Quantitative Valuation of Ecosystem Services Provided by Oyster Reefs in Mobile Bay, Alabama

by

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Abstract

Oyster reef services have been acknowledged for their ecosystem services, but globally oyster reefs are at risk due to rapid anthropogenic and natural changes. Conservation decisions for these important habitats often require cost-benefit analysis to evaluate trade-offs associated with various restoration strategies. Evaluating economic values of ecosystem services is desirable to for this purpose.

The objectives of this dissertation were to estimate: 1) The value (in dollars) of fish and crustacean production enhancement associated with current oyster reefs in Mobile Bay, Alabama; 2) The nitrogen removal services provided by these oyster reefs, and; 3) The consequences of increasing the oyster *(Crassostrea virginica)* harvest size limit on provision of ecosystem services by oyster reefs in Mobile Bay, Alabama.

This study estimated that when compared to unstructured habitats, oyster reefs in Mobile Bay resulted in enhancement of 354.09±182.62 (mean±1sd) g m^{-2} yr^{-1} of fish and crustaceans. The production attributed to commercial and recreational landings was 64.55±68.55 g m^{-2} yr^{-1} and 105.80±63.63 g m^{-2} yr^{-1}, respectively. The economic benefit estimated for the 1,045 ha of oyster reefs in the bay was \$267,000 – \$739,000 yr^{-1} from commercial landings and \$3.7 – \$12.3 million yr^{-1} from recreational fishing. In addition, the oyster reefs also were estimated to remove 26,666±2,919 kg N yr^{-1} through denitrification, the burial of biodeposits into sediments, and via oyster harvest, comprising an additional \$106,397±11,646 yr^{-1} in economic benefit.

Results from a model that evaluated oyster growth indicated that a proposed change to an 89mm harvest size limit would lower harvest production from 46% to 72% compared to the

76mm size limit. The economic benefit from nitrogen removal services associated with changing the harvest regulation was very small (\$8,127 yr^{-1}) compared to the loss of oyster production (\$308,000 – \$482,000) due to estimated high natural mortality associated with poor water quality for oysters

Results (e.g., fish enhancement, nitrogen removal benefits) can be used by decision makers or the public to estimate the economic return of oyster habitat restoration investment in Alabama. Oysterrowth models did not support increasing harvest size limit to 89mm but fishery managers could monitor oyster mortality in the bay to reduce uncertainty related to proposed changes in harvest size limit in the future.

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Table of Contents

List of Tables

List of Figures

Chapter 1 Introduction

Eastern oyster (*Crassostrea virginica),* also known as American oyster, is an important commercial and recreational species with a native range from the Gulf of St. Lawrence, Canada to the Gulf of Mexico. Their typical habitats are estuaries, sounds, and bays with hard bottoms and salinities ranging from 5 to 27ppt (Kennedy et al. 1996). Eastern oysters (hereafter: oysters) in aggregation were once a dominant structural habitat of estuaries on the U.S. Atlantic coast and in the Gulf of Mexico (Kennedy et al. 1996; Leard et al. 1999). However, oyster reefs are one of the most threatened marine habitats. A recent study (zu Ermgassen et al. 2012) reported that U.S. oyster reefs have lost 64% of their historical spatial habitats and 88% of their biomass over the last century due to impacts from overharvest, disease, and poor water quality (Mackenzie 2007; Beck et al. 2011).

In Alabama, oysters are found in Mobile Bay and the Mississippi Sound from Gaillard Island down to Little Dauphin Island and Porterville Bay in the west, and to Bon Secour Bay at the east end of Mobile Bay (Wallace et al. 1999). Compared to the declining trend of oyster habitats on U.S. coasts overall, oyster habitats in Mobile Bay have decreased by only 10%, but oyster density has declined by 60% over the last century (zu Ermgassen et al. 2016b). The most productive oyster and only commercial harvest reefs are located near Cedar Point (zu Ermgassen et al. 2016b).

Oyster reefs are becoming widely recognized for providing ecosystem services including protecting shorelines from wave action, removing excess nutrients from seawater and providing shelter and food for fish, crustaceans and other invertebrates (Meyer et al. 1997; Coen et al.

2007; Grabowski and Peterson 2007; Scyphers et al. 2011; Grabowski et al. 2012). These ecosystem services are defined as the benefits that people obtain from the ecosystems (Millennium Ecosystem Assessment 2005) and consist of direct and indirect contributions to human well-being (USEPA 2009). These ecosystem services are often designated into four groups based on their functioning: supporting services, provisioning services, regulating services and culture services. Oyster ecosystem services encompass all of these services and their true value to society should be properly identified and accounted for (Coen et al. 2007; Grabowski and Peterson 2007; Grabowski et al. 2012).

Supporting services are the primary services for the production of other ecosystem services. Some examples of supporting services include biomass production and habitat formation (Millennium Ecosystem Assessment 2005). Oysters in aggregation form structural habitats which provide shelter, spawning and foraging grounds for fish, crustaceans, and other invertebrates (Coen et al. 2007; Grabowski and Peterson 2007; Scyphers et al. 2011; Grabowski et al. 2012). Peterson et al. (2003) and zu Ermgassen et al. (2016a) have conducted meta-analyses to quantify fish and crustacean enhancement benefits provided by oyster reefs compared to unstructured habitats throughout the South and Mid-Atlantic coasts of the USA and the northern Gulf of Mexico. Oyster reefs are expected to enhance fish and crustacean production by 260 g m^{-2} yr^{-1} (South Atlantic coast), 218 g m^{-2} yr^{-1}(Mid-Atlantic coast), and 289 g m^{-2} yr^{-1} (Gulf of Mexico). Several other studies have estimated the economic value of fish and crustacean enhancement by oyster reefs using the angler Willingness-To-Pay method (WTP, Grabowski et al. 2011; Kroeger 2012). Grabowski et al. (2011) estimated that a restored oyster reef in North Carolina resulted in an additional economic value of \$10,516 ha^{-1} yr^{-1} more than an unstructured habitat. Kroeger (2012) estimated the economic value of fish production enhancement was

$11,800 ha^{-1} yr^{-1} for Barton and Swift reefs in Mobile Bay. The economic estimation of fishery enhancement from oyster reefs will vary depending on specific data requested from anglers (i.e., WTP for more fish versus heavier fish), but these economic valuation approaches are important to policy makers and managers (Mendelsohn and Olmstead 2009; Pendleton 2010) for understanding the dynamics and interaction across natural and social-science disciplines so as to make effective implementation of ecosystem-based management (Grabowski et al. 2012).

Provisioning services are products or material benefits people obtain from ecosystems including food, fiber, or genetic resources, as examples. (Millennium Ecosystem Assessment 2005). These services are often the first and foremost services traded in markets. Oysters began to be exploited by early settlers and were one of the most important fishery commodities in the early 20th century in many estuaries in the U.S. (Kennedy et al. 1996). The dockside value of oyster harvest in 2008 was $122 million representing almost 3% of the total U.S. seafood values (Vanderkooy 2012). Therefore, oyster restoration embraces a vast potential direct economic benefit to society.

Regulating services are benefits which are obtained from the regulation of ecosystem processes, for example, the regulation of water quality, nutrient cycling, or erosion (Millennium Ecosystem Assessment 2005). These services are often invisible and difficult to quantify. As their usage is mostly non-excludable, they are taken for granted (FAO 2018). Quantifying these services is important to evaluate their loss and degradation. Hence, the true value of these services could be accounted for in decision making frameworks (De Groot et al. 2012).

As an active suspension filter feeder, oysters help to increase water quality by transferring suspended particles from the water column to sediment layers where bacteria continue the physiological process to denitrify and release nitrogen from the water system (Newell et al.

2005). This is the most important functional process performed by oysters (Dame 1996), and quantifying these services either explicitly or implicitly have been made for many estuaries located along U.S. coasts (Newell et al. 2005; Kasperski and Wieland 2009; Piehler and Smyth 2011; Grabowski et al. 2012; Pollack et al. 2013). There are different methods to estimating the economic value of these services. For example, market price is often used when these services are explicitly traded in the market (i.e., nutrient exchange market in North Carolina; Piehler and Smyth 2011). Indirect valuation techniques (i.e., replacement cost method) are used when there are no direct markets for services, or when market evaluations do not adequately capture social values (Farber et al. 2002). The replacement cost method using an engineering solution as a proxy for nitrogen removal services by oyster reefs has been used to estimate nitrogen removal services in the Mission-Aransas estuary, Texas (Pollack et al. 2013). The replacement cost method can be used when three conditions are met: 1) the engineered system provides the same services as the natural system, 2) the engineering alternative is the least expensive (De Groot et al. 2012), and 3) the services are demanded by society (Shabman and Batie 1978; Farber et al. 2002).

Culture services are non-material benefits people obtain from ecosystems through spiritual enrichment, recreation, aesthetic experience and/or education (Millennium Ecosystem Assessment 2005). These services are among the most important services that connect people with nature and are embedded in human-environment interactions (FAO 2018). It is not only about food and income but also a way of life in some communities. Failure to recognize these services will create negative impacts on communities (Poe et al. 2014) whose cultural values are associated with these ecosystems. Understanding the cultural values and heritage of oystermen communities is important to gain community cooperation and political support for any oyster restoration and conservation strategy (La Peyre et al. 2012; Vanderkooy 2012).

Expressing multiple dimensions (ecological, socio-cultural and economic) of ecosystem services in monetary units is important and often necessary to: 1) justify restoration decisions; 2) evaluate trade-offs associated with various restoration strategies (Barbier et al. 2011); 3) calculate the economic return of restoration activities (Peterson and Lipcius 2003; Primack 2006); and 4) improve decision making in an effective and transparent manner (De Groot et al. 2012). Quantitative valuation of ecosystem services could also raise public awareness about various characteristics of harvest and non-harvest resources, improve and promote sustainable ecosystem management (De Groot et al. 2012), and create incentives for public and private sector investments if a payment reward system is available (Farley and Costanza 2010). In fact, oyster reef services, excluding oyster harvests, have been estimated to provide between \$5,500 and \$99,000 ha^{-1} yr^{-1} in economic value, depending on where the reef is located Grabowski et al. (2012).

Ecosystem services vary temporally and spatially (Ruckelshaus et al. 2013; La Peyre et al. 2014) depending on the condition of the resources and also the interaction between the resources and their surrounding environment (Gregalis et al. 2009). Communicating these uncertainties is a critical step for using an ecosystem system approach to inform decisions (Ruckelshaus et al. 2013), especially when the gains in ecosystem services and other values associated with oyster reef restoration have been poorly documented (La Peyre et al. 2014).

Oyster reef restoration in Alabama began in the 1800s on private riparian oyster bottoms, and the first publicly funded restoration efforts took place in 1910 on natural public reefs (Wallace et al. 1999). Oyster reef restoration consisted mostly of shell cultch planting, and the quantity of deposited shells varied yearly depending on funding and shell availability with the greatest deposit of 12,691 m^3 of shells recorded in 1990 (Wallace et al. 1999). More recently the Alabama Department of Conservation and Natural Resources began depositing an average of 2,300 m^3 of shell cultch per year in Alabama waters to enhance the oyster fishery (Gregalis et al. 2008) and to maintain oyster ecosystem services.

Several management decisions have been made to protect oyster reefs in Alabama including setting minimum harvest size to 76mm on public reefs, stopping oyster dredging on public reefs, truncating daily harvest hours from 7 am to 2 pm (ALDCNR 2017), and requiring the oyster industry to purchase oyster tags to create funding for oyster cultch planting (Wallace et al. 1999). Since 2001, community-based oyster restoration programs, known as oyster gardening, have also been initiated to restore oyster reefs in the Mobile Bay and Mississippi Sound (Waters 2001). Construction of a larger scale oyster reef began in 2011 to restore 160 km of oyster reefs in coastal Alabama. Since then, 1.2 km of oyster reefs have been constructed in the Bay (Alabama Coastal Foundation 2017). Off-bottom oyster culture has a potential to reduce the pressure of oyster harvests on natural reefs and provide good quality oysters for the premium half-shell market. However, this technique in Alabama is relatively new and faces some challenges for expansion, including obtaining permits to establish an oyster farm (Walton et al. 2013). Therefore, oyster restoration in Alabama may provide not only increased oyster harvest but also enhanced ecosystem services associated with oyster reefs. The economic estimation of ecosystem services provided by oyster reefs will provide a justification and cost-benefits analysis for oyster restoration in Alabama, and also raise public awareness about the importance of oyster reefs.

The objectives of my Doctoral research were to estimate: 1) the value (in dollars) of fish and crustacean production enhancement associated with oyster reefs in Mobile Bay, Alabama; 2) nitrogen removal services provided by oyster reefs in Mobile Bay, Alabama, and 3) effects of increasing the oyster *(Crassostrea virginica)* harvest size limit on provision of ecosystem services by oyster reefs in Mobile Bay, Alabama.

This dissertation focuses on quantifying fish and crustacean production enhancement and nitrogen removal services based on the simple assumption that these services are relatively homogenous across different oyster reef structures and can be scaled up to the entire oyster reefs in Mobile Bay, Alabama from a basic measuring unit (m^2). Therefore, the result could be useful for decision makers who seek to justify decisions regarding oyster restoration in Mobile Bay. Other services exhibit extreme spatial heterogeneity (i.e., shoreline protection; Grabowski et al. 2012) or difficult to estimate (i.e., cultural values; Mehvar et al. 2018) and are not within the scope of this dissertation.

Study location

Mobile Bay, Alabama is in the Gulf of Mexico with an area of 1,059 km^2 which is approximately 52km tall (north to south) and 37km wide (east to west). Its mouth is formed by the Fort Morgan Peninsula on the eastern side and Dauphin Island, a barrier island on the western side (Mobile Bay Estuary Program). The bay is relatively shallow with an average depth of 3m (USEPA 1999). Oyster reefs primarily exist in the southwest corner of the bay near Mississippi Sound. The Cedar Point area (southwest part of Mobile Bay) has the most productive reefs and the only commercial harvest reefs in Mobile Bay, where Tatum et al. (1995) estimated 1,407 ha of subtidal oyster reef coverage. Recently, oyster reef habitats in the bay were estimated to be around 1,045 ha (Figure 1-1) (zu Ermgassen et al. 2016b). The details of the oyster reef locations within Mobile Bay are reported in Tatum et al. (1995) and zu Ermgassen et al. (2016b).

This dissertation is presented in five chapters: Chapter 1 introduces the research setting for the work; Chapter 2 presents analysis of the quantity and value of harvestable fish and crustacean production associated with oyster reefs in Mobile Bay, Alabama; Chapter 3 provides an estimate of nitrogen removal services provided by oysters in Mobile Bay, Alabama; Chapter 4 investigates the consequences of increasing the oyster harvest size limit on provision of ecosystem services by oyster reefs in Mobile Bay, Alabama; and Chapter 5 is the synthesis of the research and provides management implications and future directions of this study.

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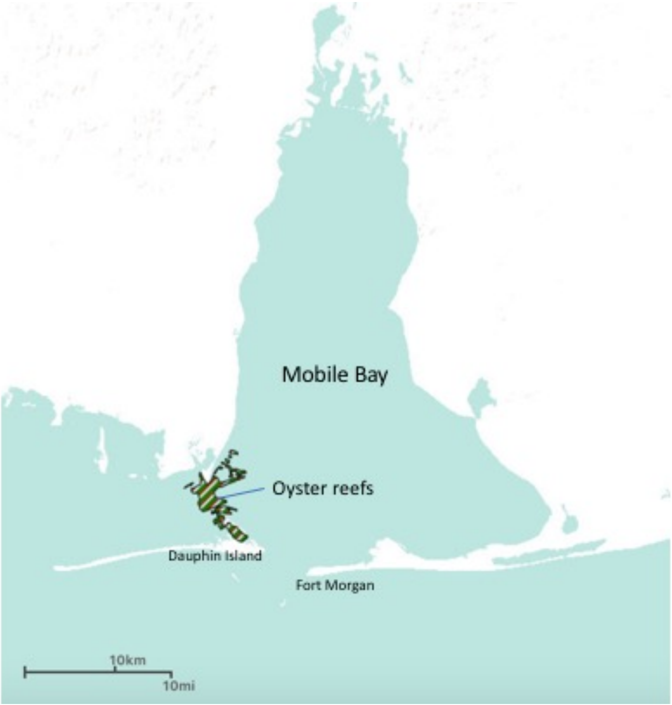

Figure 1-1: Map of the location of oyster reefs in Mobile Bay, AL. Adapted from http://maps.coastalresillience.org/

Chapter 2 Quantifying harvestable fish and crustacean production enhancement and associated economic values from oyster reefs in Mobile Bay, Alabama.

Abstract

Quantifying ecosystem services will assist decision makers and the public regarding their understanding about resources and may justify limited funding for restoration. This study provided an estimate of the economic value of fish and crustacean production enhancement provided by oyster reefs in Mobile Bay, Alabama. Of the estimated 354.09±182.62 (mean±1sd) g m^{-2} yr^{-1} of fish and crustaceans enhanced, results indicated that 170.35±112.34 g m^{-2} yr^{-1} was economically quantifiable: 64.55±68.55 g m^{-2} yr^{-1} (or \$267,000 – \$739,000 yr^{-1}) from commercial production, 105.80±63.63 g m^{-2} yr^{-1} (\$3.7 – \$12.3 million yr^{-1}) from recreational landings. The results demonstrated a substantial positive economic benefit of ecosystem services from oyster reefs associated with fishery production and the estimates could be used to justify oyster habitat restoration investment in Alabama, and elsewhere in the Gulf of Mexico.

Introduction

Oyster reef services provided by aggregations of Eastern Oyster (*Crassostrea virginica*; hereafter, oysters) have been acknowledged for their importance in protecting shorelines from wave action, removing excess nutrients from seawater and providing shelter and food for fish, crustacean and other invertebrates (Coen et al. 2007; Grabowski and Peterson 2007; Scyphers et al. 2011; Grabowski et al. 2012). However, oyster reefs are one of the most threatened marine habitats; their extent has diminished by 85% compared to their historic levels due to rapid anthropogenic impacts (i.e., overharvest, disease, poor water quality; Beck et al. 2011) and more frequent natural changes (i.e., hurricanes; Livingston et al. 1999). Quantitative assessments of the ecological benefits and the economic value of services are needed to provide a strong argument for costly restoration efforts (Peterson and Lipcius 2003; zu Ermgassen et al. 2016a). However, these analyses are generally not available to assist conservation and decision makers in determining potential gains or losses from management interventions, establishment of long-term management goals (La Peyre et al. 2014b).

Oyster reefs increase fish and crustacean (hereafter, fish) production by enhancing recruitment of reef-dependent species and survival of other species that spend all or some fraction of their life near the reefs on activities such as foraging, taking refuge from predation, or spawning (Peterson et al. 2003). Peterson et al. (2003) conducted a meta-analysis of six studies throughout the South Atlantic and Mid-Atlantic coasts (USA) to quantify fish enhancement benefits provided by oyster reefs compared to unstructured habitats. In that study, they reported total fish production enhancement as the combination of the production enhancement of life-time reef-associated species and the fraction of production of species that preyed on reef-associated species. Later, zu Ermgassen et al. (2016a) conducted a similar study for the Gulf of Mexico, South Atlantic and Mid-Atlantic coasts but identified the total enhancement production for life-time reef-associated species and incorporated temporal and spatial fish density uncertainty into their calculation to provide more meaningful estimates with broader application for policy and management (zu Ermgassen et al. 2016a). However, their study did not include uncertainty from fish life-history that exhibits great variability for some species (i.e., Blue crab *Callinectes sapidus*), and which could affect the level of confidence in the estimates.

Despite the complexity of ecological models, decision-makers and public typically ask for simple, easy-to-use and understandable decision support tools (Ruckelshaus et al. 2013) that can 1) justify restoration decisions; 2) evaluate trade-offs associated with various restoration strategies (Barbier et al. 2011; La Peyre et al. 2014); 3) calculate the economic return of restoration activities (Peterson and Lipcius 2003; Primack 2006); and 4) improve decision making in an effective and transparent manner (De Groot et al. 2012). Economic valuation of ecosystem services provides a means to compare cost-benefit analysis of ecological outcomes in comparable terms that will facilitate the allocation of our limited resources to manage ecosystems more effectively (Grabowski et al. 2012).

Although, economic estimation of oyster ecosystem services have been established in the literature, the estimations vary dependent on location, availability of alternatives and the valuation techniques (Farber et al. 2002). Grabowski et al. (2012) estimated that oyster reefs providing economically valuable ecosystem services, excluding oyster harvest, range between \$5,500 and \$99,000 ha^{-1} yr^{-1}, depending on where the reef was located and the services it provided. Others such as Grabowski et al. (2011) and Kroeger (2012) estimated the economic value of fish enhancement by oyster reefs. Grabowski et al. (2011) used an angler's Willingness-To-Pay (WTP) method and estimated \$10,516 ha^{-1} yr^{-1} of additional economic value by increasing angler trips to a restored oyster reef in North Carolina. Kroeger (2012) also used angler's WTP data from the Atlantic Ocean and Florida to estimate fish enhancement production associated with Barton and Swift reefs in Mobile Bay, Alabama as \$11,800 ha^{-1} yr^{-1}. Diversifying valuation techniques and approaches for estimation of economic gain for a service will not confound the information for policy and management but support broader use of the information for restoration efforts.

To further contribute to economic evaluation of fish production enhancement from oyster reefs, I used data published in zu Ermgassen et al. (2016a) and an angler's WTP survey data (Johnston et al. 2006) to estimate harvestable fish production enhancement for Mobile Bay, Alabama. The specific objectives of my study were to: 1) use published parameters to construct fish production and biomass models for harvest sized fish species associated with oyster reefs in Mobile Bay; 2) apply fishery landing data (2005-2015) from the bay to partition recreational and commercial portions of the production estimates; 3) simulate uncertainty boundaries due to fish density and life-history parameters around the estimates of harvestable, commercial and recreational production enhancement provided by oyster reefs in the bay; and 4) quantify the economic benefit of the enhanced harvestable fish production from oyster reefs.

Methods

Species selection for Mobile Bay

A species is enhanced by oyster reefs when there is clear evidence of its production and abundance within oyster reef habitat is higher than non-reef habitat. Production and density enhancement refers to the differences of production and density of the species within oyster reef habitats compared to non-reef habitats (zu Ermgassen et al. 2016a).

A list of species in the Gulf of Mexico (zu Ermgassen et al. 2016a) was used as a primary reference to identify species for production enhancement estimates in Mobile Bay. Then the list was customized for Mobile Bay based on other published studies (Gregalis et al. 2009; Geraldi et al. 2009; Scyphers et al. 2011) regarding species associated with oyster reefs in Mobile Bay. Any excluded species (i.e., Striped blenny *Chasmodes bosquianus*) were then reviewed for distribution using fishbase.org to confirm if they occurred in Mobile Bay and Northern Gulf of Mexico waters and warranted inclusion in the study.

Production calculation

The density of each enhanced species at age-0.5 (individuals m^{-2}) in Mobile Bay was assumed to be within the range zu Ermgassen et al. (2016a) reported for oyster reefs in the Gulf of Mexico. This density was used as an input to predict how much annual production enhancement would be expected from $1m^2$ oyster reef in Mobile Bay by applying the growth and mortality from age-0.5 to the species maximum age (t_{max}). The annual production enhancement for each species was the sum of products between age-class-weight increments with the number of fish that survive through that age class (Peterson et al. 2003; zu Ermgassen et al. 2016a)..

For each species, the growth in length at age (L_t; cm) was first predicted using the von Bertalanffy equation for fish from age-0.5 to their maximum age (t_{max}).

$$L_t = L_{inf}\{1–e^{[–K (t – t0)]}\} \qquad (1)$$

where: L_{inf} (cm) is the asymptotic maximum length; K is the Brody growth coefficient; and t_0 is the age at zero length.

The length-weight relation was then used to convert growth in length (L_t; cm) to growth in weight (W_t ; g):

$$W_t = aL_t^b \qquad (2)$$

where: a and b are specific species constant coefficients.

Size dependent natural mortality (M_t) was estimated for all size classes using the Lorenzen (2000) equation:

$$M_t = M\, L_m / L_t \qquad (3)$$

where: *M* is instantaneous natural mortality at maturity; L_m is length at maturity available from published literature or estimated from L_{inf} (Froese and Binohlan 2000).

The number of surviving individuals (N_t) at each age class from age class $t_{0.5}$ (ref., zu Ermgassen et al. 2016a) to t_{max} for each species was calculated by multiplying the number of individuals at t-1 (N_{t-1}) by the associated survival rate at t-1 ($e^{-M_{t-1}}$) (zu Ermgassen et al. 2016a).

$$\mathrm{Nt} = N_{t-1}\, e^{-M_{t-1}} \qquad (4)$$

The annual production enhancement (P in g) is the sum of products of weight (g) increment ($W_t - W_{t-1}$) multiplied by surviving individuals (N_t) through that age class (Peterson et al. 2003; zu Ermgassen et al. 2016a):

$$P = \sum_{0.5}^{tmax} N_t(W_t - W_{t-1}) \qquad (5)$$

To estimate production enhancement of all species within the same year (i.e., on extant reefs with stable age distribution for all enhanced fish), short-lived species were extended to the time of the longest-lived species (i.e., 17 years) without changing production beyond their own t_{max}. The net annual production was deemed to be the sum of all species production enhancement. Blue crab (*Callinectes sapidus),* Brown shrimp (*Farfantepenaeus aztecus)* and White shrimp (*Litopanaeus setiferus)* are special cases as these species recruit at age-0.25 (zu Ermgassen et al. 2016a) so their production enhancement was estimated from age-0.25.

Harvestable production was the fraction of annual production enhancement that was contributed from fish above the harvest size limit. Therefore, harvest size limits for Alabama were applied (i.e., Sheepshead: 30.5cm and Blue Crab: 12.7cm) to truncate the production of individuals that had not recruited to harvestable size. For other unregulated species, I assumed that anglers would not want fish smaller than 10cm so I used 10cm as a size limit.

The fish density was assumed to be homogeneous regardless of oyster reef structure (i.e., oyster density and reef height) and a oyster reef carrying capacity relation was not limiting in Mobile Bay. Therefore, I linearly scaled production enhancement from 1m^2 up to 1,045 ha of oyster reef in Mobile Bay to estimate total net production enhancement.

Production uncertainty

To calculate uncertainty around production enhancement estimates, uncertainty from life-history parameters and the density of the enhanced species were used. The life-history parameters of enhanced species were compiled from studies conducted in the Gulf of Mexico (Appendix 2-1). In cases where the parameters were not available, the studies in the Atlantic or similar species were employed as proxy (see zu Ermgassen et al. 2016a). The average values were used when multiple studies existed for the same species. The variance of 10% from the mean value was applied to generate random parameters for the fish growth simulation. Due to its sensitivity to weight increments, the coefficient b in the length-weight relation was allowed to vary by only 5% from the mean. Maximum recorded coefficient b (i.e., fishbase.org) was used when necessary (i.e., Spadefish *Chaetodipterus faber)* to truncate the extreme weight values.

To reduce independent combinations of life-history parameters when simulating fish growth, one hundred thousand suites of parameters (i.e., L_{inf} K t_0) were drawn from a multivariate normal distribution (mvtnorm package in R program) with the mean equal to the average values of parameters, covariance matrix with diagonal elements equal to parameter variances of each species, and off-diagonal elements were estimated from parameter correlations multiplied by species specific parameter variances. Due to inadequate information for estimating parameter correlation for every species, the parameter correlation (i.e., L_{inf} K t_0; a,b) for Sheepshead (*Archosargus probatocephalus)* was used to estimate off-diagonal elements for each species.

$$off\text{-}diagonal_{species(i)} = variances_{species(i)} \times correlation_{sheepshead} \quad (6)$$

A separate multivariate normal distribution was produced to generate length-weight parameters (a,b) to align with the simulated length-at-age parameters (L_{inf} K t_0) as inputs into the production estimate. The length at maturity (L_m) and natural mortality at maturity (M) were assumed to be invariant and were used as a baseline for generating uncertainty for size dependent natural mortality (Equation 3).

Density of the enhanced species at age-0.5 (reported in zu Ermgassen et al. 2016a was modeled as a lognormal distribution to constrain negative values because the presence of oyster reefs does not lead to the reduction in fish abundance (zu Ermgassen et al. 2016a). This lognormal distribution is different from the methods of zu Ermgassen et al. (2016a) who modeled the density enhancement as a non-negative normal distribution. The parameters of the lognormal distribution were selected such that the mean and standard deviation (before bias correction for lognormal) of the distribution matched the mean and standard error from zu Ermgassen et al. (2016a). This selection is to reduce over-dispersion in simulating lognormal data for some species (i.e., Silver perch *Bairdiella chrysoura)* which sometimes produced ~6,000 fish m^{-2}. Blue crab was a special case when the lognormal (mean=1.317, se=3.093 before bias correction for lognormal) still produced extremely high density values. I assumed that Blue crab density was not higher than the mean density of all species combined (~15 individuals m^{-2}). Therefore, I used 15 as truncation value for Blue crab density (Evastats package in R). This truncation also reduced the lognormal parameter dispersion when simulating density values (mean=1.454 individuals m^{-2} after truncation). One hundred thousand samples were also drawn from the lognormal distribution to coincide with the samples from the multivariate normal distribution of life-history parameters to produce 100,000 outputs for annual net and harvestable production. The mean, first standard deviation, and lower and upper quartiles of the distribution of the production enhancement for each species were reported.

Economic evaluation

The annual harvestable production of each species was comprised of commercial and recreational production shares. These shares were assumed to reflect average harvest production throughout Mobile Bay. Average fishery landing data from 11 years were available from National Oceanic and Atmospheric Administration (NOAA) for Alabama (NOAA-ALABAMA 2005-2015) and were used to estimate shares for each species. Those species that lacked landing data (commercial or recreation), such as Silver perch were assumed to be unimportant for that sector, so their shares were treated as zero. Harvestable production was then multiplied to these shares to calculate commercial and recreational production (g m^{-2} yr^{-1}) for each species. A flow chart showing the economic calculation procedures of fish enhancement is presented in Figure 2-1.

To account for the uncertainty of inter-annual variability of production for each species, the mean and standard deviation derived from the 11-year dataset (2005-2015) were modeled as the percentage share from a beta distribution. One hundred thousand samples were randomly generated from the beta distribution and were multiplied by the harvestable production to have annual commercial and recreational production. The mean, standard deviation, and lower and upper quartiles of the distribution of the commercial and recreational production for each species were reported.

<u>Commercial value</u>: Based on the NOAA commercial landing price in 2014 and the annual commercial production enhancement for each species, the net economic value of the commercial portion of fish enhancement was estimated. The benefit ratio of wild fish production is usually not available (Milon 1989; Lovell et al. 2007) and varies depending on different factors such as location and availability of resources, and could range from 21% to 58% (Lovell et al. 2007; Kroeger 2012). This range was used to calculate the range in the expected net value attributable to commercial fishing.

Recreational value: Data from a Saltwater Angler's Willingness-To-Pay (WTP) survey for bottom fish (e,g, Pinfish, Pigfish) caught in the Gulf of Mexico was used as reference for the enhanced species values in Mobile Bay (Johnston et al. 2006). The WTP for an additional fish caught (marginal value) in the Gulf of Mexico ranged from \$2.21 to \$7.23 (Johnston et al. 2006). The average weight of a fish caught on reef was assumed to be about 0.325kg derived from average recreational landing data from the NOAA dataset for the enhanced species allowing estimation of the WTP value at \$6.81 - \$22.26 kg^{-1}.

To evaluate the portion of enhanced fish production that could be potentially considered as additional catch, Kroeger (2012) asserted that fish production enhancement was additional catch for Barton and Swift reefs in Mobile Bay, Alabama based on: (1) evaluation and monitoring data from the Mobile Bay revealed that the populations of most species in the bay have remained stable (Mobile Bay National Estuary Program 2008) indicating harvest and natural mortality were in equilibrium with recruitment; (2) recreational fishing pressure is high in Mobile Bay (Dute 2011); and (3) enhancement production is already corrected for natural mortality and fish below harvest size limit. Hence, I assumed that the production enhancement provided by oyster reefs in Mobile Bay was fully available as additional harvest.

However, the marginal value of each unit of ecosystem goods and services often decreases as more goods and services become available (Grabowski and Peterson 2007; Grabowski et al. 2012). To be conservative when scaling the marginal value to entire oyster reefs in Mobile Bay, I assumed the WTP value was 50% lower (\$3.41 - \$11.13 kg^{-1}) than the WTP for a newly restored reef (\$6.81 - \$22.26 \$ kg^{-1}).

All simulations were performed using Program R and R code is appended to this chapter (Version 1.1.383; R Core Team 2013; Appendix 2-2). Data in the study were reported using the format (mean ± 1sd).

Results

I found 16 species associated with oyster reefs in Mobile Bay Alabama (Table 2-1). Of these, 14 species were used for calculating production enhancement. Two species, including Brown shrimp and White shrimp were identified as enhanced species; however, they were not included in the estimates because of reported high natural mortality rates (M=18, Appendix 2-1) used in the simulation that caused their populations to crash within six months from recruitment at 0.25-years.

Among 14 species included in production enhancement, seven species, including the Darter goby (*Ctenogobius boleosoma)*, Skilletfish (*Gobiesox strumosus)*, Naked goby (*Gobiosoma bosc)*, Feather blenny (*Hypsoblennius hentz)*, Freckled blenny (*Hypsoblennius ionthas)*, Gulf toadfish (*Opsanus beta)* and Stone crab (*Menippe mercenaria)* were identified as species with minimal to zero economic value based on the NOAA landing data (2005-2015). Of the remaining seven species, three species including Sheepshead, Spadefish and Spot (*Leiostomus xanthurus)* had both commercial and recreational value; another three species, Silver perch (*Bairdiella chrysoura)*, Pinfish (*Lagodon rhomboids)* and Pigfish (*Orthopristis chrysoptera)* had only recreational value; the remaining species, Blue crab, had only commercial value (Table 2-1).

Growth projections for both mean length-at-age (Figure 2-2) and mean weight-at-age (Figure 2-3) were similar among all species; the fastest growing species was Spadefish and the slowest growing was Naked goby. The longest-lived species was Sheepshead (age 17) and the shortest-lived were Darter goby and Skilletfish (age 2).

Predicted density (# m^{-2}) varied by age and species as the result of uncertainty in the estimation of density at age-0.5 and the impact of size dependent mortality on the survival of each species (Figure 2-4). At age-0.5, Stone crab had the highest density (1.936±0.214 m^{-2} ;Figure 2-5); however, at the maximum age, Freckled blenny had the highest density (0.129±0.081 m^{-2} ; Figure 2-6). Consequently, this uncertainty is incorporated in the net production uncertainty in Equation 5 (Figure 2-7).

The net production enhancement is production on a yearly basis where 1m^2 of oyster reef encompasses all year classes with their corresponding year-class density (N_t) for each species. Oyster reefs in Mobile Bay were estimated to provide approximately 354.09 ± 182.62 g m^{-2} yr^{-1} more in fish production than unstructured habitat (Table 2-1). Of this production, Sheepshead and Blue crab were most productive; they contributed 35% and 20% respectively of the total. Five other species, Silver perch, Pinfish, Spot, Gulf toadfish and Stone crab accounted for an additional 40%; whereas the remaining 5% was from the other seven species.

Harvestable production which included the proportion of production above the harvest size limits of commercial and recreational species was 170.35±112.34 g m^{-2} yr^{-1} or 48% of the total net production. Harvestable production was dominated by Sheepshead accounting for 46% and Blue crab accounting for 21%, although there was a high variation in their production estimate (Figure 2-8). Silver perch, Pinfish and Spot accounted for 29% and the remaining 4% was shared by the other two species: Spadefish and Pigfish. Gulf toadfish and Stone crab, despite accounting for 23% of the total net production enhancement, were not considered species of recreational or commercial interest based on the NOAA data.

The annual harvestable production was comprised of approximately 64.55±68.55 g m^{-2} yr^{-1} in commercial production (37%) and 105.80±63.63 g m^{-2} yr^{-1} in recreational production (63%). Blue crab accounted for 55% of commercial production and Sheepshead accounted for 60% of recreational production. The production by commercial species, Sheepshead, Spadefish and Spot, was characterized by inter-annual variability (Figure 2-9). For example, most of the commercial production share for Spot was between 48% - 96% and for Spadefish between 1% - 31%. This variation in the commercial share affected the variation in the recreational share, accordingly. Blue crab production was attributable mostly to commercial harvest. Despite existing recreational value, harvest is likely low (i.e., ~4% recreational harvest in Louisiana; Bourgeois et al. 2014).

Based on the commercial landing price in 2014 and benefit ratios of 21% and 58%, the oyster reefs resulted in an addition of \$0.0256±0.023 – \$0.0707±0.063 m^{-2} yr^{-1} in direct economic value for fishers. The value corresponded to \$256±230 – \$707±630 ha^{-1} yr^{-1} or \$267,597±240,350 – \$739,077±658,350 yr^{-1} for 1,045 ha of oyster reefs in Mobile Bay, Alabama (Table 2-2).

Salt water Alabama angler willingness to pay for the enhanced species was \$3.41- \$11.13 kg^{-1}. The oyster reefs in Mobile Bay enhanced approximately 1,100 tons yr^{-1} (1,105,610±664,934 kg yr^{-1}) of additional fish that contributed to recreational fishing. The economic value of this enhancement in Alabama for all oyster reefs was approximately \$3.7 – \$12.3 million yr^{-1} (\$3,770,130±2,267,423 - 12,305,439±7,400,709 yr^{-1}), which equaled \$3,600 – 11,700 ha^{-1} yr^{-1} (\$3,607±2,169 - 11,775±7,082 ha^{-1} yr^{-1}).

Mean economic value of harvestable fish enhancement from oyster reefs in Alabama (commercial and recreational values) was about \$8.5 million yr^{-1} (\$8,541,121 yr^{-1}) or \$8,173 ha^{-1} yr^{-1} in 2014, of which, approximately 5.8% was attributable to commercial landings and 94.2% was from recreational fishing.

Discussion

This study provided an estimation of enhanced net and harvestable production of fish and mobile crustaceans attributable to oyster reefs in Mobile Bay, Alabama. The harvestable production was broken down into commercial and recreational production to better estimate their economic values. The incorporation of life-history uncertainty of enhanced species provided more confidence in the production estimates than previous studies in the Gulf of Mexico (Peterson et al. 2003; zu Ermgassen et al. 2016a).

The estimated enhancement production associated with oyster reefs in Mobile Bay were from sixteen species in this study compared to nineteen species reported from the entire Gulf of Mexico (zu Ermgassen et al. 2016a). Three species including Frillfin goby (*Bathygobius soporator*), Striped blenny (*Chasmodes bosquianus*), and Sea robin (*Prionotus spp*) were distributed mostly from the Atlantic Coast to the Florida Keys (fishbase.org) and were not found associated with oyster reefs in Mobile Bay (Gregalis et al. 2009; Geraldi et al. 2009; Scyphers et al. 2011).

The identification of species as having minimal to no economic value, as well as the partitioning of the production into commercial and recreational harvests based on NOAA reports may contain some potential biases. For example, NOAA does not report both commercial and recreational landing data for Stone crab and only commercial harvest for Blue crab, which leads to categorizing Stone crab as a non- economically valuable species and Blue crab as commercial species only. However, these biases appear to be relatively minor and did not contribute substantial error to the economic estimates. For example, Stone crab is mostly harvested for personal consumption in Mobile Bay (Kroeger 2012) and recreational harvest of Blue crab was estimated to contribute only about 4% in nearby Louisiana (Bourgeois et al. 2014).

Incorporating uncertainty is a critical step for using an ecosystem valuation approach to informing decisions (Ruckelshaus et al. 2013). However, data for uncertainty estimates were not always available and consistent. For example, there were insufficient life history parameter data for many species considered in this study. These parameters had to be obtained from different areas of the Gulf of Mexico and/or the Atlantic Ocean, therefore introducing potential bias in the production estimates for the enhanced species in Mobile Bay. Zu Ermgassen et al. (2016a) illustrated that a key driver for production uncertainty was the mortality estimates that were applied to their models of production and concluded that the sensitivity of the production estimates was related to the fact that natural mortalities are poorly understood. For example, estimates of high natural mortality rates in my study led to both species of shrimp dying before reaching 6 months in age in my model. Because Mobile Bay has a thriving shrimp industry we assume that the early life history mortality estimates were uncertain or wrong. Incorporation of variation in species specific mortality estimates should be an objective of any future estimation of fish and crustacean enhanced production associated with oyster reef restoration.

This study produced similar estimates to previous studies which estimated the net production enhancement as 370 g m^{-2} yr^{-1} (zu Ermgassen et al. 2016a) and 260 g m^{-2} yr^{-1} (Peterson et al. 2003) in the Gulf of Mexico. However, my result incorporated uncertainty into the models by introducing life-history parameter uncertainty for all species considered. As a result, this study could offer a greater level of confidence to fishery managers and decision makers who seek to justify decisions regarding oyster restoration in Mobile Bay and elsewhere in the northern Gulf of Mexico.

The magnitude of oyster reefs for supporting fish and crustaceans is likely influenced by the amount and structure of existing oyster reef habitat available for these species (Grabowski et al. 2012). Fish production enhancement would likely not increase linearly with oyster reef area through time and fish production enhancement is expected to asymptote when habitat is no longer a limiting factor for fish enhancement (i.e., carrying capacity; Peterson et al. 2003; zu Ermgassen et al. 2016a). The time frame when carrying capacity is met will likely vary depending on location and reef conditions (La Peyre et al. 2014b). There are also reported interactions among season, reef location, and reef design that influence differences in fish communities benefitting from oyster reefs (Gregalis et al. 2009). Therefore, the linear scaling production enhancement from 1m^2 up to 1,045 ha of oyster reefs in Mobile Bay is another source of uncertainty in my model that should be the subject of future study.

The findings that the recreational value greatly outweighed the commercial value, both in terms of enhanced production and economic values, are important data for managers of fisheries and other coastal resources (e.g., tourism). My results were similar to others that estimated recreational production, in the Gulf of Mexico (Bell 1997; Coleman et al. 2004) where recreational fishing pressure is high (Dute 2011). Also similar to my findings, O'Higgins et al. (2010) estimated that recreational fishing comprised 98% of the economic value in dollars for the fishery in Weeks Bay, Alabama.

Some differences in the economic estimates of this study compared to studies conducted for Barton and Swift reefs in Mobile Bay (Kroeger 2012) were mainly due to the different methods employed. Kroeger (2012) used a WTP survey conducted on the Atlantic Coast and estimated the economic benefit for his study oyster reefs as \$11,800 ha^{-1} yr^{-1} for the recreational sector; my study estimated a lower benefit of \$8,037 yr^{-1} ha^{-1}. It is likely that demographics of anglers (e.g., income, living standard) and availability of resources define how much the angler was willing to pay (Mendelsohn and Olmstead 2009; Pendleton 2010) so that a Gulf of Mexico angler was likely willing to pay less for accessing the resources compared to the Atlantic angler. This reflects how the economic estimation is sensitive to the specifics of WTP surveys as well as social and cultural differences among anglers.

zu Ermgassen et al. (2016a) and Peterson et al. (2003) reported a fraction of production enhancement for species such as Southern Kingfish (*Menticirrhus americanus*), Southern Flounder (*Paralichthys lethostigma*), Black Drum (*Pogonias cromis*), Cownose Ray (*Rhinoptera bonasus*), and Red drum (*Sciaenops ocellatus*) which utilize oyster reefs during later life stages (Powers et al. 2003). However, it is not known to what degree these species benefit from the reefs (zu Ermgassen et al. 2016a), so they were not included in my production estimation, potentially making my estimation more conservative. Separation of the enhanced fish into different categories in my study (harvestable, commercial and recreational fish) may also have improved the accuracy of the economic estimation. Kroeger (2012) estimated the economic impact (i.e., job creation, whole/retain sales) that restoration of two reefs in Mobile Bay would have on the commercial fishery as $39,000 per year (in 2010 dollars); based on my findings, inclusion of the impact on recreational fisheries would likely increase this estimate dramatically.

There is uncertainty from yearly variation in estimating the percentage share attributable to commercial and recreational fish production of enhanced species. De Mutsert et al. (2008) and Kroeger (2012) both cautioned against the usage of NOAA landing data for analysis because the data do not always reflect true fish population characters and actual catch rates. I acknowledged and treated these percentage shares as another source of uncertainty to foster greater confidence in production estimates for both commercial and recreational harvests.

Application of fish production enhancement estimates with associated uncertainty in Mobile Bay could assist the Alabama Department of Conservation and Natural Resources and other management agencies in providing inference regarding different benefits related to habitat restoration. The harvestable production estimate has management implications when evaluating the economic return of restoring or protecting oyster reefs; whereas the net production estimate provides a description of the ecological role that oyster reefs play in support of fish and crustaceans in the bay.

The economic estimation in my study provided a different view of the resources and could be used to justify public resource allocation in an effective and transparent manner toward oyster reef protection and restoration. The magnitude of the economic estimation depended on the valuation method especially for non-market resources like recreational fishing. The economic estimation in this study was conservative and should be considered as the lowest in terms of economic contribution of the oyster reefs to the fishery industry because of all of the indirect benefits which were excluded.

Henderson and O'Neil (2003) estimated that in terms of oyster harvest benefits it would take 14 years to recover the initial cost of new reef construction. Using the Henderson and O'Neil (2003) construction cost of \$53,000 ha^{-1} (in 2014 dollars), I estimated that it would take only about 5-6 years to recover the investment cost by the combination of oyster harvest and fish production enhancement. Other important services of oyster reefs which include nitrogen regulation, water clarity and shoreline stabilization have been qualified (Newell et al. 2005; Swann 2008; Scyphers et al. 2011; Carmichael et al. 2012; Pollack et al. 2013) and could be added to reduce the economic recovery time further.

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Table 2-1: Net, harvestable, commercial and recreational productions (g m^{-2} yr^{-1}) of enhanced species. The commercial share and its variation was retrieved from 11 years of landing data for Alabama water (NOAA-ALABAMA 2005-2015). The numbers are in format mean±1sd

	Net production enhancement g m^{-2} yr^{-1}	Harvestable g m^{-2} yr^{-1}	Commercial share %	Commercial production g m^{-2} yr^{-1}	Recreational production g m^{-2} yr^{-1}
Sheepshead *Archosargus probatocephalus*	125.39±66.95	78.48±54.84	18±9	14.16±13.15	64.32±45.80
Silver Perch *Bairdiella chrysoura*	19.28±16.59	17.12±16.75	0	0	17.12±16.75
Spadefish *Chaetodipterus faber*	3.97±2.63	3.91±2.65	16±15	0.62 ±0.82	3.28 ±2.34
Pinfish *Lagodon rhomboides*	22.56 ±12.35	14.69 ±12.41	0	0	14.69±12.41
Spot *Leiostomus xanthurus*	18.49±9.17	18.49±9.17	72±24	13.34±8.22	5.15±5.60
Pigfish *Orthopristis chrysoptera*	1.46±0.90	1.09±0.94	0	0	1.09±0.94
Darter goby *Ctenogobius boleosoma*	0.49±0.31	NA	NA	NA	NA
Skilletfish *Gobiesox strumosus*	2.23±1.08	NA	NA	NA	NA
Naked goby *Gobiosoma bosc*	1.46±0.64	NA	NA	NA	NA
Feather Blenny *Hypsoblennius hentz*	0.43±0.19	NA	NA	NA	NA
Freckled Blenny *Hypsoblennius ionthas*	2.08±1.34	NA	NA	NA	NA
Gulf Toadfish *Opsanus beta*	56.04±50.19	NA	NA	NA	NA
Stone crab *Menippe mercenaria*	27.86 ±21.35	NA	NA	NA	NA
Blue crab	72.40±104.44	36.41±62.39	100	36.41±62.39	0

Callinectes sapidus					
Brown shrimp *Farfantepenaeus aztecus*	NA	NA	NA	NA	NA
White shrimp *Litopanaeus setiferus*	NA	NA	NA	NA	NA
Total	**354.09 ±182.62**	**170.35±112.34**		**64.55 ±68.55**	**105.80 ±63.63**

Table 2-2: Commercial landing prices of enhanced species in Mobile Bay, Alabama. Landing prices were reported for 2014 data retrieved from NOAA-ALABAMA (2005-2015). The net value was 21% - 58% of the gross value which included costs such as labor, operation and maintenance. The numbers are in format mean±1sd are reported.

Common names/ *Scientific name*	Price $ g^{-1}	Commercial production g m^{-2} yr^{-1}	Gross value $ m^{-2} yr^{-1}	Net value $ m^{-2} yr^{-1}	
				21% ratio	58% ratio
Sheepshead *Archosargus probatocephalus*	0.00143	14.16±13.15	0.0203	0.0043	0.0117
Spadefish *Chaetodipterus faber*	0.00174	0.62±0.82	0.0011	0.0002	0.0006
Spot Croaker *Lagodon rhomboides*	0.00086	13.34±8.22	0.0115	0.0024	0.0066
Blue crab *Callinectes sapidus*	0.00245	36.41±62.39	0.0891	0.0187	0.0517
Total m^{-2}				0.0256±0.023	0.0707±0.063
Total ha^{-1}				256±230	707±630
Total in Mobile Bay				**267,597±240,350**	**739,077±658,350**

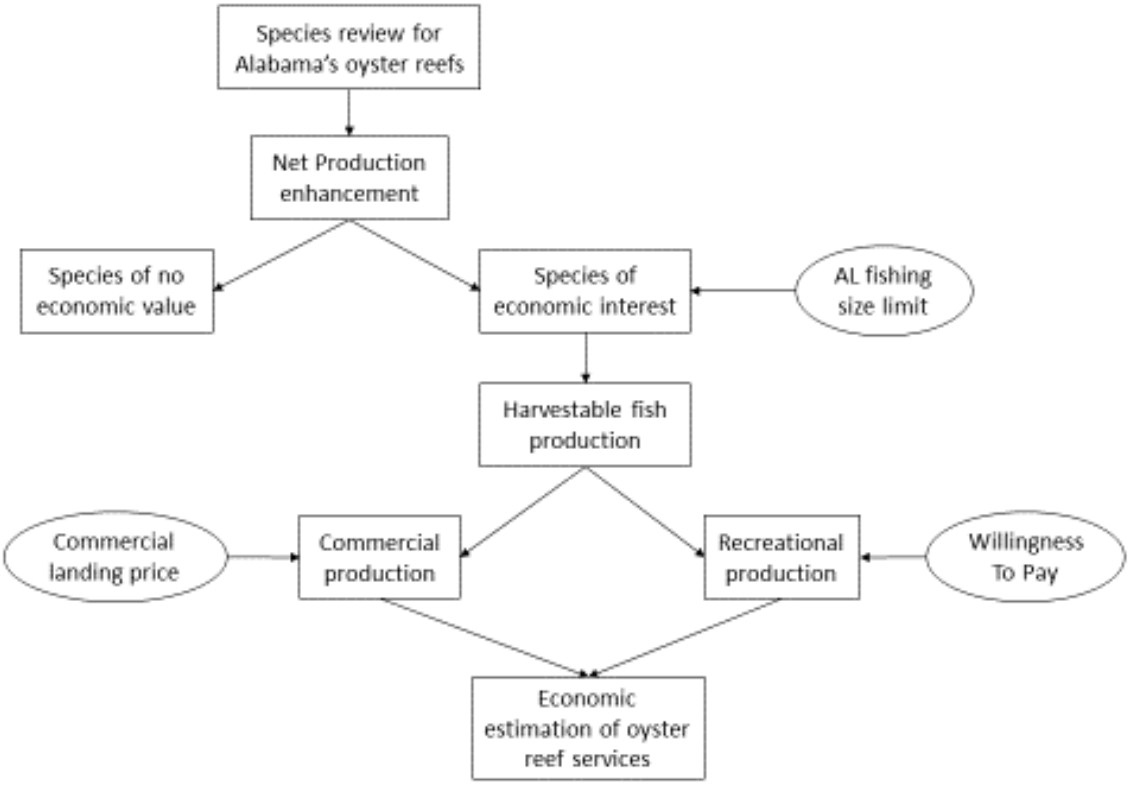

Figure 2-1: Flow chart showing the economic calculation procedures of fish and crustacean enhancement provided by oyster reefs in Mobile Bay, Alabama

Figure 2-2: Predicted length (cm) at age (von Bertalanffy model: Equation 1) of enhanced species from age-0.5 to tmax. All parameters used for the model are described in Appendix 2-1.

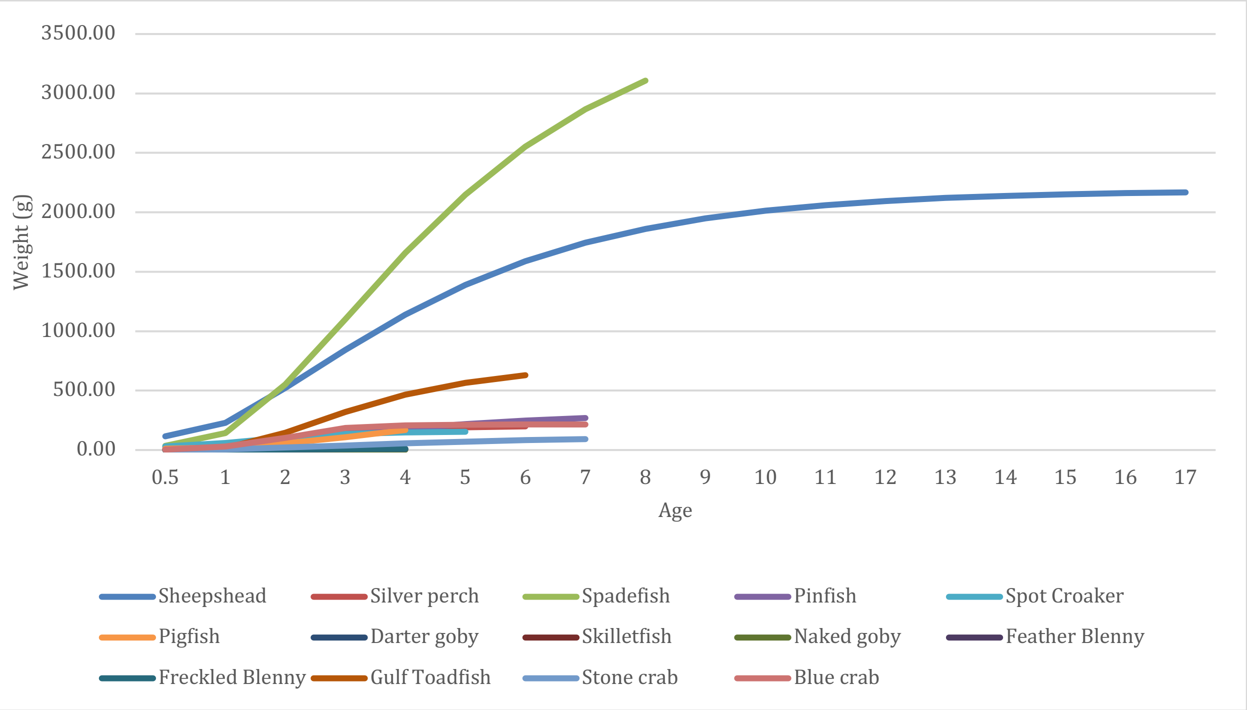

Figure 2-3: Predicted weight growth(g) at age (Equation 2) of enhanced species from age-0.5 to tmax. All parameters used for the model are described in Appendix 2-1.

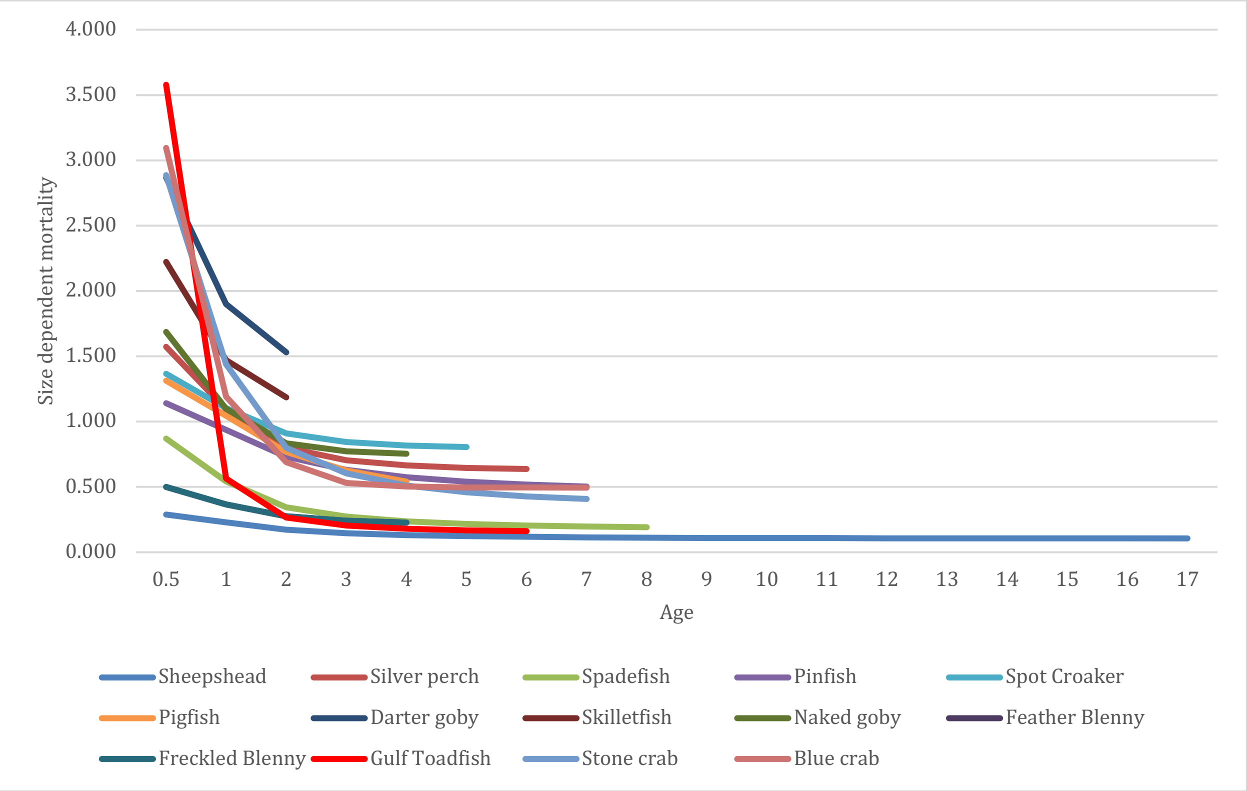

Figure 2-4: Predicted size dependent mortality of enhanced species (Equation 3) from age-0.5 to tmax. All parameters used for the model are described in Appendix 2-1.

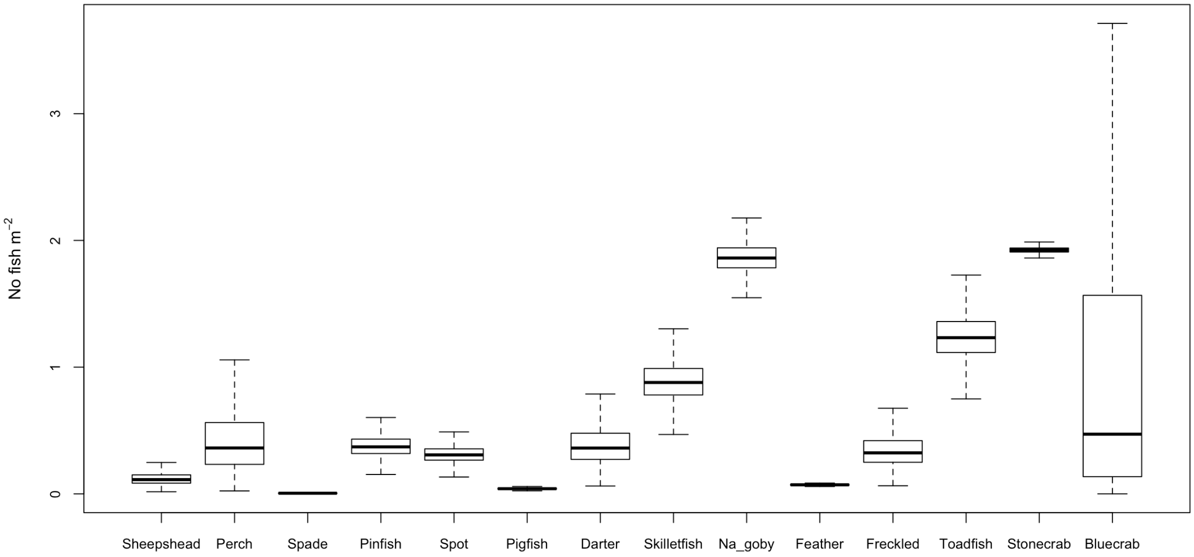

Figure 2-5: Densities of individual fish m^{-2} at age-0.5 for enhanced species. Data were published in zu Ermgassen et al. (2016a). The plot represents the mean, upper and lower quartiles and minimum and maximum generated from 100,000 draws. Outliers were removed from the plot.

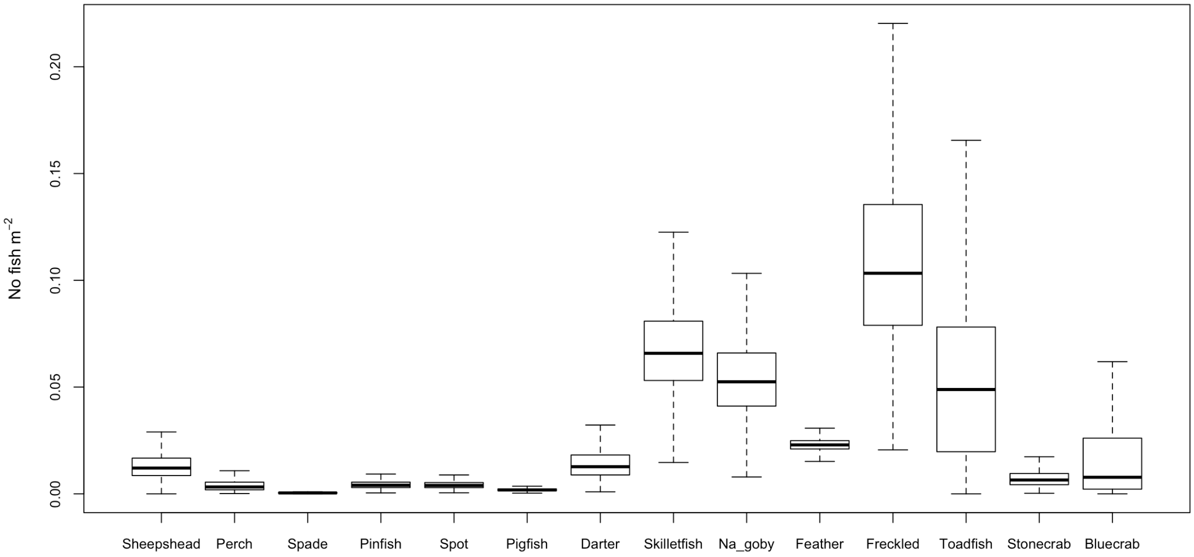

Figure 2-6: Predicted densities of individual fish m^{-2} at maximum age for enhanced species. The plot is the result of simulating from density from age-0.5 to their (each species) tmax and represents the mean, upper and lower quartiles and minimum and maximum from 100,000 simulation outcomes. Outliers were removed from the plot.

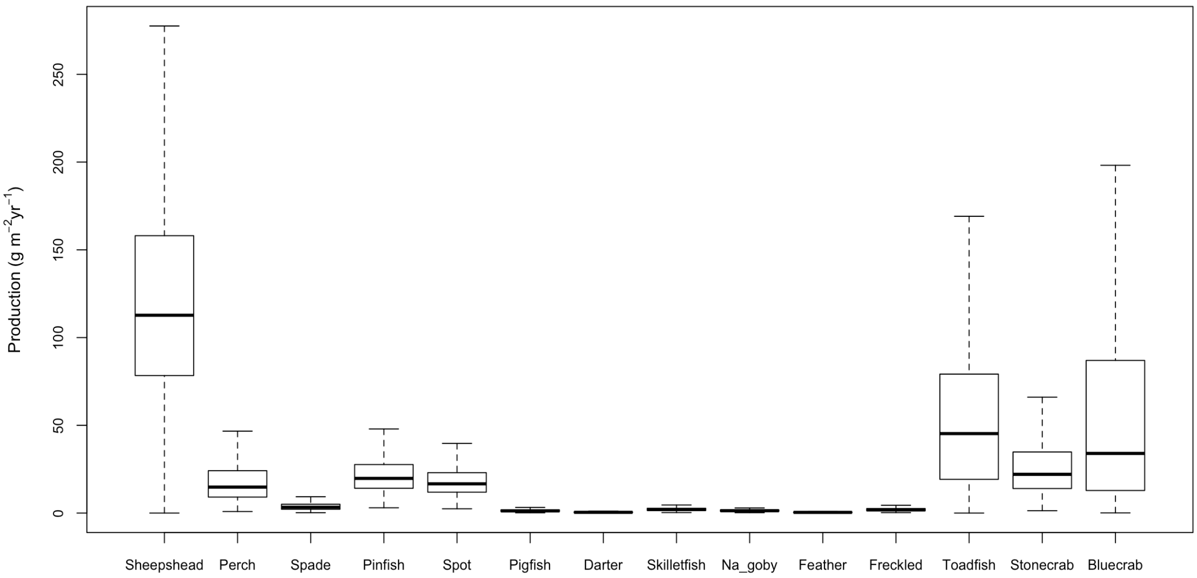

Figure 2-7: Predicted net production g m^{-2} yr^{-1} of enhanced species. The plot represents the mean, upper and lower quartiles and minimum and maximum from 100,000 outputs from model simulation. Outliers were removed from the plot.

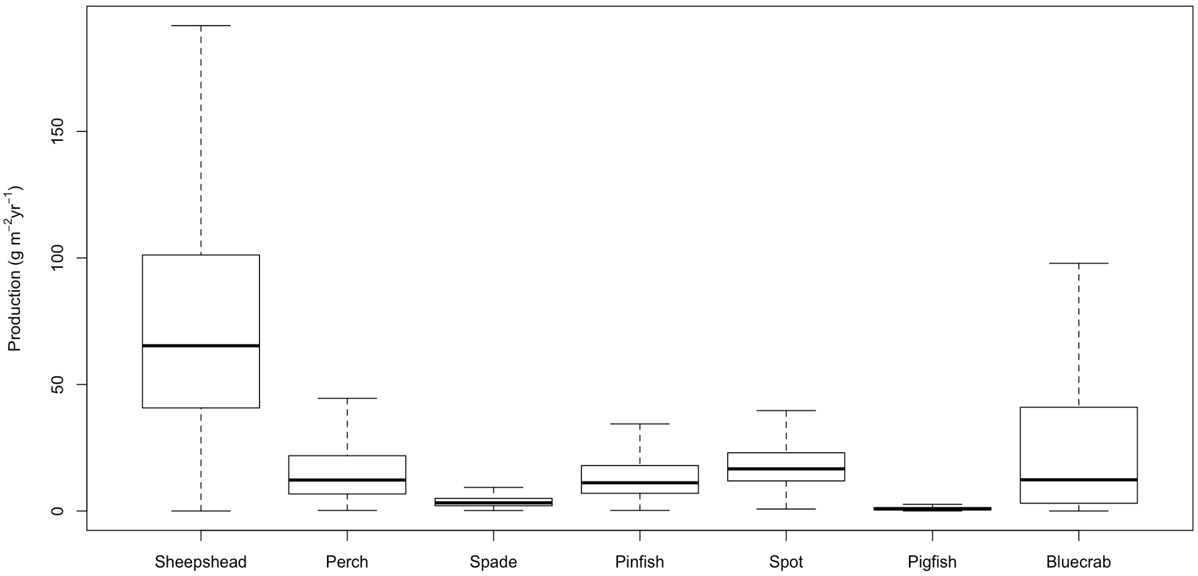

Figure 2-8: Predicted harvestable production (g m-2 yr-1) of the species that had economic value. The plot represents the mean, upper and lower quartiles and minimum and maximum from 100,000 outputs from model simulation. Outliers were removed from the plot.

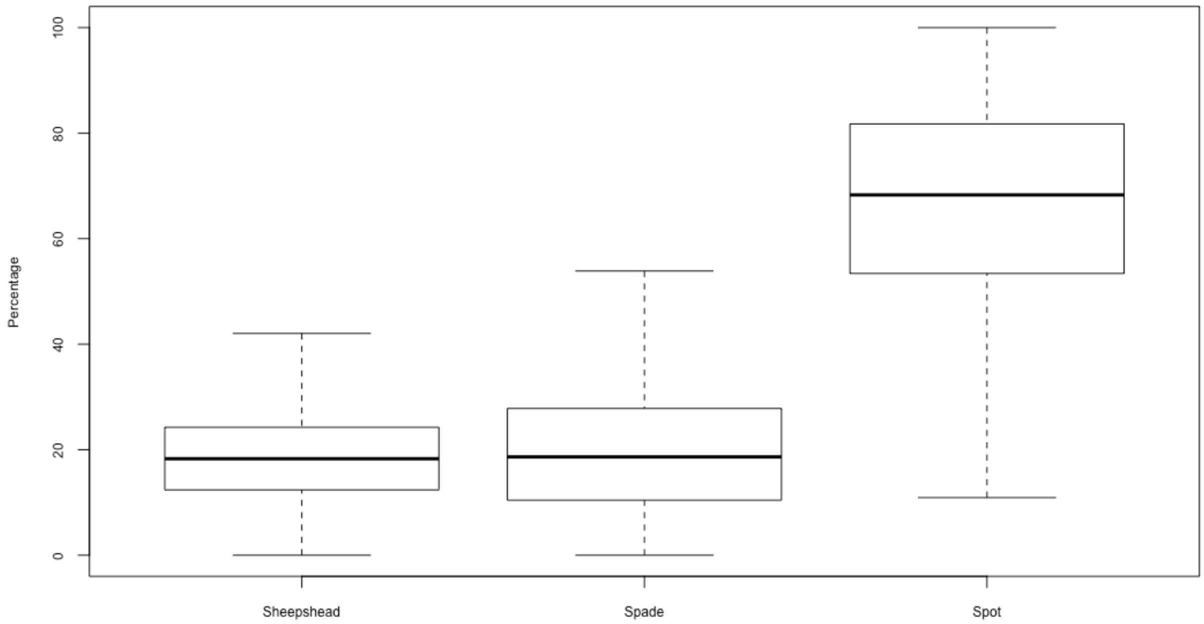

Figure 2-9: Commercial share (%) of three species which had both commercial and recreational values. The plot represents the mean, upper and lower quartiles and minimum and maximum from 100,000 draws using mean and standard deviation from 11 years commercial landing data 2005-2015 in Mobile Bay, Alabama (NOAA-ALABAMA 2005-2015). Outliers were removed from the plot.

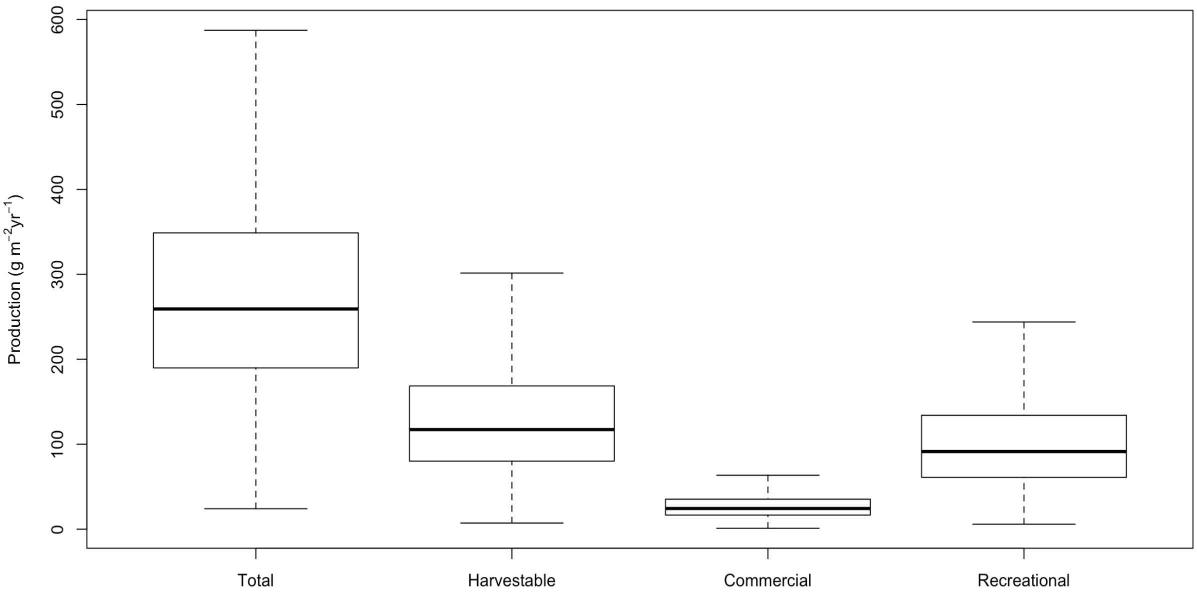

Figure 2-10: Total net production (g m^{-2} yr^{-1}), harvestable commercial and recreational of enhanced species. The plot is the graphical illustration of data from Table 2-1 and represents the mean, upper and lower quartiles and minimum and maximum.

Appendix 2-1: Life history parameters of enhanced species. M is natural mortality at maturity; L_∞ is the asymptotic maximum length; K is the Brody growth coefficient; and t_0 is the age at zero length, t_{max} is maximum age ($L_t = L_\infty\{1 – e^{[–K\,(t – t0\,)\,]}\}$, $L_{t:}$ length at age t); *a* and *b* are constant coefficients for weight and length relation ($W_t = aL_t^b$, W_t (g) is weight at age t); L_m (cm) is length at maturity (with asterisks is estimated from L_{inf}). Mean fish density (0.5-age ind m^{-2}) were derived from (zu Ermgassen et al. 2016a).

Study	Mean enhancement 0.5-age ind m^{-2}	L_{inf}	K	t0	a	b	tmax	M	Lm
Sheepshead *Archosargus probatocephalus*									
Murphy and MacDonald 2000		45.1	0.24	-1.170	0.0237	3.04	16	0.2	
VanderKooy 2006 - Alabama		49.1	0.32	-0.470					
Dutka-Gianelli and Murie 2001		49.0	0.26	-0.420	0.0342	2.89	15		24.0
Beckman et al. 1991		43.3	0.40	-0.965	0.0396	2.86	20		
Brown-Peterson et al. 2005		44.0	0.52	-1.294	0.0239	2.91			
Winner et al. 2017		41.9	0.27	-0.980	0.0310	2.93			
Average	0.139±0.101	45.4	0.33	-0.883	0.0305	2.93	17	0.2	24.0
Silver perch *Bairdiella chrysoura*									
Ayala-Pérez et al. 2006		27.0	0.69	-0.24	0.0114	3.00	6		10
Welsh and Breder 1923		23.0						1.39	15
Fishbase.org ±Froese, R., J. Thorson and R.B. Reyes Jr., 2013)		30.0			0.0107	3.08			9.3
Grammer et al. 2009		20.8							
Average	0.501±0.481	25.2	0.69	-0.24	0.0111	3.04	6	1.39	11.4
Spadefish *Chaetodipterus faber*									
Hayse 1990; Vianna et al. 2004		49.0	0.34	-0.18	0.0373	2.96	8	0.55	16
Average	0.006 ±0.004	49.0	0.34	-0.18	0.0373	2.96	8	0.55	16

Pinfish *Lagodon rhomboides*									
Nelson 2002		22.0	0.33	-1.10	0.0292	3.07	7	0.78	13.2
Muncy 1984					0.0355	2.90			
Average	0.415±0.209	22.0	0.33	-1.10	0.0323	2.99	7	0.78	13.2
Spot *Leiostomus xanthurus*									
zu Ermgassen et al. 2016		23.9	0.89	-0.04	0.0092	3.07	4	1.08	
Florida Fish and Wildlife Commission 2016		24.1	0.73	-1.13			6		
Average	0.342±0.167	24	0.81	-0.58	0.0092	3.07	5	1.08	17.7*
Pigfish *Orthopristis chrysoptera*									
Tpwd.texas.gov: *Orthopristis chrysoptera*		31.7							
zu Ermgassen et al. 2016		47.5	0.16	-1.14	0.0128	3.06	4	0.6	20
Average	0.044±0.018	39.6	0.16	-1.14	0.0128	3.06	4	0.6	20*
Darter Goby *Ctenogobius boleosoma*									
zu Ermgassen et al. 2016		8.0	1.46	0.02	0.0094	3.06	2	2.14	5.4*
Average	0.234±0.169	8.0	1.46	0.02	0.0094	3.06	2	2.14	5.4*
Skilletfish *Gobiesox strumosus*									
zu Ermgassen et al. 2016; Chesapeak Bay Program 2017		8.6	1.46	0.02	0.0128	3.04	2	2.14	4.5
Average	0.959±0.420	8.6	1.46	0.02	0.0128	3.04	2	2.14	4.5
Naked Goby *Gobiosoma bosc*									
zu Ermgassen et al. 2016		6.5	1.10	-0.03	0.0105	2.99	4	1.08	4.5*
Average	1.920±0.488	6.5	1.10	-0.03	0.0105	2.99	4	1.08	4.5*

Feather Blenny *Hypsoblennius hentz*									
zu Ermgassen et al. 2016; Ditty et al. 2005		10.7	0.62	-0.39	0.0110	2.96	4	1.08	2.1
Average	0.074±0.020	10.7	0.62	-0.39	0.0110	2.96	4	1.08	2.1
Freckled Blenny *Hypsoblennius ionthas*									
zu Ermgassen et al. 2016; Ditty et al. 2005		10.7	0.62	-0.39	0.0110	2.96	4	1.08	2.1
Average	0.392±0.269	10.7	0.62	-0.39	0.0110	2.96	4	1.08	2.1
Toadfish *Opsanus beta*									
Malca et al. 2009		29.6	0.55	0.42	0.0063	3.28	6	0.60	7.6
López et al. 2017					0.0389	2.82			
					0.0506	2.77			
Average	1.325±0.527	29.6	0.55	0.42	0.0320	2.96	6	0.60	7.6
Blue crab *Callinectes sapidus*									
Murphy et al. 2007		17.6	1.45	0.13	1.1474	1.86	6	1.00	9
					0.7634	2.1			4.7
					0.0040	1.87			12.5
					0.0055	2.14			
					0.1255	2.64			
					0.1080	2.77			
Average	1.317±3.093	17.6	1.45	0.13	0.3590	2.23			8.7
Stone crab *Menippe mercenaria*									
Gerhart and Bert 2008; zu Ermgassen et al. 2016		13.1	0.46	0.26	0.2885	3.05	7	0.7	7
Savage and Sullivan 1978; Peterson et al. 2003		14.0	0.17	-0.40	0.1170	3.30			
Average	1.936±0.214	13.6	0.31	0.07	0.2028	3.17	7	0.7	7
Brown shrimp *Farfantepenaeus aztecus*									
Arreguin-Sanchez 1999; Minello et al. 2008		19.1	1.14	-0.29	0.0071	3.07	2	18	
Average	1.036±0.627	19.1	1.14	-0.29	0.0071	3.07	2	18	

White shrimp *Litopanaeus setiferus*									
Arreguin-Sanchez 1999; Minello et al. 2008		19.1	1.14	-0.29	0.0065	3.00	2	18	
Average	4.640±2.726	19.1	1.14	-0.29	0.0065	3.00	2	18	

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Appendix 2-2. R codes

```
#####        Sheepshead     #######

## covariance for growth parameters of sheepshead

linf_sheepshead <- log(c(45.1,49.1, 49.0, 43.3, 44.0, 41.9))

k_sheepshead <- log(c(0.24, 0.32, 0.26, 0.40, 0.52, 0.27))

t0_sheepshead<- c(-1.170, -0.470, -0.420, -0.965, -1.294, -0.981)

P_Shep=cbind(linf_sheepshead,k_sheepshead,t0_sheepshead)

sigma_shep=cov(P_Shep)  ## variance-covariance matrix of growth-length: Sheepshead

cor_mat=cor(P_Shep) ## corelation matrix

P_mean_shep=apply(P_Shep,2,mean) ##  vector for mvt run

library(mvtnorm)

set.seed(1)

sheepshead=rmvnorm(n=100000,mean=P_mean_shep,sigma=sigma_shep) ## generate Von-Bert paramaeters for Sheepshead

hist(exp(sheepshead[,1]))

hist(exp(sheepshead[,2]))

hist(sheepshead[,3])


##Predict length at age - Von Bert

Linf_shep=matrix(rep(exp(sheepshead[,1])),nrow=length(sheepshead[,1]),ncol=18) ##  Length infinity of sheepshead

hist(Linf_shep)
```

```
K_shep=matrix(rep(exp(sheepshead[,2])),nrow=length(sheepshead[,2]),ncol=18) ##  Length infinity of sheepshead
hist(K_shep)
t0_shep=matrix(rep(sheepshead[,3]),nrow=length(sheepshead[,3]),ncol=18)  ## t0 of sheepshead
t0_shep[t0_shep>=0.5]=0.5 ## Constrain t0 so Length do no have nagetive value
hist(t0_shep)
age_shep=matrix(rep(c(0.5,1,2,3,4,5,6,7,8,9,10,11,12,13,14,15,16,17)),nrow=100000,ncol=18,byrow=TRUE)
L_shep=matrix(NA,nrow=100000,ncol=18,byrow=TRUE)
L_shep=Linf_shep*(1-exp(-K_shep*(age_shep-t0_shep)))
mean_length_shep=apply(L_shep,2,FUN=mean)
sd_length_shep=apply(L_shep,2,FUN=sd)
plot(mean_length_shep)
hist(L_shep)
matplot(t(apply(L_shep,2,quantile,c(0.025,0.5,0.975))),type='l')
summary(L_shep)

### covariance analysis of weight and length of sheepshead
a_Sheepshead=log(c(0.0237, 0.0342, 0.0396, 0.0239,  0.0310))
b_Sheepshead=log(c(3.040, 2.890,   2.860, 2.912, 2.930))
PW_Shep=cbind(a_Sheepshead,b_Sheepshead)
sigmaW_shep=cov(PW_Shep)  ## variance-covariance matrix of weight-length: Sheepshead
sigmaW_shep
```

```
Wcor_mat=cor(PW_Shep) ## correlation matrix for weight
PW_mean_shep=apply(PW_Shep,2,mean) ## vector for mvt run
set.seed(1)
sheepshead_W=rmvnorm(n=100000,mean=PW_mean_shep,sigma=sigmaW_shep) ## generate paramaeters
hist(exp(sheepshead_W[,2]))

## Predict Weight as function of length
a_Shep=matrix(rep(exp(sheepshead_W[,1])),nrow=100000,ncol=18) ## a coefficent for length weight relationship
hist(a_Shep)
b_Shep=matrix(rep(exp(sheepshead_W[,2])),nrow=100000,ncol=18)     ## b coefficent for length weight relationship
hist(b_Shep)
W_shep=matrix(NA,nrow=100000,ncol=18)
W_shep=a_Shep*L_shep^b_Shep          ## Length weight relationship
matplot(t(apply(W_shep,2,quantile,c(0.01,0.5,0.99))),type='l')
summary(W_shep)
W_increase_shep=matrix(NA,nrow=100000,ncol=18,byrow = TRUE) ## Weight increasement of Sheepshead
for(j in 1:100000) {
  W_increase_shep[j,1]=W_shep[j,1]
  for (i in 2:18) {
```

```
    W_increase_shep[j,i]=W_shep[j,i]-W_shep[j,i-1]
  }
  W_increase_shep
}
Lm_shep=24.03 ### Length at maturity
Mm_shep=0.2 ## natural mortality at size Lm
M_shep=Mm_shep*Lm_shep/L_shep ### Size dependent mortality
summary(M_shep)
summary(L_shep)
matplot(t(apply(M_shep,2,quantile,c(0.01,0.5,0.99),na.rm=T)),type='l')

## Density enhancement
set.seed(1)
mean05_Shep=0.139 ## Mean density enhancement of 0.5-year from Zu Ermgassen 2016
SE05_Shep=0.101 ## SE density enhancement of 0.5-year from Zu Ermgassen 2016
cv05_shep=SE05_Shep/mean05_Shep # coefficient of variation of 0.5-year density
shape2_Shep=log(1+cv05_shep^2) ## parameter for log normal distribution
shape1_Shep=log(mean05_Shep)-shape2_Shep/2 ## parameter for log normal distribution
hist(rlnorm(100000,shape1_Shep,shape2_Shep))
Ni_shep=matrix(NA,nrow=100000,ncol=18)
for (i in 3:18) {
  Ni_shep[,1]=rlnorm(100000,shape1_Shep,shape2_Shep) ### Density at age-0.5 per m2
  Ni_shep[,2]=Ni_shep[,1]*exp(-M_shep[,1]/2)     ### Density at age-1 per m2
```

```
  Ni_shep[,i]=Ni_shep[,i-1]*exp(-(M_shep[,i-1])) ### Density at age-2 per m2
}
matplot(t(apply(Ni_shep,2,quantile,c(0.00001,0.5,0.99))),type='l')
summary(Ni_shep) ### Density of Sheephead / m2
Pn_shep=matrix(NA,nrow = 100000,ncol = 18)
for (j in 1:100000) {
  for (i in 1:18) {
    Pn_shep[j,i]=Ni_shep[j,i]*W_increase_shep[j,i] ### Production of sheephead per m2
  }
}
Pn_shep
matplot(t(apply(Pn_shep,2,quantile,c(0.00001,0.5,0.99999),na.rm=T)),type='l')
summary(Pn_shep)
mean_Pn_shep_total=mean(apply(Pn_shep,1,FUN=sum)) ##  mean of Sheepshead production
SD_Pn_shep_total=sd(apply(Pn_shep,1,FUN=sum)) ## SD of Sheepshead production
L_shep_underharvest=ifelse(L_shep<30.5,0,1) ## Create a matrix to remove under harvest size limit
Pn_shep_harvest=apply(Pn_shep*L_shep_underharvest,1,FUN=sum)   # mean harvestable production
mean(apply(Pn_shep*L_shep_underharvest,1,FUN=sum))
sd(apply(Pn_shep*L_shep_underharvest,1,FUN=sum))


#### Beta distribution for commercial and recreational shares
```

```
beta.commercial.percent<-function(mu,sd){
a=mu*(mu*(1-mu)/sd^2-1)
b<-(1-mu)*((mu*(1-mu)/sd^2)-1)
c(a,b)
}
beta_shep=beta.commercial.percent(0.18,0.09) ## Beta for sheeepshead
set.seed(1)
Pn_shep_commercial_share=rbeta(100000,beta_shep[1],beta_shep[2]) ## Generate commercial share
hist(Pn_shep_commercial_share)
Pn_shep_commercial_production=mean(Pn_shep_harvest*Pn_shep_commercial_share) ### Generate mean of commercial production
sd(Pn_shep_harvest*Pn_shep_commercial_share) ### Generate SD of commercial production
Pn_shep_recreational_share=1-Pn_shep_commercial_share ## Generate recreational share
Pn_shep_recreational_production=mean(Pn_shep_harvest*Pn_shep_recreational_share) ### mean of recreational production
sd(Pn_shep_harvest*Pn_shep_recreational_share) ###  SD of recreational production

########        Silver Perch        #######
## Length at age
P_mean_Per=c(25.2,0.69,-0.24) ## Mean value of Linf, K0 and t0 of Silver Perch
cv_perch=0.10         ## 10% variance of the mean
log_Para_Perch=sqrt(log(1+rep(cv_perch,3)^2)) ## correct for the log scale of Linf, K0
```

```
log_Para_Perch[3]=0.24*0.10 ## t0 in normal scale = 10% variance of the mean
sigma_Per=log_Para_Perch%o%log_Para_Perch*cor_mat
library(mvtnorm)
set.seed(1)
SilverPerch=rmvnorm(n=100000,mean=c(log(P_mean_Per[1:2]),P_mean_Per[3]),sigma=sigma_
Per)
hist(exp(SilverPerch[,1]))
hist(exp(SilverPerch[,2]))
hist(SilverPerch[,3])
Linf_per=matrix(rep(exp(SilverPerch[,1])),nrow=length(SilverPerch[,1]),ncol=18) ##  Length
infinity of Per
hist(Linf_per)
K_per=matrix(rep(exp(SilverPerch[,2])),nrow=length(SilverPerch[,2]),ncol=18) ##  K for Per
hist(K_per)
t0_per=matrix(rep(SilverPerch[,3]),nrow=length(SilverPerch[,3]),ncol=18)  ## t0 of Per
hist(t0_per)
age_per=matrix(rep(c(0.5,1,2,3,4,5,6,6,6,6,6,6,6,6,6,6,6,6)),nrow=100000,ncol=18,byrow=TRU
E) ## Extend tmax to longest live species: 17 years
L_per=matrix(NA,nrow=100000,ncol=18,byrow=TRUE)
L_per=Linf_per*(1-exp(-K_per*(age_per-t0_per))) ## Von Bert Length at age
mean_length_per=apply(L_per,2,FUN=mean)
plot(mean_length_per)
hist(L_per)
```

```
matplot(t(apply(L_per,2,quantile,c(0.025,0.5,0.975))),type='l')
summary(L_per)


## Weight at age
PW_mean_Per=c(0.0111,3.04) ## Mean value of a and b for weight growth of Silver Perch
W_cv_perch=c(0.1,0.05) ## 10% and 5% variance of mean
W_log_Para_Perch=sqrt(log(1+W_cv_perch^2)) ## correct for the log scale of a and b
sigmaW_Per=W_log_Para_Perch%o%W_log_Para_Perch*Wcor_mat
SilverPerch_W=rmvnorm(n=100000,mean=c(log(PW_mean_Per[1:2])),sigma=sigmaW_Per)
diag(sigmaW_Per)[1:2]/2),sigma=sigmaW_Per)
hist(exp(SilverPerch_W[,1]))
hist(exp(SilverPerch_W1[,1]))
hist(exp(SilverPerch_W[,2]))
hist(exp(SilverPerch_W1[,2]))
a_Per=matrix(rep(exp(SilverPerch_W[,1])),nrow=100000,ncol=18) ## a coefficent for length
weight relationship
b_Per=matrix(rep(exp(SilverPerch_W[,2])),nrow=100000,ncol=18)     ## b coefficent for length
weight relationship
W_per=matrix(NA,nrow=100000,ncol=18)
W_per=a_Per*L_per^b_Per          ## Length weight relationship
matplot(t(apply(W_per,2,quantile,c(0.01,0.5,0.99))),type='l')
mean_W_per=apply(W_per,2,FUN=mean)
plot(mean_W_per)
```

```
W_increase_per=matrix(NA,nrow=100000,ncol=18,byrow = TRUE) ## Weight increasement of Perch
for(j in 1:100000) {
  W_increase_per[j,1]=W_per[j,1]
  for (i in 2:18) {
    W_increase_per[j,i]=W_per[j,i]-W_per[j,i-1]
  }
  W_increase_per
}
matplot(t(apply(W_increase_per,2,quantile,c(0.01,0.5,0.99))),type='l')
summary(W_increase_per)
Lm_per=11.4  ## Length at maturity
Mm_per=1.39 ## Natural mortality at Length at maturity
M_per=Mm_per*Lm_per/L_per ## Size dependent mortality
summary(M_per)
matplot(t(apply(M_per,2,quantile,c(0.01,0.5,0.99),na.rm=T)),type='l')
mean_M_per=apply(M_per,2,FUN=mean)
plot(mean_M_per)

## Density enhancement
mean05_Per=0.501 ## Mean density enhancement of 0.5-year fish from Zu Ermgassen 2016
SE05_Per=0.481 ## SE density enhancement of 0.5-year from Zu Ermgassen 2016
cv05_per=SE05_Per/mean05_Per # coefficient of variation of 0.5-year density
```

```
shape2_per=log(1+(cv05_per^2)) ## parameter for log normal distribution

shape1_per=log(mean05_Per)-shape2_per/2 ## parameter for log normal distribution

hist(rlnorm(100000,shape1_per,shape2_per))

Ni_per=matrix(NA,nrow=100000,ncol=18)

for (i in 3:18) {

  Ni_per[,1]=rlnorm(100000,shape1_per,shape2_per) ### Density at age-0.5 per m2

  Ni_per[,2]=Ni_per[,1]*exp(-M_per[,1]/2)     ### Density at age-1 per m2

  Ni_per[,i]=Ni_per[,i-1]*exp(-(M_per[,i-1])) ### Density at age-2 per m2

}

matplot(t(apply(Ni_per,2,quantile,c(0.00001,0.5,0.99))),type='l')

summary(Ni_per) ### Density of Silverperch / m2

Pn_per=matrix(NA,nrow = 100000,ncol = 18)

for (j in 1:100000) {

  for (i in 1:18) {

    Pn_per[j,i]=Ni_per[j,i]*W_increase_per[j,i] ### Production of SilverPerch per m2

  }


}

Pn_per

matplot(t(apply(Pn_per,2,quantile,c(0.00001,0.5,0.99999),na.rm=T)),type='l')

summary(Pn_per)

mean_Pn_per_total=mean(apply(Pn_per,1,FUN=sum)) ##  mean of Silver Perch production

SD_Pn_per_total=sd(apply(Pn_per,1,FUN=sum)) ## SD of Silver Perch production
```

```
L_per_underharvest=ifelse(L_per<10,0,1) ## Create a matrix to remove under harvest size limit
Pn_per_harvest=apply(Pn_per*L_per_underharvest,1,FUN=sum)   # mean harvestable production
mean(apply(Pn_per*L_per_underharvest,1,FUN=sum))
sd(apply(Pn_per*L_per_underharvest,1,FUN=sum))

#################  Spadefishes    #######
## Length at age
P_mean_spad=c(49,0.34,-0.18) ## Mean value of Linf, K0 and t0 of Spadefishes
cv_spad=0.1         ## CV of Spadefishes from literature
log_Para_spad=sqrt(log(1+rep(cv_spad,2)^2)) ## correct for the log scale of Linf, K0
log_Para_spad[3]=0.18*0.1 ## t0 in normal scale from report
sigma_spad=log_Para_spad%o%log_Para_spad*cor_mat
library(mvtnorm)
Spadefishes=rmvnorm(n=100000,mean=c(log(P_mean_spad[1:2]),P_mean_spad[3]),sigma=sigma_spad)
hist(exp(Spadefishes[,1]))
hist(exp(Spadefishes[,2]))
hist(Spadefishes[,3])
Linf_spad=matrix(rep(exp(Spadefishes[,1])),nrow=length(Spadefishes[,1]),ncol=18) ##  Length infinity
K_spad=matrix(rep(exp(Spadefishes[,2])),nrow=length(Spadefishes[,2]),ncol=18) ##  K infinity
t0_spad=matrix(rep(Spadefishes[,3]),nrow=length(Spadefishes[,3]),ncol=18)  ## t0
```

```
hist(t0_spad)
age_spad=matrix(rep(c(0.5,1,2,3,4,5,6,7,8,8,8,8,8,8,8,8,8,8)),nrow=100000,ncol=18,byrow=TR
UE) ## Extend tmax to longest live species: 17 years
L_spad=matrix(NA,nrow=100000,ncol=18,byrow=TRUE)
L_spad=Linf_spad*(1-exp(-K_spad*(age_spad-t0_spad))) ## Von Bert Length at age
mean_length_spad=apply(L_spad,2,FUN=mean)
plot(mean_length_spad)
hist(L_spad)
matplot(t(apply(L_spad,2,quantile,c(0.025,0.5,0.975))),type='l')
summary(L_spad)

## Weight at age
PW_mean_spad=c(0.0373,2.96) ## Mean value of a and b for weight growth of Spadfish
W_cv_spad=c(0.1,0.05)
W_log_Para_spad=sqrt(log(1+W_cv_spad^2)) ## correct for the log scale of Linf, K0
sigmaW_spad=W_log_Para_spad%o%W_log_Para_spad*Wcor_mat
Spadefishes_W=rmvnorm(n=100000,mean=c(log(PW_mean_spad[1:2])),sigma=sigmaW_spad)
hist(exp(Spadefishes_W[,1]))
hist(exp(Spadefishes_W[,2]))
a_spad=matrix(rep(exp(Spadefishes_W[,1])),nrow=100000,ncol=18) ## a coefficent for length
weight relationship
b_spad=matrix(rep(exp(Spadefishes_W[,2])),nrow=100000,ncol=18)     ## b coefficent for
length weight relationship
```

```
b_spad[b_spad>3.06]=3.06 ## constrain b not too hight (Fishbase.org) and replace by mean value
hist(b_spad)
W_spad=matrix(NA,nrow=100000,ncol=18)
W_spad=a_spad*L_spad^b_spad          ## Length weight relationship
matplot(t(apply(W_spad,2,quantile,c(0.01,0.5,0.99))),type='l')
mean_W_spad=apply(W_spad,2,FUN=mean)
plot(mean_W_spad)
W_increase_spad=matrix(NA,nrow=100000,ncol=18,byrow = TRUE) ## Weight increasement
for(j in 1:100000) {
  W_increase_spad[j,1]=W_spad[j,1]
  for (i in 2:18) {
    W_increase_spad[j,i]=W_spad[j,i]-W_spad[j,i-1]
  }
  W_increase_spad
}
matplot(t(apply(W_increase_spad,2,quantile,c(0.01,0.5,0.99))),type='l')
summary(W_increase_spad)
Lm_spad=16  ## Length at maturity
Mm_spad=0.55 ## Natural mortality at Length at maturity
M_spad=Mm_spad*Lm_spad/L_spad ## Size dependent mortality
summary(M_spad)
matplot(t(apply(M_spad,2,quantile,c(0.01,0.5,0.99),na.rm=T)),type='l')
```

```
## Density enhancement
set.seed(12)
mean05_spad=0.006 ## Mean density enhancement of 0.5-year fish from Zu Ermgassen 2016
SE05_spad=0.004 ## SE density enhancement of 0.5-year from Zu Ermgassen 2016
cv05_spad=SE05_spad/mean05_spad # coefficient of variation of 0.5-year density
shape2_spad=log(1+(cv05_spad^2)) ## parameter for log normal distribution
shape1_spad=log(mean05_spad)-shape2_spad/2 ## parameter for log normal distribution
hist(rlnorm(100000,shape1_spad,shape2_spad))
Ni_spad=matrix(NA,nrow=100000,ncol=18)
for (i in 3:18) {
  Ni_spad[,1]=rlnorm(100000,shape1_spad,shape2_spad) ### Density at age-0.5 per m2
  Ni_spad[,2]=Ni_spad[,1]*exp(-M_spad[,1]/2)     ### Density at age-1 per m2
  Ni_spad[,i]=Ni_spad[,i-1]*exp(-(M_spad[,i-1])) ### Density at age-2 per m2
}
matplot(t(apply(Ni_spad,2,quantile,c(0.00001,0.5,0.99))),type='l')
summary(Ni_spad) ### Density of Sheephead / m2
Pn_spad=matrix(NA,nrow = 100000,ncol = 18)
for (j in 1:100000) {
  for (i in 1:18) {
    Pn_spad[j,i]=Ni_spad[j,i]*W_increase_spad[j,i] ### Production of SilverPerch per m2
  }
```

```
}
Pn_spad
matplot(t(apply(Pn_spad,2,quantile,c(0.00001,0.5,0.99999),na.rm=T)),type='l')
summary(Pn_spad)
mean_Pn_spad_total=mean(apply(Pn_spad,1,FUN=sum)) ##  mean of Spadefish production
SD_Pn_spad_total=sd(apply(Pn_spad,1,FUN=sum)) ## SD of Spadefish production
L_spad_underharvest=ifelse(L_spad<10,0,1) ## Create a matrix to remove under harvest size
limit
Pn_spad_harvest=apply(Pn_spad*L_spad_underharvest,1,FUN=sum)   # mean harvestable
production
mean(apply(Pn_spad*L_spad_underharvest,1,FUN=sum))
sd(apply(Pn_spad*L_spad_underharvest,1,FUN=sum))
#### Beta distribution for commercial and recreational shares
beta_spad=beta.commercial.percent(0.16,0.15) ## Beta for Spadefish
set.seed(1)
Pn_spad_commercial_share=rbeta(100000,beta_spad[1],beta_spad[2]) ## Generate commercial
share
hist(Pn_spad_commercial_share)
Pn_spad_commercial_production=mean(Pn_spad_harvest*Pn_spad_commercial_share) ###
Generate mean of commercial production
sd(Pn_spad_harvest*Pn_spad_commercial_share) ### Generate SD of commercial production
Pn_spad_recreational_share=1-Pn_spad_commercial_share ## Generate recreational share
```

```
Pn_spad_recreational_production=mean(Pn_spad_harvest*Pn_spad_recreational_share) ### mean of recreational production
sd(Pn_spad_harvest*Pn_spad_recreational_share) ###  SD of recreational production


############# Pinfish ################
P_mean_Pin=c(22,0.33,-1.1) ## Mean value of Linf, K0 and t0 of Pinfish
cv_Pin=0.10         ## 10% variance of the mean
log_Para_Pin=sqrt(log(1+rep(cv_Pin,2)^2)) ## correct for the log scale of Linf, K0
log_Para_Pin[3]=1.1*0.10 ## t0 in normal scale = 10% variance of the mean
sigma_Pin=log_Para_Pin%o%log_Para_Pin*cor_mat
library(mvtnorm)
set.seed(1)
Pinfish=rmvnorm(n=100000,mean=c(log(P_mean_Pin[1:2]),P_mean_Pin[3]),sigma=sigma_Pin)
hist(exp(Pinfish[,1]))
hist(exp(Pinfish[,2]))
hist(Pinfish[,3])
Linf_pin=matrix(rep(exp(Pinfish[,1])),nrow=length(Pinfish[,1]),ncol=18) ##  Length infinity of Pin
K_pin=matrix(rep(exp(Pinfish[,2])),nrow=length(Pinfish[,2]),ncol=18) ##  K for Pin
t0_pin=matrix(rep(Pinfish[,3]),nrow=length(Pinfish[,3]),ncol=18)  ## t0 of Per
age_pin=matrix(rep(c(0.5,1,2,3,4,5,6,7,7,7,7,7,7,7,7,7,7,7)),nrow=100000,ncol=18,byrow=TRUE) ## Extend tmax to longest live species: 17 years
```

```
L_pin=matrix(NA,nrow=100000,ncol=18,byrow=TRUE)
L_pin=Linf_pin*(1-exp(-K_pin*(age_pin-t0_pin))) ## Von Bert Length at age
mean_length_pin=apply(L_pin,2,FUN=mean)
## Weight at age
PW_mean_Pin=c(0.0323,2.986) ## Mean value of a and b for weight growth of Pinfish
W_cv_pin=c(0.1,0.05) ## 10% and 5% variance of mean
W_log_Para_Pin=sqrt(log(1+W_cv_pin^2)) ## correct for the log scale of a and b
sigmaW_Pin=W_log_Para_Pin%o%W_log_Para_Pin*Wcor_mat
Pinfish_W=rmvnorm(n=100000,mean=c(log(PW_mean_Pin[1:2])),sigma=sigmaW_Pin)
hist(exp(Pinfish_W[,1]))
hist(exp(Pinfish_W[,2]))
a_Pin=matrix(rep(exp(Pinfish_W[,1])),nrow=100000,ncol=18) ## a coefficent for length weight
relationship
b_Pin=matrix(rep(exp(Pinfish_W[,2])),nrow=100000,ncol=18)     ## b coefficent for length
weight relationship
W_pin=matrix(NA,nrow=100000,ncol=18)
W_pin=a_Pin*L_pin^b_Pin          ## Length weight relationship
matplot(t(apply(W_pin,2,quantile,c(0.01,0.5,0.99))),type='l')
W_increase_pin=matrix(NA,nrow=100000,ncol=18,byrow = TRUE) ## Weight increasement of
Pin
for(j in 1:100000) {
  W_increase_pin[j,1]=W_pin[j,1]
  for (i in 2:18) {
```

```
    W_increase_pin[j,i]=W_pin[j,i]-W_pin[j,i-1]
  }
  W_increase_pin
}
Lm_pin=13.2  ## Length at maturity
Mm_pin=0.78 ## Natural mortality at Length at maturity
M_pin=Mm_pin*Lm_pin/L_pin ## Size dependent mortality
## Density enhancement
mean05_Pin=0.415## Mean density enhancement of 0.5-year fish from Zu Ermgassen 2016
SE05_Pin=0.209 ## SE density enhancement of 0.5-year from Zu Ermgassen 2016
cv05_pin=SE05_Pin/mean05_Pin # coefficient of variation of 0.5-year density
shape2_pin=log(1+(cv05_pin^2)) ## parameter for log normal distribution
shape1_pin=log(mean05_Pin)-shape2_pin/2 ## parameter for log normal distribution
hist(rlnorm(100000,shape1_pin,shape2_pin))
Ni_pin=matrix(NA,nrow=100000,ncol=18)
for (i in 3:18) {
  Ni_pin[,1]=rlnorm(100000,shape1_pin,shape2_pin) ### Density at age-0.5 per m2
  Ni_pin[,2]=Ni_pin[,1]*exp(-M_pin[,1]/2)     ### Density at age-1 per m2
  Ni_pin[,i]=Ni_pin[,i-1]*exp(-(M_pin[,i-1])) ### Density at age-2 per m2
}
matplot(t(apply(Ni_pin,2,quantile,c(0.00001,0.5,0.99))),type='l')
Pn_pin=matrix(NA,nrow = 100000,ncol = 18)
for (j in 1:100000) {
```

```
  for (i in 1:18) {

    Pn_pin[j,i]=Ni_pin[j,i]*W_increase_pin[j,i] ### Production of Pinfish per m2

  }


}

Pn_pin

matplot(t(apply(Pn_pin,2,quantile,c(0.00001,0.5,0.99999),na.rm=T)),type='l')

summary(Pn_pin)

mean_Pn_pin_total=mean(apply(Pn_pin,1,FUN=sum)) ##  mean of Pinfish production

SD_Pn_pin_total=sd(apply(Pn_pin,1,FUN=sum)) ## SD of Pinfish production

L_pin_underharvest=ifelse(L_pin<10,0,1) ## Create a matrix to remove under harvest size limit

Pn_pin_harvest=apply(Pn_pin*L_pin_underharvest,1,FUN=sum)   # mean harvestable
production

mean(apply(Pn_pin*L_pin_underharvest,1,FUN=sum))

sd(apply(Pn_pin*L_pin_underharvest,1,FUN=sum))


#############     Spot       ###########

P_mean_spot=c(24,0.81,-0.585) ## Mean value of Linf, K0 and t0 of spot

cv_spot=0.10         ## 10% variance of the mean

log_Para_spot=sqrt(log(1+rep(cv_spot,2)^2)) ## correct for the log scale of Linf, K0

log_Para_spot[3]=0.585*0.10 ## t0 in normal scale = 10% variance of the mean

sigma_spot=log_Para_spot%o%log_Para_spot*cor_mat

library(mvtnorm)
```

```
set.seed(1)
Spotfish=rmvnorm(n=100000,mean=c(log(P_mean_spot[1:2]),P_mean_spot[3]),sigma=sigma_spot)
hist(exp(Spotfish[,1]))
hist(exp(Spotfish[,2]))
hist(Spotfish[,3])
Linf_spot=matrix(rep(exp(Spotfish[,1])),nrow=length(Spotfish[,1]),ncol=18) ##  Length infinity of Spot
K_spot=matrix(rep(exp(Spotfish[,2])),nrow=length(Spotfish[,2]),ncol=18) ##  K for Spot
t0_spot=matrix(rep(Spotfish[,3]),nrow=length(Spotfish[,3]),ncol=18)  ## t0 of Spot
age_spot=matrix(rep(c(0.5,1,2,3,5,5,5,5,5,5,5,5,5,5,5,5,5,5)),nrow=100000,ncol=18,byrow=TRUE) ## Extend tmax to longest live species: 17 years
L_spot=matrix(NA,nrow=100000,ncol=18,byrow=TRUE)
L_spot=Linf_spot*(1-exp(-K_spot*(age_spot-t0_spot))) ## Von Bert Length at age
mean_length_spot=apply(L_spot,2,FUN=mean)
matplot(t(apply(L_spot,2,quantile,c(0.025,0.5,0.975))),type='l')
summary(L_spot)
## Weight at age
PW_mean_spot=c(0.0092,3.07) ## Mean value of a and b for weight growth of Spot
W_cv_spot=c(0.1,0.05) ## 10% and 5% variance of mean
W_log_Para_spot=sqrt(log(1+W_cv_spot^2)) ## correct for the log scale of a and b
sigmaW_spot=W_log_Para_spot%o%W_log_Para_spot*Wcor_mat
Spotfish_W=rmvnorm(n=100000,mean=c(log(PW_mean_spot[1:2])),sigma=sigmaW_spot)
```

```
hist(exp(Spotfish_W[,1]))
hist(exp(Spotfish_W[,2]))
a_spot=matrix(rep(exp(Spotfish_W[,1])),nrow=100000,ncol=18) ## a coefficent for length
weight relationship
b_spot=matrix(rep(exp(Spotfish_W[,2])),nrow=100000,ncol=18)    ## b coefficent for length
weight relationship
b_spot[b_spot>3.23]=3.23
hist(b_spot)
W_spot=matrix(NA,nrow=100000,ncol=18)
W_spot=a_spot*L_spot^b_spot        ## Length weight relationship
matplot(t(apply(W_spot,2,quantile,c(0.01,0.5,0.99))),type='l')
summary(W_spot)
W_increase_spot=matrix(NA,nrow=100000,ncol=18,byrow = TRUE) ## Weight increasement
of Perch
for(j in 1:100000) {
  W_increase_spot[j,1]=W_spot[j,1]
  for (i in 2:18) {
    W_increase_spot[j,i]=W_spot[j,i]-W_spot[j,i-1]
  }
}
matplot(t(apply(W_increase_spot,2,quantile,c(0.01,0.5,0.99))),type='l')
summary(W_increase_spot)
Lm_spot=17.7  ## Length at maturity
```

```
Mm_spot=1.08 ## Natural mortality at Length at maturity

M_spot=Mm_spot*Lm_spot/L_spot ## Size dependent mortality

## Density enhancement

mean05_spot=0.342 ## Mean density enhancement of 0.5-year fish from Zu Ermgassen 2016

SE05_spot=0.167 ## SE density enhancement of 0.5-year from Zu Ermgassen 2016

cv05_spot=SE05_spot/mean05_spot # coefficient of variation of 0.5-year density

shape2_spot=log(1+(cv05_spot^2)) ## parameter for log normal distribution

shape1_spot=log(mean05_spot)-shape2_spot/2 ## parameter for log normal distribution

hist(rlnorm(100000,shape1_spot,shape2_spot)) ##

Ni_spot=matrix(NA,nrow=100000,ncol=18)

for (i in 3:18) {

  Ni_spot[,1]=rlnorm(100000,shape1_spot,shape2_spot) ### Density at age-0.5 per m2

  Ni_spot[,2]=Ni_spot[,1]*exp(-M_spot[,1]/2)     ### Density at age-1 per m2

  Ni_spot[,i]=Ni_spot[,i-1]*exp(-(M_spot[,i-1])) ### Density at age-2 per m2

}

matplot(t(apply(Ni_spot,2,quantile,c(0.00001,0.5,0.99))),type='l')

Pn_spot=matrix(NA,nrow = 100000,ncol = 18)

for (j in 1:100000) {

  for (i in 1:18) {

    Pn_spot[j,i]=Ni_spot[j,i]*W_increase_spot[j,i] ### Production of Spotfish per m2

  }


}
```

```
matplot(t(apply(Pn_spot,2,quantile,c(0.00001,0.5,0.99999),na.rm=T)),type='l')
summary(Pn_spot)
mean_Pn_spot_total=mean(apply(Pn_spot,1,FUN=sum)) ##  mean of Spotfish production
SD_Pn_spot_total=sd(apply(Pn_spot,1,FUN=sum)) ## SD of Spotfish production
L_spot_underharvest=ifelse(L_spot<10,0,1) ## Create a matrix to remove under harvest size
limit
Pn_spot_harvest=apply(Pn_spot*L_spot_underharvest,1,FUN=sum)   # mean harvestable
production
mean(apply(Pn_spot*L_spot_underharvest,1,FUN=sum))
sd(apply(Pn_spot*L_spot_underharvest,1,FUN=sum))
#### Beta distribution for commercial and recreational shares
beta_spot=beta.commercial.percent(0.72,0.24) ## Beta for spotfish
set.seed(1)
Pn_spot_commercial_share=rbeta(100000,beta_spot[1],beta_spot[2]) ## Generate commercial
share
hist(Pn_spot_commercial_share)
Pn_spot_commercial_production=mean(Pn_spot_harvest*Pn_spot_commercial_share) ###
Generate mean of commercial production
sd(Pn_spot_harvest*Pn_spot_commercial_share) ### Generate SD of commercial production
Pn_spot_recreational_share=1-Pn_spot_commercial_share ## Generate recreational share
Pn_spot_recreational_production=mean(Pn_spot_harvest*Pn_spot_recreational_share) ###
mean of recreational production
sd(Pn_spot_harvest*Pn_spot_recreational_share) ###  SD of recreational production
```

```
#####      Pigfish ###########
## Length at age
P_mean_Pig=c(39.6,0.16,-1.14) ## Mean value of Linf, K0 and t0 of Pigfish
cv_pig=0.10      ## 10% variance of the mean
log_Para_Pig=sqrt(log(1+rep(cv_pig,2)^2)) ## correct for the log scale of Linf, K0
log_Para_Pig[3]=1.14*0.10 ## t0 in normal scale = 5% variance of the mean
sigma_Pig=log_Para_Pig%o%log_Para_Pig*cor_mat
library(mvtnorm)
set.seed(10)
Pigfish=rmvnorm(n=100000,mean=c(log(P_mean_Pig[1:2]),P_mean_Pig[3]),sigma=sigma_Pig)
hist(exp(Pigfish[,1]))
hist(exp(Pigfish[,2]))
hist(Pigfish[,3])
Linf_pig=matrix(rep(exp(Pigfish[,1])),nrow=length(Pigfish[,1]),ncol=18) ##  Length infinity of Pig
K_pig=matrix(rep(exp(Pigfish[,2])),nrow=length(Pigfish[,2]),ncol=18) ##  K for Pig
t0_pig=matrix(rep(Pigfish[,3]),nrow=length(Pigfish[,3]),ncol=18)  ## t0 of Pig
age_pig=matrix(rep(c(0.5,1,2,3,4,4,4,4,4,4,4,4,4,4,4,4,4,4)),nrow=100000,ncol=18,byrow=TRUE) ## Extend tmax to longest live species: 17 years
L_pig=matrix(NA,nrow=100000,ncol=18,byrow=TRUE)
L_pig=Linf_pig*(1-exp(-K_pig*(age_pig-t0_pig))) ## Von Bert Length at age
mean_length_pig=apply(L_pig,2,FUN=mean)
```

```
matplot(t(apply(L_pig,2,quantile,c(0.025,0.5,0.975))),type='l')

## Weight at age

PW_mean_Pig=c(0.0128,3.06) ## Mean value of a and b for weight growth of Pig

W_cv_pig=c(0.1,0.05) ## 10% and 5% variance of mean

W_log_Para_Pig=sqrt(log(1+W_cv_pig^2)) ## correct for the log scale of a and b

sigmaW_Pig=W_log_Para_Pig%o%W_log_Para_Pig*Wcor_mat

Pigfish_W=rmvnorm(n=100000,mean=c(log(PW_mean_Pig[1:2])),sigma=sigmaW_Pig)

hist(exp(Pigfish_W[,1]))

hist(exp(Pigfish_W[,2]))

a_Pig=matrix(rep(exp(Pigfish_W[,1])),nrow=100000,ncol=18) ## a coefficent for length weight
relationship

b_Pig=matrix(rep(exp(Pigfish_W[,2])),nrow=100000,ncol=18)     ## b coefficent for length
weight relationship

W_pig=matrix(NA,nrow=100000,ncol=18)

W_pig=a_Pig*L_pig^b_Pig          ## Length weight relationship

matplot(t(apply(W_pig,2,quantile,c(0.01,0.5,0.99))),type='l')

mean_W_pig=apply(W_pig,2,FUN=mean)

W_increase_pig=matrix(NA,nrow=100000,ncol=18,byrow = TRUE) ## Weight increasement of
Pig

for(j in 1:100000) {

  W_increase_pig[j,1]=W_pig[j,1]

  for (i in 2:18) {

    W_increase_pig[j,i]=W_pig[j,i]-W_pig[j,i-1]
```

```
  }
  W_increase_pig
}
matplot(t(apply(W_increase_pig,2,quantile,c(0.01,0.5,0.99))),type='l')
Lm_pig=20  ## Length at maturity
Mm_pig=0.6 ## Natural mortality at Length at maturity
M_pig=Mm_pig*Lm_pig/L_pig ## Size dependent mortality
matplot(t(apply(M_pig,2,quantile,c(0.01,0.5,0.99))),type='l')
## Density enhancement
mean05_Pig=0.044 ## Mean density enhancement of 0.5-year fish from Zu Ermgassen 2016
SE05_Pig=0.018 ## SE density enhancement of 0.5-year from Zu Ermgassen 2016
cv05_pig=SE05_Pig/mean05_Pig # coefficient of variation of 0.5-year density
shape2_pig=log(1+(cv05_pig^2)) ## parameter for log normal distribution
shape1_pig=log(mean05_Pig)-shape2_pig/2 ## parameter for log normal distribution
hist(rlnorm(100000,shape1_pig,shape2_pig))
Ni_pig=matrix(NA,nrow=100000,ncol=18)
for (i in 3:18) {
  Ni_pig[,1]=rlnorm(100000,shape1_pig,shape2_pig) ### Density at age-0.5 per m2
  Ni_pig[,2]=Ni_pig[,1]*exp(-M_pig[,1]/2)     ### Density at age-1 per m2
  Ni_pig[,i]=Ni_pig[,i-1]*exp(-(M_pig[,i-1])) ### Density at age-2 per m2
}
matplot(t(apply(Ni_pig,2,quantile,c(0.00001,0.5,0.99))),type='l')
Pn_pig=matrix(NA,nrow = 100000,ncol = 18)
```

```
for (j in 1:100000) {
  for (i in 1:18) {
    Pn_pig[j,i]=Ni_pig[j,i]*W_increase_pig[j,i] ### Production of Pigfish per m2
  }

}
matplot(t(apply(Pn_pig,2,quantile,c(0.00001,0.5,0.99999))),type='l')
mean_Pn_pig_total=mean(apply(Pn_pig,1,FUN=sum)) ##  mean of Pigfish production
SD_Pn_pig_total=sd(apply(Pn_pig,1,FUN=sum)) ## SD of Pigfish production
L_pig_underharvest=ifelse(L_pig<10,0,1) ## Create a matrix to remove under harvest size limit
Pn_pig_harvest=apply(Pn_pig*L_pig_underharvest,1,FUN=sum)   # mean harvestable
production
mean(apply(Pn_pig*L_pig_underharvest,1,FUN=sum))
sd(apply(Pn_pig*L_pig_underharvest,1,FUN=sum))
######       Darter goby #######
P_mean_Dar=c(8,1.46,0.02) ## Mean value of Linf, K0 and t0 of Darter goby
cv_Dar=0.10         ## 10% variance of the mean
log_Para_Dar=sqrt(log(1+rep(cv_Dar,3)^2)) ## correct for the log scale of Linf, K0
log_Para_Dar[3]=0.02*0.10 ## t0 in normal scale = 10% variance of the mean
sigma_Dar=log_Para_Dar%o%log_Para_Dar*cor_mat
library(mvtnorm)
set.seed(11)
```

```
Dartergoby=rmvnorm(n=100000,mean=c(log(P_mean_Dar[1:2]),P_mean_Dar[3]),sigma=sigma_Dar)
hist(exp(Dartergoby[,1]))
hist(exp(Dartergoby[,2]))
hist(Dartergoby[,3])
Linf_Dar=matrix(rep(exp(Dartergoby[,1])),nrow=length(Dartergoby[,1]),ncol=18) ##  Length infinity of Darter goby
K_Dar=matrix(rep(exp(Dartergoby[,2])),nrow=length(Dartergoby[,2]),ncol=18) ##  K for
t0_Dar=matrix(rep(Dartergoby[,3]),nrow=length(Dartergoby[,3]),ncol=18)  ## t0 of
age_Dar=matrix(rep(c(0.5,1,2,2,2,2,2,2,2,2,2,2,2,2,2,2,2,2)),nrow=100000,ncol=18,byrow=TRUE) ## Extend tmax to longest live species: 17 years
L_Dar=matrix(NA,nrow=100000,ncol=18,byrow=TRUE)
L_Dar=Linf_Dar*(1-exp(-K_Dar*(age_Dar-t0_Dar))) ## Von Bert Length at age
mean_length_Dar=apply(L_Dar,2,FUN=mean)
## Weight at age
PW_mean_Dar=c(0.0094,3.06) ## Mean value of a and b for weight growth of Darter goby
W_cv_Dar=c(0.1,0.05) ## 10% and 5% variance of mean
W_log_Para_Dar=sqrt(log(1+W_cv_Dar^2)) ## correct for the log scale of a and b
sigmaW_Dar=W_log_Para_Dar%o%W_log_Para_Dar*Wcor_mat
Dartergoby_W=rmvnorm(n=100000,mean=c(log(PW_mean_Dar[1:2])),sigma=sigmaW_Dar)
hist(exp(Dartergoby_W[,1]))
hist(exp(Dartergoby_W[,2]))
```

```
a_Dar=matrix(rep(exp(Dartergoby_W[,1])),nrow=100000,ncol=18) ## a coefficent for length
weight relationship
b_Dar=matrix(rep(exp(Dartergoby_W[,2])),nrow=100000,ncol=18)     ## b coefficent for length
weight relationship
W_Dar=matrix(NA,nrow=100000,ncol=18)
W_Dar=a_Dar*L_Dar^b_Dar          ## Length weight relationship
matplot(t(apply(W_Dar,2,quantile,c(0.01,0.5,0.99))),type='l')
W_increase_Dar=matrix(NA,nrow=100000,ncol=18,byrow = TRUE) ## Weight increasement of
Perch
for(j in 1:100000) {
  W_increase_Dar[j,1]=W_Dar[j,1]
  for (i in 2:18) {
    W_increase_Dar[j,i]=W_Dar[j,i]-W_Dar[j,i-1]
  }
  W_increase_Dar
}
matplot(t(apply(W_increase_Dar,2,quantile,c(0.01,0.5,0.99))),type='l')
Lm_Dar=5.4 ### Length at maturity
Mm_Dar=2.14 ## natural mortality at size Lm
M_Dar=Mm_Dar*Lm_Dar/L_Dar ### Size dependent mortality
matplot(t(apply(M_Dar,2,quantile,c(0.01,0.5,0.99))),type='l')
## Density enhancement
mean05_Dar=0.234 ## Mean density enhancement of 0.5-year fish from Zu Ermgassen 2016
```

```
SE05_Dar=0.169 ## SE density enhancement of 0.5-year from Zu Ermgassen 2016
cv05_Dar=SE05_Dar/mean05_Dar # coefficient of variation of 0.5-year density
shape2_Dar=log(1+(cv05_Dar^2)) ## parameter for log normal distribution
shape1_Dar=log(mean05_Dar)-shape2_Dar/2 ## parameter for log normal distribution
hist(rlnorm(100000,shape1_Dar,shape2_Dar))
Ni_Dar=matrix(NA,nrow=100000,ncol=18)
for (i in 3:18) {
  Ni_Dar[,1]=rlnorm(100000,shape1_per,shape2_Dar) ### Density at age-0.5 per m2
  Ni_Dar[,2]=Ni_Dar[,1]*exp(-M_Dar[,1]/2)     ### Density at age-1 per m2
  Ni_Dar[,i]=Ni_Dar[,i-1]*exp(-(M_Dar[,i-1])) ### Density at age-2 per m2
}
matplot(t(apply(Ni_Dar,2,quantile,c(0.00001,0.5,0.99))),type='l')
summary(Ni_Dar) ### Density of Silverperch / m2
Pn_Dar=matrix(NA,nrow = 100000,ncol = 18)
for (j in 1:100000) {
  for (i in 1:18) {
    Pn_Dar[j,i]=Ni_Dar[j,i]*W_increase_Dar[j,i] ### Production of Darter goby per m2
  }


}
matplot(t(apply(Pn_Dar,2,quantile,c(0.00001,0.5,0.99999))),type='l')
summary(Pn_Dar)
mean_Pn_Dar_total=mean(apply(Pn_Dar,1,FUN=sum)) ##  mean of Darter goby production
```

```
SD_Pn_Dar_total=sd(apply(Pn_Dar,1,FUN=sum)) ## SD of Darter goby production

#######      Skilletfish      ####
P_mean_Skil=c(8.6,1.46,0.02) ## Mean value of Linf, K0 and t0 of Skilletfish
cv_Skil=0.10         ## 10% variance of the mean
log_Para_Skil=sqrt(log(1+rep(cv_Skil,3)^2)) ## correct for the log scale of Linf, K0
log_Para_Skil[3]=0.02*0.10 ## t0 in normal scale = 10% variance of the mean
sigma_Skil=log_Para_Skil%o%log_Para_Skil*cor_mat
library(mvtnorm)
set.seed(1)
Skilletfish=rmvnorm(n=100000,mean=c(log(P_mean_Skil[1:2]),P_mean_Skil[3]),sigma=sigma_Skil)
hist(exp(Skilletfish[,1]))
hist(exp(Skilletfish[,2]))
hist(Skilletfish[,3])
Linf_Skil=matrix(rep(exp(Skilletfish[,1])),nrow=length(Skilletfish[,1]),ncol=18) ##  Length infinity of Skilletfish
K_Skil=matrix(rep(exp(Skilletfish[,2])),nrow=length(Skilletfish[,2]),ncol=18) ##  K for Per
t0_Skil=matrix(rep(Skilletfish[,3]),nrow=length(Skilletfish[,3]),ncol=18)  ## t0 of Per
age_Skil=matrix(rep(c(0.5,1,2,2,2,2,2,2,2,2,2,2,2,2,2,2,2,2)),nrow=100000,ncol=18,byrow=TRUE) ## Extend tmax to longest live species: 17 years
L_Skil=matrix(NA,nrow=100000,ncol=18,byrow=TRUE)
L_Skil=Linf_Skil*(1-exp(-K_Skil*(age_Skil-t0_Skil))) ## Von Bert Length at age
```

```
mean_length_Skil=apply(L_Skil,2,FUN=mean)
hist(L_Skil)
matplot(t(apply(L_Skil,2,quantile,c(0.025,0.5,0.975))),type='l')
summary(L_Skil)
## Weight at age
PW_mean_Skil=c(0.0128,3.04) ## Mean value of a and b for weight growth of Skilletfish
W_cv_Skil=c(0.1,0.05) ## 10% and 5% variance of mean
W_log_Para_Skil=sqrt(log(1+W_cv_Skil^2)) ## correct for the log scale of a and b
sigmaW_Skil=W_log_Para_Skil%o%W_log_Para_Skil*Wcor_mat
Skilletfish_W=rmvnorm(n=100000,mean=c(log(PW_mean_Skil[1:2])),sigma=sigmaW_Skil)
hist(exp(Skilletfish_W[,1]))
hist(exp(Skilletfish_W[,2]))
a_Skil=matrix(rep(exp(Skilletfish_W[,1])),nrow=100000,ncol=18) ## a coefficent for length weight relationship
b_Skil=matrix(rep(exp(Skilletfish_W[,2])),nrow=100000,ncol=18)     ## b coefficent for length weight relationship
W_Skil=matrix(NA,nrow=100000,ncol=18)
W_Skil=a_Skil*L_Skil^b_Skil          ## Length weight relationship
matplot(t(apply(W_Skil,2,quantile,c(0.01,0.5,0.99))),type='l')
mean_W_Skil=apply(W_Skil,2,FUN=mean)
plot(mean_W_Skil)
W_increase_Skil=matrix(NA,nrow=100000,ncol=18,byrow = TRUE) ## Weight increasement of Skil
```

```
for(j in 1:100000) {
  W_increase_Skil[j,1]=W_Skil[j,1]
  for (i in 2:18) {
    W_increase_Skil[j,i]=W_Skil[j,i]-W_Skil[j,i-1]
  }
  W_increase_Skil
}
matplot(t(apply(W_increase_Skil,2,quantile,c(0.01,0.5,0.99))),type='l')
summary(W_increase_Skil)
Lm_Skil=4.5 ### Length at maturity
Mm_Skil=2.14 ## natural mortality at size Lm
M_Skil=Mm_Skil*Lm_Skil/L_Skil ### Size dependent mortality
## Density enhancement
mean05_Skil=0.959 ## Mean density enhancement of 0.5-year fish from Zu Ermgassen 2016
SE05_Skil=0.420 ## SE density enhancement of 0.5-year from Zu Ermgassen 2016
cv05_Skil=SE05_Skil/mean05_Skil # coefficient of variation of 0.5-year density
shape2_Skil=log(1+(cv05_Skil^2)) ## parameter for log normal distribution
shape1_Skil=log(mean05_Skil)-shape2_Skil/2 ## parameter for log normal distribution
hist(rlnorm(100000,shape1_Skil,shape2_Skil))
Ni_Skil=matrix(NA,nrow=100000,ncol=18)
for (i in 3:18) {
  Ni_Skil[,1]=rlnorm(100000,shape1_Skil,shape2_Skil) ### Density at age-0.5 per m2
  Ni_Skil[,2]=Ni_Skil[,1]*exp(-M_Skil[,1]/2)     ### Density at age-1 per m2
```

```
  Ni_Skil[,i]=Ni_Skil[,i-1]*exp(-(M_Skil[,i-1])) ### Density at age-2 per m2
}
Pn_Skil=matrix(NA,nrow = 100000,ncol = 18)
for (j in 1:100000) {
  for (i in 1:18) {
    Pn_Skil[j,i]=Ni_Skil[j,i]*W_increase_Skil[j,i] ### Production of Skil per m2
  }

}
mean_Pn_Skil_total=mean(apply(Pn_Skil,1,FUN=sum)) ## produce mean of total production
SD_Pn_Skil_total=sd(apply(Pn_Skil,1,FUN=sum)) ## produce SD of total production
#####         Naked goby   ####
P_mean_Nak=c(6.5,1.1,-0.03) ## Mean value of Linf, K0 and t0 of Naked goby
cv_Nak=0.10         ## 10% variance of the mean
log_Para_Nak=sqrt(log(1+rep(cv_Nak,3)^2)) ## correct for the log scale of Linf, K0
log_Para_Nak[3]=0.03*0.10 ## t0 in normal scale = 10% variance of the mean
sigma_Nak=log_Para_Nak%o%log_Para_Nak*cor_mat
library(mvtnorm)
set.seed(1)
Nakedgoby=rmvnorm(n=100000,mean=c(log(P_mean_Nak[1:2]),P_mean_Nak[3]),sigma=sigm
a_Nak)
hist(exp(Nakedgoby[,1]))
hist(exp(Nakedgoby[,2]))
```

```
hist(Nakedgoby[,3])
Linf_Nak=matrix(rep(exp(Nakedgoby[,1])),nrow=length(Nakedgoby[,1]),ncol=18) ##  Length
infinity of Nakedgoby
K_Nak=matrix(rep(exp(Nakedgoby[,2])),nrow=length(Nakedgoby[,2]),ncol=18) ##  K for
Nakedgoby
t0_Nak=matrix(rep(Nakedgoby[,3]),nrow=length(Nakedgoby[,3]),ncol=18)  ## t0 of Nakedgoby
age_Nak=matrix(rep(c(0.5,1,2,3,4,4,4,4,4,4,4,4,4,4,4,4,4,4)),nrow=100000,ncol=18,byrow=TRU
E) ## Extend tmax to longest live species: 17 years
L_Nak=matrix(NA,nrow=100000,ncol=18,byrow=TRUE)
L_Nak=Linf_Nak*(1-exp(-K_Nak*(age_Nak-t0_Nak))) ## Von Bert Length at age
mean_length_Nak=apply(L_Nak,2,FUN=mean)
hist(L_Nak)
matplot(t(apply(L_Nak,2,quantile,c(0.025,0.5,0.975))),type='l')
## Weight at age
PW_mean_Nak=c(0.0105,2.99) ## Mean value of a and b for weight growth of Naked goby
W_cv_Nak=c(0.1,0.05) ## 10% and 5% variance of mean
W_log_Para_Nak=sqrt(log(1+W_cv_Nak^2)) ## correct for the log scale of a and b
sigmaW_Nak=W_log_Para_Nak%o%W_log_Para_Nak*Wcor_mat
Nakedgoby_W=rmvnorm(n=100000,mean=c(log(PW_mean_Nak[1:2])),sigma=sigmaW_Nak)
hist(exp(Nakedgoby_W[,1]))
hist(exp(Nakedgoby_W[,2]))
a_Nak=matrix(rep(exp(Nakedgoby_W[,1])),nrow=100000,ncol=18) ## a coefficent for length
weight relationship
```

```
b_Nak=matrix(rep(exp(Nakedgoby_W[,2])),nrow=100000,ncol=18)     ## b coefficent for length weight relationship
W_Nak=matrix(NA,nrow=100000,ncol=18)
W_Nak=a_Nak*L_Nak^b_Nak          ## Length weight relationship
matplot(t(apply(W_Nak,2,quantile,c(0.01,0.5,0.99))),type='l')
mean_W_Nak=apply(W_Nak,2,FUN=mean)
plot(mean_W_Nak)
W_increase_Nak=matrix(NA,nrow=100000,ncol=18,byrow = TRUE) ## Weight increasement of Nak
for(j in 1:100000) {
  W_increase_Nak[j,1]=W_Nak[j,1]
  for (i in 2:18) {
    W_increase_Nak[j,i]=W_Nak[j,i]-W_Nak[j,i-1]
  }
  W_increase_Nak
}
matplot(t(apply(W_increase_Nak,2,quantile,c(0.01,0.5,0.99))),type='l')
Lm_Nak=4.5 ### Length at maturity
Mm_Nak=1.08 ## natural mortality at size Lm
M_Nak=Mm_Nak*Lm_Nak/L_Nak ### Size dependent mortality
## Density enhancement
mean05_Nak=1.920 ## Mean density enhancement of 0.5-year fish from Zu Ermgassen 2016
SE05_Nak=0.488 ## SE density enhancement of 0.5-year from Zu Ermgassen 2016
```

```
cv05_Nak=SE05_Nak/mean05_Nak # coefficient of variation of 0.5-year density
shape2_Nak=log(1+(cv05_Nak^2)) ## parameter for log normal distribution
shape1_Nak=log(mean05_Nak)-shape2_Nak/2 ## parameter for log normal distribution
hist(rlnorm(100000,shape1_Nak,shape2_Nak))
Ni_Nak=matrix(NA,nrow=100000,ncol=18)
for (i in 3:18) {
  Ni_Nak[,1]=rlnorm(100000,shape1_Nak,shape2_Nak) ### Density at age-0.5 per m2
  Ni_Nak[,2]=Ni_Nak[,1]*exp(-M_Nak[,1]/2)     ### Density at age-1 per m2
  Ni_Nak[,i]=Ni_Nak[,i-1]*exp(-(M_Nak[,i-1])) ### Density at age-2 per m2
}
Pn_Nak=matrix(NA,nrow = 100000,ncol = 18)
for (j in 1:100000) {
  for (i in 1:18) {
    Pn_Nak[j,i]=Ni_Nak[j,i]*W_increase_Nak[j,i] ### Production of Skil per m2
  }

}
Pn_Nak
mean_Pn_Nak_total=mean(apply(Pn_Nak,1,FUN=sum)) ##  mean of total production
SD_Pn_Nak_total=sd(apply(Pn_Nak,1,FUN=sum)) ##  SD of total production

##########   Feather Blenny ###########
P_mean_Fea=c(10.7,0.62,-0.39) ## Mean value of Linf, K0 and t0 of Feather Blenny
```

```
cv_Fea=0.10         ## 10% variance of the mean
log_Para_Fea=sqrt(log(1+rep(cv_Fea,3)^2)) ## correct for the log scale of Linf, K0
log_Para_Fea[3]=0.39*0.10 ## t0 in normal scale = 10% variance of the mean
sigma_Fea=log_Para_Fea%o%log_Para_Fea*cor_mat
library(mvtnorm)
set.seed(1)
FeatherBlenny=rmvnorm(n=100000,mean=c(log(P_mean_Fea[1:2]),P_mean_Fea[3]),sigma=sigma_Fea)
hist(exp(FeatherBlenny[,1]))
hist(exp(FeatherBlenny[,2]))
hist(FeatherBlenny[,3])
Linf_Fea=matrix(rep(exp(FeatherBlenny[,1])),nrow=length(FeatherBlenny[,1]),ncol=18) ## Length infinity of FeatherBlenny
K_Fea=matrix(rep(exp(FeatherBlenny[,2])),nrow=length(FeatherBlenny[,2]),ncol=18) ##  K for FeatherBlenny
t0_Fea=matrix(rep(FeatherBlenny[,3]),nrow=length(FeatherBlenny[,3]),ncol=18)  ## t0 of FeatherBlenny
age_Fea=matrix(rep(c(0.5,1,2,3,4,4,4,4,4,4,4,4,4,4,4,4,4,4)),nrow=100000,ncol=18,byrow=TRUE) ## Extend tmax to longest live species: 17 years
L_Fea=matrix(NA,nrow=100000,ncol=18,byrow=TRUE)
L_Fea=Linf_Fea*(1-exp(-K_Fea*(age_Fea-t0_Fea))) ## Von Bert Length at age
mean_length_Fea=apply(L_Fea,2,FUN=mean)
hist(L_Fea)
```

```
matplot(t(apply(L_Fea,2,quantile,c(0.025,0.5,0.975))),type='l')
## Weight at age
PW_mean_Fea=c(0.0110,2.96) ## Mean value of a and b for weight growth of Naked goby
W_cv_Fea=c(0.1,0.05) ## 10% and 5% variance of mean
W_log_Para_Fea=sqrt(log(1+W_cv_Fea^2)) ## correct for the log scale of a and b
sigmaW_Fea=W_log_Para_Fea%o%W_log_Para_Fea*Wcor_mat
FeatherBlenny_W=rmvnorm(n=100000,mean=c(log(PW_mean_Fea[1:2])),sigma=sigmaW_Fea)
hist(exp(FeatherBlenny_W[,1]))
hist(exp(FeatherBlenny_W[,2]))
a_Fea=matrix(rep(exp(FeatherBlenny_W[,1])),nrow=100000,ncol=18) ## a coefficent for length weight relationship
b_Fea=matrix(rep(exp(FeatherBlenny_W[,2])),nrow=100000,ncol=18)     ## b coefficent for length weight relationship
W_Fea=matrix(NA,nrow=100000,ncol=18)
W_Fea=a_Fea*L_Fea^b_Fea          ## Length weight relationship
matplot(t(apply(W_Fea,2,quantile,c(0.01,0.5,0.99))),type='l')
mean_W_Fea=apply(W_Fea,2,FUN=mean)
plot(mean_W_Fea)
W_increase_Fea=matrix(NA,nrow=100000,ncol=18,byrow = TRUE) ## Weight increasement of Fea
for(j in 1:100000) {
  W_increase_Fea[j,1]=W_Fea[j,1]
  for (i in 2:18) {
```

```
    W_increase_Fea[j,i]=W_Fea[j,i]-W_Fea[j,i-1]
  }
  W_increase_Fea
}
matplot(t(apply(W_increase_Fea,2,quantile,c(0.01,0.5,0.99))),type='l')
Lm_Fea=2.1 ### Length at maturity
Mm_Fea=1.08 ## natural mortality at size Lm
M_Fea=Mm_Fea*Lm_Fea/L_Fea ### Size dependent mortality
## Density enhancement
mean05_Fea=0.074 ## Mean density enhancement of 0.5-year fish from Zu Ermgassen 2016
SE05_Fea=0.020 ## SE density enhancement of 0.5-year from Zu Ermgassen 2016
cv05_Fea=SE05_Fea/mean05_Fea # coefficient of variation of 0.5-year density
shape2_Fea=log(1+(cv05_Fea^2)) ## parameter for log normal distribution
shape1_Fea=log(mean05_Fea)-shape2_Fea/2 ## parameter for log normal distribution
hist(rlnorm(100000,shape1_Fea,shape2_Fea))
Ni_Fea=matrix(NA,nrow=100000,ncol=18)
for (i in 3:18) {
  Ni_Fea[,1]=rlnorm(100000,shape1_Fea,shape2_Fea) ### Density at age-0.5 per m2
  Ni_Fea[,2]=Ni_Fea[,1]*exp(-M_Fea[,1]/2)     ### Density at age-1 per m2
  Ni_Fea[,i]=Ni_Fea[,i-1]*exp(-(M_Fea[,i-1])) ### Density at age-2 per m2
}
Pn_Fea=matrix(NA,nrow = 100000,ncol = 18)
for (j in 1:100000) {
```

```
  for (i in 1:18) {
    Pn_Fea[j,i]=Ni_Fea[j,i]*W_increase_Fea[j,i] ### Production of Fea per m2
  }

}
mean_Pn_Fea_total=mean(apply(Pn_Fea,1,FUN=sum)) ##  mean of total production
SD_Pn_Fea_total=sd(apply(Pn_Fea,1,FUN=sum)) ##  SD of total production
######## ###       Freckled Blenny ####
P_mean_Frec=c(10.7,0.62,-0.39) ## Mean value of Linf, K0 and t0 of Freckled Blenny
cv_Frec=0.10         ## 10% variance of the mean
log_Para_Frec=sqrt(log(1+rep(cv_Frec,3)^2)) ## correct for the log scale of Linf, K0
log_Para_Frec[3]=0.39*0.10 ## t0 in normal scale = 10% variance of the mean
sigma_Frec=log_Para_Frec%o%log_Para_Frec*cor_mat
library(mvtnorm)
set.seed(1)
FreckledBlenny=rmvnorm(n=100000,mean=c(log(P_mean_Frec[1:2]),P_mean_Frec[3]),sigma=
sigma_Frec)
hist(exp(FreckledBlenny[,1]))
hist(exp(FreckledBlenny[,2]))
hist(FreckledBlenny[,3])
Linf_Frec=matrix(rep(exp(FreckledBlenny[,1])),nrow=length(FreckledBlenny[,1]),ncol=18) ##
Length infinity of FeatherBlenny
```

```
K_Frec=matrix(rep(exp(FeatherBlenny[,2])),nrow=length(FreckledBlenny[,2]),ncol=18) ##  K for FreckledBlenny
t0_Frec=matrix(rep(FreckledBlenny[,3]),nrow=length(FreckledBlenny[,3]),ncol=18)  ## t0 of FreckledBlenny
age_Frec=matrix(rep(c(0.5,1,2,3,4,4,4,4,4,4,4,4,4,4,4,4,4,4)),nrow=100000,ncol=18,byrow=TRUE) ## Extend tmax to longest live species: 17 years
L_Frec=matrix(NA,nrow=100000,ncol=18,byrow=TRUE)
L_Frec=Linf_Frec*(1-exp(-K_Frec*(age_Frec-t0_Frec))) ## Von Bert Length at age
mean_length_Frec=apply(L_Frec,2,FUN=mean)
## Weight at age
PW_mean_Frec=c(0.0110,2.96) ## Mean value of a and b for weight growth of FreckledBlenny
W_cv_Frec=c(0.1,0.05) ## 10% and 5% variance of mean
W_log_Para_Frec=sqrt(log(1+W_cv_Frec^2)) ## correct for the log scale of a and b
sigmaW_Frec=W_log_Para_Frec%o%W_log_Para_Frec*Wcor_mat
FreckledBlenny_W=rmvnorm(n=100000,mean=c(log(PW_mean_Frec[1:2])),sigma=sigmaW_Frec)
hist(exp(FreckledBlenny_W[,1]))
hist(exp(FreckledBlenny_W[,2]))
a_Frec=matrix(rep(exp(FreckledBlenny_W[,1])),nrow=100000,ncol=18) ## a coefficent for length weight relationship
b_Frec=matrix(rep(exp(FreckledBlenny_W[,2])),nrow=100000,ncol=18)     ## b coefficent for length weight relationship
W_Frec=matrix(NA,nrow=100000,ncol=18)
```

```
W_Frec=a_Frec*L_Frec^b_Frec          ## Length weight relationship
W_increase_Frec=matrix(NA,nrow=100000,ncol=18,byrow = TRUE) ## Weight increasement of Fea
for(j in 1:100000) {
  W_increase_Frec[j,1]=W_Frec[j,1]
  for (i in 2:18) {
    W_increase_Frec[j,i]=W_Frec[j,i]-W_Frec[j,i-1]
  }
  W_increase_Frec
}
Lm_Frec=2.1 ### Length at maturity
Mm_Frec=1.08 ## natural mortality at size Lm
M_Frec=Mm_Frec*Lm_Frec/L_Frec ### Size dependent mortality
## Density enhancement
mean05_Frec=0.392 ## Mean density enhancement of 0.5-year fish from Zu Ermgassen 2016
SE05_Frec=0.269 ## SE density enhancement of 0.5-year from Zu Ermgassen 2016
cv05_Frec=SE05_Frec/mean05_Frec # coefficient of variation of 0.5-year density
shape2_Frec=log(1+(cv05_Frec^2)) ## parameter for log normal distribution
shape1_Frec=log(mean05_Frec)-shape2_Frec/2 ## parameter for log normal distribution
hist(rlnorm(100000,shape1_Frec,shape2_Frec))
Ni_Frec=matrix(NA,nrow=100000,ncol=18)
for (i in 3:18) {
  Ni_Frec[,1]=rlnorm(100000,shape1_Frec,shape2_Frec) ### Density at age-0.5 per m2
```

```
  Ni_Frec[,2]=Ni_Frec[,1]*exp(-M_Frec[,1]/2)     ### Density at age-1 per m2
  Ni_Frec[,i]=Ni_Frec[,i-1]*exp(-(M_Frec[,i-1])) ### Density at age-2 per m2
}
Pn_Frec=matrix(NA,nrow = 100000,ncol = 18)
for (j in 1:100000) {
  for (i in 1:18) {
    Pn_Frec[j,i]=Ni_Frec[j,i]*W_increase_Frec[j,i] ### Production of Fea per m2
  }

}
mean_Pn_Frec_total=mean(apply(Pn_Frec,1,FUN=sum)) ##
SD_Pn_Frec_total=sd(apply(Pn_Frec,1,FUN=sum)) ##

######## #####     Gulf Toadfish ###########
P_mean_Gulf=c(29.6,0.55,0.42) ## Mean value of Linf, K0 and t0 of Gulf Toadfish
cv_Gulf=0.10         ## 10% variance of the mean
log_Para_Gulf=sqrt(log(1+rep(cv_Gulf,3)^2)) ## correct for the log scale of Linf, K0
log_Para_Gulf[3]=0.42*0.10 ## t0 in normal scale = 10% variance of the mean
sigma_Gulf=log_Para_Gulf%o%log_Para_Gulf*cor_mat
library(mvtnorm)
set.seed(1)
GulfToadfish=rmvnorm(n=100000,mean=c(log(P_mean_Gulf[1:2]),P_mean_Gulf[3]),sigma=sig
ma_Gulf)
```

```
hist(exp(GulfToadfish[,1]))
hist(exp(GulfToadfish[,2]))
hist(GulfToadfish[,3])
Linf_Gulf=matrix(rep(exp(GulfToadfish[,1])),nrow=length(GulfToadfish[,1]),ncol=18) ## Length infinity of GulfToadfish
K_Gulf=matrix(rep(exp(GulfToadfish[,2])),nrow=length(GulfToadfish[,2]),ncol=18) ##  K for GulfToadfish
t0_Gulf=matrix(rep(GulfToadfish[,3]),nrow=length(GulfToadfish[,3]),ncol=18)  ## t0 of GulfToadfish
t0_Gulf[t0_Gulf>=0.5]=0.5
hist(t0_Gulf)
age_Gulf=matrix(rep(c(0.5,1,2,3,4,5,6,6,6,6,6,6,6,6,6,6,6,6)),nrow=100000,ncol=18,byrow=TRUE) ## Extend tmax to longest live species: 17 years
L_Gulf=matrix(NA,nrow=100000,ncol=18,byrow=TRUE)
L_Gulf=Linf_Gulf*(1-exp(-K_Gulf*(age_Gulf-t0_Gulf))) ## Von Bert Length at age
mean_length_Gulf=apply(L_Gulf,2,FUN=mean)
plot(mean_length_Gulf)
hist(L_Gulf)
matplot(t(apply(L_per,2,quantile,c(0.025,0.5,0.975))),type='l')
summary(L_Gulf)
## Weight at age
PW_mean_Gulf=c(0.032,2.96) ## Mean value of a and b for weight growth of Gulf Toadfish
W_cv_Gulf=c(0.1,0.05) ## 10% and 5% variance of mean
```

```
W_log_Para_Gulf=sqrt(log(1+W_cv_Gulf^2)) ## correct for the log scale of a and b
sigmaW_Gulf=W_log_Para_Gulf%o%W_log_Para_Gulf*Wcor_mat
GulfToadfish_W=rmvnorm(n=100000,mean=c(log(PW_mean_Gulf[1:2])),sigma=sigmaW_Gulf)
hist(exp(GulfToadfish_W[,1]))
hist(exp(GulfToadfish_W[,2]))
a_Gulf=matrix(rep(exp(GulfToadfish_W[,1])),nrow=100000,ncol=18) ## a coefficent for length weight relationship
b_Gulf=matrix(rep(exp(GulfToadfish_W[,2])),nrow=100000,ncol=18)     ## b coefficent for length weight relationship
b_Gulf[b_Gulf>3.2]=3.2
hist(b_Gulf)
W_Gulf=matrix(NA,nrow=100000,ncol=18)
W_Gulf=a_Gulf*L_Gulf^b_Gulf          ## Length weight relationship
summary(W_Gulf)
W_increase_Gulf=matrix(NA,nrow=100000,ncol=18,byrow = TRUE) ## Weight increasement of Fea
for(j in 1:100000) {
  W_increase_Gulf[j,1]=W_Gulf[j,1]
  for (i in 2:18) {
    W_increase_Gulf[j,i]=W_Gulf[j,i]-W_Gulf[j,i-1]
  }
  W_increase_Gulf
```

```
}
Lm_Gulf=7.6 ### Length at maturity
Mm_Gulf=0.6 ## natural mortality at size Lm
M_Gulf=Mm_Gulf*Lm_Gulf/L_Gulf ### Size dependent mortality
summary(M_Gulf)
matplot(t(apply(M_Gulf,2,quantile,c(0.01,0.5,0.99),na.rm=T)),type='l')
mean_M_Gulf=apply(M_Gulf,2,FUN=mean)
plot(mean_M_Gulf)
## Density enhancement
mean05_Gulf=1.325 ## Mean density enhancement of 0.5-year fish from Zu Ermgassen 2016
SE05_Gulf=0.527 ## SE density enhancement of 0.5-year from Zu Ermgassen 2016
cv05_Gulf=SE05_Gulf/mean05_Gulf # coefficient of variation of 0.5-year density
shape2_Gulf=log(1+(cv05_Gulf^2)) ## parameter for log normal distribution
shape1_Gulf=log(mean05_Gulf)-shape2_Gulf/2 ## parameter for log normal distribution
hist(rlnorm(100000,shape1_Gulf,shape2_Gulf))
Ni_Gulf=matrix(NA,nrow=100000,ncol=18)
for (i in 3:18) {
  Ni_Gulf[,1]=rlnorm(100000,shape1_Gulf,shape2_Gulf) ### Density at age-0.5 per m2
  Ni_Gulf[,2]=Ni_Gulf[,1]*exp(-M_Gulf[,1]/2)     ### Density at age-1 per m2
  Ni_Gulf[,i]=Ni_Gulf[,i-1]*exp(-(M_Gulf[,i-1])) ### Density at age-2 per m2
}
Pn_Gulf=matrix(NA,nrow = 100000,ncol = 18)
for (j in 1:100000) {
```

```
  for (i in 1:18) {
    Pn_Gulf[j,i]=Ni_Gulf[j,i]*W_increase_Gulf[j,i] ### Production of Gulf per m2
  }


}
mean_Pn_Gulf_total=mean(apply(Pn_Gulf,1,FUN=sum)) ##
SD_Pn_Gulf_total=sd(apply(Pn_Gulf,1,FUN=sum)) ##


########Blue crab###########
## Length at age
P_mean_blue=c(17.6,1.45,0.13) ## Mean value of Linf, K0 and t0 of Blue crab
cv_blue=0.10         ## 10% variance of the mean
log_Para_blue=sqrt(log(1+rep(cv_blue,3)^2)) ## correct for the log scale of Linf, K0
log_Para_blue[3]=0.13*0.10 ## t0 in normal scale = 10% variance of the mean
sigma_blue=log_Para_blue%o%log_Para_blue*cor_mat
library(mvtnorm)
set.seed(1)
Bluecrab=rmvnorm(n=100000,mean=c(log(P_mean_blue[1:2]),P_mean_blue[3]),sigma=sigma_blue)
hist(exp(Bluecrab[,1]))
hist(exp(Bluecrab[,2]))
hist(Bluecrab[,3])
```

```
Linf_blue=matrix(rep(exp(Bluecrab[,1])),nrow=length(Bluecrab[,1]),ncol=18) ##  Length infinity of Per
K_blue=matrix(rep(exp(Bluecrab[,2])),nrow=length(Bluecrab[,2]),ncol=18) ##  K for Per
t0_blue=matrix(rep(Bluecrab[,3]),nrow=length(Bluecrab[,3]),ncol=18)  ## t0 of Per
age_blue=matrix(rep(c(0.25,0.5,1,2,3,4,5,6,6,6,6,6,6,6,6,6,6,6)),nrow=100000,ncol=18,byrow=TRUE)
#age_blue=matrix(rep(c(0.25,0.5,1,2,3,3,3,3,3,3,3,3,3,3,3,3,3,3)),nrow=100000,ncol=18,byrow=TRUE) ## Extend tmax to longest live species: 17 years
L_blue=matrix(NA,nrow=100000,ncol=18,byrow=TRUE)
L_blue=Linf_blue*(1-exp(-K_blue*(age_blue-t0_blue))) ## Von Bert Length at age
mean_length_blue=apply(L_blue,2,FUN=mean)
hist(mean_length_blue)
summary(L_blue)
matplot(t(apply(L_blue,2,quantile,c(0.025,0.5,0.975))),type='l')
## Weight at age
PW_mean_blue=c(0.359,2.23) ## Mean value of a and b for weight growth of Blue crab
W_cv_blue=c(0.1,0.05) ## 10% and 5% variance of mean
W_log_Para_blue=sqrt(log(1+W_cv_blue^2)) ## correct for the log scale of a and b
sigmaW_blue=W_log_Para_blue%o%W_log_Para_blue*Wcor_mat
Bluecrab_W=rmvnorm(n=100000,mean=c(log(PW_mean_blue[1:2])),sigma=sigmaW_blue)
hist(exp(Bluecrab_W[,1]))
hist(exp(Bluecrab_W[,2]))
```

```
a_blue=matrix(rep(exp(Bluecrab_W[,1])),nrow=100000,ncol=18) ## a coefficent for length
weight relationship
b_blue=matrix(rep(exp(Bluecrab_W[,2])),nrow=100000,ncol=18)     ## b coefficent for length
weight relationship
W_blue=matrix(NA,nrow=100000,ncol=18)
W_blue=a_blue*L_blue^b_blue          ## Length weight relationship
summary(W_blue)
mean_W_blue=apply(W_blue,2,FUN=mean)
plot(mean_W_blue)
matplot(t(apply(W_blue,2,quantile,c(0.01,0.5,0.99))),type='l')
W_increase_blue=matrix(NA,nrow=100000,ncol=18,byrow = TRUE) ## Weight increasement
of Perch
for(j in 1:100000) {
  W_increase_blue[j,1]=W_blue[j,1]
  for (i in 2:18) {
    W_increase_blue[j,i]=W_blue[j,i]-W_blue[j,i-1]
  }
}
summary(W_increase_blue)
matplot(t(apply(W_increase_blue,2,quantile,c(0.01,0.5,0.99))),type='l')
Lm_blue=8.7  ## Length at maturity
Mm_blue=1 ## Natural mortality at Length at maturity
M_blue=Mm_blue*Lm_blue/L_blue ## Size dependent mortality
```

```
matplot(t(apply(M_blue,2,quantile,c(0.00001,0.5,0.99))),type='l')
## Density enhancement
mean05_blue=1.317 ## Mean density enhancement of 0.5-year fish from Zu Ermgassen 2016
SE05_blue=3.093 ## SE density enhancement of 0.5-year from Zu Ermgassen 2016
cv05_blue=SE05_blue/mean05_blue # coefficient of variation of 0.5-year density
shape2_blue=log(1+(cv05_blue^2)) ## parameter for log normal distribution
shape1_blue=log(mean05_blue)-shape2_blue/2 ## parameter for log normal distribution
hist(rlnorm(100000,shape1_blue,shape2_blue))
mean(rlnorm(100000,shape1_blue,shape2_blue))
library(EnvStats) ## to truncate lognomal
hist(rlnormTrunc(100000,meanlog=shape1_blue,sdlog=shape2_blue,min=0,max=15))
mean(rlnormTrunc(100000,meanlog=shape1_blue,sdlog=shape2_blue,min=0,max=15))
hist(rnorm(10000,1.317,3.093))
Ni_blue_test=rnorm(10000,1.317,3.093)
Ni_blue_test[Ni_blue_test<0]=0
hist(Ni_blue_test)
Ni_blue=matrix(NA,nrow=100000,ncol=18)
for (i in 4:18) {


  Ni_blue[,1]=rlnormTrunc(100000,meanlog=shape1_blue,sdlog=shape2_blue,min=0,max=15)
### Density at age-0.25 per m2
  #Ni_blue[,1]=Ni_blue_test
  Ni_blue[,2]=Ni_blue[,1]*exp(-M_blue[,1]*0.25)     ### Density at age-0.5 per m2
```

```
  Ni_blue[,3]=Ni_blue[,2]*exp(-M_blue[,2]*0.5)      ### Density at age-1 per m2
  Ni_blue[,i]=Ni_blue[,i-1]*exp(-(M_blue[,i-1])) ### Density at age-2 per m2


}
matplot(t(apply(Ni_blue,2,quantile,c(0.00001,0.5,0.99))),type='l')
mean_Ni_blue=apply(Ni_blue,2,FUN=mean)
Pn_blue=matrix(NA,nrow = 100000,ncol = 18)
for (j in 1:100000) {
  for (i in 1:18) {
    Pn_blue[j,i]=Ni_blue[j,i]*W_increase_blue[j,i] ### Production of Blue crab per m2
  }
}
matplot(t(apply(Pn_blue,2,quantile,c(0.00001,0.5,0.99999))),type='l')
mean_Pn_blue_total=mean(apply(Pn_blue,1,FUN=sum)) ##  mean of Blue Crab production
SD_Pn_blue_total=sd(apply(Pn_blue,1,FUN=sum)) ## SD of Blue Crab production
summary(apply(Pn_blue,1,FUN=sum))
L_blue_underharvest=ifelse(L_blue<12.7,0,1) ## Create a matrix to remove under harvest size limit
summary(L_blue_underharvest)
Pn_blue_harvest=apply(Pn_blue*L_blue_underharvest,1,FUN=sum)   # mean harvestable production
mean(apply(Pn_blue*L_blue_underharvest,1,FUN=sum))
sd(apply(Pn_blue*L_blue_underharvest,1,FUN=sum))
```

```
#### Stone crab########
## Length at age
P_mean_stone=c(13.6,0.31,0.07) ## Mean value of Linf, K0 and t0 of stone crab
cv_stone=0.10          ## 10% variance of the mean
log_Para_stone=sqrt(log(1+rep(cv_stone,3)^2)) ## correct for the log scale of Linf, K0
log_Para_stone[3]=0.07*0.10 ## t0 in normal scale = 5% variance of the mean
sigma_stone=log_Para_stone%o%log_Para_stone*cor_mat
library(mvtnorm)
set.seed(1)
Stonecrab=rmvnorm(n=100000,mean=c(log(P_mean_stone[1:2]),P_mean_stone[3]),sigma=sigma_stone)
hist(exp(Stonecrab[,1]))
hist(exp(Stonecrab[,2]))
hist(Stonecrab[,3])
Linf_stone=matrix(rep(exp(Stonecrab[,1])),nrow=length(Stonecrab[,1]),ncol=18) ##  Length infinity of Per
K_stone=matrix(rep(exp(Stonecrab[,2])),nrow=length(Stonecrab[,2]),ncol=18) ##  K for Per
t0_stone=matrix(rep(Stonecrab[,3]),nrow=length(Stonecrab[,3]),ncol=18)  ## t0 of Per
age_stone=matrix(rep(c(0.5,1,2,3,4,5,6,7,7,7,7,7,7,7,7,7,7,7)),nrow=100000,ncol=18,byrow=TRUE) ## Extend tmax to longest live species: 17 years
L_stone=matrix(NA,nrow=100000,ncol=18,byrow=TRUE)
L_stone=Linf_stone*(1-exp(-K_stone*(age_stone-t0_stone))) ## Von Bert Length at age
```

```
mean_length_stone=apply(L_stone,2,FUN=mean)
matplot(t(apply(L_stone,2,quantile,c(0.025,0.5,0.975))),type='l')
## Weight at age
PW_mean_stone=c(0.2028,3.17) ## Mean value of a and b for weight growth of Blue crab
W_cv_stone=c(0.1,0.05) ## 10% and 5% variance of mean
W_log_Para_stone=sqrt(log(1+W_cv_stone^2)) ## correct for the log scale of a and b
sigmaW_stone=W_log_Para_stone%o%W_log_Para_stone*Wcor_mat
Stonecrab_W=rmvnorm(n=100000,mean=c(log(PW_mean_stone[1:2])),sigma=sigmaW_stone)
hist(exp(Stonecrab_W[,1]))
hist(exp(Stonecrab_W[,2]))
a_stone=matrix(rep(exp(Stonecrab_W[,1])),nrow=100000,ncol=18) ## a coefficent for length weight relationship
b_stone=matrix(rep(exp(Stonecrab_W[,2])),nrow=100000,ncol=18)     ## b coefficent for length weight relationship
W_stone=matrix(NA,nrow=100000,ncol=18)
W_stone=a_stone*L_stone^b_stone          ## Length weight relationship
matplot(t(apply(W_stone,2,quantile,c(0.01,0.5,0.99))),type='l')
W_increase_stone=matrix(NA,nrow=100000,ncol=18,byrow = TRUE) ## Weight increasement of Perch
for(j in 1:100000) {
  W_increase_stone[j,1]=W_stone[j,1]
  for (i in 2:18) {
    W_increase_stone[j,i]=W_stone[j,i]-W_stone[j,i-1]
```

```
  }
}
matplot(t(apply(W_increase_stone,2,quantile,c(0.01,0.5,0.99))),type='l')
summary(W_increase_stone)
Lm_stone=7  ## Length at maturity
Mm_stone=0.7 ## Natural mortality at Length at maturity
M_stone=Mm_stone*Lm_stone/L_stone ## Size dependent mortality
matplot(t(apply(M_stone,2,quantile,c(0.01,0.5,0.99),na.rm=T)),type='l')
## Density enhancement
mean05_stone=1.936 ## Mean density enhancement of 0.5-year fish from Zu Ermgassen 2016
SE05_stone=0.214 ## SE density enhancement of 0.5-year from Zu Ermgassen 2016
cv05_stone=SE05_stone/mean05_stone # coefficient of variation of 0.5-year density
shape2_stone=log(1+(cv05_stone^2)) ## parameter for log normal distribution
shape1_stone=log(mean05_stone)-shape2_stone/2 ## parameter for log normal distribution
hist(rlnorm(100000,shape1_stone,shape2_stone))
mean(rlnorm(100000,shape1_stone,shape2_stone))
Ni_stone=matrix(NA,nrow=100000,ncol=18)
for (i in 3:18) {
  Ni_stone[,1]=rlnorm(100000,shape1_stone,shape2_stone) ### Density at age-0.5 per m2
  Ni_stone[,2]=Ni_stone[,1]*exp(-M_stone[,1]*0.5)     ### Density at age-1 per m2
  Ni_stone[,i]=Ni_stone[,i-1]*exp(-(M_stone[,i-1])) ### Density at age-2 per m2
}
matplot(t(apply(Ni_stone,2,quantile,c(0.00001,0.5,0.99))),type='l')
```

```
Pn_stone=matrix(NA,nrow = 100000,ncol = 18)
for (j in 1:100000) {
  for (i in 1:18) {
    Pn_stone[j,i]=Ni_stone[j,i]*W_increase_stone[j,i] ### Production of Stonecrab per m2
  }
}
matplot(t(apply(Pn_stone,2,quantile,c(0.00001,0.5,0.99999))),type='l')
mean_Pn_stone_total=mean(apply(Pn_stone,1,FUN=sum)) ##  mean of Stonecrab production
SD_Pn_stone_total=sd(apply(Pn_stone,1,FUN=sum)) ## SD of Stonecrab production
Pn_stone_harvest=0.2*mean_Pn_stone_total  # for claw only and = about 20% of total
production
SD_Pn_stone_harvest=sd(apply(0.2*Pn_stone,1,FUN=sum))
#### Net production enhancement #####
Pn=apply(Pn_shep,1,FUN = sum)+apply(Pn_per,1,FUN=sum)+apply(Pn_spad,1,FUN=sum)+
  apply(Pn_pin,1,FUN=sum)+apply(Pn_spot,1,FUN=sum)+apply(Pn_pig,1,FUN=sum)+
  apply(Pn_Dar,1,FUN=sum)+apply(Pn_Skil,1,FUN=sum)+apply(Pn_Nak,1,FUN=sum)+
  apply(Pn_Fea,1,FUN=sum)+apply(Pn_Frec,1,FUN=sum)+apply(Pn_Gulf,1,FUN=sum)+
  apply(Pn_stone,1,FUN=sum)+ apply(Pn_blue,1,FUN=sum)## Total production enhancement
all species
mean_Pn=mean(Pn) ## mean total enhancement
SD_Pn=sd(Pn) ### Sd total enhancement
mean(apply(Pn_spot,1,FUN=sum))
```

```
#### Harvestable production enhancement #####
Pn_harvest=Pn_shep_harvest+Pn_per_harvest+Pn_spad_harvest+Pn_pin_harvest+Pn_spot_harv
est+Pn_pig_harvest+
  Pn_blue_harvest
mean(Pn_harvest)## mean harvestable production
sd(Pn_harvest) ### Sd total enhancement

#### Commercial production enhancement #####
Pn_commercial_production=(Pn_shep_harvest*Pn_shep_commercial_share)+(Pn_spad_harvest
*Pn_spad_commercial_share)+
  (Pn_spot_harvest*Pn_spot_commercial_share)+Pn_blue_harvest
mean(Pn_commercial_production) ## mean commercial enhancement
sd(Pn_commercial_production) ### Sd commercial enhancement
#### Recreational production enhancement #####
Pn_recreational_production=(Pn_shep_harvest*Pn_shep_recreational_share)+
  Pn_per_harvest+(Pn_spad_harvest*Pn_spad_recreational_share)+
  Pn_pin_harvest+(Pn_spot_harvest*Pn_spot_recreational_share)+
  Pn_pig_harvest
mean(Pn_recreational_production) ## mean recreational enhancement
sd(Pn_recreational_production) ### Sd recreational enhancement
```

Chapter 3 Estimating nitrogen removal services of eastern oyster *(Crassostrea virginica)* in Mobile Bay, Alabama in Mobile Bay, Alabama

Abstract

Eastern oysters have been acknowledged for their important contribution to human well-being by providing goods and services including nitrogen removal from water bodies. In this study, I estimated nitrogen removal rates and associated economic benefits provided by oyster reefs in Mobile Bay, Alabama. Published data and parameters were used to construct models to estimate denitrification rates, burial of biodeposits in sediments, and loss of nitrogen through oyster harvest from reefs in Mobile Bay, Alabama. The estimated total nitrogen removal services provided by oyster reefs in Mobile Bay was 26,666±2,919 kg N yr^{-1} (mean ± 1sd). To estimate the economic value of the services, the replacement cost of removing nitrogen from an Alabama sewage water treatment plant using a Biological Nutrient Removal process was calculated, resulting in an estimated economic benefit of nitrogen removal services of \$106,397±11,646 yr^{-1} which is \$101±11 ha^{-1} yr^{-1}. These results provide another economic benefit to the overall estimation of oyster reef ecosystem services in Alabama that can be used by decision makers or the public to estimate the economic return of oyster habitat restoration investment in Alabama waters.

Introduction

Estimating and valuating services of an ecosystem is often demanding when there is a need to justify restoration decisions and to calculate the recovery of post dollar investments (Peterson and Lipcius 2003; Primack 2006). Ecological restoration is often initiated as a means to cease or reverse the trend of degraded ecosystem and/or species loss caused by human-induced impacts or others. The underlying purpose of restoration is to bring the system back to the point where it can continue to function well for provision of goods and services (Bradshaw 1996) for humans directly, indirectly or both. However, decisions for conserving, restoring and protecting imperiled species and degraded ecosystems often are made when the ecosystems are brought to a point of near collapse (Primack 2006). This is the case for Eastern oyster (*Crassostrea virginica,* hereafter, oysters) and the reef ecosystems that they inhabit (Grabowski et al. 2012).

Impacts from overharvest, disease and poor water quality are primary causes of substantial declines of oyster reefs globally (Beck et al. 2011). The decline of oyster biomass is a strong contributing factor that has resulted in major shifts to microbial food webs and increased summer anoxia in deeper waters of the Chesapeake Bay (Newell 1988; Ulanowicz and Tuttle 1992). The declines have impaired the capacity of oyster reefs themselves to curb excessive eutrophication in many other estuaries in the U.S (zu Ermgassen et al. 2012). Oyster filtering capacity has declined by 85% in U.S. estuaries and by 79% in Mobile Bay, Alabama, respectively, over the last century (zu Ermgassen et al. 2012). Newell et al. (2005) suggested that oyster restoration could be considered as a means to achieve the long-term goal of improving water quality because of oysters' high filtration rates (Dame 1996).

As an active suspension filter feeder, oysters directly capture small seston particles (i.e., > 5µm in diameter) from the water column with high efficiency (Kennedy et al. 1996). The particles are sorted out and the rich nutritious particles are ingested, and the remaining particles are bound together in mucus pellets and ejected immediately into sediment as pseudofeces (Kennedy et al. 1996). The ingested nutritious particles are assimilated, and undigested particles are excreted as feces. Through these processes, phytoplankton and suspension particles are transferred from water column to the benthic system around the oyster reefs as biodeposits (pseudofeces and feces) that can lead to enhanced water clarity (Newell et al. 2005; Dame 1996). In the sediment layer around the oyster reefs, nitrogen captured in the biodeposits is microbially mediated in a coupled nitrification and denitrification process that causes a proportion of nitrogen loss as gas, another proportion can be buried in the sediment and the rest becomes inorganic nitrogen added to the dissolved inorganic nitrogen pool in the water column (Newell et al. 2005; Voss et al. 2011).

The capacity and rate of filtering particles by oysters has been studied extensively and these rates are known to be regulated by many environmental factors such as temperature, seston concentration, food and body size (Newell and Langdon 1996); salinity (Shumway 1996); and/or water velocity (Dame et al. 1985). Oysters can maintain filtering activity up to 24 hours without a diurnal rhythm (Newell 1988) but the filtering response is complex in response to temperature variation and seston concentration (Newell and Langdon 1996). Although, oyster filtration rates models have been established in literature (Powell et al. 1992; Cerco and Noel 2005; Fulford et al. 2007), the model parameters are often assumed to be constant due to a limited understanding about their variation (zu Ermgassen et al. 2012). Communicating model uncertainty will increase model credibility and provide critical insights on model implications.

When filtration rates are combined with estimated assimilation efficiency rates and Chlorophyll-*a* concentration in the water column (Newell et al. 2005; Pollack et al. 2013), the estimate of nitrogen removal capacity of oysters can be made based on the coupled nitrification-denitrification process of oyster biodeposists in the sediments (Newell et al. 2002). Both conceptual models of the potential for oysters to enhance estuarine denitrification (Newell et al.

2005) and directly measures of denitrification rates in oyster reef sediments (Piehler and Smyth 2011) have been presented in literature, which indicated the denitrification rates were highest in the summer coinciding with higher filtration rates and higher metabolism (Newell et al. 2005; Piehler and Smyth 2011).

As oysters assimilate nutritious particles for growth, nitrogen is stored in their shells and tissues. Nitrogen concentrations are generally similar across sites and growth types (reefs and aquaculture) approximating from about 7.4 to 11.8% and 0.20% to 0.26% nitrogen in tissue and shell dry weight, respectively (Kellogg et al. 2014). This nitrogen can be physically removed from the water by oyster harvest (Vitousek et al. 1997).

Oyster reefs have demonstrated higher rates of denitrification than other coastal habitats such as submerged aquatic vegetation, salt marshes and unstructured habitats, especially during warmer seasons (Piehler and Smyth 2011). However, compared to other structured habitats, oyster reef restoration has been the focus of substantial restoration efforts only over the last decade (Coen and Luckenbach 2000; Grabowski and Peterson 2007). Valuation of these reef services can provide evidence of the necessity to restore and manage resources properly and the ecosystems that provide them (Grabowski et al. 2012). Assigning a monetary value to these services is an effective method for communicating to the public about the need of restoration actions and assisting decision makers in choosing among restoration alternatives (Barbier et al. 2011).

To value nitrogen removal services, the cost of providing nitrogen removal using an engineering solution is often considered as a replacement cost for these services by oyster reefs (Pollack et al. 2013). The replacement cost can be used to value ecosystem regulating services (De Groot et al. 2012) when three conditions are met: 1) the engineered system provides the same services as the natural system, 2) the engineered alternative is the least expensive, and 3) the services are demanded by society (Shabman and Batie 1978; Farber et al. 2002).

Recent focus on oyster restoration in Mobile Bay, Alabama (e.g., the100-1000 Restore Coastal Alabama Project; Alabama Coastal Foundation 2017) has illustrated the need to estimate benefits of oyster reef restoration. The objectives of this study were to: 1) integrate published filtration rate and ingestion rate models to provide estimation of nitrogen removal services from denitrification and burial services provided by oyster reefs in Mobile Bay; 2) apply oyster landing data (2008 – 2016) from the bay to estimate nitrogen removal from shell and tissue when oysters were harvested; and 3) use a replacement cost method to estimate the economic value of nitrogen removal by oysters in Mobile Bay.

Methods

Modeling Approach

An individual filtration rate model was estimated for oysters in Mobile Bay, Alabama, using daily environmental inputs (temperature, salinity and chlorophyll-*a*). Oysters can assimilate an average of 50% of the particulate organic nitrogen filtered for growth, and the remaining 50% is voided as biodeposits into sediments (Newell and Jordan 1983). Because denitrification efficiency (90 – 100% of benthic inorganic N) does not vary greatly temporally (Piehler and Smyth 2011; Smyth et al. 2013, 2015, 2016), a denitrification rate of 20% of biodeposits organic nitrogen input derived from a laboratory study of oysters (Newell et al. 2002), was applied to estimate the amount of nitrogen removed by a coupled nitrification-denitrification process. Another 10% nitrogen was removed from the biodeposits by nitrogen burial in sediment (Boynton et al. 1995). Therefore, nitrogen removal varied daily based on variation in the filtration rate. The annual nitrogen removal (kg N yr^{-1}) was the sum of the daily removal over

365 days. The yearly nitrogen removal from 2008 to 2016 expected from oyster reefs in Mobile Bay, Alabama, was estimated by using environmental data and average oyster density in the bay.

Nitrogen stored in oyster tissues and shells was also removed from the water as oysters were harvested. A conceptual model of nitrogen flow associated with oysters is provided in Figure 3-1.

Environmental variables

Temperature and salinity: Daily temperature and salinity data from 2008 to 2016 were retrieved from the Mobile Bay National Estuary Program (NEP-CedarPoint 2008-2016) at the Cedar Point Station where the most productive oyster reefs are located. Daily values of temperature and salinity are presented in Figure 3-2 and Figure 3-3.

Chlorophyll-*a* and Turbidity: Chlorophyll-*a* and Turbidity data were obtained from the National Water Information System for Mobile Bay, Alabama at the Cedar Point station (USGS-WQ-CedarPoint 2016). Daily data of Chlorophyll-*a* and Turbidity were linearly interpolated from monthly data recorded in 2016. Due to the lack of yearly data from 2008 to 2016 for Chlorophyll-*a* and Turbidity at Cedar Point reefs, the interpolated daily data were replicated 9 times to align with the temperature and salinity data above as inputs into the nitrogen removal model (Wang et al. 2008). Daily values of Chlorophyll-*a* and Turbidity are presented in Figure 3-4 and Figure 3-5.

Filtration rate model

A universal filtration rates model is described as a function of oyster biomass (Newell and Langdon 1996), and is modified under limiting environmental factors (Cerco and Noel 2007; Fulford et al. 2007; Ehrich and Harris 2015) as:

$$FR = aW^b * f(T) * f(S) \qquad (1)$$

where: FR is an individual oyster filtration rate (l h^{-1}), W is oyster dry weight (g DW), $\underline{a}$ is filtration rate per gram dry weight, $\underline{b}$ is the weight exponent scaling filtration rate nonlinearly as a function of oyster biomass (Newell and Langdon 1996). *f(T)* and *f(S)* are temperature and salinity limitation to the filtration rate.

Coefficient $\underline{a}$, is theoretically assumed to be constant (Newell and Langdon 1996; Cerco and Noel 2007; Fulford et al. 2007; zu Ermgassen et al. 2012). A recent review by Ehrich and Harris (2015) recommended incorporating uncertainty (CV=40%) to the average value of $\underline{a}$ to estimate filtration rate in model simulation. Considering these, an average $\underline{a}$ value of 8.02 reported in zu Ermgassen et al. (2012) and a standard deviation of 40% from the mean were used to model coefficient $\underline{a}$ from a lognormal distribution. The lognormal distribution was applied to constrain the coefficient $\underline{a}$ from approximating a negative value. Then, 1,000 values of $\underline{a}$ were randomly drawn from the lognormal distribution and applied to the filtration rate model. The nitrogen estimate was then replicated 1,000 times corresponding to each $\underline{a}$ value.

Coefficient $\underline{b}$ is also often assumed to be constant (Cranford et al. 2011; La Peyre et al. 2014) due to the complexity of the correlation between $\underline{a}$ and $\underline{b}$. Efforts to describe the relation from field data for oysters has been limited (zu Ermgassen et al. 2012). Therefore, Ehrich and Harris (2015) recommended using constant $\underline{b}$ while introducing variability into the coefficient $\underline{a}$. The average constant value of $\underline{b}$ = 0.58 reported in zu Ermgassen et al. (2012) and Cranford et al. (2011) was used in the filtration rate model for oysters in Mobile Bay.

Oyster dry weight (g DW) was converted from oyster shell height (L; mm) using the previously reported conversion equation (Aransas Bay, Texas; Pollack et al. 2011):

$$W = 7\,L^{3.876}\,10^{-8} \tag{2}$$

The *f(T)* is the temperature (T; °C) limitation equation (Cerco and Noel 2005)

$$f(T) = e^{[-0.015((T-27)^2)]} \tag{3}$$

and *f(S)* is the salinity limitation equation (Cerco and Noel 2005) that is incorporated to modify the filtration rate at salinity below 7.5ppt (La Peyre et al. 2014)

$$f(S) = 0.5(1 + \tanh(Salinity - 7.5)) \quad (4)$$

Oyster filtration rates was also modulated when seston concentrations were below 0.005 g l^{-1} and above 0.025 g l^{-1} (Cerco and Noel 2005; La Peyre et al. 2014). However, the seston concentrations in this study were well within this range (Figure 3-5); therefore, a seston limiting factor was not incorporated to modify filtration rates in this study.

Denitrification and nitrogen burial services provided by oyster reefs

It is common for oysters and other bivalves to void approximate 50% of their ingestion food as biodeposits into sediments (Newell and Jordan 1983; Dame 1996). A denitrification rate of 20% (Newell et al. 2002) and 10% burial rate (Boynton et al. 1995), which is common to other studies (Newell et al. 2005; North et al. 2010; Carmichael et al. 2012; Pollack et al. 2013), was applied to the daily particulate organic nitrogen in the oyster biodeposits to estimate the daily amount of nitrogen removal. The daily rate was summed over 365 days to estimate the annual rate of nitrogen removal (kg N yr^{-1}) in 1,045 ha of oyster reefs in Mobile Bay.

The amount of food available for oysters in the water column was correlated with Chlorophyll-*a* concentration, which was used as the index of food available for oysters (Soniat et al. 1998; Hyun et al. 2001)

$$f = 0.088\, Chl_{\alpha} + 0.520 \qquad (5)$$

where *f* is food (mg l^{-1} DW) and *Chl_α* is Chlorophyll-*a* concentrations in the water column (µg l^{-1}). Food expressed in dry weight units (mg l^{-1} DW) was converted to carbon and then to nitrogen units (N mg l^{-1}) using: a food DW-Carbon ratio of 2.14:1 (Widdows et al. 1979) and a

Carbon-Nitrogen ratio of 6.9:1 (Newell 1982). Food from Equation 5 was then expressed in nitrogen units (N mg l^{-1}) in the form

$$f_N = 0.006\, Chl_\alpha + 0.035 \qquad (6)$$

The conversion from food dry weight (mg l^{-1} DW) to food in nitrogen unit (N mg l^{-1}) was to applied to avoid the straight conversion from Chlorophyll-a to food (N mg l^{-1}) using a Chlorophyll-a -Nitrogen ratio of 1:14 (i.e., Newell et al. 2005; Pollack et al. 2013).

The ingestion rate of an oyster (I --N mg h^{-1}) was represented as a function of available food and filtration rate (Powell et al. 1995).

$$I = f_N \times FR \qquad (7)$$

The hourly filtration rate (FR l h^{-1}) and ingestion rate (I --N mg h^{-1}) were multiplied by 24 to obtain ingestion daily rates (Newell 1988). The individual nitrogen removal rate was scaled up to encompass the entire oyster reef extent in Mobile Bay using the average oyster density from published studies in the Bay: 11.2 individual m^{-2} (mean length = 51mm shell height; zu Ermgassen et al. 2016).

Nitrogen removal from oyster harvest

Nitrogen removal from Mobile Bay due to oyster harvest was estimated using 9 years of harvest data from 2008 to 2016 (Figure 3-4). To account for the uncertainty of inter-annual variability of oyster harvest, mean and standard deviation of the 9-year oyster harvest data were used to model the oyster harvest from a normal distribution with minimum and maximum values during the 9-year period (truncnorm package in R). Dalrymple (2013) estimated that nitrogen contained in oyster tissues and shells in Mobile Bay, Alabama, was 11.8% and 0.26% dry weight, respectively.

In order to convert wet weight harvest to dry weight harvest for estimating nitrogen contained in tissue, a conversion equation developed for Aransas Bay, Texas was used (Pollack et al. 2011)

$$W_{dry} = 0.179\, W_{wet} - 0.113 \qquad (8)$$

where W_{dry} (g) is dry tissue and W_{wet} (g) is wet tissue.

Shell dry weight (W_{shell}) was estimated from tissue dry weight (W_{dry}) using average ratio for market sized oysters from Sapelo Island, Georgia (Mercado-Silva 2005).

$$W_{shell} = \frac{W_{dry}\, 100}{2.462} \qquad (9)$$

Economic valuation of nitrogen removal services

Using the replacement cost method developed for oyster reefs in the Mission-Aransas estuary, Texas (Pollack et al. 2013), nitrogen removal cost ($ kg^{-1}) was estimated from the Opelika East Side Wastewater Treatment Plant, Alabama (GMC 2005), where a Biological Nutrient Removal (BNR) process is used for sewage water treatment and this cost was applied to estimate the economic value of nitrogen removal services provided by oyster reefs in Mobile Bay. The BNR process uses microorganisms to remove total nitrogen and phosphorus (USEPA, Office of Water 2007), which is similar to the process in oyster reefs (Pollack et al. 2013). Estimating the replacement cost depends on the plant investment, capacity, operation and efficiency (Pollack et al. 2013). A summary of steps and data used for the estimation is presented in Table 3-1, and the present study's data were compared to other studies in the literature.

All simulations were performed using Program R and R code is appended to this chapter (Version 1.1.383; R Core Team 2013; Appendix 3-1). Data in the study are reported using the format (mean ± 1sd).

Results

Water temperature did not vary much from year to year and showed a general trend of seasonal variation in Mobile Bay (Figure 3-2). A general trend for salinity was also observed showing low salinity during spring, and higher salinity in summer and fall, except for 2009 and 2013, which exhibited low salinity during fall (Figure 3-3). Chlorophyll-*a* was high in early spring and summer and low in late fall and early winter (Figure 3-4). Turbidity was the highest in February (0.022 g l^{-1}) and the lowest in July (0.011 g l^{-1}) (Figure 3-5).

The simulation of filtration rate based on daily environmental inputs from 2008 to 2016 estimated that on average the maximum filtration rate was in 2012 (24.0±3.5 l h^{-1} m^{-2}) and the minimum was in 2014 (17.5±2.6 l h^{-1} m^{-2}). The yearly average oyster filtration rate was 20.0±4.3 l h^{-1} m^{-2}. (Figure 3-6); however, the incorporation of uncertainty into the filtration rate model (uncertainty due to coefficient $\underline{a}$) resulted in a range from 15.65 (lower quartiles) l h^{-1} m^{-2} to 26.22 (upper quartiles) l h^{-1} m^{-2} for simulated oysters in Mobile Bay.

Denitrification and nitrogen buried in sediments were a fraction of voided biodeposits in sediments. Therefore, nitrogen removal was highest in 2012 (0.0028±0.0004 kg N m^{-2} yr^{-1}) and the lowest was in 2014 (0.0019±0.0003 kg N m^{-2} yr^{-1}) (Figure 3-7). Scaling up to 1,045 ha of oyster reefs in Mobile Bay, nitrogen removal ranged from 29,008±4,264 to 20,202±2,969 kg N yr^{-1}. The average nitrogen removal rate was 24,185±3,555 kg N yr^{-1} in which 16,123±2,370 kg N yr^{-1} was removed by denitrification and 8,061±1,185 kg N yr^{-1} by nitrogen buried in sediments (Table 3-2).

There was high variation in oyster harvest each year from 2008 to 2016. The maximum harvest was 134,254 kg wet weight yr^{-1} in 2011 and the minimum was 10,442 kg wet weight yr^{-1} in 2009 (Figure 3-8). The average harvest during this period was 50,470±45,900 kg wet weight yr^{-1} that was approximately 9,034±8,216 kg yr^{-1} of dry tissue and 366,941±333,710 kg yr^{-1} of shell weight. Nitrogen contained in these tissues and shells are physically removed from the bay when the oysters are harvested. Approximately 1,313±652 kg N yr^{-1} from oyster tissues and 1,175± 583 kg N yr^{-1} from oyster shells was removed annually (Table 3-2). Nitrogen removal from oyster harvest was equal to 12% of combined nitrogen removal from the denitrification and the nitrogen buried in sediments.

The nitrogen removal cost ($ kg^{-1}) estimated from the medium sized wastewater treatment plant, the Opelika East Side Wastewater Treatment Plant, Alabama was $3.99 kg^{-1} N. The nitrogen removal capacity of oysters in Mobile Bay was about 20% of the plant which was 128,302 kg N yr^{-1} (Table 3-1). Using this replacement cost, the economic benefit of nitrogen removal services provided by the oyster reefs in Mobile Bay was estimated to be about $106,397±11,646 yr^{-1} (Table 3-2) which was $101±11 ha^{-1} yr^{-1}.

The cost of nitrogen removal services used in this study was much more conservative compared to previous studies (Table 3-3) because of different estimation techniques and data inputs.

Discussion

Estimating and valuing nitrogen removal services have been conducted for oyster reefs in many estuaries draining to the Atlantic Ocean and the Gulf of Mexico. By integration of work conducted in previous studies, this study provided an estimation of nitrogen removal services and their equivalent economic value in the Mobile Bay, Alabama.

In this study, average filtration rate was calculated using the daily environmental inputs from 2008 to 2016 as opposed to previous studies which used yearly (La Peyre et al. 2014), seasonal (Pollack et al. 2013) or monthly environmental data (Newell et al. 2005) as model inputs. For example, using average summer temperature, zu Ermgassen et al. (2012) estimated that the filtration capacity of the current oyster density in Mobile Bay is 600 m^3 h^{-1} ha^{-1} which is 3 times higher than the filtration estimated in this study. Although, the time span over which filtration rates were estimated depends on the purpose of each study, the incorporation of daily values may be more precise.

The filtration rate model applied in this study has the same model structure but different parameter values (*a* & *b* = 8.02 and 0.58 versus 0.17 and 0.75) than a recent review by Ehrich and Harris (2015) that resulted in slightly different (~8%) estimates. The combination between parameters *a* and *b* is still poorly understood (zu Ermgassen et al. 2012).

The inclusion of parameter uncertainty and environmental variables results in estimated filtration rate (l h^{-1} m^{-2}) variation of 21% from the mean value. There is little information on how to include uncertainty from both coefficients $\underline{a}$ and $\underline{b}$ (zu Ermgassen et al. 2012). The filtration rate model also requires assumptions of environmental thresholds such as optimum temperature for filtration: 27°C; a constant that controls temperature effect on filtration: 0.015 $^{\circ}C^{-2}$ and a salinity threshold at which filtration rate is halved (7.5ppt) (Cerco and Noel 2007). Although only one parameter uncertainty is included, the degree of uncertainty reported in this study can provide better insights on the confidence about the filtration rate value that decision makers and public would expect from current oyster populations in Mobile Bay and so as to set objectives for oyster restoration.

Oyster restoration has been proposed as a management strategy for improving water quality (Newell et al. 2005; Kellogg et al. 2014; zu Ermgassen et al. 2016) based on the high filtering capacity of oysters, and high denitrification rates around oyster reefs compared to other structured and unstructured habitats (i.e., marsh, submerged aquatic vegetation, intertidal and subtidal flats; Piehler and Smyth 2011; Smyth et al. 2013, 2015, 2016). Therefore, oyster density is often used as proxy for setting restoration targets (La Peyre et al. 2014; zu Ermgassen et al.

2016) to both reduce existing water pollution and treating runoff into the estuary (Kasperski and Wieland 2009). Cerco and Noel (2007) predicted that 10-fold increase in Chesapeake Bay oyster biomass could reverse water eutrophication in the bay and oysters could remove 30,000 kg N day^{-1} through denitrification. In Mobile Bay, 100 miles of oyster reef restoration has been implemented to restore oyster reefs back to their historical extent (Alabama Coastal Foundation 2017). This study with its findings hopes to provide more information about the gains in ecosystem services in a form that decision makers can utilize for justifying oyster restoration in Mobile Bay .

Quantification of nitrogen removal services provided by oysters has been demonstrated in several estuaries. Newell et al. (2005) estimated 753 kg N yr^{-1} was removed by denitrification and burial services per a million market size oysters (>76mm) in the Chesapeake Bay. My estimation was approximately 701 kg N yr^{-1} removed per million market size oysters (80mm) in Mobile Bay. Compared to Pollack et al. (2013) who estimated that oysters in the Mission-Aransas estuary, Texas removed 7.5 kg N ha^{-1} yr^{-1}, my results indicated higher removal rates (23 kg N ha^{-1} yr^{-1}) through denitrification and burial services in Mobile Bay. The differences likely arose from different environmental conditions and specific filtration rate models from Powell et al. (1992) which Ehrich and Harris (2015) asserted resulted in lower filtration rates.

Denitrification rates in oyster reef sediments commonly show seasonal patterns, with higher rates (kg N m^{-2}) occurring in the warmer months (Piehler and Smyth 2011) but denitrification efficiency does not. Normally 90-100% of inorganic nitrogen in the sediment was denitrified (Piehler and Smyth 2011; Smyth et al. 2013, 2015, 2016). Therefore, the application of a constant denitrification rate of 20% from a laboratory study to temporal variation in oyster biodeposits for estimating variation of nitrogen removal rates (kg N m^{-2}) is defendable.

Nitrogen removal from oyster harvest contributed a small fraction (12%) in total nitrogen removal in this study. Oyster harvest during this period (2018-2016) in Mobile Bay was low compared to earlier periods (2004-2005) which was 3 - 40 times higher. The low production of oyster harvest during 2008-2009 and 2012-2015 represented the combined impacts of drought that caused oyster drill (*Stramonita haemastoma*) proliferation and the long term destructive effects of hurricanes Ivan and Katrina, which depleted Alabama's oyster reefs (Vanderkooy 2012).

The economic value of nitrogen removal depends on location, availability of alternatives, the inconvenience or deleterious effects that would have incurred in the absence of the services and the valuation techniques (Farber et al. 2002). A nitrogen trading program such as North Carolina's Nutrient Offset Credit Program (North Carolina Division of Mitigation Services 2017) provides an example of how the market could function for ecosystem services (Piehler and Smyth 2011). However, the direct market exchange like the one in North Carolina does not often exist. Instead, indirect valuation techniques should be used when there are no explicit markets for services or when market evaluations do not adequately capture social values (Farber et al. 2002). The replacement cost method is usually used to provide economic benefit estimates in such cases (Pollack et al. 2013; Bricker et al. 2017). The economic estimate of nitrogen removal in this study was conservative compared to previous studies. It is also probable because it was derived from local based replacement cost estimates and it passed the three conditional tests raised by Shabman and Batie (1978): 1) the treatment process provided by oysters was similar to the technology applied in the BNR water treatment plant (Pollack et al. 2013); 2) the BNR was a technology with an advanced form of wastewater treatment (84% efficiency) and was used widely (Foley et al. 2007; USEPA, Office of Water 2007), so the technology was assumed the least expensive in terms of efficiency; and 3) the services were highly valued based on Newell's (1988) results that indicated the decline of oyster biomass results in summer anoxia in some areas in of Chesapeake Bay. These conditions coupled with the high level of support for oyster reef restoration in the Gulf of Mexico indicates that services are highly valued by society (La Peyre et al. 2012).

Oyster reefs present a valuable solution for improving water quality especially for many estuaries where eutrophication was caused by non-point sources (i.e., agricultural run-off). Therefore, measures to restore and protect oyster habitats in these estuaries have significant benefits. Oyster restoration in Mobile Bay presents an excellent example where oyster filtering capacity has been reduced by 79% over the last century (zu Ermgassen et al. 2012). Restoration of oyster reefs could improve water quality in the bay and provide other ecosystem services such as fish enhancement or shoreline protection.).).

There are obvious trade-offs between harvesting oysters and leaving them in the water to provide their ecological functions. Newell et al. (2005) reported that keeping oysters in the water for 10 years for nitrogen removal services would double the value of a one-time harvest of all oysters in the Choptank River estuary (Maryland). Kasperski and Wieland (2009) discussed options of either an oyster harvest moratorium or reduction of oyster harvest rates in the Chesapeake Bay, which would both result in higher net values of oyster resources (nitrogen removal service and oyster harvest) and allow oyster stocks to recover. Any of these options would reduce profits to oyster fishers but would increase overall benefits for society. While I do not recommend any of these options for Mobile Bay, Alabama, it would be worth considering an increased oyster harvest size limit to allow oysters to provide more ecological services before harvest by increasing resident time. This option would be possible if increasing their resident time did not decrease the production of oysters due to natural mortality.

As oyster density increases, oyster filtering capacity decreases (Cerco and Noel 2007), and the value of nitrogen removal likely decreases when water becomes clearer (Kasperski and Wieland 2009). However, I do not expect that oysters in Mobile Bay will be restored to their historic density quickly, so I believe my cost estimation is appropriate.

Oysters reduce suspended particles that increase water clarity to which light can penetrate into the bottom layer to support aquatic vegetation growth (zu Ermgassen et al. 2016). Oyster reefs can remove more nitrogen than these vegetation habitats (Piehler and Smyth 2011), but support fewer mobile fishes and crustaceans (Geraldi et al. 2009). Therefore, decision makers have to consider carefully these types of trade-offs when considering one kind of habitat restoration versus another.

This study provided an estimation of nitrogen removal services provided by oyster reefs in Mobile Bay, Alabama to increase the awareness of the public about the importance of protecting and restoring oyster reefs because of their provision of ecological services. In addition, the work provided decision makers with economic estimation of the oyster reefs services to help value and justify decisions related to oyster reef restoration.

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Table 3-1: Summary of steps and data that were used to estimate the nitrogen removal cost ($ kg^{-1}) from the Opelika East Side Wastewater Treatment Plant, Alabama using a replacement cost method (Pollack et al. 2013).

			References
1	Plant investment	$ 6,918,000	GMC 2005
2	Plant capacity for water treatment	14,000,000 *l* day^{-1}	GMC 2005
3	Life span	15 years	Foley et al. 2007
4	Maintenance and operation costs of the plant	11% of annual capital	USEPA, Office of Water 2007
5	Plant efficiency	25.1 mg N *l*$^{-1}$ removed by the plant	USEPA, Office of Water 2007
6	N removal capacity of the plant	128,302 kg N yr^{-1}	[2]*[5]*365 days
7	N Removal cost	$3.99 kg^{-1} N	{([1] + [1]*[4])/[3]}/[6]

Table 3-2: Summary of nitrogen removal services and economic benefit estimation provided by oyster reefs in Mobile Bay, Alabama. The amount of nitrogen removal (Kg N yr^{-1}) were average values from 2008 to 2016. The economic values were estimated by multiplying nitrogen removal with the replacement cost (\$3.99 kg^{-1} N). The numbers are in format mean±1sd are reported.

	Nitrogen removal (Kg N yr^{-1})	Benefit estimation (\$ yr^{-1})
Denitrification	16,123±2,370	64,330±9,456
Burial	8,061±1,185	32,163±4,728
Tissues	1,313±652	5,238±2,601
Shells	1,175±583	4,688±2,326
Total	26,666±2,919	106,397±11,646

Table 3-3: The values ($/kg N) and valuation techniques were applied at different places to estimate economic value of nitrogen removal services provided by oyster reefs.

Source	Valuation techniques	Site	Value ($/kg N)
Piehler and Smyth (2011) Grabowski et al. (2012)	Direct exchange value in North Carolina nutrient offset payment marketplace.	Bogue Sound, NC North Carolina	13.00 28.23
Newell et al. (2005) Kasperski and Wieland (2009)	Average cost from $4.6 planting cover crops to $1,125 erosion and sediment control	Chesapeake Bay	24.07
Pollack et al. (2013)	Replacement cost from a water treatment plant in Maryland	Mission – Aransas estuary, Texas	8.30
This study	Replacement cost from a water treatment plant in Alabama	Mobile Bay, Alabama	3.99

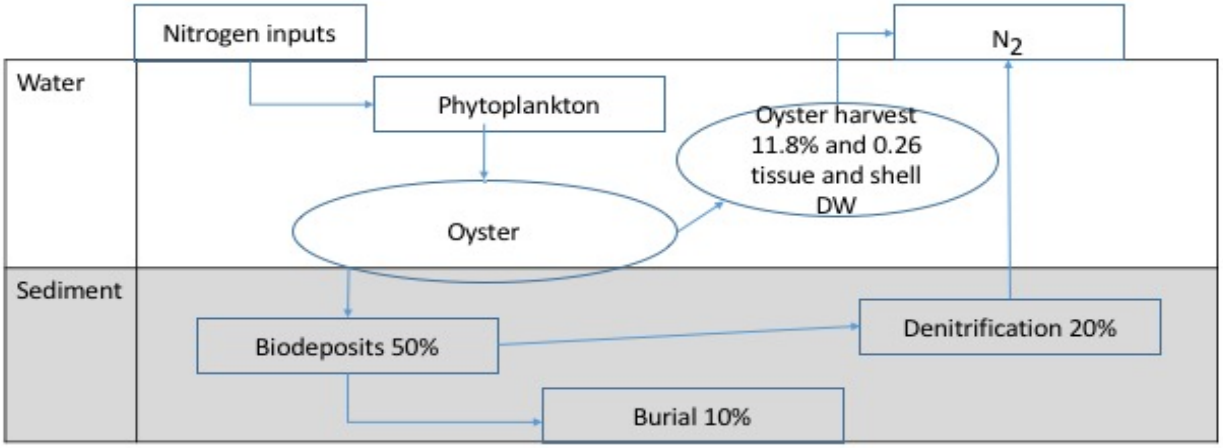

Figure 3-1: Nitrogen flow input from water to oyster and associated nitrogen removal percentages. Summary percentages were from Newell et al. (1983) and (2005)

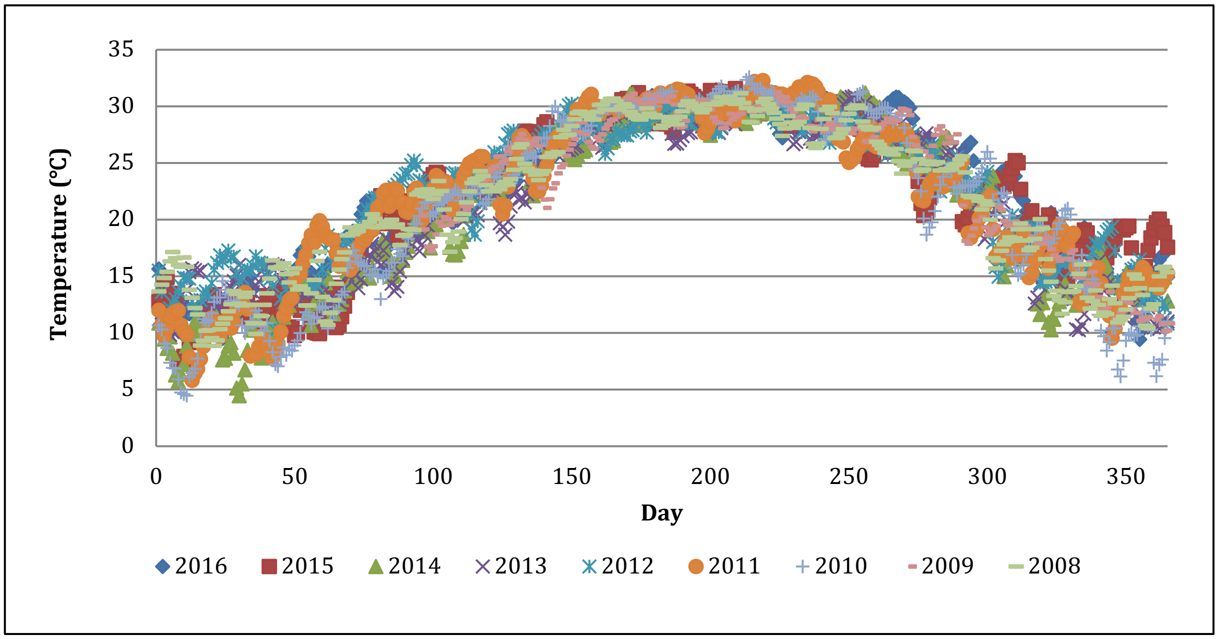

Figure 3-2: Daily temperature (2008 – 2016) was taken from the Mobile Bay National Estuary Program (NEP-CedarPoint 2008-2016) at Cedar Point Station

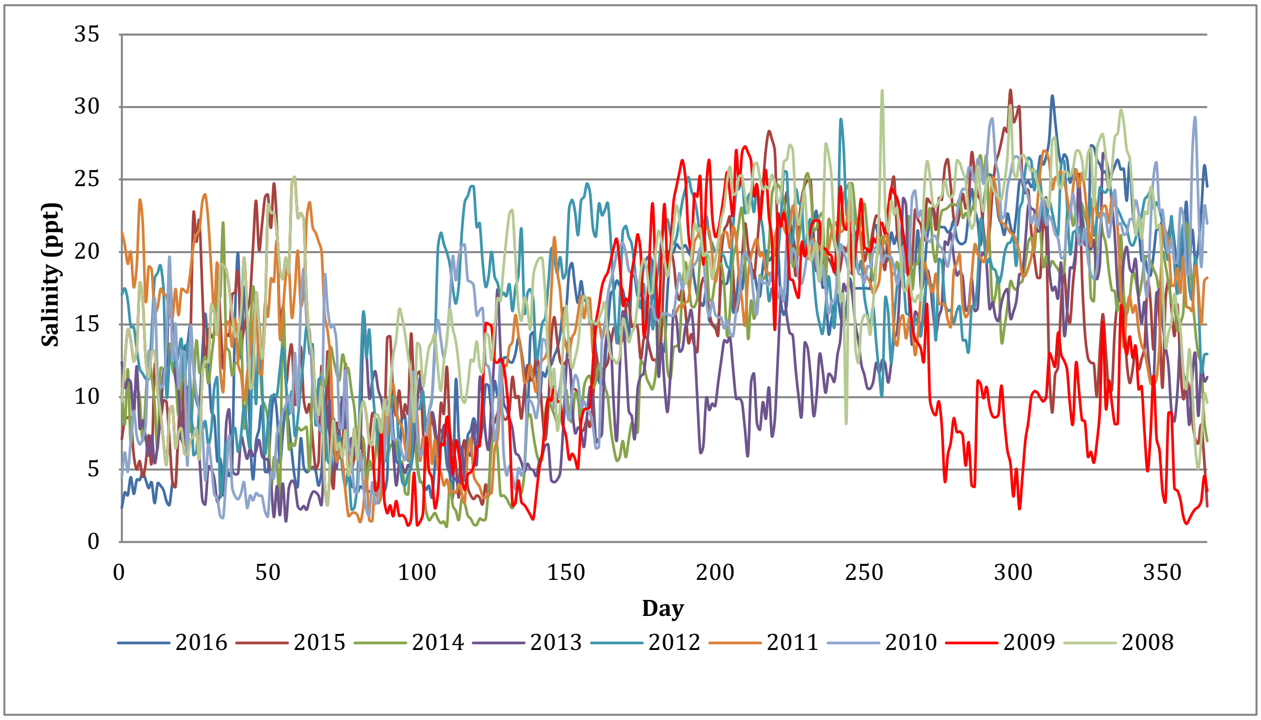

Figure 3-3: Daily salinity (2008 – 2016) was taken from the Mobile Bay National Estuary Program (NEP-CedarPoint 2008-2016) at Cedar Point Station

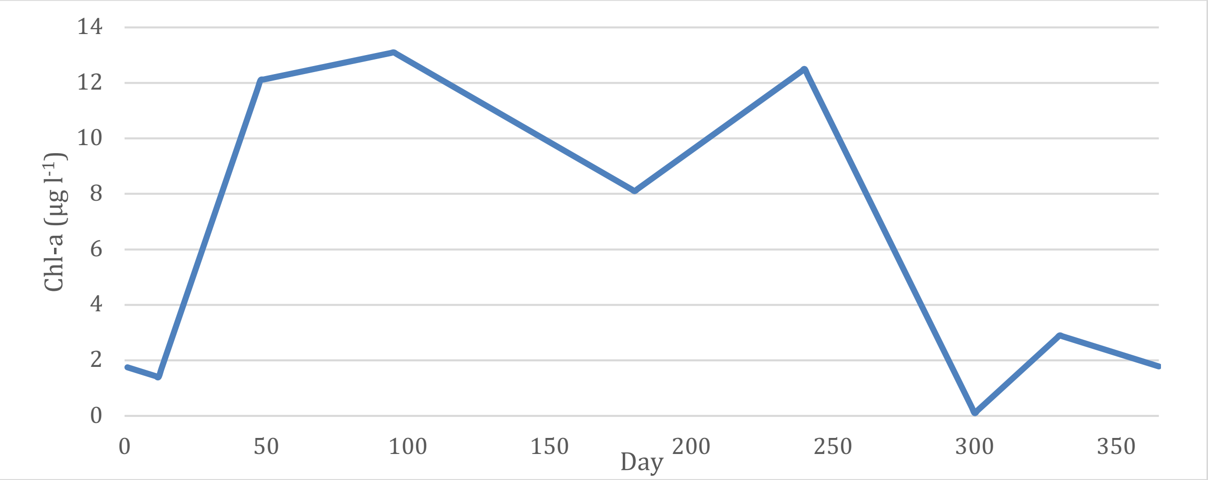

Figure 3-4: Daily Chlorophyll data were obtained from the National Water Information System for Mobile Bay, Alabama at the Cedar Point station (USGS-WQ-CedarPoint 2016).

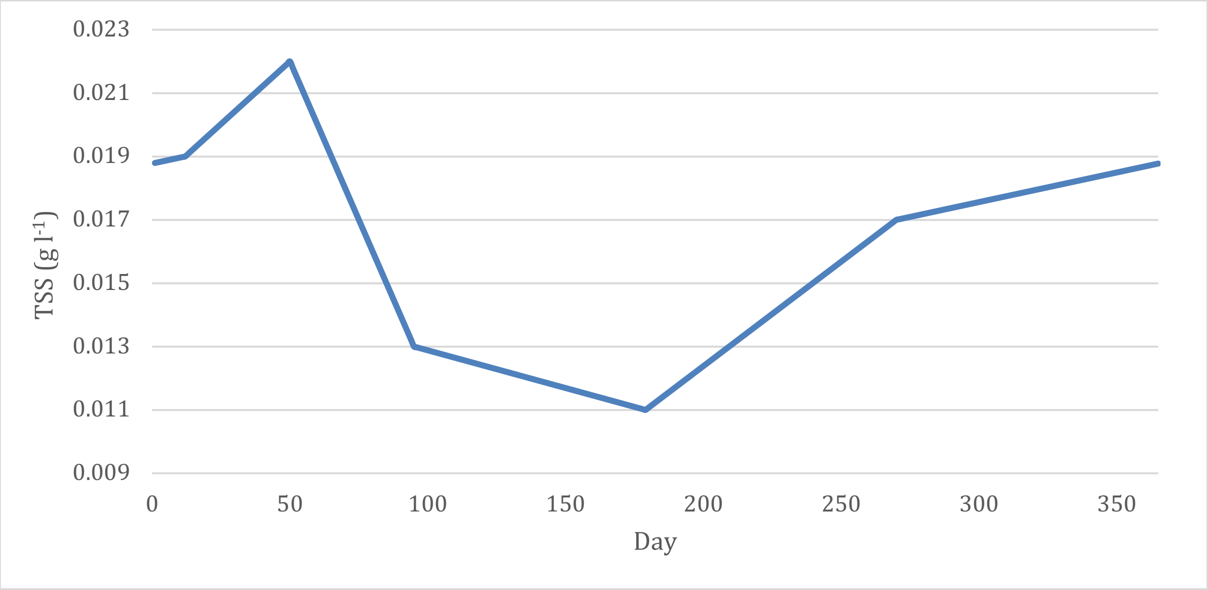

Figure 3-5: Daily Turbidity data were obtained from the National Water Information System for Mobile Bay, Alabama at the Cedar Point station (USGS-WQ-CedarPoint 2016).

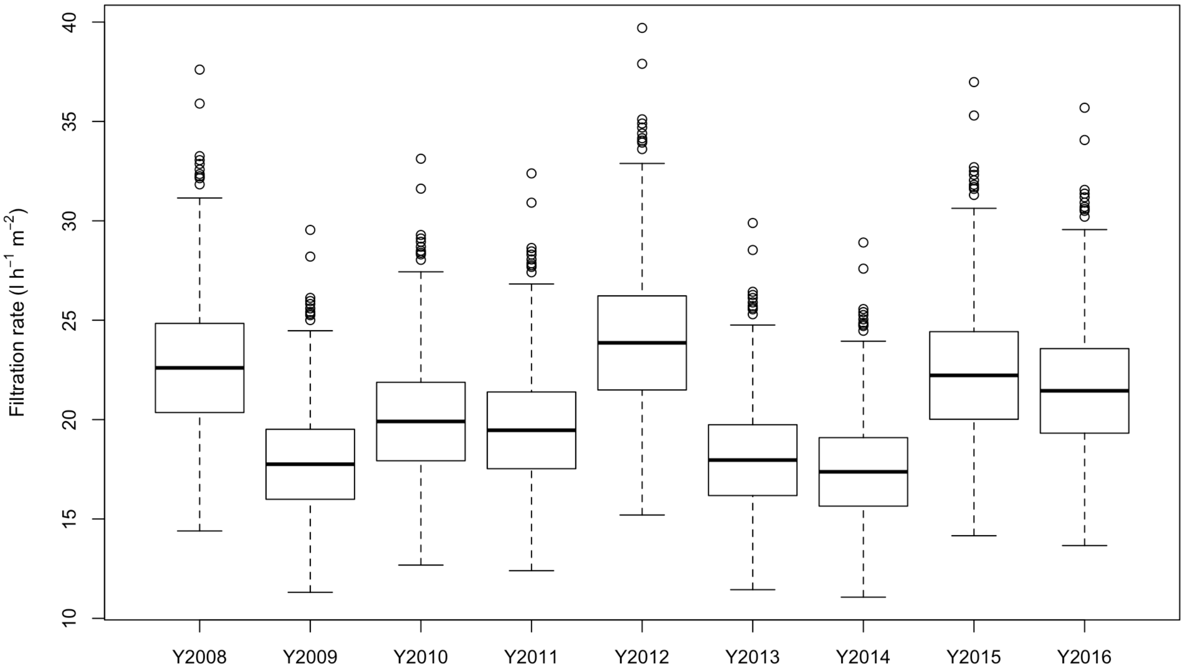

Figure 3-6: Average filtration rate (*l* h^{-1}) of 1 m^2 from oyster reefs in Mobile Bay. Each box presents mean, upper and lower quartiles and minimum and maximum filtration rates (*l* h^{-1}) of 1 m^2 oyster reefs from 1,000 simulation outputs. The highest average filtration rate was in 2012 and the lowest was in 2014. The yearly average oyster filtration rate was 20.0±4.3 *l* h^{-1} m^{-2}

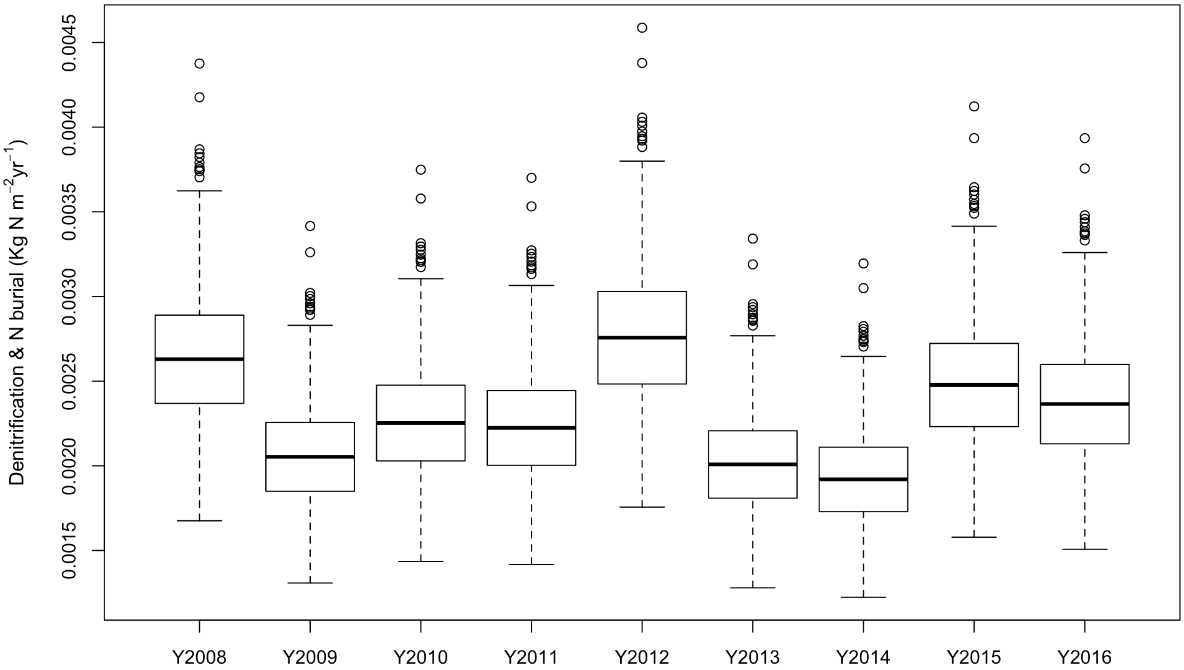

Figure 3-7: Nitrogen removal (Kg N m^{-2} yr^{-1}) from denitrification and nitrogen burial services. The highest removal rate was 2012 and the lowest was in 2014 corresponding to the filtration rates presented in Figure 3-6. The yearly average removal rate was 0.0023±0.00034 kg N m^{-2} yr^{-1}

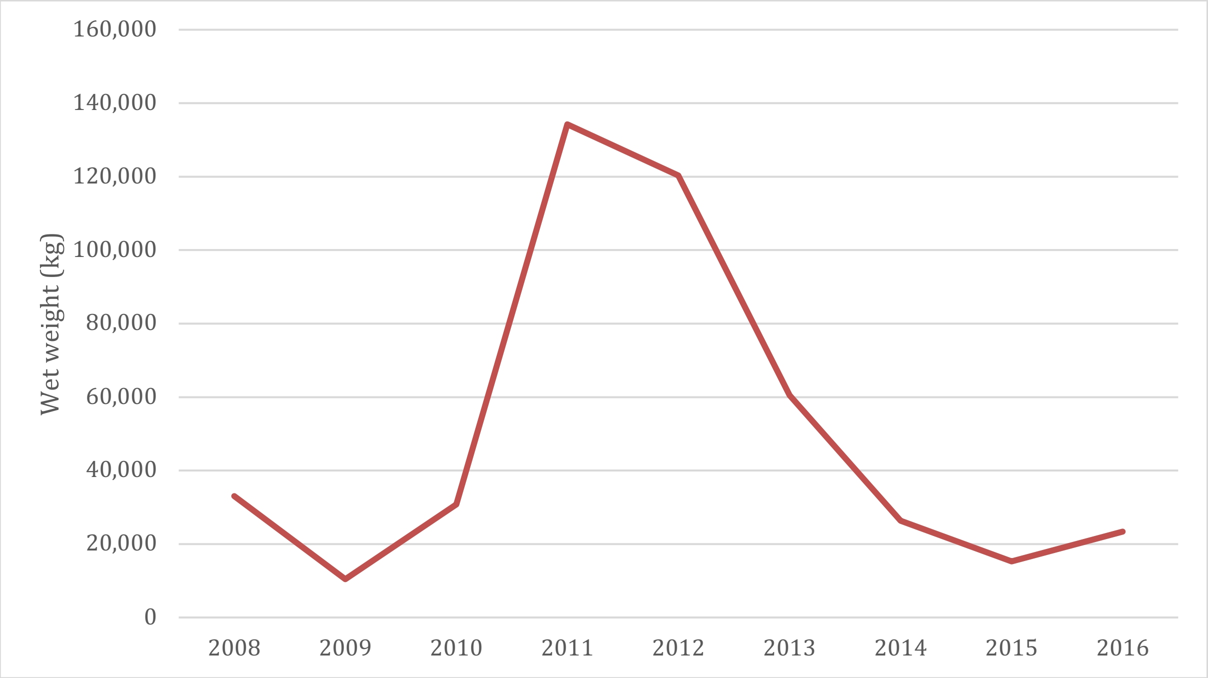

Figure 3-8: Oyster harvest (Kg wet weight yr^{-1}) from Mobile Bay, Alabama (2008-2016). Data were retrieved from NOAA-ALABAMA (2008-2016).

Appendix 3-1: R codes

```
Env=read.csv(file.choose())

str(Env)
Temp=cbind.data.frame(Env$Temp2008,Env$Temp2009,Env$Temp2010,Env$Temp2011,Env$
Temp2012,Env$Temp2013,
         Env$Temp2014,Env$Temp2015,Env$Temp2016)
str(Temp)

Sal=cbind.data.frame(Env$Sal2008,Env$Sal2009,Env$Sal2010,Env$Sal2011,Env$Sal2012,Env
$Sal2013,
                 Env$Sal2014,Env$Sal2015,Env$Sal2016)
str(Sal)

food=matrix(rep(Env$food,9),ncol=9)

str(food)

factor_Temp=exp(-0.015*(Temp[,]-27)^2) # Temperature limiting factorr

factor_Sal=0.5*(1+tanh(Sal[,]-7.5))    # Salinity limiting factor
factor_Sal[factor_Sal>0.5]=1           # There is no impact when Salinity >7.5ppt

mean_a=8.02                        # Mean coeffecient a
sd_a=3.18                         # SD coeffecient a

shape2_a=log(1+(sd_a/mean_a)^2) ## parameter for log normal distribution

shape1_a=log(mean_a)-shape2_a/2 ## parameter for log normal distribution

hist(rlnorm(1000,shape1_a,shape2_a))

set.seed(3)
a=rlnorm(1000,shape1_a,shape2_a)

b=0.58

########## Nitrogen removal of spat#######

#### Filtrationate rate of one oyster

W2=0.29   ## oyster dry weight converted from shell height (51mm) using Polack 2011

Density2=11.2
```

```
FR2008_seed=matrix(NA,nrow = 365,ncol = 1000) ## filtration rate 2008
for (i in 1:1000){
  FR2008_seed[,i]=a[i]*W2^b*factor_Temp[,1]*factor_Sal[,1]
}

hist(FR2008_seed[,1])
plot(FR2008_seed[,1],type='l')

Total_FR2008_seed=apply(FR2008_seed,2,FUN=sum)*24/1000 ## Annual m3 water filtered by
one seed oyster a year
## 24 is hours; 1000 is to convert from little to cubic meter
mean(Total_FR2008_seed)
sd(Total_FR2008_seed)

FR2009_seed=matrix(NA,nrow = 365,ncol = 1000) ## filtration rate 2009
for (i in 1:1000){
  FR2009_seed[,i]=a[i]*W2^b*factor_Temp[,2]*factor_Sal[,2]
}

FR2010_seed=matrix(NA,nrow = 365,ncol = 1000) ## filtration rate 2010
for (i in 1:1000){
  FR2010_seed[,i]=a[i]*W2^b*factor_Temp[,3]*factor_Sal[,3]
}

FR2011_seed=matrix(NA,nrow = 365,ncol = 1000) ## filtration rate 2011
for (i in 1:1000){
  FR2011_seed[,i]=a[i]*W2^b*factor_Temp[,4]*factor_Sal[,4]
}

FR2012_seed=matrix(NA,nrow = 365,ncol = 1000) ## filtration rate 2012
for (i in 1:1000){
  FR2012_seed[,i]=a[i]*W2^b*factor_Temp[,5]*factor_Sal[,5]
}

FR2013_seed=matrix(NA,nrow = 365,ncol = 1000) ## filtration rate 2013
for (i in 1:1000){
  FR2013_seed[,i]=a[i]*W2^b*factor_Temp[,6]*factor_Sal[,6]
}

FR2014_seed=matrix(NA,nrow = 365,ncol = 1000) ## filtration rate 2014
for (i in 1:1000){
  FR2014_seed[,i]=a[i]*W2^b*factor_Temp[,7]*factor_Sal[,7]
}

FR2015_seed=matrix(NA,nrow = 365,ncol = 1000) ## filtration rate 2015
for (i in 1:1000){
```

```
  FR2015_seed[,i]=a[i]*W2^b*factor_Temp[,8]*factor_Sal[,8]
}

FR2016_seed=matrix(NA,nrow = 365,ncol = 1000) ## filtration rate 2016
for (i in 1:1000){
  FR2016_seed[,i]=a[i]*W2^b*factor_Temp[,9]*factor_Sal[,9]
}

hist(FR2016_seed[,1])

##Average filtration rates l/h/m2 in Mobile Bay

Total_FR2008=apply(FR2008_seed,2,FUN=mean)*Density2
Total_FR2009=apply(FR2009_seed,2,FUN=mean) *Density2
Total_FR2010=apply(FR2010_seed,2,FUN=mean) *Density2
Total_FR2011=apply(FR2011_seed,2,FUN=mean) *Density2
Total_FR2012=apply(FR2012_seed,2,FUN=mean) *Density2
Total_FR2013=apply(FR2013_seed,2,FUN=mean) *Density2
Total_FR2014=apply(FR2014_seed,2,FUN=mean) *Density2
Total_FR2015=apply(FR2015_seed,2,FUN=mean) *Density2
Total_FR2016=apply(FR2016_seed,2,FUN=mean)*Density2

par(mar=c(5.1,5.1,4.1,2.1))
boxplot(Total_FR2008,Total_FR2009,Total_FR2010,Total_FR2011,
        Total_FR2012, Total_FR2013, Total_FR2014,Total_FR2015,

Total_FR2016,names=c("Y2008","Y2009","Y2010","Y2011","Y2012","Y2013","Y2014","Y20
15","Y2016"),
        ylab=expression(paste("Filtration rate ","(",l," ",h^-1," ",m^-
2,")")),cex.lab=1,cex.axis=0.95)

summary(Total_FR2009)
mean(Total_FR2014)
sd(Total_FR2012)

Total_FR=rowMeans(cbind(Total_FR2008,Total_FR2009,Total_FR2010,Total_FR2011,Total_
FR2012,Total_FR2013,
                        Total_FR2014,Total_FR2015,Total_FR2016)) ## Average filtration rate l/h/m2
mean(Total_FR)
sd(Total_FR)

## Denitrification and nitrogen burial

Density2=11.2  ## Density No of seed oyster/m2

#for 2008
```

```
Inges2008=FR2008_seed*food[,1]*24 ## 24 is 24 hours a day

Remo_day_2008=0.5*Inges2008*0.3*Density2*10^-6  ## Kg N remove from 1 m2 of a oyster a
day.
#10^-6 to convert from mg to kg

Remo_year_2008=apply(Remo_day_2008,2,FUN=sum) ## Kg N remove from 1 m2 of oyster
seed a year

Remo_year_2009=apply((0.5*FR2009_seed*food[,2]*24*0.3*Density2*10^-6),2,FUN=sum)
#for 2009: Kg N remove from 1 m2 of an oyster a year
Remo_year_2010=apply((0.5*FR2010_seed*food[,3]*24*0.3*Density2*10^-6),2,FUN=sum)
#for 2010:
Remo_year_2011=apply((0.5*FR2011_seed*food[,4]*24*0.3*Density2*10^-6),2,FUN=sum)
#for 2011:
Remo_year_2012=apply((0.5*FR2012_seed*food[,5]*24*0.3*Density2*10^-6),2,FUN=sum)
#for 2012:
Remo_year_2013=apply((0.5*FR2013_seed*food[,6]*24*0.3*Density2*10^-6),2,FUN=sum)
#for 2013:
Remo_year_2014=apply((0.5*FR2014_seed*food[,7]*24*0.3*Density2*10^-6),2,FUN=sum)
#for 2014:
Remo_year_2015=apply((0.5*FR2015_seed*food[,8]*24*0.3*Density2*10^-6),2,FUN=sum)
#for 2015:
Remo_year_2016=apply((0.5*FR2016_seed*food[,9]*24*0.3*Density2*10^-6),2,FUN=sum)
#for 2016:
hist(Remo_year_2016)

par(mar=c(5.1,5.1,4.1,2.1))
boxplot(Remo_year_2008,Remo_year_2009,Remo_year_2010,Remo_year_2011,
      Remo_year_2012, Remo_year_2013, Remo_year_2014,Remo_year_2015,

Remo_year_2016,names=c("Y2008","Y2009","Y2010","Y2011","Y2012","Y2013","Y2014","Y
2015","Y2016"),
      ylab=expression(paste("Denitrification & N burial ","(","Kg ","N ",m^-2,yr^-
1,")")),cex.lab=1,cex.axis=0.95)

mean(Remo_year_2014)
sd(Remo_year_2014)

Total_remove=rowMeans(cbind(Remo_year_2008,Remo_year_2009,Remo_year_2010,Remo_y
ear_2011,Remo_year_2012,Remo_year_2013,
                      Remo_year_2014,Remo_year_2015,Remo_year_2016)) ## Average filtration
rate l/h/m2
mean(Total_remove)
sd(Total_remove)
```

```
area=1045*10000 ## Total area of oyster reefs in m2
Mobie_2012=Remo_year_2012*area  ##Kg N remove a year by oyster reefs in Mobile
mean(Mobie_2012)
sd(Mobie_2012)

Mobie_2014=Remo_year_2014*area  ## Min removal
mean(Mobie_2014) ##
sd(Mobie_2014)

Mobie_average=Total_remove*area  ## Average removal
mean(Mobie_average)
sd(Mobie_average)

par(mar=c(5.1,5.1,4.1,2.1))
boxplot(Remo_year_spat,Remo_year_seed,Remo_year_market,names=c("Spat","Sub-
Legal","Market-Size"),
      ylab=expression(paste("Denitrification & N burial ","(","Kg ","N ",m^-2,yr^-
1,")")),cex.lab=1,cex.axis=0.95)

################

###### Estimate variation for oyster harvest####
library(truncnorm)

Oyster_harvest=rtruncnorm(100000,a=10442,b=134254,mean=50470,sd=45900) # value in kg
wet tissue weight
Oyster_harvest_dry=0.179*Oyster_harvest-0.113 ## value in kg dry tissue weight
Oyster_harvest_dry_shell=Oyster_harvest_dry*100/2.462  ## shell dry in kg
N_removal_tissue=Oyster_harvest_dry*0.118 ### Nitrogen removal from tissue in kg
mean(N_removal_tissue)  ## mean value N removal from tissue
sd(N_removal_tissue)  ## SD value N removal from tissuee

N_removal_shell=Oyster_harvest_dry_shell*0.0026
mean(N_removal_shell) ##mean value N removal from shell
sd(N_removal_shell)  ## SD value N removal from shell

a=rnorm(100000,16123,2370) ### Denitrification
b=rnorm(100000,8061,1185) ## Burial
Total_N_removal=N_removal_tissue+N_removal_shell+a+b  ### sum of N removal from tissue
and tissuee
mean(Total_N_removal)
sd(Total_N_removal)
```

Chapter 4 The consequences of increasing the oyster *(Crassostrea virginica)* harvest size limit to provision of ecosystem services by oyster reefs in Mobile Bay, Alabama.

Abstract

A 3 inch (76mm) oyster harvest size limit is commonly adopted to regulate oyster fisheries in the U.S., but there is little justification as to why this size limit has been applied. Research implying that retention of oysters on reefs increases ecosystem services exists. To examine the impacts on production and benefits to ecosystem services of increasing the oyster harvest size limit on public reefs in Mobile Bay, Alabama, I simulated oyster growth from 76mm (3 inches) to 89mm (3.5 inches). Results indicated that oysters took from 55 to 444 days to reach 89mm shell height from 76mm depending on starting month of the simulation. However, the 89mm harvest scheme would lower production by 42% to 72% due to high natural mortality. The total amount of nitrogen removal from water by changing the harvest size limit was 2,037±236 kg N (mean±1sd). This nitrogen removal benefit was very small compared to the loss of oysters, which was about 78±12% due to very high natural mortality. The regulating agencies could implement a monitoring program and associated analysis to quantify oyster mortality for informing implications related to any change in the harvest size limit of oysters.

Introduction

Oysters, one of the most threatened marine species, have long been acknowledged for their importance as a commercial commodity, as well as for having recreational and ecological value to human beings (Coen et al. 2007; Grabowski and Peterson 2007; Scyphers et al. 2011;

Grabowski et al. 2012). However, oyster reefs and oyster population biomass have diminished by 64% and 88%, respectively, in estuaries of the United States over the last century (zu Ermgassen et al. 2012). In the Gulf of Mexico, oyster reef restoration has been ongoing for decades; however, the gains in ecosystem and other values associated with these efforts have been poorly documented (La Peyre et al. 2014). Quantifying these services is needed to justify restoration decisions, as well as to evaluate trade-offs associated with various restoration strategies (Barbier et al. 2011).

In Alabama, oyster reef restoration has taken place since at least the 1880s (Wallace et al. 1999). Despite that, Alabama's estuaries have still seen a 60% decline in oyster density and market size (zu Ermgassen et al. 2016) and 79% decrease in oyster filtering capacity (zu Ermgassen et al. 2013). The Alabama Department of Conservation and Natural Resources (ADCNR) in consultation with the Conservation Advisory Board may promulgate rules or regulations designed for protection and conservation of all fishery resources such as size, bag limits, or harvest season. Oysters harvested on most public reefs in Alabama for commercial or recreational purposes must be taken by hand or with oyster-tongs and be at least 76mm in size (Wallace 2003; Vanderkooy 2012). A 76mm oyster harvest size limit is commonly adopted as a regulation for harvest from public reefs in U.S. coastal regions. However, there is little information as to why the 76mm limit was adopted. Vanderkooy (2012) speculated that it originated from the Chesapeake Bay where the 63mm (2.5 inches) harvest size limit in 1890 was increased to 76 mm in 1927 in response to a decline in oyster harvest. The harvest continued to decline; however, the 76mm regulation has remained in effect until today (Rothschild et al. 1994).

Although it has been typical to value oysters as a fishery commodity, there is scientific evidence of oyster reefs providing economically valuable ecosystem services; supporting and provisioning of food and shelter for many (estimated ~360) marine species (Wallace 2003; Gregalis et al. 2008; Grabowski et al. 2012; zu Ermgassen et al. 2016),; filtering excessive water nutrients and maintaining viability in coastal communities where oysters are valued both economically and culturally.

Increasing ecosystem services such as nitrogen removal as an oyster restoration goal is often considered during discussions regarding oyster management (La Peyre et al. 2014; zu Ermgassen et al. 2016). For example: Newell et al. (2005) suggested that keeping oysters in the water for 10 years for nitrogen removal services would double the value of a one-time harvest of all oysters in the Choptank River estuary (Maryland). Kasperski and Wieland (2009) proposed that imposing an oyster harvest moratorium or limiting harvest efforts would create more economic incentives than oyster harvest itself in Chesapeake Bay. However, management options that increase harvest size limit to achieve dual goals of oyster production and enhanced ecosystem values have not been discussed in the literature.

Oysters can become reproductively mature four weeks after settling; and effective spawning ensues when oysters reach 50mm in size (Hayes and Menzel 1981). Oysters in the Gulf of Mexico spawn throughout the year with multiple spawning events, depending on environmental conditions and can produce as many 100 million eggs per female in a season (Hayes and Menzel 1981). The analysis of factors contributing to the oyster collapse in Apalachicola Bay, Florida in 2012 demonstrated that the collapse was driven by reduced cultch areas available for oyster settlement rather than overharvest (Pine et al. 2015). The productive waters in Mobile Bay support rapid oyster growth (Walton et al. 2012) and oysters can reach the harvest size limit of

76mm in 12-18 months from settling (Ingle and Dawson Jr 1952). Increasing oyster resident time likely would increase supporting and regulating services provided by oysters, however, there is also the risk of increasing oyster exposure to disease and predators (Hofstetter et al. 1965) leading to increased oyster mortality. An 89mm minimum harvest size limit of oyster was once maintained in Texas from 1925 to 1963, then was reduced to 76mm limit similar to other regions primarily due to high oyster mortality (Hofstetter 1963).

In this study, I hypothesized that increasing the harvest size limit from 76mm (3 inches) to 89mm (3.5 inches) in Mobile Bay, Alabama would not reduce the overall production of those oysters due to natural mortality because of compensatory benefits provided by larger oysters. Increasing the size limit would also increase oyster resident time on reefs to generate additional benefits in the form of ecosystem services. Therefore, I simulated oyster production as oyster growth from 76mm to 89mm under different growth rates and mortality due to the influence of environmental conditions in Mobile Bay, and then estimated the additional benefit from nitrogen removal services due to increasing oyster resident time.

Methods

Modeling approach

The oyster growth model (post-settlement energy growth model) used in this study was originally developed by Powell et al. (1992) that predicts oyster daily growth rates as functions of environmental variable inputs. The growth model was assumed to be applicable to Mobile Bay, as it was successfully applied to resident oysters in Galveston Bay, Texas (Powell et al. 1992; Hofmann et al. 1994; Dekshenieks et al. 2000), Apalachicola Bay, Florida and Breton Sound Estuary, Louisiana (Wang et al. 2008, 2017). Therefore, no attempt was made to modify the model parameters for Mobile Bay, Alabama. A conceptual model describing oyster growth in relation to the input of environmental variables is presented in Figure 4-1. The details of post settlement growth model equations are described in Appendix 4-1, illustrating individual oyster growth with a daily time step. Oyster growth is defined as somatic growth (cal ind^{-1} day) and is then converted to oyster shell height (mm) by standard conversion equations reported in Appendix 4-1. All model parameters are assumed to be constant (Powell et al. 1992; Wang et al. 2008, 2017).

The daily growth of a cohort of individual oysters at 76mm (~ 0.52 g ash-free-dry-weight, hereafter: AFDW) exposed to daily environmental variables of water temperature, salinity, turbidity and food (Chlorophyll-*a*) from Mobile Bay was simulated until the oysters attained 89mm (~0.94 g AFDW). The simulation began on the first day of each month (January-December) to provide a basic comparison of how the growth rate would vary among different times of year and how long it would be expected for the oysters to attain the 89mm shell height based on the time of recruitment at 76mm. Daily growth was replicated using 9 years of environmental data from 2008 to 2016 to evaluate the variation in growth rates in the bay. For example, the simulation started from January each year to compare the growth rate of January oysters between years. For oysters that took longer than a year to attain 89mm (i.e., fall oysters), environmental data from the next year were used to simulate the growth until oysters attained 89mm. Similar to other bivalves, oyster soft tissue growth increases with shell size in response to increased food supply and favorable conditions, (i.e., Quahogs *Mercenaria mercenaria*, and Softshell Clams *Mya arenaria*; Carmichael et al. 2004) but oysters also lose soft tissue biomass during unfavorable conditions (usually in winter; Powell et al. 1992), however the shell size does not change. This is basic for my assertion that it would be most beneficial in terms of production biomass if oysters were harvested when they first attained a desirable size (i.e., 0.94 g AFDW ~

89mm shell height). Therefore, I assumed that the 89mm shell height oysters were all harvested, then compared the production of the larger oysters to the production of oysters at 76mm shell height if they were harvested at the smaller size.

However, the decision to harvest oysters at 89mm versus 76mm shell height is influenced by natural mortality which was modelled as a function of temperature and salinity.

The daily instantaneous natural mortality rate (M_t) was derived from a mortality study in Texas (Hofstetter et al. 1965) by dividing the reported monthly finite rate by 30 days.

$$M_t = \frac{-\ln(1-finite\ rate)}{30} \tag{1}$$

The daily natural mortality then was regressed as function of temperature and salinity and was assumed to apply to oysters in Mobile Bay:

$$M_t = -0.0539+0.00189*T+0.000977*S \ (p<0.05, R^2= 0.62) \tag{2}$$

where M_t is instantaneous daily mortality rate, T (°C) is daily temperature and S (ppt) is daily salinity.

The average number of oysters harvested each month during 2008 – 2016 was assumed to be at 76mm shell height. Therefore, I used the average number of 76mm oysters in each month as the initial number to simulate surviving individuals each day from the first day of the simulation to the day that oysters attained 89mm shell height. The daily surviving individuals (N_t) is the product of the number of individuals at t-1 (N_{t-1}) and the survival rate at t-1 ($e^{-M_{t-1}}$) as:

$$\text{Nt} = N_{t-1}\, e^{-M_{t-1}} \tag{3}$$

where: $e^{-M_{t-1}}$ is daily survival rate

The production at the day that oysters attained 89mm shell height (P in g AFDW) is the product of oyster weight (~0.94 g AFDW) and the surviving individuals (N_t) at that day:

$$P_t = N_t W_t \tag{4}$$

The comparison of oyster production at 89mm versus 76mm shell height was described by percentage of production gained or lost.

Environmental variables

Temperature and salinity: Daily temperature and salinity data from 2008 to 2016 were obtained from the Mobile Bay National Estuary Program's Cedar Point Station (NEP-CedarPoint 2008-2016) near the most productive oyster reefs in Mobile Bay. Daily values of temperature and salinity are presented in Figure 3-2 and Figure 3-3 in Chapter 3.

Chlorophyll-*a* and Turbidity: Chlorophyll-*a* and Turbidity data were obtained from the National Water Information System for Mobile Bay, Alabama at the Cedar Point station (USGS-WQ-CedarPoint 2016). Daily data of Chlorophyll-*a* and Turbidity were linearly interpolated from monthly data recorded in 2016. Due to the lack of yearly data (2008-2015) for Chlorophyll-*a* and Turbidity at Cedar Point reefs, the interpolated daily data were replicated 9 times to align with the temperature and salinity data above as inputs into the growth model (Wang et al. 2008). Daily values of Chlorophyll-*a* and Turbidity are presented in Figure 3-4 and Figure 3-5.

Chlorophyll-*a* values were then converted to food (Soniat et al. 1998; Hyun et al. 2001) for the oyster growth model

$$f = 0.088 \, x \, Chl + 0.520 \qquad (5)$$

where: f is food content (mg l^{-1}); Chl is Chlorophyll-*a* concentration in the water column (µg l^{-1}).

Nitrogen removal services provided by delayed oyster harvest

A daily denitrification and nitrogen burial service was estimated for individual oysters as described in Chapter 3. The daily nitrogen removal benefit was estimated by multiplying daily nitrogen removal rate with the number of oysters surviving through that day. The total nitrogen removal benefit of the delayed harvest was the sum of the daily nitrogen benefit from the first day of simulation to the day when oysters attained 89mm shell height.

Results

Oyster growth rates were highly variable. The time to grow from 76mm to 89mm shell height ranged from 55 to 445 days and was dependent on the start month of the simulation. The fastest oyster growth rates were observed when simulations began in July (69±29 days) and August (70±23 days), and the slowest growth rates were for oysters simulated from September (334±98 days), October (286±85days) and November (293±44 days) (Table 4-1, Figure 4-2) (hereafter oysters which were simulated beginning in July will be referred to as July oysters, those simulated beginning in August. August oysters, and so forth). Oysters grew rapidly during the summer simulations (June-August oysters) and oysters were predicted to reach 89mm in about two to three months. Oyster growth rates during summer were similar among years except for in 2013 (Figure 4-3). All oysters simulated from the winter and summer months (January-August oysters) reached 89mm within the same calendar year (Figure 4-4); simulated growth rates were fastest in 2012 and slowest in 2013. The yearly variation in growth rates is likely due to only salinity regime because the temperature showed a similar trend and the Chlorophyll-*a* was assumed to be invariant among years in the bay (Figure 3-2, 3-3,3-4 in Chapter 3). Oysters simulated beginning in the fall (September- December oysters) grew slower and reached 89mm in the next spring or fall (from 153 to 445 days) depending on the year (Figure 4-5).

Daily mortality (instantaneous daily mortality rate) was very high especially during the summer. Summer mortality (June- August) contributed to about 60% of annual mortality (Figure 4-6). Despite the fast-growing rates, oyster production still decreased by 46% to 72% a consequence of changing the harvest size limit (Table 4-1). There were exceptions; February 2008 oysters, October 2008 oysters and October 2010 oysters gained 54%, 5% and 16% in their production respectively (Figure 4-7). Although these oysters were not the fastest growing oysters, they did reach 89mm before the high mortality season (summer) started. Overall, fall oysters (September-December) tended to lose more production on average than other oysters because of their longer resident time.

Nitrogen removal benefit depended on the number of oysters surviving and the subsequent additional resident time. Due to the high mortality rates, the number of oysters remaining in the water to provide the service was low, as was the amount of nitrogen removed by these oysters. September oysters were predicted to have the lowest survival rates (14±13%) and July oysters had the highest survival rates (35±5%) at the end of the simulations (Figure 4-8). The lowest nitrogen benefit was 9±2kg N from June oysters and the highest benefit was 739±168kg N from November oysters (Table 4-1, Figure 4-9). The total amount of nitrogen removal from the water by changing the harvest size limit from 76mm to 89mm was 2,037±236 kg N, which was equal to \$8,127 yr^{-1} (\$3.99 kg^{-1} N) in economic benefit. This nitrogen removal benefit was very small as compared to the loss of oysters 28,408 – 44,465 kg wet weight, which was equal to \$308,000 – \$482,000 (\$10.85 kg^{-1} oyster) due to assumed high natural mortality.

Discussion

The growth simulations indicated that the time interval for oysters to attain 89mm shell height from 76mm depended on the starting month of the simulation. The fastest predicted growth rates during the summer (June – August), which is common to oysters in the Gulf of Mexico (Ingle 1950; Livingston et al. 1999, 2000), were likely the result of the combination of the imposed environmental variables such as temperature, salinity and food in the simulation.. In this simulation, summer oysters were predicted to gain 13mm in length in 55-90 days. These growth rates seemed to be very high for market size oysters which tend to grow slower as the oysters get larger. However, Ingle (1950) reported that oysters in Florida could achieve the growth of 2.7mm in length per week in summer months providing inference that predicted growth rates in my study are feasible even for large oysters. Higher growth rates also coincided with the higher daily values of food (Chrolorophyll-*a*) available to oysters (Hofmann et al. 1994; Powell et al. 1995), which was highest during the summer months in my study. The slower growth rates for summer 2013 oysters likely corresponded to the lowest monthly average salinities (~10ppt); average salinity usually ranges from 17ppt to 25ppt in Mobile Bay during summer (Figure 3-3 in Chapter 3). Wang et al. (2008) reported lower growth rates at lower salinity; () a salinity of 10ppt is the minimum level that adult oysters can grow at normal rates (Kennedy et al. 1996).

There is natural variation in the growth of oysters, which exhibit faster growth rates during summer but slower growth in winter (i.e., Pine III et al. 2015). The fall oysters (October-December) took a longer time to attain 89mm shell height because these oysters tended to lose soft tissue biomass under unfavorable conditions during the winter (se also Powell et al. 1992). However, the faster growth rates resumed again in the next summer, compensating for the loss in biomass (see also Powell et al. 1992).

Overall, this simulation predicted that oysters in Mobile Bay were fast growing under the assumption that model parameters are applicable and constant for influencing oyster growth in the Bay. The variation of growth using nine years of environmental data signified a strong environmental influence. In addition to temperature and salinity, the growth rates were also sensitive to Chrolorophyll-*a* concentration, however, the daily values of Chrolorophyll-*a* were not available for 2008 – 2016 which could introduce bias in the model (see Wang et al. 2008). I predict that if daily variation in values of Chlorophyll-*a* were used in the simulation, more variation in growth rates would be observed.. Therefore, Chrolorophyll-*a* remained to be the main source of uncertainty in the model estimation.

Mortality is likely the factor that ultimately will affect any decision toward changing the minimum harvest size limit. Despite fast growth, the gain in oyster biomass under a delayed harvest action was not able to offset for the loss in production, under the assumption of high mortality rates. That scenario presented a potential economic loss to fishers if the 89mm minimum harvest size limit was applied. Natural mortality rate variation has been as reason to change harvest size limits in some fisheries (e.g., Texas Hofstetter 1963). The average mortality rates applied in that study were similar to the reported summer daily mortality rates in Mobile Bay, Alabama for smaller size oysters (Gregalis et al. 2008). However, it is not uncommon that larger size oysters have higher rates of mortality depending on temperature and salinity regimes (Hofstetter et al. 1965; Rybovich et al. 2016). The mortality rates also depend on reef structures where mortality may be lower in high density reefs (Pine III et al. 2015) and likely vary with reef elevation (i.e., low reefs versus high reefs, Gregalis et al. 2008).

High oyster mortalities in Alabama waters are known to be caused by Southern Oyster drill (*Thais haemastoma*) and Dermo (*Perkinsus marinus*) (May 1968, 1971; Gregalis et al. 2008; Scyphers et al. 2011), which are most abundant in more saline part of estuary (Butler 1985) and during summer (Jordan 1996; Hamilton et al. 2005; Vølstad et al. 2008). At salinity higher than 15ppt, Dermo starts to become prolific and causes oyster mortality (Kennedy et al. 1996; Vanderkooy 2012). The high mortality also impacts off-bottom oyster aquaculture. Hamilton et al. (2005) reported oyster mortality ranged from 44% to 70% after 36 weeks for off-bottom oysters cultured on the northern side of Dauphin island. My study predicted higher mortality (78±12%) on average at the end of the simulations.

Compared to other simulation studies, the mortality applied in this study (i.e., 1.8-3.4/year or 0.005-0.009/day) derived from Hofstetter et al. (1965) was much higher. Pine III et al. (2015) assumed yearly instantaneous natural mortality rates for oysters in Apalachicola bay were 1.2/year. In the same bay, Wang et al. (2008) used constant daily mortality rates from 0.0002/day to 0.00122/day. It is likely that the effects of mortality (i.e., Dermo and Oyster drill) will define oyster population structure (Jordan 1996). Further mortality research in Mobile Bay, Alabama could elucidate which is the best harvest size limit: 76mm, 89mm or even 63mm (2.5 inches) for the provision of ecosystem services by oysters in the bay.

The estimation of the economic benefit provided by nitrogen removal services from delaying or increasing oyster harvest size limit suggested that the nitrogen removal services should be considered as a complement to the oyster harvest in Mobile Bay rather than a factor to change the harvest regime to harvest moratorium or limiting oyster harvest as Kasperski and Wieland (2009) suggested for the Chesapeake Bay. Based on this study simulation, it would be more beneficial to keep the harvest size limit at 76mm instead of increasing to 89mm shell height. This study suggested that management agencies could monitor and study oyster mortality and measures to control oyster mortality in Mobile Bay as a foundation for considering changing the minimum harvest size limit of oysters.

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Table 4-1: Summary of the oyster growth model simulation. Recruitment time is the time (month) when the growth simulation began with 76mm oysters. Number of oysters to start the simulation is the average number oysters harvested each month from 2008 to 2016. Number of days to attain 89mm (0.94 g AFDW) shell height is the number of days of simulation from 76mm (0.52 g AFDW). Number of oysters at 89mm is the number of oysters surviving to the end of the simulation. Oyster production gain/loss (%) by increasing harvest size limit and associated nitrogen benefit (kg N). The number format in the table is mean and first standard deviation (mean±1sd) are reported.

Recruitment time	**No oysters to start**	**No of days to attain 89mm**	**No oysters at 89mm**	**Production gained/loss (%)**	**Nitrogen benefits (kg N)**
January	593,925	224±46	150870±65775	-53±18	151±18
February	426,817	194±52	116441±97634	-46±41	89±15
March	287,678	176±40	55106±17804	-63±12	51±8
April	243,493	149±44	44739±14303	-64±13	33±7
May	263,235	118±34	46500±10320	-68±8	25±6
June	141,489	93±31	26540±5191	-66±4	9±2
July	213,879	69±29	55731±7693	-51±7	11±3
August	161,232	70±23	45605±5095	-46±10	9±3
September	92,132	334±98	12662±12013	-72±25	17±5
October	1,122,040	286±85	288229±250028	-52±41	284±45
November	2,512,252	293±44	472541±361773	-64±26	739±168
December	2,070,157	264±44	435578±255387	-60±22	619±58
Total	**8,128,329**		**1,750,540±690,840**		**2,037±236**

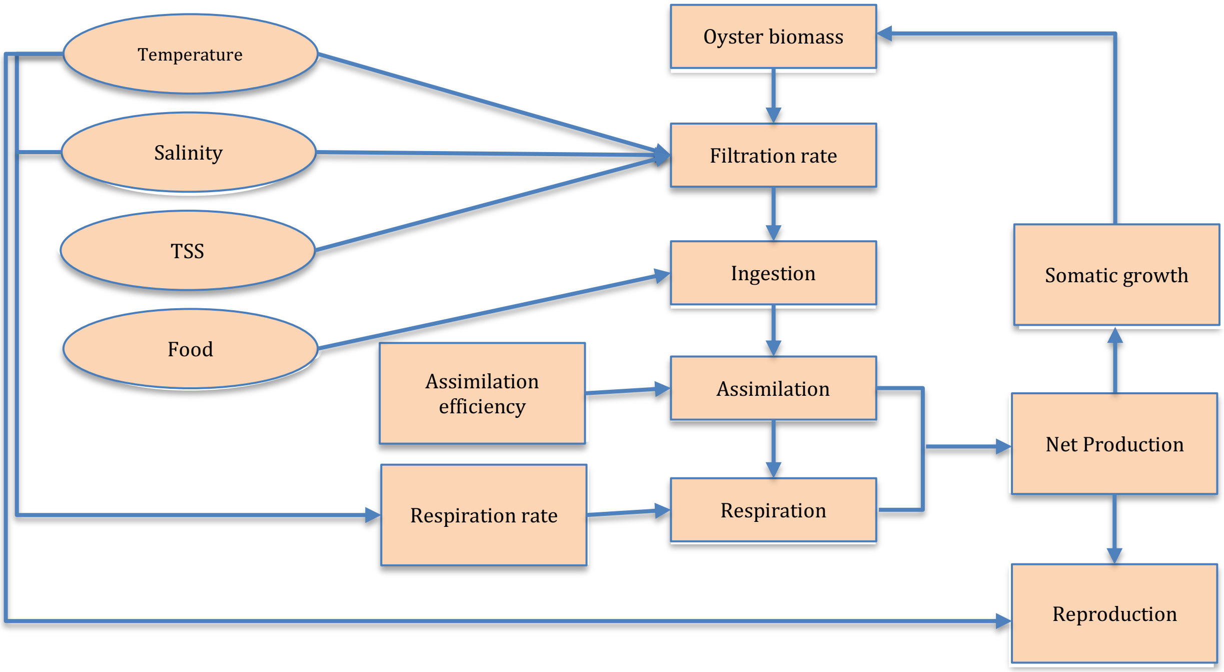

Figure 4-1: Conceptual post settlement model (modified from Hofmann et al. 1994; Powell et al. 1994; Hofmann et al. 2006)

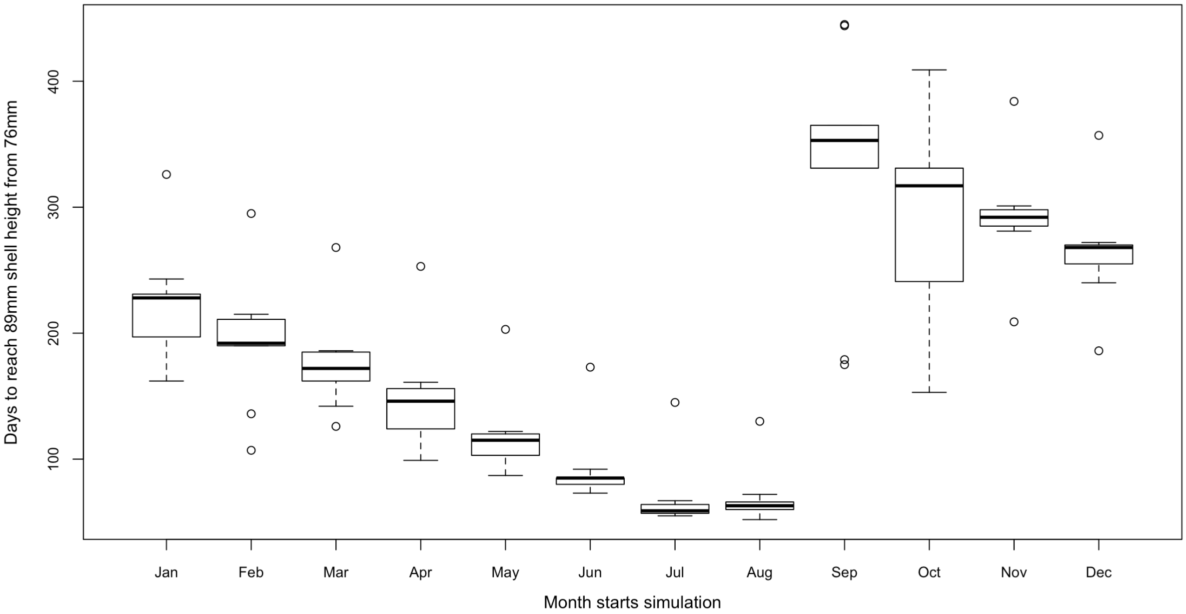

Figure 4-2: Days to reach 89mm from 76mm shell height. The x axis displays the month when the growth simulation began. The y axis is the number of days from the first day of the simulation to the day oysters attain 89mm shell height. Each box presents mean, upper and lower quartiles and minimum and maximum days that oysters attain 89mm under different environmental conditions from 2008 to 2016. Summary of the simulation outputs in mean and standard deviation were presented in Table 4-1.

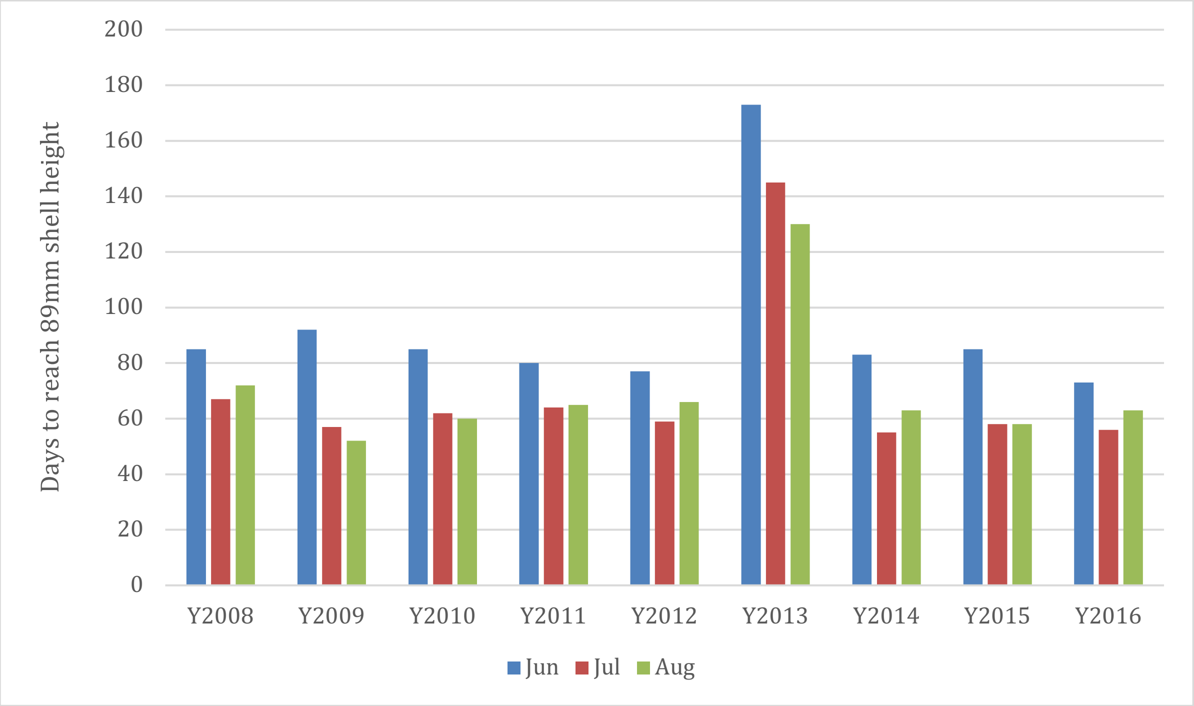

Figure 4-3: Number of days to reach 89mm from 76mm shell height for oysters simulated during summer months. The plot represents yearly variation in growth rates for summer oysters. The x axis is the month in each year when the growth simulation began. The y axis is the number of days from first day of the simulation to the day the oysters attain 89mm shell height.

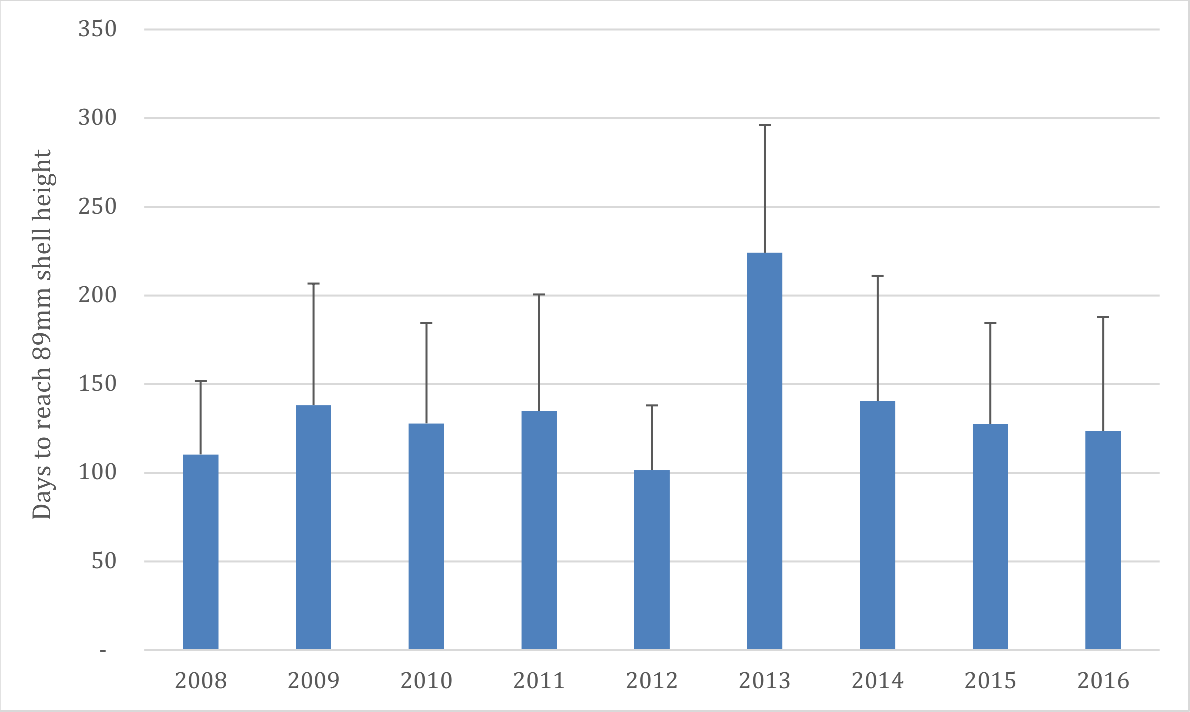

Figure 4-4: Average days to reach 89mm from 76mm shell height for oysters simulated from January to August each year. Oyster can attain the 89mm within the same calendar year. The plot shows oysters grew fastest in 2012 and slowest in 2013. The x axis presents the year of simulation. The y axis is the average days from first day of the simulation to the day oysters attain 89mm shell height. Error bars show fist standard deviation.

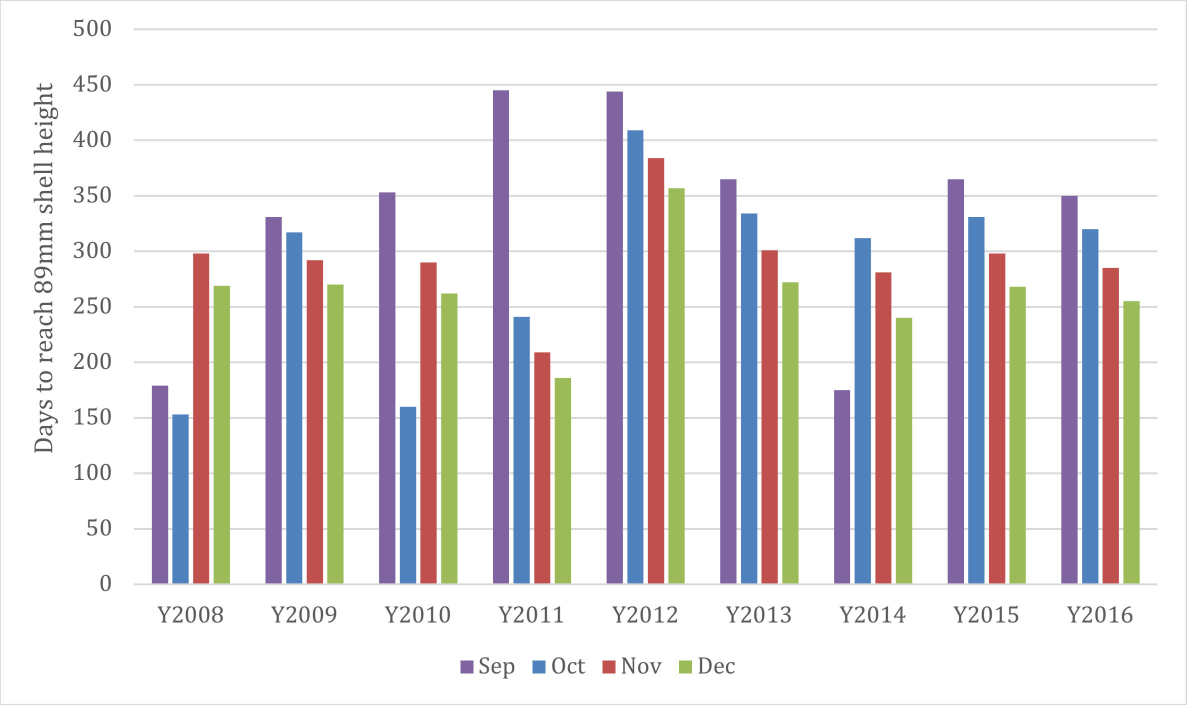

Figure 4-5: Number of days to reach 89mm from 76mm shell height for oysters stimulated during fall months. The plot represents yearly variation in growth rates for fall oysters. The x axis is the month in each year when the growth simulation began. The y axis is the number of days from first day of the simulation to the day the oysters attain 89mm shell height.

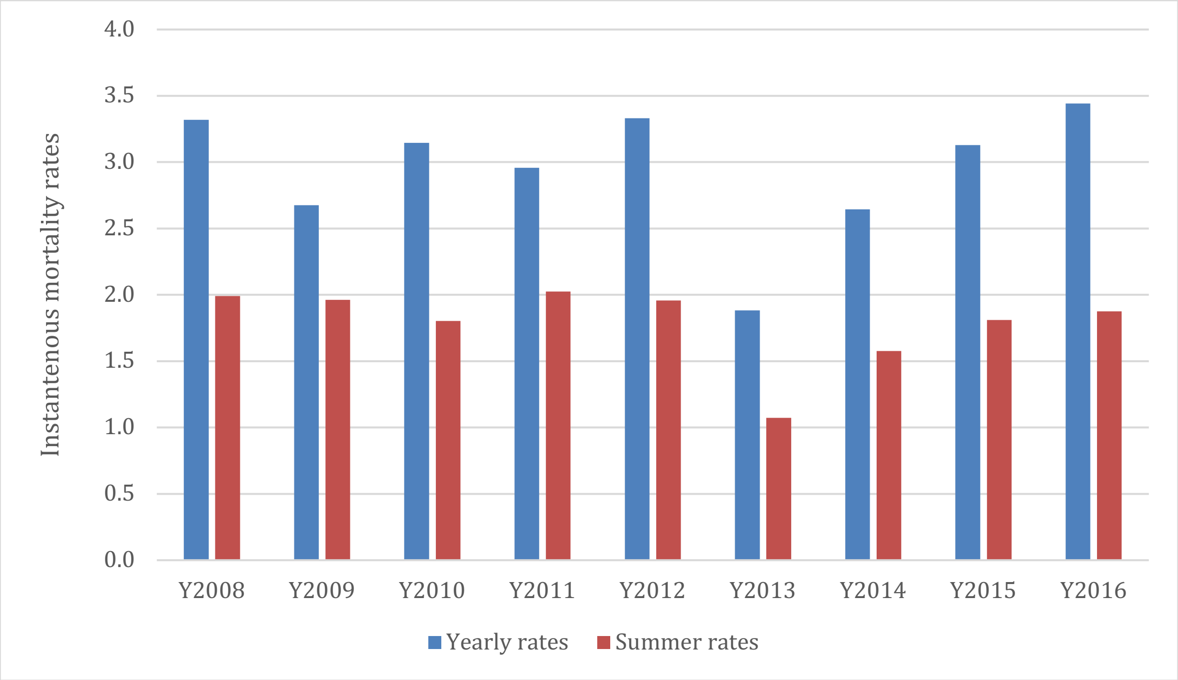

Figure 4-6: Instantaneous yearly mortality rates compared to summer mortality rates (June, July, August). The mortality rates were derived from Equation 1 by summing instantaneous daily rates in a full year and for only days in the summer months. The plot presents the yearly variation in mortality rates.

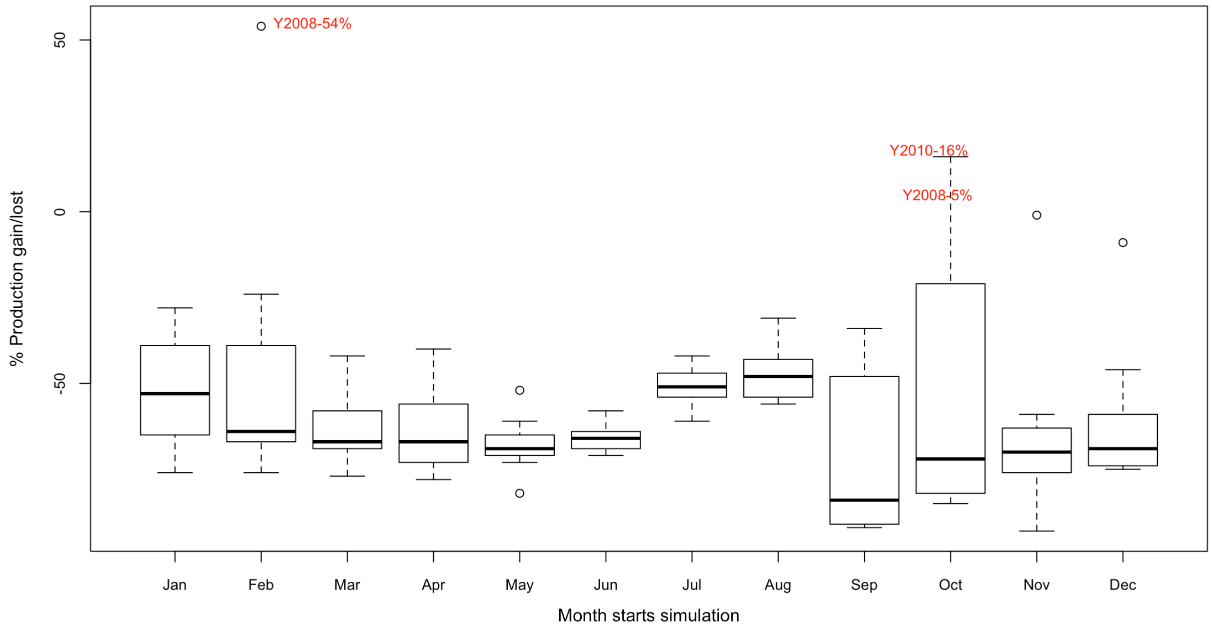

Figure 4-7: Predicted productions gain or loss (%) if oysters were harvested at 89mm compared to 76mm shell height. The x axis is the month when the growth simulation began. The y axis is the percentage difference of production between the two harvest scenarios. The negative number indicates the percentage lost by the delayed harvest. The positive number (red number) shows the percentage gained by the delayed harvest. Each box represents mean, upper and lower quartiles and minimum and maximum production gained/lost at 89mm compared to76mm among years. Summary of the simulated mean and standard deviation were presented in Table 4-1.

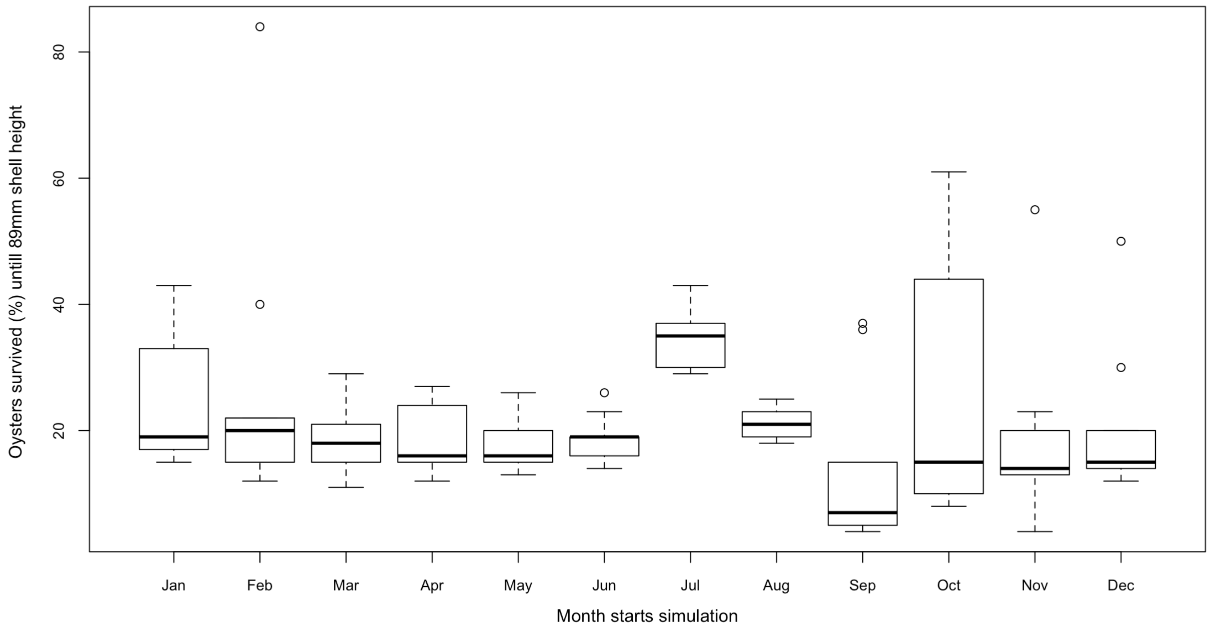

Figure 4-8: Proportions of oysters that survive until they attain 89mm shell height from 76mm. The x axis is the month when the growth simulation began. The y axis is the proportion of oysters that survived until the end of the simulation. Each box presents mean, upper and lower quartiles and minimum and maximum proportion of oysters that survived to 89mm compared to 76mm among years. Detailed numbers of individuals that survived until the end of the simulation outputs were presented in Table 4-1.

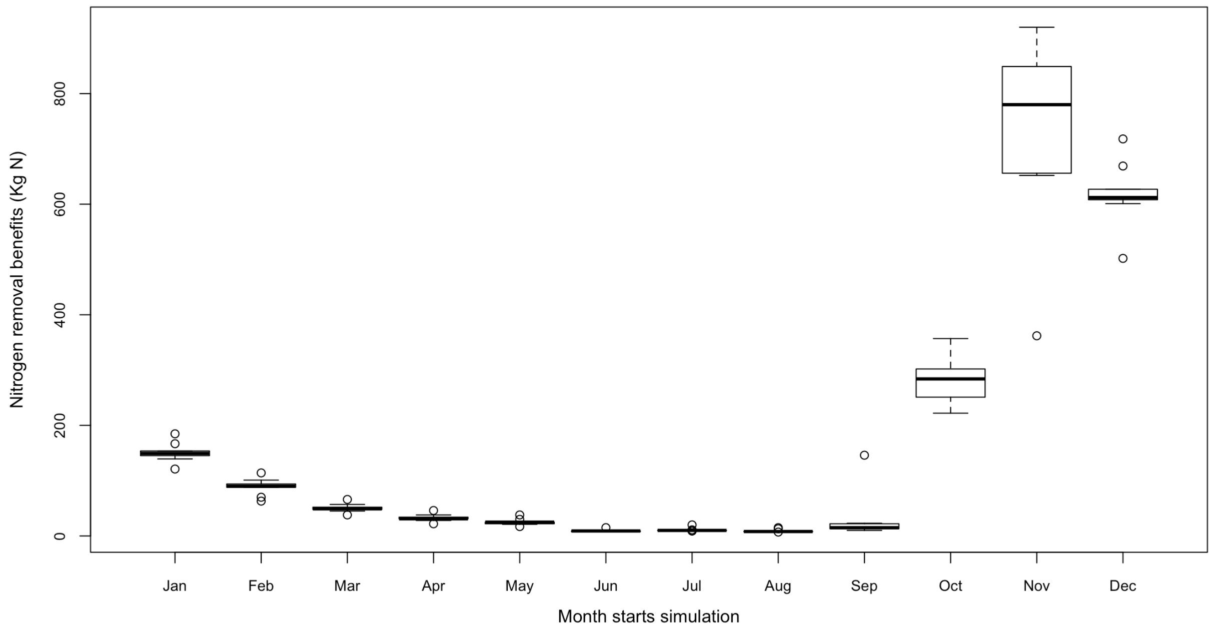

Figure 4-9: Nitrogen removal benefits (kg N removal) from increasing harvests size to 89mm shell height from 76mm. The x axis is the month when the growth simulation began. The y axis is the sum of nitrogen removal benefits from the first day to the end of the simulation. Each box represents mean, upper and lower quartiles and minimum and maximum nitrogen removal benefits among years. A summary of means and standard deviations of nitrogen removal benefits were presented in Table 4-1.

Appendix 4-1: Post-settlement model

1. Governing equation

$$NP = P_g + P_r = A - R \quad (1)$$

Where: NP is net production (cal ind^{-1} day^{-1})

P_g is energy for growth (cal ind^{-1} day^{-1})

P_r is reproduction energy (cal ind^{-1} day^{-1}). See equation 5

A is assimilation (cal ind^{-1} minute^{-1}). See equation 9

R is respiration rate (µg l^{-1} oxygen h^{-1} g^{-1} AFDW). See equation 10

2. Filtration

$$FR = \left(\frac{L^{0.96}T^{0.95}}{2.95}\right) \qquad (2)$$

$$L = W^{0.317}10^{0.669} \qquad (3)$$

Where

FR is filtration rate (cal ind^{-1} minute^{-1}),

L is oyster shell height estimated from ash free dry weight, and

W is ash free dried weight (g)

T is temperature (^{0}C).

Filtration rate and salinity

$$FR_S = \begin{cases} FR & at\ S \geq 7.5ppt \\ \frac{FR(S-3.5)}{4.0} & at\ 3.5\ ppt < S < 7.5\ ppt \\ 0 & at\ S \leq 3.5\ ppt \end{cases} \qquad (4)$$

Where: S is salinity (ppt)

Filtration rate and turbidity

$$FR_\tau = FR_S\left[1 - 0.01\left(\frac{log_{10}\tau + 3.38}{0.0418}\right)\right] \quad (5)$$

Where: τ is total particulate (inorganic and organic) content (g 1^{-1})

3. Ingestion and assimilation

$$I = f \times FR_\tau \qquad (6)$$

Where: *I* is ingestion (mg/ind/min) and *f* is food content (mg 1^{-1})

$$f = 0.088 \; x \; Chl + 0.520 \qquad (7)$$

Where: *Chl* is chlorophyll-a concentration in water column (μg l^{-1})

$$A = I \times A_{eff} \qquad (8)$$

Where: A_{eff} is assimilation efficiency. A_{eff}=0.5 and 0.75 was applied to compare the growth from two different assimilation efficiencies.

4. Respiration

$$R = \begin{cases} R_t & at\ S \geq 15ppt \\ R_t\left(1 + \left(\frac{(15-S)(R_r-1)}{5}\right)\right) & at\ 10ppt < S < 15ppt \\ R_tR_r & at\ S \leq 10ppt \end{cases} \qquad (9)$$

Respiration and temperature

$$R_t = (69.7 + 12.6T)W^{b-1} \quad \text{with b=0.75} \quad (10)$$

Respiration and salinity

$$R_r = \begin{cases} 0.007T + 2.099 & at\ T \leq 20^0C \\ 0.0915T + 1.324 & at\ T \geq 20^0C \end{cases} \qquad (11)$$

5. Reproduction

$$P_r = R_{eff}NP \qquad \textit{(12)}$$

Where: R_{eff} is temperature dependent reproductive efficiency

$$R_{eff} = 0.054T - 0.729\ (January - June) \qquad (13)$$

$$R_{eff} = 0.0047T - 0.809\ (July - December) \qquad (14)$$

Maximum reproduction efficiency was set equal to 0.8 (Ingle and Dawson Jr 1952; Livingston et al. 2000; Wang et al. 2008).

6. Spawning

Spawning occurs when the cumulative reproductive biomass exceeds 20% of total biomass and at temperature greater than 25^{0}C (Ingle and Dawson Jr 1952).

7. Caloric conversions

$W = \left(\frac{L}{10^{1.957}}\right)^{\frac{1}{0.266}}$; W is oyster weight (g AFDW), L is oyster shell height (mm)

Oyster: 6100 cal/g AFDW

Food: 5168 cal/g AFDW

Oyster eggs: 6133 cal/g AFDW

Chapter 5 Conclusions

Fish enhancement

Estimating economic value of ecosystem services provided by oyster reefs is not new, but this is the first estimate conducted for oyster reefs in Mobile Bay, Alabama that incorporates uncertainty of life-history parameters in the estimates of enhanced fish production. For fish enhancement services, I separated fish production into discrete categories so that I could apply appropriate valuation techniques for estimating the economic contribution of these services: commercial versus recreational production, economic versus non-economic species, total versus harvestable fish production. The oyster reefs in Alabama produced an additional of 354.09±182.62 (mean±1sd) g m^{-2} yr^{-1} of fish and crustaceans, of which 48% was economically quantifiable. Production associated with recreational fishing was about 2 times higher than commercial production for those enhanced species. The recreational fishing in Mobile Bay contributed about 94% to the total economic value compared to 6% from commercial landings. Taking this total economic value into consideration when estimating the recovery cost of new oyster reef construction will reduce the recovery time from 14 years to 5-6 years. This result may change the view of many people who see oyster reefs just as a source of food rather than for their role in supporting fish production and recreational fishing. The results provided quantification of the importance of oyster reefs which can be used by Alabama decision makers and the public to maximize reef restoration efforts.

Future research should focus on updating life-history parameters which will increase the accuracy of the fish and crustacean production estimates especially in relation to environmental variation in Mobile Bay. A willingness to pay survey for people who reside in Alabama or do fishing in Mobile Bay is needed to increase the reliability of the economic estimate.

Nitrogen removal services

For nitrogen removal services provided by oyster reefs were estimated to remove 26,666±2,919 kg N_2 yr^{-1} (mean ± 1sd) through denitrification, burial of biodeposits into sediments, and oyster harvests in Mobile Bay, Alabama. I demonstrated that using a replacement cost from a sewage water treatment plant in Alabama for the nitrogen removal services provided by oyster reefs in Mobile Bay is applicable and appropriate. The economic benefit of the above nitrogen removal was 106,397±11,646 yr^{-1} which is \$101±11 ha^{-1} yr^{-1}.

The nitrogen removal cost in this study was low compared to other studies because of the nature of oyster reef location and the cost estimation techniques. If a nitrogen exchange program ever exists in Mobile Bay, similar to the one in North Carolina, the estimation value would be higher. In that sense, the nitrogen removal cost applied in this study should be considered as the lowest estimate on the nitrogen removal cost spectrum.

A future study could be conducted to examine the conversions between wet weight, dry weight, and shell height of oysters in Mobile Bay. A Chlorophyll-*a* monitoring study could be combined with ongoing monitoring of other water variables as a foundation to measure annual nitrogen removal provided by oysters in the bay.

Oyster harvest size limit

The results from the oyster growth simulation indicated that the 89mm (3.5 inches) harvest scheme would decrease production by 42% to 72% due to high natural mortality. The result demonstrated that oysters in Mobile Bay were fast growing and all 76mm oysters simulated in the spring and summer will reach 89mm in the same calendar year, while fall oysters would attain 89mm in the next spring or fall. The benefit provided by nitrogen removal services from delaying harvest or increasing oyster harvest size limit was only \$8,127 yr^{-1} in Mobile Bay, Alabama. This ecosystem services will not likely compensate for the reduction of oyster harvest production which cause \$308,000 – \$482,000 in economic loss under high mortality levels in the bay.

A study of oyster growth in Mobile Bay is needed to fine-tune the oyster growth model and its parameters. This study also suggested that the agencies put in place a monitoring program for oyster mortality in addition to measures to control oyster mortality in the bay. This may provide a foundation for considering a change in the oyster minimum harvest size limit in the future. Measures to control mortality will likely involve regulating salinity because high mortality rates caused by disease and oyster predators are often associated with high salinity levels in the bay.