0
26	microzooplankton	0.001	0.01	0	0.05	0	0.15	0	0	0.25	0.05	0.15	0.02	0.1	0.35	0.29	0.05	0	0	0.01	0.045	0	0.1	0.1	0.1	0.7	0
27	SAVbenthicalgae	0.001	0.01	0	0	0	0.02	0	0	0	0.01	0.02	0.01	0	0	0	0.02	0	0.05	0.1	0	0	0	0.07	0.05	0	0
28	phytoplankton	0.001	0.001	0	0.01	0.001	0.16	0	0	0.001	0.1	0.05	0.01	0.01	0	0.25	0.13	0	0.02	0.5	0.01	0	0	0	0.4	0.25	0.7
29	detritus	0.02	0.02	0	0.03	0	0	0.01	0.05	0	0.25	0.05	0.05	0.18	0	0.2	0	0.5	0	0.36	0.28	0.2	0.595	0.15	0.2	0.05	0.3
30	import	0.01	0.005	0	0.04	0	0.05	0	0	0	0.22	0.02	0.02	0.01	0	0.15	0.012	0	0	0	0.02	0	0	0.08	0	0	0
	Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	(1 - Sum)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

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