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Connectivity patterns among coral reef systems in the southern Gulf of Mexico

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ABSTRACT: This study simulated the connectivity patterns among 7 coral reef systems in the southern Gulf of Mexico. Two subgroups of reefs were considered: one near the mainland over the narrow western shelf, and the other over the wide Campeche Bank (CB). A particle-tracking module was coupled to a realistic simulation with the Hybrid Coordinate Ocean Model in order to study the transport and dispersion of particles in near surface waters. The simulation consisted of the launch of 100 passive particles (virtual larvae) from each reef, every 24 h over a 5 year period; it considered species lasting up to 35 d in the plankton and assumed no seasonality in reproduction. On the western shelf, connection was northwards from March to August, and southwards from September to February; over the CB edge, the connection was northwestwards throughout the year. Over the western shelf, reefs showed a strong degree of interconnectivity and high particle retention. Higher self-recruitment was most likely due to the passage of synoptic-scale atmospheric systems and their associated changes in wind and current direction. In contrast, CB reefs exhibited lower connectivity and less larval retention. Over the western edge of the Bank, connectivity was almost unidirectional because of the influence of the cyclonic gyre in the Campeche Bay, which causes particles to disperse over a wide area with low probabilities of self-recruitment. The main connection pathway was the confluence zone between neritic and oceanic waters over the outer shelf of the Bank. Connection between the 2 groups of reefs was weak.

KEY WORDS: Ecological network · Dispersal pathways · Self-recruitment · Source–sink sites · Numerical circulation models · Marine protected areas

INTRODUCTION

Coral reefs are unique ecosystems in the oceans. They support a vast biological diversity, harboring perhaps one-quarter to one-third of all marine species (Sheppard et al. 2009). However, most species remain undescribed and it is possible that only 10% of species may have been discovered so far (Knowlton et al. 2010). Because of this high biodiversity, coral reefs display per unit area more types of feeding mechanisms, reproduction, growth, locomotion or predatory behavior than any other marine ecosystem (Sheppard et al. 2009). Coral reefs are among the few ecosystems that construct their own substratum, and their complex 3-dimensional structure provides shoreline protection against strong oceanic currents and waves. Furthermore, they also supply the human population with goods and services of great alimentary, biomedical and recreational value (Moberg & Folke 1999, Sheppard et al. 2009). In spite of the biological, ecological and economic importance of these systems, they did not become a priority conservation

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concern in Mexico until the 1970s; and since then, there has been an increasing interest from scientists, government agencies and the general public about the biota and ecological relationships of coral reefs, as well as in the processes that affect their structure and function (Jordán-Dahlgren & Rodríguez-Martínez 2003). Whereas corals in the Mexican Caribbean can form large barriers, coral reefs in the southern Gulf of Mexico are less developed and are patchily distributed. In the southwestern Gulf, over the narrow continental shelf, reefs lie near the shore (<22 km), and consequently are exposed to human activities. On the southeastern side, reefs occur primarily near the shelf edge to about 100 to 200 km from the shore, forming a broad arc running from the north-central portion of the broad Yucatan shelf towards the southwest (Liddell 2007).

Most of the biological literature concerning coral reef communities from the southern Gulf has reported basic information on species distribution (Moore 1958, Kornicker et al. 1959, Rice & Kornicker 1962, Farrell et al. 1983, Sanvicente-Añorve et al. 2012b), although some studies have provided important insights on ecological aspects of the species (Hicks et al. 2001, Escobar-Vásquez & Chávez 2012, Sanvicente-Añorve et al. 2012a). Far from being isolated ecosystems, coral reefs in the southern Gulf are embedded in an ecological network whose degree of connectivity is unknown. Former attempts to understand the ecological connectivity among these reefs have addressed the distribution and abundance of individual coral species (Jordán-Dahlgren 2002, Chávez-Hidalgo et al. 2008, 2009). However, there is still a need for research on these marine ecosystems within a quantitative approach through the use of high-resolution circulation models. Among them, the Hybrid Coordinate Ocean Model provides some advantages because it uses several approaches to represent vertical coordinates. In particular, the model is well designed to study the transition between oceanic and neritic waters (Bleck 2002). In the Gulf of Mexico and Caribbean Sea, previous studies have used this model to solve network connectivity problems of some marine populations (Butler et al. 2011, Johnson et al. 2013).

Demographically, the term 'connectivity' refers to the linking of local populations through the dispersal of individuals (larvae, juvenile or adults) (Sale et al. 2005). Understanding connectivity patterns is important because of their role in maintaining resilience of local and linked populations, but also because it enables measures to protect threatened ecosystems (Barber et al. 2002, McCook et al. 2009). Several factors are expected to influence the degree of marine population connectivity. The pelagic larval duration of species associated with the current regime evidently influences the dispersal pattern of populations; however, the extent of larval dispersal also depends on taxa, swimming ability, vertical migration, environmental tolerances of species, regions or habitats (Lester et al. 2007, Munday et al. 2009). Since many coral reef-associated species display a planktonic larval dispersal phase that is variable in duration, it is fundamental to comprehend the ecological connectivity patterns among coral reef patches that result from larval dispersal. Thus, the aim of the present study was to analyze connectivity patterns among the main coral reef systems of the southern Gulf of Mexico through the use of numerical circulation simulations. To this purpose, the objectives were as follows: (1) to quantify the degree of connectivity among 7 coral reefs in the southern Gulf of Mexico based on a high-resolution hydrodynamic model, (2) to analyze the connectivity network structure among these 7 reefs, (3) to examine seasonal variations in these connectivity patterns, (4) to test whether reefs in close proximity to each other also have the highest degree of connectivity, (5) to identify whether a reef habitat is a source or a sink, (6) to analyze the degree of self-recruitment of each reef, (7) to determine the main dispersal pathways of planktonic larvae, and (8) to provide management guidelines for the protection of coral reefs in the southern Gulf of Mexico.

METHODS

Study area

Circulation in the Gulf of Mexico is strongly affected by the Caribbean Current System. Water flowing through the Yucatan Channel provides most of the renewal water to the Gulf of Mexico and to the Loop Current (Duncan et al. 1977). Currents and other oceanographic conditions in the Gulf are influenced by fluctuations in the Loop Current, which occasionally sheds anti-cyclonic eddies which travel towards the west and eventually dissipate near the shelf (Alvera-Azcárate et al. 2009).

Surface currents in the Bay of Campeche display seasonal differences between neritic and oceanic waters. Whereas circulation in the open ocean is mainly cyclonic throughout the year, water transport over the shelf is strongly seasonal, driven mainly by wind stress (Zavala-Hidalgo et al. 2003, Vázquez-de la Cerda et al. 2005, Pérez-Brunius et al. 2013). In the western Gulf, over the narrow shelf, the main water transport flows towards the northwest from May to August, and towards the southeast from September to March. On the eastern side, over the wide continental shelf, the surface circulation flows southwestward throughout the year. Hence, 2 currents meet in the southernmost Gulf and induce an offshore current during the fall-winter period (Zavala-Hidalgo et al. 2003).

The shelves bordering the Gulf of Mexico display a wide range of sedimentary composition, morphologies and relative orientation of their main axis with the dominant winds. In the southwestern Gulf, the continental shelf is less than 50 km wide and has a terrigenous origin. It is also marked by the influence of continental river discharges and by considerable anthropogenic activity. In spite of the terrigenous sediment input in the area, coral reef patches develop along this portion of the coastal plain (Liddell 2007). On the southeastern side, the shelf features strongly contrast with those of the western shelf. This region, the Campeche Bank, is a wide submarine continuation of the carbonate plateau that constitutes the Yucatan Peninsula; it extends for ~650 km along the western and northern side of Yucatan, reaching ~240 km in width (Macintyre et al. 1977, Tunnell & Chapman 2000, Liddell 2007). The outer shelf has many shoals and submerged coral banks, as well as 4 groups of emergent reef structures differing in size, morphology, number of cays or islands, degree of development, flora, fauna, and distance from the shore (Paynter 1953, Tunnell & Chapman 2000, Liddell 2007).

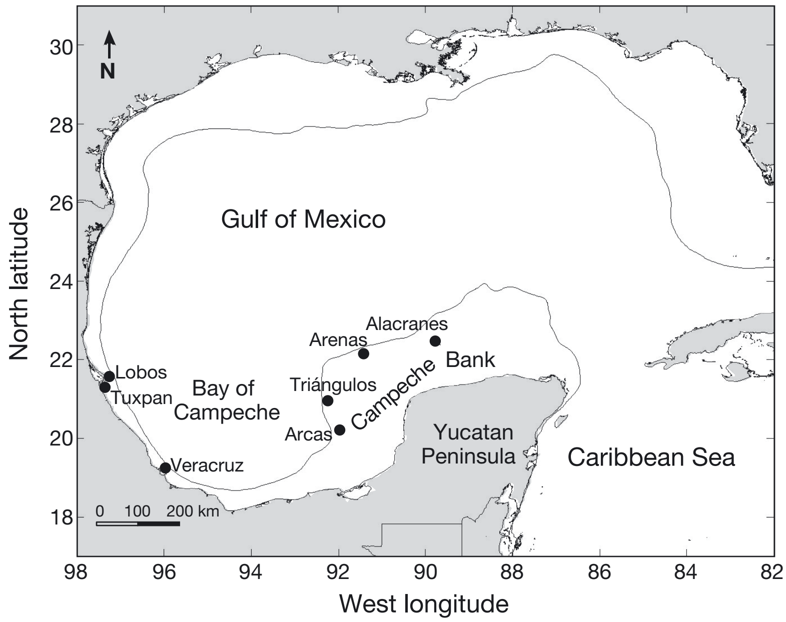

Fig. 1. Study area and location of the 7 reef systems. Black line: continental shelf

The reefs studied here are in the southern Gulf of Mexico south of 23° N. Anti-clockwise from the west they are: Lobos (centered at 21.51° N, 97.25° W), Tuxpan (21.08° N, 97.23° W), Veracruz (19.16° N, 96° W), Arcas (20.21° N, 91.97° W), Triángulos (20.93° N, 92.26° W), Arenas (22.11° N, 91.39° W) and Alacranes (22.48° N, 89.7° W) (Fig. 1). The first 3 systems are on the western narrow shelf; the other 4 are on the eastern side, over the Campeche Bank. Brief descriptions (Paynter 1953, Tunnell & Chapman 2000, Liddell 2007) of each reef complex are given below:

Lobos is the northernmost reef complex on the southwestern coast of the Gulf of Mexico. It is the northern subgroup of the Lobos-Tuxpan Reef System, and is composed of 3 emergent platform-type reefs located less than 15 km from the coastline. The Lobos-Tuxpan Reef System was designated a National Park in 2009.

Tuxpan constitutes the southern group of the Lobos-Tuxpan Reef System and it includes 3 emergent platform-type reefs. It lies 40 km south of the Lobos reefs, near the continental margin.

Veracruz, which is considered highly endangered, consists of 25 platform-type coral reefs located less than 22 km from the coastline. Owing to the influence of fluvial sediment discharges, which restrict coral development, 2 groups of reefs can be recognized: the northern group in front of Veracruz and the southern group off the village of Antón Lizardo. The whole system was designated as a National Park in August 1992.

Arcas is the southernmost coral structure of the group known as the Campeche Bank Reefs, and among them, it is the most affected by anthropogenic activity. This system, 143 km from the mainland, is composed of 3 emergent sand cays, the largest being ~900 m long and ~300 m wide. This area supports crude oil storage and transfer facilities for the Mexican oil company PEMEX. Arcas is not a marine protected area.

Triángulos is an emergent platform reef that forms part of the Campeche Bank Reefs. Lying ~190 km from the mainland, this system consists of 2 small submerged ridges, 10 km apart, each with emergent islands. The western ridge has the largest sand island of the area, whereas the eastern ridge is composed of several small islands close together. Triángulos reef is not a marine protected area.

Arenas, in northwestern region of the Campeche Bank at ~168 km from the shore, is composed by 4 small emergent islands. It is not a marine reserve.

Alacranes is an emergent platform-type reef 140 km north of the Yucatan Peninsula and the largest coral reef complex in the Bank. Five sandy islands are included in the reef area. Alacranes was designated a National Park by the Mexican government and as a Biosphere Reserve by UNESCO in 1994.

The model

The circulation model used here is the regional real time Gulf of Mexico adapted to the Hybrid Coordinate Ocean Model, hereafter called the GOM-HYCOM. The HYCOM is a primitive equation general circulation model that combines isopycnic vertical coordinates in the open stratified ocean, z-level coordinates in the weakly stratified upper-ocean mixed layer, and sigma coordinates in shallow coastal waters (Bleck 2002). The data assimilation uses the Navy Coupled Ocean Data Assimilation (NCODA) scheme. The horizontal resolution of the GOM-HYCOM is 1/25 degree; it has 20 vertical layers and takes boundary conditions from the 1/12° Atlantic HYCOM (http://hycom.org/). We used daily issues of the GOM-HYCOM upper layer to estimate the mean monthly current vectors at surface waters. This climatology encompassed a 5 yr period (2006 through 2010).

The Lagrangian trajectories of particles were simulated by the use of solutions from a hindcast based on the GOM-HYCOM. The simulation consisted of the release of 100 passive particles (virtual larvae or propagules) every 24 h from the center of each reef for 5 yr. A total of 1 278 200 larval trajectories were then simulated, and virtual larvae were tracked for 35 d. A Lagrangian particle-tracking subroutine was coupled to the circulation model in order to simulate the transport and dispersion of particles in surface waters. Larval trajectories were calculated integrating the following equations (Marinone et al. 2004):

$$\frac{dx}{dt} = u_* + u_d \quad (1)$$

$$\frac{dy}{dt} = v_* + v_d \quad (2)$$

where u_* and v_* are particle velocities that are interpolated from the model Eulerian velocity field grids using a bilinear interpolation. Equations were integrated with a second order Runge-Kutta algorithm and a time step of 6 h. The terms u_d and v_d are random velocities having a Gaussian distribution (mean = 0, variance = 1) multiplied by a dispersion coefficient. The Gaussian distribution is commonly used for turbulent processes and is based in an expected similar solution to that of the diffusion equation. The random walk simulates the subgrid processes and different values of the dispersion coefficient were tried, choosing one that keeps the larvae within a radius less than or equal to that of the grid cell.

Connectivity was expressed as the percentage of particles released from one site that arrived at another site at the end of a certain period (Xue et al. 2008). Values of connectivity were included in a square connectivity matrix in which the rows correspond to the starting sites of particles, and the columns to the final destination. The time periods considered here for constructing connectivity matrices were 0–15, 16–25 and 26–35 days of particle drifting, each of them representing marine species with different pelagic larval duration (PLD). In order to simplify results, a global connectivity matrix (0–35 d) was also constructed. The diagonal cells of matrices, corresponding to an estimation of self-recruitment of species, were more precisely analyzed by computing the percentage of particles retained day-to-day by the starting site. A successful event was considered to have occurred if particles arrived within a circular area (radius 10 km), centered on each reef. In order to standardize particle density conditions, the number of particles released per reef and the larval retention area were the same in all cases. A 10 km radius approximates the mean size for the reefs. Moreover, the role of currents in the larval dispersal was tested by comparing the minimum arrival time among reefs and geographical distance matrices, using a Mantel test (1000 permutations).

The percentages of particles successfully emitted or received by the reefs allowed identification of the sites that could function as a 'sink' when immigrants exceeded emigrants, or as a 'source', when emigrants exceeded immigrants.

This study represents a baseline case to understand connectivity patterns in the southern Gulf. The connectivity matrices presented here may represent a variety of coral reef fishes, such as *Haemulon flavolineatum* (PLD = 13 to 20 d), *Hypoplectrus nigricans* (13 to 22 d), *Stegastes partitus* (25 to 45 d) and *Chaetodon capistratus* (20 to 57 d), which spawn throughout the year in the Caribbean (Puebla et al. 2012).

Since knowledge on vertical swimming behavior of fish larvae is still limited, we decided to use surface current data because larvae concentration in the southern Gulf of Mexico is higher in the upper 30 m layer (Sanvicente-Añorve et al. 2007). Also, the similarity of currents in the upper 30 stratum was tested by correlating the *U* (east–west direction) and the *V* (north–south) velocity values at surface and at 30 m depth at three 20.5° N sites: western shelf (96.6° W), deep sea basin (94° W) and eastern shelf (92° W). In the 5 yr data scatter plots (U_{surface} vs. U_{30m} and V_{surface} vs. V_{30m}), the correlation was higher than 0.93 in all cases, indicating a high consistency in the current's direction in the upper 30 m stratum.

RESULTS

In order to identify seasonal patterns in the water transport, a monthly climatology of surface circulation was generated from 5 years of data (2006 through 2010) from the upper layer of the GOM-HYCOM. According to this, the main circulation feature in the southern Gulf of Mexico was a well-defined cyclonic gyre in the deep sea basin throughout the year. Most of the time, this gyre extended from the southwestern shelf slope to approximately 94° W to the east, and 21° N to the north. The position of the gyre corresponded with the deepest area of the Bay of Campeche, and during December and January this gyre elongated in the northwest–southeast direction. Surface circulation over the narrow western shelf displayed strong seasonal variations. From March to August, currents run towards the northwest, reaching their highest speeds in the May–July period. In September, the current reversed and flowed at low speeds towards the southeast, a trend that continued until February. According to the model, circulation patterns over the broad Campeche Bank differ between the inner and outer shelves: over the inner part, currents flow westward off the northern Yucatan Peninsula, whereas in the western region of the Bank, they flow southwestward. By contrast, the current's direction on the outer shelf was strongly influenced by oceanographic features of the deep-sea waters. On the western edge of the Bank, currents followed the cyclonic conditions of the deep basin, with the highest speeds in September and October and the lowest from December to February (Fig. 2).

Connectivity matrices regarding 3 different PLD (Table 1a–c) showed that the highest connection values were among the reefs of the western side, especially for species whose PLD was less than 16 d (Table 1). The coral ecosystems over the Campeche Bank were less interconnected, with the major connection being from Arcas with its neighbor Triángulos, and for species with PLD less than 16 d. Connectivity between the Campeche Bank reefs and those of the western shelf was very weak, even at the end of a 35 d period, regardless of the stage of development (Table 1d). The main connection between the 2 groups was from Veracruz reef, which successfully emitted only 1.08% of virtual larvae to Triángulos reef (Table 1d). As expected, matrices of minimum time of arrival (Table 2) among reefs indicated that reefs in close spatial proximity were close in connection time. Minimum connection times corresponded to the reefs over the narrow shelf, varying between 1 and 7 d, whereas in the Campeche reefs times varied between 1 and 18 d. The 2 groups of reefs connected via Veracruz; this site registered the shortest times for connection to the reefs of the Bank. Also, the Mantel test showed a highly significant association ($r = 0.58$, $p < 0.001$) between geographical distance among reefs and the minimum time of arrival; a second trial, excluding Alacranes reef, showed a higher correlation ($r = 0.89$, $p < 0.001$) between the 2 matrices.

Degree and direction of connectivity displayed strong seasonal variations, particularly among the western reefs. Regarding the Lobos-Tuxpan pair, the major connection was northwards during March–August, and southwards during September–February. The Tuxpan-Veracruz pair exhibited a similar seasonal pattern (Fig. 3). In the northern Campeche Bank, Alacranes reef showed its major connection value with its neighbor Arenas from September to February, for several PLDs (Table 1). Along the western edge of the Bank, connection was northward throughout the year, that is, from Arcas to Alacranes and Arenas (Fig. 3). Regarding the annual amount of immigrants and emigrants, Lobos, Veracruz, Triángulos and Arenas reefs were identified as areas of potentially high recruitment (sink) of larvae, whereas Tuxpan, Arcas and Alacranes may be recognized as areas of larval emission (source) (Fig. 4).

The highest larval retention occurred in the reefs close to the mainland, over the narrow continental platform. At the end of the 35 d study period, Tuxpan accounted for 1.18% of the initial particle number within its area (Fig. 5). This percentage refers to virtual larvae retained or returned to the reef area. Lobos and Veracruz had smaller values (0.38%) at the end of the period. Coral ecosystems of the wide Campeche Bank, far from the mainland, displayed lower self-recruitment values. Five days after mod-

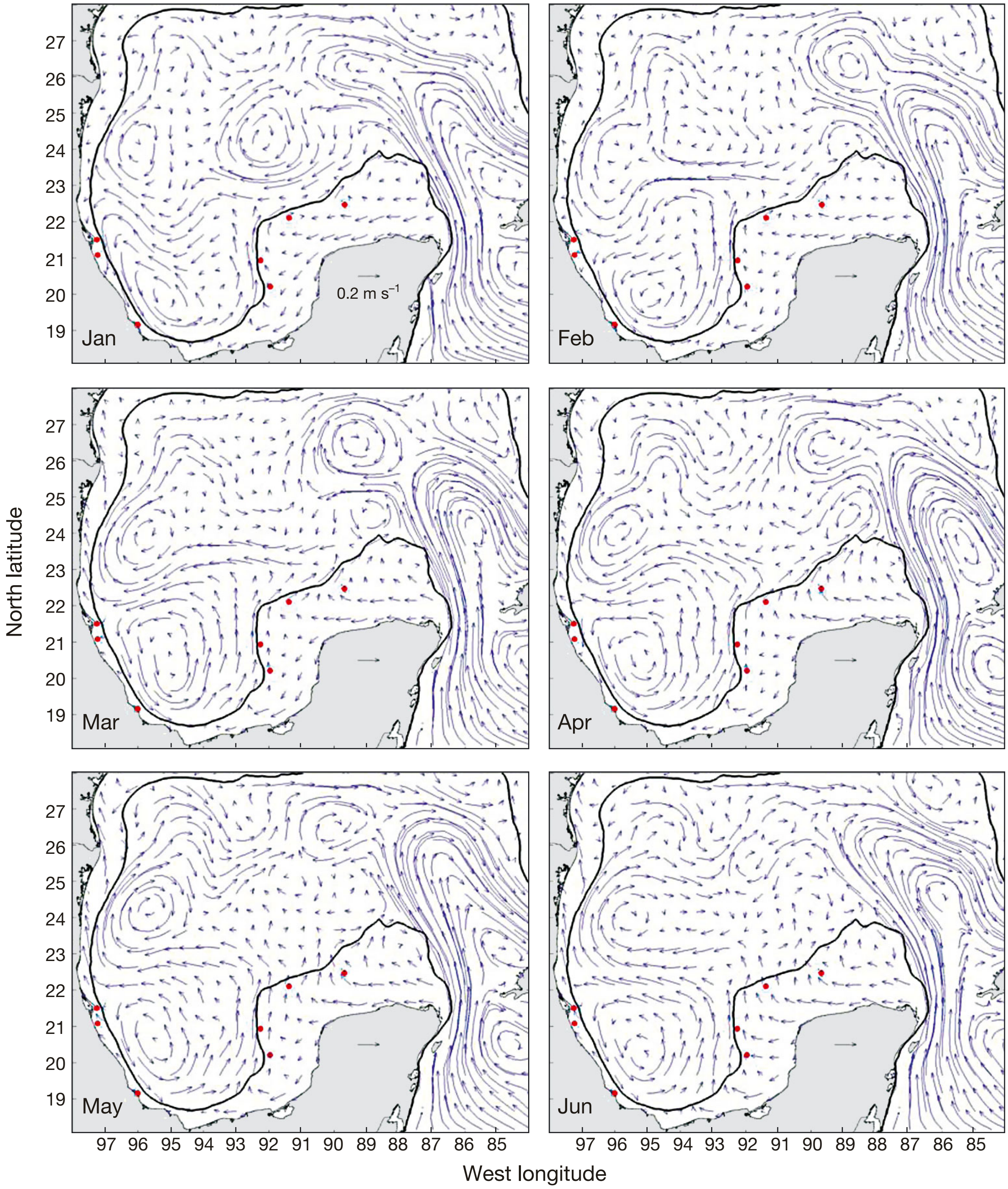

Fig. 2. Long-term (2006 through 2010) monthly mean surface circulation in the southern Gulf of Mexico throughout a year. Red dots represent the coral reef systems. Black line: continental shelf

eled particle launching, Triángulos reef had only 1.13 % of the initial value, and at the end of the period the larval retention was low (0.04 %) and similar to those of Arenas and Alacranes (Fig. 5).

Main dispersal pathways were fairly variable throughout the year. On the western shelf, the principal pathway reached its northern limit (~26° N) in June-July, whereas in October the highest particle concentrations reached only 23° N. Over the Campeche Bank, the dispersal pathway corresponded to the shelf edge from Alacranes to Arcas, with no evident seasonality (Fig. 6).

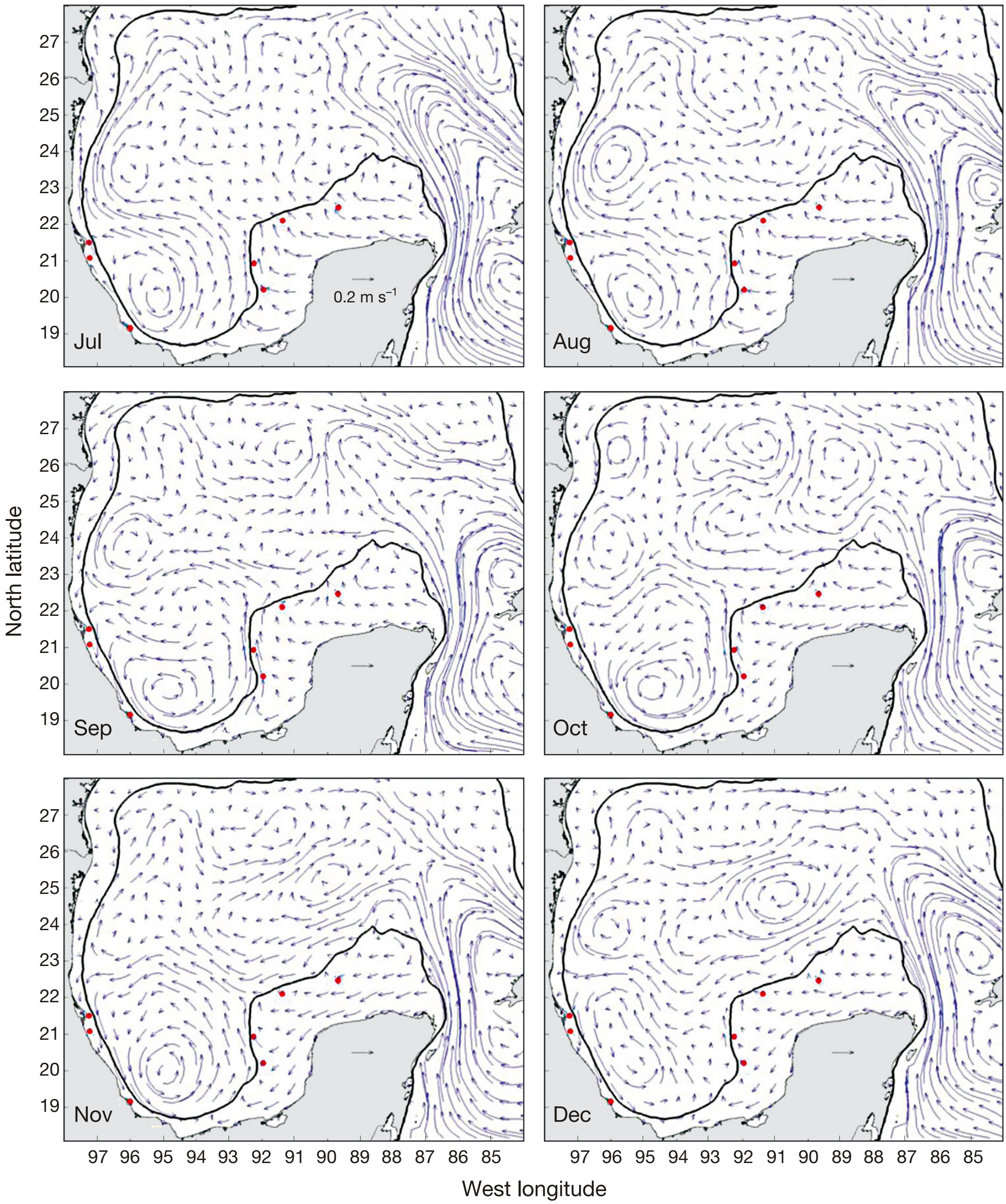

Fig. 2 (continued)

DISCUSSION

Owing to the intrinsic difficulties of doing a field study of the physical and biological variability affecting ecosystems dynamics, the use of high-resolution circulation models arises as an outstanding tool to analyze the dispersal pathways of species and the successful exchange of organisms among distant habitats (Cowen et al. 2006, Jones et al. 2009). The only previous quantitative study addressing connectivity in the southern Gulf of Mexico modeled red snapper larval transport starting over the Campeche Bank (Johnson et al. 2013); however, coral reef ecosystems have not been treated before. Therefore, this study

Table 1. Yearly mean (±SD) connectivity matrix among 7 coral reef systems in the southern Gulf of Mexico with pelagic larval durations of 0–15, 16–25, 26–35 and 0–35 d. Rows = starting sites of particles; columns = final destinations

	Lobos	Tuxpan	Veracruz	Arcas	Triángulos	Arenas	Alacranes
(a) 0–15 d							
Lobos	90.055 ± 0.4	27.378 ± 1.9	1.656 ± 0.8	0.0	0.0	0.0	0.0
Tuxpan	34.725 ± 4.6	93.933 ± 0.5	1.606 ± 0.7	0.0	0.0	0.0	0.0
Veracruz	0.441 ± 0.6	0.796 ± 0.7	87.878 ± 0.4	0.012 ± 0.0	0.044 ± 0.0	0.0	0.0
Arcas	0.0	0.0	0.0	88.840 ± 0.3	14.198 ± 5.3	0.420 ± 0.3	0.004 ± 0.0
Triángulos	0.0	0.0	0.0	0.720 ± 0.7	85.905 ± 1.1	1.737 ± 0.5	0.008 ± 0.0
Arenas	0.0	0.0	0.0	0.003 ± 0.0	0.308 ± 0.4	87.786 ± 0.4	0.115 ± 0.1
Alacranes	0.0	0.0	0.0	0.0	0.0	0.368 ± 0.3	88.235 ± 0.5
(b) 16–25 d							
Lobos	6.141 ± 1.6	9.305 ± 1.7	2.474 ± 0.9	0.001 ± 0.0	0.011 ± 0.0	0.0	0.0
Tuxpan	8.484 ± 2.1	14.018 ± 3.0	2.687 ± 1.0	0.005 ± 0.0	0.015 ± 0.0	0.0	0.0
Veracruz	1.034 ± 0.8	1.933 ± 1.2	5.817 ± 1.3	0.125 ± 0.1	0.417 ± 0.2	0.014 ± 0.0	0.0
Arcas	0.0	0.0	0.003 ± 0.0	3.508 ± 1.2	3.499 ± 0.7	1.198 ± 0.5	0.005 ± 0.0
Triángulos	0.003 ± 0.0	0.0	0.001 ± 0.0	0.410 ± 0.5	0.981 ± 1.0	1.225 ± 0.6	0.017 ± 0.0
Arenas	0.0	0.0	0.0	0.084 ± 0.1	0.635 ± 0.7	1.449 ± 0.3	0.116 ± 0.1
Alacranes	0.0	0.0	0.0	0.049 ± 0.1	0.035 ± 0.0	1.391 ± 1.0	1.229 ± 0.3
(c) 26–35 d							
Lobos	3.339 ± 1.4	5.123 ± 1.3	2.050 ± 0.5	0.027 ± 0.0	0.098 ± 0.0	0.003 ± 0.0	0.0
Tuxpan	4.480 ± 1.8	7.010 ± 2.4	2.380 ± 0.5	0.020 ± 0.0	0.077 ± 0.0	0.006 ± 0.0	0.0
Veracruz	1.139 ± 0.6	1.916 ± 1.0	2.884 ± 1.0	0.224 ± 0.1	0.626 ± 0.2	0.073 ± 0.1	0.0
Arcas	0.015 ± 0.0	0.013 ± 0.0	0.033 ± 0.0	1.624 ± 0.7	1.812 ± 0.5	1.006 ± 0.3	0.025 ± 0.0
Triángulos	0.060 ± 0.0	0.040 ± 0.0	0.034 ± 0.1	0.159 ± 0.2	0.428 ± 0.5	0.494 ± 0.3	0.032 ± 0.0
Arenas	0.029 ± 0.0	0.013 ± 0.0	0.005 ± 0.0	0.196 ± 0.2	0.515 ± 0.5	0.586 ± 0.2	0.044 ± 0.0
Alacranes	0.001 ± 0.0	0.0	0.0	0.180 ± 0.1	0.214 ± 0.1	1.070 ± 0.7	0.388 ± 0.2
(d) 0–35 d							
Lobos	90.664 ± 0.5	31.515 ± 2.0	5.447 ± 1.6	0.028 ± 0.0	0.108 ± 0.0	0.003 ± 0.0	0.0
Tuxpan	42.414 ± 6.2	94.363 ± 0.5	5.882 ± 1.5	0.024 ± 0.0	0.091 ± 0.1	0.006 ± 0.0	0.0
Veracruz	2.508 ± 1.7	3.674 ± 2.2	88.433 ± 0.5	0.345 ± 0.2	1.079 ± 0.3	0.085 ± 0.1	0.0
Arcas	0.015 ± 0.0	0.013 ± 0.0	0.036 ± 0.0	89.188 ± 0.4	18.996 ± 5.2	2.471 ± 0.9	0.033 ± 0.0
Triángulos	0.062 ± 0.0	0.040 ± 0.0	0.035 ± 0.1	1.128 ± 1.2	86.054 ± 1.2	3.192 ± 1.1	0.053 ± 0.1
Arenas	0.029 ± 0.0	0.013 ± 0.0	0.005 ± 0.0	0.266 ± 0.2	1.321 ± 1.4	87.964 ± 0.4	0.252 ± 0.2
Alacranes	0.001 ± 0.0	0.0	0.0	0.210 ± 0.1	0.239 ± 0.1	2.616 ± 1.7	88.348 ± 0.5

Table 2. Minimum arriving times in days among 7 coral reef systems in the southern Gulf of Mexico. Values were obtained from dispersal simulations of particles launched every 24 h for 5 yr (2006 through 2010) and tracked for 35 d. *Particles launched every 10 d for 3 yr (2006 through 2008) and tracked for 400 d. Rows = starting sites of particles; columns = final destinations

	Lobos	Tuxpan	Veracruz	Arcas	Triángulos	Arenas	Alacranes
Lobos	–	1	4	20	20	28	288*
Tuxpan	1	–	4	21	20	30	210*
Veracruz	7	5	–	10	9	16	72*
Arcas	27	27	23	–	1	6	10
Triángulos	24	26	26	2	–	3	8
Arenas	29	27	29	13	4	–	5
Alacranes	30	63*	63*	19	18	7	–

represents the first quantitative approach in the knowledge of connectivity patterns among the emerged reef systems in the southern Gulf of Mexico.

Connectivity matrices referring to a range of PLDs (Table 1a–c) indicated that reef systems from the western side (Lobos, Tuxpan and Veracruz) were connected only weakly with those of the Campeche Bank (Arcas, Triángulos, Arenas and Alacranes), even over a 35 d period (Table 1d). Jordán-Dahlgren (2002) deduced, from direct observations of the distribution and abundance of 31 gorgonian coral species, that there was limited connectivity between the Campeche Bank reefs and those of the western side. Moreover, Johnson et al. (2013) simulated the dispersion of particles released from a regular grid across the Campeche Bank after 31 d of planktonic drift, and concluded that a small proportion (<1%) of propagules arrived in shelf waters elsewhere in the Gulf. Their model showed the connection from the Campeche Bank to the western Gulf to be limited because of the long time scales of the westward eddies

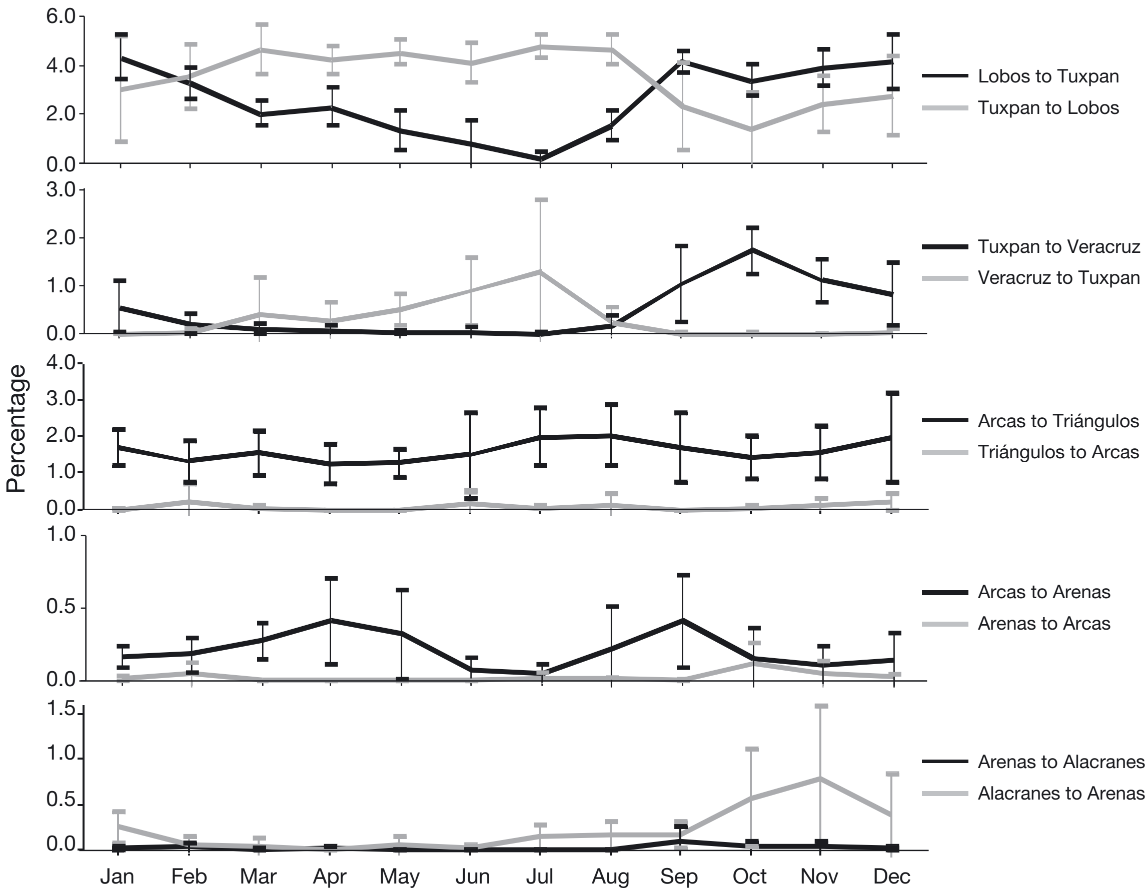

Fig. 3. Monthly mean percentage of particles emitted and received by different reef pairs in the southern Gulf of Mexico. Values were obtained from dispersal simulations of particles launched every 24 h for 5 yr (2006 through 2010) and tracked for 35 d

derived from the Loop Current and the relatively short duration of the larval stage. For species with a PLD of ≤35 d (i.e. *Haemulon flavolineatum* and *Hypoplectrus nigricans*), model results indicated that the main connection route between the 2 areas was in the southern Gulf, from Veracruz to Triángulos reefs, and that these had a low proportion of exchange (Table 1d).

Temporally, direction and degree of connectivity among reefs were strongly coupled with seasonal variations of surface circulation (Fig. 2), and intra-annual changes in the connectivity patterns were more evident in the reef structures of the southwestern Gulf of Mexico. For instance, the Tuxpan–Lobos connection was higher during the March–August period (Fig. 3), when the surface currents were predominantly northwards (Fig. 2; Zavala-Hidalgo et al. 2003, Drubanna et al. 2011). By contrast, from September to February, the connection was higher in the Lobos–Tuxpan direction, when the currents were mainly southwards (Figs. 2 & 3). Similar results were exhibited in the Tuxpan-Veracruz pair. Our results agree with those of Drubanna et al. (2011), who analyzed the trajectories of surface drifters over the western shelf and found that during March to August most drifters moved northwards, and during September to February most drifters moved southwards, recognizing the wind stress as the main driving force.

On the western edge of the Campeche Bank, the main connection was towards the north all the year. Hence, the number of particles released from Arcas reef that arrived at Triángulos or Arenas was higher than the number of particles arriving in the opposite direction (Fig. 3). According to Zavala-Hidalgo et al. (2003), neritic and oceanic waters in the southern Gulf have a semi-decoupled circulation pattern. As stated, deep-sea ocean circulation is cyclonic, whereas over the wide eastern continental shelf, currents flow southwestwards throughout the year. Vázquez-de la Cerda et al. (2005) suggested that the circulation along the outer shelf is likely to be influenced by the mesoscale cyclonic gyre. Supporting

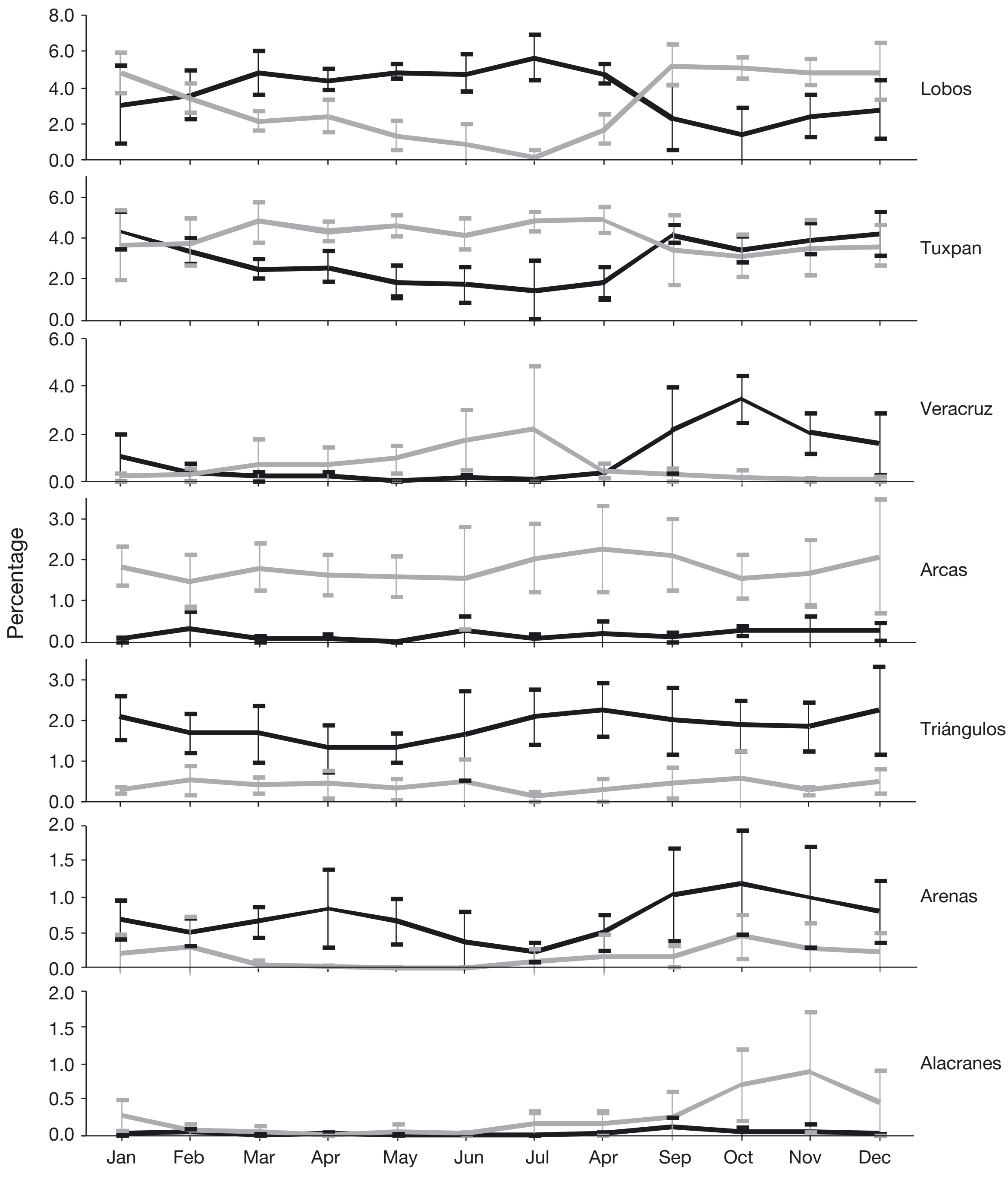

Fig. 4. Monthly mean percentage of particles successfully emitted (gray) and received (black) for each reef, based on the whole connectivity among 7 coral reef systems in the southern Gulf of Mexico. Values were obtained from dispersal simulations of particles launched every 24 h for 5 yr (2006 through 2010) and tracked for 35 d

this suggestion, connectivity results indicated that ecosystems at the western edge of the Campeche Bank (Arcas, Triángulos and Arenas) were more influenced by the circulation pattern in the deep basin (Fig. 2). In the northern Campeche Bank, westward connection dominated, and was highest during the September to January period (Fig. 3). Even when the degree of connectivity from Alacranes with the remainder Campeche Bank reefs was low, the highest connection period was consistent with the high energy wind season. In the northern Yucatan Peninsula, winds are stronger during the fall and winter

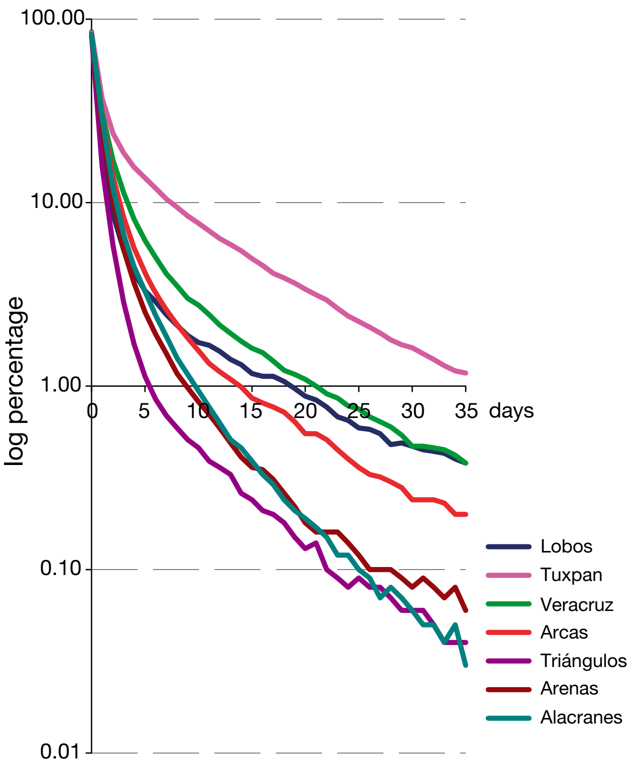

Fig. 5. Daily mean percentage of larval retention within a 10 km radius of each of the 7 coral reef systems in the southern Gulf of Mexico

months, when the winds blow towards the west and southwest at approximate speeds of 4 to 5 m s^{-1} (Gutiérrez-de Velasco & Winant 1996).

The highest values of larval retention corresponded to the reefs over the western shelf, contrasting with the low values of the reefs on the Campeche Bank (Fig. 5). As stated, Drubanna et al. (2011) observed that drifters over the western shelf preferentially moved northwards from March to August, and southwards from September to February; however, they could also move in either direction, particularly south of 21° N and during the warmer months. Those authors obtained a high correlation coefficient between the wind stress and the alongshore currents, indicating that surface currents are strongly driven by the wind along the shelves. Therefore, self-recruitment values of coral reef associated species of the western Gulf were probably due to the passage of synoptic-scale atmospheric systems that make local winds to change between northwestward and southwestward in short periods (2 to 10 d), depending on the position of the atmospheric pressure systems. Regarding the Campeche reefs, the lower retention values of virtual larvae may be due to more stable oceanographic conditions throughout the year. Semi-permanent circulation over the outer shelf (Fig. 2) limits the possibilities of particles returning to the reefs, and allows them to disperse over the wide Bank and adjacent oceanic region. Tuxpan reef had the highest self-recruitment values, and Arenas, the lowest (Fig. 5). Species lasting 13 to 20 d in the plankton, such as *Haemulon flavolineatum*, exhibit a higher probability (3.37 to 5.51 %) to be self-recruited in Tuxpan than in Arenas (0.18 to 0.49 %). In contrast, species with longer PLD, such as *Stegastes partitus* and *Chaetodon capistratus*, reduce in both cases the possibilities to be self-recruited.

Model and Mantel test results ($r = 0.58$, $p < 0.001$) also indicated that reefs in close proximity showed a higher degree of connectivity and shorter connection times. According to Friedlander et al. (2009), the scales and rates of successful exchanges among distant marine populations have profound implications for the dynamics and genetic structure of populations. For instance, over the western shelf, the exchange of individuals can occur not only for species having a very short pelagic phase (Table 2), but also for species lasting more than 25 d in the plankton (Table 1c), such as *Stegastes partitus* and *Chaetodon capistratus*. Also, migration of individuals from the Bank to the western slope is only possible for species whose PLDs last more than 24 d; nevertheless, migration in the opposite direction is feasible for species with a PLD of only 9 d, such as some pomacentriid species. This difference is due to an asymmetry in the minimum arriving times between the 2 groups of reefs (Table 2). Mantel test results, when Alacranes reef is excluded, exhibited a higher correlation ($r = 0.89$, $p < 0.001$) between geographical distances and connection times. This finding indicates that Alacranes reef is isolated from the other reefs because the main current patterns in the southern Gulf do not favor the connection with the other reefs (Fig. 2). The connection between Arcas, Triángulos, and Arenas is higher than that with Alacranes, as was previously explained.

Triángulos and Arenas reefs functioned as sink sites throughout the year (Fig. 4). As observed in other ecosystems, the existence of sink sites is the result of highly unidirectional larval dispersal pattern (Bode et al. 2006), as in the present case. Arcas reef functioned as a source site and represented the main larval supply for its northern neighbors Triángulos and Arenas, all 3 lying on the western edge of the Bank and strongly influenced by the cyclonic gyre prevailing in the basin throughout the year. In particular, Triángulos site, the main connection node with the western group, might harbor high species richness due to its strategic position in the whole network.

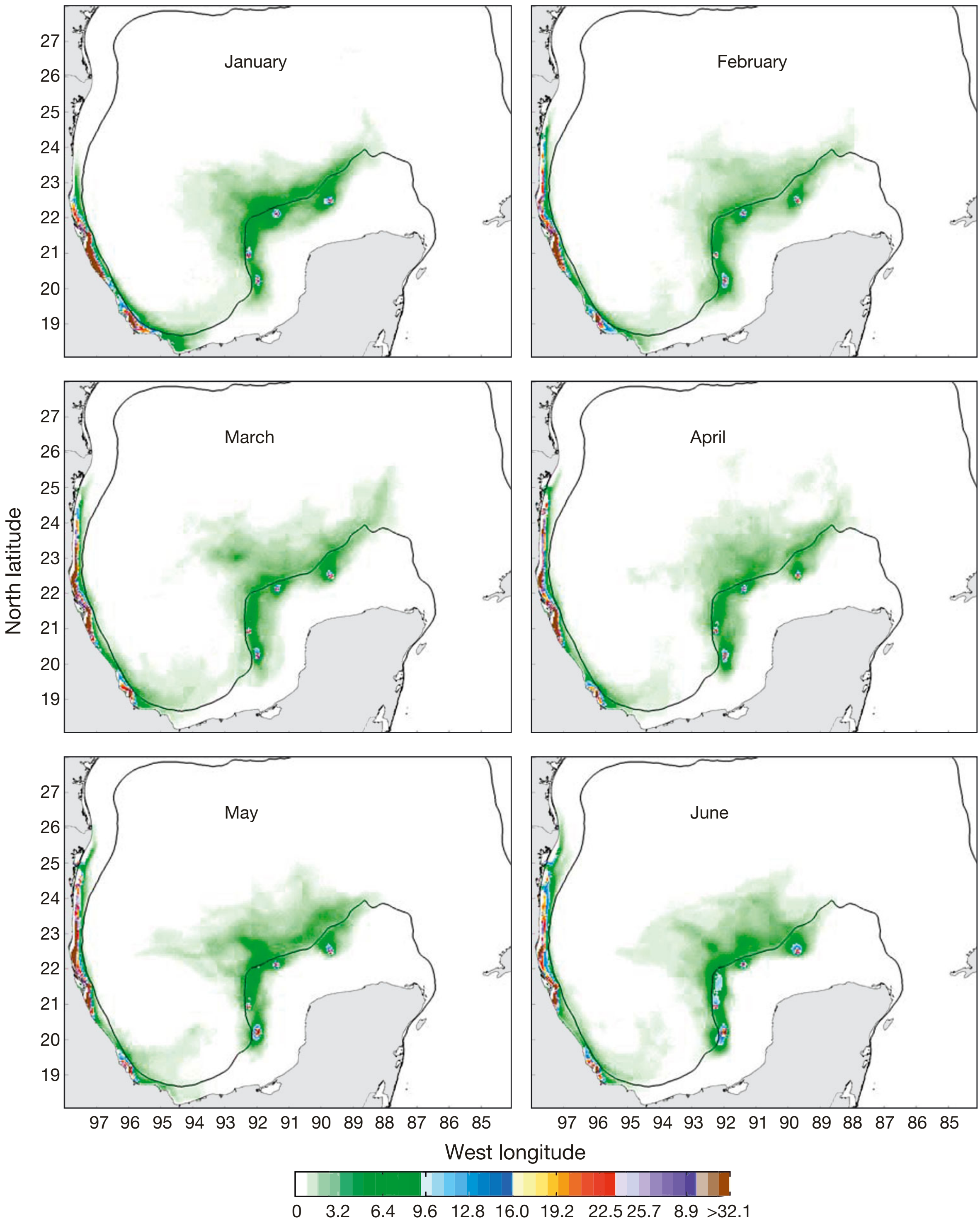

Fig. 6. Ensemble of pathways of particles released during 5 yr and tracked for 35 d from 7 coral reef systems in the southern Gulf of Mexico. Values (%) are related to the maximum number of particles per area. Black line: continental shelf

The ensemble of dispersion routes of the 1 278 200 virtual larvae released from the 7 reefs over 5 years led us to infer the main dispersal pathways of larvae. In the southwestern region, the main pathway corresponded to shelf waters, whereas on the Campeche Bank the principal route of the particles was the western platform edge (Fig. 6). In the case of particles released over the western shelf, it is

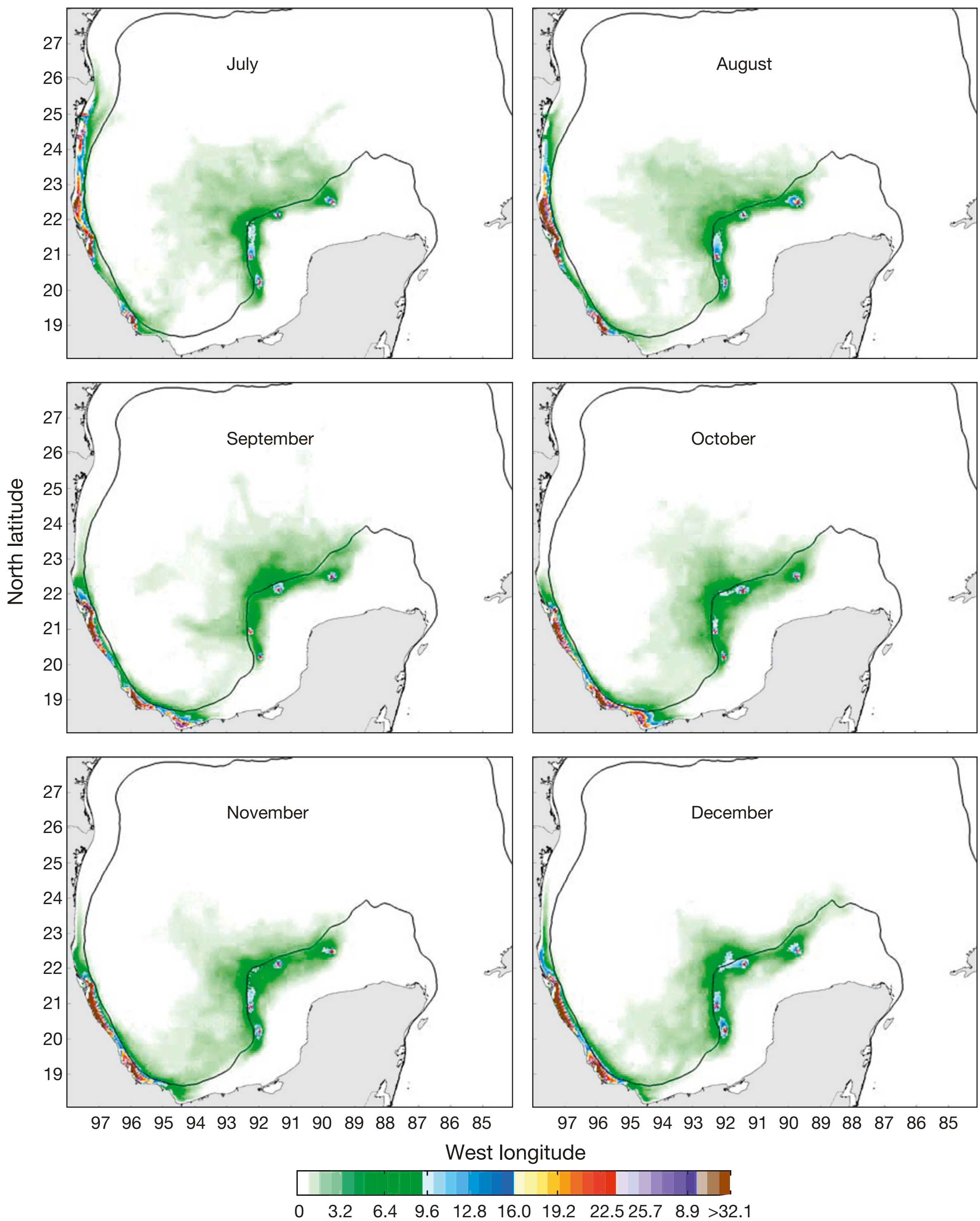

Fig. 6 (continued)

suggested that the semi-decoupled circulation pattern between neritic and oceanic waters in the southern Gulf (Zavala-Hidalgo et al. 2003) allows more particles to remain trapped in the surface currents over the narrow western shelf. In contrast, particles released in the Bank reefs distributed over a wide region that included the broad continental shelf and oceanic waters. However, it was possible to distinguish a pathway of high particle concentration (Fig. 6), coincident with the region and periods of low current velocities, near the shelf break (Fig. 2). This result suggested that the area of confluence between oceanic and neritic waters over the Bank edge constitute an important habitat for zooplanktonic organisms, and the principal connecting route among the Campeche reefs. In agreement with this, marine field observations indicated high concentrations of zooplankton at convergence zones and along boundaries between waters of different densities; this, in turn, may attract predators from higher trophic levels (Davis et al. 2002, Bost et al. 2009).

Quantitative simulations of larval dispersal contribute to the identification of ecosystem networks that should be considered for recognition of marine protected areas. Although any conservation strategy must depend on the local economic, social and ecological conditions, in the case of the reef systems in the southern Gulf of Mexico the strongest measures are needed. These should include not only the reef areas, but also the larvae dispersal pathways that connect the reefs, i.e. the narrow western continental shelf, bounded by 25° N and 18.5° N, and the western edge of the Campeche Bank, from Arcas to Alacranes. As Akçakaya et al. (2007) stressed, protection of habitat pathways benefits reproducing species in several temporal scales. In addition, these pathways offer a continuous stretch of habitat for populations, they improve connectivity among distant sites, they contribute to the total abundance of populations and they act as a buffer against catastrophic events. Conservation measures should also pay special attention to local sites of the metapopulation that cannot independently persist through time, such as Lobos, Veracruz, Triángulos and Arenas — reefs identified here as sinks. Finally, we suggest that Arcas reef must be designated a marine protected area, legislated by appropriate conservation and security measures, considering its high ecological importance and economic value: as a source site in the reef ecological network and as one of the main oil storage and exporting ports in the Mexican Gulf.

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