



# Article Larval Transport Pathways for *Lutjanus peru* and *Lutjanus argentiventris* in the Northwestern Mexico and Tropical Eastern Pacific

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Abstract: Understanding how ocean currents influence larval dispersal and measuring its magnitude is critical for conservation and sustainable exploitation, especially in the Tropical Eastern Pacific (TEP), where the larval transport of rocky reef fish remains untested. For this reason, a lagrangian simulation model was implemented to estimate larval transport pathways in Northwestern Mexico and TEP. Particle trajectories were simulated with data from the Hybrid Ocean Coordinate Model, focusing on three simulation scenarios: (1) using the occurrence records of *Lutjanus peru* and *L. argentiventris* as release sites; (2) considering a continuous distribution along the study area, and (3) taking the reproduction seasonality into account in both species. It was found that the continuous distribution scenario largely explained the genetic structure previously found in both species (genetic brakes between central and southern Mexico and Central America), confirming that the ocean currents play a significant role as predictors of genetic differentiation and gene flow in Northwestern Mexico and the TEP. Due to the oceanography of the area, the southern localities supply larvae from the northern localities; therefore, disturbances in any southern localities could affect the surrounding areas and have impacts that spread beyond their political boundaries.

Keywords: oceanographic modelling; connectivity networks; cross-boundary larval transport

# 1. Introduction

*Lutjanus peru* and *L. argentiventris* are essential economic resources for most coastal communities in the Tropical Eastern Pacific (TEP) [1] due to the quality of their meat and commercial value [2]; in Mexico, in the last 26 years, the catches have increased to 21,617 tons/year, generating an income close to MXN \$533 million [3]. Additionally, these species play an important ecological role by transferring energy to other trophic levels [2,3]. Both demersal species share much of their distribution range: *L. argentiventris* ranges from Southern California, U.S.A., to Northern Peru, while *L. peru* ranges from Bahía Magdalena, Mexico, to Northern Peru [4,5]. Despite their overlapping ranges, the spawning periods of these species differ across regions [5–11].

During the larval stage, as with most marine species, ocean currents are a critical factor in the dispersal of larvae [12], directly affecting population demographics, genetic connectivity, population structure, and recruitment patterns [13,14]. In addition to ocean currents, other physical and biological factors such as spawning site and season, planktonic



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**Copyright:** © 2024 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). larval duration (PLD), and habitat availability for species that use one or more habitats throughout their life cycle also contribute to their marine connectivity [12–16]. Specifically, Lutjanidae larvae have a PLD of approximately 30 days [17–19], during which, in the first 15 days, they are unable to swim against currents stronger than 0.1 m/s [4,20–22], which suggests that larval dispersal during this period is primarily passive. This process allows for the connection and replenishment of demersal fish populations since recruitment habitats for juveniles and adults are often patchy and isolated [23].

Direct observations of larval transport are nearly impossible due to the difficulty of tracking larvae in the open ocean [14]; oceanographic models have become valuable tools for measuring larval transport patterns. These models enable researchers to generate hypotheses about the currents' scale, direction, and strength that disperse gametes, eggs, and larvae across the marine environment [23].

Northwestern Mexico and the TEP are highly dynamic regions, characterized by oceanographic features such as currents, eddies, meanders, and filaments, all of which have been linked to larval dispersal in previous studies [24–29]. These complex oceanographic structures make this area particularly suitable for studying how oceanography affects the larval transport of *L. peru* and *L. argentiventris* [30]. For example, the larval transport of L. peru and L. argentiventris has been explicitly studied in the Southern Gulf of California (SGC). For *L. peru*, the strong asymmetry in ocean currents along the western coast of the SGC caused variations in larval connectivity depending on the season [27]. In contrast, for L. argentiventris, larval transport and genetic connectivity between the peninsular and mainland coasts of the SGC have been confirmed [28]. Despite these localized studies, the effects of larval transport on the population structure of both species at larger scales remain untested. However, efforts to understand how TEP hydrodynamics influence larval dispersal have been made in other marine organisms, such as corals, where ecoregions from Mexico to Ecuador were connected using a PLD ranging from 30 to 150 days [31–33]. Genetic markers have also been used to assess genetic connectivity among adult fish populations in the TEP. These studies suggest that the absence of gene flow between regions may be attributed to the patchy nature of juvenile and adult recruitment habitats or environmental gradients [30,34–36].

Understanding how ocean currents affect larval dispersal, and predicting where larvae will settle at the end of their PLD, is crucial for conservation efforts and sustainable fishery management [13,23]. The direction, magnitude, and geographic scale of larval dispersal are key parameters affecting the persistence of marine metapopulations [37]. Management interventions including seasonal fishing closures during reproduction, individual size, and catch limits could have a higher impact on the recovery of fish biomass if they are effectively implemented at the upstream sites that act as main larval sources for downstream fishing areas [27,38]. This study aims to provide new insights into how larval transport shapes these economically essential species' genetic diversity and distribution. A Lagrangian simulation model was implemented to estimate the effects of three different simulation scenarios on the larval transport of *L. peru* and *L. argentiventris* across Northwestern Mexico and the TEP. The most suitable simulation was validated using genetic data from a previous study [36].

#### 2. Materials and Methods

#### 2.1. Larval Transport Simulations

This study developed a Matlab (R2022b) code to simulate the passive larvae transport of *Lutjanus peru* and *L. argentiventris* along Northwestern Mexico and TEP. The larvae trajectories were simulated using the Hybrid Ocean Coordinate Model (HYCOM) data [39,40], which has a spatial resolution of 1/12°, a temporal resolution of three hours, and 40 vertical layers (depth). More precisely, only the U and V components of the current velocity vectors at a 30 m depth layer (where a higher abundance of lutjanid larvae has been reported [41]) were obtained from 1 December 2016 to 30 November 2017 (https://tds.hycom.org/thredds/catalog.html; accessed on 1 November 2021). This

year was simulated because most of the previous study's genetic samples were collected throughout 2017 [36].

In addition, to evaluate the simulated larvae's subsequent initial and final positions, a layer with 115 polygons (with 75 km of length) covering the continental shelf of Northwestern Mexico and TEP was used (Figure 1). The length of each polygon (along the coast) was 75 km, which is approximately half the distance covered by lutjanid larvae for a PLD of 20 to 26 days [27,28,42]. For the design of the 115 polygons, bathymetric data were obtained from the General Bathymetric Chart of the Oceans (GEBCO, https://www.gebco.net; accessed on 1 November 2021). The isobaths between zero and 200 m or 1000 m [only in zones with very narrow shelf (<30 km wide), like the Mexican Tropical Pacific and some areas of Central America] were used as a proxy of the continental shelf. The extension to 1000 m was made due to the lack of HYCOM data in the first 20 km from the coastline to the ocean.



**Figure 1.** Study area (**a**). Northwestern Mexico (**b**), Mexican Tropical Pacific (**c**), and Central America and Colombia (**d**). The blue polygons are the counting areas for the connectivity networks (the numbers represent the polygons' order). The continuous and dashed red lines are the sites where the genetic brakes were found for *L. peru* and *L. argentiventris*, respectively [36]. Baja California Sur (BCS), Nayarit (NAY), Colima (CMA), Oaxaca (OAX), Panama (PAN), and Colombia (COL).

Three distinct scenarios served as the basis for the simulations, and each one considered a different set of criteria to determine the larvae release points.

## 2.1.1. Occurrence Records Scenario

The first scenario consisted of obtaining the coordinate occurrence records for *L. peru* (113) and *L. argentiventris* (571) from the Global Biodiversity Facility (GBIF) [43,44],

selecting the records with human observation, material sample, and preserved specimen. A buffer of  $0.3^{\circ}$  limited to the continental shelf was made at each record to compensate for the lack of occurrences in the study area. Of the total pixels (representing coordinates) within the buffer, only 10% of the pixels that had the highest probability of being closest to the occurrence point were chosen as release points (4789 points for *L. peru* and 9626 for *L. argentiventris*) (Figure 2a,b).



Figure 2. Larval seeding points for Lutjanus peru (a), Lutjanus argentiventris (b), and centroids (c).

Random dates were generated for each year's season [winter (December 2016–February 2017), spring (March–May 2017), summer (June–August 2017), and autumn (September–November 2017)] throughout the release points for both species to simulate spawns. The larval transport simulations were initiated at 18:00 UTC-7 and tracked for 30 days [17,19]; these characteristics remained for the other scenarios. The number of simulated larvae trajectories was 4789 for *L. peru* and 9626 for *L. argentiventris* at each season.

# 2.1.2. Continuous Distribution Scenario

A continuous distribution scenario was simulated to evaluate the whole potential distribution range of *L. peru* and *L. argentiventris*. It consisted of obtaining the centroid of the 115 polygons (Figure 1b–d), which were the release points of *L. peru* and *L. argentiventris* larvae (Figure 2c). From each centroid, 60 trajectories were simulated, totaling 6900 for each year season, and random dates were assigned (from 1 December 2016 to 31 November 2017) with normal distribution.

#### 2.1.3. Continuous Distribution and Reproductive Season Scenario

This scenario used the information generated by the continuous distribution scenario, limiting it to the reproductive season of each species (Table 1). For *L. peru* 13,012 trajectories were used, and for *L. argentiventris*, 15,433.

**Table 1.** Reproductive season of *Lutjanus peru* and *L. argentiventris* along its distribution range. Nayarit (NAY), Jalisco (JAL), Colima (CMA), Revillagigedo (REV), Michoacan (MIC), Guerrero (GUE), Chiapas (CHI), Pacific (PAC), Gulf of California—peninsula (GC-PEN), Gulf of California—mainland (GC-M), El Salvador (ES), Nicaragua (NIC), Costa Rica (CRA), Panama (PAN), and Colombia (COL).

Specie	Zone	Season 1	Season 2	Season 3	
L. peru	Zone A	May–July	September-November		
	Zone B (NAY-JAL)	March–June	August-September	November-December	
	Zone B (CMA-REV)	November–June	August-September		
	Zone B (MIC)	April–May	August–December		
	Zone B (GUE-CHI)	March–May	July-September		
	Zone C	January–April			
L. argentiventris	Zone A (PAC)	May-September			
	Zone A (GC-PEN)	May-September			
	Zone A (GC-M)	November–March	July-October		
	Zone B	February–April	July–November		
	Zone C (ES-NIC)	September–January	-		
	Zone C (CRA-PAN)	January–December			
	Zone C (COL)	November–December	May-August		

Note: Reproductive season information from: [5,7–11,45–52]

#### 2.2. Data Analysis

The velocity and direction of the simulated trajectories were calculated in Matlab R2022b. Because the three simulation scenarios were executed with the same HYCOM data, the information from each scenario was summarized by zones (A, B, and C).

To obtain the connectivity networks in Northwestern Mexico and TEP for the three scenarios, the data trajectories were evaluated at 30 and 15 days of PLD. At 15 days of PLD, the larvae are in the flexion stage [4,20–22] and considered inert particles. Nevertheless, the PLD ends at 30 days [45], and the larval development can vary depending on the sea temperature [53–56]. For this reason, both periods were considered. The initial and final positions of the simulated larvae trajectories were associated with and accounted for their respective release and arrival polygons to make connectivity matrices in Matlab R2022b. Then, a graph-theoretical approach [57] was implemented in ArcMap 10.5 to construct a spatial network describing the percentage of larval dispersal between polygons. The percentage was obtained based on the total simulated trajectories of the entire study area.

In addition, the connectivity network information was summarized globally (a summary of all the connectivity network percentages for the study area was made), representing the total trajectories that finished inside a polygon (connectivity and self-recruitment), as well as the percentage of lost trajectories (that did not reach any polygon). Also, the connectivity networks were summarized by zones, where the percentage of connectivity and self-recruitment was calculated.

Finally, to find the most probable simulation scenario, the connectivity networks obtained in this study by modeling larval dispersal were compared with the genetic structure and connectivity found by Reguera-Rouzaud et al. [36] (Table S1).

#### 3. Results

## 3.1. Circulation and Main Trajectory Patterns

The California Current and mesoscale activity in the Gulf of California (GC) controlled the mean circulation at 30 m depth in zone A. In total, 28% and 33% of the trajectory direction moved to the south–southeast in the spring and winter, respectively. In contrast, 25% moved to the northwest (Figure 3a,d). In the summer, the California Current intensity decreased, and a cyclonic circulation was seen in the GC (Figure 4c), with the main larvae trajectories going to the northwest (35%; Figure 3b). The California Current shifted to the northwest in the fall, and cyclonic and anticyclonic eddies formed in the GC; the simulated trajectories mostly followed directions to the northwest and south–southeast (Figures 3c and 4d). The velocity at which the simulated larvae were transported ranged from 0.79 to 1.11 m/s, with a predominant frequency of 0.05 to 0.2 m/s (Figure S1a–d).



**Figure 3.** Direction and distance traveled by the simulated trajectories obtained with the HYCOM for the zone A (**a**–**d**), zone B (**e**–**h**), and zone C (**i**–**l**). Spring (March (M), April (A), May (M)); Summer (June (J), July (J), August (A)); Autumn (September (S), October (O), November (N)); Winter (December (D), January (J), February (F)).

The Tehuantepec Bowl, the Costa Rica Coastal Current (CRCC), and the Mexican Coastal Current were the primary structures influencing coastal circulation in zone B. In total, 26% to 45% of the simulated trajectories along the year were to the northwest (Figures 3e–h and 5a–d). The strength of coastal currents diminished throughout the summer months, and two main trajectory directions predominated: northwest and southeast (Figures 3f and 5c). The larval trajectories had velocities ranging from 0.95 to 1.7 m/s, with a prevalent frequency of 0.05 to 0.35 m/s (Figure S2a–d).



**Figure 4.** Mean seasonal circulation pattern obtained with the HYCOM for zone A during (**a**) winter, (**b**) spring, (**c**) summer, and (**d**) autumn from 2017. The color bar represents the velocity of the mean seasonal circulation in m/s, and the arrows indicate the direction.



**Figure 5.** Mean seasonal circulation pattern obtained with the HYCOM for zone B during (**a**) winter, (**b**) spring, (**c**) summer, and (**d**) autumn from 2017. The color bar represents the velocity of the mean seasonal circulation in m/s, and the arrows indicate the direction.

The presence of the CRCC, the Gulf of Panama Current, and the Colombia Current was appreciated in zone C throughout the year (Figure 6a–d). These currents affected

the simulated paths and 30% to 40% of the trajectories stayed oriented to the northwest (Figure 3i–l). During the winter and spring, a cyclonic eddy formed between Panama and Colombia, which weakened in the summer and turned into an anticyclonic eddy in the fall (Figure 6a–d). The trajectory velocities ranged from 1.14 to 1.4 m/s, with a predominant frequency of 0.05 to 0.35 m/s (Figure S3a–d).



**Figure 6.** Mean seasonal circulation pattern obtained with the HYCOM for zone C during (**a**) winter, (**b**) spring, (**c**) summer, and (**d**) autumn from 2017. The color bar represents the velocity of the mean seasonal circulation in m/s, and the arrows indicate the direction.

## 3.2. The Most Suitable Model

The continuous distribution was the scenario that better represented the genetic structure previously described by Reguera-Rouzaud et al. [37]. The gene flow barriers for *L. peru* between the Gulf of California–Nayarit, Nayarit–Oaxaca, and Oaxaca–Panama were represented in the three simulation scenarios, as well as the barriers for *L. argentiventris* between Espiritu Santo Island–San Bruno, and Colima–Panama (except for the reproductive season scenario). Regarding connectivity between locations for *L. peru*, only the continuous distribution and the reproductive season scenario represented the connectivity between the southern tip of Baja California Sur with the entrance of the Gulf of California and Panama–Colombia; for *L. argentiventris*, the connectivity between Espiritu Santo Island (peninsula)–Altata (mainland) and Gulf of California–Colima were only represented for the continuous distribution scenario (Table S1).

The continuous distribution was the scenario that better represented the genetic structure previously described by Reguera-Rouzaud et al. [36]. This scenario adequately represented 47.5% and 53.1% of the sites where connectivity was present and gene flow barriers were located for *L. peru* and *L. argentiventris*, respectively. The remaining simulated scenarios represented less than 47% for *L. peru* and less than 50% for *L. argentiventris* (Table S1).

Hereafter, the results are focused on the continuous distribution model, except when noted otherwise.

Due to the large amount of data, only the simulation scenario and the seasons that better represented the connectivity networks and connectivity brakes at both PLD periods are shown as figures (see Figures S4–S19 for detailed information).

## 3.3. Simulation Scenarios

From the 6900 simulated larvae trajectories for each year's season, approximately 60% ended inside polygons, while the other 40% were considered lost (Table 2). For coordinate occurrence records (4789 and 9626 simulated trajectories at each year season, for *L. peru* and *L. argentiventris*, respectively) and reproductive season simulations (*L. peru* 13,012, and *L. argentiventris* 15,433 trajectories used), the proportions between larvae trajectories that ended inside polygons and lost trajectories were very similar (Tables S2 and S3).

**Table 2.** Percentages of self-recruitment and connectivity for the continuous distribution scenario at 15 and 30 days of pelagic larval duration (PLD). Winter (W), Spring (SP), Summer (S), and Autumn (A).

	PLD 15				PLD 30			
	W	SP	S	Α	W	SP	S	Α
Global connectivity and self-recruitment	60.94	60.42	57.43	58.63	58.13	58.18	55.37	57.47
Global lost trajectories	39.06	39.58	42.57	41.37	41.87	41.82	44.63	42.53
Self-recruitment zone A	12.92	12.18	11.98	12.9	11.87	11.33	11.58	12.35
Self-recruitment zone B	12.8	11.93	10.75	11.62	12.3	11.67	10.07	11.14
Self-recruitment zone C	10.85	10.7	8.91	10.13	10	10.04	8.3	9.34
Connectivity zone A	8.36	8.56	9.24	7.51	8.58	8.84	9.77	8.19
Connectivity zone B	4.94	4.67	3.96	4.07	5.14	4.79	4.31	4.36
Connectivity zone C	11.09	12.38	12.59	12.4	10.24	11.51	11.34	12.09

#### 3.3.1. Zone A

In general, the percentage of self-recruitment in zone A oscillated between 11.33 and 12.92%, while the connectivity varied between 7.51 and 9.77% (Table 2). For the coordinate occurrence records and reproductive season scenarios, the self-recruitment ranged from 10.57 to 13.79% and 8.03 to 10.66%, respectively, while the connectivity ranged from 7.51 to 9.77% and 4.87 to 7.62%, respectively (Tables S2 and S3).

Nine and four connectivity networks were found in Northwestern Mexico over the 15 and 30 days of PLD, respectively. In general, there was constant connectivity between the peninsular and mainland sides of the northern GC (Figures 7a,d, S12 and S13); this characteristic network appears in the other two scenarios (Figures 8a,d and 9a,d). Also, 30 days after PLD, the adjacent Pacific was connected to the southern GC (Figure 6d). This connectivity was also observed in the *L. peru* occurrence record scenario (Figure 8d) and in the reproductive scenario (Figure 10a,d). Also, connectivity in the center and southern GC between the mainland and peninsular sides was observed (Figure 7d). The percentage of connectivity between polygons at zone A oscillates between 0.06 and 0.2% for both PLD periods (Figure 7a,d).

Regarding the interruptions in the connectivity networks, two constant brakes were found in all the simulated scenarios in the middle part of Sonora and northern Sinaloa (Figures 7a,d, 8a,d, 9a and 10a,d), with an approximate extension of 90 to 150 km. For the continuous distribution scenario, other brakes were found at the center of Baja California (Pacific side) and the northern and southern Baja California Sur (in the GC), spanning 150 to 250 km (Figure 7a,d).



**Figure 7.** Connectivity networks for the continuous distribution scenario (for both species) during winter (**a**–**c**) and spring (**d**–**f**) for 15 and 30 days of larval dispersal (PLD), respectively. The red dots represent the centroids, the colored lines represent the connectivity networks, and the tick represents the percentage of connectivity between polygons. Baja California (BC), Baja California Sur (BCS), Sonora (SON), Sinaloa (SIN), Nayarit (NAY), Colima (CMA), Guerrero (GUE), Oaxaca (OAX), Panama (PAN), and Colombia (COL).



**Figure 8.** Connectivity networks for the occurrence records of *Lutjanus peru* during winter for 15 (**a**–**c**) and 30 (**d**–**f**) days of larval dispersal (PLD), respectively. The red dots represent the centroids, the colored lines represent the connectivity networks, and the tick represents the percentage of connectivity between polygons. Baja California (BC), Baja California Sur (BCS), Sonora (SON), Sinaloa (SIN), Nayarit (NAY), Colima (CMA), Guerrero (GUE), Oaxaca (OAX), Panama (PAN), and Colombia (COL).



**Figure 9.** Connectivity networks for the occurrence records of *Lutjanus argentiventris* during summer (**a**–**c**) and autumn (**d**–**f**) for 15 and 30 days of larval dispersal (PLD), respectively. The red dots represent the centroids, the colored lines represent the connectivity networks, and the tick represents the percentage of connectivity between polygons. Baja California (BC), Baja California Sur (BCS), Sonora (SON), Sinaloa (SIN), Nayarit (NAY), Colima (CMA), Guerrero (GUE), Oaxaca (OAX), Panama (PAN), and Colombia (COL).



**Figure 10.** Reproductive season scenario at 15 days of pelagic larval duration (PLD) for *Lutjanus peru* (**a**–**c**) and *L. argentiventris* (**d**–**f**). The red dots represent the centroids, the colored lines represent the connectivity networks, and the tick represents the percentage of connectivity between polygons. Baja California (BC), Baja California Sur (BCS), Sonora (SON), Sinaloa (SIN), Nayarit (NAY), Colima (CMA), Guerrero (GUE), Oaxaca (OAX), Panama (PAN), and Colombia (COL).

## 3.3.2. Zone B

In general, for the three scenarios, the percentage of self-recruitment was higher than that of connectivity. For the continuous scenario, the self-recruitment ranged from 10.07 to 12.8%, while the connectivity ranged from 3.96 to 5.14% (Table 2). In the coordinate occurrence records scenario, self-recruitment ranged from 11.53 to 16.59% for *L. peru* and 6.98 to 10.29% for *L. argentiventris* (Table S2), while in the reproductive scenario, it ranged from 11.62 to 14.33% (Table S3). The percentage of connectivity ranged from 11.53 to

15.75% for *L. peru*, 5.26 to 6.75% for *L. argentiventris* (Table S2), and 4.31 to 5.14% (Table S3), respectively. The Mexican Tropical Pacific comprised three networks for both PLD periods, where the connectivity percentage between polygons ranged from 0.1 to 0.9% (Figure 7b,e). It was found two common connectivity brakes at the center and southern Mexico, spanning 80 to 90 km, respectively (Figure 7b,e); those brakes were also found in the other scenarios (Figures 8b,e, 9b,e and 10b). Although the extension of the connectivity brakes differed between scenarios, for the occurrence records, the brakes spanned from 200 to 350 km for *L. peru* (Figure 8b,e) and from 75 to 150 km for *L. argentiventris* (Figure 9b,e), while for the reproductive scenario, the brake found was of 75 km for *L. peru* (Figure 10b).

## 3.3.3. Zone C

In this area, the percentage of self-recruitment was less than the connectivity for the three simulation scenarios. The self-recruitment at the continuous scenario oscillated between 8.3 and 10.85% (Table 2); these values were similar to the reproductive scenario (9.29 to 13.45%, both species) and the occurrence records scenario (10.43 to 14.35% for *L. argentiventris*), except for *L. peru*, where the percentage ranged from 1.89 to 3.39% (Tables S2 and S3). Regarding the percentage of connectivity, the continuous scenario ranged between 10.24 and 12.59% (Table 2), as well as the reproductive scenario for both species (9.97 to 16.46%) and the occurrence records scenario for *L. argentiventris* (15.12 to 20.19%) (Tables S2 and S3). Only *L. peru* presented lower values, ranging from 1.42 to 5.46% (Table S2).

The Central America and Colombia regions were composed of three and two connectivity networks for 15 and 30 PLD periods, respectively (Figure 7c,f). One of the connectivity networks for the 30 PLD period extended to zone B (Figures 7f and S14i–l), as well as for the other two scenarios (Figures 9c,f and 10c,f). Except for the coordinate occurrence records scenario for *L. peru*, the connectivity networks were small and only connected to neighboring areas (Figure 8c,f).

The percentage of connectivity between polygons for the continuous scenario ranged from 0.01 to 3.6% (Figure 7c,f).

On the other hand, two interruptions in the connectivity networks were found, one in the middle part of Panama (15 PLD) and the other in southern Colombia (both PLD periods), spanning 170 and 75 km, respectively (Figures 7c,f, S12i,j and S14i,j). This last brake was shared with the other two scenarios for both PLD periods (Figures 8c,f, 9c,f and 10c,f).

## 4. Discussion

## 4.1. Comparison Between Scenarios

The three simulation scenarios for both species generally represented the genetic structure (Table S1). Nevertheless, only the continuous distribution model interpreted the connectivity between locations for *L. peru* and *L. argentiventris* found by Reguera-Rouzaud et al. [36].

The occurrence simulation scenario had the advantage of considering the real organism records as spawning points. However, it is possible that the occurrence records underestimated the species' distribution because more populations could exist along the TEP [5,58]. This still needs to be documented in the Global Biodiversity Facility, especially in Central America and Colombia. Even though the model has good coastal resolution [39], more was needed to consider the occurrences closest to the coast, especially the coordinate records in the upper GC, where there was a lack of HYCOM data in the first 70 km in this area.

On the other hand, the continuous distribution scenario had the advantage of considering all the potential distributions of both species along the TEP as possible spawning sites. The release larvae points were situated at the centroid of the polygons, adapting them to the spatial resolution of the HYCOM and avoiding the problem from the first simulation scenario.

Finally, the results for the reproductive season scenario (both species) were uncertain because the available information on the reproductive seasons was extrapolated to broad

regions throughout Northwestern Mexico and the TEP, resulting in extensive connectivity networks that did not agree with the genetic structure previously found [36].

Although the occurrence records and the reproductive season scenarios had real biological data, the lack of information in both scenarios caused an overestimation of the connectivity via larval dispersal; this suggests that there is more variation in the reproductive seasons throughout the study area than was expected and that the distribution of *L. peru* and *L. argentiventris* is more continuous than suggested by the GBIF data. In contrast, the continuous distribution scenario fulfilled the weak points of the other two scenarios. It better explained the barriers to gene flow and the genetic connectivity between localities, making it the most suitable larval dispersal model for this case study.

Currently, no other research has investigated the larval transport of rocky reef fishes in the TEP. Still, there are a few investigations on corals in this region: Romero-Torres et al. [33] used HYCOM data to simulate four different scenarios depending on the coral species PLD; due to the uncertain PLD for the corals in the TEP, they used information from other world areas, and as a result, they had the same extensive connectivity networks as we have. On the other hand, simulations with the Regional Ocean Model System (ROMS) in the marine protected areas from the TEP resulted in less extensive connectivity networks. However, the release of particles was only one per month [59]. However, our simulation model and the previously described models agreed that Central America is well connected via larval dispersal.

The following discussion is based on the continuous distribution scenario because it is the most suitable.

## 4.2. Effects of Pelagic Larval Duration

The genetic connectivity found by Reguera-Rouzaud et al. [36] was better represented by connectivity networks formed with a PLD of 15 days for the Mexican Tropical Pacific and Central America. In contrast, genetic connectivity in Northwestern Mexico was better represented by connectivity networks formed with a PLD of 30 days. According to the larval development in the simulated zone, this could indicate a strong larval selection.

It has been documented for marine fish that changes in ocean temperature could directly influence larval development and PLD; in warmer waters, metabolic rates and growth increase compared with those in colder waters [53–55,60]. Northwestern Mexico is considered a temperate region, where the ocean temperatures oscillate between 14 °C (winter) and 30 °C (summer), while the TEP is considered a tropical region with more stable temperatures ranging from 25 °C to 30 °C [24,61,62]. Therefore, *L. peru* and *L. argentiventris* larvae could present slower development in Northwestern Mexico than in the TEP.

This thought is supported by studies in the laboratory with fish larvae, models evaluating the relationship between temperature and PLD supported by laboratory results, and otolith evaluations in marine fishes; all these investigations confirm that ocean temperature and hatching season are predictors with significant influence on the early life history of fishes; at lower temperatures, the PLD of fish species increase compared with those at higher temperatures [53,55,56].

The fact that Northwestern Mexico and the TEP have different environmental conditions [36,62] for *L. peru* and *L. argentiventris* larvae could have implications for ecological processes, such as the distance of larval dispersal, population connectivity, and recruitment dynamics [55,60]. It has been reported for other fish species that at higher temperatures, there is an increase in larval retention by improving larval swimming abilities; this means that the connectivity between populations via larval dispersal decreases; this agrees with the genetic population structure previously found by Reguera-Rouzaud et al. [36] and the connectivity networks found at 15 days of PLD for the TEP, in contrast with Northwestern Mexico, especially in the Gulf of California, where at higher PLD, the connectivity between populations was higher between the mainland and the peninsular sides and along their respective coasts.

#### 4.3. Are Larval Transport Pathways Consistent with the Genetic Structure?

Most of the genetic populations were well represented by the connectivity networks from the model. At the moment, it has been established that there are three genetic boundaries for *L. peru*: (1) between GC and Nayarit, (2) between Nayarit and Oaxaca, and (3) between Oaxaca and Panama; and for *L. argentiventris*, (1) in the middle portion of Baja California Sur, (2) between Colima and GC, and (3) between Colima and Panama [36], (Figure 1).

Specifically, in the Gulf of California, some research with genetic data and otolith chemistry supports the three connectivity networks (northern, center, and southern) found during spring to autumn (Figures 7 and S10) for both species at 30 days of PLD. The genetic population structure found in L. argentiventris in the Gulf of California has been previously attributed to the patchy distribution and small number and size (<1 km) of mangroves [36], in addition to the significant differences in otolith microchemistry in juveniles between the three regions [63]. Although our connectivity networks showed no connections between the central and southern Gulf of California, it has been documented that for L. peru there was genetic homogeneity in this area, probably caused by the relative continuous distribution of rocky reefs (adult habitat) and sandy bottoms (juvenile habitat) [36]. In addition, the connectivity network from the Southern Gulf of California for L. peru and L. argentiventris was supported by the genetic homogeneity found between the peninsular and mainland coasts [28,36]. Our simulation based on HYCOM data, as well as the Hamburg Shelf Ocean Model (HAMSOM) and the Region Ocean Model System (ROMS) simulation [28,64–66], suggested that seasonally reversing currents and the mesoscale eddies exchange migrants (larvae) between both coasts (Figure 3).

The connectivity networks generated by the HYCOM data at 15 days of PLD indicated that the northern Mexican Pacific supplied the southern Gulf of California with larvae (Figures 6 and S12) via the Mexican coastal current [26]. This asseveration is inconsistent with the genetic data found for *L. peru* and *L. argentiventris* (except for one location inside the southern Gulf of California that has genetic homogeneity with the northern Mexican Pacific); however, it has been reported for other fish species that other ecological factors could be restricting the gene flow between zones A and B, like habitat discontinuities (Sinaloan gap) [67–69] and significant environmental differences between the ecoregions and oceanographic structures like eddies, fronts, and upwelling zones in the mouth of the Gulf of California, where the California Current and Mexican Coastal Current converge [30,36,70–72].

For *L. peru* and *L. argentiventris*, there were interruptions in the connectivity networks at 15 days of PLD, separating Central (Colima) and Southern Mexico (Oaxaca) from Panama, consistent with the genetic structure of both species. However, the genetic structure between Oaxaca and Panama from *L. peru* was inconsistent [36]. Other marine species have shown a genetic barrier between Central/Southern Mexico and Central America. In contrast, connectivity between Colombia and Panama due to the Colombian Current and the cyclonic circulation of the Panama Bight [24,61,73] was well represented by the larval dispersal in this study and supported by genetic data from *L. peru* [36] and *L. guttatus* [74].

In addition to previously described ecological and environmental factors (isolation by distance, lack of suitable habitat, and significant environmental differences) [30,34,75,76], larval transport was a primary determinant shaping the genetic structure in Northwestern Mexico and TEP.

#### 4.4. Cross-Boundary Genetic Populations

The southern localities generally export larvae to northern localities. The primary direction from the simulated larvae in zones B and C was towards the north–northwest (Figures 5 and 6).

The Mexican Coastal Current exported migrants along the Mexican Pacific (Figures 7b and S12e–h), and the Costa Rica Coastal Current exported larvae from Northern Panama to Guatemala; in some cases, the migrants reached Southern Mexico, while

the Colombia Current and the cyclonic eddy in Panama facilitated the transport between Colombia to Southern Panama (Figures 7c and S12i–l); these connections are supported by genetic connectivity found in *L. guttatus* and *L. peru* [36,74].

Therefore, disturbances in any southern localities could affect the surrounding areas and have impacts that spread beyond its political boundaries [77]. Establishing fisherymanagement strategies that consider the connectivity and source–sink dynamics between neighboring states or countries and promoting socio-economic agreements that match the geographic scale of ecological connectivity could improve regional fisheries' benefits [78]. For example, the monitoring of reference points, fishery assessments, and the establishment of total allowable catch should be designed and implemented within each genetic stock identified, implying collaborations between inter-state and international fisheries authorities [38].

#### 5. Conclusions

Coupled with the other ecological and environmental drivers, larval transport is a primary determinant shaping the genetic structure in Northwestern Mexico and the Tropical Eastern Pacific, not only in rocky reef fish like *Lutjanus peru* and *L. argentiventris* but also in reef-associated fish species and corals. In addition, the environmental differences (primary temperature) could accelerate or slow larval development, affecting the PLD and the connectivity or retention rates. In this sense, the TEP could exhibit more larval retention than Northwestern Mexico; nevertheless, even with a PLD of 15 days, Colombia and Central American were countries demonstrated to be well connected via larval dispersal, and on some occasions (during spring and autumn), the countries of the north of Central America connected with the southern states from Mexico.

It is shown that the supply of larvae to other populations of *L. peru* and *L. argentiventris* depends on their neighbors' countries or states (in the case of Mexico), due to most larval pathways being towards the north. Therefore, disturbances in any southern localities could affect the surrounding areas and have impacts that spread beyond political boundaries.

The continuous distribution scenario largely explained the genetic structure in both species, confirming that the ocean currents play a significant role as predictors of genetic differentiation and gene flow in Northwestern Mexico and TEP. However, further research is needed in the areas of reproductive biology (especially along Central America) and larval development (affectation in growth by temperature, mortality, and vertical movement) for *L. peru* and *L. argentiventris* to incorporate this information in a more realistic biophysical model.

Supplementary Materials: The following supporting information can be downloaded at: https://www. mdpi.com/article/10.3390/w16213084/s1, Figure S1. Velocity at which the simulated trajectories were transported at the zone A during (a) winter, (b) spring, (c) summer, and (d) autumn. Figure S2. Velocity at which the simulated trajectories were transported at the zone B during (a) winter, (b) spring, (c) summer, and (d) autumn. Figure S3. Velocity at which the simulated trajectories were transported at the zone C during (a) winter, (b) spring, (c) summer, and (d) autumn. Figure S4. Connectivity networks presented for the occurrence records of Lutjanus peru during winter (a-c), spring (d-f), summer (g-i), and autumn (j-l) for 15 days of larval dispersal. Figure S5. Connectivity matrix for the occurrence records of Lutjanus peru 15 days of larval dispersal for the zone A (a-d), B (e-h) and C (i-l). Figure S6. Connectivity networks presented for the occurrence records of Lutjanus peru during winter (a-c), spring (d-f), summer (g-i), and autumn (j-l) for 30 days of larval dispersal. Figure S7. Connectivity matrix for the occurrence records of Lutjanus peru at 30 days of larval dispersal for the zone A (a–d), B (e–h) and C (i–l). Figure S8. Connectivity networks presented for the occurrence records of Lutjanus argentiventris during winter (a-c), spring (d-f), summer (g-i), and autumn (j–l) for 15 days of larval dispersal. Figure S9. Connectivity matrix for the occurrence records of Lutjanus argentiventris at 15 days of larval dispersal for the zone A (a–d), B (e–h) and C (i–l). Figure S10. Connectivity networks presented for the occurrence records of Lutjanus argentiventris during winter (a-c), spring (d-f), summer (g-i), and autumn (j-l) for 30 days of larval dispersal. Figure S11. Connectivity matrix for the occurrence records of Lutjanus argentiventris at 30 days

of larval dispersal for the zone A (a-d), B (e-h) and C (i-l). Figure S12. Connectivity networks presented for the continuous distribution scenario during winter (a-c), spring (d-f), summer (g-i), and autumn (j-l) for 15 days of larval dispersal. Figure S13. Connectivity matrix for the continuous distribution scenario at 15 days of larval dispersal for the zone A (a-d), B (e-h) and C (i-l). Figure S14. Connectivity networks presented for the continuous distribution scenario during winter (a-c), spring (d-f), summer (g-i), and autumn (j-l) for 30 days of larval dispersal. Figure S15. Connectivity matrix for the continuous distribution scenario at 30 days of larval dispersal for the zone A (a-d), B (e-h) and C (i-l). Figure S16. Connectivity networks presented for the reproductive season scenario for Lutjanus peru for 15 (a-c), and 30 (d-f) days of larval dispersal. Figure S17. Connectivity matrix for the reproductive season for Lutjanus peru at 15 (a-c) and 30 days (d-f) of larval dispersal. Figure S18. Connectivity networks presented for the reproductive season scenario for Lutjanus for 15 (a-c), and 30 (d-f) days of larval dispersal. Figure S19. Connectivity matrix for the reproductive season for Lutianus argentiventris at 15 (a-c) and 30 days (d-f) of larval dispersal. Table S1. Comparison between the three simulation scenarios with the genetic results. The checkmark ( $\checkmark$ ) indicates that the gene flow barriers and the genetic connectivity between locations agree with the dispersal model. Table S2. Percentage of self-recruitment and connectivity for the coordinate occurrence records scenario, for a pelagic larval duration (PLD) of 15 and 30 days for Lutjanus peru and, L. argentiventris. Table S3. Percentage of self-recruitment and connectivity for the reproductive scenario at 15 and 30 days of pelagic larval duration (PLD). Lutjanus peru (LPE), and L. argentiventris (LAR).

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**Data Availability Statement:** HYCOM data can be found at https://tds.hycom.org/thredds/catalog. html (accessed on 1 November 2021). Datasets from GOFS 3.1: 41-layer HYCOM + NCODA Global 1/12° Analysis (NRL): GLBv0.08/expt\_57.2 (1 May 2016 to 31 January 2017), GLBv0.08/expt\_57.7 (1 June 2017 to 30 September 2017), GLBv0.08/expt\_92.8 (1 February 2017 to 31 May 2017), and GLBv0.08/expt\_57.2 (1 May 2016 to 31 January 2017).

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