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ESTIMATING SUSTAINABLE HARVESTS OF EASTERN OYSTERS, *CRASSOSTREA VIRGINICA*

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ABSTRACT Sustainability of a fishery is traditionally and typically considered achieved if the exploited population does not decline in numbers or biomass over time as a result of fishing relative to biological reference point goals. Oysters, however, exhibit atypical population dynamics compared with many other commercial species. The population dynamics often display extreme natural interannual variation in numbers and biomass, and oysters create their own habitat—the reef itself. With the worldwide decline of oyster reef habitat and the oyster fisheries dependent thereon, the maintenance of shell has received renewed attention as essential to population sustainability. We apply a shell budget model to estimate the sustainable catch of oysters on public oyster grounds in Louisiana using no net shell loss as a sustainability reference point. Oyster density and size are obtained from an annual stock assessment. The model simulates oyster growth and mortality, and natural shell loss. Shell mass is increased when oysters die in place, and is diminished when oysters are removed by fishing. The shell budget model has practical applications, such as identifying areas for closure, determining total allowable catch, managing shell planting and reef restoration, and achieving product certification for sustainability. The determination of sustainable yield by shell budget modeling should be broadly applicable to the eastern oyster across its entire range.

KEY WORDS: *Crassostrea virginica*, oyster, fisheries modeling, stock assessment, sustainability, shell budget, biological reference point

INTRODUCTION

Sustainability of a fishery is traditionally and typically considered achieved if the exploited population does not decline in numbers or biomass over time as a result of fishing (Ricker 1975). In the modern era, management of most U.S. fisheries resources has focused on biological reference points that support maximum sustainable yield (Applegate et al. 1998, Restrepo et al. 1998, Rothschild et al. 2012). Although this approach is not without controversy or implementation challenges (Hilborn 2002, Mangel et al. 2002, Maunder 2012, Punt & Szuwalski 2012), the imposition of biological reference points—essentially, goals for stock biomass and fishing mortality that support sustainability—have resulted in significant improvement in U.S. fish stocks nationwide. Oysters, however, exhibit atypical population dynamics compared with many other commercial species. Their population dynamics display extreme natural interannual variation in numbers and biomass (e.g., Jordan 1995, Powell et al. 2008, Soniat et al. 2012, Louisiana Department of Wildlife & Fisheries 2012, Louisiana Department of Wildlife & Fisheries 2013) more often associated with short-lived species such as squid (Dawe et al. 2000, Zuur & Pierce 2004, Powell et al. 2005), and oysters create their own habitat—the reef itself. This last is unique among widespread commercially exploited species.

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Coincident with the decline of oyster fisheries and oyster reefs nationally and worldwide (Mann & Powell 2007, Beck et al. 2009, Beck et al. 2011), the maintenance of shell has received renewed attention as essential to population sustainability (Powell et al. 2006, Powell & Klinck 2007, Waldbusser et al. 2011a, Waldbusser et al. 2011b, Waldbusser et al. 2013). Oyster shell is an essential and limiting resource subject to the vicissitudes of dissolution (Cubillas et al. 2005, Waldbusser et al. 2011a), biodegradation (Carver et al. 2010, Powell et al. 2011), sedimentation (Davies et al. 1989, Smith et al. 2001, Jordan-Cooley et al. 2011), and subsidence (Gagliano et al. 1981, Yuill et al. 2009). Oyster reefs are enhanced by the addition of shell through natural mortality and are degraded by shell loss. Sufficient numbers of large oysters must die in place to compensate for natural shell loss (Mann & Powell 2007, Mann et al. 2009a). Furthermore, fishing, which removes shell, and disease (Powell et al. 2012) and frequent freshets (Cake 1983, LaPeyre et al. 2009, LaPeyre et al. 2013), which prevent oysters from achieving full size, are detrimental to reef accretion.

The extreme natural variation in oyster numbers and biomass limits the application of equilibrium yield as a sole biological reference point (Powell et al. 2012). Powell et al. (2006) and Powell and Klinck (2007) endorse the application of a second biological reference point as appropriate for oysters—namely, no net shell loss—because only if habitat integrity is preserved can oyster populations achieve sustainability over the long term. Soniat et al. (2012) developed a numerical model that incorporates the concept of no net shell loss as a standard for reef and fisheries sustainability; they applied the model using historical stock assessment data from the Louisiana Primary State Seed Grounds east of the Mississippi River to estimate annual sustainable harvests retrospectively. The purpose of this contribution is to estimate sustainable oyster harvest prospectively using the shell budget modeling approach in a larger scale application. The estimation of sustainable harvest for the 2013/2014 oyster season on all Louisiana public oyster grounds is used as an example.

MATERIALS AND METHODS

Study Area

Oyster (*Crassostrea virginica*) samples were collected by Louisiana Department of Wildlife and Fisheries biologists from public oyster grounds in Louisiana in June and July 2013. The state has 667,731 ha of public oyster grounds, of which about 24,000 ha are hard reef bottom (Louisiana Department of Wildlife & Fisheries 2012). Predicting oyster harvest on the 155,802 ha of privately leased bottom is not part of this study.

Coastal Louisiana is broadly divided into the Deltaic Plain in the east and the Chenier Plain in the west. The Deltaic Plain extends from the Louisiana/Mississippi border to Vermilion Bay and is characterized by lobate shorelines of active and degrading deltas. The Chenier Plain includes a series of high ridges (cheniers) that run roughly parallel to a relatively strait shoreline and extends from Vermilion Bay to the western boundary of Louisiana, Sabine Lake. Cheniers are former shore-side dunes that became isolated inland as the westward drift and subsequent deposition of sediment, largely from the Mississippi and Atchafalaya rivers, built new shorelines. In the Deltaic Plain, subtidal oysters are found in mesohaline portions of the interdistributary bays that form between the natural levees of the Mississippi River and its distributaries (Mackin & Hopkins 1961, Coleman & Gagliano 1964, Melancon et al. 1998). An exception is the Vermilion Bay area, where copious outflows of freshwater from the Atchafalaya River push mesohaline conditions beyond the coastline, and where oysters extend onto the shallow continental shelf (Price 1954). Intertidal oysters occur on the backside of the barrier islands of the Deltaic Plain; they are not harvested by fishermen, nor are they sampled by Louisiana Department of Wildlife & Fisheries personnel, and they are not considered here. Oysters along the Chenier Plain are found in bays that are characterized by single narrow connections with the Gulf of Mexico and receive freshwater independent of the Mississippi River and its distributaries.

The Louisiana Department of Wildlife & Fisheries, which is responsible for the management of the state's oyster industry, divides the coast into hydrological and management units called coastal study areas (CSAs). Historically, 7 CSAs were designated. Starting in 2011, the Louisiana Department of Wildlife & Fisheries adopted a new classification with 5 CSAs (Fig. 1). For the sake of simplicity and historical continuity, the original designation is used to describe CSA boundaries: CSA 1, Mississippi Line to Mississippi River gulf outlet; CSA 2, Mississippi River gulf outlet to Empire; CSA 3, Empire to Bayou Lafourche; CSA 4, Bayou Lafourche to Caillou Boca; CSA 5, Caillou Boca to Atchafalaya River; CSA 6, Atchafalaya River to Freshwater Bayou; CSA 7, Freshwater Bayou to Sabine Pass. CSA 1 includes the Louisiana portion of Mississippi Sound, Lake Borgne, Chandeleur Sound, and adjacent waters. Coastal study area 2 encompasses Breton Sound and contiguous bays such as Bay Gardene, Bay Crabe, Black Bay, and California Bay. Coastal study area 3 is the Barataria Bay system, which includes the public grounds of Little Lake, Hackberry Bay, and the Barataria Bay Public Oyster Seed Grounds. Coastal study area 4 is the Terrebonne Basin and includes public grounds in Lakes Felicity, Chien, Tambour, Sister (= Caillou), and Mechant, and Bay Junop. Vermilion Bay, East and West Cote Blanche Bays, and Atchafalaya Bay fall within the boundaries of CSA 6. Coastal study areas 1–6 are part of the Deltaic Plain. Public oyster grounds in CSA 7 are found in Lake Calcasieu and Sabine Lake. Coastal study area 7 lies within the Chenier Plain

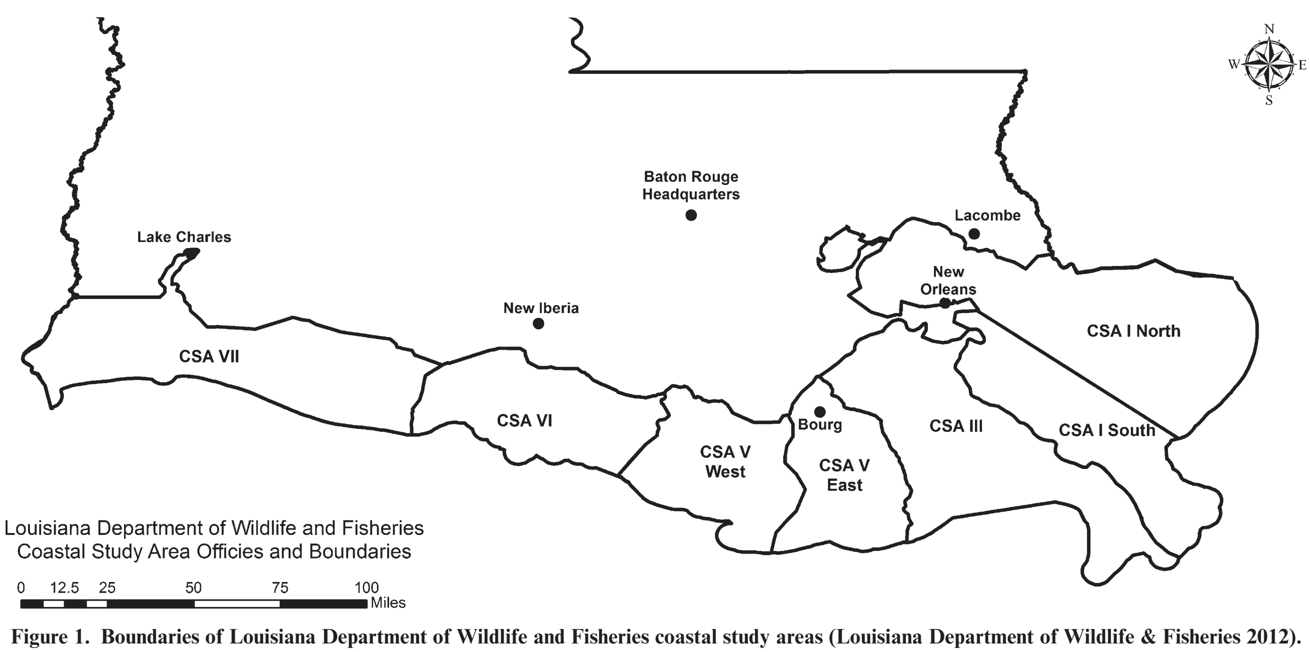

Figure 1. Boundaries of Louisiana Department of Wildlife and Fisheries coastal study areas (Louisiana Department of Wildlife & Fisheries 2012).

(Louisiana Department of Wildlife & Fisheries 2012). The new CSA system absorbs CSA 2 into CSA 1, with the former CSA 1 called CSA 1North (1N) and the former CSA 2 called CSA 1South (1S); CSA 3 remains unchanged; CSA 4 is combined with CSA 5, with the former CSA 4 designated as CSA 5East (5E) and the former CSA 5 now called CSA 5West (5W); and CSAs 6 and 7 remain unchanged.

Stock Assessment

In 2013, the Louisiana Department of Wildlife & Fisheries collected 490 samples from 98 stations; oysters were collected from 5 replicate 1-m^2 grids by divers using scuba gear. Oysters were enumerated, sized, and grouped into 5-mm bins. Data from replicates were combined to produce average numbers of spat (≤25 mm), seed (26–74 mm), and sack oysters (≥75 mm) per station. The average number of oysters per replicate was multiplied by the station's acreage to estimate the number of oysters per station. In some cases, large reefs have multiple stations and the acreage is partitioned equally; in the case of CSA 6, reef acreages are roughly estimated in consultation with Louisiana Department of Wildlife & Fisheries biologists (Table 1). The 2012 Stock Assessment (Louisiana Department of Wildlife & Fisheries 2012) included, for the first time, quantitative estimates of the quality and quantity of the cultch. Brown (surface) and black (muddy, buried) substrate were collected from 1-m^2 grids and weighed. These measurements were repeated during the 2013 Stock Assessment sampling (Louisiana Department of Wildlife & Fisheries 2013). The substrate was assigned to a series of categories: muddy oyster shell, brown oyster shell, muddy limestone, brown limestone, muddy clamshell, brown clamshell, muddy concrete, brown concrete, muddy other substrate, and brown other substrate. The substrates limestone, clamshell (mostly *Rangia cuneata*), and concrete represent substrates added during reef replenishment and recruitment enhancement activities (Soniat et al. 1991, Soniat & Burton 2005, Louisiana Department of Wildlife & Fisheries 2004). Although the quantity (grams per square meter) of all the various substrate types was sampled in the 2013 stock survey, only the 91 reefs (Table 1) with measureable brown shell were used in the current study.

Data Management

Oyster abundance and size from the 2013 Louisiana Department of Wildlife & Fisheries Stock Assessment (Louisiana Department of Wildlife & Fisheries 2013) for all public oyster areas in all CSAs were input using an automated data entry form available via http://www.oystersentinel.org. The digitized data were queried by the numerical model (Soniat et al. 2012) through a model setup utility. Oyster density and size frequency, and brown oyster shell quantity were input into the model to evaluate the number of sacks of seed and sack oysters that could be removed during the 2013 season with no net loss of shell.

Model Overview

The model calculates growth, natural mortality, fishing mortality, cultch density, and sacks of seed and sack (market) oysters fished (Fig. 2). Oysters that are not lost to natural mortality or removed by fishing grow and enter new size classes over time. Natural mortality provides new shell to the reef, whereas fishing removes it. Natural shell loss occurs from taphonomic processes, mostly dissolution and biodegradation. Change in cultch density is thus a function of initial cultch density, initial population numbers, size–frequency distribution, shell growth, natural mortality, fishing mortality, and natural shell loss. Through a series of numerical trials of fishing rates and times using the model, we determined a sustainable harvest, defined here as harvests that result in no net loss of shell. This follows a recommendation originally forwarded by Klinck et al. (2001) that, when faced with an inability to estimate a desired goal for a resource, the conservative approach is to manage at no net change (see also Mann and Powell [2007]). Mathematical and procedural details of the model are provided by Soniat et al. (2012), Cooper (2013), and Soniat et al. (2013). Fishing rates were varied to identify a rate that resulted in no net loss of cultch. Initial simulations were conducted for all stations (reefs and cultch plants) without fishing (Table 1); only those with a gain of cultch mass over 1 y without fishing were deemed potentially "fishable" (Figs. 3–8).

Simulations

Simulations were conducted to estimate sustainable harvests from all CSAs (Fig. 1) and by summation statewide harvest from all public oyster areas. For those areas deemed fishable (Figs. 3–8) by having the desirable characteristic of potentially accumulating shell throughout the year, fishing rates were varied to identify the maximum rate that resulted in no net loss of shell. Reefs and cultch plants that were deemed "fishable" and that were open for harvest (as designated by the Louisiana Department of Wildlife & Fisheries) were subsequently simulated to determine a sustainable total allowable catch (TAC). Sustainability in simulations is achieved by manipulating fishing effort to achieve no net loss of shell. The temporal distribution of fishing, fishing effort (approximate monthly effort as a percent of total effort), and fishing type (sack, seed) is informed by weekly fisheries-dependent observations (boarding reports) from the 2012 fishing season provided by the Louisiana Department of Wildlife & Fisheries (Table 2).

RESULTS

Simulated TACs for sack and seed oysters for the various CSAs and the statewide total are summarized in Table 3. From CSA 1N, Petit Island, Johnson Bayou, and East and West Karako showed a positive shell balance and are designated open to fishing (Table 1, Fig. 3), thus they are included in the assessment of the TAC. Coastal study area 1N supports a combined TAC of 9,936 sacks of sack oysters and 6,464 sacks of seed oysters (Table 3). (A Louisiana sack is 1.5 U.S. bushels or 0.053 m^3.)

The CSA 1S stations of Snake Island, Jessie Island, Lonesome Island, West Bay Crabe, and Horseshoe Reef show a positive shell balance (Table 1, Fig. 4), are planned to be open for fishing (Table 1), and are thus included in the estimation of the regional TAC (Table 3). The combined TAC for CSA 1S is estimated to be 10,098 sacks of sack oysters and 1,416 sacks of seed.

In CSA 3, the Lower, Middle, and Upper Hackberry Bay stations; the 2004 North and South Hackberry Bay Shell Plants; and the 2008 and 2012 cultch plants in Hackberry Bay showed a positive shell balance without fishing (Fig. 5).

TABLE 1.

Region name (coastal study area [CSA]), station names, location, and associated reef size (acres).

Region name	Station name	Coordinates	Reef Size	Cultch loss (%)	Fishable	Open	Simulated
CSA1	Grassy	30.15000° N, 89.46667° W	2,283	7.1	False	True	False
CSA1	Petit	30.09806° N, 89.47889° W	2,283	–15.2	True	True	True
CSA1	Three Mile	30.03917° N, 89.35278° W	1,529	7.0	False	True	False
CSA1	Grand Pass	30.14278° N, 89.23972° W	600	10.0	False	True	False
CSA1	Cabbage Reef	30.15306° N, 89.22556° W	600	7.3	False	True	False
CSA1	Turkey Bayou	30.10472° N, 89.29861° W	600	4.0	False	True	False
CSA1	Millennium Reef	30.11278° N, 89.44611° W	70	10.0	False	True	False
CSA1	Johnson Bayou	30.08750° N, 89.31083° W	200	–58.2	True	True	True
CSA1	Shell Point	30.02306° N, 89.35194° W	47	–10.8	True	True	True
CSA1	E. Karako	30.02000° N, 89.23389° W	764	–7.9	True	True	True
CSA1	W. Karako	30.01190° N, 89.28306° W	764	–8.4	True	True	True
CSA1	Grand Banks	30.14778° N, 89.36028° W	100	0.9	False	True	False
CSA2	Snake	29.63397° N, 89.56423° W	506	–5.5	True	True	True
CSA2	Jessie	29.63502° N, 89.61820° W	59	–4.2	True	True	True
CSA2	N. Lonesome	29.62153° N, 89.56430° W	896	1.8	False	True	False
CSA2	N. Black Bay	29.61278° N, 89.50900° W	157	10.0	False	True	False
CSA2	Bayou Lost	29.60080° N, 89.61727° W	118	9.4	False	True	False
CSA2	Lonesome	29.61355° N, 89.55680° W	273	–4.6	True	True	True
CSA2	Black Bay	29.59685° N, 89.56500° W	301	8.8	False	True	False
CSA2	W. Bay Crabe	29.56522° N, 89.58660° W	501	–12.1	True	True	True
CSA2	Stone	29.57612° N, 89.54145° W	461	6.8	False	True	False
CSA2	S. Black Bay	29.56033° N, 89.53443° W	145	7.5	False	True	False
CSA2	Elephant Pass	29.54125° N, 89.56410° W	339	10.0	False	True	False
CSA2	Curfew	29.53685° N, 89.53348° W	425	7.8	False	True	False
CSA2	N. California Bay	29.52700° N, 89.54102° W	109	7.4	False	True	False
CSA2	California Bay	29.51112° N, 89.56667° W	7	2.9	False	True	False
CSA2	Telegraph	29.51600° N, 89.53232° W	127	9.5	False	True	False
CSA2	Sunrise Point	29.49475° N, 89.56655° W	174	4.5	False	True	False
CSA2	Bay Long	29.50833° N, 89.59167° W	572	10.0	False	True	False
CSA2	E. Pelican	29.49952° N, 89.52645° W	782	6.5	False	True	False
CSA2	Mangrove Point	29.47900° N, 89.54032° W	937	10.0	False	True	False
CSA2	W. Pelican	29.50695° N, 89.54583° W	293	8.2	False	True	False
CSA2	Bay Crabe	29.55697° N, 89.57682° W	659	9.3	False	True	False
CSA2	E. Bay Crabe	29.55665° N, 89.56982° W	122	10.0	False	True	False
CSA2	E. Bay Gardene	29.58167° N, 89.62195° W	28	6.5	False	False	False
CSA2	Bay Gardene	29.58272° N, 89.64577° W	69	9.2	False	False	False
CSA2	Battledore Reef	29.46412° N, 89.42875° W	1,419	10.0	False	True	False
CSA2	Horseshoe Reef	29.60261° N, 89.49386° W	158	–5.1	True	True	True
CSA2	S. Lake Fortuna	29.65020° N, 89.50435° W	2,144	4.0	False	True	False
CSA2	Wreck	29.56472° N, 89.48306° W	2,276	4.3	False	True	False
CSA2	E. Stone	29.58306° N, 89.51472° W	105	9.0	False	True	False
CSA2	N. Lake Fortuna	29.67940° N, 89.48472° W	2,144	6.6	False	True	False
CSA3	Lower Hackberry	29.38822° N, 90.05253° W	5	–31.1	True	True	True
CSA3	Middle Hackberry	29.40169° N, 90.02917° W	5	–109.3	True	True	True
CSA3	Upper Hackberry	29.42164° N, 90.03069° W	5	–13.3	True	True	True
CSA3	2004 N. Hackberry Shell Plant	29.41722° N, 90.03250° W	10	–10.4	True	True	True
CSA3	2004 S. Hackberry Shell Plant	29.38833° N, 90.05250° W	25	–5.3	True	True	True
CSA3	2004 Barataria Bay Cultch Plant	29.33028° N, 89.94000° W	40	9.1	False	True	False
CSA3	2008 Cultch Plant	29.42528° N, 90.01528° W	50	–25.4	True	True	True
CSA3	2012 Cultch Plant	29.41525° N, 90.05232° W	200	–9.7	True	False	False
CSA4	Lake Felicity	29.31500° N, 90.44444° W	40	1.7	False	False	False
CSA4	2004 Lake Chien	29.33417° N, 90.44722° W	15	–13.7	True	False	False
CSA4	2009 Lake Chien	29.33472° N, 90.43778° W	22	–3.5	True	False	False
CSA5	2009 SL Cultch Plant	29.24583° N, 90.91000° W	156	–38.4	True	True	True

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TABLE 1.

continued

Region name	Station name	Coordinates	Reef Size	Cultch loss (%)	Fishable	Open	Simulated
CSA5	Buckskin Bayou Junop	29.26556° N, 91.02917° W	17	–63.4	True	False	False
CSA5	Grand Pass	29.25806° N, 90.93333° W	322	–565.9	True	True	True
CSA5	Junop Bayou DeWest	29.21056° N, 91.05167° W	33	7.0	False	False	False
CSA5	Lake Mechant	29.31111° N, 90.94750° W	30	9.3	False	True	False
CSA5	Mid 94 Shell Plant	29.23806° N, 90.92611° W	187	–33.3	True	True	True
CSA5	Mid Bay Junop	29.24556° N, 91.05250° W	73	–15.8	True	False	False
CSA5	Mid Sister Lake	29.23333° N, 90.92750° W	270	–266.6	True	True	True
CSA5	N. 94 Shell Plant	29.25083° N, 90.92528° W	139	–208.6	True	True	True
CSA5	N. 95 Shell Plant	29.25694° N, 90.93611° W	167	–113.8	True	True	True
CSA5	Old Camp	29.21611° N, 90.94444° W	220	9.7	False	True	False
CSA5	Rat Bayou	29.21861° N, 91.04806° W	33	1.8	False	False	False
CSA5	S. 94 Shell Plant	29.22056° N, 90.90889° W	117	10.0	False	True	False
CSA5	SL 2004 Cultch Plant	29.22361° N, 90.91500° W	97	–66.9	True	True	True
CSA5	Walkers Point	29.24750° N, 90.93806° W	119	–53.9	True	True	True
CSA6	South Point	29.48333° N, 91.75750° W	75	10.0	False	True	False
CSA6	Big Charles	29.61433° N, 91.98621° W	15	10.0	False	True	False
CSA6	Indian Point	29.68633° N, 91.90183° W	50	9.1	False	True	False
CSA6	Dry Reef	29.62500° N, 92.00833° W	20	8.8	False	True	False
CSA6	Bayou Blanc	29.51333° N, 91.75833° W	15	10.0	False	True	False
CSA6	Sally Shoals	29.65444° N, 91.87111° W	5	10.0	False	True	False
CSA6	Rabbit	29.51106° N, 91.59756° W	15	10.0	False	True	False
CSA6	Lighthouse Point	29.57944° N, 92.03444° W	15	9.4	False	True	False
CSA6	Middle Reef	29.45281° N, 91.72397° W	20	10.0	False	True	False
CSA6	N. Reef	29.47892° N, 91.80803° W	5	10.0	False	True	False
CSA7	Sabine Lake 1	29.77917° N, 93.90778° W	260	–149.2	True	False	False
CSA7	Sabine Lake 2	29.78611° N, 93.90444° W	260	–127.2	True	False	False
CSA7	Sabine Lake 3	29.78500° N, 93.91806° W	260	–165.5	True	False	False
CSA7	Sabine Lake 4	29.79917° N, 93.91667° W	260	–146.1	True	False	False
CSA7	Sabine Lake 5	29.82333° N, 93.91972° W	219	–145.8	True	False	False
CSA7	Sabine Lake 6	29.81000° N, 93.88556° W	219	–150.9	True	False	False
CSA7	Big Washout	29.85667° N, 93.33383° W	474	10.0	False	False	False
CSA7	Little Washout	29.85028° N, 93.34083° W	474	10.0	False	False	False
CSA7	Mid Lake	29.85417° N, 93.32889° W	474	10.0	False	False	False
CSA7	Southeast Rabbit	29.84306° N, 93.37556° W	560	–140.2	True	True	True
CSA7	Northeast Rabbit	29.85694° N, 93.38222° W	1,134	3.2	False	True	False
CSA7	W. Cove Transplant	29.84780° N, 93.36972° W	560	–59.6	True	True	True
CSA7	W. Rabbit	29.84694° N, 93.39500° W	1,134	6.2	False	True	False

Negative values for cultch loss indicate a shell gain. Reefs showing a shell gain in initial simulations were deemed fishable (indicted by True in the Fishable column). Reefs open for fishing are indicated by True in the Open column. Reefs both fishable and open were simulated to determine sustainable catch, as indicated by True in the Simulated column.

Of these, only the 2012 cultch plant is planned to be closed to fishing (Table 1). The combined TAC for CSA 3 is estimated to be 1,085 sacks of sack oysters and 1,349 sacks of seed (Table 3).

None of the former CSA 4 stations (Table 1) are included in the calculation of TAC because they are planned to be closed to fishing. Fishable and open stations from CSA 5E and CSA 5W, used in the calculation of the TAC, include the 2009 Sister Lake shell plant, Mid Sister Lake, the N 94 and 95 shell plants, the Sister Lake 2004 cultch plant, and Walker's Point (Table 3, Fig. 6). The combined TAC for CSA 5 is 25,573 sacks of sack oysters and 10,413 sacks of seed (Table 3).

None of the stations in CSA 6 were considered fishable (Fig. 7). Low densities or no oysters on the reefs there resulted in negative shell budgets; that is, shell loss is expected to exceed shell gain through natural mortality of living oysters. The Sabine Lake stations (CSA 7) showed a shell gain without fishing (Fig. 8, Table 1); however, they are not planned to be open to fishing (Table 1) and thus are not included in the estimation of the TAC. Only Southeast Rabbit Island and the West Cove transplant sites (Fig. 8, Table 1) were used in the determination of TAC for CSA 7. The CSA 7 TAC is 30,070 sacks of sack oysters. As a general industry practice, no fishing of seed oysters occurs in CSA 7 (Table 2).

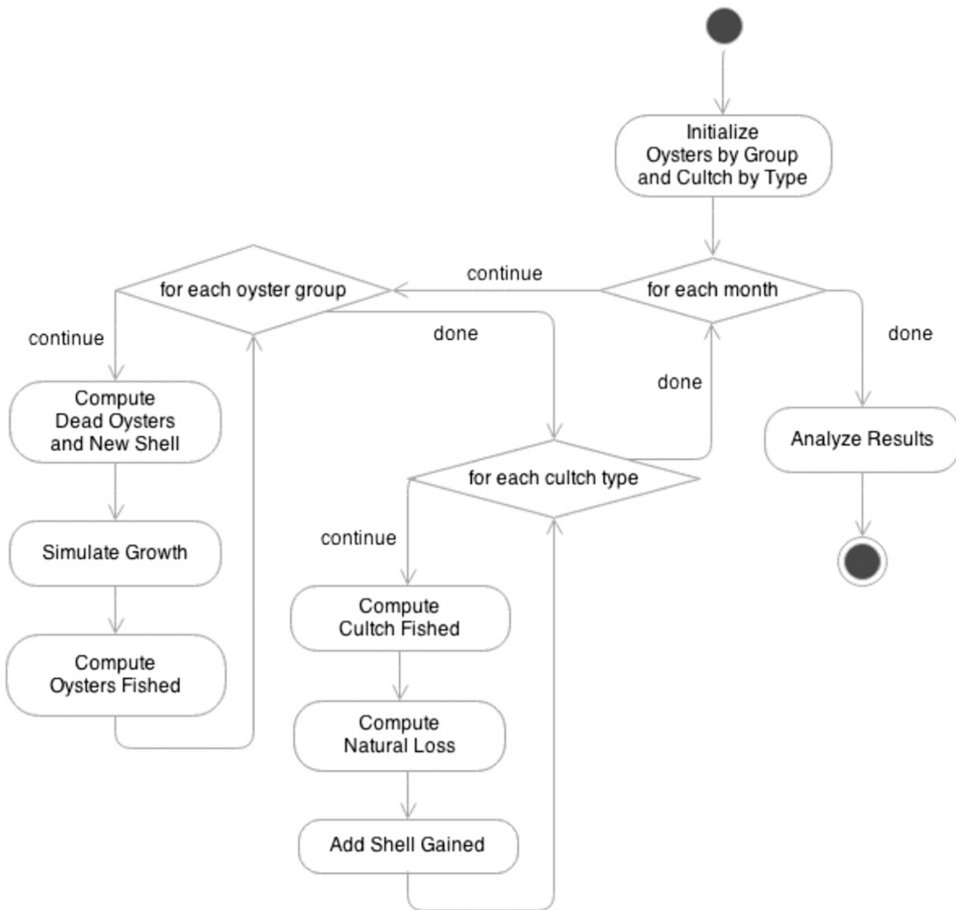

Figure 2. Schematic of major oyster model processes.

Of the 91 reefs considered herein, 37 (40.6%) were deemed fishable (Table 1). In total, the 2013 statewide estimated combined TAC is 76,763 sacks of sack oysters and 19,642 sacks of seed. This compares with a 2012 estimated *harvest* of 64,897 sacks of sack oysters and 13,014 sacks of seed from the public oyster areas of the state. Thus, the predicted sustainable catch for the 2013 season is comparable with and greater than the actual harvest for 2012. Note that the statewide estimated stock abundance in 2012 is 1,461,706 sack equivalents of sack (market) oysters and 1,006,948 sack equivalents of seed oysters (Louisiana Department of Wildlife & Fisheries 2012); the statewide stock abundance estimate in 2013 is 328,708 sacks of market oysters and 1,302,052 sacks of seed oysters (Louisiana Department of Wildlife & Fisheries 2013). This represents a 29.3% increase in seed oysters and 77.5% decrease in sack oysters in 2013 compared with 2012.

DISCUSSION

Fishable Reefs

Some reefs were projected to lose shell during 2013 even if closed to fishing. These reefs have an imbalance between anticipated shell input from natural mortality and loss through taphonomy. In most cases, low abundance of living oysters is the primary source of this imbalance. However, a suite of reefs was projected to see a positive shell balance during 2013. These were defined as fishable reefs. An evaluation of the characteristics of fishable reefs is instructive. Of the 37 fishable reefs, 7 are recent (since 2004) cultch plants; 6 are in Sabine Lake, where fishing is prohibited; 4 are in Lake Calcasieu, where only limited harvest (10 sacks per day) is allowed; and 6 are in Hackberry Bay, which was subject to a special management experiment in 2012 (Table 1). Thus, only 14 reefs exposed to standard fishing practices were characterized by a projected shell gain if were fishing not to occur on them in 2013.

The Hackberry Bay Public Oyster Seed Reservation was used as a test site for an initial model application in 2012. Sustainable harvest estimates from Hackberry Bay generated from the 2012 stock assessment data were used to set a TAC of 7,000 sacks of seed and 4,700 sacks of sack oysters. Harvest was monitored closely by Louisiana Department of Wildlife & Fisheries biologists, and the season closed when the estimated harvest appeared to reach the projected TAC. Actual harvest as a percent of the TAC was 71.9% for seed and 109.6% for sack oysters (Soniat 2013). The 2012 experiment was successful. Fishing in Hackberry Bay in 2012 was limited per model predictions; as a consequence, reef quality was apparently maintained, and the reefs encompassed by the experiment were deemed fishable again for the 2013 season (Table 1).

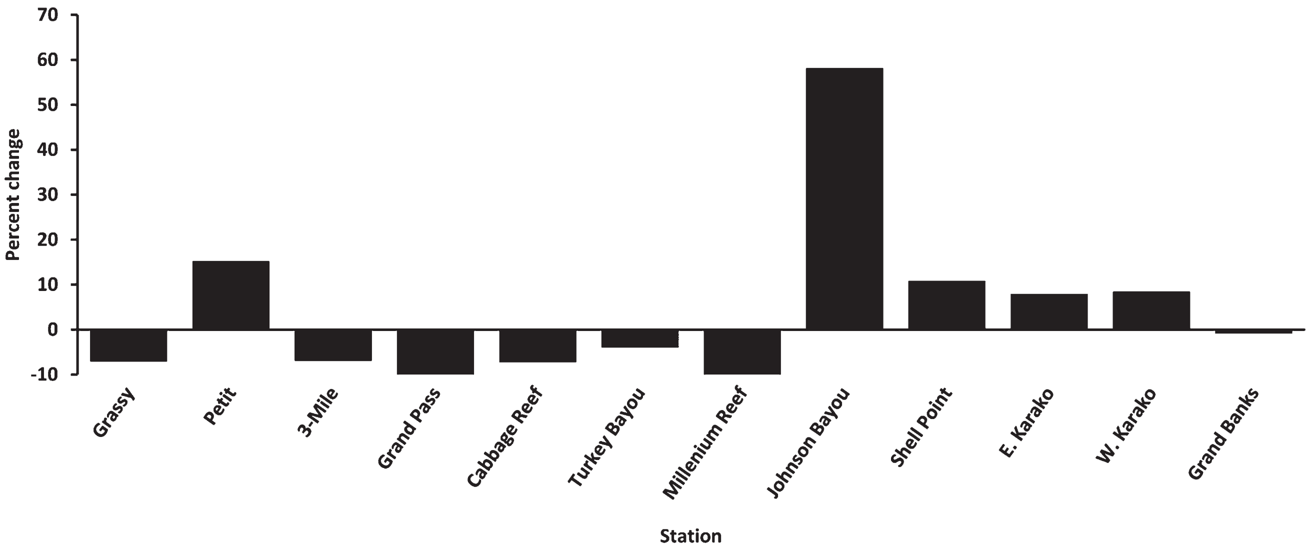

Figure 3. Initial simulations to determine percent change in cultch mass without fishing (CSA 1N). Positive change indicates that the reef or shell plant is fishable.

In the following sections, we discuss application of the shell budget model to reef closures, TAC, cultch planting and restoration, and resource sustainability and product certification in Louisiana. We conclude with a discussion of the broader significance of the no-net-shell-loss reference point.

Reef Closures

Area closures and time restrictions are common tools used in fisheries management and conservation (FAO 1997, Horwood et al. 1998, Santopietro et al. 2009). Depending on the species and application, these management measures are used to maintain critical spawning stocks, to protect critical life stages, and to preserve habitat (Hart 2001, Kasperski & Wieland 2010, Munroe et al. 2013a). Until now, closure rules applied to oyster reefs have relied on the comparison of stock abundance with reference points that expressed a desired stock abundance based, for example, on surplus production (e.g., Klinck et al. 2001) or time–series of population performance (e.g., Powell et al. 2009b). A no-net-shell-loss reference point was identified by Mann and Powell (2007) and Powell et al. (2012) as important to ensure sustainability of oyster reef habitat over the long term and was explored further by Soniat et al. (2012). We suggest that the no-net-shell-loss reference point provides a rational basis for determining reef closures. Simulations reveal conditions under which no fishing is possible, using cultch sustainability as the desired end point (Table 1). Prudent management dictates that reefs that do not accrete shell in model simulations without fishing should not be subjected to fishing in actual practice, because all these reefs need carbonate production for the year added to the shell bed.

We note that very little information is available that would permit the establishment of a reference point goal based on cultch density. The current estimates of TAC are based on

TABLE 2.

Fishing effort by month for sack and seed oysters.

CSA	Effort type	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
CSA 1N	Sack effort	0.00	0.20	0.35	0.25	0.10	0.05	0.05	0.00	0.00	0.00	0.00	0.00
	Seed effort	0.00	0.70	0.10	0.00	0.00	0.10	0.10	0.00	0.00	0.00	0.00	0.00
CSA 1S	Sack effort	0.00	0.20	0.30	0.20	0.10	0.05	0.05	0.10	0.00	0.00	0.00	0.00
	Seed effort	0.00	0.70	0.10	0.00	0.00	0.10	0.10	0.00	0.00	0.00	0.00	0.00
CSA 3	Sack effort	0.00	0.50	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Seed effort	0.00	0.70	0.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CSA 5E	Sack effort	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Seed effort	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CSA 5W	Sack effort	0.00	0.50	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Seed effort	0.00	0.70	0.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CSA 6	Sack effort	0.00	0.10	0.20	0.20	0.20	0.10	0.10	0.10	0.00	0.00	0.00	0.00
	Seed effort	0.60	0.10	0.05	0.05	0.05	0.05	0.05	0.05	0.00	0.00	0.00	0.00
CSA 7	Sack effort	0.00	0.00	0.20	0.35	0.05	0.10	0.15	0.15	0.00	0.00	0.00	0.00
	Seed effort	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Numbers are percent effort expended per month as a portion of the overall effort. Data are anticipated fishing effort based on the previous (2012) season.

TABLE 3.

Simulated sustainable catch (sacks) for reefs both fishable and open.

CSA	New CSA	Fishing mode	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Total
1	1N	Sack	0	0	2,405	3,741	2,205	830	382	373	0	0	0	0	9,936
1	1N	Seed	0	0	4,550	628	0	0	645	642	0	0	0	0	6,464
2	1S	Sack	0	0	6,122	3,705	0	126	45	38	63	0	0	0	10,098
2	1S	Seed	0	0	1,101	155	0	0	160	0	0	0	0	0	1,416
3	3	Sack	0	0	561	524	0	0	0	0	0	0	0	0	1,085
3	3	Seed	0	0	968	381	0	0	0	0	0	0	0	0	1,349
4	5E	Sack	Not fished*												
4	5E	Seed													
5	5W	Sack	0	0	13,887	11,686	0	0	0	0	0	0	0	0	25,573
5	5W	Seed	0	0	7,529	2,884	0	0	0	0	0	0	0	0	10,413
6	6	Sack	Not fishable†												
6	6	Seed													
7	7	Sack	0	0	0	6,844	11,042	1,398	2,843	4,075	3,868	0	0	0	30,070
7	7	Seed	0	0	0	0	0	0	0	0	0	0	0	0	0
Sack total															76,763
Seed total															19,642

* A region closed to fishing (CSA 4 or CSA 5E). † None of the open reefs in the region support a sustainable harvest (CSA 6).

cultch stasis, not enhancements to desired end points (Mann et al. 2009b). Because sustainable fishing estimates are based on no net loss of cultch, a poor-quality reef before fishing remains a poor-quality reef after fishing. To improve reef quality, fishing can be diminished to produce a shell gain on those reefs that do not meet a predetermined standard of cultch density. Thus, the current reference point, although important in setting a minimal goal for management, does not invoke the option of obtaining a desired cultch density. Such a reference point would permit development of a rebuilding plan to rehabilitate reefs where cultch density is inadequate, regardless of the 1-y status of the shell budget. Powell et al. (2012) examined the population dynamics necessary to engender reef accretion, and Mann et al. (2009a) and Southworth et al. (2010) reviewed the cultch status for a number of reefs in the Chesapeake Bay. DeAlteris (1988) inferred accretion rates for 1 reef in the James River of the Chesapeake Bay, and Powell et al. (2012) suggested that reef accretion was unlikely under typical population dynamics observed at this time. Recent observations of the expansion of *Crassostrea gigas* in the Wadden Sea, on the other hand, show the capability of this genus to foster reef expansion under favorable conditions (Troost 2010). Nevertheless, details of the biological process of recruitment as a function of shell availability and broodstock remain unknown (Ritchie & Menzel 1969, Hidu et al. 1978, Powell et al. 2009a, Troost et al. 2009), and such information would be required to establish optimal shell resource criteria. Thus, we propose a conservative option that merely seeks to limit a further decline of shell stock beyond that already observed

Total Allowable Catch

By fishing only those reefs that potentially accrete shell (Table 1), and adjusting fishing rates to match fishing practices

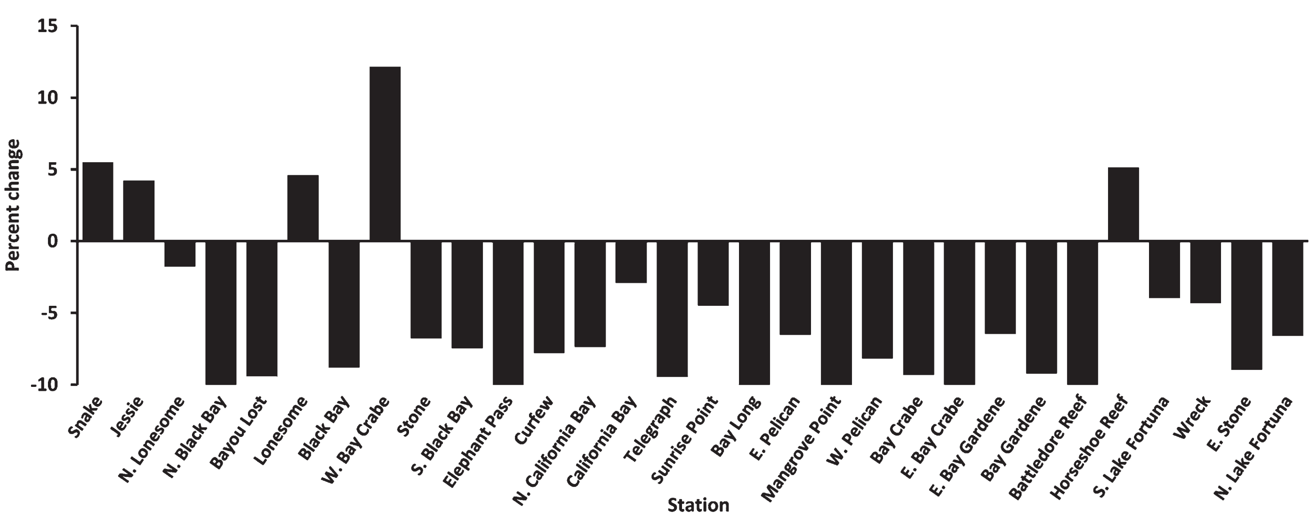

Figure 4. Initial simulations to determine percent change in cultch mass without fishing (CSA 1S). Positive change indicates that the reef or shell plant is fishable.

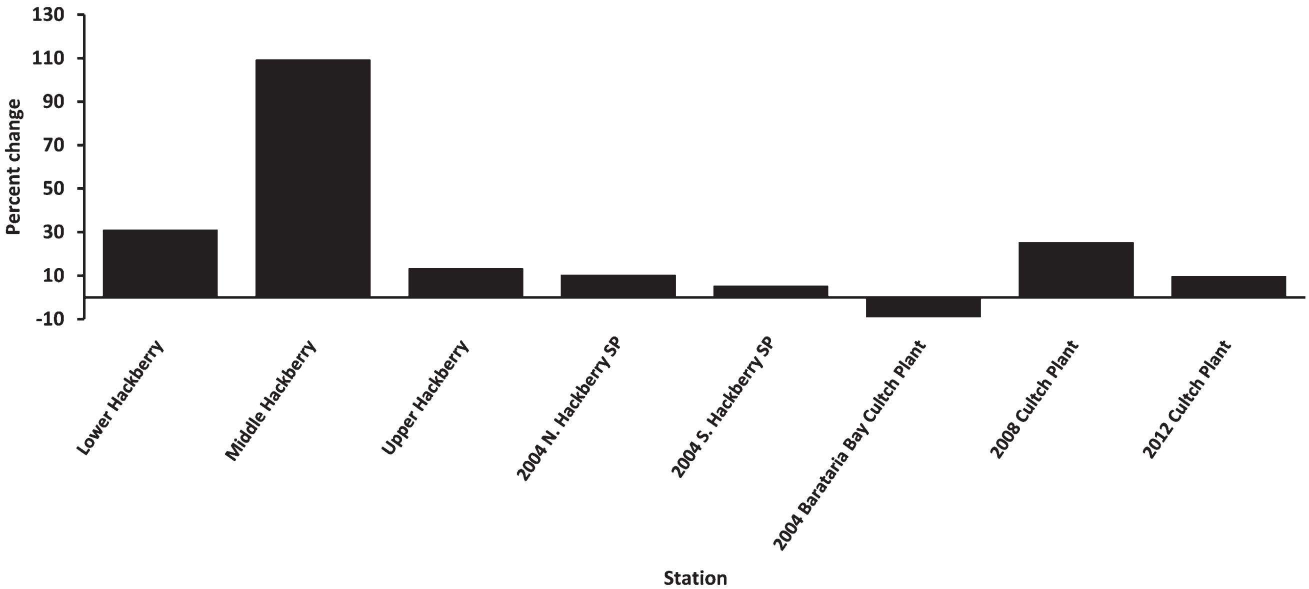

Figure 5. Initial simulations to determine percent change in cultch mass without fishing (CSA 3). Positive change indicates that the reef or shell plant (SP) is fishable.

(Table 2), within a constraint of shell stasis, we generate TAC. The approach can be used to generate TAC for a seed fishery, a sack fishery, or, as is the routine approach for our study region, a combination thereof. This combined TAC for seed and market-size oysters for the upcoming season, estimated under the no-net-shell-loss reference point for the public grounds, is itemized in Table 3. Imposing TAC *a priori,* together with monitoring of catch on the public grounds, can be used to curtail fishing effort when TAC is approached, and thereby minimize the chance of overfishing as defined under the reference point goal.

Cultch Planting and Reef Restoration

Since 1917, the state of Louisiana has planted approximately 1.39 million m^3 of cultch on the public grounds (Louisiana Department of Wildlife & Fisheries, unpubl. data). It is unlikely that the current level of fishing on the public grounds is sustain-

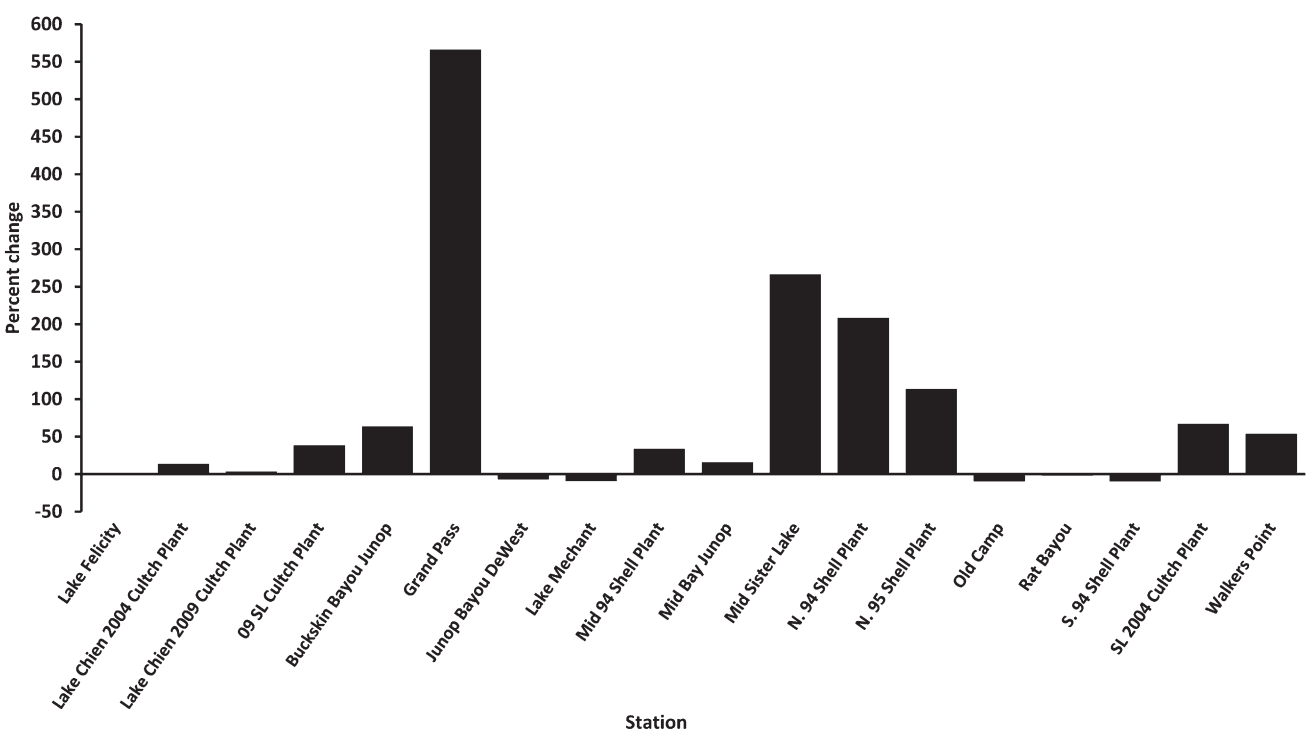

Figure 6. Initial simulations to determine percent change in cultch mass without fishing (CSA 5). Positive change indicates that the reef or shell plant is fishable. SL, Sister Lake.

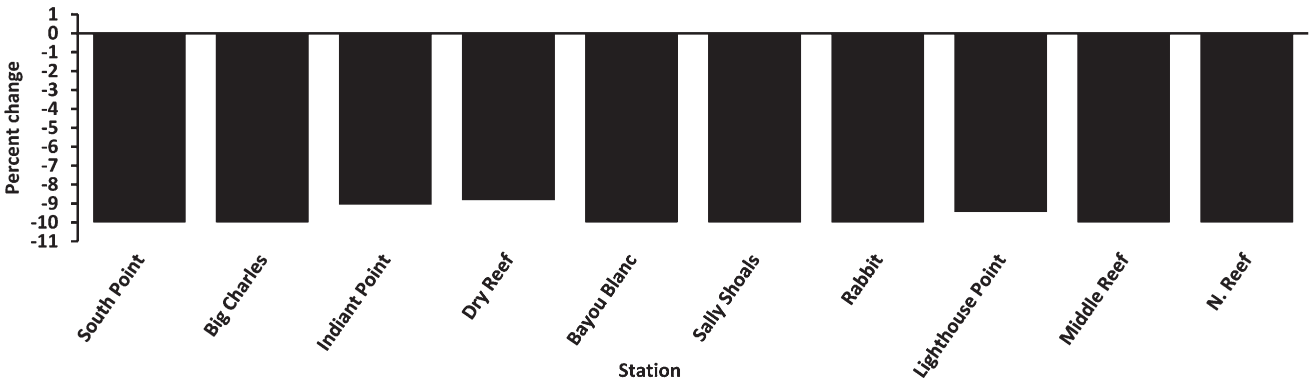

Figure 7. Initial simulations to determine percent change in cultch mass without fishing (CSA 6). Positive change indicates that the reef or shell plant is fishable. None of the stations in CSA 6 show a gain in cultch mass.

able without substantial and continuous cultch additions. The large number of reefs failing to meet even our conservative definition of fishable is demonstrative (Table 1). The industry depends on seed oysters taken from the public grounds and transferred to private leases, where they grow and are subsequently harvested. (Market-size oysters are sometimes harvested from public grounds and marketed directly.) The fishing of seed oysters is especially detrimental to the shell budget in part because seed are not easily or routinely culled from cultch (Soniat et al. 2012; see also Harding et al. 2010), thus the living population of adults must provide a large number of deaths to resupply the reef with the carbonate removed by the seed fishery. In contrast, the sack fishery removes little carbonate from the shell bed; rather, it limits the rate of carbonate addition that, although nontrivial in its implications, is less pernicious than the removal of carbonate already added to the shell bed by the seed fishery. Munroe et al. (2013a) expressed additional concerns about the deleterious influence of a seed fishery on oyster population dynamics.

The shell budget model can be used to balance shell budgets and to determine locations for cultch enhancement. Addition of cultch is used either to enhance recruitment or to improve or expand the reef footprint (e.g., Nestlerode et al. 2007, Powers et al. 2009, Dumbauld et al. 2011). Although such projects are manifold and of highly varying success, a core requirement of management should be optimizing production on extant reefs. Assuming that the population dynamics permits an evaluation of potential surplus production in the occupying population, the shell budget can be used as a mechanism to identify locations where addition of cultch would have value and, as important, permit the retention of gains made through that activity. Cultch additions are, in the context of the current model, shell subsidies that permit an increase in TAC under the no-net-shell-loss reference point, but also a mechanism to lock in gains during habitat restoration. Moreover, as an alternative to costly shell subsidies, the current modeling exercise suggests how public reefs can be managed without a shell subsidy. An economic analysis of these alternatives, including a scaled combination of both, would be informative.

Resource Sustainability and Product Certification

The FAO code of conduct for responsible fisheries (FAO 1997) establishes principles and criteria for the elaboration and implementation of policies for the conservation, management, and development of fisheries worldwide. Prominent among these principles is the concept of resource sustainability, and that management measures be commensurate with the productive capacity of the resource. With the model applied herein, and previously described in mathematical detail (Soniat et al. 2012),

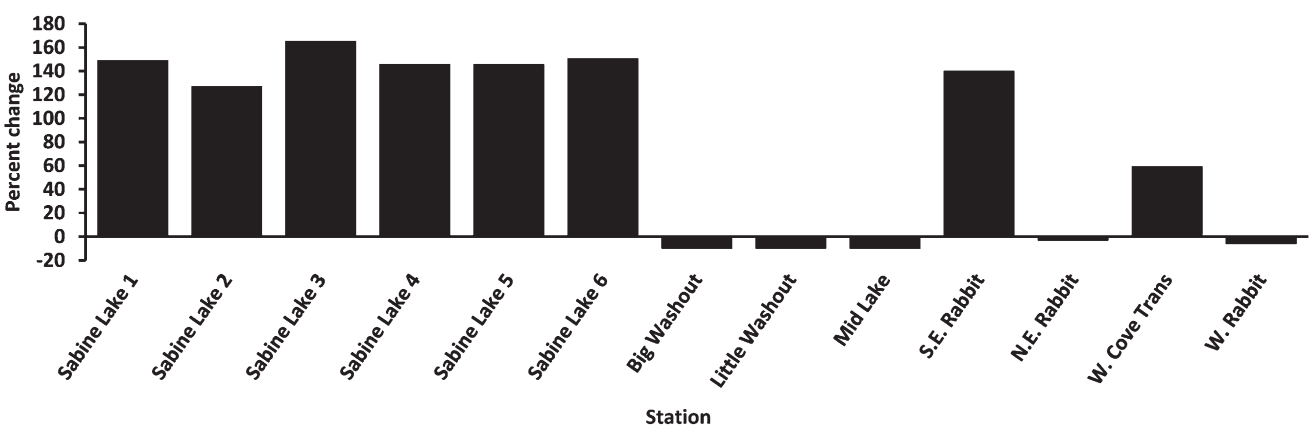

Figure 8. Initial simulations to determine percent change in cultch mass without fishing (CSA 7). Positive change indicates that the reef or shell plant is fishable.

it is now possible to estimate sustainable yields for eastern oysters and implement focused management practices to maintain productive capacity.

Resource sustainability is a key requirement for product certification, which is becoming an increasingly significant feature of domestic and international market share (Washington & Ababouch 2011). To date, through a peer-review process only the Delaware Bay oyster fishery has been found to be sustainable (Haskin Shellfish Research Laboratory 2012). The purchasing policies of most large retailers are typically guided by the requirements of ecolabels that certify that sustainable practices and procedures are implemented and followed (Sainsbury 2010). Sustainability has a number of definitions (e.g., Flaaten 1991, Applegate et al. 1998, Zabel et al. 2003). The concept of a sustainable stock, under federal guidelines articulated by the Magnuson-Stevens Fishery Conservation and Management Act, is expressed in the concepts of ''overfishing'' and an ''overfished'' stock. Under federal guidelines, the term ''overfishing'' represents a comparison of the current fishing mortality rate relative to the rate permitted at maximum sustainable yield (*Fmsy*). The term ''overfished'' refers to the biomass of the stock relative to the biomass at maximum sustainable yield (*Bmsy*). These concepts do not depend on the history of the stock or the fishery prior to the year of the assessment; rather, the concepts are yearly designations that express the conditions that exist in the assessment year (or the year of most recent survey data).

Oyster populations are difficult to fit within federal guidelines for a number of reasons. The vast majority of populations are impacted significantly by disease. Disease limits population surplus production from which maximum sustainable yield guidelines are directly defined or indirectly inferred (e.g., Maunder 2003, Haltuch et al. 2008, Maunder 2012, Punt & Szuwalski 2012). Populations with enhanced adult mortality resulting from disease have not been and likely cannot be addressed by standard *Bmsy* and *Fmsy* criteria (Powell et al. 2012). Powell et al. (2009b) report the only estimate of a maximum sustainable yield-type stock reference point for oysters and note that, although an abundance goal could be estimated akin to *Bmsy*, the partner fishing mortality rate resulting in maximum sustainable yield was poorly constrained. The Haskin Shellfish Research Laboratory (2012) argued, based on this analysis, that stock stability was the most important objective, and that stability of the market-size population was the most desirable approach because, even with aperiodic disease epizootics, this component of the population was inherently more stable temporally, and is also more important reproductively and as the principal carbonate producer. Thus, no-net-change reference points offer the best current-day option to manage oyster stocks sustainably.

Furthermore, a no-net-change reference point for the stock itself inherently invokes the important concept of surplus production, because no net change in market-size abundance requires that the fishery be limited by the number of submarket animals growing to market size debited by natural mortality (e.g., Klinck et al. 2001). This is a useful measure of surplus production because most production occurs in the growing animals rather than the larger adults. In this context, ''overfishing'' represents a state wherein the market-size component of the stock declines throughout the year. The volatility imposed by disease means that oyster populations will wax and wane over time, as climate cycles influence disease intensity and hence adult abundance (e.g., Soniat et al. 2006, Soniat et al. 2009, Bushek et al. 2012). Thus, evidence of an overfished stock would be a decline in market-size abundance from 1 epizootic cycle to the next, as recovery of abundance during the nadir cycle would be limited by excessive fishery removals. That is, stock sustainability has a multiyear dimensionality imposed by the highly unstable natural mortality rate, but with an underlying premise that no net change can be expressed over a multiannual period established by the periodicity of disease.

Applying the no-net-change approach to the shell bed opens up a new long-term dimensionality. Shell loss rates are inherently multiyear signals. Half-lives tend to be on the order of half-decadal to decadal (e.g., Powell et al. 2006). These time frames are as long, if not longer, than the cycles controlling adult mortality (e.g., Soniat et al. 2006, Soniat et al. 2009, Bushek et al. 2012). Furthermore, stability of the shell bed cannot be achieved without a substantive adult population producing through natural—not fishing—mortality sufficient carbonate to compensate for the loss, as, in most oyster reefs, the volume of exposed carbonate as cultch far exceeds the volume of living carbonate housed in the market-size population (Mann et al. 2009a, Powell et al. 2012). Thus a no-net-change reference point applied to cultch inherently encompasses a sustainability requirement for the living population. Last, the shell bed is inherently the most stable component of the reef (Powell et al. 2008). As a consequence, management for sustainable cultch inherently requires long-term sustainability of the market-size population without requiring precision in the year-to-year management of the market-size stock.

Shell Budget Versus Equilibrium Yield Models

Equilibrium models presuppose a carrying capacity (*K*)—a relatively constant maximum number of organisms supportable by a given environment over a multigenerational time frame. Also implicit in equilibrium models is the assumption that the habitat itself is relatively constant. These assumptions, although routinely violated to some degree (e.g., Steele & Henderson 1984, Mangel & Tier 1994, Moilanen 2000), provide the basis for most biological reference points (e.g., Powell et al. 2009b, Maunder 2012, Rothschild et al. 2012). The equilibrium assumption is, however, *severely* violated by oyster populations, which show great interannual variations in numbers and biomass, and whose functional reef habitat contracts or expands with annual mean shifts in salinity (Soniat et al. 2013) for two reasons. First, freshets introduce aperiodic, but severe, mortalities on the upestuary portion of the oyster's range (La Peyre et al. 2009, Pollack et al. 2011, Munroe et al. 2013b). Second, disease epizootics impose large interannual variations in adult mortality (Powell et al. 2008, Mann et al. 2009a, Bushek et al. 2012). The shell budget model described and applied herein is an exemplar of a nonequilibrium yield model; it does not assume a relatively constant equilibrium yield of oyster numbers or biomass, but presupposes shell stasis as the basis of sustainable oyster production. An evaluation of a 54-y time series of oyster production of Delaware Bay oysters in New Jersey waters (Powell et al. 2008, Powell et al. 2009a, Powell et al. 2009b) identifies oyster populations as characterized by regime shifts between persistent periods of high and low abundance. A time series of stock abundance of Louisiana oysters on public oyster grounds, although of shorter duration, shows a similar cycle—in this case, abundance from 1992 to 2001, bracketed by scarcity from 1982 to 1991 and 2002 to 2013 (Louisiana Department of Wildlife & Fisheries 2013). Similar variations are recorded in the Chesapeake Bay (Mann et al. 2009b, Southworth et al. 2010).

An insistence on maintaining equilibrium yields of oyster numbers or biomass amidst extreme stock variability is a recipe for managerial failure. Alternatively, the shell budget approach defines sustainability as shell stasis and determines sustainable yield based on the ability of the measured stock to maintain reef habitat quality. The determination of sustainable yield by shell budget modeling should be broadly applicable to the eastern oyster across its entire range. Furthermore, the approach facilitates the imposition of successful rebuilding plans because stock rebuilding in oyster populations is principally accomplished by the addition of carbonate. Expecting that added carbonate be maintained as a long-term resource requires that the management of the living population encompasses the continuing needs for additional production of carbonate and its addition to the reef through the mortality principally of the market-size individuals.

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