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APPLICATION OF REMOTE SENSING TO THE STUDY OF THE PELAGIC SPINY LOBSTER LARVAL TRANSPORT IN THE TROPICAL ATLANTIC*

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ABSTRACT

The connectivity of marine populations via larval dispersal is crucial for the maintenance of fisheries production and biodiversity. Because larval dispersion takes place on different spatial scales, global operational satellite data can be successfully used to investigate the connectivity of marine populations on different spatial and temporal scales. In fact, satellite data have long been used for the study of the large and mesoscale biological processes associated with ocean dynamics. This paper presents simulations of spiny lobster larvae transport in the Tropical Atlantic using the geostrophic currents, generated by altimetry that feeds an advection/diffusion model. Simulations were conducted over the Tropical Atlantic (20ºN to 15ºS), considering four larvae release areas: the Cape Verde Archipelago, the Ivory Coast, Ascension Island and Fernando de Noronha Archipelago. We used mean geostrophic current (MGC) calculated from 2001 to 2005 to represent the mean circulation of the Tropical Atlantic. We also ran the model for the El Niño geostrophic current regime (ENGC) using part of the MGC data, representing the El Niño 2002/2003 event. Results suggest that the intensification of the mesoscale ocean processes associated with El Niño events promotes the connectivity between populations, increasing the chances of a genetic flux among different stocks. We concluded that the altimetry geostrophic current data together with a relatively simple advection/diffusion model can provide useful information about the physical dynamics necessary to conduct studies on larval dispersion.

RESUMO

A conectividade de populações marinhas através da dispersão larval é crucial para a manutenção da produção pesqueira e da biodiversidade. A dispersão de larvas ocorre em diferentes escalas espaciais e temporais, de forma que o recobrimento global e escala sinóptica fazem dos dados de satélite ferramentas importantes para esses estudos. O objetivo deste artigo é apresentar os resultados do uso de dados de correntes geostróficas derivadas de satélites altímetros para simular o transporte de larvas de lagosta espinhosa no oceano Atlântico Tropical. As simulações foram realizadas ao longo do Atlântico Tropical (20ºN - 15ºS), iniciando em quatro locais (Cabo Verde, Costa do Marfim, Ilha de Ascensão e Arquipélago de Fernando de Noronha). Foi utilizado um modelo advectivo/difusivo forçado com o campo médio de circulação geostrófica calculado entre 2001 e 2005 e outro forçado com campo correspondente ao evento de El Niño 2002/2003. Os resultados obtidos sugerem que há uma intensificação de processos oceânicos de meso-escala durante o ano de El Niño, que promove a conectividade entre diferentes estoques e aumenta as chances de ocorrer um fluxo genético. Os dados de correntes geostróficas gerados a partir de satélites altímetros incorporados a um modelo advectivo/difusivo simples podem prover informações importantes acerca da dinâmica física necessárias para conduzir estudos sobre dispersão larval.

Descriptors: Satellite data, Altimetry, Larval transport, El Niño.
Descritores: Dados de satélite, Altimetria, Transporte de larvas, El Niño.

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INTRODUCTION

Many marine benthic species have populations connected by larval transport during their planktonic phases. Connectivity depends largely on the larval duration in the plankton, the spatial heterogeneities in physical conditions such as advection and diffusion, vertical larval migration, and mortality (COWEN et al., 2000; BECKER et al., 2007). These are important elements in fisheries management and in the design of marine protected areas (MPAs) that have fuelled the debate over the relative importance of size and spacing of MPAs (HASTINGS; BOTSFORD, 2006; ALMANY et al., 2007). Connectivity among spatially structured marine populations is also known to be important to support sustainable fisheries.

Because larval dispersion takes place on different spatial scales, it has become increasingly evident that satellite data can be successfully used to investigate the connectivity of marine populations on different spatial and temporal scales. For example, since the mid-seventies, maps of sea surface temperature (SST) have been derived from infrared radiometers onboard NOAA (National Oceanic and Atmospheric Administration) satellites. Based on these SST maps it is possible, for instance, to extract information about the ocean currents, their frontal zones, meanderings and eddy shedding. Long-term global SST data sets derived from satellites are also considered one of the most useful indicators of climate change. Ocean color sensors have been used to monitor variations of chlorophyll-a concentrations on a global scale, which are of great importance for biological studies of marine ecosystems and to climate change, considering that the CO_2 oceanic intake is controlled by the planktonic photosynthesis. Altimetric radar such as TOPEX/Poseidon (T/P), European Remote-Sensing satellite (ERS) and Jason provide information to produce maps of dynamic height on an operational and global basis, and derive geostrophic current maps with a temporal resolution of 7-10 days. These maps can be used to force advection/diffusion models of marine larvae, particularly for spiny lobster larvae that can be advected for long periods by ocean currents.

It is possible to simulate larval advection using the current field generated as the output of ocean models. These rather complex models are normally initialized with climatological fields of temperature and salinity and are forced by either climatological or satellite winds. However, geostrophic current fields derived from spaceborne altimetry data can be used to force much simpler advection/diffusion models.

Modeling Early Life Stages

The majority of marine organisms exhibit a complex life cycle that includes separate planktonic larval and bottom-dwelling juvenile and adult phases. Dispersal in its broadest sense means movement away from the birthplace (SUGDEN; PENNISI, 2006). Besides the physical conditions affecting larval dispersion, biological parameters are extremely important. Among the most important biological parameters, two deserve special attention: the time of development and the swimming behavior of larvae. The first one should be divided into two categories: short-lived planktonic larvae (e.g. reef fish larvae and other invertebrate larvae) and long-lived planktonic larvae (e.g. spiny lobster larvae). Short-lived planktonic larvae, especially fish larvae, seem to present a self-recruitment process more intense and efficient than previously thought (COWEN et al., 2006; ALMANY et al., 2007).

Fish larvae present intense swimming abilities; therefore models should better address mesoscale features and, if possible, simulate the water column's behavior (LEIS, 2006; MONTGOMERY et al., 2006). In contrast, the pelagic larvae of spiny lobsters (called phyllosoma) show some adaptations inherent to holoplankton (i.e. a transparent and dorsoventrally flattened leaf-like body) and are associated with their ability to withstand up to 12 months in the plankton. These characteristics and the lack of swimming abilities allow spiny lobster larvae to be transported for long distances by ocean currents away from the spawning area (PHILLIPS et al., 1980; PHILLIPS; SASTRY, 1980; BOOTH; PHILLIPS, 1994).

Studies on lobster larval dispersion using geostrophic currents derived from altimetry data include that of Chiswell and Booth (1999) near the Wairarapa eddy (New Zealand), using T/P satellite data. Polovina et al. (1999) also used T/P data to force an advection/diffusion model for *P. marginatus* in the Hawaiian Archipelago. Griffin et al. (2001) developed a quantitative biophysical model of lobster larval (*P. cygnus*) transport using a T/P geostrophic velocities field. More recently, Chiswell et al. (2003) used geostrophic current fields derived from altimetry to run a larval transport model in the Tasman Sea.

In the Tropical Atlantic Ocean there are five spiny lobster species of the genus *Panulirus*, of which *P. argus*, *P. leavicauda* and *P. echinatus* occur in Brazilian waters, including the oceanic islands of the Atol das Rocas, the Fernando de Noronha and the São Pedro São Paulo archipelago (HOLTHUIS, 1991). There is a predominance of *P. echinatus* in the oceanic islands of Ascension, São Pedro and São Paulo, Fernando de Noronha and the Atol das Rocas

(COELHO; RAMOS-PORTO, 1998; TAVARES, 2003). The species *P. echinatus*, *P. regius* and *P. charlestoni* are known to occur off the northwestern African coast. However, Freitas and Castro (2005) reported the occurrence of *P. argus* in the Cape Verde Archipelago and also cited other occurrences off the Ivory Coast (see also Tavares, 2003).

Grimm (1999) suggests a few basic rules when dealing with ecological models: (i) models should be kept as simple as possible; (ii) the final importance of the model is to understand the processes involved, and (iii) modelers should adopt an experimental attitude.

In the present paper we show how geostrophic currents generated by altimetry can be used to simulate the transport of spiny lobster larvae, addressing the implications for the connectivity of potential spawning grounds. We also evaluate the influence of El Niño in changing the velocity fields and the connectivity among these spawning grounds.

Materials and Methods

Ocean Current Data

We used the geostrophic surface current velocity fields obtained from altimetry, distributed by AVISO (http://www.aviso.oceanobs.com/), to run the advection/diffusion model. This database is a result of merged observations from T/P, Jason and ERS altimeters to achieve improved spatial and temporal resolutions of 1/3 degree and 7 days in a global coverage. Poleward of 5ºN and 5ºS the zonal (u) and meridional (v) geostrophic velocity components are calculated from the meridional and zonal slopes of the dynamic height (ζ) derived from the sea level anomalies (SLA). In the ±5° equatorial band, where the geostrophic assumption becomes weak, velocities are calculated using the second derivative of ζ according to Picaut (1989) and Lagerloef et al. (1999). The absolute dynamic topography used in the calculations of u and v are obtained by adding SLA to the mean dynamic topography (MDT), the latter being estimated by subtracting the standard geoid from the mean sea surface height (MSH).

We calculated the mean values of the zonal (u) and meridional (v) components using the AVISO database from 2001 to 2005 for each week of the year (1 to 52), obtaining the mean geostrophic current (MGC). This was the velocity field used to advect the particles, representing the surface circulation of the Tropical Atlantic for a typical year. We also ran the model for the El Niño geostrophic current regime (ENGC) using part of the MGC data relative to the El Niño event that occurred between 2002 and 2003. The El Niño period was determined using the *Oceanic Niño Index* (ONI), one of the standard indices used by NOAA to characterize El Niño events. This Index refers to the sea surface temperature anomaly (SSTA) taken in the Tropical Pacific (5°N-5°S and 120°-170°W) based on the climatology from 1971 to 2000. According to NOAA, El Niño and La Niña periods are identified in the series when a 0.5°C negative (El Niño) or positive (La Niña) anomaly occurs during 5 consecutive months. According to this Index we selected the geostrophic current velocities database from April 3rd 2002 to April 2nd 2003 time-series to represent the El Niño phenomenon.

We correlated the u ($r = 0.93, p=0.05, n = 70$) and v ($r = 0.63, p=0.05, n = 51$) velocity components from MGC with coincident velocities obtained by drifting-buoys (Global Drifter Program - GDP/SVP, http://www.meds-sdmm.dfo-mpo.gc.ca/) for the study area (excluding buoys without drogue).

With the same GDP/SVP drifter database we calculated the zonal (*kx*) and meridional (*ky*) eddy-diffusion coefficients, using only buoys with the drogue attached (n=377), in accordance with the methodology proposed by Assireu (2003). We calculated *kx* and *ky* for 35 boxes of 2°x2° distributed over the Tropical Atlantic, however, to represent the turbulence in the study area, our model used mean values for *kx* ($3.97\mathrm{x}10^{7}$cm²/s) and *ky* ($2.05\mathrm{x}10^{7}$cm²/s).

Advection/Diffusion Model

The advection/diffusion model was run by iteratively applying successive advective displacements due to water flow with added random displacement (ε) associated with diffusion.

Starting at a chosen x_t and y_t initial position, the new location ($x_{t+\Delta t}$, $y_{t+\Delta t}$) of each virtual larvae after a time interval Δt, is updated in time by the equations 1 and 2 (POLOVINA et al., 1999).

$$x_{t+\Delta t} = x_t + \frac{[u_{(xt,yt,t)}\Delta t + \varepsilon\sqrt{kx\Delta t}]}{\cos(y_t)} \qquad (1)$$

$$y_{t+\Delta t} = y_t + [v_{(xt,yt,t)}\Delta t + \varepsilon\sqrt{ky\Delta t}] \qquad (2)$$

where:

t = time (day);
x and y = position of the larvae (degrees of longitude and latitude);
u and v = zonal and meridional geostrophic velocity components (degree/day);
ε = normal distributed random variable (zero mean, unit standard deviation);
kx and *ky* = zonal and meridional eddy-diffusion coefficients (degree^2/day).

The first and second terms inside the brackets correspond to the advective and the diffusive displacements, respectively. The cosine function in the first equation corrects for the poleward convergence of meridians with latitude.

The time step was set to one day (Δt=1) with 365 iterations representing one year of simulation. Larvae have a new position each day, calculated using the u and v geostrophic velocities linearly interpolated from the four closest grid points. The simulation is halted when the larvae hit the coastline or whenever any of the four grid interpolating points touches land. Forcing altimeter geostrophic velocities are updated every seven days and no daily interpolation of this data set was performed between successive weeks.

Simulations

Simulations were conducted over the Tropical Atlantic (20°N to 15°S) starting during the spawning peak seasons of April and September (CAVALCANTE-SOARES; FONTELES-FILHO, 2000) from four different sites known to have adult populations: Cape Verde, Ivory Coast, Ascension Island and Fernando de Noronha Archipelago (Fig. 1). Each model run released 5000 virtual larvae (hereafter termed only larvae) from randomly chosen points inside a 1°lat x 1°long rectangle. Larvae were advected for 365 days using mean geostrophic current (MGC) and the El Niño geostrophic current regime (ENGC).

Results

Plots of larval trajectories readily allow differentiation between the advective fields from the MGC and the ENGC. The only exception is the Ivory Coast where simulations show almost no differences (Fig. 2).

All other larval drifts from the El Niño simulations present wider dispersal ranges when compared to MGC runs (Fig. 3-5). Considering the spawning ground of the Cape Verde Archipelago (Fig. 3), when MGC data are used, dispersal boundaries are somewhat confined for both spawning periods (April and September) and meridional larval transport did not reach 5° N. The ENGC simulations, in contrast, indicate that larvae can drift as far south as the equator when spawning occurs in September. Trajectories simulated for April have comparable boundaries but the ENGC dispersion is less compact during the El Niño period.

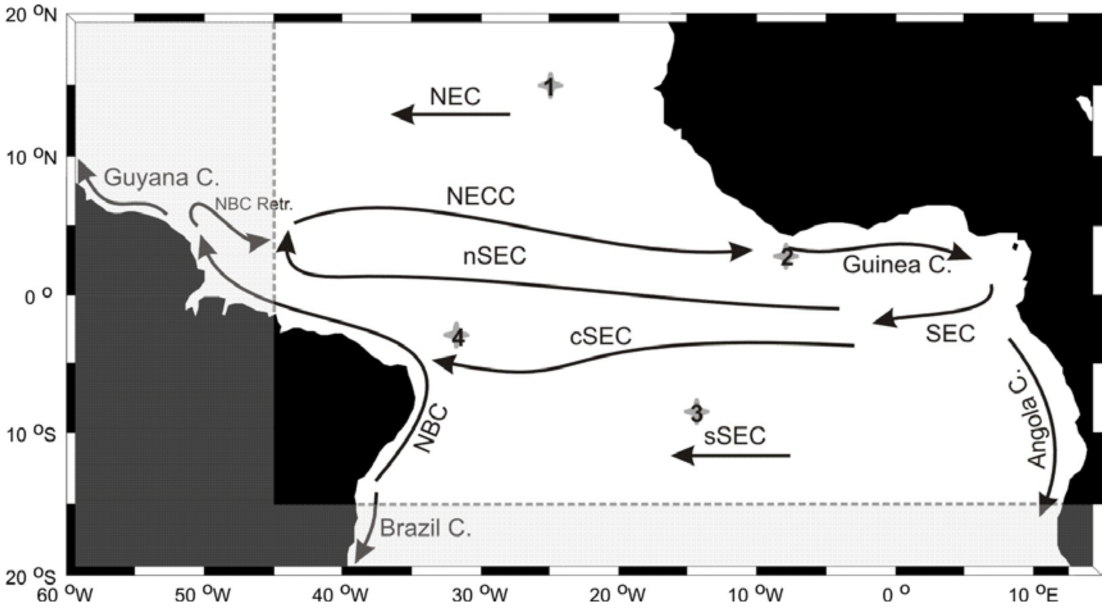

Fig. 1. Tropical Atlantic and study area (dashed rectangle). Main superficial ocean currents are indicated by arrows, including the North Equatorial Current NEC, North Equatorial Countercurrent NECC, Guinea Current, Angola Current, northern, central and southern branches of the South Equatorial Current SEC, Brazil Current, Guyana Current, North Brazil Current NBC and its retroflection (NBC Retr.) (Adapted from Lumpkin and Garzoli, 2005). The stars (✦) mark the release areas used to start the simulations: 1 - Cape Verde (24-25ºW, 15-16ºN); 2 - Ivory Coast (7-8ºW, 3-4ºN); 3 - Ascension Island (14-15ºW, 7-8ºS); 4 - Fernando de Noronha Archipelago (31-32ºW, 3-4ºS).

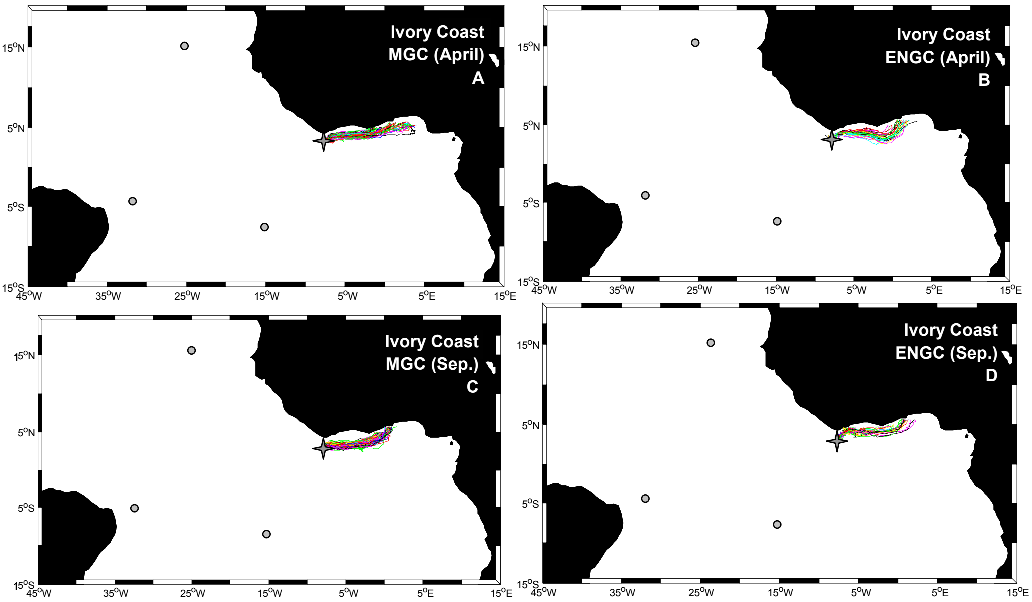

Fig. 2. Trajectories of virtual larvae (n= 5000) based on simulations starting in April (top) and September (bottom) from Ivory Coast (✦). Right-hand maps represent El Niño geostrophic currents (ENGC) and left-hand maps represent mean geostrophic currents (MGC). Circles indicate other adult stock populations to help visualize the connectivity among sites. Larvae trajectories are colored to improve visualization.

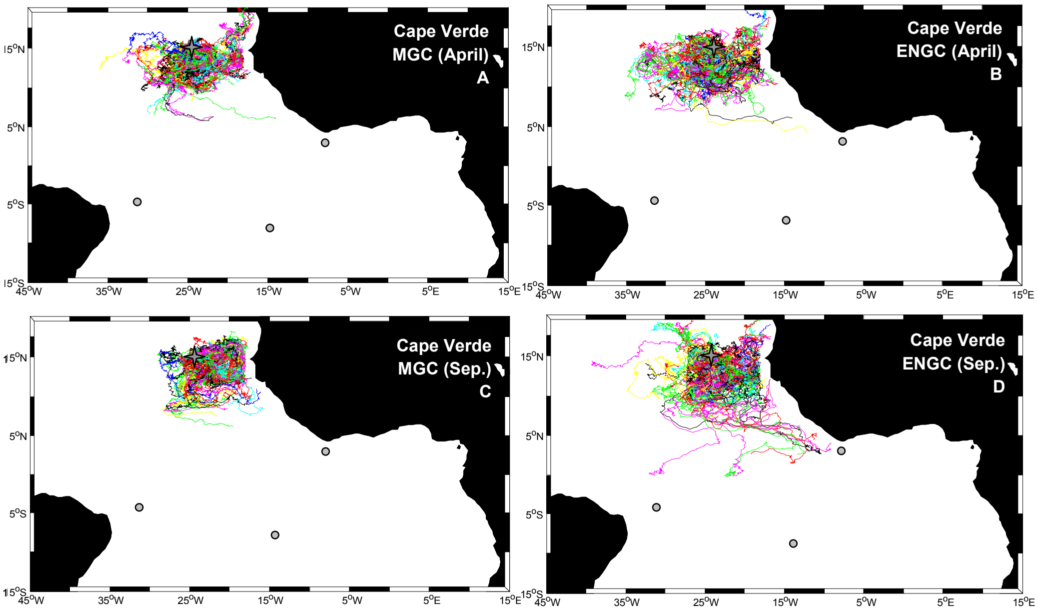

Fig. 3. Trajectories of virtual larvae (n= 5000) based on simulations starting in April (top) and September (bottom) from Cape Verde (✦). Right-hand maps represent El Niño geostrophic currents (ENGC) and left-hand maps represent mean geostrophic currents (MGC). Circles indicate other adult stock populations to help visualize the connectivity among sites. Larvae trajectories are colored to improve visualization.

Larval drifts originating from Ascension Island have more impressive differences between spawning seasons and geostrophic current data. The MGC-based simulations display a more compact trajectory pattern than the ENGC simulations, the latter extending zonally further to the east and meridionally to the north and south (Fig. 4). These north-south extensions of trajectories extrapolate for just a few degrees but what seems more relevant is the lack of compactness observed in the trajectories generated with the ENGC data. The simulation of trajectories departing from Ascension Island using the MGC data starting in September (Fig. 4C) is the only one that shows no extensions towards the Brazilian coast beyond 5ºS.

Spawning simulations dispersing from the Fernando de Noronha Archipelago also show a distinct behavior during the El Niño period (Fig. 5). In this release area larvae trajectories display a wider dispersion as compared to the MGC scenario, reaching more eastern longitudes but also being found closer to the northern Brazilian NE coast. It is clear that surface advection around the Fernando de Noronha Archipelago has a comparatively weaker meridional component because most simulated trajectories have a predominant east-west orientation. An example of this zonal advection is the ENGC scenario starting in September, by which some larvae were advected as far as 22ºW (Fig. 5D).

The overall intensification of the magnitudes of ENGCs relative to MGCs for the whole Tropical Atlantic is shown in Table 1. Except for the austral summer period, maximum weekly average velocities are higher during the El Niño period than during the rest of the year. Maximum average velocity was particularly high during the El Niño winter.

The spatial and seasonal variations in the ENGC magnitudes of the geostrophic current anomalies (relative to MGC) for the El Niño period were calculated at each grid point for the Tropical Atlantic. The results are displayed in Figure 6 superimposed on the mean geostrophic current vectors calculated using the MGC database. Anomalies were calculated based on the resultant of the two geostrophic velocity components (*u* and *v*), so that anomalies represent changes in magnitude (but not in direction). We can observe the MGC flow direction and intensity by looking at the vectors overlying these anomalies graphs. An increase in the magnitude of geostrophic currents is most evident in the North Brazil Current retroflection region during austral spring and winter and a weakening during the austral summer. Of greater importance, however, are the positive and negative anomalies seen throughout the equatorial Atlantic during the austral autumn and winter seasons, respectively.

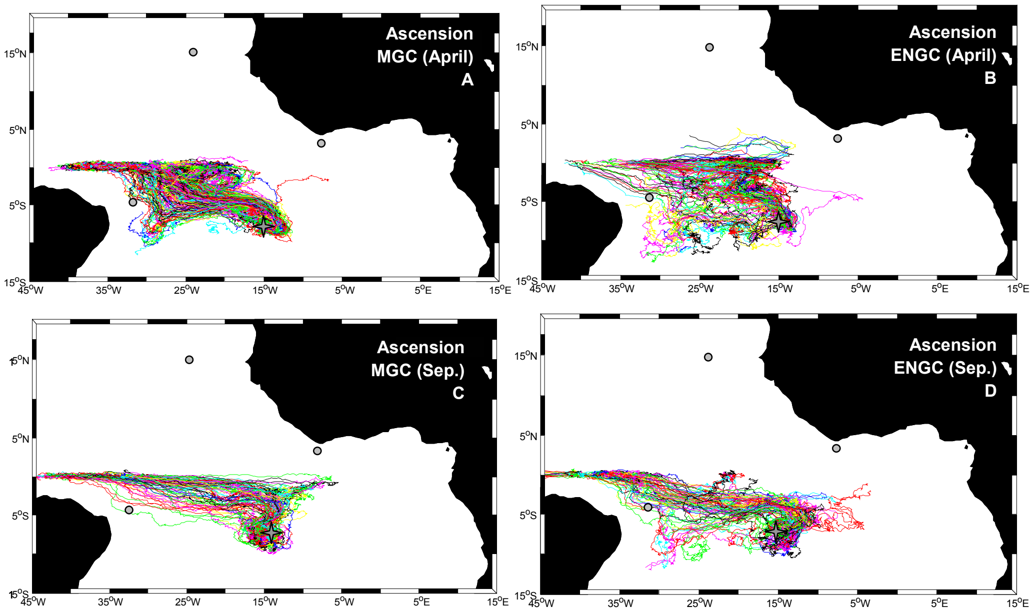

Fig. 4. Trajectories of virtual larvae (n= 5000) based on simulations starting in April (top) and September (bottom) from Ascension (✦). Right-hand maps represent El Niño geostrophic currents (ENGC) and left-hand maps represent mean geostrophic currents (MGC). Circles indicate other adult stock populations to help visualize the connectivity among sites. Larvae trajectories are colored to improve visualization.

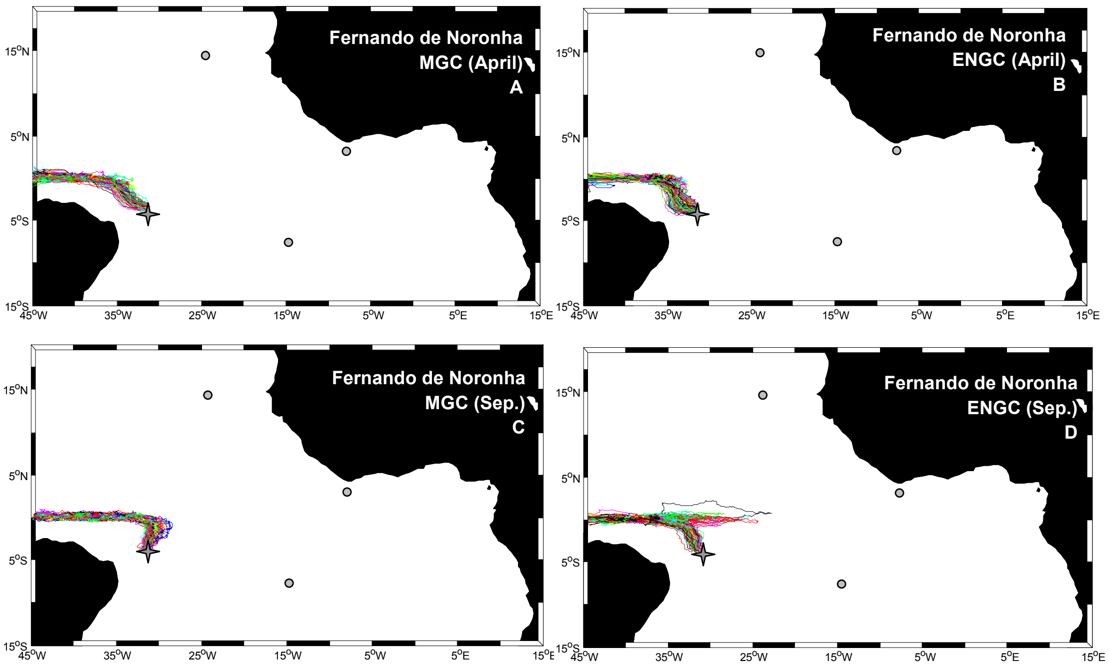

Fig. 5. Trajectories of virtual larvae (n= 5000) based on simulations starting in April (top) and September (bottom) from Fernando de Noronha (✦). Right-hand maps represent El Niño geostrophic currents (ENGC) and left-hand maps represent mean geostrophic currents (MGC). Circles indicate other adult stock populations to help visualize the connectivity among sites. Larvae trajectories are colored to improve visualization.

Table 1. Maximum geostrophic velocities for the Tropical Atlantic from SSALTO/DUACS data base (MGC) and data for the El Niño period.

	Mean Geostrophic Current (MGC)	**El Niño (ENGC)**
	Maximum	**Maximum**
Summer	64.76	41.52
Autumn	38.93	54.33
Winter	45.02	91.28
Spring	58.13	63.93

The observed geostrophic velocity anomalies during an El Niño year suggest large spatial and seasonal variabilities. This indicates that the greatest impact of an El Niño event upon larval dispersion will depend on the relative positions of the larvae cloud and the regions of maximum geostrophic velocity anomalies.

Discussion

There is a permanent tropical circulation composed of several zonal current and countercurrent bands in the equatorial Atlantic. As a consequence, the connectivity of adult lobster populations via larval dispersion in the Tropical Atlantic operates within a complex system. For example, the Cape Verde Archipelago located in the Tropical Eastern Atlantic, is subject to different oceanographic regimes (STRAMMA et al., 2005), including major large scale surface flow fields of the eastward North Equatorial Counter Current (NECC) and the Cape Verde frontal zone (CVFZ) (ZENK et al., 1991) between the North Equatorial Current (NEC) and the northern branch of the North Equatorial Counter Current (nNECC). It is also close to mesoscale variabilities such as tropical

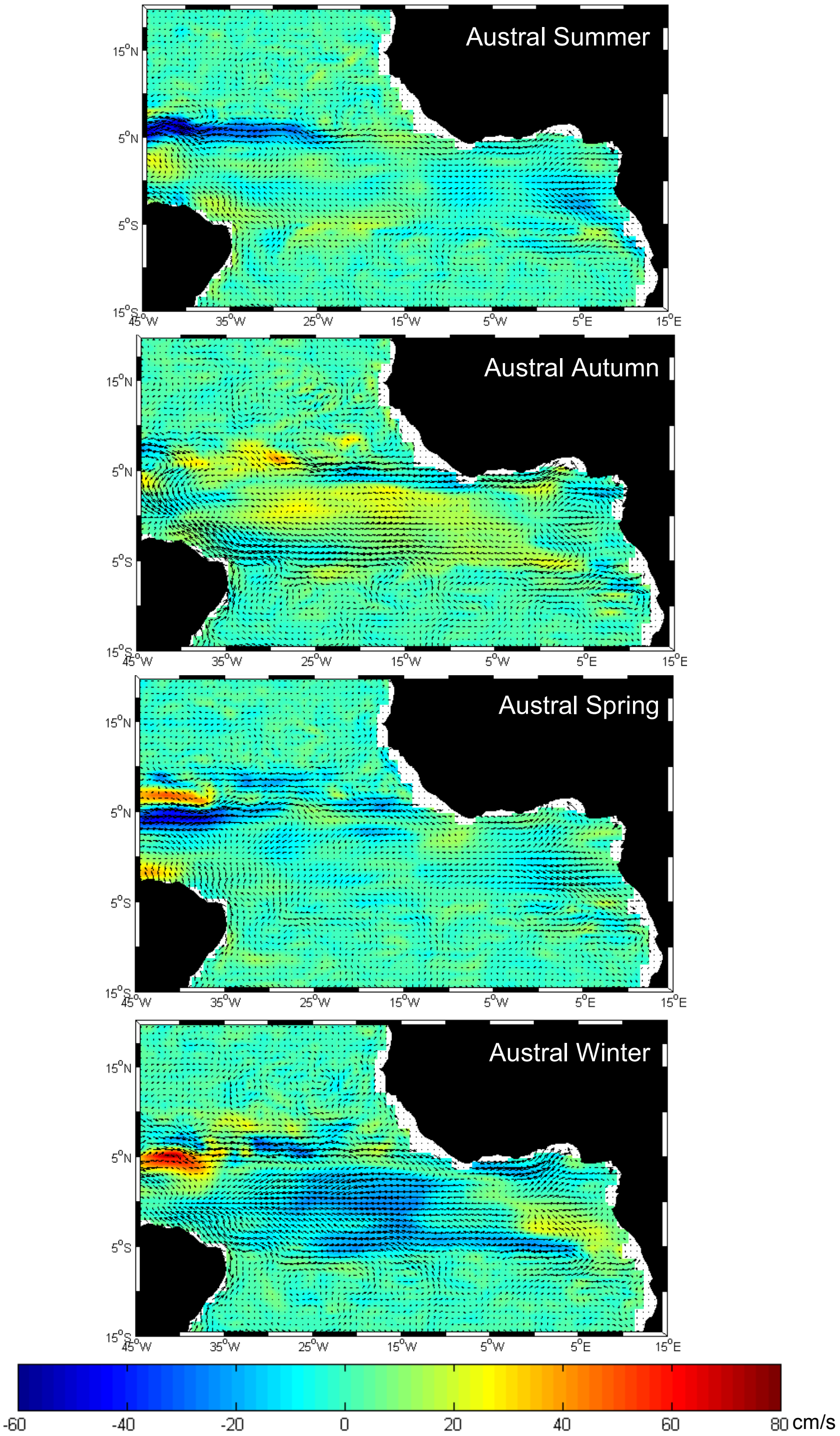

Fig. 6. Magnitudes of the seasonal geostrophic current anomalies (scale in colors) for the El Niño period calculated from the four year mean (MGC). These magnitudes are superimposed by the four year mean geostrophic velocity vectors (black arrows).

instability vortices and zonal fronts. These perturbations originate from mid-May to September in the central and eastern basin translating westward with a maximum speed of 40 cm s^{-1} (FOLTZ et al., 2004). Our simulations of larval dispersal from Cape Verde capture this dynamically complex scenario as showed by wider dispersion trajectories beginning in April (Fig. 3A). During the El Niño period, these mesoscales features are intensified and larvae can be advected further southeast, connecting lobster stocks from Cape Verde and Ivory Coast (Fig. 3 B, 3D). Both larval retention (Fig. 3A) and dispersion are ecologically relevant, the former contributing to the self-recruitment or self-seeding processes (e.g., Sammarco and Andrews, 1988; Almany et al., 2007), and the latter to the connectivity among populations on larger scales than the ecological timescale. For example, results of a density-independent matrix population model suggest that a spatially structured fishery resource connectivity is as important as the productivity. Sink areas also may be essential for the persistence of a network (HASTINGS; BOTSFORD, 2006).

The advection/diffusion model did not demonstrate a clear connection between the eastern and western Tropical Atlantic lobster populations. However, the release of larvae from Ascension Island during El Niño simulations, resulted in the largest zonal dispersal distance (Fig. 4B, 4D). In this case, larval trajectories reach further east and southwest, allowing the connection among populations of Ascension and those located in the northeastern Brazil section beyond the 5º S limit. Simulations also indicate connectivity of Ascension Island with the Fernando de Noronha Archipelago and the northeast of Brazil under the influence of the North Brazil Current, northwards of 5º S. We suggest that these islands constitute a system of stepping-stones for marine species in the Tropical Atlantic with a long-lived larval phase, since they are positioned centrally in the southern portion of the Tropical Atlantic.

Looking at the predominantly unidirectional pattern of the trajectories of larvae released from the Fernando de Noronha Archipelago (as well as from the Ivory Coast) one can appreciate the influence exercised by the geographical location of the spawning areas relative to both large scale, basinwide currents as well as to mesoscale instability features. Adding to the influence of mean advective fields, larval trajectories are also subject to seasonal changes and interannual variabilities such as those depicted by simulations starting in different periods of the year (April and September) and during El Niño years.

The fact that we have extracted the weekly geostrophic fields for the El Niño period from the same database used for the 2000/2003 mean currents highlights the intrinsic variability captured by the model outputs. On the other hand, it also shows that regional instabilities have to be considered in any analysis of either short or long-lived larval dispersion of marine organisms as these may contribute to larval retention or long-distance dispersion. We contend that an unbiased interpretation of larval trajectories and the connectivity they promote must necessarily be based on a sound understanding of the dynamics of surface ocean circulation and their mesoscale turbulence processes.

Our results shed light on the complex connective pathways among Tropical Atlantic spiny lobster stocks against which contemporary gene flow and historical biogeography hypotheses may be tested. The genetic structure and variability between close and distant Tropical Atlantic pools of spiny lobster stocks should also be addressed to investigate the influence of the simulated trajectories on the spatial genetic heterogeneity (i.e., heterozygosity). Assuming that global climatic events such as the El Niño Southern Oscillation do impact fisheries in many different ways, it is important to preserve rare alleles to increase fitness under unusual environmental conditions (see Pérez-Ruzafa et al., 2006 and references therein).

CONCLUSIONS

The simulations performed show that extreme episodes such as those associated with strong El Niño events could promote connectivity between adult spiny lobster stocks over the Tropical Atlantic, making possible a genetic flux by larval transport. Results also indicate the occurrence of both retention and long-distance dispersal of spiny lobster larvae within the Tropical Atlantic.

As a final remark, we conclude that the use of altimetry geostrophic current data, combined with a relatively simple advection/diffusion model, can provide the physical dynamics background required to adequately address larval transport patterns. Synoptic views of larval distribution for a range of geographical, hydrodynamic and climatic conditions on different spatial and temporal scales are useful to place fisheries management decisions within the seascape/biogeographical context.

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