REPORT DOCUMENTATION PAGE	*Form Approved* *OMB No. 0704-0188*

1. REPORT DATE *(DD-MM-YYYY)* 11-05-2015

2. REPORT TYPE Journal Article

3. DATES COVERED *(From - To)*

4. TITLE AND SUBTITLE
Transport of blue crab larvae in the northern Gulf of Mexico during the Deepwater Horizon oil spill

5a. CONTRACT NUMBER

5b. GRANT NUMBER

5c. PROGRAM ELEMENT NUMBER

5d. PROJECT NUMBER

5e. TASK NUMBER

5f. WORK UNIT NUMBER
73-4799-02-5

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8. PERFORMING ORGANIZATION REPORT NUMBER
NRL/JA/7320--13-1796

9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES)
Office of Naval Research
One Liberty Center
875 North Randolph Street, Suite 1425
Arlington, VA 22203-1995

10. SPONSOR/MONITOR'S ACRONYM(S)
Univ of Miami

11. SPONSOR/MONITOR'S REPORT NUMBER(S)

12. DISTRIBUTION/AVAILABILITY STATEMENT
Approved for public release, distribution is unlimited.

13. SUPPLEMENTARY NOTES

14. ABSTRACT

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15. SUBJECT TERMS
Lagrangian particle tracking · Graph-theoretic metric · Shannon index · Vertex degree · Betweenness centrality · Potential connectivity

16. SECURITY CLASSIFICATION OF: a. REPORT	b. ABSTRACT	c. THIS PAGE	17. LIMITATION OF ABSTRACT	18. NUMBER OF PAGES	19a. NAME OF RESPONSIBLE PERSON
Unclassified	Unclassified	Unclassified	UU	14	Dong Shan Ko

19b. TELEPHONE NUMBER *(Include area code)*
(228) 688-5448

Reset

13-1231-1925

PUBLICATION OR PRESENTATION RELEASE REQUEST

Pubkey: 8837 NRLINST 5600.2

Ref: (a) NRL Instruction 5600.2
(b) NRL Instruction 5510.40D

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( ) Journal article (not refereed)
( ) Oral Presentation, not published

STRN NRL/JA/7320-13-1796
Route Sheet No. 7320/
Job Order No. 73-4799-02-5
Classification X U C
Sponsor U of Miami
approval obtained ___ yes X no

Title of Paper or Presentation
Potential Population Connectivity of Blue Crabs (Callinectes sapidus) in the Northern Gulf of Mexico Using Lagrangian Particle-tracking and Graph-theory

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It is intended to offer this paper to the ____________________
(Name of Conference)

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and/or for publication in **Marine Ecology Progress Series, Unclassified** ____________________
(Name and Classification of Publication) (Name of Publisher)

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It is the opinion of the author that the subject paper (is ____) (is not X) classified, in accordance with reference (b).
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CODE	SIGNATURE	DATE	COMMENTS
Author(s) Ko	Dong Shan Ko	06/06/13	Need by 21 Jun 13
			Publicly accessible sources used for this publication
			This is a Final Security Review. Any changes made in the document, after approved by Code 1231, nullify the Security Review.
Section Head Allard	R. Allard	6-6-13	
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Security, Code 1231		6/11/13	1. Paper or abstract was released. 2. A copy is filed in this office.
Office of Counsel, Code 1008.3	Kathy Chapman	6/14/13	Sponsor Approval Attached
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Public Affairs (Unclassified/ Unlimited Only), Code 7030.4	Shannon Mensi	6-12-13	
Division, Code			
Author, Code			

HQ-NRL 5511/6 (Rev. 12-98) (e)

THIS FORM CANCELS AND SUPERSEDES ALL PREVIOUS VERSIONS

Vol. 527: 143–156, 2015
doi: 10.3354/meps11238

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published May 7

Transport of blue crab larvae in the northern Gulf of Mexico during the Deepwater Horizon oil spill

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ABSTRACT: To better understand population connectivity of the blue crab *Callinectes sapidus* and how it may have been affected by the Deepwater Horizon oil spill, we simulated larval dispersal with a biophysical model of the coastal waters from western Louisiana to the Florida panhandle. We investigated connectivity patterns, intra-annual variability, and potential impacts of the Deepwater Horizon oil spill during the spring and summer of 2010. Overall, we found that the Mississippi River delta (MRD) is a barrier to dispersal, and that local retention was high; of the 7.7% of larvae that successfully settled, 37.5% returned to their natal estuary and 28.5% to an adjacent one. We used network metrics to assess the overall diversity of population connectivity and the importance of individual estuaries to maintaining connectivity. The proportion of larvae that successfully settle does not significantly change during the spawning season, but connectivity among estuaries significantly declines. Estuaries near the MRD were most important for maintaining connectivity, likely because they were the primary source of the few larvae that crossed the MRD. These patterns influence the distribution of settlement locations for larvae that were potentially exposed to oil. A total of 38.1% of the simulated larvae were potentially exposed to oil, and these larvae were concentrated on the eastern side of the MRD. For some spawning events, up to 96.3% of the larvae that successfully settled east of the MRD were potentially exposed to oil, which may have substantial implications for population dynamics. These results provide quantitative predictions regarding blue crab connectivity in the northern Gulf of Mexico that can be corroborated with data. The predictions can be applied for disaster management planning and for management of this environmentally and economically important species.

KEY WORDS: Lagrangian particle tracking · Graph-theoretic metric · Shannon index · Vertex degree · Betweenness centrality · Potential connectivity

INTRODUCTION

Connectivity has been identified as an important driver of population dynamics in theoretical (Hastings & Harrison 1994, Botsford et al. 2001, Hastings & Botsford 2006, Bode et al. 2008, Kininmonth et al. 2010b) and empirical studies (Meynecke et al. 2008, Rooker et al. 2008, Hinrichsen et al. 2011) of marine populations. Population connectivity may be defined as the successful exchange of individuals among spatially separated sub-populations that constitute a single metapopulation (Cowen et al. 2007). It includes the rate, extent, and spatial structure of such exchange (Cowen et al. 2006), as well as the tempo-

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ral variance of these components. High levels of connectivity may increase resilience to local overharvesting and local disturbances (Strathmann et al. 2002), adaptability to climate change through migration (Peterson et al. 2002, Harley et al. 2006), and adaptability to regional level shifts via gene flow and genetic diversity (Bohonak 1999, Garant et al. 2007). High connectivity thus decreases the impact of local, regional, and global disturbances on the population (Cowen & Sponaugle 2009).

For many marine organisms, dispersal occurs primarily during a planktonic larval phase (Kinlan & Gaines 2003). Studying movements of these larvae in the field is challenging because of their small size and high natural mortality rates. Direct estimates of larval connectivity can sometimes be obtained using mark-recapture of artificially tagged larvae (Thorrold et al. 2002) or by analyzing geochemical signatures in calcified structures (Thorrold et al. 2007). However, applying these methods is difficult or impossible for some taxa, particularly crustacean larvae, which contain no calcified parts and molt frequently. Indirect estimates of connectivity can be obtained using genetic markers, although the costs required for developing appropriate genetic markers are prohibitively high for most researchers at this time (Hedgecock et al. 2007). Lagrangian particle tracking is an increasingly common method for estimating potential connectivity that can be applied to a wide variety of taxa. This method simulates the movement of individual particles ('larvae') through hydrological flow fields. Applications of Lagrangian particle tracking to larval dispersal have been facilitated by advances in computing and the availability of high-resolution hydrodynamic data sets. These models have been used by many studies for a variety of applications. Examples include estimating the proportion of larvae locally retained (Cowen et al. 2000), investigating how larval behavior influences dispersal distance (Paris et al. 2007, North et al. 2008), and determining the optimal spatial design of marine reserves (Hinrichsen et al. 2009, Costello et al. 2010, Kininmonth et al. 2011).

In this study, we coupled a Lagrangian particle-tracking model to output from a high-resolution hydrodynamic model to estimate potential connectivity of the blue crab *Callinectes sapidus* in the northern Gulf of Mexico (nGOM). The blue crab is an abundant, estuarine-dependent species in the western Atlantic and Gulf of Mexico (GOM), where it supports profitable commercial and recreational fisheries (Guillory et al. 2001). Blue crab fisheries were once considered inexhaustible because of the crab's high fecundity and rapid growth rates, but recent declines in the historically strong Chesapeake Bay stock has highlighted the need for better management of this species (Miller et al. 2005). In the US GOM, the stock fluctuates from year to year (Van Voorhees 2012), but there has been no apparent downward trend in blue crab abundance, and the industry has recently been certified as sustainable by the Marine Stewardship Council (DeAlteris et al. 2012). Currently, the US GOM blue crab stock is managed at the state level as 5 separate fisheries (Texas, Louisiana, Mississippi, Alabama, and Florida), but the spatial structure of the blue crab population and degree of dispersal between the states is unknown. Decades of research in the areas surrounding the Delaware and Chespeake Bays demonstrated that blue crab larvae are most likely to recruit to their natal bay (Epifanio & Tilburg 2008), but connectivity in the nGOM may be different because nearshore circulation in the nGOM is primarily driven by wind, outflow from the Mississippi River, and intrusions of the Loop Current and its periodic eddies (Ward 1980). Some previous genetic studies have found evidence for overall Gulf-wide panmixia (McMillen-Jackson & Bert 2004), but others have found evidence for significant structure over shorter spatial and temporal scales (Kordos & Burton 1993, Darden 2004, Yednock & Neigel 2014). This suggests that long-distance dispersal occurs frequently enough to keep the populations panmictic, but also that dispersal could be limited at scales relevant to ecological processes.

We ran simulations over the course of April to October 2010 over a spatial domain of coastal waters from western Louisiana to the Florida panhandle. The spatial extent and time frame allowed us to estimate potential effects of the Deepwater Horizon (DWH) oil spill. The DWH spill, the largest accidental marine oil spill in US history (Graham et al. 2011), started when the DWH oil platform, situated 80 km southeast of Venice, Louisiana, exploded and sank on 20 April 2010. An estimated 4.0 million barrels of oil were subsequently released from the broken wellhead at a depth of 1500 m until the well was capped on 15 July 2010. Much of the oil remained deep, but about 50% rose to the sea surface, forming slicks that were visible in satellite imagery (Peterson et al. 2012). We expect that blue crab larvae came into contact with the surface oil because they are surface-dwelling organisms, found at depths of 1–3 m (Epifanio & Tilburg 2008), and the release of oil occurred during their primary spawning season (Guillory et al. 2001).

A variety of methods are available for extracting meaningful information from the output of Lagrangian particle-tracking models; we present our analysis in the context of graph theory. Graph theory is a field of mathematics that analyzes the encoding and properties of the connections among a set of discrete objects, and the field offers many usable metrics for analysis of Lagrangian model output. Graph-level metrics, such as diameter, degree distribution, and minimum path length, have been used in a small number of marine studies to characterize the structure of networks (Treml et al. 2008, Kininmonth et al. 2010a, 2011, Holstein et al. 2014), and are widely used for the assessment of connectivity patterns in other fields. Other metrics are used to identify important vertices within the network. These include basic metrics such as the number of settlers arriving to (destination strength) or coming from (source strength) a particular vertex (Mitarai et al. 2009, Watson et al. 2010), and measures of centrality that consider the importance of a vertex to the entire network (e.g. closeness centrality, betweenness centrality, eigenvalue centrality; Treml et al. 2008, Kininmonth et al. 2010a, Watson et al. 2011). Although many of the graph metrics have equivalent operations in linear algebra or other fields of mathematics, presenting the results in the context of graph theory retains the ecological interpretation of our system as a network of interconnected populations. In this study, we generated a small network with 14 vertices, where the vertices represent estuaries in the nGOM and the edges between vertices represent the probability of larvae traveling between pairs of estuaries. We generate overall connectivity matrices for the network from our simulations. To estimate the importance of individual estuaries in maintaining connectivity throughout the region, we calculate betweenness centrality (the proportion of the most probable pathways that pass through each vertex) for each estuary. To quantify the overall level of connectivity in the network, we use a combination of average vertex degree, average vertex source strength, and average vertex Shannon index. The vertex out-degree and vertex source strength are measures of the route-specific flux through a vertex (Rayfield et al. 2011), and the Shannon index measures the topological diversity of the network (Eagle et al. 2010). Vertex degree is the number of possible destinations for particles that originate at that vertex. Source strength is the sum of these outgoing edges and represents the probability that a particle released at that vertex will successfully settle. The Shannon index combines these indices into a single metric that quantifies both the number and evenness of the dispersal probabilities. It was originally derived as an entropy measure of the maximum amount of information that can be transmitted in a finite length message (Shannon 1948), and has been applied in ecology as a measure of species diversity (Good 1953, Margalef 1958) and community stability (MacArthur 1955). We apply it to measuring metapopulation stability. In a graph-theoretic context, the Shannon index for a vertex is maximized for a fully and uniformly connected vertex. A vertex with fewer connections or a non-uniform distribution of larvae traversing each outbound connection will have a lower Shannon index.

Using these techniques, we describe and quantify the patterns of population connectivity for *C. sapidus* in the nGOM and investigate how those patterns may have been influenced by larval exposure to oil from the DWH oil spill. We examine the locations of settlement of larvae that were potentially exposed to oil. Using graph metrics, we quantify the connectivity and the changes in connectivity over the course of a single season, and the importance of different regions to maintaining connectivity. Using sensitivity analyses, we demonstrate that our main conclusions are robust to assumptions made by our model.

METHODS

We modeled larvae as planktonic particles and simulated their movement using a Lagrangian Individual Based Model (IBM), then assessed the potential dispersal patterns and destinations of larvae whose trajectories crossed surface oil slicks from the DWH oil spill.

Hydrodynamic model

The IBM is forced by oceanographic data from the Northern Gulf of Mexico Nowcast/Forecast System (NGOMNFS). NGOMNFS is a free surface, data-assimilating, hydrodynamic model based upon NCOM (Martin et al. 2009) that solves the primitive equations for incompressible, hydrostatic flow with the finite difference method (http://www7320.nrlssc.navy.mil/IASNFS_WWW/NGOMNFS_WWW/NGOMNFS.html; Ko et al. 2008). The inputs to NGOMNFS include bathymetry that is based upon the 2-min resolution NRL DBDB2 data set and improved with 1-min resolution NOAA NGDC data, and NGOMNFS assimilates sea surface height from satellite altimeters (GFO-1, Jason-1, and ERS-2) and sea surface temperature from MODIS and AVHRR via the NRL MODAS (Fox et al. 2003). Three-hourly wind stress, sea-level air pressure and heat fluxes from NOGAPS and COAMPS atmospheric prediction systems are applied for surface forcing. Tidal forcing and freshwater discharges from 112 rivers or runoff points are also applied, and open boundary conditions are provided by the large-scale Intra-Americas Sea Nowcast/Forecast System (Ko et al. 2003). NGOMNFS produces hourly 1/72° (~1.9 km) 3D current velocity, temperature, and salinity nowcasts for the nGOM above 27.5° N and from 92° W to 86° W at 37 vertical sigma levels. NGMONFS output is available from 2001 until the present. Validation with NOAA tidal observations shows that NGOMNFS performs very well in the prediction of tides and subtidal wind-driven sea-level variation (r ~ 0.9), and NGOMNFS output has been applied in various studies (e.g. D'Sa & Ko 2008, Green et al. 2008).

Individual-based model

The IBM advects and diffuses particles in 3 dimensions, and implements swimming behavior that restricts larvae to the surface layer. Particle trajectories are advected using a 4th-order Runga-Kutta scheme and fixed hourly time step. Within each grid cell, velocities are interpolated to the particle position using a tri-linear interpolation. Although linear interpolations are divergent, the NGOMNFS output is of high resolution, and the interpolation errors are minor relative to the broader problem of how well the ocean model simulates the ocean dynamics. Therefore, we used the computationally efficient linear interpolation scheme. Sub-grid-scale diffusion is simulated using a random flight model, as has been done in similar studies (Marinone et al. 2004, Johnson et al. 2013). The random flight model assumes that sub-grid-scale turbulence is isotropic in the horizontal direction. It uses normally distributed random samples, the time step duration, and a diffusion coefficient to adjust the particle position in the x and y directions at each time step. We chose a diffusion coefficient of 1.21 m^2 s^{-1} based upon the linear relationship between length scale and diffusion presented by Okubo (1971) and the characteristics of NGOMNFS. In addition to the passive advection and diffusion of particles, we implemented vertical swimming behavior that maintains them near the surface because field and laboratory studies show that the larvae inhabit surface water throughout their larval development (Epifanio 1988, Epifanio & Tilburg 2008). In the model, if the depth of a larva was at least 2 m, then a simple linear function of $z_{t+1} = 0.1z_t$ was applied, where z_t is the vertical position of the larva at time t. This formulation assumes that larvae swim upward more forcefully in response to increased downward transport. This function is consistent with the zoeal swimming speeds of 0.005 m s^{-1} measured by Sulkin et al. (1980).

Using this IBM together with spawning and larval behavior parameters from the known natural history of blue crabs, we ran 24 simulations of blue crab dispersal. Exact spawning locations are mostly unknown in the nGOM (but see Gelpi et al. 2009), so we released larvae throughout the plausible region of potential sites. We identified locations within the NGOMNFS domain of 3–10 m depth and at least 22 ppt salinity, which are the known conditions necessary for blue crab spawning (Guillory et al. 2001, Rittschof et al. 2010). The release points were a uniform grid of 200 potential spawning locations throughout this region (Fig. 1). Assessing population connectivity patterns requires us to quantify both larval dispersal and the movements of ovigerous females from estuaries to spawning habitat. During the analyses, we assume that each spawning site may contain spawning females from any estuary within 100 km, and that the proportion of females from each estuary is inversely proportional to the distance between the estuary and the spawning site. For example, a spawning location that was 75 km from estuary i and 25 km from estuary j would be assumed to have 25% of its larvae sourced from i and 75% from j. Because the choice of migration distance for ovigerous females was arbitrary, we performed a sensitivity analysis to this parameter.

Each of the 24 simulations began at the local nocturnal ebbing tide (Provenzano et al. 1983) on the date of each quarter of the moon phase, to match the observed highest spawning events (Ziegler 2002) from 1 April 2010 until 30 September 2010, which is the primary spawning season for blue crabs in the nGOM (Guillory et al. 2001). For each spawning site, tide data were obtained for the closest location available on the NOAA Tides and Currents database (https://tidesandcurrents.noaa.gov).

At each of the 200 spawning sites, we simulated the release and subsequent hourly movements of 10000 super-individuals. Each super-individual is assumed to represent a large number of larvae, which has been used in prior studies where the number of larvae spawned each year greatly exceeds computational capacities (Scheffer et al. 1995, Woods 2005, Tian et al. 2009). Larvae, once spawned, are assumed

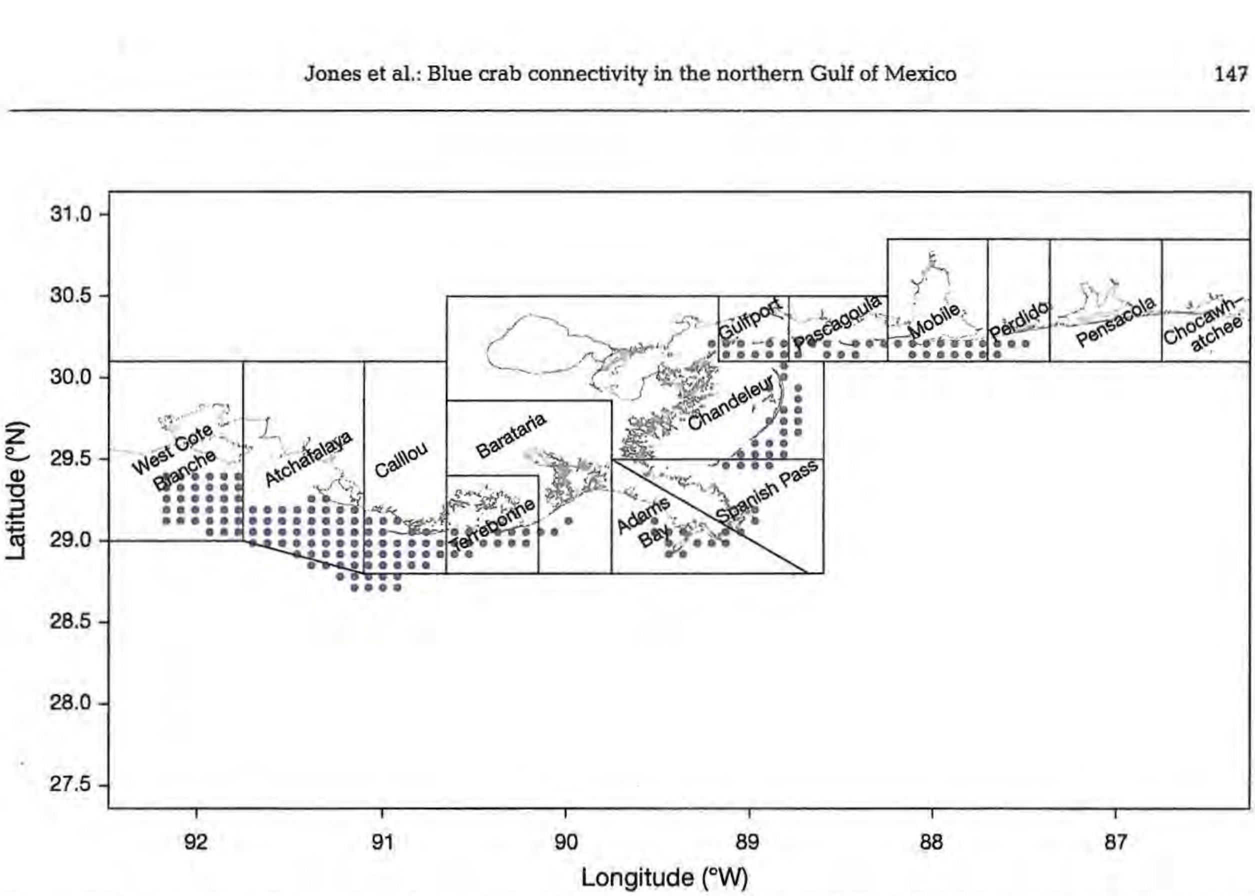

Fig. 1. The study region. The Northern Gulf of Mexico Nowcast/Forecast System model includes the coastal waters north of 27.5° N and between 92° W and 86° W. The 14 labeled estuaries represent our division of adult habitat. We assume that ovigerous female crabs (*Callinectes sapidus*) migrate from these estuaries to the spawning sites that are indicated by blue dots. The boxes surrounding each estuary depict the settlement area. Additional details about the spawning and settlement criteria are provided in the 'Individual-based model' section of the text

to remain within the plankton for at least 27 d, which is the average larval development period observed in the laboratory (Zmora et al. 2005). Larvae are deemed to settle if between 27 and 60 d after spawning they are in water with a depth of less than 0.5 m. We assume that all post-larvae (megalopae) in shallow, nearshore waters are able to maneuver to a suitable settlement site via their well-documented selective tidal-stream transport mechanism (reviewed in Forward et al. 2003).

We divided the model domain into 14 estuaries as shown in Fig. 1 based upon the locations where juvenile and adult crabs are known to live. These estuaries were divided based upon the major topographic features in the region. The spawning habitat was divided among estuaries according to geographic distance as described above. Each larva that met the other criteria for settlement was deemed to settle in the nearest estuary as defined by the boundaries in Fig. 1. Neither larval development nor mortality are incorporated in the IBM; however, any larvae that fail to settle in an estuary in 60 d are assumed to either be carried by alongshore currents over the western or eastern boundaries of the model, entrained in offshore currents and carried to the deep sea off the southern boundary, or trapped by local currents offshore but within the model boundaries.

Basic dispersal metrics measured or tracked included total proportion of larvae that successfully settled into estuaries, fates of those larvae that failed to settle, and the dispersal distance for each larva. Absolute expected larvae dispersal distance from each spawning location was calculated by averaging the migration distances of successfully settled larvae in all model runs. We visually examined the larval transport trajectories and described how these patterns relate to published descriptions of the circulation patterns in the nGOM.

Metapopulation structure

We populated 24 potential connectivity matrices $\mathbf{P}_t$ whose elements p_{ij} are the proportion (probability) of larvae from source estuary i that settled in estuary j for each simulated spawning date t. The elements of the overall potential connectivity matrix $\mathbf{P}$ are the proportions of all larvae averaged across all 24 spawning dates. From the connectivity matrices, we also populated an oceanographic distance matrix $\mathbf{D}$. The elements d_{ij} are given by:

$$d_{ij} = \ln\left(\frac{1}{s \cdot p_{ij}}\right) \tag{1}$$

where s is the step discount factor that accounts for post-settlement survival and recruitment. The oceanographic distance d_{ij} is short when the probability of moving from estuary i to estuary j is high. The probability that an individual will follow an n step pathway through multiple estuaries may be computed as the product of the probabilities of following each step, discounted by s^n. Alternatively, the distance of this pathway may be computed directly by summing the distance of each step. For example, a pathway from estuary i to j to k would have probability $s^2 p_{ij} p_{jk}$ and distance $d_{ij} + d_{jk}$. Using this formulation, it is possible that a multiple step pathway is shorter and more probable than a direct pathway between any pair of estuaries. Betweenness centrality for a given estuary is the proportion of minimum length paths in the network that pass through that estuary (Freeman 1977, 1978). Estuaries with a large betweenness centrality are important for maintaining connectivity throughout the network. We measured betweenness centrality for each estuary from the graph generated from the distance matrix, $\mathbf{D}$, using the R statistical package (R Core Team 2014) with the igraph library (Csardi & Nepusz 2006). We arbitrarily set the value of s to 0.75.

To quantify the overall level of connectivity in the network over time, we computed the average source strength, average vertex degree, and Shannon index for each vertex from each potential connectivity matrix $\mathbf{P}_t$. The source strength is the proportion of particles released from an estuary that successfully settled. This metric is commonly reported in ecological network studies. Although it is an informative metric for assessing larval success rates, it ignores the number of possible destinations and evenness in connectivity across these connections. Because mathematical models have shown that connectivity network structure is an important driver of population dynamics (Kininmonth et al. 2010b), we use 2 additional metrics of population connectivity alongside source strength. The vertex degree for an estuary at a given release time is the number of destination estuaries that received settlers from that estuary. Averaging the vertex degree across all estuaries in the network provides an estimate of how many estuaries are likely to be impacted by a perturbation to a single estuary within 1 generation. The Shannon index (H_i) quantifies both the number and strength of the outgoing connections from an estuary and is given by:

$$H_i = -\sum_j p_{ij} \ln(p_{ij}) \tag{2}$$

The Shannon index provides an estimate of the stability of the metapopulation, and high values indicate a more diverse suite of connections and more stable metapopulation. We averaged each of these 3 metrics across all 14 estuaries for each release time to compute a measure of the overall connectivity of the population. To analyze temporal trends in connectivity over the season, we performed a simple linear regression of each statistic with spawning date.

Deepwater Horizon oil spill

We used data from NOAA Satellite Derived Surface Oil Analysis Products for Deepwater Horizon (www.ssd.noaa.gov/PS/MPS/deepwater.html) to determine the daily location and extent of oil slicks. When data were unavailable for a specific day, we used data from the previous day. When 2 consecutive days had no data available, we used data from the previous day for the first day and data from the following day for the second day. If a larva encountered an oil slick at any point during its trajectory, we designated that larva as 'oiled'. We quantified the potential decrease in connectivity if 'oiled' particles were removed from the simulation. We computed the total number of successfully settling larvae that were potentially exposed to oil, as well as the location of settlement for these larvae. From these, we calculated the total proportion of settlers to each estuary and from each release time that were potentially exposed to oil. Under the worst-case scenario that exposure to oil is always fatal to larvae, we reassessed the spatial structure of population connectivity in the region. Although this assumption is unlikely to be realistic, it provides a worst-case bound on the impacts of the Deepwater Horizon oil spill on blue crabs during the dispersal phase.

Model sensitivity analyses

To confirm that our results are robust to the assumptions made in the model, we ran a number of sensitivity analyses. Our primary sensitivity analysis was to the spawning schedule. There is some evidence for lunar periodicity in blue crab spawning

(Ziegler 2002), so we examined the scenario in which blue crab spawning events coincide with the full and new moons. In our analysis, we assume that the maximum distance migrated by ovigerous female crabs is 100 km. There is no strong consensus in the literature as to the distance migrated by female crabs, so we tested the effects of doubling and halving this distance on our results.

RESULTS

Over all time periods, 7.7 % of the simulated larvae settled within the region. The remaining 92.3 % were removed from the model because they were predicted to move out of the model domain or remain offshore until the megalopae were no longer competent to settle. Of the total 48 million larvae simulated, 34.8 million (72.5 %) were lost to the edges of the model domain boundaries, with 7.7 million (22.2 %) of these lost over the southern boundary, 1.7 million (4.9 %) over the eastern boundary, and 25.4 million (72.9 %) over the western boundary. This pattern of westbound transport being dominant was also exhibited by the particles that successfully settled: 75.7 % of the successful settlers returned to their origin estuary or one to the west.

The trajectories followed by the larvae were in accordance with previous descriptions of the seasonal circulation of the northern Gulf of Mexico. A cyclonic gyre dominates the circulation of the Louisiana–Texas (LATEX) shelf during the fall, winter, and spring (Smith & Jacobs 2005). Most larvae released west of the Mississippi River delta during the spring and fall releases were entrained by the strong, westward, coastal component of this gyre and transported past the western boundary of NGOM-NFS. One exception to this pattern is particles released immediately southwest of the delta itself, many of which were entrained by a small, cyclonic eddy. During the summer, flow on the LATEX shelf is predominately eastward, and many larvae were transported towards the delta, and then offshore. On the eastern side of the delta, most individuals released during the spring were transported west towards the delta, and then offshore. This pattern changed in the summer to be dominated by eastward alongshore transport, then western alongshore transport during the fall. The $\log_{10}$-transformed expected distance for larvae to be transported from the spawning site to the settlement location decreased over the course of the year (slope = -3.9 km d^{-1}, adjusted R^2 = 0.642, $p \leq 0.001$).

The model predicts a high degree of local retention of blue crabs in the nGOM. Overall, 28.5 % of larvae that successfully settled returned to their parent estuary and 37.5 % settled in an adjacent estuary. The high local retention can be seen by the strong diagonal pattern in Fig. 2. It is also clear from Fig. 2 that the MRD acts as a barrier to dispersal, as only 4 % of the settling larvae crossed the mouth of the Mississippi River. Many of the larvae that crossed the Mississippi River were swept southward offshore and did not successfully settle.

Metapopulation structure

Total potential connectivity varies across estuaries and over time. The estuaries adjacent to the Mississippi River delta have the highest values of betweenness connectivity, indicating that they are most important to maintaining the connectedness of the metapopulation (Fig. 3). The overall connectivity, as measured by the Shannon index and vertex outdegree declines over the course of the spawning season. Average vertex degree drops by approximately 0.029 links per day ($p \leq 0.001$) and the Shannon index by 0.004 per day ($p \leq 0.001$; Fig. 4). A non-significant ($p \leq 0.13$) increase was seen in source strength.

Deepwater Horizon oil spill

Of the 3.7 million successfully settling larvae, 1.4 million (38.1 %) were potentially exposed to oil during the dispersal phase. The proportion of successfully settling larvae that were potentially exposed to oil varied widely, from 0 % when there was no overlap to 93 % for larvae released on 18 June 2010, when the overlap was greatest. The majority of the potentially oiled, successfully settling larvae were released during June, with 13.8 % on 12 June 2010 and 20.9 % on 26 June 2010. The overlap of the oil slick with larval locations was much greater on the eastern side of the MRD than the western side, so it is not surprising that 79.5 % of the settled larvae that were potentially exposed to surface oil were predicted to settle in estuaries east of the MRD and only 20.5 % in estuaries west of the MRD (Fig. 5). On 26 June 2010, 96.3 % of the successful settlers east of the MRD were potentially exposed to oil.

Larvae were most likely to be exposed to oil at a young age and for a short duration: 63.2 % of the potentially exposed larvae would have been first exposed at less than 15 d of age, and 28.6 % were

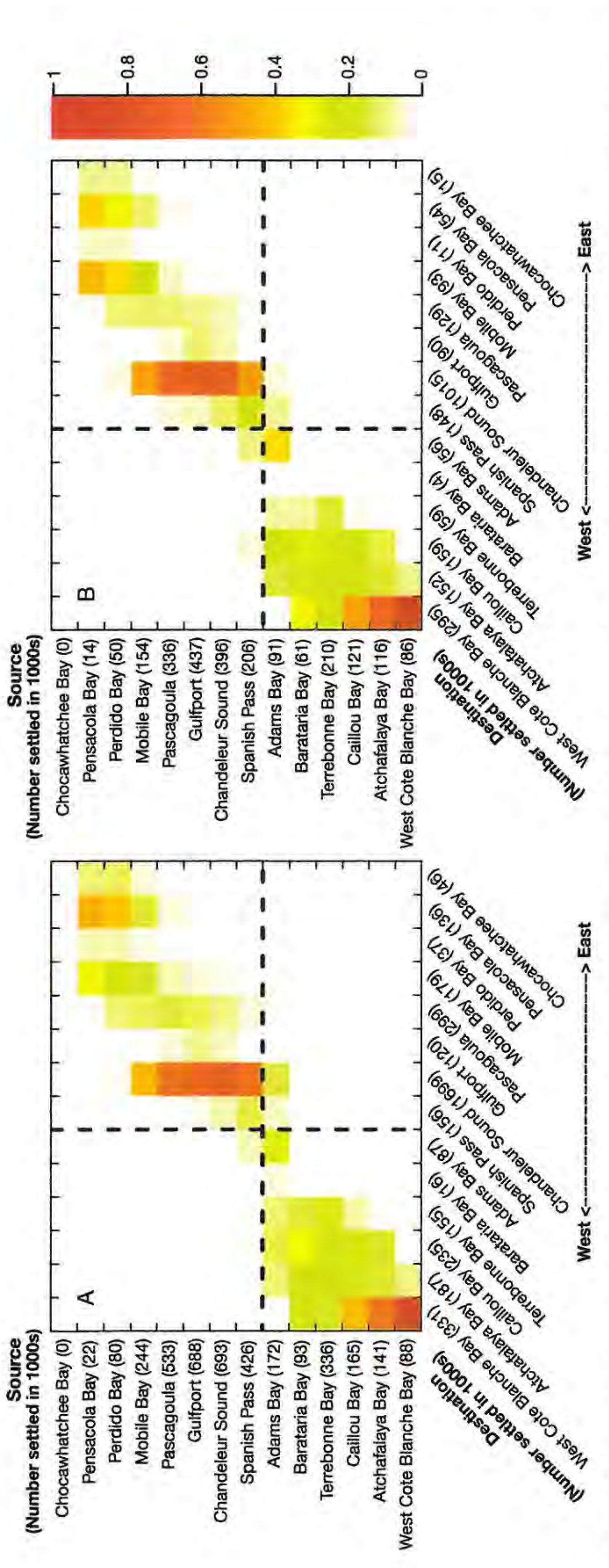

Fig. 2. Connectivity matrices from all 24 simulations. For each matrix, the vertical axis is the estimated source estuary (i.e. the estuary from which the parent crab originated) and the horizontal axis is the destination estuary in which larvae settled. The color of each block indicates the proportion of successfully settling larvae spawned at the source estuary that settled in the destination estuary and the dashed lines indicate the location of the Mississippi River delta. The numbers on the vertical axis indicate the number of successful settlers that originated at that estuary, and the numbers on the horizontal axis indicate the number of successful settlers that arrived at that estuary. (A) Connectivity matrix that results from all particles; (B) connectivity matrix with the potentially oiled particles removed. The overall connectivity patterns are similar in both panels, but the number of successful settlers is lower in B, particularly east of the Mississippi River delta

potentially exposed for only a single day. The distribution of exposure durations was approximately exponentially distributed, with a decay rate of 0.34 d^{-1}.

Assuming that exposure to oil is fatal to blue crab larvae reduces the proportion of larvae that successfully settle by 38.1%, but does not substantially influence the patterns of connectivity (Fig. 2). Overall, the proportion of successfully settling larvae from each estuary was reduced by 31.8 ± 15.3%. Larvae released from the 2 estuaries bordering the MRD were particularly heavily impacted by the oil spill, with 47.1% of the larvae leaving Adams Bay and 51.6% of the larvae leaving Spanish Pass being potentially exposed to oil. As recipients, Barataria Bay, Perdido Bay, and Chocawhatchee Bay were most heavily impacted with 78.7%, 69.7%, and 67.1% of their settlers potentially exposed to oil. These sites were particularly impacted because they already received few settlers and much of their settlement occurred during the DWH oil spill. Other sites that consistently had high settlement throughout the year (e.g. Chandeleur Sound) were less impacted by the spill. If oil exposure were fatal, Chandeleur Sound would be more important for maintaining connectivity (Fig. 3).

Because the oil slicks from DWH were present during late spring and early summer, fatality from oil would have dampened the trend that connectivity declines during the year (Fig. 4). Excluding potentially oiled larvae, the Shannon index and vertex degree declines over the course of the spawning season, but not by as much as with those larvae included. The average vertex degree drops by approximately 0.016 links per day ($p \leq 0.001$) and the Shannon index by 0.003 per day ($p \leq 0.001$). Although previously non-significant, the increase in source strength dur-

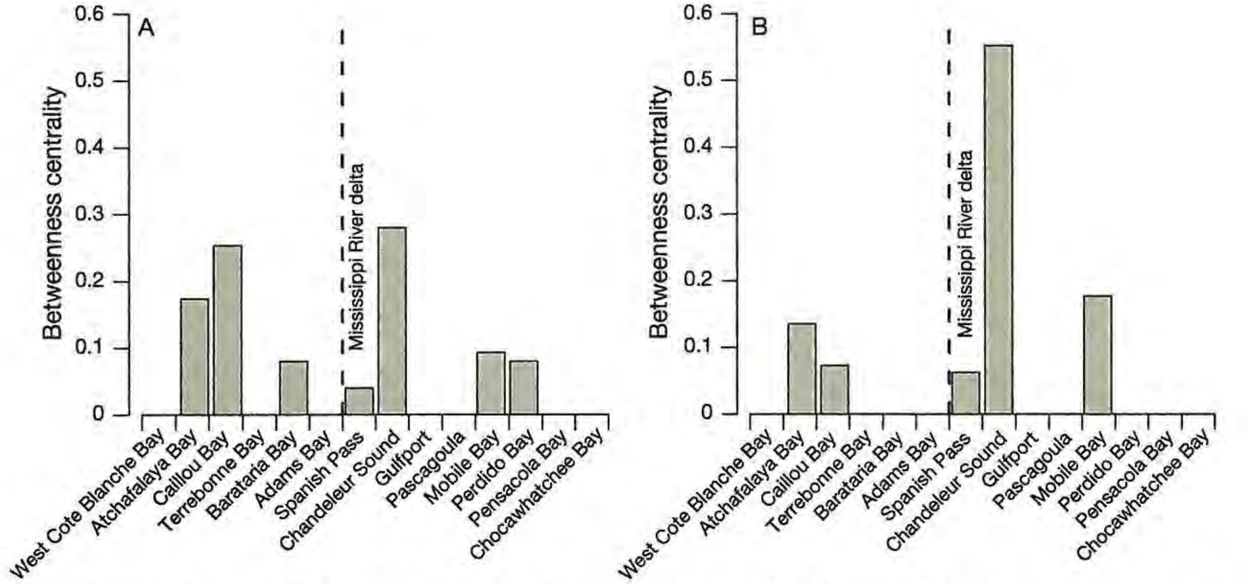

Fig. 3. Betweenness centrality of blue crab larvae calculated for each estuary as described in the 'Metapopulation structure' section of the text. This metric shows the importance of each estuary to maintaining connectivity. (A) All larvae; (B) excludes larvae that were potentially exposed to oil. In both cases, Chandeleur Sound is the most important estuary for maintaining connectivity. When particles that are potentially exposed to oil are removed, the importance of Chandeleur Sound increases

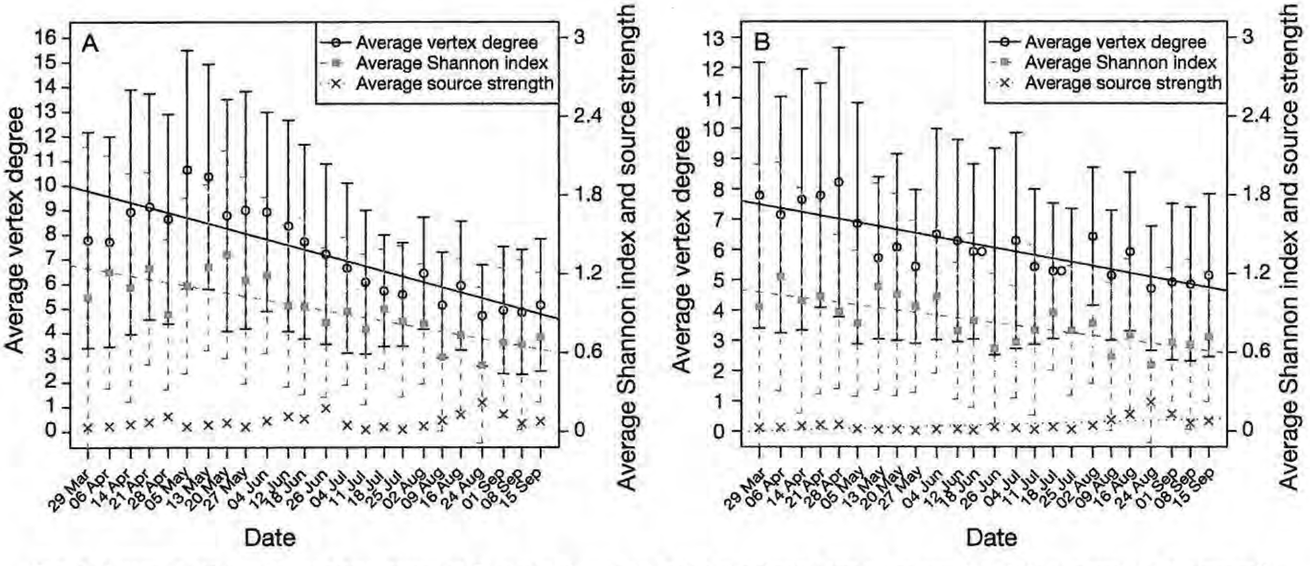

Fig. 4. Average vertex degree and average Shannon index for each simulation versus spawning date measuring the overall connectivity of the blue crab population in the network of estuaries. Error bars are ±1 SE. (A) All larvae; (B) excludes larvae that were potentially exposed to oil. The significant trend lines for average vertex degree and Shannon index are plotted in both panels. The trend for source strength is included only in (B) because it was not significant when oiled particles were included

ing the year is significant when potentially oiled larvae are excluded ($p \leq 0.005$). However, the rate of increase is small, 5.4×10^{-4} d^{-1}. These results support our conclusions from examining the connectivity matrices that the magnitude, but not patterns, of connectivity were influenced by the DWH oil spill.

Sensitivity analyses

Our sensitivity analysis to the frequency of larval release revealed that our model is not sensitive to this configuration. Assuming that blue crabs spawn only during the full and new moons reduced the number

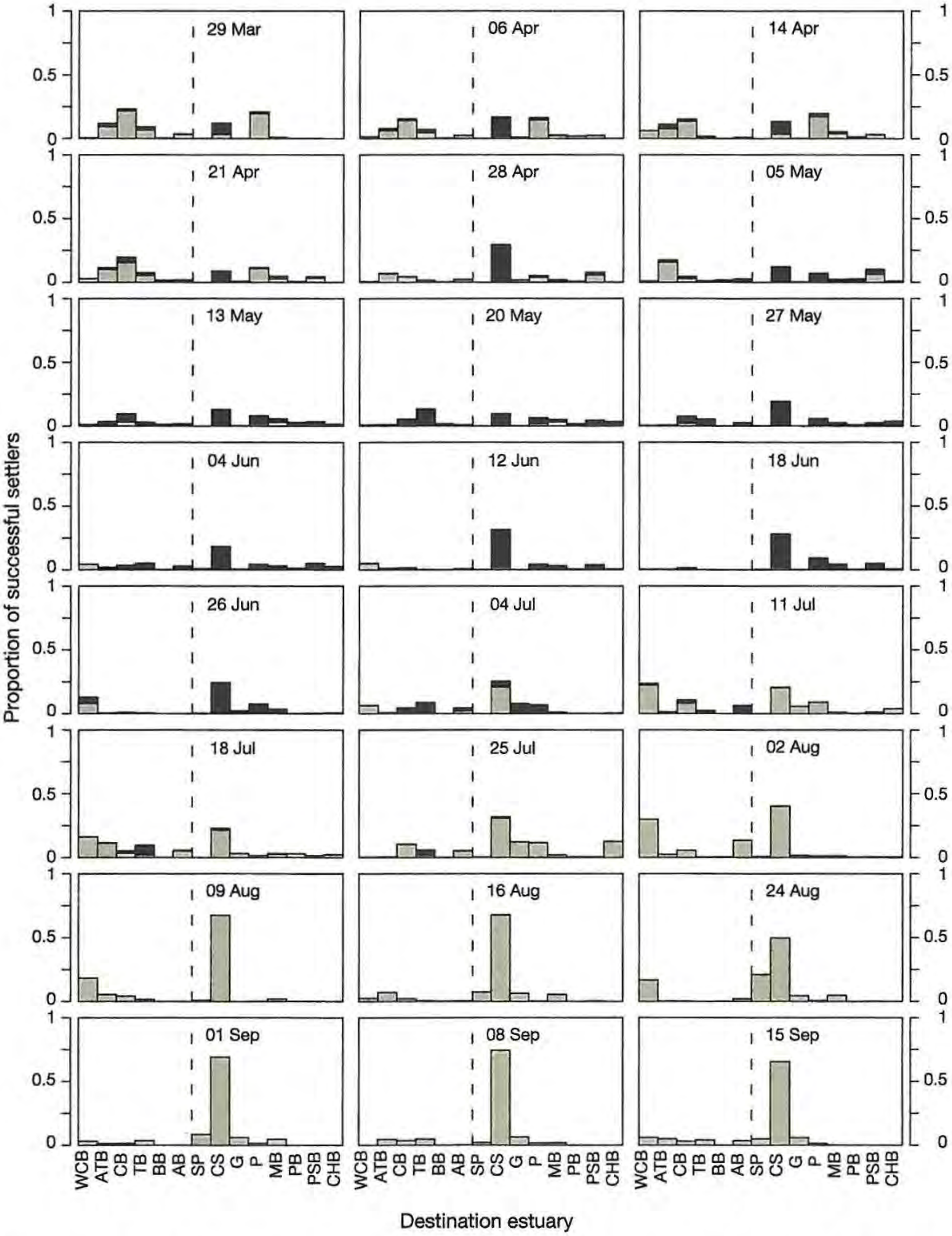

Fig. 5. Successfully settling blue crab larvae from each release time divided according to the proportion that arrives at each estuary. Grey bars indicate larvae that were not exposed to oil, and black bars indicate larvae that were potentially exposed to oil at any time during the dispersal phase. The dashed line is the location of the Mississippi River delta. Estuaries are listed from west to east (left to right). WCB: West Cote Blanche Bay; ATB: Atchafalaya Bay; CB: Caillou Bay; TB: Terrebonne Bay; BB: Barataria Bay; AB: Adams Bay; SP: Spanish Pass; CS: Chandeleur Sound; G: Gulfport; P: Pascagoula; MB: Mobile Bay; PB: Perdido Bay; PSB: Pensacola Bay; CHB: Chocawhatchee Bay

of successful larvae, but not the probability of success. In our original simulation, 7.7 % of the released larvae successfully settled. Examining the new and full moon events only, this proportion was 8.2 %. The overall patterns that the MRD is a barrier to dispersal (Fig. S1 in the Supplement at www-int-res.com/articles/suppl/m527p143_supp.pdf) and that the estuaries on either side of the MRD are most important for maintaining connectivity (Fig. S2 in the Supplement) remained. As before, we saw a significant decline in connectivity as measured by the Shannon Index ($p \leq 0.001$) and average vertex degree ($p \leq 0.001$).

Reducing the distance migrated by ovigerous females to 50 km and doubling it to 200 km does not change our results (Fig. S3 in the Supplement). The MRD remains a barrier to dispersal, and the trends in Shannon index, average vertex degree, and source strength are unchanged in all configurations. In our original parameterization, average vertex degree drops by ~0.029 links per day ($p \leq 0.001$) and the Shannon index by 0.004 per day ($p \leq 0.001$). Our results here are highly similar. Under the 50 km parameterization, average vertex degree drops by ~0.028 links per day ($p \leq 0.001$) and the Shannon index by 0.003 per day ($p \leq 0.001$). Under the 200 km parameterization, average vertex degree drops by ~0.029 links per day ($p \leq 0.001$) and the Shannon index by 0.004 per day ($p \leq 0.001$). A non-significant increase was seen in source strength in our original configuration ($p \leq 0.13$), the 50 km configuration ($p \leq 0.12$), and the 200 km configuration ($p \leq 0.13$). Overall, our results are robust to the assumptions that we have made.

DISCUSSION

The Mississippi River and its delta have a strong effect on the circulation in the nGOM. Strong currents often occur near the Mississippi River along the river plumes that advect larvae away from the river mouth, and alongshore currents form on either side of the delta, driven by the wind and, to a lesser extent, by the tides. Hence, the MRD forms a natural barrier to dispersal (Fig. 2). This has a large effect on the potential population connectivity of blue crabs within the nGOM. Our results suggest that the population east of the delta might be ecologically distinct from the population west of the delta. No evidence exists for genetic differentiation at the MRD for blue crabs, although a review of genetic studies in the Gulf does show that other species differentiate genetically at the MRD (Neigel 2009). However, differentiation in benthic species could be due to sediment differences east and west of the MRD or other factors, rather than larval transport (Neigel 2009). Furthermore, the small cross-delta movements predicted by our model may be large enough to homogenize genetic differences (Slatkin 1987), and we do not necessarily expect to find genetically differentiated populations. On ecological time scales, the larval connectivity patterns found here support managing each side of the MRD separately.

We speculate that the decline in population connectivity during the summer is primarily driven by the seasonal circulation patterns of the LATEX shelf. Whereas both average vertex degree and the Shannon index indicated a significant decline in population connectivity during the year, the source strength did not show a significant trend. Theoretical studies have found that network structure is an important driver of metapopulation dynamics (Hastings & Botsford 2006, Kininmonth et al. 2010b), so we recommend that future studies of population connectivity apply a suite of connectivity metrics. The trajectories followed by the simulated larvae are similar to published circulation patterns over the LATEX shelf. Seasonal variability in potential connectivity determines how timing of spawning peaks within the year affects dispersal distances and realized population connectivity. Because there is some interannual variability in the circulation patterns, particularly on the eastern side of the MRD (Smith & Jacobs 2005), and because stochasticity in realized connectivity lowers metapopulation growth rates (Watson et al. 2012), it would be interesting and useful to quantify the interannual variability in connectivity in this region.

Our model can only be used to predict potential connectivity as it uses assumptions of constant larval supply and does not account for larval mortality during transport or mortality at later stages. To predict realized connectivity would require knowledge of how the larval supply varies over space and time as well as more accurate information on spawning locations, larval mortality, finer-scale nearshore hydrodynamics, and post-larval behaviors that affect settlement. Such information does not exist for blue crabs in the nGOM. Since our dispersal model does not include such factors, we do not expect resulting settlement patterns predicted by our model to match data from megalopal (post-larval) collections (e.g. Rabalais et al. 1995, Perry et al. 2003, E. K. Grey et al. unpubl. data).

Use of graph-theoretic metrics improves the analysis of results from Lagrangian particle-tracking models. It can be argued that not much additional information is gained by calculating the graph-theoretic metrics for such a small network (only 14 vertices), especially when the vertices have an essentially linear geographic distribution along the coast. However, we believe that the use of graph metrics in a small network demonstrates the effectiveness and utility of the approach and of the particular metrics. For example, we expect that the estuaries immediately adjacent to the dispersal barrier imposed by the MRD will be important stepping stones since the low percentage of larvae that travel across the MRD largely originate from these estuaries. Betweenness centrality is indeed highest for those estuaries (Fig. 3), demonstrating that betweenness centrality is an effective tool for measuring the importance of individual vertices, and therefore can be used in larger networks where the geographic arrangement of vertices is more complex (e.g. Treml et al. 2008, Kininmonth et al. 2010a, Treml & Halpin 2012). Similarly, average vertex degree and the Shannon index are both effective metrics for measuring the overall connectivity of networks (Shannon 1948, MacArthur 1955).

The DWH oil spill overlapped with predicted blue crab spawning locations in late May and June 2010. Our model predicts that larvae potentially exposed to oil are most likely to settle east of the MRD, with peak settlement in late June. No catastrophic reduction in settlement is observed in this or any other region during this time period (E. K. Grey et al. unpubl. data). However, little is known about the sublethal effects of oil exposure in crabs. If effects manifest later in life, this model predicts that we would observe such effects more commonly in eastern nGOM estuaries.

Overall, we find that the MRD serves as a barrier to larval dispersal of blue crabs in the nGOM, and that the overall level of population connectivity declines during the spawning season. Our results are robust to the assumptions that we have made with regards to the distance that ovigerous female crabs migrate and the frequency of spawning. Blue crabs that were potentially exposed to oil from the DWH oil spill are predicted to have settled on the eastern side of the MRD. This study provides a valuable first estimate of the potential impacts of the DWH oil spill on larval transport.

Acknowledgements. This work was funded in part by a National Science Foundation RAPID award (PI C. Taylor, OCE-1042792) and in part by a grant from BP/The Gulf of Mexico Research Initiative (PIs J. Neigel and C. Taylor).

LITERATURE CITED

Bode M, Burrage K, Possingham HP (2008) Using complex network metrics to predict the persistence of metapopulations with asymmetric connectivity patterns. Ecol Model 214:201–209

Bohonak AJ (1999) Dispersal, gene flow, and population structure. Q Rev Biol 74:21–45

Botsford LW, Hastings A, Gaines SD (2001) Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. Ecol Lett 4:144–150

Costello C, Rassweiler A, Siegel D, De Leo G, Micheli F, Rosenberg A (2010) The value of spatial information in MPA network design. Proc Natl Acad Sci USA 107: 18294–18299

Cowen RK, Sponaugle S (2009) Larval dispersal and marine population connectivity. Annu Rev Mar Sci 1:443–466

Cowen RK, Lwiza KMM, Sponaugle S, Paris CB, Olson DB (2000) Connectivity of marine populations: open or closed? Science 287:857–859

Cowen RK, Paris CB, Srinivasan A (2006) Scaling of connectivity in marine populations. Science 311:522–527

Cowen RK, Gawarkiewicz G, Pineda J, Thorrold SR, Werner FE (2007) Population connectivity in marine systems: an overview. Oceanography 20:14–21

Csardi G, Nepusz T (2006) The igraph software package for complex network research. InterJournal Complex Syst 1695:1–9

D'Sa E, Ko D (2008) Short-term influences on suspended particulate matter distribution in the northern Gulf of Mexico: satellite and model observations. Sensors 8: 4249–4264

Darden R (2004) Population genetics of the blue crab in the Gulf of Mexico. PhD thesis, The University of Southern Mississippi, Hattiesburg, MS

DeAlteris J, Daume S, Allen R (2012) MSC public certification report: Louisiana blue crab fishery. Scientific Certification Systems, Emeryville, CA

Eagle N, Macy M, Claxton M (2010) Network diversity and economic development. Science 328:1029–1031

Epifanio CE (1988) Dispersal strategies of two species of swimming crab on the continental shelf adjacent to Delaware Bay. Mar Ecol Prog Ser 49:243–248

Epifanio CE, Tilburg CE (2008) Transport of blue crab larvae in the Middle Atlantic Bight: a wet and windy journey. J Mar Res 66:723–749

Forward R, Tankersley R, Welch H (2003) Selective tidal-stream transport of the blue crab *Callinectes sapidus*: an overview. Bull Mar Sci 72:347–365

Fox D, Teague W, Barron C, Carnes M, Lee C (2003) The modular ocean data assimilation system (MODAS). J Atmos Ocean Technol 19:240–252

Freeman LC (1977) A set of measures of centrality based on betweenness. Sociometry 40:35–41

Freeman LC (1978) Centrality in social networks conceptual clarification. Soc Networks 1:215–239

Garant D, Forde S, Hendry A (2007) The multifarious effects of dispersal and gene flow on contemporary adaptation. Funct Ecol 21:434–443

Gelpi CGJ, Condrey RE, Fleeger JW, Dubois SF (2009) Discovery, evaluation, and implications of blue crab, *Callinectes sapidus*, spawning, hatching, and foraging grounds in federal (US) waters offshore of Louisiana. Bull Mar Sci 85:203–222

Good IJ (1953) The population frequencies of species and the estimation of population parameters. Biometrika 40: 237–264

Graham B, Reilly WK, Beinecke F, Garcia TD, Murray CA, Ulmer F (2011) Deep Water: the Gulf oil disaster and the future of offshore drilling. National Commission on the BP Deepwater Horizon Oil Spill and Offshore Drilling, Washington, DC

Green R, Gould R, Ko D (2008) Statistical models for sediment/detritus and dissolved absorption coefficients in coastal waters of the northern Gulf of Mexico. Cont Shelf Res 28:1273–1285

Guillory V, Perry H, Steele P, Wagner T, Keithly W, Pellegrin B, Petterson J (2001) The blue crab fishery of the Gulf of Mexico, United States: a regional management plan. Gulf States Marine Fisheries Commission, Ocean Springs, MS

Harley CD, Hughes AR, Hultgren KM, Miner BG and others (2006) The impacts of climate change in coastal marine systems. Ecol Lett 9:228–241

Hastings A, Botsford LW (2006) Persistence of spatial populations depends on returning home. Proc Natl Acad Sci USA 103:6067–6072

Hastings A, Harrison S (1994) Metapopulation dynamics and genetics. Annu Rev Ecol Evol Syst 25:167–188

Hedgecock D, Barber PH, Edmands S (2007) Genetic approaches to measuring connectivity. Oceanography 20:70–79

Hinrichsen HH, Kraus G, Böttcher U, Köster F (2009) Identifying eastern Baltic cod nursery grounds using hydrodynamic modelling: knowledge for the design of marine protected areas. ICES J Mar Sci 66:101–108

Hinrichsen HH, Dickey-Collas M, Huret M, Peck MA, Vikebø FB (2011) Evaluating the suitability of coupled biophysical models for fishery management. ICES J Mar Sci 68:1478–1487

Holstein DM, Paris CB, Mumby PJ (2014) Consistency and inconsistency in multispecies population network dynamics of coral reef ecosystems. Mar Ecol Prog Ser 499: 1–18

Johnson DR, Perry HM, Lyczkowski-Shultz J (2013) Connections between campeche bank and red snapper populations in the Gulf of Mexico via modeled larval transport. Trans Am Fish Soc 142:50–58

Kininmonth SJ, De'ath G, Possingham HP (2010a) Graph theoretic topology of the great but small barrier reef world. Theor Ecol 3:75–88

Kininmonth SJ, Drechsler M, Johst K, Possingham HP (2010b) Metapopulation mean life time within complex networks. Mar Ecol Prog Ser 417:139–149

Kininmonth S, Beger M, Bode M, Peterson E and others (2011) Dispersal connectivity and reserve selection for marine conservation. Ecol Model 222:1272–1282

Kinlan BP, Gaines SD (2003) Propagule dispersal in marine and terrestrial environments: a community perspective. Ecology 84:2007–2020

Ko D, Preller R, Martin P (2003) An experimental real-time Intra-Americas Sea Ocean Nowcast/Forecast System for coastal prediction. Proceedings of the AMS 5th Conference on Coastal Atmospheric & Oceanic Prediction and Processes, Seattle, WA, 6–8 Aug 2003. American Meteorological Society, Washington, DC, p 97–100

Ko D, Martin J, Rowley C, Preller R (2008) A real-time coastal ocean prediction experiment for MREA04. J Mar Syst 69:17–28

Kordos L, Burton R (1993) Genetic differentiation of Texas Gulf coast populations of the blue crab *Callinectes sapidus*. Mar Biol 117:227–233

MacArthur R (1955) Fluctuations of animal populations and a measure of community stability. Ecology 36:533–536

Margalef DR (1958) Information theory in ecology. Mem R Acad Sci 32:373–449

Marinone S, Gutirrez O, Pars-Sierra A (2004) Numerical simulation of larval shrimp dispersion in the northern region of the Gulf of California. Estuar Coast Shelf Sci 60: 611–617

Martin PJ, Barron CN, Smedstad LF, Campbell TJ and others (2009) Users manual for the Navy Coastal Ocean Model (NCOM) Version 4.0. Naval Research Laboratory, Stennis Space Center, MS

McMillen-Jackson A, Bert T (2004) Mitochondrial DNA variation and population genetic structure of the blue crab *Callinectes sapidus* in the eastern United States. Mar Biol 145:769–777

Meynecke JO, Lee S, Duke NC (2008) Linking spatial metrics and fish catch reveals the importance of coastal wetland connectivity to inshore fisheries in Queensland, Australia. Biol Conserv 141:981–996

Miller T, Martell S, Bunnell D, Davis G and others (2005) Stock assessment of blue crab in Chesapeake Bay: 2005. Final Report Ref: [UMCES]CBL 05-077. UMCES Tech Ser No TS-48705-CBL. University of Maryland Center for Environmental Science Chesapeake Biological Laboratory, Solomons, MD

Mitarai S, Siegel DA, Watson JR, Dong C, McWilliams JC (2009) Quantifying connectivity in the coastal ocean with application to the Southern California Bight. J Geophys Res 114:C10026, doi:10.1029/2008JC005166

Neigel J (2009) Population genetics and biogeography of the Gulf of Mexico. In: Felder D, Camp C (eds) Gulf of Mexico—its origins, waters, and biota. Texas A&M University Press, College Station, TX, p 1353–1370

North EW, Schlag Z, Hood RR, Li M, Zhong L, Gross T, Kennedy VS (2008) Vertical swimming behavior influences the dispersal of simulated oyster larvae in a coupled particle-tracking and hydrodynamic model of Chesapeake Bay. Mar Ecol Prog Ser 359:99–115

Okubo A (1971) Oceanic diffusion diagrams. Deep-Sea Res 18:789–802

Paris CB, Chérubin L, Cowen RK (2007) Surfing, spinning, or diving from reef to reef: effects on population connectivity. Mar Ecol Prog Ser 347:285–300

Perry H, Johnson DR, Larsen K, Trigg C, Vukovich F (2003) Blue crab larval dispersion and retention in the Mississippi Bight: testing the hypothesis. Bull Mar Sci 72: 331–346

Peterson AT, Ortega-Huerta MA, Bartley J, Sánchez-Cordero V, Soberón J, Buddemeier RH, Stockwell DRB (2002) Future projections for Mexican faunas under global climate change scenarios. Nature 416:626–629

Peterson CH, Anderson SS, Cherr GN, Ambrose RF and others (2012) A tale of two spills: novel science and policy implications of an emerging new oil spill model. Bioscience 62:461–469

Provenzano AJJ, McConaugha JR, Philips KB, Johnson DF, Clark J (1983) Vertical distribution of first stage larvae of the blue crab, *Callinectes sapidus*, at the mouth of Chesapeake Bay. Estuar Coast Shelf Sci 16:489–499

R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.r-project.org

Rabalais NN, Burditt RF Jr, Coen LD, Cole BE and others (1995) Settlement of *Callinectes sapidus* megalopae on artificial collectors in four Gulf of Mexico estuaries. Bull Mar Sci 57:855–876

Rayfield B, Fortin MJ, Fall A (2011) Connectivity for conservation: a framework to classify network measures. Ecology 92:847–858

Rittschof D, Darnell K, Goldman M, Ogburn M, McDowell R (2010) Estimating relative abundance of the female blue crab spawning stock in North Carolina. In: Kruse GH, Eckert GL, Foy RJ, Lipcius RN, Sainte-Marie B, Stram DL, Woodby D (eds) Biology and management of exploited crab populations under climate change. Alaska Sea Grant, University of Alaska Fairbanks, Fairbanks, AK, p 91–108

Rooker JR, Secor DH, De Metrio G, Schloesser R, Block BA, Neilson JD (2008) Natal homing and connectivity in Atlantic bluefin tuna populations. Science 322:742–744

Scheffer M, Braveco JM, DeAngelis DL, Rose KA, Van Nes EH (1995) Super-individuals: a simple solution for modeling large populations on an individual basis. Ecol Model 80:161–170

Shannon C (1948) A mathematical theory of communication. Bell Syst Tech J 27:379–423, 623–656

Slatkin M (1987) Gene flow and the geographic structure of natural populations. Science 236:787–792

Smith S, Jacobs G (2005) Seasonal circulation fields in the northern Gulf of Mexico calculated by assimilating current meter, shipboard ADCP, and drifter data simultaneously with the shallow water equations. Cont Shelf Res 25:157–183

Strathmann R, Hughes T, Kuris A, Lindeman K, Morgan S, Pandolfi J, Warner R (2002) Evolution of local recruitment and its consequences for marine populations. Bull Mar Sci 70(Suppl 1):377–396

Sulkin S, Van Henkelem W, Kelly P, Van Henkelem L (1980) The behavioral basis of larval recruitment in the crab *Callinectes sapidus* Rathbun: a laboratory investigation of ontogenetic changes in geotaxis and barokinesis. Biol Bull 159:402–417

Thorrold SR, Jones GP, Hellberg ME, Burton RS and others (2002) Quantifying larval retention and connectivity in marine populations with artificial and natural markers. Bull Mar Sci 70:291–308

Thorrold SR, Zacherl DC, Levin LA (2007) Population connectivity and larval dispersal: using geochemical signatures in calcified structures. Oceanography 20:80–89

Tian RC, Chen C, Stokesbury KDE, Rothschild BJ and others (2009) Dispersal and settlement of sea scallop larvae spawned in the fishery closed areas on Georges Bank. ICES J Mar Sci 66:2155–2164

Treml EA, Halpin PN (2012) Marine population connectivity identifies ecological neighbors for conservation planning in the Coral Triangle. Conservation Letters 5:441–449

Treml EA, Halpin PN, Urban DL, Pratson LF (2008) Modeling population connectivity by ocean currents, a graph-theoretic approach for marine conservation. Landscape Ecol 23:19–36

Van Voorhees D (2012) Fisheries of the United States. National Marine Fisheries Service Office of Science and Technology, Silver Spring, MD

Ward G (1980) Hydrography and circulation processes of gulf estuaries. In: P Hamilton, K MacDonald (eds) Estuarine and wetland processes. Springer, New York, NY, p 183–215

Watson JR, Mitarai S, Siegel DA, Caselle JE, Dong C, McWilliams JC (2010) Realized and potential larval connectivity in the Southern California Bight. Mar Ecol Prog Ser 401:31–48

Watson JR, Siegel DA, Kendall BE, Mitarai S, Rassweiller A, Gaines SD (2011) Identifying critical regions in small-world marine metapopulations. Proc Natl Acad Sci USA 108:E907–E913

Watson JR, Kendall BE, Siegel DA, Mitarai S (2012) Changing seascapes, stochastic connectivity, and marine metapopulation dynamics. Am Nat 180:99–112

Woods J (2005) The Lagrangian ensemble metamodel for simulating plankton systems. Prog Oceanogr 67:84–159

Yednock BK, Neigel JE (2014) Detecting selection in the blue crab, *Callinectes sapidus*, using DNA sequence data from multiple nuclear protein-coding genes. PLoS ONE 9:e99081

Ziegler T (2002) Larval release of the blue crab, *Callinectes sapidus*: entrainment cues and time in different tidal regions. Florida Institute of Technology, Melbourne, FL

Zmora O, Findiesen A, Stubblefield J, Frenkel V, Zohar Y (2005) First hatchery mass production of blue crab (*Callinectes sapidus*) juveniles. Aquaculture 244:129–139

Editorial responsibility: Steven Morgan,
Bodega Bay, California, USA

Submitted: June 17, 2013; Accepted: February 11, 2015
Proofs received from author(s): April 6, 2015