

Metapopulation dynamics guide marine reserve design: importance of connectivity, demographics, and stock enhancement

B. J. PUCKETT^{1,†} AND D. B. EGGLESTON

*Department of Marine, Earth & Atmospheric Sciences, Center for Marine Sciences and Technology,
North Carolina State University, Morehead City, North Carolina 28557 USA*

Citation: Puckett, B. J., and D. B. Eggleston. 2016. Metapopulation dynamics guide marine reserve design: importance of connectivity, demographics, and stock enhancement. *Ecosphere* 7(6):e01322. 10.1002/ecs2.1322

Abstract. The concepts of metapopulation persistence and source-sink dynamics are central and often untested tenets of marine reserve networks. Effective application of these concepts to marine reserves is limited by data on demographic rates within reserves and larval connectivity among reserves. Using a network of reserves established to restore eastern oyster (*Crassostrea virginica*) in Pamlico Sound, North Carolina, USA as our model system, we integrated empirically based demographic rates and regional hydrodynamic-based connectivity estimates within a metapopulation model to (1) evaluate the potential for the reserve network to function as a self-persistent oyster metapopulation, (2) determine the relative importance of demographics vs. connectivity on reserve source-sink dynamics, (3) assess the efficacy of stock enhancement in promoting metapopulation persistence, and (4) evaluate whether application of a Few Large or Several Small reserves—a modification of the Single Large or Several Small concept—promoted greater metapopulation retention of larvae within the reserve network (i.e., local larval retention within reserves + larval connectivity among reserves). The reserve network failed to function as a self-persistent metapopulation, despite exceptional demographic rates within reserves. When considering only larval supply from reserves, local retention and connectivity were insufficient to provide annual replacement (≥ 0.25 recruits per adult). Accordingly, reserves contributed to the metapopulation primarily via production, not dispersal, of larvae and reserve source-sink dynamics were influenced more by demographics within reserves, particularly adult growth and survival, than larval connectivity among reserves. Addressing recruitment limitation via stock enhancement was not effective at augmenting projected metapopulation declines. Several small reserves initially promoted greater metapopulation retention of larvae than a few large reserves, however, as the number or area of reserves increased, metapopulation retention was equivalent among designs, suggesting that Few Large *and* Several Small reserves may be the best network design. Marine reserves can be an effective restoration tool for improving demographic rates within reserve boundaries, but designation of multiple reserves does not guarantee a functional reserve network metapopulation. Both demographics and larval connectivity are important considerations to successful application of metapopulation concepts to the design of reserve networks.

Key words: connectivity; *Crassostrea virginica*; demographics; marine reserves; metapopulation dynamics; Pamlico Sound; persistence; restoration; Single Large or Several Small; stock enhancement.

Received 13 March 2015; revised 8 December 2015; accepted 11 December 2015. Corresponding Editor: D. P. C. Peters.

Copyright: © 2016 Puckett and Eggleston. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

¹ Present address: North Carolina National Estuarine Research Reserve, 101 Pivers Island Road, Beaufort, North Carolina 28516 USA.

[†] **E-mail:** brandon.puckett@ncdenr.gov

INTRODUCTION

A metapopulation is an assemblage of subpopulations inhabiting discrete patches connected by dispersal (Levins 1969, Hanski and Gilpin 1991, Hanski 1998, Kritzer and Sale 2004). In marine systems, metapopulations persist when the interplay between subpopulation demographics and connectivity, typically the exchange of larvae among subpopulations, ensures each adult is replaced by at least one larval recruit that survives to reproduce (Hastings and Botsford 2006, Gaines et al. 2010). An extension of the metapopulation concept is the notion of source-sink dynamics. "Source" and "sink" subpopulations contribute positively and negatively to metapopulation persistence, respectively, based on their ability to produce and disperse larvae within the metapopulation (Pulliam 1988, Diffendorfer 1998, Figueira and Crowder 2006, Runge et al. 2006). Metapopulation persistence and source-sink dynamics are central and often untested tenets of many management strategies, including no-take marine reserves. Multiple marine reserves can function as networks (i.e., metapopulations), yet effective application of these concepts to the design of marine reserve networks is often limited by a lack of data on spatiotemporally explicit demographic rates within reserves and connectivity among reserves (Roberts 1998, Crowder et al. 2000, Botsford et al. 2009, Burgess et al. 2014).

Connectivity is often considered the primary driver of metapopulation and source-sink dynamics in marine systems (Caley et al. 1996, Roberts 1998, Hastings and Botsford 2006). The dispersal of larvae over potentially long distances can decouple subpopulation reproduction and recruitment, thereby reducing the influence of subpopulation demographics on metapopulation dynamics. In contrast, where subpopulation recruitment from local retention, the settlement of larvae in their natal subpopulation, equals or exceeds that from immigration via connectivity, evidence suggests that subpopulation demographic rates are potentially more important drivers of metapopulation and source-sink dynamics than connectivity. For example, in a simulated coral reef fish metapopulation where local retention was up to an order of magnitude greater than connectivity, the source-sink status of subpopulations was more sensitive to adult

and juvenile demographics than connectivity (Figueira 2009). Similarly, where empirical estimates of connectivity and local retention were approximately equal, metapopulation growth rate of two species of intertidal mussels (*Mytilus californianus* and *Mytilus galloprovincialis*) was more sensitive to adult fecundity, as well as juvenile growth and survival, than connectivity (Carson et al. 2011). Thus, spatial variation in local demographic rates may drive metapopulation growth rates, and overwhelm any source-sink designation based upon connectivity alone.

Knowledge of the relative importance of connectivity and demographics to metapopulation dynamics has important management implications. For instance, metapopulations characterized by relatively low levels of connectivity and a relatively high sensitivity to subpopulation demographics would seemingly benefit most from management actions that improve demographics. Protecting subpopulations within marine reserves is one management strategy often associated with improved demographics within reserve boundaries (Lester et al. 2009, Puckett and Eggleston 2012). Targeted stock enhancement, the hatchery-production and subsequent release of juveniles in the wild (Molony et al. 2003, Zohar et al. 2008), is another option that may improve subpopulation demographics through increases in density and subsequent increases in reproductive output (Lipcius et al. 2008). Where demographic rates associated with management actions are near maximal for a target species or connectivity among subpopulations is relatively high and demographics less important to metapopulation dynamics, management actions should focus on increasing connectivity. In a marine reserve context, managers may consider whether increasing the number or the area of reserves in the network promotes greater metapopulation retention of larvae within the reserve network (i.e., local larval retention within reserves + larval connectivity among reserves).

A classic example of trade-offs between the number and size of reserves is the debate over whether a Single Large reserve or Several Small reserves of equal cumulative area (SLOSS) provide greater conservation benefit (Diamond 1975, Simberloff and Abele 1982, McNeill and Fairweather 1993, Stockhausen and Lipcius 2001). A modification of the SLOSS approach can be used

to guide the design of reserve networks where the tradeoff may consist of a network with Few Large or Several Small reserves of equal cumulative area (FLOSS). In an application of the FLOSS concept to promote metapopulation persistence in a terrestrial system, Nicol and Possingham (2010) developed a patch-occupancy model whereby the decision to increase the number or area of metapopulation patches was dependent, in large part, on connectivity (recolonization of extinct patches in this case). At low levels of recolonization, increasing patch area reduced the probability of metapopulation extinction more so than increasing the number of patches. As recolonization increased, the preferred strategy switched from increasing patch area to increasing patch number. A key question is whether marine reserve managers should follow a similar approach to that of Nicol and Possingham (2010), where the extinction and colonization features of metapopulations have been de-emphasized (Sale et al. 2006) and marine reserves are typically too small relative to larval dispersal distances (median reserve size = 1.6 km² vs. median dispersal distance ≥20 km; Shanks et al. 2003, Spalding et al. 2010) to promote extensive local retention.

In this study, we illustrate the utility of metapopulation and source-sink concepts for assessing the function of marine reserves and the design of reserve networks. Using a network of ten reserves in Pamlico Sound, North Carolina, USA established to protect and restore eastern oyster (*Crassostrea virginica*) as our model system, we modeled metapopulation and source-sink dynamics by integrating empirically based subpopulation demographic rates and regional hydrodynamic-based connectivity estimates within a matrix model. Specifically, we (1) evaluated the potential for the reserve network to function as a self-persistent oyster metapopulation, thereby serving as a template for oyster management and restoration, (2) identified source and sink reserves to determine the relative importance of demographics vs. connectivity on reserve source-sink dynamics, (3) assessed whether stock enhancement, a common restoration strategy for multiple species, can promote metapopulation persistence, and (4) applied a modified FLOSS framework to determine whether increasing the size or number of reserves in a network promoted greater metapopulation

retention of larvae within the network, thereby enhancing metapopulation persistence.

METHODS

Model species

The general biphasic life history of oysters with sessile adults and a dispersive pelagic larval stage is similar to that of many benthic invertebrates, making them an ideal model species for testing metapopulation, source-sink, and SLOSS concepts. Along the east and gulf coasts of the USA, the native eastern oyster (*C. virginica*) is an ecologically and economically important species at historic population lows, a fate similar to many oyster species worldwide (Beck et al. 2011). Eastern oysters (hereafter oysters) are protandrous hermaphrodites, initially maturing as males, and transitioning to functional females at sizes >30 mm shell height (Burkenroad 1931, Mroch et al. 2012). Oysters spawn gametes into the water column where eggs are fertilized and subsequently develop through two planktonic larval stages during their 10–30 d pelagic larval duration (Kennedy 1996 and references therein). In Pamlico Sound (model system; see below), oyster spawning is protracted from May to October, with primary and secondary peaks in reproductive output in May and August, respectively (Eggleston et al. 2011, Mroch et al. 2012). Competent larvae seek a solid surface for settlement. Newly settled oyster (spat) remain as permanently attached epibenthic organisms (Kennedy 1996).

Model system

Pamlico Sound is a shallow (mean depth of ~4.5 m), well-mixed lagoonal estuary that responds rapidly to wind forcing, the primary driver of circulation in the system (Pietrafesa et al. 1986, Luettich et al. 2002). Wind forcing is predominately southwesterly (towards northeast) during summer (Xie and Eggleston 1999, Eggleston et al. 2010, Puckett et al. 2014) when primary and secondary peaks in oyster spawning occur. Semidiurnal tides are present, but tidal influence quickly diminishes with distance from inlets (Pietrafesa et al. 1986).

There are three distinct, yet inter-related, oyster restoration strategies in Pamlico Sound of particular relevance to this study: (1) no-harvest reserves,

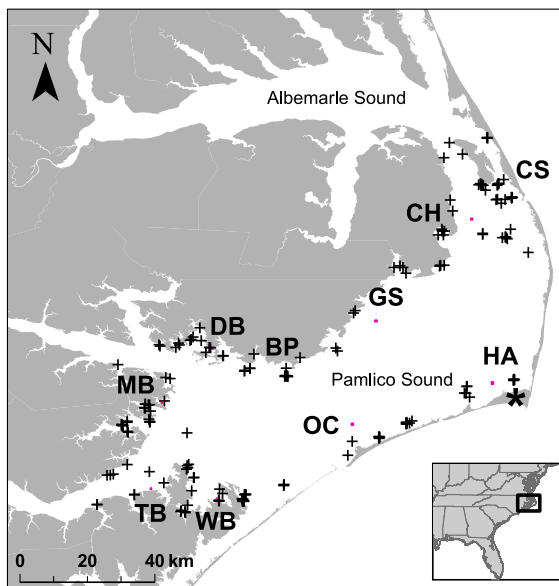


Fig. 1. Map of the Croatan-Albemarle-Pamlico-Estuarine System (CAPES) in North Carolina, USA with location of no-harvest oyster reserves (closed squares) and restored + harvested cultch-planting sites (+) in Pamlico Sound. Labeled reserves from southwest to northeast: Turnagain Bay (TB), West Bay (WB), Middle Bay (MB), Deep Bay (DB), Bluff Point (BP), Ocracoke (OC), Gibbs Shoal (GS), Hatteras (HA), Crab Hole (CH), and Croatan Sound (CS). Asterisk indicates location of wind observations at Cape Hatteras Meteorological Station used to drive the hydrodynamic model. Site symbols not to scale.

(2) stock enhancement, and (3) cultch-planting. All three strategies are used to various degrees to restore native oysters globally (Coen and Luckenbach 2000, Laing et al. 2006, Paynter et al. 2010, Beck et al. 2011). (1) Ten no-harvest, broodstock reserves were established by the North Carolina Division of Marine Fisheries (NC DMF) beginning in 1996 to protect restored subtidal oyster reefs from harvest so that oyster subpopulations within reserves functioned as a self-persistent metapopulation capable of providing larval subsidies to harvested subpopulations (Fig. 1). Reserves vary in size from 0.03 to 0.2 km² (Table 1) and are separated by distances ranging from 10 to 120 km. (2) Stock enhancement was conducted at 4 of the 10 reserves during 2006–2008 (Table 1) whereby hatchery-reared juvenile oysters were set on oyster shell and deployed at reserves to increase juvenile oyster densities and,

presumably, reproductive output from reserves. (3) Cultch-planting was conducted at 187 sites during 1995–2004 (Fig. 1), whereby a thin veneer of oyster shell was deployed to replace shell removed through the process of commercial oyster harvest. The shell (i.e., cultch) provides settlement substrate to increase larval settlement success. Cultch-planting sites are harvested once oysters reach minimum commercial size limits (76 mm).

Previous research has documented several properties of the no-harvest oyster reserves that make it an ideal model system for applying metapopulation concepts. For example, demographic rates of oysters vary significantly among reserves, with certain reserves characterized by relatively high survivorship, others relatively fast growth, and others relatively high fecundity (Mroch et al. 2012, Puckett and Eggleston 2012). Local retention of larvae within reserves and larval connectivity among reserves have been documented, but appear to be limited because reserves are generally too small to facilitate extensive local retention and spaced too far apart to facilitate extensive connectivity (Haase et al. 2012, Puckett et al. 2014). Yet, precipitous increases in oyster density have been observed within reserves (Puckett and Eggleston 2012). We were interested in whether increases in oyster density were due to reserves supporting a persistent oyster metapopulation and whether recent efforts at stock enhancement (Geraldi et al. 2013) promoted persistence.

Subpopulation demographic rates

To quantify oyster growth and survival, five replicate settlement trays were deployed at six (of 10) reserves—West Bay (WB), Ocracoke (OC), Hatteras (HA), Crab Hole (CH), Bluff Point (BP), and Deep Bay (DB) (Fig. 1)—in June 2006, August 2006, and May 2007 prior to primary and secondary peaks in oyster settlement. Trays were retrieved at bimonthly intervals from May to October 2006–2008. During the initial census, 40 individual oysters on each tray (when present) were marked and measured (Table 1). During subsequent censuses, we followed the demographic fate of each marked individual. Marked individuals were assumed to have survived if present with both valves and minimal valve gape. If present and alive, individuals were measured to the nearest 0.1 mm. For a

Table 1. Summary information on reserve area, number of oysters marked for demographic analyses, number of oysters seeded via stock enhancement, and initial population size and size structure for model simulations.

Reserve	Area (km ²)	Number marked	Stock enhancement	Initial population size (% of metapopulation)	Initial size structure (% in size class)					
					1	2	3	4	5	6
TB	0.02	n/a	5,252,790†	2,859,081 (3)	6	27	27	21	14	5
WB	0.03	513	0	3,583,233 (4)	5	30	26	19	12	8
MB	0.02	n/a	3,430,000‡	544,923 (1)	23	3	9	15	34	16
DB	0.07	379	0	1,399,915 (1)	0	2	12	22	46	18
BP	0.08	400	1,210,000‡	1,494,865 (2)	1	5	41	45	8	0
OC	0.12	520	1,675,000§	16,907,958 (17)	0	15	36	28	15	6
GS	0.12	n/a	0	8,074,711 (8)	6	15	30	25	16	8
HA	0.19	337	0	32,669,551 (34)	8	22	34	23	7	6
CH	0.13	537	0	23,757,518 (24)	13	52	21	10	3	1
CS	0.03	n/a	0	5,817,243 (6)	12	52	22	10	3	1
Total	0.81	2686	11,567,790	97,109,000	9	37	27	17	7	3

Notes: Reserve abbreviations: Turnagain Bay (TB), West Bay (WB), Middle Bay (MB), Deep Bay (DB), Bluff Point (BP), Ocracoke (OC), Gibbs Shoal (GS), Hatteras (HA), Crab Hole (CH), and Croatan Sound (CS). Size classes: 1 = 0–15 mm, 2 = 15.1–30 mm, 3 = 30.1–45 mm, 4 = 45.1–60 mm, 5 = 60.1–75 mm, 6 = 75+ mm.

† 25% of enhancement occurred in July 2006, 10% in July 2007, 10% in September 2007, 26% in May 2008, and 29% in July 2008.

‡ 100% of enhancement occurred in July 2008.

§ 76% of enhancement occurred in July 2007, 24% in September 2007.

more detailed description of growth and survival methods, see Puckett and Eggleston (2012).

To quantify size-specific oyster fecundity, oysters were collected by Mroch et al. (2012) from the same six reserves (as above; Fig. 1) during May and August of 2006–2008. Individual oysters from a given reserve were measured and separated into six size classes of 15 mm each: 0–15 mm, 15.1–30 mm, 30.1–45 mm, 45.1–60 mm, 60.1–75 mm, and 75+ mm. Ten oysters from the two smallest size classes and 20 oysters from the remaining size classes were randomly selected and processed individually to determine total egg content (i.e., per capita fecundity) by following the general procedures in Cox and Mann (1992). Mean per capita fecundity was calculated for each size class in each reserve. Males were included in calculations of mean per capita fecundity, thereby incorporating the sex ratio of a given size class within each reserve. For a more detailed description of fecundity methods, see Mroch et al. (2012).

Local retention and connectivity

To quantify local retention and inter-reserve connectivity, we used a coupled hydrodynamic and particle tracking model previously validated

and applied in our model system (Luettich et al. 2002, Reynolds et al. 2006, 2007, Haase et al. 2012, Puckett et al. 2014). The hydrodynamic model was forced with hourly wind velocities measured from May through August 2006–2010 at Cape Hatteras Meteorological Station. Current velocities were output at hourly intervals following an 8-d model “spin-up.” One thousand particles were released from evenly spaced grid nodes within each reserve at 24 h intervals over a 14 d period in May and August of each year to coincide with primary and secondary peaks in oyster reproductive output in Pamlico Sound (i.e., 28,000 particles/reserve/year). Particles (larvae hereafter) were assumed to be passive surface drifters and subjected to predicted surface currents. Previous research in this shallow, well-mixed system revealed that connectivity was driven primarily by location of natal reserve, date of spawning, and their interaction, whereas larval behavior and the number of larvae released were of secondary importance (Puckett et al. 2014).

Larvae were tracked hourly over a 21 d larval duration. We applied a proportional daily mortality rate of 0.2/d based on the relationship between larval duration and predation developed

by Jackson and Strathmann (1981) and applied to oyster larvae by Dekshenieks et al. (1997). At the beginning of each day, 20% of larvae released from a reserve were randomly removed from simulations due to mortality. Due to the stochastic implementation of mortality, we ran 10 iterations of particle tracking simulations (*sensu* Paris et al. 2007) using the average of the 10 iterations to estimate connectivity (see below). Larvae were assumed competent to settle from day 14 through day 21, after which larvae remaining in the water column died (*sensu* North et al. 2008). Settlement was assumed to occur if larvae that were competent to settle were located in reserve polygons. For a more detailed description of connectivity methods, see Puckett et al. (2014).

Connectivity matrices were generated during May–June and July–August of 2006–2010 (i.e., 2 matrices/yr \times 5 yr = 10 connectivity matrices). Matrix elements represent the proportion of larvae released from a row-referenced reserve that settled in a column-referenced reserve. *Local retention*, the proportion of larvae spawned from a reserve returning to settle within their natal reserve, was obtained from the diagonal elements of the connectivity matrix. *Inter-reserve connectivity*, the proportion of larvae spawned from a reserve that successfully settled in any non-natal reserve, was calculated by summing each row of the connectivity matrix excluding local retention. *Metapopulation retention*, the proportion of all reserve-spawned larvae retained within the metapopulation, was calculated as the sum of local retention and inter-reserve connectivity over all reserves, divided by the number of reserves.

Metapopulation model

We developed a size-structured, discrete-time matrix metapopulation model of the form,

$$n(t+1) = \mathbf{A}n(t) \quad (1)$$

where n is a vector containing the number of individuals in each size class at time t and \mathbf{A} is a metapopulation projection matrix that represents demographic transitions and per capita fecundity (Caswell 2001). Because size is the predominant mechanism underlying many ecological interactions (e.g., fecundity and natural mortality), we divided n on the basis of size

where elements in vector n contained the abundance of oysters in one of six size classes: 0–15 mm (new recruits), 15.1–30 mm (predominately males), 30.1–45 mm (reproductively mature females), 45.1–60 mm, 60.1–75 mm, and 75+ mm (harvestable size).

The model time step was divided into three intra-annual seasonal periods corresponding to demographic sampling (see *Subpopulation demographic rates* above) and oyster biology. The projection matrix, \mathbf{A} , was parameterized separately for each season: $\mathbf{A}^{\text{spring}}$ —1 May to 30 June corresponding to peak oyster fecundity, $\mathbf{A}^{\text{summer}}$ —1 July to 31 August corresponding to secondary peaks in oyster fecundity, and $\mathbf{A}^{\text{fall/winter}}$ —1 September to 30 April corresponding to no fecundity. Growth and survival also differed in each seasonal projection matrix. For example, growth was generally reduced in $\mathbf{A}^{\text{fall/winter}}$ due to temperature-induced growth stasis during winter. Projection matrices did not vary inter-annually because demographic data collected from 2006 to 2008 were pooled to ensure sufficient sample sizes for estimating demographic parameters in \mathbf{A}^x (see below; *sensu* McMurray et al. 2010).

Seasonal metapopulation projection matrices were parameterized separately for each k reserve (\mathbf{A}_k^x) and decomposed into the sum of two matrices, \mathbf{T}_k^x and \mathbf{F}_k^x where \mathbf{T}_k^x describes transition probabilities in reserve k during season x and \mathbf{F}_k^x describes per capita fecundity in reserve k during season x . The diagonal elements of \mathbf{T}_k^x describe the probability of individuals in reserve k and size-class i surviving and remaining in size-class i (i.e., stasis; $P_{i,k}$) and the subdiagonal elements describe the probability of surviving and growing into size-class j ($G_{j,k}$; Fig. 2). Transition frequency tables created from the demographic mark-recapture data collected at each of the reserves from which we sampled oysters were used to estimate reserve- and season-specific growth and survival transition probabilities (see *Subpopulation demographic rates* above; Caswell 2001). Elements along the first row of \mathbf{F}_k^x , the only non-zero values in \mathbf{F} , describe per capita fecundity of individuals in reserve k and size-class i ($F_{i,k}$; Fig. 2). Mean size class-specific, per capita fecundity was estimated from empirical data collected by Mroch et al. (2012). A log-linear analysis was used to test for differences in

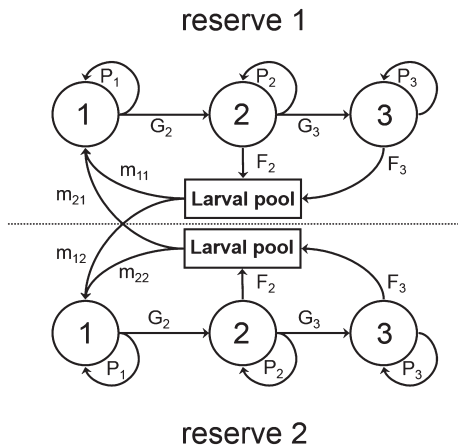


Fig. 2. A life cycle graph depicting the spatially explicit, size-structured matrix metapopulation model used in this study. For simplicity, only two subpopulations within no-harvest reserves (separated by dotted line) and three size classes (circular nodes) are shown. The model used in this study consisted of 10 reserves and six size classes. Model parameters are as follows: P_i is the probability of surviving and remaining in size-class i , G_j is the probability of surviving and growing into size class j , F_i is the per capita fecundity of size class i , and m_{jk} is the proportion of larvae spawned in reserve j that settle in reserve k .

transition frequencies among reserves, seasons, and their interaction (sensu Hill et al. 2002). Effects of each were evaluated by comparing the likelihoods (ΔG^2 with χ^2 distributions) of a hierarchical set of models beginning with the null that fate at time $t + 1$ (7 possibilities; 6 stages and death), conditional on stage (6) at time t , was independent of reserve (6) and season (3). To test whether mean per-capita fecundity varied among reserves, seasons, or their interaction, a two-way ANCOVA was used with oyster length as the covariate.

Size-specific per capita fecundity and transition probabilities of the four non-sampled reserves were interpolated using inverse distance weighting. We used a percent error-based, cross-validation “leave one out” approach to test the interpolation accuracy of four distance-decay parameters (0.1, 1, 2, and 3) that span a gradient from strong local influence (3) to small local influence (0.1) on interpolation. Additionally, we tested the accuracy of an adaptive distance-decay parameter developed by Lu

and Wong (2008). The adaptive distance-decay approach was most accurate (>50% of predictions with percent error <10%) and used for interpolations.

Empirically derived and interpolated elements of \mathbf{F}_k^x were adjusted for density-dependent fertilization success based on Levitan (1991) as:

$$\% \text{ fertilization} = 0.49 \times D^{0.72} \quad (2)$$

where D is total oyster density per m^2 . Fertilization success was capped at 100% in the event oyster densities were sufficiently high to generate fertilization success >100% in Eq. 2. The larvae spawned from reserve j were calculated as the product of a reserves per capita fecundity matrix (\mathbf{F}_j^x) and $n_{j(t)}$. Larvae were distributed among reserves based on elements of the connectivity matrix, \mathbf{M} , at time t . Elements of \mathbf{M} describe the proportion of larvae released from reserve j that survive to settle in reserve k ($m_{j,k}$; Fig. 2). Connectivity pathways included both local retention and inter-reserve connectivity. We assumed settlement occurred at the midpoint of the model time step (i.e., $t + 0.5$) and new settlers in reserve j survived to time $t + 1$ with probability $P_{1,j}^*$ adjusted for half a time step (Caswell 2001).

The complete metapopulation model was expressed as:

$$N(t+1) = \sum \begin{pmatrix} n_{1(t+1)} \\ \vdots \\ n_{10(t+1)} \end{pmatrix} = \begin{pmatrix} \mathbf{T}_{1^x} & \cdots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \cdots & \mathbf{T}_{10^x} \end{pmatrix} + \begin{pmatrix} P_{1,1}^*(m_{1,1}\mathbf{F}_1^x) & \cdots & P_{1,10}^*(m_{10,1}\mathbf{F}_{10}^x) \\ \vdots & \ddots & \vdots \\ P_{1,10}^*(m_{1,10}\mathbf{F}_1^x) & \cdots & P_{1,10}^*(m_{10,10}\mathbf{F}_{10}^x) \end{pmatrix} \begin{pmatrix} n_{1(t+1)} \\ \vdots \\ n_{10(t+1)} \end{pmatrix} \quad (3)$$

where N is metapopulation size at time t , $n_{k(t)}$ is a subvector containing the abundance of oysters in each size-class in reserve k at time t , \mathbf{T}_k^x is a submatrix representing the transition probabilities of each size-class in reserve k at time t during season x , \mathbf{F}_k^x is a submatrix representing the per capita fecundity of each size-class in reserve k at time t during season x , and $m_{j,k}$ and $P_{1,j}^*$ are defined as above (Lewis 1997, Caswell 2001). Population vectors at each reserve, n_{k^r} were initially seeded with reserve-specific empirical estimates (or interpolated for reserves not sampled) of oyster density and size structure from June 2006

scaled to reserve area (Table 1). Metapopulation abundance was projected over a 5 yr period from May 2006 to April 2011.

Metapopulation analyses

Eigen analysis of projection matrices.—We conducted eigen analyses of each reserve’s annual projection matrix (\mathbf{A}_k) to calculate the associated dominant eigenvalue (λ ; Caswell 2001). Where $\lambda > 1$, subpopulation’s within reserves are self-persistent assuming all larvae are locally retained. To determine the minimum local retention required for subpopulations within reserves to be self-persistent, we incrementally reduced fecundity in each reserve’s annual projection matrix by 0.01% until $\lambda = 1$. Using these modified annual projection matrices such that $\lambda = 1$, we conducted another eigen analysis to calculate the stable stage distribution at each reserve. On the basis of the stable stage distribution, we calculated the annual ratio of the number of recruits (i.e., stage 1) to the number of adults (i.e., stages 2–6) at each reserve to estimate the annual replacement threshold required for persistence.

Metapopulation and source-sink dynamics.—We calculated the overall metapopulation growth rate ($\lambda_M(t)$) for each time step as:

$$\lambda_M(t) = \sum_{j=1}^{10} \lambda_{C_j}(t) \left(\frac{n_{j(t)}}{N(t)} \right) \quad (4)$$

where ($\lambda_{C_j}(t)$) is reserve j ’s contribution to the metapopulation at time t (Figueira and Crowder 2006) and $N(t)$ and $n_{j(t)}$ are defined above. Values of $\lambda_M(t) \geq 1$ indicate a persistent metapopulation during time t , whereas $\lambda_M(t) < 1$ indicate a non-persistent metapopulation during time t .

Each reserve’s contribution to the metapopulation (i.e., source-sink status) was calculated based on Figueira and Crowder (2006) as:

$$\lambda_{C_j}(t) = \left[\mathbf{T}_j^x n_{j(t)} \right] + \left[\sum_{k=1}^{10} P_{1,k}^* \left(m_{jk} \mathbf{F}_j^x n_{j(t)} \right) \right] \quad (5)$$

where variables are defined as above and $\lambda_{C_j}(t) > 1$ indicates reserve j functioned as a source during time t and $\lambda_{C_j}(t) < 1$ indicates reserve j functioned as a sink during time t . By calculating reserve source-sink status in this manner,

reserves are credited with births to any reserve within the metapopulation (including itself) and penalized for deaths that occur within the reserve. By this definition, a source is a net contributor to the metapopulation regardless of whether local retention is sufficient for self-persistence (Figueira and Crowder 2006, Runge et al. 2006).

Elasticity analysis: relative importance of demographics vs. connectivity on source-sink dynamics.—To determine the relative importance of within reserve demographics, local retention, and inter-reserve connectivity on reserve source-sink status, $\lambda_{C_j}(t)$, we conducted an elasticity analysis (Caswell 2001). Elasticity values represent the proportional contribution of each model parameter to $\lambda_{C_j}(t)$ by assessing how $\lambda_{C_j}(t)$ changes in response to proportional perturbations of model parameters. Elasticity values were calculated by increasing and decreasing all elements of \mathbf{T}_k , \mathbf{F}_k , and m_j for each reserve by 5%.

Effect of initial subpopulation abundance and size structure.—To test the effect of initial subpopulation abundance and size structure on metapopulation dynamics, we modeled three scenarios in addition to the empirically based scenario detailed above (see *Metapopulation model* above; Table 1). The three additional scenarios were seeded with initial subpopulation abundances divided equally among reserves. Initial metapopulation abundance was equal among all four scenarios. Subpopulation abundance was distributed among size classes based on (1) empirical observations and interpolations, (2) an equal distribution among the six size classes, (3) distribution solely to the first stage (i.e., simulating new recruits colonizing reserves), or (4) each reserve’s stable size distribution. An ANOVA was used to compare mean metapopulation abundance and metapopulation growth rate, pooled over time, among the four initial subpopulation abundance and size structure scenarios.

Effect of stock enhancement.—To assess the potential for stock enhancement to promote metapopulation persistence by (1) directly increasing the number of juvenile oysters in certain reserves and (2) indirectly increasing recruitment via increased reproductive output, we integrated the NC DMF’s oyster stock enhancement

efforts in Eq. 3. Data on “when” and “where” enhancement occurred (Table 1) were used to model enhancement at the appropriate reserves during the appropriate model time steps. Data on the number of oysters stocked during enhancement (Table 1) were added to stage 1 of $n_{k(t)}$. We assumed that all oysters seeded during enhancement were stage 1 (0–15 mm) and grew, survived, and reproduced at the same rates as their conspecifics of the same stage at their respective reserve. A t-test was used to compare mean metapopulation abundance and growth rate in the presence and absence of stock enhancement.

To assess whether the timing and location of stock enhancement impacted its efficacy, we modeled three additional stock enhancement scenarios, whereby (1) the intra-annual timing of enhancement—May, July, or September—was altered, (2) the location of enhancement was altered to reserves with the highest λ_C , and (3) the timing—based on best timing from 1—and location—based on 2—was altered. In all scenarios, the number of reserves receiving enhancement and the total number of oysters added to the metapopulation via enhancement were equal. An ANOVA was used to compare mean metapopulation abundance and λ_M among enhancement scenarios.

Reserve network design: Few Large or Several Small

We used a modified SLOSS framework to evaluate whether a FLOSS reserves promoted greater retention of reserve-spawned larvae within the reserve network, thereby improving metapopulation persistence. We simulated the few large and several small reserve design strategies over five scales of implementation whereby reserve area or number was increased by 2×, 4×, 6×, 8×, and 10×. Total reserve area was equal in both design strategies within each implementation scale. In the few large design strategy, boundaries of the 10 existing reserves were expanded by 2×–10×. At 10×, the average reserve area was ~1 km², which is near the global median size of marine protected areas (1.6 km²; Spalding et al. 2010). Larval dispersal and connectivity was based on the expanded boundaries using the methods in *Local retention and connectivity* above. The number of larvae

released at each implementation scale increased proportional to reserve area (i.e., the number of larvae released was doubled in 2× scenario).

In the several small design strategy, we increased the number rather than the area of reserves by 2×, 4×, 6×, 8×, and 10× such that the network consisted of 20, 40, 60, 80, and 100 reserves, respectively. Reserves were added to the network from the pool of 187 cultch-planting sites (see *Model system* above; Fig. 1). Cultch-planting site boundaries were delineated to equal the average area of the 10 existing reserves (0.08 km²) to ensure the cumulative reserve area was equal between the few large and several small design strategies for a given implementation scale. Site selection was conducted (1) at random over 1000 iterations to simulate a “no-knowledge” management decision, and (2) based on a site selection algorithm that maximized connectivity between the existing reserve network and newly added reserves over the 5 yr period to simulate a “perfect knowledge” management decision. Newly added reserves were constrained to distances ≥ 1 km from reserves already within the network. Again, larval dispersal and connectivity were based on the expanded number of reserves using methods in *Local retention and connectivity* above. The total number of larvae released in the few large and several small design strategies was equal for a given implementation scale.

A two-way ANOVA was used to test the effects of two factors: (1) network design strategy (2 levels: Few Large and Several Small) and (2) implementation scale (5 levels: 2×, 4×, 6×, 8×, and 10× area or number of reserves) on three response variables: (1) mean local larval retention, (2) mean inter-reserve larval connectivity, and (3) mean metapopulation larval retention. Post hoc multiple comparisons between network designs within each scale level were conducted with a Bonferroni adjustment. Variation associated with means are reported as standard errors throughout the paper.

RESULTS

Subpopulation demographic rates

A total of 2686 oysters were tracked within reserves from June 2006 to October 2008 to estimate demographic transitions. An additional

2067 oysters from reserves were processed to estimate per-capita fecundity (Mroch et al. 2012). Oyster survival and fecundity generally increased in larger size classes, whereas growth was generally greatest in smaller size classes. Growth, survival, and fecundity varied significantly among reserves, across seasons, and the reserve \times season interaction (growth and survival: $\Delta G^2 \geq 434.2$, $\Delta df \geq 72$, $P \leq 0.004$; fecundity: $F_{20,2046} \geq 4.9$, $P \leq 0.001$). Demographic rates were not concurrently maximized during any single season or at any single reserve.

Local retention and connectivity

The dispersal of 1.4 million larvae was simulated over a 5 yr period to estimate local retention within reserves and connectivity among reserves. Local retention occurred at every reserve except Middle Bay (MB) (Fig. 3), but during no more than 3 model time steps at any reserve. Where present, mean local retention averaged across the 5 yr simulation ranged from $0.003\% \pm 0.002\%$ to $0.26\% \pm 0.2\%$ among reserves (Fig. 3).

Inter-reserve connectivity was also limited in space and time. Only 20 of the possible 90 (22%) inter-reserve connections were present over the 5 yr simulation, but all reserves except DB served as the origin or terminus of inter-reserve connections (Fig. 3). Where present, connectivity was generally directed from southwest to northeast in the direction of prevailing southwesterly winds (Fig. 3). The magnitude of inter-reserve connections averaged across the 5 yr simulation ranged from $0.004\% \pm 0.003\%$ to $0.14\% \pm 0.05\%$ among reserves.

Eigen analysis of projection matrices

Demographic rates at all reserves were sufficient to support self-persistent subpopulations in simulations where all reserve-spawned larvae were assumed to be locally retained (annual $\lambda \geq 1.2$; Fig. 4a). The minimum local retention necessary for reserves to support self-persistent subpopulations (i.e., $\lambda \geq 1$) ranged from 0.3% to 1.4% (Fig. 4b). At this self-persistence threshold, stable oyster size distributions in reserves were generally bimodal with an annual ratio of recruits (stage 1) to adults (stage 2+) ranging from 0.19:1 to 0.30:1 (Fig. 4c). Thus, on average, an annual replacement of *c.* 0.25 recruits per

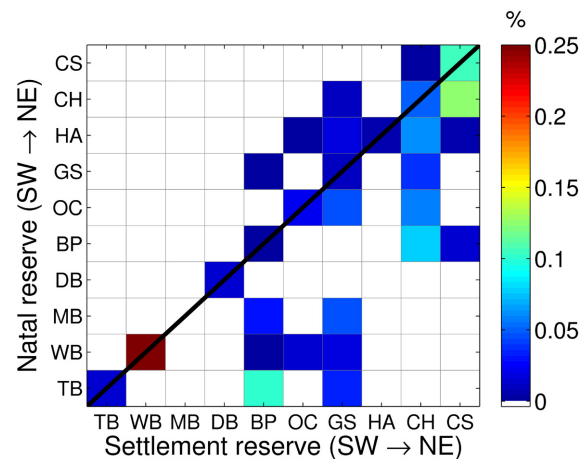


Fig. 3. Average connectivity matrix indicating proportional exchange of larvae between natal reserves (rows) and settlement reserves (columns). Average calculated over 5 yr simulation (i.e., 10 connectivity matrices; 2 spawning periods/yr \times 5 yr). The magnitude of local retention and inter-reserve connectivity is depicted by the color bar. White areas represent no local retention or connectivity. Solid line along the matrix diagonal represents local retention. Connectivity below the diagonal is generally directed from southwest to northeast and vice versa for connectivity above the diagonal. Reserve abbreviations as in Fig. 1.

adult was required to ensure persistence of subpopulations within reserves, suggesting that an average adult lived and reproduced for ~ 4 yr.

Metapopulation and source-sink dynamics

Metapopulation persistence was generally limited by low levels of local retention and inter-reserve connectivity. Only $0.12\% \pm 0.04\%$ of reserve-spawned larvae were retained, on average, within the reserve network metapopulation. Reserves received an average annual supply of $\leq 0.08 \pm 0.06$ new recruits per adult, which was $\leq 1/3$ of the recruits needed for persistence (Fig. 5a). Over the 5 yr simulation, λ_M ranged from 0.76 to 1.09, but was 0.85 ± 0.02 on average, suggesting that the reserve network was not supporting a persistent oyster metapopulation (i.e., $\lambda_M < 1$; “empirically based” line on Fig. 5b). During this time, metapopulation abundance was projected to decline by an order of magnitude from approximately

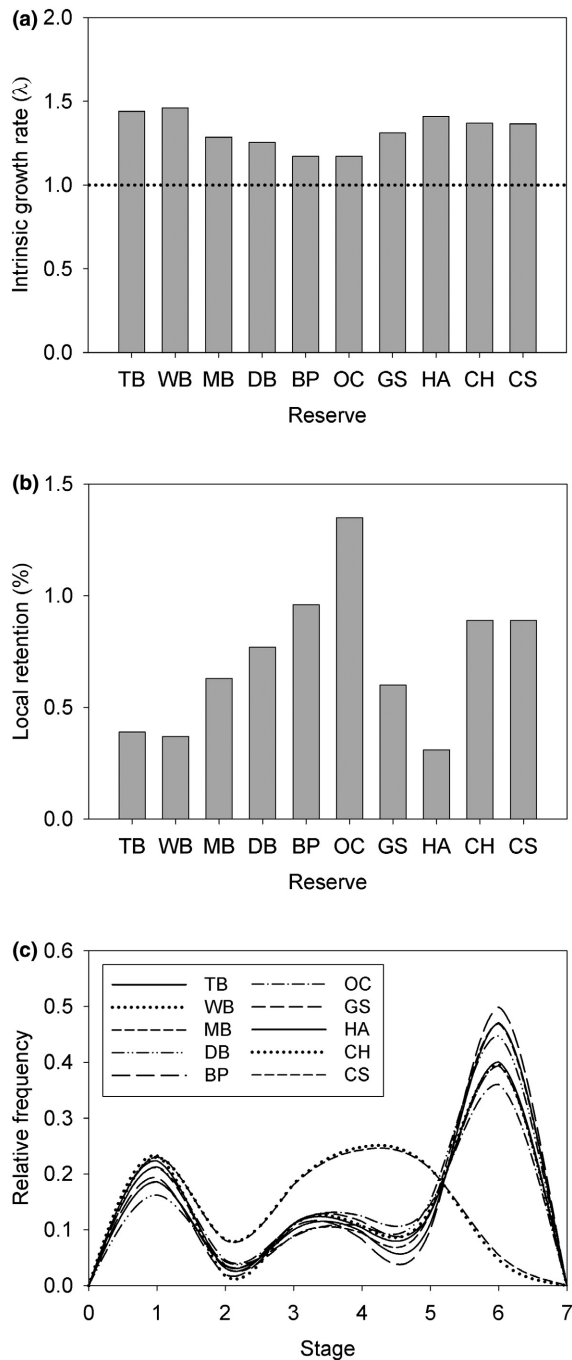


Fig. 4. (a) Intrinsic population growth rate of oyster subpopulations in no-harvest reserves assuming that all reserve-spawned larvae were locally retained. (b) Minimum local retention required at each reserve to promote self-persistent subpopulations and (c) the associated stable stage distribution of self-persistent subpopulations. Reserve abbreviations as in Fig. 1.

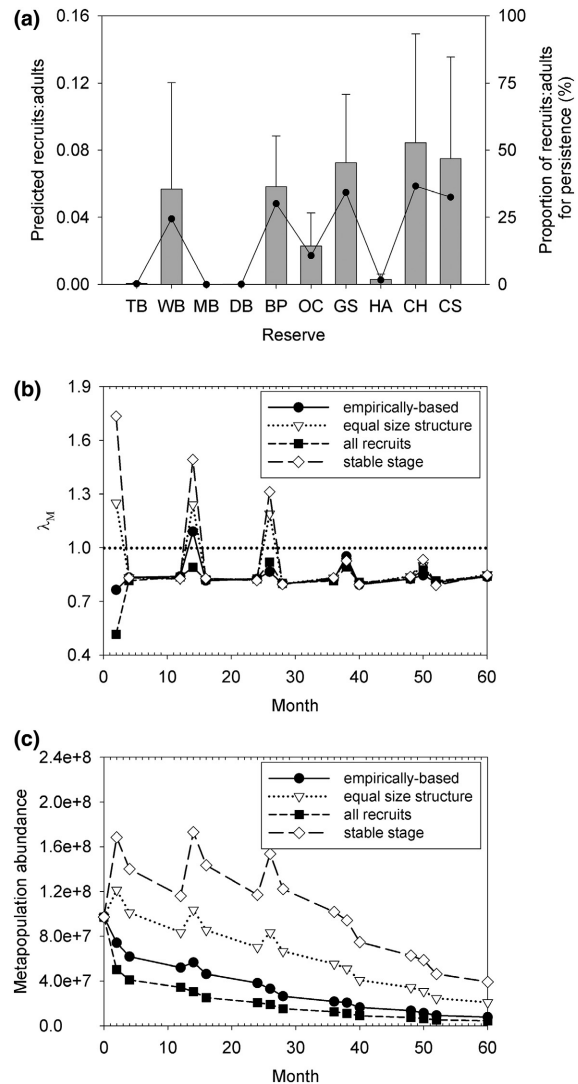


Fig. 5. (a) Ratio of recruits:adults predicted at each reserve during model simulations (bars; primary y -axis) and the proportion of recruits:adult each reserve is predicted to receive relative to what is needed for subpopulation self-persistence (line; secondary y -axis). Mean (\pm SE) values of recruits:adults calculated over 5 yr simulation. Model projections of (b) metapopulation growth rate and (c) metapopulation abundance of oysters in 10 no-harvest reserves over a 5 yr simulation in four scenarios whereby subpopulation abundance and size structure were allocated as described in the text. The dashed horizontal line in panel b is the threshold growth rate for a persistent metapopulation. Reserve abbreviations as in Fig. 1.

10×10^7 to 8×10^6 oysters (“empirically based” line on Fig. 5c). Declines of oyster abundance in reserve subpopulations exceeded 75%. Seeding the model with equal subpopulation abundance among reserves and different size structures (but the same metapopulation abundance) significantly affected mean metapopulation abundance over the 5 yr model simulation ($F_{3,56} = 25.9$, $P < 0.0001$; Fig. 5c), but not mean metapopulation growth rate (λ_M ; $F_{3,56} = 2.2$, $P = 0.09$; Fig 5b) providing further support for the inability of the network to promote metapopulation persistence.

Spatiotemporal variation in oyster demographic rates and asymmetric inter-reserve larval connectivity created source-sink structure within the reserve network. Limited local retention and inter-reserve connectivity yielded relatively few sources. Only four of 10 reserves functioned as sources ($\lambda_c > 1$) at any time over the 5 yr simulation and no reserve functioned as a source when integrated over the entire simulation (mean $\lambda_c \leq 0.97 \pm 0.07$; Fig. 6a). The model time step with the greatest number of sources (3) had the highest metapopulation growth rate ($\lambda_M = 1.09$). The location of sources and sinks was asymmetrical. The predominant southwesterly winds during oyster spawning seasons led to asymmetrical connectivity such that sources, though short-lived, were generally located in the southern-half of Pamlico Sound. Sinks were consistently located in the northern-half of Pamlico Sound (Gibbs Shoal [GS], CH, Croatan Sound [CS]; mean $\lambda_c \leq 0.8 \pm 0.02$; Fig. 6a) where reserves received the greatest number of immigrants while providing very few emigrants.

Elasticity analysis: relative importance of demographics vs. connectivity on source-sink dynamics

In general, reserve source-sink dynamics were more sensitive to changes in demographic rates than connectivity or local retention (Fig. 6b). When averaged across reserves, demographic rates associated with adult growth and survivorship (stages 3–6) had the greatest total elasticity (0.45 ± 0.13), with survival and stasis of the largest size class having the single greatest proportional influence on λ_c (0.23 ± 0.08). Adult fecundity had the second-highest total elasticity (0.17 ± 0.06 ;

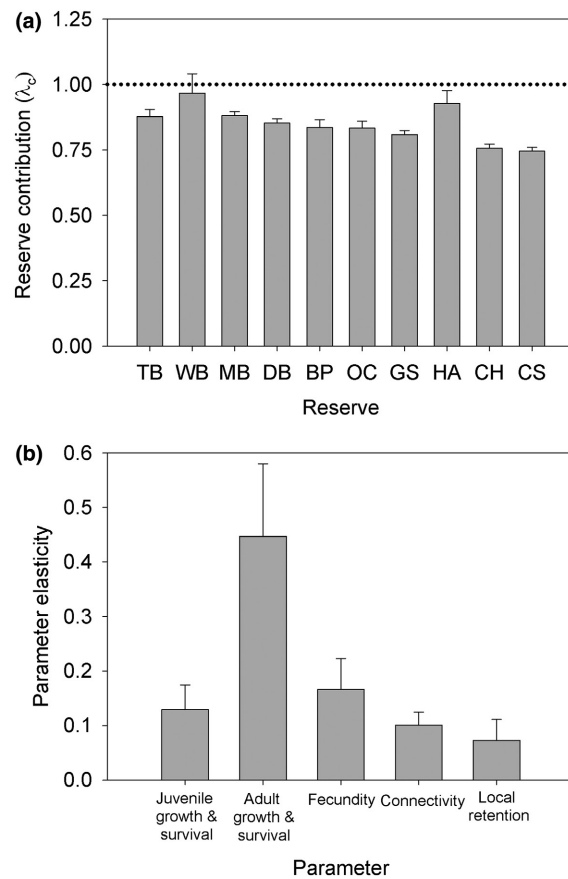


Fig. 6. (a) Reserve contribution (λ_c) to the metapopulation. The dashed horizontal line is the threshold λ_c for source ($\lambda_c > 1$) and sink ($\lambda_c < 1$) designation. Mean (\pm SE) λ_c values calculated over 5 yr simulation. (b) Elasticity values of demographic, connectivity, and local retention parameters. Demographics are sub-divided into juvenile growth and survival (stages 1–2), adult growth and survival (stages 3–6), and fecundity. Mean (\pm SE) elasticity values calculated across reserves over 5 yr simulation. Reserve abbreviations in panel a as in Fig. 1.

Fig. 6b), followed by juvenile growth and survivorship (stages 1–2), inter-reserve connectivity, and local retention, respectively (Fig. 6b).

Stock enhancement

The ~11.6 million oysters added via stock enhancement (Table 1) increased metapopulation reproductive output by 1.3×10^9 larvae over the 5 yr simulation. The increased reproductive output, however, had a minimal impact

(<20% increase) on the number of new recruits per adult at each reserve. Stock enhancement significantly increased metapopulation abundance ($t = 4.8$, $df = 14$, $P = 0.0003$) by ~2 million oysters (~25%) by the end of model simulations, but did not significantly increase λ_M ($t = 1.0$, $df = 14$, $P = 0.3$; Fig. 7a,b). Altering the timing and location of stock enhancement slightly altered the efficacy of stock enhancement, but mean metapopulation abundance and λ_M were not significantly different among the enhancement scenarios tested ($F_{5,84} \leq 0.05$, $P = 0.99$). Stock enhancement was least effective when conducted during July or September, and most effective when applied to reserves with the highest λ_C during May of a given year (Fig. 7c). Still, none of the enhancement scenarios tested were capable of increasing mean λ_M ($\leq 0.87 \pm 0.03$) above the threshold for metapopulation persistence (i.e., λ_M remained <1).

Few large or several small reserves?

Designing a reserve network with a Few Large or Several Small reserves had a significant effect on local retention, inter-reserve connectivity, and metapopulation retention (Figs. 3 vs. 8; Fig. 9a-c; Table 2). The few large design increased both mean local retention and inter-reserve connectivity by up to 475% and 650%, respectively (Figs. 3 vs. 8a; Fig. 9a,b). The several small design led to a slight decrease in mean local retention, but a rapid, albeit non-monotonic, increase in mean inter-reserve connectivity by up to 1200% (Figs. 3 vs. 8b; Fig. 9a,b). Both design strategies generally increased the proportion of larvae that were retained within the metapopulation by >575% (Fig. 9c).

The effect of design strategy on local retention, connectivity, and metapopulation retention was dependent on the scale to which each strategy was implemented (see significant interactions in Table 2). For instance, the few large design promoted greater reserve local retention than the several small design, but only as the area or number of reserves were increased by $\geq 6\times$ ($t \geq 2.9$, $P \leq 0.005$; Fig. 8a vs. b; Fig. 9a). The several small design promoted greater and more symmetrical inter-reserve connectivity than the few large design, but only as the area or number of reserves were increased by 2–6 \times ($t \geq 3.3$,

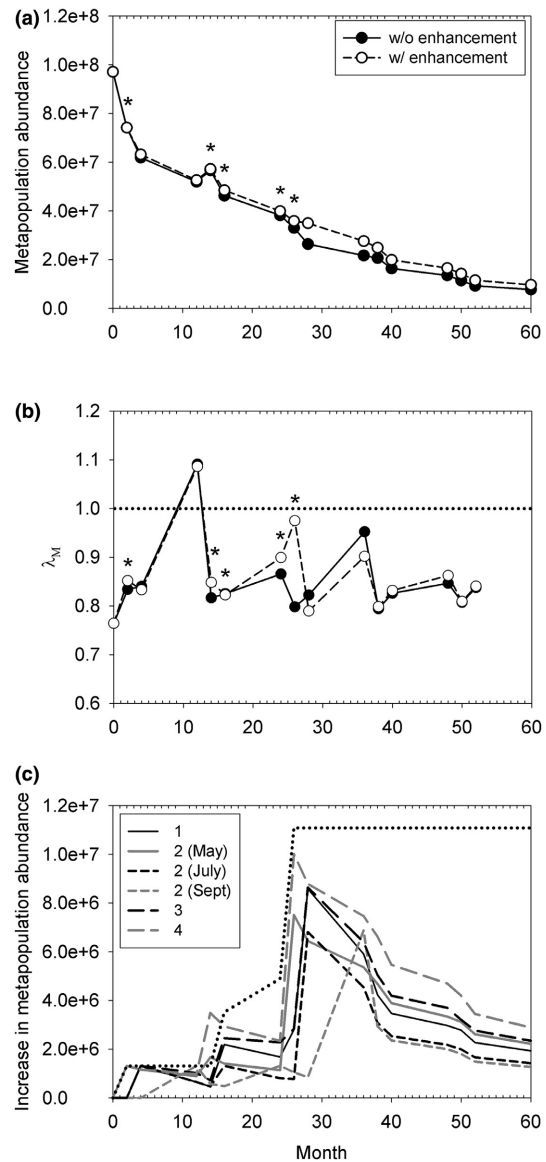


Fig. 7. Model projections of (a) metapopulation abundance and (b) metapopulation growth rate of oysters in 10 no-harvest reserves over a 5 yr simulation in scenarios with and without stock enhancement. Asterisks denote timing of stock enhancement (see Table 1). The dashed horizontal line in panel b is the threshold growth rate for a persistent metapopulation. (c) Projected increase in metapopulation abundance for various stock enhancement scenarios relative to a scenario of no stock enhancement. Scenarios 1, 2, 3, and 4 are described in the text. For scenario 2, May, July, and September indicate the month within a year that stock enhancement was conducted. The dotted line represents the cumulative number of oysters added via enhancement (timing based on scenario 1).

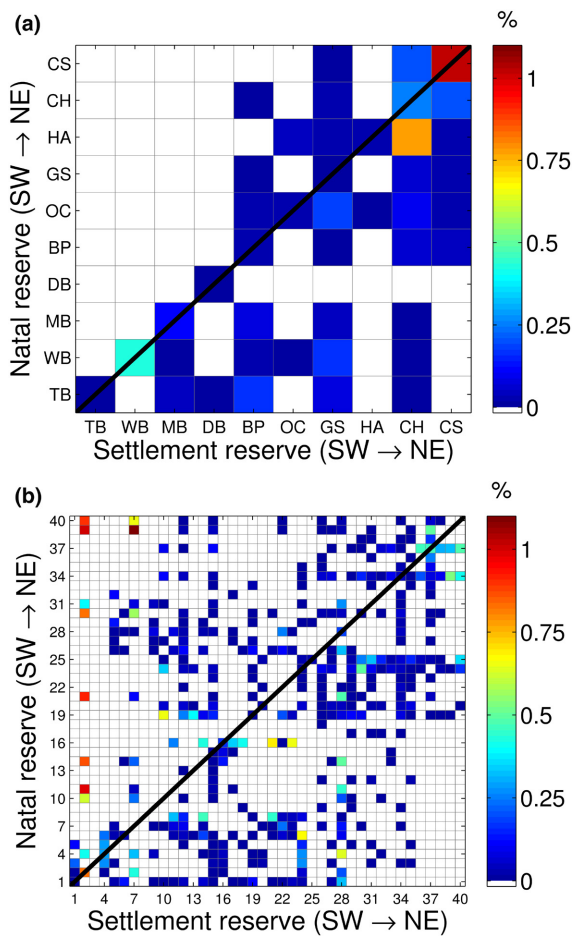


Fig. 8. Average connectivity matrices indicating proportional exchange of larvae between natal reserves (rows) and settlement reserves (columns) in a Few Large (a) and Several Small (b) reserve network design. Average calculated over 5 yr simulation (i.e., 10 connectivity matrices; 2 spawning periods/yr \times 5 yr) for each scenario. Reserve area and number were increased by 4 \times in connectivity matrices depicted in panels. The magnitude of local retention and inter-reserve connectivity is depicted by the color bar. White areas represent no local retention or connectivity. Solid line along the matrix diagonal represents local retention. Connectivity below the diagonal is generally directed from southwest to northeast and vice versa for connectivity above the diagonal. See Fig. 3 for average connectivity matrix of the original 10-reserve network over 5 yr simulation. Reserve abbreviations as in Fig. 1. In panel b, reserves correspond to the following numbers: TB = 1, WB = 4, MB = 8, DB = 16, BP = 19, OC = 20, GS = 24, HA = 25, CH = 34, and CS = 37.

$P \leq 0.001$; Fig. 8a vs. b; Fig. 9b). Similarly, meta-population retention was significantly higher in the several small design than the few large design, but only when reserve area or number was increased by 2–4 \times ($t \geq 2.8$, $P \leq 0.007$; Fig. 9c). The optimal 20- and 40-reserve networks that maximized metapopulation retention often consisted of clustered reserves that reduced the mean spacing between reserves from 26.5 ± 4.2 km to 15.4 ± 3.2 km and 10.4 ± 1.8 km, respectively (Fig. 10). Knowledge of connectivity during site selection was important; randomly adding sites to the network (i.e., “no knowledge”) reduced metapopulation retention relative to the few large design as the area or number of reserves was increased by $\geq 6\times$ ($t \geq 2.5$, $P \leq 0.01$; Table 2; Fig. 9d).

DISCUSSION

Limited local retention and inter-reserve connectivity prevented the reserve network from functioning as a self-persistent oyster meta-population, despite supporting oyster demographic rates within reserves that were some of the highest reported for the species (Puckett and Eggleston 2012 and references therein). On average, $<1/3$ of the *c.* 0.25 recruits per adult needed annually for replacement were provided via local retention or inter-reserve connectivity, indicating the network was recruitment limited when considering only larval supply from reserves. Accordingly, reserves contributed to the metapopulation primarily via production, not dispersal, of larvae and reserve source-sink dynamics were influenced more by demographics within reserves, particularly adult growth and survival, than larval connectivity among reserves. Additional restoration strategies aimed at further improving oyster demographics rates within reserves may be futile given the near maximal rates we observed for the species. For instance, stock enhancement, which should enhance recruitment success by increasing the abundance of juvenile oysters within reserves, was unable to augment projected metapopulation declines. We conclude that successful species management and restoration using reserve networks must ensure that reserves are sufficiently connected before the demographic benefits due

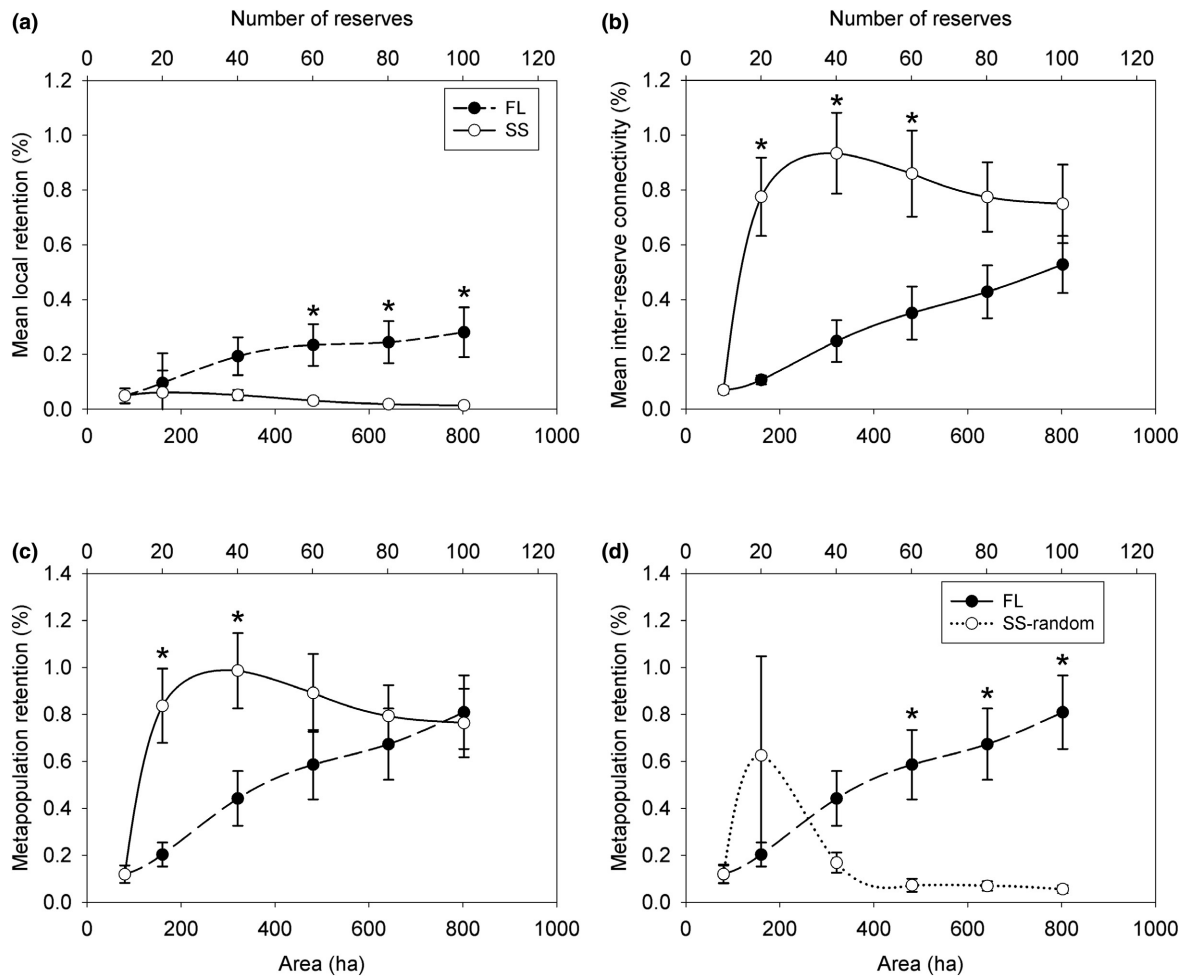


Fig. 9. Proportion of reserve-spawned larvae locally retained within reserves (a), transferred via inter-reserve connections (b), and retained within the metapopulation (c, d) for reserve network designs of Few Large reserves (FL) vs. Several Small reserves. Mean (\pm SE) values calculated across reserves over 5 yr simulation. Reserves were added to the network in the Several Small design based on knowledge of connectivity (SS, a-c) and at random (SS-random, d). Each reserve network design strategy was simulated over five implementation scales whereby the area or number of reserves was increased by 2 \times , 4 \times , 6 \times , 8 \times , and 10 \times . Significant differences between designs within a scenario are denoted by *. Secondary x-axes only applicable to SS designs. The first point in each plot represents the current reserve network.

to harvest protection or stock enhancement scale-up to benefit the overall reserve network metapopulation (Gaines et al. 2010).

Increasing the size of reserves in the network (i.e., Few Large design) promoted greater local retention of oyster larvae within reserves, whereas increasing the number of reserves in the network (i.e., Several Small design) promoted greater and more symmetrical inter-reserve larval connectivity. Of the two designs, several

small reserves promoted greater metapopulation retention of reserve-spawned larvae. This response was particularly evident and rapid with small increases in the number of reserves suggesting that initially increasing the number of reserves may provide the best “bang for the restoration buck.” As the number or size of reserves in the network continued to expand, metapopulation retention of larvae was equivalent between both designs, suggesting that

Table 2. Analysis of variance results of the effects of reserve network design strategy (Few Large or Several Small) and implementation scale (2×, 4×, 6×, 8×, and 10× reserve area or number) on mean proportion of larvae locally retained within reserves, transferred via inter-reserve connections, and retained within the metapopulation.

Response	Source of variation	df	SS	MS	F	P
Local retention	Strategy	1	0.6	0.6	25.6	<0.0001
	Scale	5	0.1	0.03	1.2	0.3
	Strategy × Scale	5	0.3	0.06	2.4	0.04
Inter-reserve connectivity	Strategy	1	4.9	4.9	42.4	<0.0001
	Scale	5	4.7	0.9	8.2	<0.0001
	Strategy × Scale	5	1.8	0.4	3.1	0.01
Metapopulation retention	Strategy	2†	9.1	4.6	23.4	<0.0001
	Scale	5	4.3	0.9	4.4	0.0009
	Strategy × Scale	10	6.6	0.7	3.4	0.0005

† Added a second Several Small design based on “no knowledge” random addition of reserves to the network.

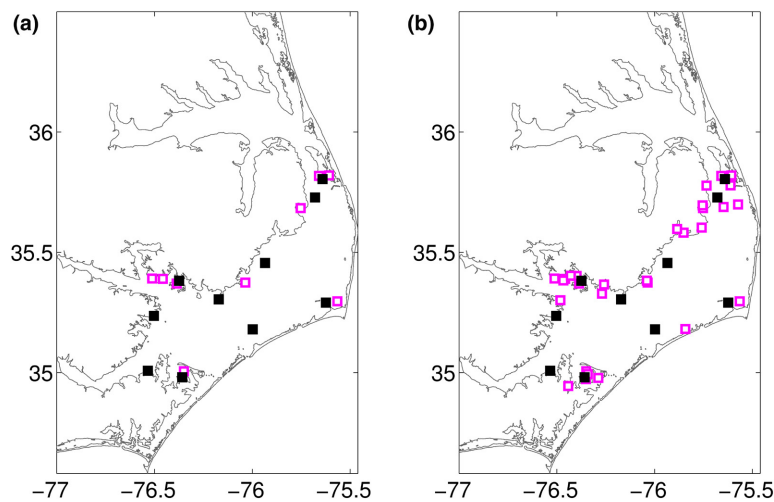


Fig. 10. The optimal Several Small reserve network consisting of (a) 20 and (b) 40 reserves. Location of 10 existing no-harvest reserves and reserves added to the network are depicted by closed and open squares, respectively.

Few Large and Several Small reserves (FLASS) may be the best long-term network design. The concept of variably sized reserves is not new; Palumbi (2004) suggested variability in reserve size was necessary to protect different species that may have different life histories and dispersal distances. Variably sized marine reserves were used in the re-zoning of the Great Barrier Reef to include 150 no-harvest reserves ranging in size from 1 to 500 km² (Almany et al. 2009, Jones et al. 2009). Even in a relatively simple setting where the focus is on a single target species, results from this study suggest that a “one-size

fits all” approach is likely not an optimal reserve network design strategy.

Caveats regarding model assumptions

We made several assumptions to simplify the metapopulation model applied in this study. First, oyster demographic rates were implicitly density-dependent (see Puckett and Eggleston 2012), but lacked a compensatory density-dependent response as densities were projected to decrease by >35% to levels below those used in estimating demographics. The demographic portion of the metapopulation model accurately

projected reserve size structure and abundance at observed oyster densities (Puckett and Eggleston unpubl. data), but as densities were projected to decline, a compensatory response or weakening of density dependence would have reduced, but likely not reversed, the rate of metapopulation decline.

Second, larval dispersal was modeled as a passive drift driven solely by surface currents despite evidence that oyster larvae migrate vertically and are generally distributed in the water column according to their ontogenetic stage (Carriker 1951, Deksheniaks et al. 1996). In stratified or partially stratified systems, such as Chesapeake Bay, larvae may respond behaviorally to features such as haloclines, which can influence larval dispersal (North et al. 2008, Narvaez et al. 2012). In well-mixed systems lacking a significant halocline such as Pamlico Sound, it remains unclear what water column features oyster larvae might respond to (if any) to regulate their depth, other than a general ontogenetic shift towards deeper depths as sinking speeds exceed swimming speeds (Deksheniaks et al. 1996). In our study system, larval dispersal and connectivity were more sensitive to location and the date of spawning than to larval behavior (Puckett et al. 2014). Including larval behavior may have reduced dispersal distances, thereby increasing local retention and decreasing inter-reserve connectivity (North et al. 2008, Puckett et al. 2014). These changes may have influenced our projection of metapopulation abundance and assessment of optimal network design strategy.

Third, oyster subpopulations within reserves were the only subpopulations included in the metapopulation model despite the presence of non-reserve oyster subpopulations in Pamlico Sound (e.g., restored cultch-planting sites and natural, non-restored reefs). These harvested oyster subpopulations likely subsidize reserves with oyster larvae (J. Peters, D. Eggleston, B. Puckett, unpublished manuscript). Discrepancies between observed >85% increases in oyster density at the six empirically sampled reserves over a 3 yr time period (Puckett and Eggleston 2012) and model projections of a >35% declines in oyster density at the same reserves over the same time period suggests that reserve subpopulations received significant larval subsidies from non-reserve subpopulations (see *Observed vs. predicted metapopulation*

dynamics below). The reserve-centric focus of this study was justified by our interest in determining whether the reserve network was capable of supporting a persistent metapopulation, an important feature of reserve networks (Gaines et al. 2010). We are currently expanding the metapopulation modeling framework applied in this study by integrating demographics and connectivity of both restored and non-restored oyster subpopulations to assess the relative benefits of restoration and harvest protection to overall oyster metapopulation dynamics in Pamlico Sound.

Metapopulation and source-sink dynamics

Observed vs. predicted metapopulation dynamics. — We projected oyster abundance within the reserve network metapopulation to decline rapidly over a relatively short, 5 yr timeframe. Yet, empirical observations at six reserves indicated oyster densities increased by ~50-fold from an average of $\sim 40 \pm 27$ oysters/m² in 2002 to $\sim 1900 \pm 127$ oysters/m² in 2008 (Powers et al. 2009, Puckett and Eggleston 2012). We have observed declines in oyster density at two reserves (HA and OC) since 2008, but not the metapopulation-wide decline projected in model simulations (Eggleston and Puckett, unpublished data).

The discrepancy between projected decreases in oyster abundance in reserves and observed increases is likely due to larval “spill-in” to reserves from cultch-planting sites and natural oyster reefs, which was not modeled in this study. Despite greater potential larval output per m² from reserves as compared to harvested reefs, the much larger sound-wide areal coverage of harvested reefs in Pamlico Sound may yield potential larval output that is up to 500% greater than that from reserves (J. Peters, D. Eggleston, B. Puckett, unpublished manuscript). Support for larval spill-in to reserves from cultch-planting sites, as well as larval “spill-over” from reserves to cultch-planting sites was provided in our network design simulations (see *Few large or several small reserves?* below), which used the pool of cultch-planting sites as potential sites to add to the reserve network.

The interaction between harvested and protected subpopulations, and between different strategies within a restoration portfolio is encouraging from a restoration and management perspective. For instance, the spill-over of larvae

from reserves to harvested areas is an important function of reserves, with the potential to enhance fisheries if a reserve-based larval subsidy leads to an increase in the number of settlers in fished subpopulations, and if larval settlement, as opposed to habitat availability, is the limiting factor for the fishery (Chiappone and Sullivan Sealy 2000). However, the dependence of reserve subpopulations on recruitment subsidies from harvested oyster subpopulations is perilous given the rapid time scale over which oysters can become commercially extinct (Jackson et al. 2001, Beck et al. 2011). We contend that a more precautionary approach should be adopted, whereby the reserve network supports a self-persistent metapopulation. Metapopulation persistence and fisheries enhancement are not mutually exclusive management objectives for marine reserve networks, but the former is necessary to derive long-term benefits from the latter.

Relative importance of demographics vs. connectivity on source-sink dynamics.—The relative contribution of subpopulation demographics vs. connectivity on metapopulation and source-sink dynamics is often unequal (Bode et al. 2006, Figueira 2009, Carson et al. 2011). Our findings that source-sink dynamics were more sensitive to changes in demographic rates (primarily adult survival) than connectivity further generalize the conclusions of Figueira (2009) and Carson et al. (2011). In their studies and this one, local retention was generally equivalent to or greater than connectivity, which strengthened the coupling between subpopulation recruitment and reproduction. Accordingly, source-sink and metapopulation dynamics were primarily driven by demographics related to larval production and subsequent juvenile and adult survival. These studies highlight the need to more carefully consider spatiotemporal variation in demographic rates in restoration strategies, when assigning source-sink status, and in marine reserve network design.

Identifying the drivers of metapopulation dynamics can assist managers with targeting actions that provide the greatest restoration and conservation benefits (Crouse et al. 1987, Lipcius et al. 2008). Where metapopulation dynamics are most sensitive to adult survival and fecundity, such as our model oyster system, marine reserves that protect adults from harvest, thereby

increasing adult density and, ultimately, reproductive output, are likely to be an effective restoration strategy. In contrast, restoration actions such as stock enhancement that primarily target the juvenile component of the life stage, may be less effective. If, however, the ultimate goal is a self-persistent reserve network metapopulation, restoring demographics alone is likely not sufficient. A strategy more likely to be effective is designating reserves to improve demographics, and designing a complimentary reserve network that promotes connectivity. In support of this notion, reserves in our study system with relatively high “demographic potential” (as measured by λ ; Fig. 4) did not necessarily contribute proportionally to the reserve network metapopulation (as measured by λ_c). Reserves such as CH and CS, with relatively high demographic potential, always functioned as sinks. In contrast, a reserve such as OC, characterized by the lowest demographic potential of any reserve, was one of only four reserves to ever function as a source due to its location in the southern portion of Pamlico Sound where predominately southwesterly wind-driven dispersal promoted connectivity with reserves located to the north.

Stock enhancement

Stock enhancement provides one direct benefit—increased juvenile abundance—and one indirect benefit—increased reproductive output—that can increase the metapopulation abundance of a species (Wootton and Bell 1992, Lipcius et al. 2008). These benefits were apparent in our simulations, where the addition of millions of juvenile oysters that survived to produce billions of larvae increased mean metapopulation abundance. The effect of stock enhancement was greatest when source-sink dynamics were incorporated. For instance, metapopulation abundance was greatest when enhancement was conducted during May at source reserves (scenario 4 in Fig. 7c). The timing of enhancement during May likely optimizes the combination of oyster growth, survival, and fecundity by enabling oysters 0–15 mm to grow to relatively fecund sizes (50–70 mm) by the following May when seasonal per capita fecundity peaks.

Stock enhancement did not, however, contribute to the inherent persistence of the reserve

network metapopulation because a majority of the increased reproductive output was not subsequently retained within the network due to limited larval connectivity and local retention. Recent empirical tests of the efficacy of oyster stock enhancement in several of the same reserves examined in this study similarly concluded that stock enhancement was unsuccessful at increasing oyster density (Geraldi et al. 2013). Wootton and Bell (1992) observed a similar pattern with stock enhancement of Peregrine Falcon, whereby enhancement was successful at increasing population size, but did not contribute to population persistence. Stock enhancement may not be a viable restoration approach to improve network persistence, but it may be an effective strategy in concert with a FLOSS network design (see below) that increases retention of larvae within the network.

Few large or several small reserves?

We evaluated whether a few large or several small marine reserves promoted greater metapopulation retention of reserve-spawned larvae. In this context, our simulations suggested that marine reserve networks configured as several small reserves performed better, on average, than a few large reserves. Increasing the number of reserves in a “Several Small” network tended to promote rapid increases in inter-reserve connectivity, but had relatively little effect on local retention. As the number of several small reserves increased, so did symmetry among inter-reserve connections. Symmetrical connectivity is a desirable feature of marine reserve networks due to its importance to population persistence and ability to rescue declining reserve subpopulations (Hastings and Botsford 2006, Almany et al. 2009, Burgess et al. 2014).

In hydrodynamically advective-environments such as Pamlico Sound, two characteristics of a several small network design (relative to a few large design) likely promoted increased inter-reserve connectivity. First, increasing the number of reserves in the network increased the perimeter:area ratio of the reserve network. As the perimeter:area ratio increases, so should the probability of intercepting dispersing larvae (Eggleston et al. 1998, 1999), although knowledge of dispersal and connectivity patterns was necessary to take advantage of this network property (Fig. 9b vs. d). Adding several small reserves at random

was not a viable solution. Second, increasing the number of reserves in the network decreased the spacing between reserves. As the spacing between reserves approaches the mean dispersal distance of the target species, inter-reserve connectivity should increase (Shanks et al. 2003). Indeed, the mean spacing between reserves in the optimal 40-reserve network (10.6 km) was similar to the mean dispersal distance of oysters in Pamlico Sound (i.e., 10 km; Puckett et al. 2014).

Our results suggest that the best design strategy for promoting both inter-reserve connectivity and local retention may be a hybrid FLOSS design. Support for a hybrid design in this study originates from observed “diminishing returns” on metapopulation retention as the number of reserves in the several small network design continued to increase (Fig. 9c). As the number of reserves in the 80- and 100-reserve network scenarios began to approach the number of potential reserve sites (i.e., 187 cultch-planting sites), suboptimal sites with limited connectivity to and from existing reserves were added to the network. At this point, the several small and few large network designs were equivalent in their ability to retain reserve-spawned larvae within the metapopulation. In adopting a FLOSS design, our results suggest that it may be most prudent to first increase the number of reserves in the network because this step provides the biggest connectivity gain per reserve footprint area. As the number of reserves increases, the network design strategy should switch focus to increasing the size of certain reserves. The point at which the transition from increasing reserve number to increasing reserve size occurs warrants further investigation—this transition occurred in our study as the number of reserves in the network approached ~1/4 of the potential reserve sites. Identifying which reserves to increase in size is also uncertain, and we suggest that knowledge of reserve source-sink dynamics would play an important role in this determination.

Conclusions

We applied an empirically based, source-sink metapopulation modeling framework to evaluate the effectiveness of management strategies, including marine reserves, stock enhancement, and FLOSS, on the metapopulation persistence of a network of no-take oyster reserves within a

shallow, primarily wind-driven estuarine system. Integration of demographic rates and connectivity within a metapopulation framework provided a single parameter used to quantify reserve source-sink status (λ_c) and metapopulation growth rate (λ_M), thereby simplifying management decisions that can be contradictory if based on demographics or connectivity alone (Haase et al. 2012, Mroch et al. 2012, Puckett and Eggleston 2012). Marine reserves can be an effective restoration tool for improving demographic rates within reserve boundaries, but designation of multiple reserves does not guarantee a functional reserve network metapopulation. Both demographics and larval connectivity are important considerations to successful application of metapopulation concepts to the design of reserve networks.

ACKNOWLEDGMENTS

We are especially grateful to the following for their field assistance, provision of data, and general insights: R. Mroch, R. Rindone, G. Plaia, A. Haase, G. Bell, C. Durham, E. Millstein, J. Wiggs, M. Moorman, M. Radlinski, and J. Eggleston, C. Hardy, S. Slade, R. Weaver, J. Gao, and Climate Office of North Carolina. We are also grateful to K. Shertzer, N. Haddad, and one anonymous reviewer for critically reviewing an earlier version of this manuscript. Funding for this project was provided by a NMFS Sea Grant Population Dynamics Graduate Fellowship (to B. Puckett; NA08OAR4170764), a North Carolina Sea Grant (to D. Eggleston), the North Carolina Fisheries Resource Grant Program (to D. Eggleston; 06-EP-03, 07-EP-04), the Blue Crab Advanced Research Consortium via the University of Maryland (to D. Eggleston), an NSA Michael Castagna Student Grant for Applied Research (to B. Puckett), a Raleigh Saltwater Sportfishing Club Dale Ward Memorial Scholarship (to B. Puckett), and NSF (OCE-1155609).

LITERATURE CITED

- Almany, G. R., S. R. Connolly, D. D. Heath, J. D. Hogan, G. P. Jones, L. J. McCook, M. Mills, R. L. Pressey, and D. H. Williamson. 2009. Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. *Coral Reefs* 28:339–351.
- Beck, M. W., et al. 2011. Oyster reefs at risk and recommendations for conservation, restoration, and management. *BioScience* 61:107–116.
- Bode, M., L. Bode, and P. R. Armsworth. 2006. Larval dispersal reveals regional sources and sinks in the Great Barrier Reef. *Marine Ecology Progress Series* 308:17–25.
- Botsford, L. W., J. W. White, M.-A. Coffroth, C. B. Paris, S. Planes, T. L. Shearer, S. R. Thorrold, and G. P. Jones. 2009. Connectivity and resilience of coral reef metapopulations in marine protected areas: matching empirical efforts to predictive needs. *Coral Reefs* 28:327–337.
- Burgess, S. C., K. J. Nickols, C. D. Griesemer, L. A. K. Barnett, A. G. Dedrick, E. V. Satterthwaite, L. Yamane, S. G. Morgan, J. W. White, and L. W. Botsford. 2014. Beyond connectivity: how empirical methods can quantify population persistence to improve marine protected-area design. *Ecological Applications* 24:257–270.
- Burkenroad, M. D. 1931. Sex in the Louisiana oyster, *Ostrea virginica*. *Science* 74:71–72.
- Caley, M. J., M. H. Carr, M. A. Hixon, T. P. Hughes, G. P. Jones, and B. A. Menge. 1996. Recruitment and the local dynamics of open marine populations. *Annual Review of Ecology and Systematics* 27:477–500.
- Carriker, M. R. 1951. Ecological observations on the distribution of oyster larvae in New Jersey estuaries. *Ecological Monographs* 21:19–38.
- Carson, H. S., G. S. Cook, P. C. Lopez-Duarte, and L. A. Levin. 2011. Evaluating the importance of demographic connectivity in a marine metapopulation. *Ecology* 92:1972–1984.
- Caswell, H. 2001. *Matrix population models: construction, analysis, and interpretation*. Second. Sinauer Associates, Sunderland, Massachusetts, USA.
- Chiappone, M., and K. M. Sullivan Sealy. 2000. Marine reserve design criteria and measures of success: lessons learned from the Exuma Cays Land and Sea Park, Bahamas. *Bulletin of Marine Science* 66:691–705.
- Coen, L. D., and M. W. Luckenbach. 2000. Developing success criteria and goals for evaluating oyster reef restoration: ecological function or resource exploitation? *Ecological Engineering* 15:323–343.
- Cox, C., and R. Mann. 1992. Temporal and spatial changes in fecundity of Eastern oysters, *Crassostrea virginica* (Gmelin, 1791), in the lower James River, Virginia, USA. *Journal of Shellfish Research* 11:49–54.
- Crouse, D., L. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology* 68:1412–1423.
- Crowder, L. B., S. J. Lyman, W. F. Figueira, and J. Priddy. 2000. Source-sink population dynamics and the problem of siting marine reserves. *Bulletin of Marine Science* 66:799–820.
- Deksheniaks, M. M., E. E. Hofmann, J. M. Klinck, and E. N. Powell. 1996. Modeling the vertical distribution of oyster larvae in response to environmental conditions. *Marine Ecology Progress Series* 136:97–110.

- Deksheniaks, M. M., E. E. Hofmann, J. M. Klinck, and E. N. Powell. 1997. A modeling study of the effects of size- and depth-dependent predation on larval survival. *Journal of Plankton Research* 19:1583–1598.
- Diamond, J. M. 1975. The island dilemma: lessons of modern biogeographic studies for the desing of natural reserves. *Biological Conservation* 7:129–146.
- Diffendorfer, J. E. 1998. Testing models of source-sink dynamics and balanced dispersal. *Oikos* 81:417–433.
- Eggleston, D. B., L. L. Etherington, and W. E. Elis. 1998. Organism response to habitat patchiness: species and habitat-dependent recruitment of decapod crustaceans. *Journal of Experimental Marine Biology and Ecology* 223:111–132.
- Eggleston, D. B., W. E. Elis, L. L. Etherington, C. P. Dahlgren, and M. H. Posey. 1999. Organism responses to habitat fragmentation and diversity: habitat colonization by estuarine macrofauna. *Journal of Experimental Marine Biology and Ecology* 236:107–132.
- Eggleston, D. B., N. B. Reyns, L. L. Etherington, G. R. Plaia, and L. Xie. 2010. Tropical storm and environmental forcing on regional blue crab (*Callinectes sapidus*) settlement. *Fisheries Oceanography* 19:89–106.
- Eggleston, D. B., B. Efland, G. R. Plaia, B. J. Puckett, R. Rindone, and K. Pierson. 2011. Ecological performance and recreational fishing impacts of large-scale, sub-tidal oyster restoration. NOAA/ARRA and NC Coastal Federation, Newport, North Carolina, USA.
- Figueira, W. F. 2009. Connectivity or demography: defining sources and sinks in coral reef fish metapopulations. *Ecological Modelling* 220:1126–1137.
- Figueira, W. F., and L. B. Crowder. 2006. Defining patch contribution in source-sink metapopulations: the importance of including dispersal and its relevance to marine systems. *Population Ecology* 48:215–224.
- Gaines, S. D., C. White, M. H. Carr, and S. R. Palumbi. 2010. Designing marine reserve networks for both conservation and fisheries management. *Proceedings of the National Academy of Sciences USA* 107:18286–18293.
- Geraldi, N. R., M. Simpson, S. R. Fegley, P. Holmlund, and C. H. Peterson. 2013. Addition of juvenile oysters fails to enhance oyster reef development in Pamlico Sound. *Marine Ecology Progress Series* 480:119–129.
- Haase, A. T., D. B. Eggleston, R. A. Luettich, R. J. Weaver, and B. J. Puckett. 2012. Estuarine circulation and predicted oyster larval dispersal among a network of reserves. *Estuarine, Coastal and Shelf Science* 101:33–43.
- Hanski, I. 1998. Metapopulation dynamics. *Nature* 396:41–49.
- Hanski, I., and M. Gilpin. 1991. Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society* 42:3–16.
- Hastings, A., and L. W. Botsford. 2006. Persistence of spatial populations depends on returning home. *Proceedings of the National Academy of Sciences USA* 103:6067–6072.
- Hill, M. F., J. D. Witman, and H. Caswell. 2002. Spatio-temporal variation in Markov chain models of subtidal community succession. *Ecology Letters* 5:665–675.
- Jackson, G. A., and R. R. Strathmann. 1981. Larval mortality from offshore mixing as a link between precompetent and competent periods of development. *American Naturalist* 118:16–26.
- Jackson, J. B. C., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–638.
- Jones, G. P., G. R. Almany, G. R. Russ, P. F. Sale, R. S. Steneck, M. J. H. van Oppen, and B. L. Willis. 2009. Larval retention and connectivity among populations of corals and reef fishes: history, advances, and challenges. *Coral Reefs* 28:307–325.
- Kennedy, V. S. 1996. Biology of larvae and spat. Pages 371–411 in V. S. Kennedy, R. I. E. Newell, and A. F. Eble, editors. *The eastern oyster Crassostrea virginica*. Maryland Sea Grant College, College Park, Maryland.
- Kritzer, J. P., and P. F. Sale. 2004. Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science. *Fish and Fisheries* 5:131–140.
- Laing, I., P. Walker, and F. Areal. 2006. Return of the native: Is European oyster (*Ostrea edulis*) stock restoration in the UK feasible? *Aquatic Living Resources* 19:283–287.
- Lester, S. E., B. S. Halpern, K. Grorud-Colvert, J. Lubchenco, B. I. Ruttenberg, S. D. Gaines, S. Airame, and R. R. Warner. 2009. Biological effects within no-take marine reserves: a global synthesis. *Marine Ecology Progress Series* 384:33–46.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15:237–240.
- Levitan, D. R. 1991. Influence of body size and population density on fertilization success and reproductive output in a free-spawning invertebrate. *Biological Bulletin* 181:261–268.
- Lewis, C. V. W. 1997. Biological-physical interactions on Georges Bank: plankton transport and population dynamics of the ocean quahog, *Arctica islandica*. Woods Hole Oceanographic Institution and Massachusetts Institute of Technology, Woods Hole, Massachusetts, USA.

- Lipcius, R. N., D. B. Eggleston, S. J. Schreiber, R. D. Seitz, J. Shen, M. Sisson, W. T. Stockhausen, and H. V. Wang. 2008. Importance of metapopulation connectivity to restocking and restoration of marine species. *Reviews in Fisheries Science* 16:101–110.
- Lu, G. Y., and D. W. Wong. 2008. An adaptive inverse-distance weighting spatial interpolation technique. *Computers and Geosciences* 34:1044–1055.
- Luettich, R. A., S. D. Carr, J. V. Reynolds-Fleming, C. W. Fulcher, and J. E. McNinch. 2002. Semi-diurnal seiching in a shallow, micro-tidal lagoonal estuary. *Continental Shelf Research* 22:1669–1681.
- McMurray, S. E., T. P. Henkel, and J. R. Pawlik. 2010. Demographics of increasing populations of the giant barrel sponge *Xestospongia muta* in the Florida Keys. *Ecology* 91:560–570.
- McNeill, S. E., and P. G. Fairweather. 1993. Single large or several small marine reserves? An experimental approach with seagrass fauna. *Journal of Biogeography* 20:429–440.
- Molony, B. W., R. Lenanton, G. Jackson, and J. Norriss. 2003. Stock enhancement as a fisheries management tool. *Reviews in Fish Biology and Fisheries* 13:409–432.
- Mroch, R. M., D. B. Eggleston, and B. J. Puckett. 2012. Spatiotemporal variation in oyster fecundity and reproductive output in a network of no-take reserves. *Journal of Shellfish Research* 31:1091–1101.
- Narvaez, D. A., J. M. Klinck, E. N. Powell, E. E. Hofmann, J. Wilkin, and D. B. Haidvogel. 2012. Circulation and behavior controls on dispersal of eastern oyster (*Crassostrea virginica*) larvae in Delaware Bay. *Journal of Marine Research* 70:411–440.
- Nicol, S. C., and H. P. Possingham. 2010. Should metapopulation restoration strategies increase patch area or number of patches? *Ecological Applications* 20:566–581.
- North, E. W., Z. Schlag, R. R. Hood, M. Li, L. Zhong, T. Gross, and V. S. Kennedy. 2008. Vertical swimming behavior influences the dispersal of simulated oyster larvae in a coupled particle-tracking and hydrodynamic model of Chesapeake Bay. *Marine Ecology Progress Series* 359:99–115.
- Palumbi, S. R. 2004. Marine reserves and ocean neighborhoods: the spatial scale of marine populations and their management. *Annual Review of Environment and Resources* 29:31–68.
- Paris, C. B., L. M. Cherubin, and R. K. Cowen. 2007. Surfing, spinning, or diving from reef to reef: effects on population connectivity. *Marine Ecology Progress Series* 347:285–300.
- Paynter, K. T., V. Politano, H. A. Lane, S. M. Allen, and D. Meritt. 2010. Growth rates and prevalence of *Perkinsus marinus* in restored oyster populations in Maryland. *Journal of Shellfish Research* 29:309–317.
- Pietrafesa, L. J., G. S. Janowitz, T.-Y. Chao, R. H. Weisberg, F. Askari, and E. Noble. 1986. The physical oceanography of Pamlico Sound. NC Sea Grant, Raleigh, North Carolina, USA.
- Powers, S. P., C. H. Peterson, J. H. Grabowski, and H. S. Lenihan. 2009. Success of constructed oyster reefs in no-harvest sanctuaries: implications for restoration. *Marine Ecology Progress Series* 389:159–170.
- Puckett, B. J., and D. B. Eggleston. 2012. Oyster demographics in a network of no-take reserves: recruitment, growth, survival, and density dependence. *Marine and Coastal Fisheries* 4:605–627.
- Puckett, B. J., D. B. Eggleston, P. C. Kerr, and R. A. Luettich. 2014. Larval dispersal and population connectivity among a network of marine reserves. *Fisheries Oceanography* 23:342–361.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–661.
- Reyns, N. B., D. B. Eggleston, and R. A. Luettich. 2006. Dispersal of early juvenile blue crabs within a wind-driven estuary. *Limnology and Oceanography* 51:1982–1995.
- Reyns, N. B., D. B. Eggleston, and R. A. Luettich. 2007. Dispersal dynamics of post-larval blue crabs, *Callinectes sapidus*, within a wind-driven estuary. *Fisheries Oceanography* 16:257–272.
- Roberts, C. M. 1998. Sources, sinks, and the design of marine reserve networks. *Fisheries* 23:16–19.
- Runge, J. P., M. C. Runge, and J. D. Nichols. 2006. The role of local populations within a landscape context: defining and classifying sources and sinks. *The American Naturalist* 167:925–938.
- Sale, P. F., I. Hanski, and J. P. Kritzer. 2006. The merging of metapopulation theory and marine ecology: establishing the historical context. Page 544 in J. P. Kritzer, and P. F. Sale, editors. *Marine metapopulations*. Elsevier Academic Press, Burlington, Massachusetts.
- Shanks, A. L., B. A. Grantham, and M. H. Carr. 2003. Propagule dispersal distance and the size and spacing of marine reserves. *Ecological Applications* 13:S159–S169.
- Simberloff, D., and L. G. Abele. 1982. Refuge design and island biogeographic theory—effects of fragmentation. *The American Naturalist* 120:41–50.
- Spalding, M., L. Wood, C. Fitzgerald, and K. Gjerde. 2010. The 10% target: where do we stand. Page 96 in C. Toropova, I. Meliane, D. Laffoley, E. Matthews, and M. Spalding, editors. *Global ocean protection: present status and future possibilities*. IUCN, Gland, Switzerland, The Nature Conservancy, Arlington, USA, UNEP-WCMC, Cambridge, UK, UNEP, Nairobi, Kenya, UNU-IAS, Tokyo, Japan, Agence des aires marines protégées, Brest, France.
- Stockhausen, W. T., and R. N. Lipcius. 2001. Single large or several small marine reserves for the

- Caribbean spiny lobster? *Marine and Freshwater Research* 52:1605–1614.
- Wootton, J. T., and D. A. Bell. 1992. A metapopulation model of the peregrine falcon in California—viability and management strategies. *Ecological Applications* 2:307–321.
- Xie, L., and D. B. Eggleston. 1999. Computer simulations of wind-induced estuarine circulation patterns and estuary-shelf exchange processes: the potential role of wind forcing on larval transport. *Estuarine Coastal and Shelf Science* 49:221–234.
- Zohar, Y., et al. 2008. The Chesapeake Bay blue crab (*Callinectes sapidus*): a multidisciplinary approach to responsible stock replenishment. *Reviews in Fisheries Science* 16:24–34.