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A SHELL-NEUTRAL MODELING APPROACH YIELDS SUSTAINABLE OYSTER HARVEST ESTIMATES: A RETROSPECTIVE ANALYSIS OF THE LOUISIANA STATE PRIMARY SEED GROUNDS

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ABSTRACT A numerical model is presented that defines a sustainability criterion as no net loss of shell, and calculates a sustainable harvest of seed (<75 mm) and sack or market oysters (≥75 mm). Stock assessments of the Primary State Seed Grounds conducted east of the Mississippi from 2009 to 2011 show a general trend toward decreasing abundance of sack and seed oysters. Retrospective simulations provide estimates of annual sustainable harvests. Comparisons of simulated sustainable harvests with actual harvests show a trend toward unsustainable harvests toward the end of the time series. Stock assessments combined with shell-neutral models can be used to estimate sustainable harvest and manage cultch through shell planting when actual harvest exceeds sustainable harvest. For exclusive restoration efforts (no fishing allowed), the model provides a metric for restoration success—namely, shell accretion. Oyster fisheries that remove shell versus reef restorations that promote shell accretion, although divergent in their goals, are convergent in their management; both require vigilant attention to shell budgets.

KEY WORDS: oyster, *Crassostrea virginica*, fisheries, modeling, stock assessment, restoration, sustainability, shell budget, Louisiana

INTRODUCTION

Copious flows of fresh water into the shallow subtropical waters of coastal Louisiana generate a broad mesohaline zone that supports abundant populations of eastern oysters, *Crassostrea virginica* (Chatry et al. 1983, Melancon et al. 1998). Louisiana typically leads the country in the production of oysters, accounting for about 34% of the nation's landings and more than 50% of the landings along the Gulf of Mexico, with a dockside value of about $35 million per year (Dugas et al. 1997, LDWF 2010). The Louisiana Department of Wildlife and Fisheries (LDWF) is charged with the management of nearly 1.7 million acres of public water bottoms, wherein it sets seasons, monitors harvest, and plants cultch. The industry also includes a private sector to which the state leases about 385,000 acres of water bottom.

Long-term annual average harvest from the public grounds is about 3 million lb. of meat, whereas private leases supply about 8 million lb. of meat per year (LDWF 2010).

The success of the Louisiana oyster industry is a result, in large part, of a public/private partnership in which the LDWF manages the public grounds for the production of seed oysters (<75 mm) for transplant to private leases, where they are cultivated and subsequently harvested. However, a significant increase in the harvest of market-size (or sack) oysters (≥75 mm) has occurred from public grounds during the past 15 y. (Market-size or sack oysters are harvested, sacked, and marketed directly whereas seed oysters are harvested, transplanted to private leases for grow-out, reharvested, and then marketed.) The quantity of shell being removed as seed, sack, and associated cultch far exceeds the quantity of cultch planted by the state, resulting in a potential net deficit of shell, and threatening the sustainability of the resource. Currently, annual stock assessments, combined with best professional judgment, are used both to inform management and to predict the success of the upcoming oyster season (e.g., LDWF 2010). Although these data provide crucial information for tracking oyster stock on an annual basis, current management has no established biological reference point and, consequently, no criterion by which sustainable harvest can be estimated.

Powell and Klinck (2007) developed 2 biological reference points for oysters: an abundance (or biomass) reference point and a substrate reference point, formalized respectively as

$$\frac{dN}{dt} = 0 \qquad (1)$$

and

$$\frac{dS}{dt} = 0 \qquad (2)$$

where N is the abundance of oysters, S is the quantity of surficial shell, and t is time. Eq (1) requires that recruitment equal

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combined fishing and natural mortalities whereas Eq (2) requires that shell lost to fishing and natural processes equal shell gains. A goal for sustainable management might demand that harvest not exceed recruitment and, simultaneously, that shell loss not exceed natural and enhanced replenishment. A number of biological reference points have been put forward that define the value of N in Eq (1) (Klinck et al. 2001, Powell et al. 2009a), but they do not necessarily establish an abundance consistent with Eq (2) (Powell et al. 2012). Arguably, the primary management and restoration goal is that expressed by Eq (2), the sustainability of substrate, rather than that expressed by Eq (1), the sustainability of abundance (Mann & Powell 2007), as the former depends ineluctably on the latter and demands a robust population density (Powell et al. 2012). Moreover, the cost of restoring abundance, although expensive, is minimal in comparison with the cost of restoring habitat. Thus, habitat, and hence shell, conservation is an economically advantageous goal. To this end, management for no net shell loss seems especially appropriate for oysters along the northern Gulf of Mexico, which are characterized by vibrant populations, good recruitment, and large interannual variations in numbers (Ingle & Dawson 1952, Butler 1953, Hopkins 1954, Hayes & Menzel 1981, Choi et al. 1994).

A numerical model for the sustainable management of oysters in Louisiana, which emphasizes the primacy of managing for no net shell loss over management for constant abundance, is presented. Annual stock assessments of oyster density and size are inputs into the model to estimate retrospectively the number of sacks of seed and market-size (sack) oysters that are harvestable with no net loss of reef shell. In doing so, sustainable fishing rates and harvest estimates are generated for both seed and sack oysters. Comparisons of actual annual harvest to simulated annual sustainable harvest reveal years that exceed and years that fall below sustainability targets.

MATERIALS AND METHODS

Study Area

The LDWF delineated 7 coastal fisheries management zones across the state, termed coastal study areas (CSAs). In October 2012, the LDWF consolidated CSA 1 with CSA 2, and CSA 4 with CSA5. There are now 5 CSAs in the state. The current study was conducted in CSA 2, located in Breton Sound, a shallow, microtidal estuary in the Mississippi River deltaic plain of southeastern Louisiana (Fig. 1). Coastal study area 2 encompasses about 300,000 of the 880,597 total acres of the Primary Public Oyster Grounds east of the Mississippi River (LDWF 2010).

Stock Assessment

Since 1988, the LDWF has conducted annual quantitative, fisheries-independent surveys on all state public seed grounds. Divers remove oysters and surficial shell from 1.0-m^2 grids at designated stations on reefs and shell plants (Fig. 1). Two to 5 grids are sampled at each station. Oysters and boxes (dead oysters with articulated shells) are enumerated, measured, and assigned to 5-mm size classes. The survey therefore provides a quantitative estimate of oyster density with a fine-scale resolution of size (length). Details and findings of the sampling program are published in annual oyster stock assessment reports (e.g., LDWF 2010). In CSA 2, 32 sampling stations are currently established on 30 reefs and 2 shell plants (Fig. 1, Table 1). Throughout the 1999 to 2011 time series used in this study, the number of stations, reefs, and shell plants has changed, as has the acreages associated with reefs and shell plants (Table 1).

Data Management

Historical records from CSA 2 1990 to 2010 stock assessments were digitized using an automated data entry form. The digitized data are managed in a database that is queried by the numerical model through a model setup utility.

Model Overview

Figure 2 shows a schematic of the primary linkages and processes of the sustainable oyster shell stock model. Input from the database includes the length and number of live oysters per square meter at each sample station. User-controlled initialization is provided by the model setup utility. The user chooses the region, year, stations, initial month, mean juvenile natural mortality rate, juvenile natural mortality range, mean adult natural mortality, adult natural mortality range, month of average natural mortality, commercial (sack) fishing fraction and season, seed fishing fraction and season, initial cultch density, shell loss rate, and the von Bertalanffy coefficients L_∞ and k for the model run. The utility computes the total area (in square meters) of reefs and shell plants for the year and stations chosen. The model then assigns individuals to 5-mm size classes, tallies the number of oysters in a size class, and designates the number of size classes represented.

Primary model components calculate growth, natural mortality, fishing mortality, cultch density, and sacks of seed and market or sack oysters fished. Oysters that are not lost to natural mortality or removed by fishing grow into new size classes over time. Natural mortality provides new shell to the reef, whereas fishing precludes it. Natural shell loss occurs from taphonomic processes, mostly dissolution and biodegradation. Change in cultch density is thus a function of initial cultch density, recruitment, initial population numbers, size class distribution, shell growth, natural mortality, fishing mortality, and natural shell loss.

The model contains 2 main loops: a monthly loop for simulating time and a size group (size class) loop within. It thus runs for all months in a chosen year and for all size groups for the stations selected (Fig. 2). The number of size groups depends on the year and stations chosen, as established in the initialization phase described earlier. Within the size group loop, size-specific natural mortality is calculated and the shell equivalent of those oysters is added to the pool of new shell. Oyster growth moves oysters into larger size classes, and the number of oysters removed by fishing is calculated. On exhaustion of the size group loop, shell loss resulting from fishing is determined, and reef cultch density is calculated after adding shell produced by natural mortality and debiting natural shell loss for all months. After the completion of the size group and monthly loops, sacks of seed and market or sack oysters fished, and shell remaining are reported per square meter and as totals for the simulated areas.

Model pseudocode, an informal high-level description of the computer program, is presented in Tables 2 and 3. The model

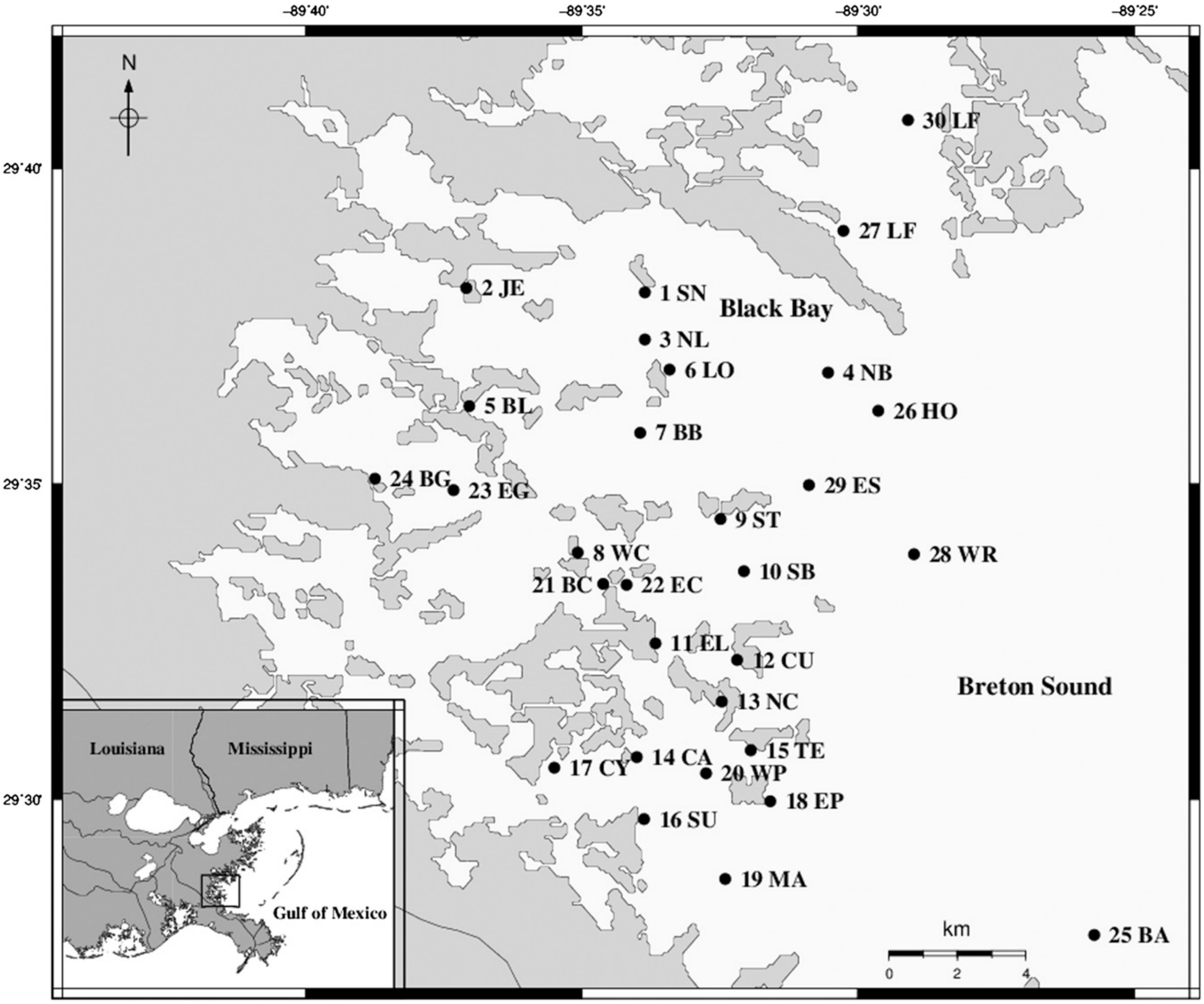

Figure 1. Map of coastal study area 2 sampling stations. Station names corresponding to station abbreviations are given in Table 1.

retrieves data from preloaded databases for a chosen year (y) and a set of chosen stations (S). These values are aggregated (GET_INPUT_RESOURCES, Table 2) to calculate the total region area (region_area) and the total number of oysters in each workgroup (N). These results are sent to the model (GET_NET_SHELL_LOSS, Table 3), which runs the simulation, calculating the net loss of cultch (shell from dead oysters). Iterative loops sum shell loss in each month and for each size group to determine a net annual loss. The simulation is initialized at $t_0 = 7$ (August), the month after the annual stock assessment. Simulations run for 12 mo ($t_{max} = 12$). Cultch mass (shell) is initialized as the initial reef shell mass (s_0). At t_0, harvest of living oysters and dead shell is initialized at 0. The variables harvest_shell and harvest_oyster track the shell mass fished and oyster sacks fished, respectively, throughout the simulation. Sack oysters, seed oysters, and shell can be fished at different rates (R_{sack}, R_{seed}, R_{shell}, respectively). Oysters experience natural mortality (MORTALITY_FRACTION), which adds shell to the reef appropriate to their length (L[g]) and its equivalent mass (OYSTER_MASS, (L[g])). Oysters grow (NEW_LENGTH) and add shell, but the shell is not credited to the reef until oysters die. Harvest and natural loss (r_n) removes shell mass from the reef. The subroutine returns net loss of shell, number of sacks harvested, and the shell mass harvested.

The equations for growth, natural mortality, fishing mortality, reef shell mass, natural shell loss, and harvest are discussed next.

Growth

Growth is the change in length (L) over time (t). Length, in turn, is time and age dependent according to a von Bertalanffy growth function:

$$L(a) = L_\infty \times \left[1 - e^{-k(t)\left(\frac{a}{12} - a_0\right)}\right] \quad (3)$$

at time t, where $L(a)$ is oyster length (in millimeters), which is a function of age a in months (months) and simulation time t in months; and $k(t)$ is a time-dependent von Bertalanffy growth coefficient. Length at infinity, L_∞ (measured in millimeters)

TABLE 1.

Louisiana Department of Wildlife and Fisheries station numbers, names, abbreviations, and areas.

Station number	Station name (abbreviation)	Area (acres)
1	Snake Island (SN)	506
2	Jessie's Island (JE)	59
3	N. Lonesome Island (NL)	896
4*	N. Black Bay (NB)	157
5	Bayou Lost (BL)	118
6†	Lonesome Island (LO)	716
6.1	2007 LO Shell Plant (P7)	200
6.2	2009 LO Shell Plant (P9)	243
7	Black Bay (BB)	301
8	W. Bay Crabe (WC)	501
9	Stone Island (ST)	461
10	S. Black Bay (SB)	145
11	Elephant Pass (EL)	339
12	Curfew (CU)	425
13	N. California Bay (NC)	109
14	California Bay (CA)	7
15	Telegraph (TE)	127
16	Sunrise Point (SU)	174
17‡	Bay Long (CY)	572
18	E. Pelican Island (EP)	782
19	Mangrove Point (MA)	937
20	W. Pelican Island (WP)	293
21	Bay Crabe (BC)	659
22	E. Bay Crabe (EC)	122
23	E. Bay Gardene (EG)	28
24	Bay Gardene (BG)	69
25	Battledore Reef (BA)	1,419
26*	Horseshoe Reef (HO)	158
27§	Lake Fortuna (LF)	2,144
28	Wreck (WR)	2,276
29‖	E. Stone Island (ES)	105
30§	Lake Fortuna (LF)	2,144

* Stations 4 and 26 were combined into 1 station, station 26 (315 acres), in year 2001.

† With a 2007 shell plant (station 6.1), acreage of station 6 was decreased by 200 acres to 516 acres, and with a 2009 shell plant (station 6.2), the acreage of station 6 was decreased by 243 acres to 273 acres. Stock assessment data from station 6.1 were collected in 2008 and 2009, and for station 6.2 in 2011.

‡ Station 17 was not sampled in years 1999 to 2008.

§ Stations 27 and 30 were combined into 1 station, station 27 (4,288 acres) in years 1999 to 2006 and 2008.

‖ Station 29 was started in 2002 but was not sampled in years 2005 and 2008.

establishes the asymptote of the von Bertalanffy growth curve (Fig. 3). Initial age, a_0, is age in years when $L = 0$. The von Bertalanffy growth coefficient is time dependent according to the equation

$$k(t) = k_0 + k_1 \times \sin\left(2\pi\left(\frac{t}{12} - t_0\right)\right), \tag{4}$$

where $k(t)$ is the von Bertalanffy growth coefficient as a function of time, t is simulation time (measured in months), k_0 is the average growth rate, k_1 is the intra-annual growth rate, and t_0 is initial time (measured in months) The time dependency of k produces a growth rate that varies seasonally (Fig. 4). The new oyster length, L_{t+1}, after a month of growth during month t is calculated as

$$L_{t+1}(L,t) = L_\infty \times \left[1 - \left(1 - \frac{L}{L_\infty}\right)e^{(-k(t)/12)}\right] \tag{5}$$

Natural Mortality

The fraction dying per time unit, $M(t, L)$, is a function of time t (measured in months) and oyster length L (measured in millimeters), expressed as

$$M(t,L) = 1 - e^{-m(t,L)/12}. \tag{6}$$

The time and length dependency of the natural mortality rate m is

$$m(t,L) = m_0 + m_1 \times \sin\left(2\pi \times \left(\frac{t - t_{avg}}{12}\right)\right), \tag{7}$$

where m_0 and m_1 are different for juveniles ($L < 25$ mm) and adults ($L \geq 25$ mm), and t_{avg} is the time (measured in months) of average mortality. The time dependency of mortality is illustrated in Figure 5. Note that the month during which mortality is average must be stipulated.

Fishing Mortality

Fishing mortality is assigned as a user option in the initiation stage. Seed and/or sack oysters can be fished simultaneously or independently. The time dependency of fishing is controlled by assigning a value (0–1.0) to the fishing coefficient for the month of interest. The fishing season is, therefore, set up as those months for which the fishing coefficient is greater than 0. Harvest is determined by the magnitude of the coefficient. For example, a 0.01 value applied to a month for seed oysters means that 1% of seed oysters are removed in that month.

Reef Cultch Density

During the initialization phase, an initial cultch density (measured in grams per square meter) for the reef is assigned. Natural mortality adds shell to the reef. Taphonomic processes diminish cultch density. New shell added from natural mortality is calculated as

$$S(d,L) = d \times s_A \times l^{s_B} \tag{8}$$

where $S(d,L)$ is new shell added as a function of d; number of dead oysters, L, is average oyster length (measured in millimeters); and s_A and s_B are the allometric coefficients relating shell length to shell mass (Fig. 6).

To determine the shell mass associated with removal by fishing requires knowledge of the number of sacks fished, number of oysters per sack (OPS; Fig. 7), the mean length of the oysters in the sack, and the mass equivalent (measured in grams) of the sack. Oysters per sack as a function of oyster length(l) is

$$OPS(l) = OPS_a \times l^{OPS_b} \tag{9}$$

where OPS_a is an oysters-per-sack coefficient and OPS_b is an exponent, both derived from the length/number relationship of Hopkins (1950). The sack equivalent $S(g)$ of a given mass of shell (measured in grams) is

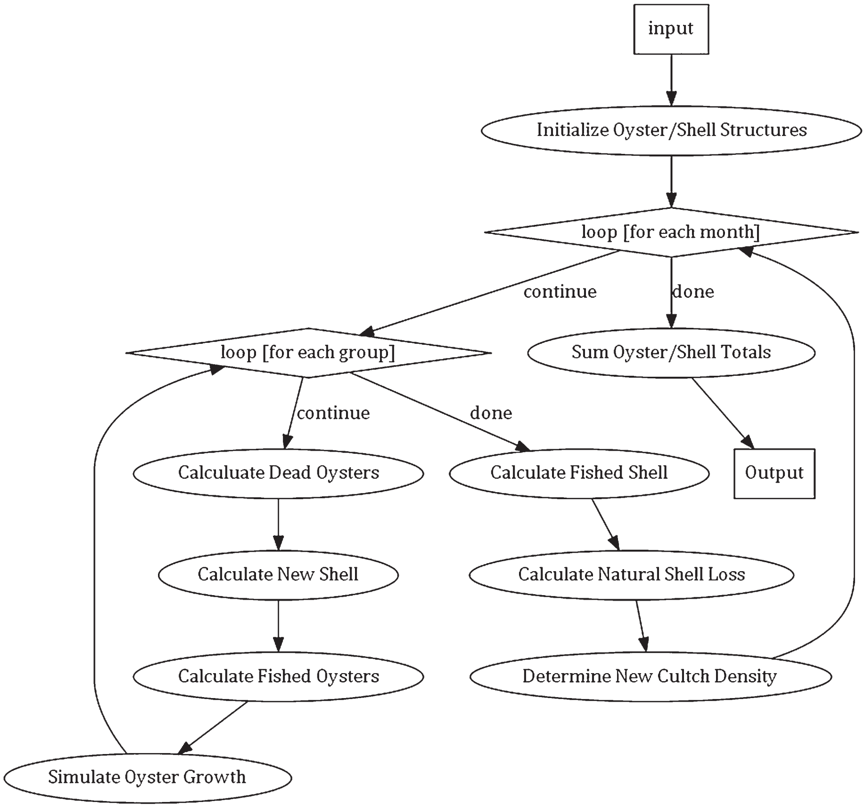

Figure 2. Schematic of major oyster model processes.

$$S(g) = \frac{g}{D \times C \times P} \tag{10}$$

where g is shell mass (measured in grams), D is shell density (measured in grams per liter), C is sack capacity (52.85 L/sack), and P is a packing coefficient, or the ratio of shell volume to expanded cultch volume.

Natural Shell Loss

Loss of surficial shell diminishes the function of the substrate to attract larvae and support newly settled ones. Natural shell loss is operationally defined as the diminution in shell mass resulting from dissolution (Waldbusser et al. 2011), biodegradation, and the export of small pieces of shell off the reef, loss of clean shell surface area resulting from burial below the oxidized layer, and fragmentation into small pieces, which are easily roiled and thus prevent settlement or survival of larvae (MacKenzie 1977, Gunter 1979). Shell loss $S_{L,t}$ (measured in grams) for a given month t is initialized as a monthly percent shell loss. Shell losses are subtracted and shell gains are added to the amount of current shell S_t (measured in grams) in a month t to determine reef cultch density for the next month ($S_{(t+1)}$) such that

$$S_{t+1} = S_t - S_{F,t} - S_{L,t} + S_{N,t} \tag{11}$$

where $S_{F,t}$ is shell removed as part of the fishing process in the current month and $S_{N,t}$ is new shell added in the current month from natural mortality. Fishing removal of shell in this case is associated primarily with seed removal, because much of the seed is attached to shell and not to live oysters. Note that cultch density in Eq (11) does not include the mass of live oysters, which is treated separately.

Harvest and Fishing

Number of commercial (sack) oysters harvested (H_C) is expressed as

$$H_C = (C_{F,C} \times N_C) \tag{12}$$

where $C_{F,C}$ is the fraction of commercial-size oysters harvested and N_C is the number of oysters in the commercial size group. Likewise, the number of seed harvested (H_S) is

$$H_S = (C_{F,S} \times N_S) \tag{13}$$

where $C_{F,S}$ is the fraction of seed size oysters harvested and N_S is the number of oysters in the seed size group. Harvest is reported in sacks by dividing the number of oysters fished in each size group (f_i) by the size-appropriate number of oysters per sack and summing across all size groups where

$$\text{Sacks Harvested} = \sum_{i=1}^{n} \left(\frac{f_i}{OPS(l_i)} \right) \tag{14}$$

Fishing Scenarios

As mentioned earlier, the time dependency of fishing and fishing effort is controlled by assigning a value (0–1.0) to the

TABLE 2.

GET_INPUT_RESOURCES pseudocode.

Symbol	Description	Example
y	The sample year	(parameter)
S	The set of stations from which to sample	(parameter)
D	Database loaded with YEAR × STATION × SAMPLE × GROUP data	(database)
A	Database loaded with STATION acreages.	(database)

```
GET_INPUT_RESOURCES(y, S)
  var region_area ← 0;
  var N ← a new array;
  var T ← a new array;
  for each station s in S
  {
    region_area ← region_area + A[s];
    for each sample n in D[y][s]
      for each group g in D[y][s][n]
        T[s][g] ← T[s][g] + D[y][s][n][g];
    for each group g from 1–40
      $N[g] \leftarrow N[g] + \frac{T[s][g]}{|D[y][s]|} \times A[s]$
  }
  return (N, region_area);
```

TABLE 3.

GET_NET_SHELL_LOSS pseudocode.

Symbol	Description	Example
N	Array of oyster group counts.	(parameter)
L	Array of oyster group lengths (mm)	(parameter)
s_0	Initial reef shell, independent of oyster mass (g)	(parameter)
R_{sack}	Array of monthly removal fractions of sack	(parameter)
R_{seed}	Array of monthly removal fractions of seed/spat	(parameter)
R_{shell}	Array of monthly removal fractions of nonoyster shell mass	(parameter)
r_n	Monthly natural loss fraction of shell	0.008895
t_0	Initial month of simulation (0 = January)	7 (August)
t_{max}	Number of months to run the simulation	12

```
GET_NET_SHELL_LOSS(N, L, $s_0$, $R_{sack}$, $R_{seed}$, $R_{shell}$)
  var t ← $t_0$
  var shell ← $s_0$
  var harvest_oysters ← 0
  var harvest_shell ← 0
  for each month in the simulation {
    var new_shell ← 0
    for each oyster group g {
      if (STAGE(L[g]) = SACK)
        var fished ← $R_{sack}$ [t] × N[g]
      else
        var fished ← $R_{seed}$ [t] × N[g]
      var dead ← MORTALITY_FRACTION(t, L[g]) × N[g]
      new_shell ← new_shell + OYSTER_MASS(L[g]) × dead
      harvest_oysters ← harvest_oysters + fished ×
        SACKS_PER_OYSTER(L[g]);
      N[g] ← N[g] – dead – fished
      L[g] ← NEW_LENGTH(t, L[g])
    }
    var shell_fished ← shell × $R_{shell}$ [t]
    var shell_lost ← shell × $r_n$
    shell ← shell + new_shell – shell_lost – shell_fished
    harvest_shell ← harvest_shell +
      SHELL_TO_SACKS(shell_fished)
    t ← t +1
  }
  var net_loss = $s_0$ – shell
  return (net_loss, harvest_oysters, harvest_shell)
```

fishing fraction coefficient (C_F) for the month of interest. However, different fishing modes result in differential incidental harvest of dead shell and live oysters. Fishing for shell, seed, and sack-size (commercial) oysters are separated explicitly in the model, allowing for the evaluation of the impact of various fishing scenarios. Three common fishing scenarios are (1) direct harvest of sack oysters, (2) fishing for seed on public grounds and planting them on private leases, and (3) wholesale planting of sack oysters, seed, and shell from public grounds to private leases. Direct harvest is selected fishing for sack oysters that are culled, sacked, and marketed immediately. Direct harvest (sacking) includes an incidental harvest of seed and shell, but for the sake of simplicity this removal is assumed to be *de minimis* and is not included in the simulations presented herein. Fishing for seed imposes a shell fishing rate equivalent to the seed fishing rate because the shell on which the seed is attached is not culled easily or routinely, whereas wholesale planting removes (at an equal rate) sack oysters, seed, and shell from the public grounds to private leases. Thus, various fishing scenarios result in differential impacts on the shell budget. In the current simulations, sack and seed oysters are fished simultaneously. Fishing effort (fishing fraction) is manipulated to achieve the sustainability criterion of no net loss of reef shell.

RESULTS

Table 4 shows the status of the initial stock, fishing effort for seed and sack oysters, and model outputs for simulations for 1999 to 2011. Shell density is initialized at 5,000 g/m^2 for all simulations. The number of oysters on the seed grounds varied from 2.95×10^9 to in 2000 to 3.89×10^7 in 2011. Likewise, oyster density showed a similar trend during the same period with a high of 45.4 oysters/m^2 in 2000 and a low of 0.58 oysters/m^2 in 2011. Oyster mass (the shell mass of living oysters) peaked at 2,519 g/m^2 in 2001 and was lowest in 2010 at 53 g/m^2. Mean oyster length varied from 76.9 mm in 2011 to 22.5 mm in 2009. Sustainable sack fishing effort ranged from 0.25/mo in 2000 to 0/mo in 2008, 2010, and 2011, whereas seed/shell

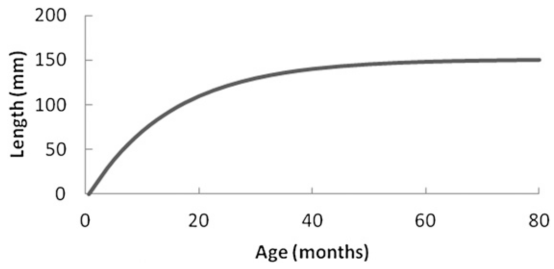

Figure 3. Oyster length as a function of age. Length at infinity, L_∞ = 151 mm.

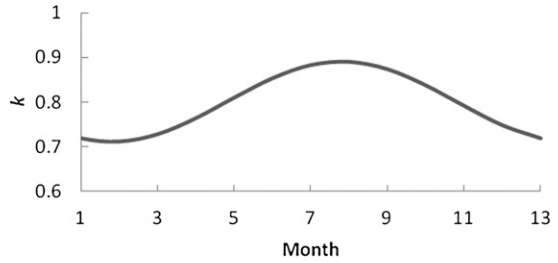

Figure 4. Time dependency of the von Bertalanffy growth coefficient, k.

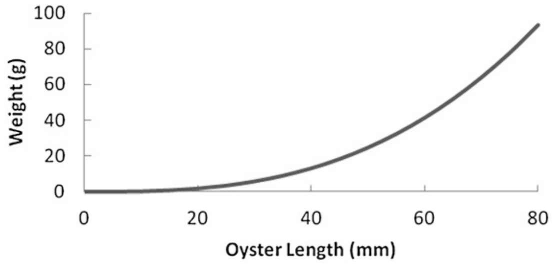

Figure 6. Conversion of oyster length to oyster shell weight.

fishing effort ranged from 0.02/mo in 2000 to 0/mo in 2005, 2008, 2010, and 2011. Average sack fishing rate for the 7-mo season over the time series was 0.102/mo versus a seed/shell fishing rate of 0.007/mo. In the simulations, the volume of shell fished varied from 661,000 sacks in 2000 to 0 sacks in 2005, 2008, 2010, and 2011, the years that no seed was fished. An attempt was made to fish at a rate such that there was no diminution of shell density (shell of dead oysters) and, because the shells of live oysters do not accrete to the reef until oysters die, no diminution of reef mass. It was not always possible to achieve an exact balance between these conditions. Emphasis was, therefore, placed on achieving no reef mass loss (±5%). In 2010 and 2011, however, when no fishing was simulated, reef mass losses exceeded 5%. Final shell density varied from 5,357 g/m^2 in 2001 to 4,372 g/m^2 in 2006. Percent shell loss varied from –7.1% in 2001 (a gain of 7%) to 12.6% in 2006. Oysters dead is the percent of oysters that died over simulated time; it varied from 46.6% in 2009 to 33.6% in 2001. Final oyster mass ranged from 2,336 g/m^2 in 2001 to 101 g/m^2 in 2011. Oyster mass as a percent change between initial and final mass ranged from 378% in 2009 to 93% in 2001. Final oyster density was greatest in 2000 (10.3 oysters/m^2) and lowest in 2011 (0.34 oysters/m^2). The highest simulated sustainable seed harvest was 816,000 sacks (year 2000); in 2005, 2008, 2010, and 2011, no amount of seed harvest was deemed sustainable. In 2001, a high of 3,066,000 sacks of sack oysters was calculated to be a sustainable harvest, whereas in some years (2008, 2010, and 2011) no amount of fishing was considered sustainable.

Table 5 provides LDWF stock assessment and harvests estimates for sack and seed oysters; harvest as a percent of available stock for sack and seed oysters is calculated. Simulated sustainable estimates of sack and seed oysters are presented, and harvest as a percent of simulated harvest for sack and seed oyster are given. Stock estimates of sack oysters range from 4,642,996 sacks in 2001 to 156,900 sacks in 2009; stock seed estimates show a 2000 high of 6,828,812 sacks and a 2008 low of 221,502 sacks. Harvest of sack oysters was greatest in 2001 (844,898 sacks) and lowest in 2009 (167,614 sacks). Seed harvest varied from 626,320 in 2003 to 58,270 in 2005. In 2008 and 2009, all the stock of sack oysters was harvested. (Values greater than 100% suggest errors in the estimate of stock abundance and/or harvest.) In contrast, only 18.2% of the stock of sack oysters was harvested in 2001. In 2008, 69.5% of available seed was harvested, whereas in 2000 only 3.0% was taken. Sustainable estimates for allowable catch of sack oysters varied from 3,065,531 (2001) to 0 sacks (2008). No fishing of sack oysters was considered sustainable in 2008, yet 265,581 sacks were harvested; in 2005 harvest also exceeded sustainability estimates. In year 2000, only 13.2% of the sustainable sack estimate was harvested. In most years (2002 to 2005, 2007, 2008), the harvest of seed oysters exceeded sustainable harvest estimates. In 2005 and 2008, no harvest of seed was considered sustainable, yet 58,270 sacks were harvested in 2005 and 154,006 sacks were harvested in 2008. In contrast, in the 2000 oyster season, only 201,560 sacks of seed (24.7%) of the simulated sustainable catch of 816,468 sacks were harvested.

DISCUSSION

Sustainable fishing rates for seed oysters appear to be about an order of magnitude less than sustainable fishing rates for sack oysters. In most years the harvest of seed was not sustainable, whereas sustainability goals were often achieved for sack oysters. A notable exception was 2000, a year of abundant seed oysters in which less than 25% of the sustainability goal for seed oysters was harvested. For both seed and sack oysters the general trend in the simulated time series is from sustainable harvests in the early years of abundance to unsustainable harvests in the recent years of paucity. In some years toward

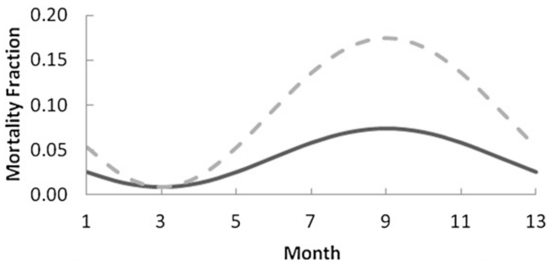

Figure 5. Time dependency of monthly natural mortality fraction. Dashed line, juveniles (L < 25 mm); solid line, adults ($L \geq$ 25 mm).

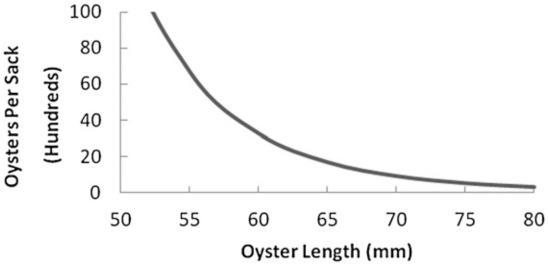

Figure 7. Number (hundreds) of oysters per sack for oysters of various length.

TABLE 4.

Initial oyster stock, sustainable fishing efforts, and model simulation outputs for 1999 to 2011.

	Year												
	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
Initial stock													
Shell density (g/m^2)	5,000	5,000	5,000	5,000	5,000	5,000	5,000	5,000	5,000	5,000	5,000	5,000	5,000
Oyster count (10^3)	1,927,151	2,952,714	2,264,214	1,203,688	947,604	773,613	481,309	1,522,752	1,212,731	201,380	1,352,198	81,908	38,946
Oyster density ($oysters/m^2$)	29.6	45.4	34.8	18.4	14.5	11.8	7.4	23.3	18.8	3.1	20.2	1.2	0.58
Oyster mass (g/m^2)	1,376	1,382	2,519	1,004	671	577	383	392	381	137	294	53	73
Mean length (mm)	51.5	46.1	66.5	46.9	50.9	53.1	52.5	31.6	26.4	43.4	22.5	49.1	76.9
Fishing effort													
Sack fishing frac (mo)	0.15	0.25	0.125	0.1	0.1	0.1	0.05	0.2	0.1	0	0.15	0	0
Seed fishing frac (mo.)	0.01	0.02	0.01	0.005	0.0025	0.0025	0	0.015	0.01	0	0.01	0	0
Shell fishing frac (mo)	0.01	0.02	0.01	0.005	0.0025	0.0025	0	0.015	0.01	0	0.01	0	0
Model output													
Shell fished (10^3 sack)	337	661	358	168	88	82	0	474	315	0	324	0	0
Shell density (g/m^2)	4,908	4,667	5,357	4,857	4,821	4,761	4,741	4,372	4,484	4,593	4,449	4,535	4,531
Net shell loss (%)*	1.8	6.7	–7.1	2.9	3.6	4.8	5.2	12.6	10.3	8.1	11.0	9.3	9.4
Oysters dead (%)	36.5	33.9	33.6	41.6	38.0	36.7	39.5	40.4	45.9	43.3	46.6	41.3	41.1
Oyster mass (g/m^2)	1,694	1,815	2,336	1,296	1,105	937	742	1,235	1,156	356	1,110	154	101
Mass change (%)	123	131	93	129	165	163	194	315	304	260	378	291	138
Oyster density ($oysters/m^2$)	8.8	10.3	9.7	6.7	5.5	4.6	3.5	8.2	7.7	1.7	8.0	0.7	0.34
Seed fished (10^3 sack)	372	816	385	176	88	87	0	537	340	0	354	0	0
Sack fished (10^3 sack)	2,012	3,049	3,066	1,005	751	638	235	795	414	0	447	0	0
Reef mass loss (%)*	–3.6	–1.6	–2.3	–2.5	–4.5	–2.2	–1.9	–4.0	–4.8	3.6	–5.0	7.2	8.7

* Negative loss percentages indicate a net gain. frac, fraction.

TABLE 5.

Stock assessment and harvest estimates from the Louisiana Department of Wildlife and Fisheries, and harvest as a percent of the available stock for sack and seed oysters.

Year	Stock sack (sacks)	Stock seed (sacks)	Harvest sack (sacks)	Harvest seed (sacks)	% Harvest/stock (sack)	% Harvest/stock (seed)	Sim. sack fished (sacks)	Sim. seed fished (sacks)	% Harvest/Sim. (sack)	% Harvest/Sim. (seed)
1999	1,989,508	3,382,040	700,617	138,056	35.2	4.1	2,012,018	372,441	34.8	37.1
2000	1,754,696	6,828,812	403,374	201,560	23.0	3.0	3,049,175	816,468	13.2	24.7
2001	4,642,996	3,851,418	844,898	318,490	18.2	8.3	3,065,531	385,332	27.6	82.7
2002	1,937,488	1,201,982	704,284	281,766	36.4	23.4	1,004,700	176,001	70.1	160.1
2003	1,134,036	1,598,908	286,963	626,320	25.3	39.2	751,139	87,736	38.2	713.9
2004	741,188	1,497,112	535,936	391,072	72.3	26.1	634,174	86,670	84.5	451.2
2005	598,628	778,146	271,271	58,270	45.3	7.5	234,559	0	115.7	*
2006	308,986	2,215,294	183,355	221,134	59.3	10.0	794,925	536,576	23.1	41.3
2007	619,124	902,068	278,580	347,170	45.0	38.5	414,042	340,485	67.3	102.0
2008	248,786	221,502	265,581	154,006	106.8	69.5	0	0	*	*
2009	156,900	483,524	167,614	165,376	106.8	34.2	476,887	354,295	35.1	46.7

* Results for which a division by 0 would occur, indicating harvest greatly exceeds simulation estimate.

Sustainable catch from the model simulation and harvest as a percent of the sustainable catch for sack and seed oysters. Data from the Louisiana Department of Wildlife and Fisheries for 2010 and 2011 have not been released. Sim., simulation.

the end of the time series, no level of fishing was considered sustainable. That is, insufficient oysters were present at the beginning of the season to support the deaths needed to offset the loss of shell resulting from natural processes (Powell et al. 2006, Powell & Klinck 2007, Waldbusser et al. 2011).

As argued by Powell et al. (2009a, 2009b), extreme annual variation in oyster stocks precludes the application of standard biological reference points such as carrying capacity. Good years often follow good years and bad years often follow bad years, punctuated by regime shifts (Powell et al. 2008). Oyster reefs exhibit a system memory provided through the persistence (or loss) of cultch, the shell mass associated with living oysters, and the number of surviving oysters that constitute the spawning stock. Sustainable harvest of oysters in Louisiana, and likely elsewhere, as indicated by application of this shell-neutral model, is an annual moving target that precludes the application of standard production and maximum sustained yield models.

The assumption of an initial cultch density made it possible to determine sustainable harvests in the absence of measured cultch densities; however, sustainable fishing rates and associated harvest allotments are dependent, in part, on the assumption of the initial cultch mass. With a high initial cultch mass, more natural shell loss occurs, and to compensate, more oysters must remain on the reef and die there. In the simulations, it was assumed that the reef was in good condition (initial cultch = 5000 g m^{-2}; Mann et al. 2009), and harvest was not diminished to build reef (i.e., for a shell gain). The modeling exercise clearly demonstrates the need to monitor cultch density and adopt a reference point that constitutes adequate cultch. A measured value for initial cultch density would then establish reef condition, and fishing could be adjusted to achieve the reference point goal at the end of the season. The measurement of cultch density the following stock assessment would indicate if the cultch reference goal was achieved.

The model permits area management by grouping stations with similar attributes and treating them as a functional unit. Attributes of particular importance are oyster growth and mortality, especially because they vary across the salinity gradient. However, in the simulations described herein, a single value each month for growth and mortality across all years and stations was used. Further model refinement would involve empirically based parameterization of the growth and mortality equations. Regional environmental and climatic variability have been shown to alter oyster growth and mortality ratesdramatically (La Peyre et al. 2009, Soniat et al. 2009), and experimental work has demonstrated that growth and mortality may vary substantially between years, across stations, and by size class (La Peyre et al. 2003, La Peyre et al. 2009, Eberline 2012). For example, in a recent 2-year study in Breton Sound, growth ranged from a mean monthly rate as low as 0.2 mm/mo to as high as 7.9 mm/mo across stations, years, and size classes (Eberline 2012). These differences are suggested to be related to the local salinity regime, which may be influenced by regional climatic patterns and local water management (Klinck et al. 2002, Powell et al. 2003, Wang et al. 2008, La Peyre et al. 2009). Refining the growth and mortality equations to account for this level of variation should improve model predictions significantly.

The no-net-shell-loss approach to sustainability is broadly applicable to the eastern oyster, a quintessentially r-selected species that also builds the substrate on which its future generations depend. The population dynamics of *Crassostrea virginica* in the Gulf of Mexico have many r-selected attributes, even though the species is iteroparous. Growth rates and mortality rates are high, life span is often limited to 1–2 years, and 2 generations per year are often possible. In more northern climes, *C. virginica* population dynamics take on more of the bet-hedging lifestyle, and iteroparity and long life become increasingly important components of species persistence. Although applied initially to the Louisiana fishery, with local parameterization the model should prove useful in estimating sustainable harvests and in evaluating the success of reef restoration of the eastern oyster across its entire range. Oyster fisheries that remove shell versus reef restorations that promote shell accretion, although divergent in their goals, are convergent in their management; both require vigilant attention to shell budgets.

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