Appendix 2

Age-structured population dynamics model development

Growth

In our age-structured model (Appendix 1), growth of oysters is first described using standard von Bertalanffy growth parameters (Walters and Martell 2005). For Apalachicola Bay, we estimated these parameters using incremental growth measurements obtained from oyster growth experiments conducted by the Florida Department of Environmental Protection (DEP) during 2004-2009 (J. Harper, DEP, *personal communication*). We then used the Ford-Brody representation of growth (Equation 2), which is a relatively simple bioenergetics model derived from the von Bertalanffy assumptions that: (1) anabolic (feeding) rates vary as the 2/3 power of body weight, (2) catabolic (metabolic) rates are proportional to body weight, and (3) body length varies as the 1/3 power of body weight. The Ford-Brody α parameter (Equation 3) can be expressed in terms of the asymptotic maximum body length L_∞ (Equation 4). As noted by Walters and Post (1993), L_∞ represents effects of both feeding and metabolic rates, and is likely to vary inversely with population density. Both feeding and metabolic rates are likely to vary with water temperature, but lead to the same L_∞ if both rates vary with the same Q_{10} or Arrhenius power of temperature. Using these relationships, we expect L_∞ to vary with population density but not temperature, and ρ (the slope of the Ford-Brody plot) to vary only with temperature. Hence we assume $\rho_m=e^{-Km}$ to vary in a sinusoidal pattern; variation in K_m is due to variation in monthly average temperature, and α varies both with density and monthly temperature. In the von Bertalanffy model, feeding or filtering rate is assumed to vary as the square of body length.

The use of monthly time steps in our age-structured model allows for the incorporation of seasonal variation in growth (Appendix Figure A2.1). In Florida, there is wide divergence in reported oyster growth rates with estimated age (*a*) of recruitment to the legal size (76.4 mm) ranging from about *a* = 7 months (Ingle and Dawson 1952) to *a* = 15 months or more (L. Sturmer, University of Florida, *unpublished information*). Growth has also been reported to be seasonal (Ingle and Dawson 1952; Hayes and Menzel 1981) with average growth rates of about 0.05 mm/day in the winter and 0.15 mm/day in the summer. We examined a large sample of individual Apalachicola Bay oyster growth curves from 2004-2009 (data from J. Harper, DEP, *personal communication*) and did not find evidence for strong seasonality in growth. We fit these growth measurements to the Ford-Brody growth model and found best fit with weak seasonal growth (Appendix Figure A2.1) and constant L_∞ = 90 mm and K = 0.1/month. It is unclear from the literature how strong density-dependent effects on oyster growth might be, and our attempts to include density dependent effects on Apalachicola Bay oyster growth did not improve model fit.

Survival

In our population dynamics model, we assume that survival rates $S_{a,t}$ (1 = natural mortality) in Equation 1 were assumed to vary with oyster age and body length, according to the Lorenzen survival function (mortality rate inversely proportional to body length). We assumed a base natural mortality rate (around 0.1/month) for larger oysters that had reached near asymptotic length and applied an annual relative mortality rate scaler (P_y, varying around 1.0) to represent changes in natural mortality rate (e.g., from salinity, predation, disease, etc.). Based on field observations, the net mortality rate of oysters in a dense "clump" may be very low and the oyster populations persist for a long time. This is accounted for in our model in Equation 5 which can predict a "stagnant" high density situation where $L_{\infty,t}$ has been severely reduced through competition when most oysters have reached this length or larger.

We assumed that the vulnerability of oysters to harvesting ($v_{a,t}$ in Equation 1) varies with body length and the legal minimum length for harvest (in Apalachicola Bay, L_{legal} = 76.2 mm) according to a logistic function that represents variation in size at age around the mean length $L_{a,t}$ (Equation 6). Monthly exploitation rates U_t are predicted in our model from fishing efforts using a standard Baranov catch equation (Equation 7; Hilborn and Walters 1992). This catch equation assumes density dependence and variation in vulnerable biomass in catchability (q) according to a type II functional response (Equation 8). Note that Equation 8 can represent combined effects of nonrandom searching for oysters by fishermen, handling and processing time, and caps on daily harvests by regulation or orders from wholesale oyster dealers per oyster license holder.

In the population dynamics model, information on annual oyster recruitment is required to drive initial oyster year class size in each year. For Apalachicola bay, we developed a standardized index of oyster recruitment using fisheries independent survey data of oysters by 5-mm size classes collected by the Florida Department of Agriculture and Consumer Services (DACS) on the major commercial fishing reefs in Apalachicola Bay (available from 1990-2013). As a tong fishery, a fishing trip in Apalachicola Bay consists of a number of oyster tong lifts that each "sweep" some area a_{lift} of the bottom. From our assessment of the fisheries independent survey data, it appears that when fishing effort is measured by the number of oyster fishing trips annually, q varies as predicted by Equation 8. The DACS survey data also provided annual estimates of mean legal oyster biomass per unit area D_{year}. The catch per trip should thus vary as catch-per-unit-effort (CPUE) $=a_{lift}$ x number of lifts per trip x D_{year}. If lifts per trip were constant and lift locations were random with respect to fine-scale variation in oyster densities, CPUE should be proportional to D_{year} (i.e., q measured as a_{lift} x number of lifts per trip should be constant). However, when we plot the observed ratio of CPUE to mean DACS density, we see instead that the apparent q has increased considerably when densities have been low (Appendix Figure A2.2). Apalachicola oyster fishermen have told us that they do indeed stay out longer and make more lifts when oyster abundance is low, and typically end each trip when their catch approaches trip limits imposed by regulations or daily limits based on market orders from dealers.

Recruitment

Monthly recruitment $N_{1,t}$ (Equation 9) to the population is predicted as a function of larval oyster settlement (Equation 10, 10a) and available shell material with a density-dependent mortality function applied during the first month of settlement to match observed survival patterns (Equation 11). We examined an alternative model for larval settlement where base settlement rate was made a power function of the relative spawning biomass index SB_t (Equation 10a).

Shell Accumulation

A key aspect of our population dynamics model is the development of an accounting and prediction system for oyster shell biomass and the explicit linkage in our model between oyster recruitment, oyster mortality rates, and availability of shell material for spat settlement

(Equations 9-13). This is an original contribution. In our model, if shell persistence (shell survival) is high (S_{shell} = 0.99) this implies slow deterioration in the shell substrate base available for oyster settlement and recruitment. Under sustainable oyster harvesting regimes, the suitable shell area AS_t is predicted in our shell budget to approach a nonzero equilibrium value (i.e., shell "recruitment" exceeds removals from harvest). However, the possibility of long term deterioration in oyster population carrying capacity would result if abundances $N_{a,t}$ are severely reduced through harvesting, leading to declines in AS_t. This suggests that there is a critical oyster stock size below which the oyster population will tend toward zero unless recruitment onto the oyster bars is assumed to be supported by adult oysters invulnerable to the fishery (the power function for larval settlement LS_t in equation 10a $\beta < 1.0$). Early attempts to fit the model by allowing β to vary always led to $\beta = 0$ (similar to Equation 10), but full use of both oyster harvest and relative abundance information suggests the opposite result: that β is larger and generally approaches the constraint $\beta = 1$. In our model, Equation 12 predicts that on average the ratio of dead shells to total live oysters, AS/N, should be near $(1-S_{live})/(1-S_{shell})$, where S_{live} is the average of $S_{a,t}$ weighted by $N_{a,t}/N$. From field observations we have seen highly variable AS/N, but typically we see ratios near 1.0, where the number of recently dead shells is about equal to the number of live oysters. This implies S_{shell} should be about equal to S_{live}, in the range 0.8-0.9. For our Apalachicola Bay analysis, we assumed a relatively conservative value 0.8 for the analysis. Our model assumes an exponential form of the larval production rate proportional to live biomass, which implies an overall long term Ricker stock-recruitment relationship (Hilborn and Walters 1992) for the population. This allows for depensatory decrease in recruitment at low oyster population stock sizes due to the shell area dynamics factor AS_t (Equation 13).

Parameter Scaling

We used scaling parameters (i.e., k_{growth}) to link oyster and fishery rate processes (growth, catchability, biomass) with oyster abundance as measured by the sum of squared lengths and biomass (Equations 14-15). Appropriate values for these parameters depend on the units of measurement of length, and scaling of overall population size so as to match historical abundance and catch data. This scaling is simplified by specifying an overall average natural recruitment rate R_o and corresponding Botsford incidence functions that sum up age specific quantities weighted by survivorship to age assuming equilibrium (Walters and Martell 2004, Box 3.1, page 56) for natural survivorships to age x natural age-specific quantities (L^2, W; Equations 16-22). In our model, as R_o is varied by the user or by Solver in Excel (Microsoft Corporation, Redmond, Washington), the scaling parameters are varied so as to predict growth and survival rates that will make R_o close to a stable equilibrium value without harvesting. That is, the model predicts base numbers and sizes at age $N_{a,0}$ by assuming $N_{a,0} = R_o l_{a,0}$ where $l_{a,0}$ is natural survivorship to age *a*, given a base or natural growth curve $L_{a,0}$ with associated base predictions of $M_{a,o}$. These base numbers and sizes are used in the model to predict base values for the sums over ages that appear in the various dynamic equations. The dynamic equations are then solved for the scaling parameters (*k*) given these base values. Given the season and density effects parameterized in the model and observed in the data, this solution for the *k* values is not exact but is sufficient to avoid strong transient changes as the model dynamics "spin up" over time.

To further simplify the parameter scaling in our stock assessment model, key quantities like maximum oyster catchability q_{max} and body size $L_{\infty max}$ were assumed as ratios to either base unfished values or to likely values at some sustainable fished equilibrium. We specified a base exploitation rate U_o in which case the population is assumed to have been fished at this rate (and to be near equilibrium with respect to it) for enough time for abundances and sizes to have reached equilibrium. These initial equilibrium values are used to set $N_{a,1}$ (numbers at age in the first simulation month) and catchability scaling parameter k_q that will give a catchability q_o that insures U_t=U_o when effort is at its initial time value E_1.

Alternative Model Formulation to Check Model Assumptions and Predictions

We were concerned that the Ricker functional form for density dependent early survival in our model may have a dome shape, and hence may provide overly optimistic predictions about recruitment changes when oyster stock size is reduced. To check this possibility, we ran the model with an alternative stock-recruitment relationship of Beverton-Holt form (described in Equations 23-25, final form Equation 26). This alternative model was derived by assuming that larval settlement LS_t has a mass-action relationship to both relative egg production (relative spawning biomass index SB_t) and relative effective shell settlement area A_{set}.

Equilibrium Analysis Using Growth Type Group Splitting of Recruitment

We were also concerned that the population dynamics model could give misleading predictions of length distribution patterns if the length distribution predictions are based on treating the length distribution at each age as "regenerating" each month by having constant standard deviation independent of harvesting effects (Walters and Martell 2004). In reality, faster growing individuals from each cohort will reach legal size sooner and be removed by fishing, which progressively distorts the length distribution for each age. The distortion could be represented by dividing each cohort into a set of growth types, and tracking size and survival (natural and fishing) separately for each group. However, this computation would result in extremely complex monthly accounting unless it was used simply to predict average or equilibrium length distributions over periods of stable growth and exploitation rate in a growth type group (GTG) model structure (Walters and Martell 2004, Box 5.3, p. 121). Using this simplified method, equilibrium length frequency predictions were made for five-year periods from 1990-2012.

The equilibrium GTG predictions were constructed by first dividing a typical cohort of N = 1.0 recruits into 21 growth types *g*, each initialized at 1 month age to $N_{g,1}$ = p(g) recruits where p(g) is the proportion of recruits assigned to group *g*. All groups were assumed to have the same von Bertalanffy K value, and distinct maximum lengths $L_\infty(g)$ given by $L_\infty(g) = L_\infty[1+CV\Delta(g-11)]$ where CVL_∞ is the standard deviation of L_∞ among individuals (we assumed CV = 0.1). We also assumed that Δ is the standard normal distribution increment between groups and we set Δ such that the groups vary in L_∞ over two standard deviations from average, with *g* = 11 representing the average group. Applying the von Bertalanffy growth equation by *g* and age results in a 21 x 36 matrix $L_{g,a}$ of predicted lengths at age, we then applied the basic survival equation (Equation 1) to each group over age to predict the 21 x 36 matrix $N_{g,a}$, using the Lorenzen size-dependent survival rate for each $L_{g,a}$ (Equation 5) and vulnerability $v_{g,a}$ to fishing set at 0.0 for predicted lengths at age < 75 mm and at 1.0 for lengths 75 mm and larger (approximate legal size of harvest in Florida). Finally, the equilibrium length distribution was obtained by simply summing all the $N_{g,a}$ by 5-mm length bins, with length bin assignment determined by the $L_{g,a}$ lengths.

Population Dynamics Model Parameter Estimation for Apalachicola Bay

Our basic approach to estimate as many of the model parameters as possible involved (1) estimating oyster growth and recruitment timing parameters from independent data sources and inputting these values, then (2) fitting the model to a set of time series data using a "stock synthesis" approach where the model equations are solved over time given only initial stock structure, effort time series, and relative recruitment and mortality time series. This is a harsh test of the model structure, since the equations could easily diverge greatly from patterns evident in the data if the model parameter values were far off.

Three time series were available for estimation of model parameters for the Apalachicola Bay oyster population: (1) monthly meat weight of oysters landed C_t for 1986-2012, (collected by FWC), (2) monthly fishing efforts (daily fishing trips) E_t for these same months (collected by FWC), and (3) annual survey estimates for 1990-2012 of absolute density of oysters (numbers/m^2) by 5-mm size increments, from 10-40 0.25 m^2 quadrats per year (collected by DACS). We aggregated the DACS survey densities by size to numbers of sublegal (20-75 mm) and legal (> 75 mm) oysters per m^2. The more detailed 5-mm interval length distributions were compared to model-predicted distributions only after fitting, since these detailed distributions are "contaminated" by interannual changes in seasonal timing of recruitment not fully captured in the basic model.

Unfortunately, the DACS data cannot be used directly to estimate total population size, since the total oyster bar area to which the sampled densities apply is not known. Estimates of oyster bar area based on geological sampling (Twichell et al. 2006, 2010) and available GIS layers (Apalachicola National Estuarine Research Reserve; January 2013) suggest a total area A_{total} of at least 40 km^2, whereas the DACS density estimates and fishery catch data imply that the observed catches might be coming from as little as 2-4 km^2 of productive bottom. In directly comparing the DACS data to catches, we noted a useful conversion factor: a DACS legal density (> 75 mm) of 30/m^2 corresponds to a live weight harvestable biomass of 0.45 kg/m^2 (1 lb/m^2), so densities of 30/m^2 represent about 453,492 kg/km^2 (1 million lb/km^2).

Also unfortunately, only a few of the DACS sampling areas have been visited consistently since 1990 (Table 1) and these areas are known only based on the name of the oyster bar and not a specific location on the bar. This creates a need to estimate missing area-year data combinations based on persistent differences among areas and shared temporal patterns (Equation 27). Fishery CPUE (C_t/E_t) has varied less than the DACS legal density estimates DL_y over time (Appendix Figure A2.2), suggesting as indicated above that CPUE has been strongly hyperstable (i.e., CPUE does not decline as fast as abundance).

Based on our growth assessments, the majority of sublegal oysters (DS_y) counted in any year of the DACS survey data probably did not become legal until the next year (average sublegal length was about 40 mm, implying about a year to reach legal length). This suggests that the ratio DL_{y+1}/DS_t is a reasonable estimator of the annual survival rate of sublegal oysters and $M = -\ln(DL_{y+1}/DS_t)/12$ is a reasonable estimator of the monthly natural mortality rate of sublegal oysters. Indeed, we would not even attempt to estimate the annual relative mortality multipliers P_y in Equation 5 if it were not for the direct information about annual carryover rates evident in the DACS data. The most realistic average mortality rates were obtained when the model M_o value was set to 0.1/month (Appendix Table 3).

Population Dynamics Model Estimation Procedure for Apalachicola Bay Oyster Fishery

We maximized a concentrated log likelihood function for the time series data (Equation 28) using Solver, by varying the following parameters:

$$\{R_o, l_o, U_o, q_{max}, M_o, P_{1986}\text{-}P_{2012}, RY_{1986}\text{-}RY_{2012}\}$$

where R_o sets the basic simulated population scale, l_o determines resilience (how low the population can be driven before recruitment fails), base exploitation rates U_o and q_{max} determine average monthly exploitation rate U_t given effort E_t and harvestable biomasses B_t, P_y drives interannual variation in natural mortality rate, and RY_y drives interannual changes in relative recruitment rate. Note that we would not ordinarily try to estimate both fishing (U_o, q_{max}) and natural mortality (M_o) rates at the same time, but having sublegal and legal density estimates from the DACS data makes this possible. As recommended by Walters and Ludwig (1994), SS_{DACS} (Equation 29) is evaluated at the conditional maximum likelihood estimate of q_s. As an alternative to this SS that assumed q_s to be unknown, we note that given the DACS units of measurement (counts/m^2), q_s can be interpreted as $1/A_{total}$, where A_{total} is the total productive area of the fishery. For some fitting trials, we froze A_{total} to various reasonable values, ranging from 2.0 km^2 to 10 km^2. The “penalty” terms for recruitment and survival anomalies (Equations 30 and 31) are the same as assuming RY_y and $PY_y = e^{\xi y}$, where ξ_y is assumed to be normally distributed with mean zero.

The estimation criterion defined by Equation 28 requires an estimate of the four σ^2 variances: catch, survey abundance, recruitment, natural mortality. However, we were unsure how to estimate these variances, or what to assume about their structure. We initially attempted to estimate them as additional unknown parameters [by changing from SS/variance to (n/2)ln(SS) terms in Equation 28, thus evaluating the normal log likelihood terms at their conditional maximum likelihood variance estimates], but this led to unrealistically high estimates of RY_y variation and no variation in P_y, basically “ignoring” evidence of mortality variation in the DACS data in favor of fitting the catch data more precisely. To force the model to better fit the DACS data, we assumed relatively high variance in the catch σ^2_C =1.0, and low DACS variance σ^2_{DACS}=0.04 based on coefficient of variation of the annual abundance estimates of around 0.2 based on observed variation in densities among bars sampled each year. We also tried various combinations of values for σ^2_{RY} and σ^2_P, generally in the range 0.1-1.0, to represent alternative hypotheses about how much of the observed variation has been due to recruitment versus survival variation.

Age-structured Population Model Results

Model estimates of natural mortality (M_o = 0.095/month) and exploitation rates (averaging 5%-10% per month) from our stock assessment model are quite reasonable and the q_s estimate implies a productive area of around 2 km^2. When we used the Beverton-Holt formulation for recruitment (Equation 26), best fits were obtained at unrealistically high unfished recruitments R_o (huge productive area), low productivity (α), and unrealistically low exploitation rates U_t. That is, the Ricker stock-recruitment formulation indicated a small, productive stock while the Beverton-Holt indicated a large, unproductive one.

The DACS data represents the best available information on trends in abundance and oyster size composition of areas fished. Because of uncertainty in the total area (A_{total}) of oysters to which the DACS surveys apply, we systematically varied A_{total} from low to high while allowing all other model parameters in the model to vary. This was done to try and determine whether the fishery was supported from a small highly productive oyster population or a large low-productivity oyster population. It resulted in almost identical fits to the catch and survey data from either the small productive or large unproductive oyster stock scenario (sums of squares based on the catch data or the DACS survey data, Equation 23). For both scenarios (small productive or large unproductive) the best model fits (lowest sums of squares, Equation 23) show a substantial increase in the Apalachicola Bay oyster population from 1990 until about 2000, then a persistent decline (Appendix Figure A2.3). Estimated exploitation rates during this time period of increasing population were lower during the years 1990-2000 than in recent years when oyster populations have declined (Figure 4; Appendix Figure A2.3). How were the same results and model fits found from models with very different A_{total}? For the large, low productivity stock scenario (high values of A_{total}) the best model fit was made by estimating high M_o and by attributing the patterns in oyster abundance and landings mainly to large recruitment and mortality anomalies (SS_P, SS_{RY} components of the likelihood function, Equation 23). For the small, highly productive stock, the patterns in oyster abundance and landings are attributed by the model more to effects of fishing (i.e., estimating low exploitation rates during the mid-1990s, much higher exploitation rates at present), leading to considerably smaller recruitment and natural mortality anomalies and hence lower SS_P, SS_{RY} in the likelihood function (Equation 23).

We had hoped that close examination of the DACS length frequency data for legal oysters would demonstrate changes in exploitation rate, at least between the lower exploitation period of the mid-1990s compared to the higher exploitation from about 2008-2013, through reduced relative abundance of larger oysters in the high exploitation period (Figures 4 and Appendix Figure A2.3). However, the data show no such pattern; if anything they seem to support the hypothesis that monthly exploitation rates have never been high enough to severely distort the size distribution based on the available data. As an example, a comparison of predicted and observed length frequencies for oysters by year suggests either no change, or possibly that survival rates to larger sizes were lower in the early to mid-1990s than indicated by model estimates of exploitation rates (Appendix Figures A2.4 and A2.5, see 1992-99 as examples where observations are lower than predictions for legal size oysters).

Comparison of the full model length distributions to DACS length frequencies (Appendix Figure A2.5) shows that the model does not correctly predict the observed sublegal (< 75 mm) size distribution in late fall for most years. The model predicts a more pronounced peak in the size distribution near 40 mm (Appendix Figure A2.5, solid line) than was observed in most years (Appendix Figure A2.5, dots), indicating a wider spread in settlement timing than assumed. For recent years the observed length distribution has peaks at smaller sizes (15-20 mm), presumably representing later seasonal timing of successful settlement than assumed in the model. The late settlement years in the DACS data (1993, 1995, 2000, 2002, 2005-2011) are not obviously correlated with any known environmental factor such as Apalachicola River discharge (average monthly, total annual and total monthly, CV on annual discharge, mean seasonal, or total seasonal). We could have forced the model to fit the juvenile patterns more closely by estimating a set of nuisance parameters representing annual recruitment timing variation, but this would not change the model's basic predictions about abundance trends and harvest impacts, and would instead give a false impression about the model's precision in explaining observed data.

Growth Type Group Model Results

The equilibrium GTG model gives average exploitation rates by 5-year period similar to those resulting from fitting the age-structured model with A_{total} = 5 km^2 (Appendix Table A2.2), provided the natural mortality parameter M_o is set to 0.1 (M = K assumption, also best M_o from that same age-structured model fit). These fits were obtained by visual comparison of the model and observed legal length proportions (Appendix Figures A2.4 and A2.5). For alternative estimates of the monthly exploitation rate, comparisons based on a binomial likelihood comparison of observed and predicted proportions resulted in somewhat higher exploitation rates, for reasons that are unclear. Unfortunately, the reasonable agreement between the age-structured and GTG model predictions is not good evidence that the monthly exploitation rate is indeed low, since the best GTG estimate of exploitation rate is highly sensitive to the assumed M_o; lower exploitation rates are obtained when M_o is increased and higher rates when it is decreased. Absent independent estimates of M from unexploited populations, the GTG model does not resolve the issue of how large the productive area A_{total} really is.

Table A2.1. Model equations

Accounting equations		
Equation 1	$N_{a+1,t+1}=N_{a,t}S_{a,t}(1-v_{a,t}U_t)$	Oyster population numbers at age *a* and time *t*. $S_{a,t}$ is the monthly natural survival rate of age a oysters in month t, $v_{a,t}$ is the relative vulnerability of age a oysters to harvest, U_t is the monthly exploitation rate of fully vulnerable oysters in month t
Equation 2	$L_{a+1,t+1}=\alpha_t+\rho_m L_{a,t}$	α_t is the Ford-Brody (incremental von Bertalanffy) growth intercept (or size at age 1 month) parameter, and ρ_m is the Ford-Brody metabolic parameter (equal to e^{-K} where K is the monthly von Bertalanffy metabolic parameter for length growth). New recruits $N_{1,t}$ are added to the population each month, at body length $\alpha_{,t}$
Growth equations		
Equation 3	$\alpha_t=(1-\rho_m)L_{\infty,t}$	Ford-Brody growth intercept
Equation 4	$L_{\infty,t}=L_{\infty max}/(1+k_{growth}\Sigma N_{a,t}L_{a,t}^2)$	$L_{\infty max}$ is the maximum asymptotic length that would be achieved at low population densities, k_{growth} is a scaling constant for effect of population density, and $\Sigma N_{a,t}L_{a,t}^2$ is the sum of numbers at age times L^2 as an index of relative feeding
Survival equations		
Equation 5	$S_{a,t}=\exp\{-P_y M_o L_{\infty,t}/L_{a,t}\}$	Natural survival rates, assumed to vary with age and shell length, M_o base natural mortality rate (around 0.1/month), $L_{\infty,t}$ is the time and possibly density dependent maximum length (equation 4), and P_y is an annual relative mortality rate scaler.
Vulnerability to harvest		
Equation 6	$v_{a,t}=1/(1+\exp\{-(L_{a,t}-L_{legal})/s_a\})$	Vulnerability of oysters to harvesting ($v_{a,t}$) represented by logistic function that represents variation in size at age around mean length $L_{a,t}$. where s_a=CV/1.7 x L_∞ with CV around 0.13 represents variation in length at age. An s_a of around 5 implies length at age near the legal size varying with a standard deviation of around 5/1.7 or 2.9 mm.
Equation 7	$U_t=1-\exp(-q_t E_t)$	Monthly exploitation rates U_t are predicted from fishing efforts E_t
Equation 8	$q_t=q_{max}/(1+k_q B_t)$ where $B_t=\Sigma_a N_{a,t}W_{a,t}v_{a,t}$	$W_{a,t}$=weight at age, q_{max} is maximum catchability (fishing mortality rate per unit effort) at low stock size, and k_q is a scaling constant such that q is reduced to $q_{max}/2$ when

		B_t is half of its unfished level (i.e. k_q=2/B_o where B_o is the predicted average biomass of the stock absent harvesting)
Recruitment and shell accumulation		
Equation 9	$N_{1,t} = LS_t\ AS_t\ SL_t$	$N_{1,t}$ = monthly recruitment where LS_t= annual and seasonally varying larval settlement per unit suitable shell area, AS_t= suitable shell area generated from natural mortality, SL_t= density-dependent survival of pre or post settlement juveniles.
Equation 10	$LS_t = l_o R_y R_m SB_t$ where $SB_t = \Sigma_a N_{a,t} L^3_{a,t}$	LS_t = Larval settlement rate where, l_o = average settlement rate, R_y = interannual variation in larval production estimated from data, R_m monthly variation in spawning and predation rate on larvae and spat, SB_t spawning biomass that is proportion to body weights at age
Equation 10a	$LS_t = l_o R_y R_m (SB_t/SB_o)^{\beta}$	Alternative model for larval settlement assuming a power function of SB_t. Power parameter β represents possible density dependence in larval or early juvenile survival rats, and/or delivery of a substantial proportion of the larvae from non-harvested spawning sources (e.g. intertidal areas where oysters never reach legal size).
Equation 11	R_m=spawning component x predation component	Monthly variation in spawning and predation rate set by user in spreadsheet model to vary seasonally following either a unimodal spat settlement pattern peaking midsummer, bimodal recruitment pattern with high mid-summer predation loss, or unimodal spring or fall peak with high predation rates in spring or fall (patterns similar to Appendix Figure A2.1).
Equation 12	$AS_{t+1} = S_{shell} AS_t + k_{shell} \Sigma_a N_{a,t} (1-S_{a,t}) L_{a,t}^2$	AS_t = Shell area available for recruitment following a balance rate of shell survival $S_{survival}$ (persistence of old shell) and recruitment of new shell due to natural mortality of live oysters 1-$S_{a,t}$. k_{shell} is an arbitrary area scaling constant = 10^{-4} . By summing over ages of numbers, times squares of lengths, this represents age-size variation in shell area per dying oyster
Equation 13	$SL_t = \exp\{-k_{density} \Sigma_a N_{a,t} L_{a,t}^2\}$	Density-dependent effects on larval survival and/or survival over the first month after settlement. $k_{density}$ is a scaling constant for the effect per unit live oyster area present on survival rate.

Scaling parameters

Equation 14	$l_{1,0}= l_{1,fished}=1.0$, $l_{a,0}=l_{a-1,0}S_{a-1},0$ a >1	Unfished survivorship to age
Equation 15	$l_{a,fished}=l_{a-1,fished}S_{a-1},0(1-v_{a,0}U_o)$ where a>1	Fished survivorship to age
Equation 16	$\varphi_{L2,0}=\Sigma_a l_{a,0}L_{a,0}^2$	Incidence function, squared lengths
Equation 17	$\varphi_{SH,0}=k_{shell}\Sigma_a l_{a,0}(1-S_{a,0})L_{a,0}^2$	Incidence function, shell production
Equation 18	$\varphi_{B,0}=\Sigma_a l_{a,0}v_{a,0}W_{a,0}$	Incidence function, vulnerable biomass
Equation 19	$\varphi_{E,0}=\Sigma_a l_{a,0}vL^3_{a,0}$	Incidence function, relative spawning biomass, equation 10
Equation 20	$k_{growth}=(L_{\infty,max}/L_{\infty,0}-1)/(R_o\ \varphi_{L2,0})$	Growth scaling constants based on assuming recruitment R_o, given $\beta=0$
Equation 21	$k_q=(q_{max}/q_o-1)/(R_o\varphi_{B,0})$	Catchability scaling constants based on assuming recruitment R_o, given $\beta=0$
Equation 22	$k_{density}=-\ln[(1-S_{shell})/(l_o\varphi_{SH,0})]/(R_o\ \varphi_{L2,0})$	Density scaling constants based on assuming recruitment R_o, given $\beta=0$

Beverton-Holt stock recruitment

Equation 23	$LS_t=kSB_tA_{set}$	LS_t = larval settlement at time t related to both relative egg production SB_t and relative effective shell settlement area A_{set} and a constant k
Equation 24	$N_{t+1}=akSB_tA_{set}/(1+bkSB_tA_{set})$	Predicted recruitment following density dependent mortality of spat following settlement
Equation 25	$A_{set}=\xi AS_t/(1+\xi AS_t)$	Equation describing the relationship between effective shell settlement area A_{set} and shell area AS_t. where ξ is a constant that determines the shell area needed to achieve half of the maximum possible effective settlement area ($1/\xi$ is the shell area needed to obtain $A_{set}=0.5$, ½ of its maximum 1.0)
Equation 26	$N_{1t}=\alpha R_yR_mSB_tAS_t/[1+AS_t(\xi+\beta SB_t]$	Simplified Beverton-Holt stock recruitment function based on relationships in Equations 23-25 after combining constants and including seasonal and annual relative recruitment multipliers (R_y, R_m) where α represents the steepness of the stock-recruitment relationship and β represents density-dependent mortality effects. Other terms as defined previous.
Equation 27	$\ln(D_{x,y})=\mu_x+\tau_y + e_{x,y}$	Log-linear model used to estimate oyster densities for different area-year data combinations. $D_{x,y}$ is the observed mean density for area x in year y, $e_{x,y}$ is combined process and sampling error for that observation, area means μ_x were estimated as the mean density for each

		area x over time, while the year effects τ_y were estimated as the mean of the deviations $D_{x,y}- \mu_x$ in year y from the overall mean densities for the areas sampled in year y. corrected density estimates $D'_{x,y}=\exp(\mu_x+\tau_y)$ were then averaged using stratum weights equal to estimated bar areas for each x to give weighted density estimates DS_y for sublegal sized oysters and DL_y for legal sized oysters for each year
Estimation procedure		
Equation 28	$\ln L= -0.5[SS_C/\sigma^2_C+SS_{DACS}/\sigma^2_{DACS} + SS_{RY}/\sigma^2_{RY}+SS_P/\sigma^2_P]$	Log-likelihood function for time series data assuming log-normal variation in all observed quantities, recruitment, and mortality anomalies and weighting the sums of squares deviations by assumed variances.
Equation 29	$SS_{DACS}=\Sigma_y[\ln(DS_y/NS_y)-\ln(q_s)]^2+\Sigma_y[\ln(DL_y/NL_y)-\ln(q_s)]^2$	SS_{DACS} calculated by assuming observed values have averages proportional to model sublegal and legal abundances (NS_y and NL_y) obtained by adding abundances over the simulated age structure in an index month (August) each year, with constant of proportionality or survey catchability q_s (q_s is interpreted as the inverse of the number of square kilometers of oyster bar habitat at DACS densities needed to produce the model abundances). The MLE $\ln(q_s)$ is the arithmetic average over all DACS estimates of the $\ln(D_y/N_y)$ ratios.
Equation 30	$SS_{RY} =\Sigma_y \ln^2(R_y)$	Penalty term for recruitment anomalies
Equation 31	$SS_P =\Sigma_y \ln^2(P_y)$	Penalty term for recruitment anomalies

Table A2.2a-d. Estimates of raw and interpolated mean oyster density (number/m^2) for sublegal (20-75 mm shell length) and legal (> 75 mm) oysters from Florida Department of Agriculture and Consumer Services surveys on major oyster bars in Apalachicola Bay.

(a) Raw mean oyster density (number/m^2) for sublegal oysters

	Cat Point	Dry Bar	East Hole	Eleven Mile Bar	Lighthouse Bar	Normans South	Platform Bar	Porters Bar
1990	267.4		166.0		108.1			
1991	220.2	257.4	158.7		244.8		340.9	
1992	274.9	242.0	237.1		315.6			502.4
1993	237.5	151.8	333.4		246.0	298.0		140.8
1994	287.7	305.4	525.2	132.1	214.9	332.8		152.9
1995	180.7	216.8	721.4	119.6	256.8		344.9	
1996	341.6	225.4	293.8		516.9	430.8		
1997	377.7	122.7	460.8	106.4	360.4	329.2		
1998	191.7	105.8	174.1		317.2	320.4		
1999	244.3	562.8	443.6		246.0	192.1		
2000	379.1	199.6	332.8					
2001	266.1	516.8	415.2					138.4
2002	286.4	412.8	211.6	62.5				85.2
2003	353.7	283.2	167.2	164.8				184.8
2004	681.7	144.1	685.8	40.0				657.4
2005	180.3	119.7	184.0					92.9
2006	178.0	500.4	124.4	462.4				42.5
2007	350.5	618.4	158.8	253.6				168.0
2008	148.6	418.6	198.6	200.2	170.0	189.1	256.4	253.3
2009	154.1	261.9	186.1	169.5			229.7	172.7
2010	172.1	242.3	247.2	139.9	309.2	224.1	439.7	
2011	587.9	401.2				297.6		
2012	48.5	80.0	34.5		194.9	219.6		

(b) Interpolated mean oyster density (number/m^2) for sublegal oysters using log-linear model with bar and year effects

	Cat Point	Dry Bar	East Hole	Eleven Mile Bar	Lighthouse Bar	Normans South	Platform	Porters Bar
1990	168.2	170.3	165.9	95.0	172.0	186.8	213.8	113.4
1991	225.1	227.9	222.0	127.1	230.2	250.0	286.2	151.7
1992	325.1	329.2	320.6	183.6	332.5	361.1	413.4	219.1
1993	233.6	236.5	230.3	131.9	238.8	259.4	297.0	157.4
1994	285.5	289.0	281.5	161.2	291.9	317.0	362.9	192.4
1995	272.4	275.8	268.6	153.8	278.5	302.5	346.3	183.6
1996	338.5	342.7	333.8	191.1	346.1	375.9	430.3	228.1
1997	273.8	277.2	270.0	154.6	280.0	304.0	348.1	184.5
1998	199.6	202.0	196.8	112.7	204.1	221.6	253.7	134.5
1999	302.7	306.5	298.5	170.9	309.5	336.2	384.8	204.0
2000	293.2	296.9	289.2	165.6	299.9	325.7	372.8	197.6
2001	329.2	333.3	324.6	185.9	336.6	365.6	418.5	221.9
2002	203.7	206.2	200.9	115.0	208.3	226.2	258.9	137.3
2003	266.4	269.8	262.7	150.4	272.4	295.9	338.7	179.6
2004	341.8	346.0	337.0	193.0	349.5	379.5	434.5	230.3
2005	153.0	154.9	150.9	86.4	156.5	169.9	194.5	103.1
2006	224.7	227.5	221.6	126.9	229.8	249.6	285.7	151.5
2007	329.1	333.2	324.5	185.8	336.5	365.5	418.4	221.8
2008	235.3	238.3	232.1	132.9	240.6	261.3	299.2	158.6
2009	217.0	219.7	214.0	122.5	221.9	241.0	275.9	146.3
2010	245.6	248.7	242.3	138.7	251.2	272.8	312.3	165.6
2011	396.7	401.6	391.2	224.0	405.6	440.5	504.3	267.3
2012	87.2	88.3	86.0	49.3	89.2	96.9	110.9	58.8

(c) Raw mean oyster density (number/m^2) for legal oysters

	Cat Point	Dry Bar	East Hole	Eleven Mile Bar	Lighthouse Bar	Normans South	Platform	Porters Bar
1990	23.4		17.3		11.9			
1991	17.0	16.4	14.8		40.8		45.5	
1992	20.7	22.4	18.2		51.6			49.6
1993	41.9	30.6	63.8		126.8	134.0		24.8
1994	29.7	18.5	83.2	23.9	48.3	98.0		44.9
1995	46.4	45.6	184.4	92.8	74.8		87.9	
1996	31.0	77.8	203.6		133.9	209.2		
1997	56.5	46.9	82.8	51.2	101.6	169.6		
1998	34.8	35.4	58.9		61.6	100.4		
1999	33.7	24.0	34.4		45.6	79.9		
2000	81.0	168.0	93.8					
2001	41.1	59.2	54.4					62.4
2002	24.1	103.6	32.0	32.7				23.6
2003	31.4	45.2	18.0	32.8				17.2
2004	38.6	40.5	40.2	47.2				181.6
2005	29.1	17.3	48.2					55.9
2006	45.0	49.0	23.2	61.6				8.3
2007	37.0	68.7	42.8	36.0				18
2008	36.2	42.1	32.3	59.0	40.4	41.6	48.4	35.9
2009	20.6	18.4	18.5	27.6			18.9	11.5
2010	19.7	24.4	25.6	34.3	33.2	32.7	51.5	
2011	24.3	29.6				75.2		
2012	15.9	20.0	16.3		48.3	40.0		

(d) Interpolated mean oyster density (number/m^2) for legal oysters using log-linear model with bar and year effects

	Cat Point	Dry Bar	East Hole	Eleven Mile Bar	Lighthouse Bar	Normans South	Platform	Porters Bar
1990	13.0	15.4	16.8	17.4	22.1	34.4	18.7	13.0
1991	18.3	21.7	23.5	24.5	31.1	48.3	26.3	18.2
1992	24.2	28.7	31.2	32.4	41.2	64.0	34.9	24.1
1993	41.4	49.1	53.3	55.4	70.4	109.4	59.6	41.3
1994	30.6	36.4	39.5	41.0	52.1	81.0	44.1	30.5
1995	60.2	71.4	77.5	80.5	102.4	159.0	86.7	60.0
1996	72.5	86.0	93.4	97.0	123.3	191.6	104.5	72.3
1997	52.5	62.4	67.7	70.3	89.4	138.9	75.7	52.4
1998	36.6	43.4	47.1	48.9	62.2	96.6	52.7	36.5
1999	27.1	32.2	35.0	36.3	46.2	71.7	39.1	27.1
2000	94.1	111.7	121.3	126.0	160.2	248.8	135.7	93.9
2001	48.2	57.3	62.2	64.6	82.1	127.5	69.5	48.1
2002	31.3	37.2	40.4	41.9	53.3	82.8	45.1	31.2
2003	23.4	27.8	30.2	31.4	39.9	61.9	33.8	23.4
2004	48.3	57.4	62.3	64.7	82.2	127.7	69.6	48.2
2005	30.7	36.5	39.6	41.1	52.3	81.2	44.3	30.6
2006	26.4	31.3	34.0	35.3	44.9	69.8	38.0	26.3
2007	32.2	38.2	41.5	43.1	54.8	85.1	46.4	32.1
2008	29.9	35.5	38.5	40.0	50.9	79.0	43.1	29.8
2009	15.6	18.5	20.1	20.8	26.5	41.2	22.4	15.5
2010	21.0	24.9	27.0	28.1	35.7	55.4	30.2	20.9
2011	25.8	30.6	33.2	34.5	43.9	68.2	37.2	25.7
2012	17.1	20.3	22.0	22.9	29.1	45.2	24.6	17.0

Table A2.3. Estimates of monthly exploitation rate from the age-structured model with A_{total} = 5 km^2, compared to estimates from fitting the growth type group model to the average legal size distribution over 5-year periods.

Period	Age model	GTG model
1990-1994	0.067	0.06
1995-1999	0.02	0.04
2000-2004	0.03	0.02
2005-2009	0.045	0.06
2010-2012	0.075	0.05

Table A2.4. Apalachicola Bay oyster resource management recommendations compiled from reports from local symposia or agency assessments.

Swift 1898

- Maintain dredge fishery ban
- Extend harvest closure period to April 15 through October 15 in order to protect early spawning season
- Adhere strictly to laws regarding culling and taking of small oysters
- Improve enforcement of harvest laws and laws protecting oyster planters
- Break up and separate transplanted clusters of overcrowded oysters in order to improve growth
- Use shell as cultch for new planting locations to create productive beds
- Add cultch to depleted beds and allow to recuperate for a year or two
- Improve communication with oystermen to reduce mistrust of planting laws

Whitfield and Beaumariage 1977

- Balance protection of resources and enhancement of product marketability through technological innovation and modernization of industry
- Develop non-destructive mechanical harvesting technology
- Construct state-sponsored oyster fattening plants to allow year-round culture
- Shorten harvest season to November 1 through May 1
    - Refuse demands by oystermen for legislation allowing year-round harvest
- Adhere vigorously to harvest regulations
- Amend anti-leasing laws to encourage private management and reef development
- Continue State-directed construction of new oyster reefs and rehabilitation of existing reefs
- Inform general public on impacts of development and upstream health on coastal economy and food production
- Have resource managers work closely with resource users to implement management plans
- Initiate FDA-sponsored oyster marketing and sanitation inspection program to improve product quality
- Expand sanitary surveillance of harvesting waters
- Discourage further development, channelization, and dam construction on Apalachicola River

Andree 1983

- Environmental effects on productivity of oysters
    - Correlate biological productivity of oysters with rainfall, salinity, density of predators, and other environmental parameters
    - Map substrate bottom types and locations in order to improve oyster cultch planting efforts in suitable locations
    - Examine sedimentation and current scour in relation to oyster spat survival in order to improve reef construction site selection
- Management and regulation of fishery resources
    - Re-examine laws on undersized oyster harvest, oyster transport, and summer harvest to make law enforcement more efficient

- Re-examine potential for submerged bottom leasing in unproductive areas that are not likely to be developed by the state's reef construction program
- Continue Florida Department of Natural Resources oyster reef construction program, but improve site selection, construction methods, and reef monitoring
- Improve communication between state agencies, researchers, and the industry through an annual forum, possibly led by the Apalachicola National River and Estuarine Sanctuary
- Develop better economic guidance for oyster dealers and oystermen
- Create functional long-range resource use plan for oysters

- Maintenance of a quality product for the market
  - Increase cooperation between law enforcement, management agencies, oystermen, and oyster dealers to reduce undersized oyster harvest
  - Establish water quality control procedures in oyster processing houses
  - Develop simple, adequate test for *Vibrio* bacteria in oyster meats in order to avoid costly consumer scares
- Miscellaneous discussion
  - Potential for hybridization and genetic manipulation
  - Exploration of alternative and "non-traditional" seafood products
  - Preliminary oyster "relay" projects highly successful

Arnold and Berrigan 2002

- Florida FWC should closely monitor ACF River Basin Allocation Formula agreements between Florida, Alabama, and Georgia, and should intervene to protect oyster resources in Apalachicola Bay if these freshwater allocations threaten them
- Florida FWC should carefully manage other Florida oyster resources to ensure that alternative sources are available if/when natural or anthropogenic factors result in the collapse of Apalachicola Bay oyster populations

Havens et al. 2013

- Monitoring
  - Continue monitoring oyster landings and expand fisheries independent monitoring program
  - Include oysters in list of species routinely assessed by FWRI
- Management and restoration
  - Improve acceptance and enforcement of rules regarding size limits, spatial restrictions, and seasonal closures
  - Explore oyster leases as possible alternative to open-access fisheries (e.g. Territorial User Rights Fisheries)
  - Evaluate efficacy and cost effectiveness of different shell planting materials and strategies, and expand cultching efforts
  - Involve state agencies and university experts in long-term fishery management process
  - Evaluate "relay" practices and potential for recruitment overfishing
- Research
  - Identify optimal approach for monitoring long-term oyster characteristics
  - Quantify interactions of oyster population dynamics, product quality, and the

    - fishery with river flow, nutrients, salinity, harvesting intensity, and restoration methods
    - Assess oystermen harvesting practices and adaptation to changes in oyster abundance
    - Use ECOSPACE model to identify effects of varying flow regimes and flow alternatives on oyster population dynamics and harvest potential
- Outreach and education
    - Develop community-based outreach and education program
    - Involve oyster harvesters and processors in research and restoration projects
- Miscellaneous discussion
    - Exploration of alternative and “non-traditional” seafood products

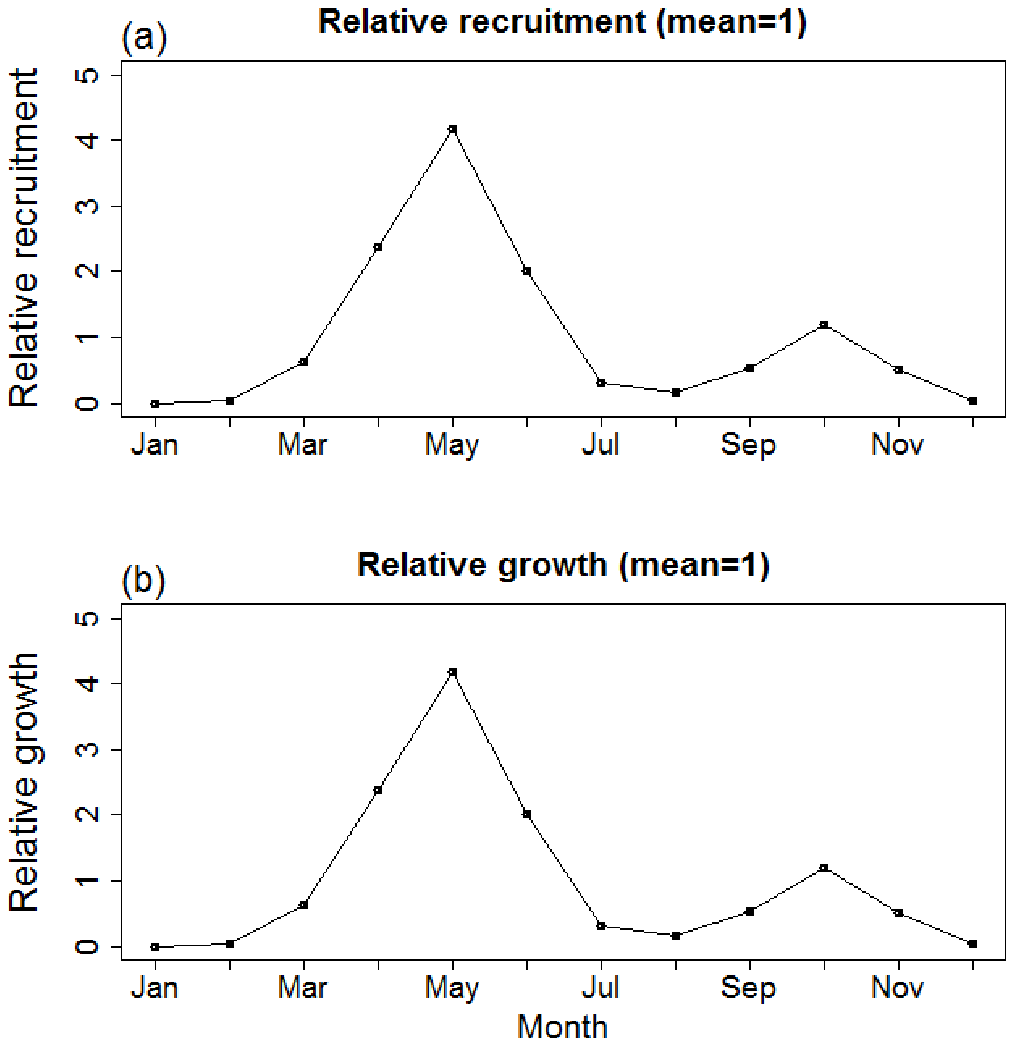

Figure A2.1. Monthly relative recruitment (a) and growth patterns (b) assumed for oysters in Apalachicola Bay, Florida based on empirical assessment of growth patterns and literature review.

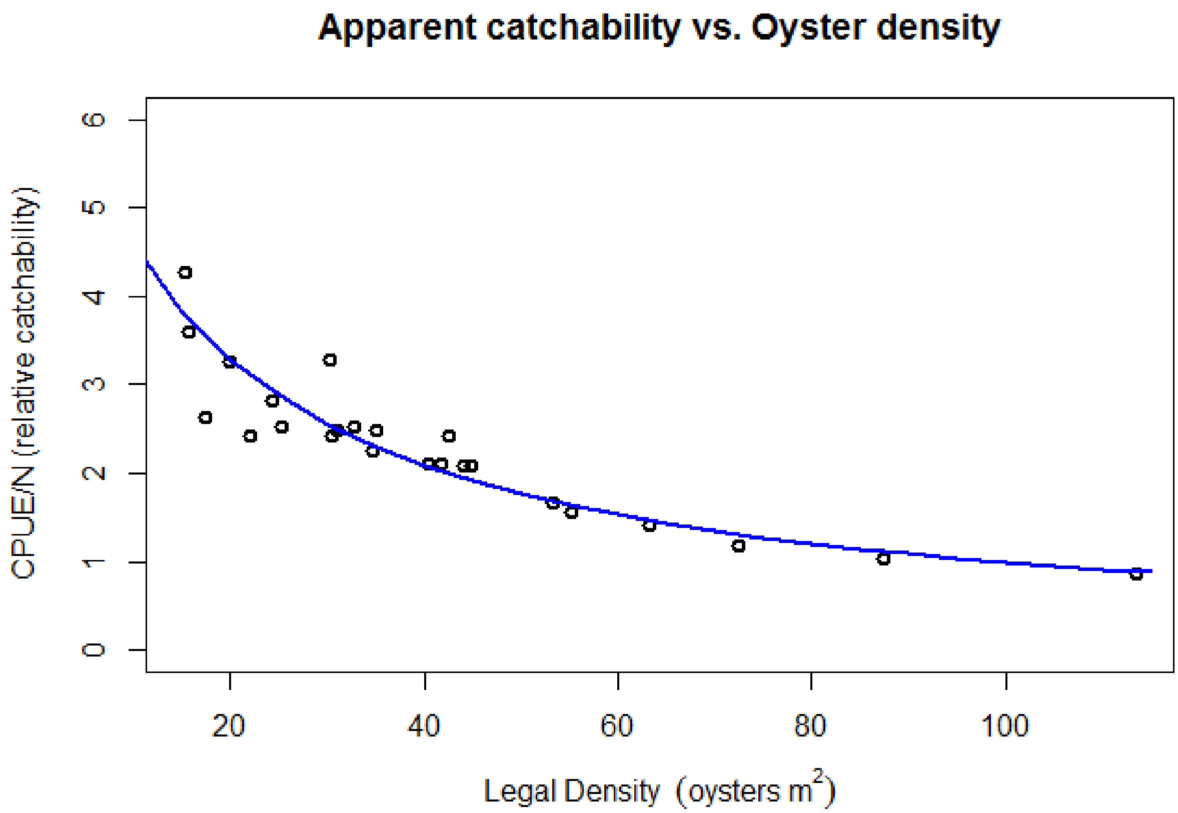

Figure A2.2. Density dependence in relative catchability *q* as evidenced by variation in mean annual catch per unit effort (CPUE), measured as trips per year divided by mean legal oyster density from DACS surveys. Assuming constant area swept per tong lift, this relationship implies that number of tong lifts per trip increases by a factor of about 4 when densities drop from around 100 legal oysters/m^2 to the observed low of near 10/m^2.

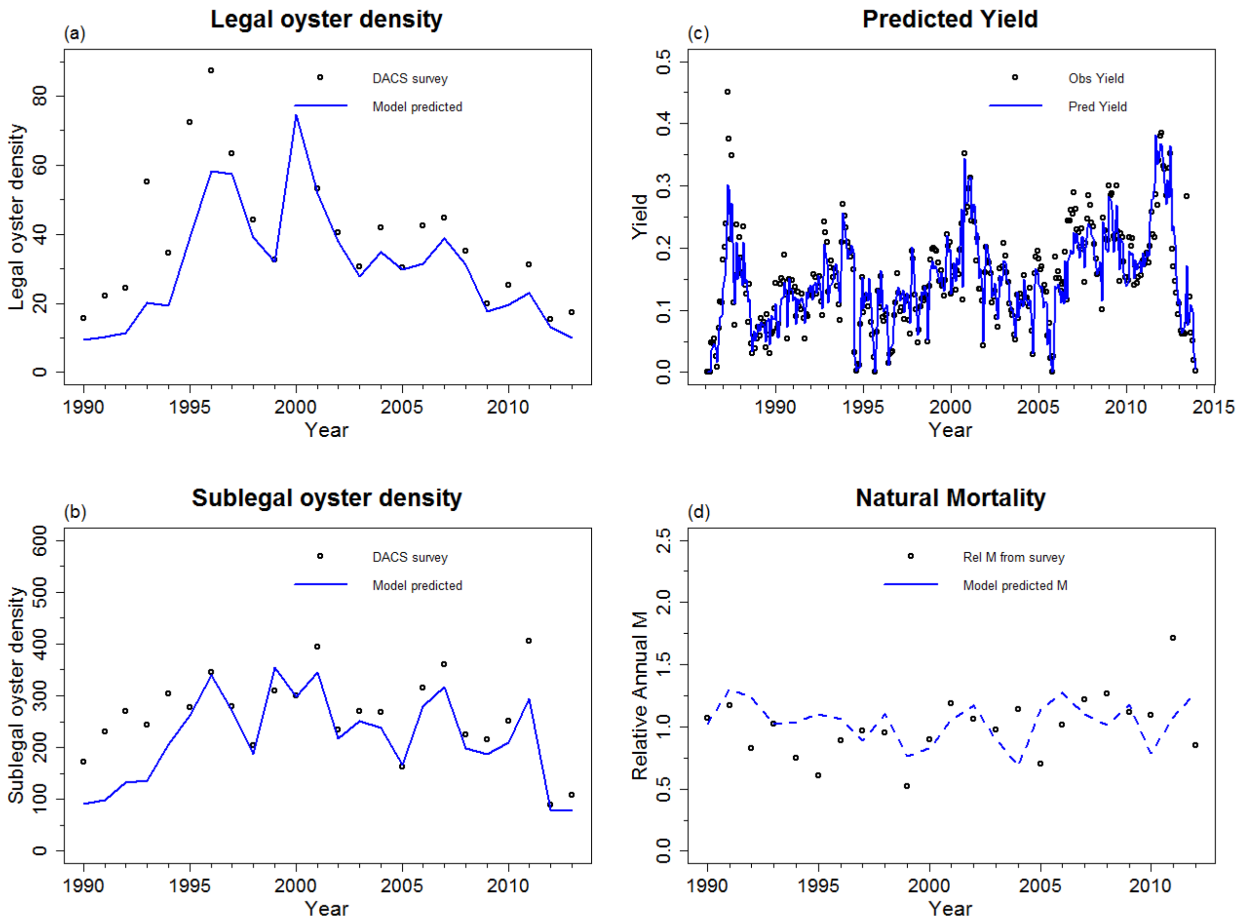

Figure A2.3. Observed (black circles) and model predicted (blue line) trends in legal (> 76.2 mm, panel (a) and sub-legal (b) oyster abundance, predicted oyster fishery yield (c), and estimated natural mortality rate (d) in Apalachicola Bay from 1990-2013. Model prediction results are from applying the parameter estimation procedure assuming balanced impacts of variation in natural mortality rate and recruitment rate. Observed data are from Florida Department of Agriculture and Consumer Sciences (DACS) fisheries independent surveys and predictions are from age-structured model described in this paper for comparison. Note large reduction in recruitment rates for 2012-3 implied by forcing the model to fit the DACS density estimates.

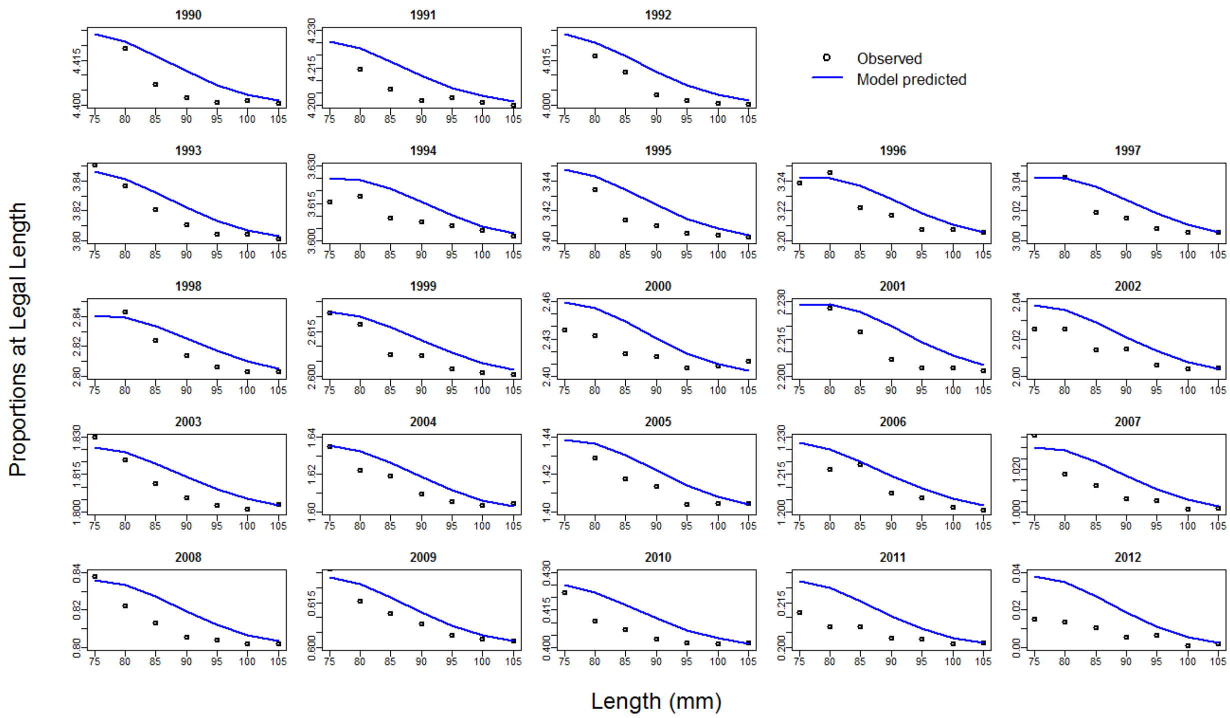

Figure A2.4. Comparison of model-predicted length proportions of legal sized oysters in Apalachicola Bay, Florida during fall (blue line) and observed length proportions of legal size oysters (black circles) in fisheries independent surveys conducted in fall by the Florida Department of Agriculture and Consumer Services.

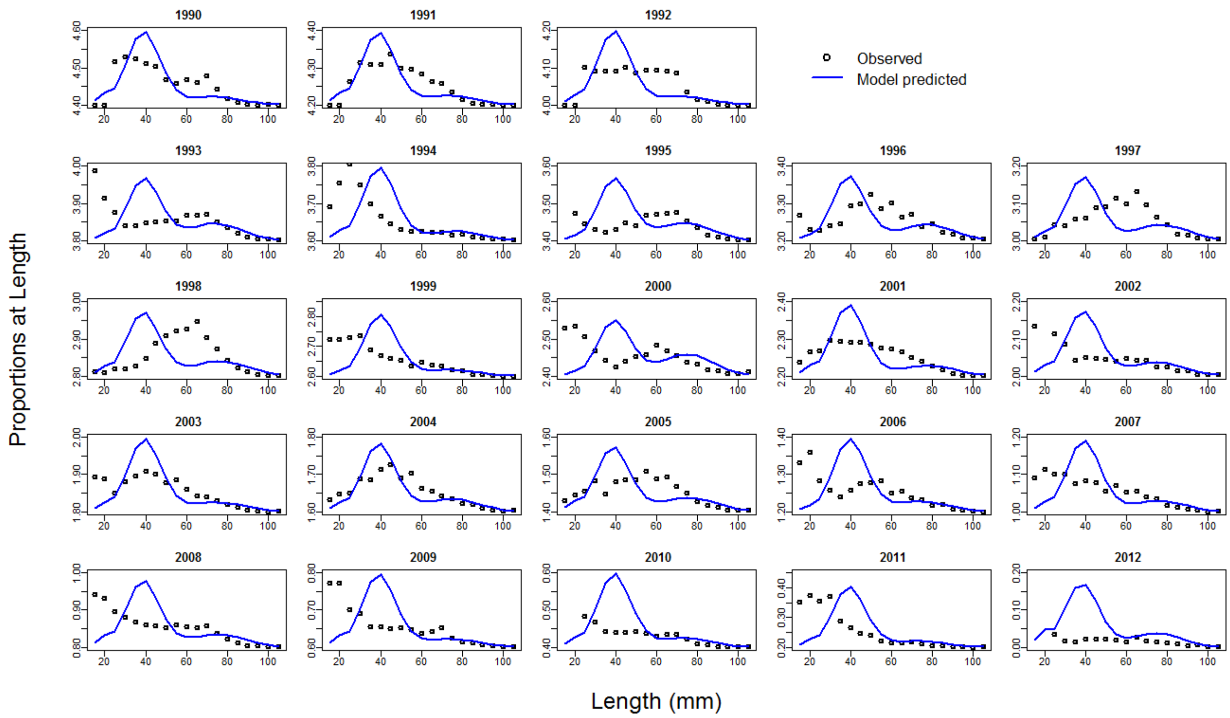

Figure A2.5. Comparison of model predicted length proportions of oysters 15-105 mm in size from Apalachicola Bay, Florida during fall (blue line) and observed length proportions of legal size oysters (black circles) from fisheries independent surveys conducted in fall by the Florida Department of Agriculture and Consumer Services.

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