Pathways of connectivity amongst Western Caribbean spiny lobster stocks

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Abstract. The long larval period of spiny lobster may be a factor influencing the connectivity of stocks, where larvae may drift with the currents. We hypothetized that some evidence of this could be found by examining the age structure of the stocks exploited in the west Caribbean countries where main sea current pathways move from south to north. Age structure of stocks from ten countries exploiting spiny lobster was used to test connectivity links. Fifteen years of catch data were obtained from the FAO statistical records and were transformed into numbers per age class throughout these years by using population parameter values and simulation. We analyzed the correlation between total adults in a country and age I juveniles one year after in another, comparing data from pairs of countries. We found low but significant correlations in most cases. Higher values of $R^2 = 0.7$ to 0.8 were found in the Dominican Republic as a source and Florida and Mexico as destinations, and between Haiti as a source for Cuba. Source-destination correlations at the level of $R^2 = 0.8$ to 0.9 were found between Mexico with Cuba; Florida with Mexico, Belize with Mexico, Florida and Honduras; Haiti with Honduras, Belize, Mexico, Florida, and Dominican Republic; Colombia with Honduras, Belize, Mexico and Cuba; the Bahamas with Cuba; and Nicaragua with Colombia, Belize, Mexico, Cuba, and Haiti. A strong correlation ($R^2 > 0.9$) was found between Honduras with Mexico and Cuba; Belize with Cuba; Nicaragua with Honduras; and in the Bahamas with Haiti, Honduras, Belize, Mexico, and Colombia. Our results provide evidence on the most likely patterns of connectivity amongst spiny lobster populations of the western Caribbean, reinforcing the recommendation that these fisheries should be managed by an international entity.

Key words. Spiny lobster, connectivity, Western Caribbean, correlations.

Introduction

Coral reefs are open systems, exchanging organisms, nutrients and reproductive products among themselves and with other reef systems. All of these exchanges are likely mediated by water flow (Jordán-Dahlgren 2002; Sale, 2004). Coral reef connectivity results from the export and import of species or reproductive products between localities (Paris & Cowen, 2004; Chavez-Hidalgo et al. 2009; Steneck et al. 2009). The Caribbean lobster *Panulirus argus* (Latreille) is usually recorded from shallow waters but may occur down to 90 m or even deeper. Lobsters are found among rocks, on reefs, in eelgrass beds, or in any habitat providing shelter. The species is gregarious and migratory. Females move to deeper water for spawning. Mass migrations have been reported in the autumn when single files of up to 50 individuals move in a certain direction in daytime, each animal having body contact with the next through the antennae. It is by far one of the most important species exploited on Caribbean coral reefs.

The extent of larval dispersal and recruitment to the adult population is different for each species. The chances of dispersal largely depend on the speed of the currents and the time of the larval stage. It has been reported that Caribbean lobster larvae are in the water column for nearly nine months. Despite that a large proportion of the offspring settle in the same area where they were born (Black 1993; Jordan-Dahlgren 2002; Butler et al. 2009), a significant number of larvae drift and are taken away by the currents (Roberts 1997; Jordán-Dahlgren & Rodriguez-Martinez 2003; Butler et al. 2009). Therefore, the present paper aims to provide evidence of connectivity between Caribbean lobster populations, based on temporal similarities of spatially separated main stocks exploited in the Caribbean waters. The working hypothesis was that given the nature of its distribution and the high uncertainty associated with physical variables in the Caribbean, there would be no significant correlations among the stocks in terms of their dynamics.

Material and Methods

Caribbean lobster fisheries in 10 main countries (Bahamas, Belize, Colombia, Cuba, Dominican Republic, Florida (USA), Haiti, Honduras, Mexico, Nicaragua, and the whole Caribbean) were analyzed.

In each case, the catch data of fifteen years (1989 to 2007, downloaded from the FAO statistic records http://www.fao.org/fishery/fishfinder), were transformed into age structure by using the FISMO simulation model (Chavez 2005). This allowed estimation of the numbers per age class in each fishery examined.

Estimations of the age structure were made for each stock where a constant age of first catch was applied (tc = 2), such that these and older age groups were subjected to natutral and fishig mortality. Then each stock size was evaluated applying the catch equation. Cohorts were linked over time with the Beverton-Holt recruitment model, where age-I juveniles were considered as recruits instead of newborn larvae; it was was made this way to reduce uncertainty in their estimation. These analyses were made using the age structure values of the reconstructed population over the fifteen years that the FISMO model uses. Once the age structure was defined for each fishery, we compared the absolute number of adults in a given stock with the absolute number of one year-old juveniles in another stock with one year lag. It was made by combining all pairs of age groups. This approach was made on the assumption that a larval stage of 7 – 9 months allows a passive drift of a significant proportion of the offspring. Then regression analysis of two kinds was performed, in the first one, simple regressions of second order were applied, where the independent variable was the number of adults of each country, and the dependent variable was the number of one year-old juveniles one year later. The second type was the multiple regression analysis, where each series of age I of the years 2 to 15 was the dependent variable and series of adults of all other stocks of the years 1 to 14 were independent variables.

Results

As a result of the simple regression analysis, R^2 values found were very high, denoting high correlations, but only in nine pairs of comparisons the R^2 were higher than 0.9. The results of multiple regression analysis indicate surprisingly very high significant correlations in all tests, but on examining the coefficient values, a few are high, as seen in Table 1, where the coefficients of the three main variables are displayed; these results are rather confusing. The most likely explanation of this is that in the case of simple regression analysis first performed, the numbers of dependent variable are similar to those of independent variables; when the multiple regression analysis was made, the numbers of independent variables increased by tenfold ratio; another possible explanation is that so many variables involved may mask the correlations that were expressed more clearly when comparisons were made just by pairs as in the first case.

Therefore, results described in the following lines are referred to simple regressions of second order, from which Figs. 1A and 1B display the highest correlations found: In the base map (redrawn after Carpenter 2002 and used as background), the spiny lobster distribution range generally accepted, is represented as a shade along the shoreline. Here, shades describing the degree of correlation amongst the countries were superimposed; the highest correlations had $R^2 > 0.9$. These strong connections occur between Nicaragua with Honduras; Bahamas with Colombia, Honduras, Belize, and Mexico; Belize with Cuba; and Honduras with Mexico and Cuba (Fig. 1B). Weaker correlation ($R^2 = 0.8 – 0.9$) was found in twenty other combinations (values ommited for lacking of space). Haiti was connected with five countries: Honduras, Belize, Mexico, Florida and Haiti. At the same level of correlation, Belize is connected with Honduras, Mexico, and Florida; Mexico with Cuba; and Florida with Mexico. The same level of correlation was observed between Colombia with Honduras, Belize, Mexico, and Cuba, as well as Bahamas with Cuba; and Nicaragua with Colombia, Haiti, Belize, Mexico, and Cuba.

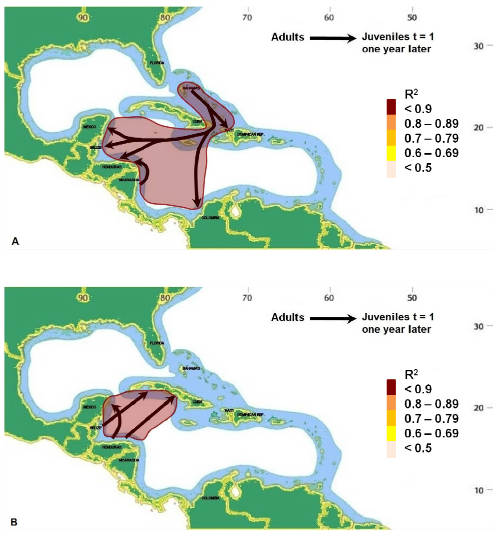

Fig.1. Pathways of connectivity of the Caribbean lobster, evidenced as result of applying regressions of second order, using the number of adults as an independent variable in a given country and the number of one year-old juveniles in another country one year later as dependent variable. In all combinations, the correlations are significant; however, the shades represent values of $R^2 > 0.9$. The arrows point towards the direction of flows. a) Main directions of connectivity from Bahamas, to Haiti, Colombia, Honduras, Belize, and Mexico; from Nicaragua to Honduras. b) from Honduras to Mexico and Cuba and from Belize to Cuba.

Table 1. Caribbean countries as post-larval sinks (left column). The multiple regressions R^2 and the level of significance (p-values) are shown, evidencing a high correlation with adult stocks from all other countries as potential sources. Fifteen-year data series of one year-old juveniles at each country were used as dependent variables and series of fifteen-year data of adult numbers one year before from all other Caribbean countries were the independent variables. The three main coefficients of the multiple regressions are indicated in the three columns on the right side. The subscript letters on the first column and on the coefficient values identify each country.

Sink	R^2	p-value	Main Coefficients of Sources		
$Bahamas_A$	0.9999	$5.66e^{-06}$	525.359_F	1.7071_H	0.4632_C
$Belize_B$	0.9999	$7.24e^{-06}$	146.173_F	2.408_B	0.3178_C
$Colombia_c$	0.9999	$6.06e^{-06}$	84.232_F	0.3188_H	0.0861_G
$Cuba_D$	0.9999	$5.49e^{-06}$	2.1314_F	0.0104_B	0.0049_H
$Dominican_E$	0.9998	$1.48e^{-05}$	5.76_F	2.668_B	0.231_G
$Florida_F$	0.9996	$6.22e^{-05}$	3.132_B	0.558_C	0.083_J
$Haiti_G$	0.9999	$8.82e^{-0.6}$	1.845_H	1.802_B	0.1755_C
$Honduras_H$	0.9999	$7.24e^{-06}$	146.173_F	2.4077_B	0.3187_C
$Mexico_I$	0.9998	$1.82e^{-05}$	5.0568_B	0.2498_A	0.2423_J
$Nicaragua_J$	0.9999	$1.10e^{-05}$	1648.184_F	13.571_B	3.5893_C

Discussion

The Yucatan Current, which circulates in the Yucatan Channel in the northwestern Caribbean, is one of the most dynamic boundary currents on the planet. These waters are characterized by high transparency and strong flow from south to north with mean speeds of 1.5 m^{-s}, with fluctuations of up to $3m^{-s}$, creating meanders, eddies and a complex vertical structure (Chavez & Hidalgo 1988; Marin et al. 2008). This stream also feeds the principal bodies of water to the region, passing through the Yucatan Strait and up on the platform, resulting in a northwesterly direction in a nutrient-rich flow (Roberts 1997; CONANP, 2004; Carrillo et al. 2007; Marin et al. 2008). A hurricane can induce a large shift in a short period of time with vertical and horizontal mixing of the water column, causing dispersal of larvae (Lugo-Fernández et al. 2001). Some of the distribution links shown here are reasonably explained by the hypothesis that the reefs of the western Gulf of Mexico and the Caribbean are more similar because these areas are less affected by hurricanes (Chavez-Hidalgo et al. 2009; Steneck et al. 2009). This also suggests that the dispersal of larvae produced on the reef is modified by the effects of hurricanes (Lugo-Fernandez et al. 2001).

Our results are consistent with the opinions of other authors (Lugo-Fernandez et al. 2001; Roberts, 2001; CONANP, 2004; Sale, 2004), who based their assumptions mostly on the pathways of oceanic currents. Connectivity results from the export and import of species or reproductive products amongst Coral reefs, as open systems exchanging organisms, reproductive products, nutrients, and pollutants.

The lobster stocks in the wider Caribbean have high connectivity by larval dispersal through their oceanic larval stage (5-9 months), which is largely influenced by the system of ocean currents and large-scale sporadic events such as hurricanes. Local populations can be formed both by recruits that originate from postlarvae from stocks in other areas, and recruits from local shallow or deep areas, as a result of ontogenetic and migratory movements (Ramirez-Estevez et al. 2010).

In the southwestern shelf of Cuba it has been found that the seasonal distribution of stage I of *P. argus* shows good agreement with the cycle of reproduction, displaying increased numbers in the spring and summer. It has also been shown that the main distribution pattern of phyllosoma larvae decreases towards offshore (Hernandez & Pineiro, 2003).

Exchange pathways between the Caribbean reef ecosystems are not known. It is assumed that reefs of the northwestern Caribbean may play a significant role as sources of larvae moving along the Yucatan channel, that the eddies in the central Gulf of Mexico may be a significant sink, and that these factors may have imposed patterns of similarity over the evolutionary process. Geographical distance and the days of transport by currents and sea surface temperature are considered as the main driving forces supporting the idea that biological similarity agrees with the general pattern of ocean circulation (Butler et al. 2009). Knowledge of the processes involved in the connectivity of spiny lobster stocks should provide the basis for informed management and conservation actions. Aspects of connectivity of spiny lobster fisheries should be explored with an international perspective. Informed management must be at this scale, because incorrect fishing practices in one place and time may have undesirable effects in another place and time.

The proposed routes of connectivity are due largely the predominant current flow, and in some cases, the only reasonable explanation was the transport by other occasional events like hurricanes (Lugo-Fernández et al. 2001; Jordán-Dahlgren 2002; Presley & Willig 2008), which is consistent with the pattern of connectivity found with stony corals in Mexican coral reefs.

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