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Travel Times of Passive Drifters from the Western Caribbean to the Gulf of Mexico and Florida–Bahamas

ALEXIS LUGO-FERNÁNDEZ

Travel times of passive drifters along five predetermined routes connecting coral reefs in the western Caribbean with reefs in the Gulf of Mexico and Florida–Bahamas are provided. Mean surface velocities used to estimate time were derived from ship drifts and from satellite-tracked drifters. Estimated times include 55–135 d between Belize and the Flower Garden Banks, 26–42 d between Belize/Yucatan and Florida–Bahamas, and 31 d from Campeche to Vera Cruz. These results agree with the time of waterborne pathogen arrival at the Flower Garden Banks from Belize and an oil slick reaching Texas from Campeche.

Larval dispersal in marine environments is an important and relevant problem, because about 70% of all marine benthic invertebrates have a pelagic stage that is subject to dispersion (Karlson and Levitan, 1990). A majority (~ 75% of all species) of scleractinian corals broadcast gametes for fertilization near the surface in synchronized mass events that facilitate their dispersion by surface currents (Veron, 1995). Coral larvae remain at the sea surface as passive drifters because of their limited swimming capabilities (Kingsford et al., 2002) and remain viable for recruitment for a maximum of 120 d (Wilson and Harrison, 1998). Factors affecting dispersion include horizontal and vertical velocities (Sammarco and Andrews, 1989; Sammarco, 1994), physiological characteristics such as duration of larvae stage (Mora and Sale, 2002), and larvae behavior such as swimming ability (Olson and Carlson, 1993). Prediction of larval dispersion is a very complex problem.

Dispersion has large evolutionary and ecological consequences. Some evolutionary consequences include flow of genes and lower rates of genetic divergence; ecological consequences include colonization of new habitats and recolonization of devastated communities (Karlson and Levitan, 1990). Connectivity is strongly controlled by dispersion (Mora and Sale, 2002) and it affects material exchanges (e.g., nutrients, sediments, pollutants, and larvae), genetic flow, invasive species, and delineation and management of preservation areas (Olson and Carlson, 1993; Roberts, 1997; Lesios et al., 1984). Although dispersion occurs at short and long ranges (Sammarco and Andrews, 1989), this work focuses only on the long-range aspect of dispersion. Specifically, the long-range dispersion between western Caribbean reefs (Belize and Yucatan) and the Gulf of Mexico, Florida, and Bahamas reefs is examined.

The circulation of the Gulf of Mexico is dominated by the Loop Current and its associated eddies. The Loop Current enters the Gulf of Mexico through the Yucatan Channel as a jet of warm waters ($T \sim 25\text{--}26\text{ C}$) with speeds of 1–2 m/s (Badan et al., 2005), extends northward up to 28°N, and turns clockwise to exit through the Florida Straits. When the Loop Current reaches its maximum northern position, it usually sheds a large clockwise-rotating eddy with diameter of 200–400 km at intervals of 0.5–18.5 mo (Leben, 2005). These eddies travel to the western Gulf at speeds of 1–8 km/d (Vukovich and Crissman, 1986) and have life spans of about 1 yr (Elliot, 1982).

In the Caribbean Sea, mass spawning events occur in summer (Hagman et al., 1998). This fact suggested constraining this work to the summer season, because its objective was to study connectivity between reefs. Thus, we selected the summer average surface ship-drift velocities, Fig. 1A (U.S. Navy, 1986), and 10-yr (1989–1999) average velocities from satellite-tracked drifters, Figure 1B (Nowlin et al., 2001) to drive the advection along the routes. Both data sets are needed to overcome the surface mass accumulation in the western Gulf observed in the ship-drift data (Sturges and Kenyon, unpublished data). Previous analyses of surface drifters (Lugo-Fernández et al., 2001a) showed that drifters released in the Yucatan area reach the western Gulf and eastern Florida, suggesting that these areas are connected. On the basis of this information, the routes were subjectively established by connecting current vectors joining the point of origin (Belize and Yucatan) to final destinations [Flower Garden Banks (FGB) and Florida–Bahamas]. The routes (Fig. 2) were subdivided in segments that allow estimation of travel times to intermediate areas of interest such as Contoy, Campeche, Vera Cruz, and southern Texas. The speed and

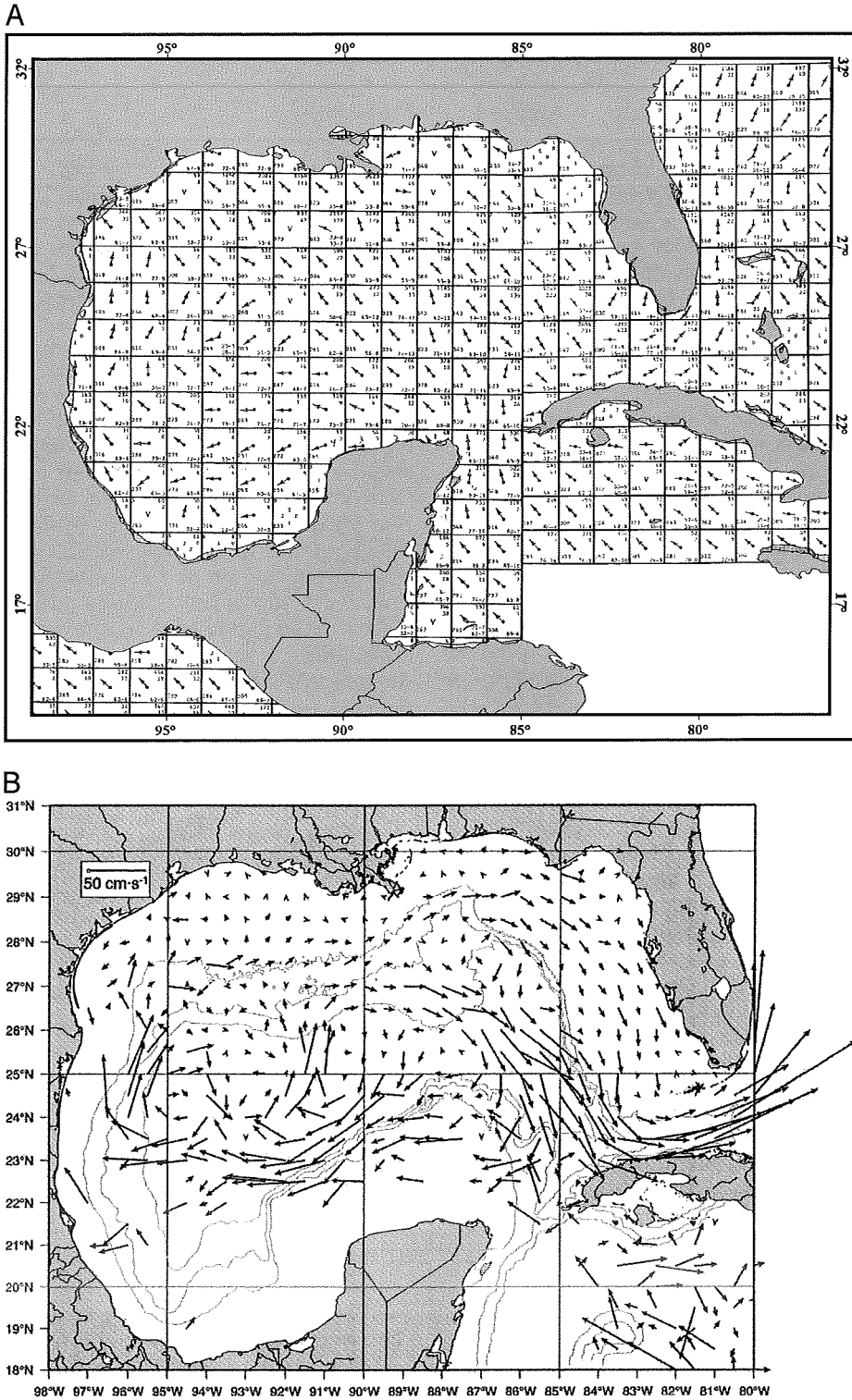


Fig. 1. (A) Surface velocity from ship drift from U.S. Navy (1986) used to estimate drifting time. (B) Surface velocity from satellite tracked drifters from Nowlin et al. (2001) used to estimate drifting time.

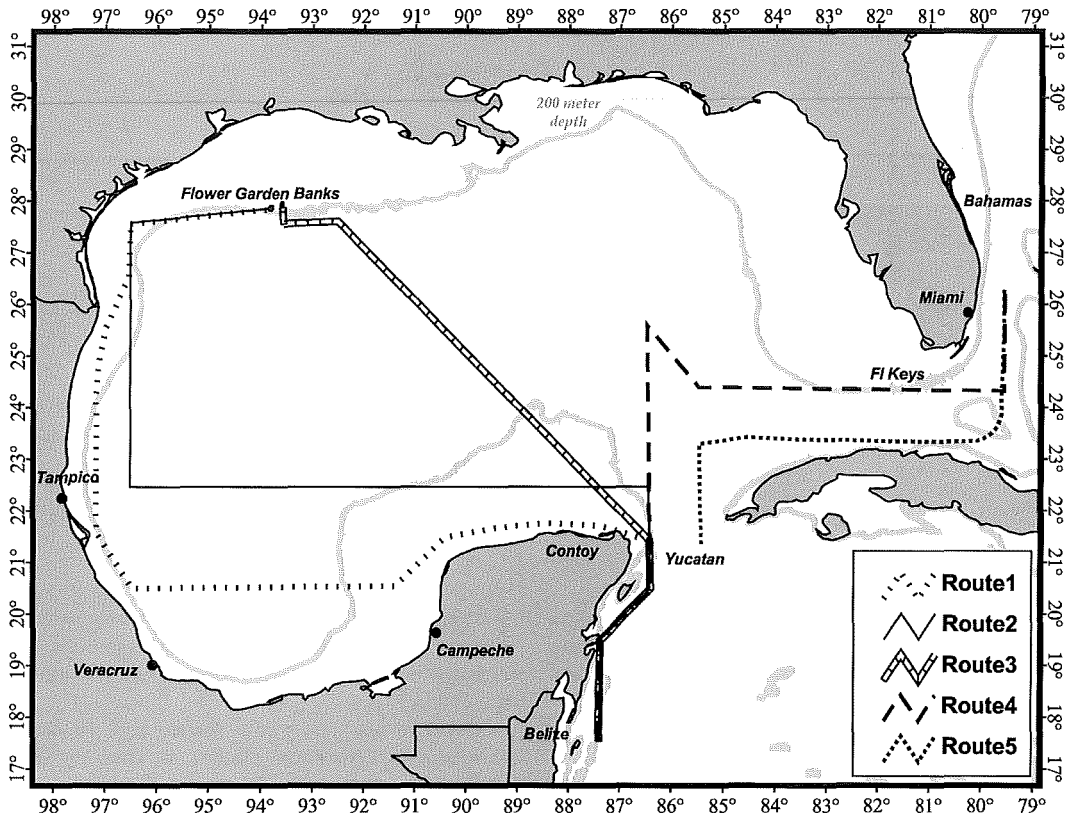


Fig. 2. Study area depicting the five routes employed in this work. Route 1: Belize to Flower Garden Banks (FGB) along Mexico–Texas; Route 2: Belize–FGB along the southern Gulf; Route 3: Belize–FGB across the central Gulf; Route 4: Belize–Bahamas along the eastern Gulf; and Route 5: Yucatan–Bahamas.

direction for each $1^\circ \times 1^\circ$ square were entered in a spreadsheet and the north–south or west–east components were calculated. Components parallel to the route were selected and plotted against distance [60–nautical mile (nm) increments], and a least-square polynomial was fitted to the observations to interpolate speeds at 30-nm increments for each route; see Figure 3 for an example. The order of the polynomial was chosen when the r -squared was ≥ 0.90 . With the polynomial equation, a table of distance and speed was constructed; from the table a travel time between neighboring points was computed with the use of:

$$T_i = 2d / (v_i + v_f)$$

where d equals 30 nm, and $v_{f(i)}$ represents the final (initial) speed in knots. Travel time (T) was estimated by summing individual times between the points of interest, which is a numerical integration by the trapezoidal method. Physically, this approach is justified by noting that long-range larval movement can be approximated through examination of the mean

surface circulation or path lines. Path lines are defined by $dx_i/dt = u_i(x_i, t)$ where the subscript represents the x (east–west) or y (north–south) coordinates (Currie, 1974).

RESULTS

Five routes were established with the use of the scheme described above (see Fig. 2). Routes 1–3 connect reefs in Belize and Yucatan to reefs of the FGB and southwestern Mexico; Route 4 connects reefs in Belize and Yucatan to reefs in Florida–Bahamas; and Route 5 connects Yucatan reefs to Bahamian reefs. Routes 1 and 2 are described in the literature, e.g., Rezak et al. (1983) and Jordan-Dahlgren (2002). A study of numerical drifters released in the Gulf (Welsh and Inoue, 2002) showed that drifters generally move from east to west inside the Gulf by entrainment in Loop Current eddies. However, Route 3 is seldom mentioned in the literature, because it represents a direct path over deep waters. Satellite-tracked drifters released in the Yucatan Channel from

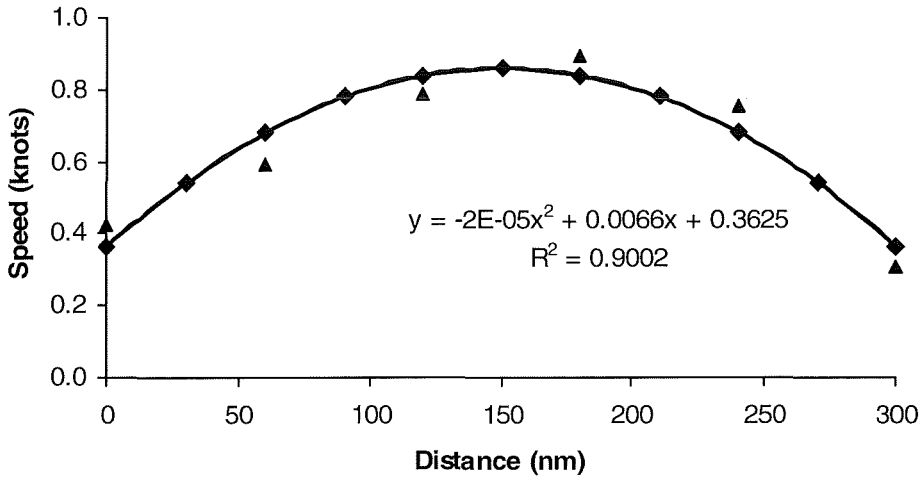


Fig. 3. Speed (\blacktriangle) with least-square polynomial fit (thick line) and speeds calculated from the polynomial (\blacklozenge) along a segment of Route 2.

September 1999 through January 2000 revealed that some drifters traveled along the western edge of the Loop Current, separated from it, and flowed westward along the northern Gulf of Mexico to near the FGB, similar to Route 3 (Badan et al., 2001). Routes 4 and 5 are also described in the literature, because the connection of corals between the Caribbean and Florida–Bahamas is well accepted (Phinney et al., 2001). The satellite drifters also provide evidence for transport into the Campeche Bank, supporting Routes 1 and 2.

TABLE 1. Estimated travel times (days) between selected points along routes.

Segments/Routes	Route 1	Route 2	Route 3	Route 4	Route 5
Belize–FGB	134	110	55	—	—
Contoy–FGB	125	99	45	—	—
Campeche–FGB	97	—	—	—	—
Vera Cruz–FGB	66	65	—	—	—
Belize–Contoy	11	11	11	11	—
Contoy–Campeche	27	—	—	—	—
Campeche–Vera Cruz	31	—	—	—	—
Western Campeche Bank–South Texas	—	38	—	—	—
Vera Cruz–South Texas	15	—	—	—	—
Belize–Bahamas	—	—	—	42	—
Contoy–Vera Cruz	58	34	—	—	—
Contoy–Bahamas	—	—	—	32	—
Contoy–FL Keys	—	—	—	30	—
Yucatan–Bahamas	—	—	—	—	26
FL Keys–Bahamas	—	—	—	2	—

A recent study of ecological connectivity also shows that the Belize–Yucatan area is connected with the Florida–Bahamas region (Cowen et al., 2006).

Travel times for each route and between points of interests are shown in Table 1. The times range from a high of 135 d (4.5 mo) to a low of 2 d and represent a drift or advection time and not a diffusion time. Notice that from Belize to the FGB travel times range from 1.8 to 4.5 mo, depending on the route; from Belize to Bahamas, the travel time is 1.4 mo; and from the Yucatan to Bahamas, it is 0.9 mo. Travel time from Campeche to the FGB is 97 d (~ 3 mo) and from Vera Cruz to the FGB 66 d (~ 2 mo). From Contoy/Campeche to Vera Cruz travel time ranges from 27 to 58 d (1–2 mo) and from Florida Keys to Bahamas it is only 2 d. These estimates represent minimum times for two basic reasons: (1) the routes selected are straight, whereas real ones display a series of close loops caused by tides and eddies that are well known in the Gulf of Mexico (Kirwan et al., 1984); and (2) the currents are very variable and seldom behave as averages suggest.

DISCUSSION

This work is an analysis of advection of passive drifters along five routes connecting the western Caribbean reefs to reefs in the western Gulf of Mexico and Florida–Bahamas. Although they are subjectively defined, these routes are also supported by observations. For example, the routes along the southern Gulf are suggested by distributions of gorgonians and corals (Jordan-Dahlgren, 2002). Other

works that support these two routes are Jordan-Dahlgren and Rodríguez-Martínez (2003) and Lugo-Fernández et al. (2001a). Routes to the Florida–Bahamas are supported by Jordan-Dahlgren (2002), Phinney et al. (2001), and Lugo-Fernández et al. (2001a). Numerical studies of drifters also support these routes (Cowen et al., 2006; Welsh and Inoue, 2002). Route 3, a direct path to the FGB from the western Caribbean over deep waters, appears to be less known, as no information was found in the literature reviewed. However, drifter data over 2 yr (Badan et al., 2001) show that larvae entrained in the Loop Current are carried to both the western Gulf and the Florida–Bahamas regions. These drifter data also suggest that over short times, Routes 3–5 are more prevalent than Routes 1 and 2. But Routes 1 and 2 are also active. It also appears that Route 1 is reversible, as shown by satellite-tracked drifters that reach Vera Cruz from the FGB in ~ 90 d, which is less than the 135 d estimated here (Lugo-Fernández et al., 2001b). In conclusion, it can be inferred that these routes are supported by current biological knowledge of distributions of corals in the study region and drifters released in the Yucatan Channel.

Are these travel times reasonable? An indication of how realistic these results are can be obtained by comparing the estimates herein with known dispersion and drift events. For example, the estimated travel time from Belize to Contoy is 10.5 d; Lessios et al. (1984) reports that, during the *Diadema* sea urchin die-off, the pathogen traveled from Belize to Cozumel in days. The same pathogen reached the FGB in 2–4 mo (Rezak et al., 1985; Phinney et al., 2001), which compares very well with the estimates provided (~ 2–4 mo). The pathogen traveled from Cozumel to Tortugas in about 1.5 mo and from Cozumel to Florida Keys in 0.5 mo (Lessios et al., 1984); the estimated time from Contoy to south Florida is 1 mo. During the IXTOC blowout in Campeche, the released oil arrived in Texas about 63 d later; estimated time from Campeche to south Texas is ~ 46 d by Route 1, and from the western Campeche Bank to south Texas the time is ~ 38 d by Route 2; both estimates are reasonable, considering the simplifications in this work. Furthermore, Bright et al. (1991) reported a drifting time of 4–9 wk (1–4 mo) from Yucatan and Tampico to the northwestern Gulf, which compares well to the results herein. Arrival of the pathogen responsible for the sea urchin die-off appears to have followed Routes 1 and 2, which put the pathogen at the FGB by Nov. 1983 (Rezak et al., 1985); but if it arrived in

Sept. 1983 (Phinney et al., 2001), then it probably followed Route 3, as it is the shortest one. Jordan-Dahlgren (2002) reports a drifting time of 50–60 d from Campeche to the SW Gulf; the time herein is 31–58 d from Contoy/Campeche to Vera Cruz. Drifters released in Yucatan Channel (Badan et al., 2001) provide the best direct evidence to confirm results herein. Drifters reach the northwestern Gulf along a route very similar to Route 3 in about 40–45 d; the estimated time along Route 3 from Contoy to FGB is 45 and 55 d from Belize to FGB. The drifters reach the Campeche area in about 32 d, the estimate herein is 27 d; time to Florida Keys and Bahamas is about 15–18 d vs 26–32 d; finally, from Florida to Bahamas is 1–3 d or so vs 2 d estimated. The estimated drifting times compare very well with times from actual dispersion events observed in the study area and support the claim that the dominant mechanism of dispersion in this work is drifting by near-surface currents and not diffusion.

These results can shed light on recent dispersal events in the Gulf of Mexico. The recent expansion of *T. coccinea* in the Gulf (Fenner, 2001; Sammarco et al., 2004) can be explained by dispersion along Routes 1–3, which then explains its presence in the southern Gulf and along the northwestern Gulf; see Figure 1 in Fenner (2001). Another recent event is the sighting of *A. palmata* in 2001 at the FGB (Aronson et al., 2005). This new expansion could be an example of a stepping or hopping effect from the Caribbean, since the *A. palmata* larvae is pelagic for ~ 20 d (Baums et al., 2005) and it takes 55–135 d to get to the FGB. The 135-d trip along Route 1 implies a very low probability of recruitment since coral larvae are viable for only 120 d. If it is assumed that the release of larvae occurs in August, then the 135-d estimated travel time falls in winter when temperature stress and the high wave and strong currents could combine to exert large stresses on the larvae, making recruitment and dispersal arduous. Similar conditions may also explain the absence of gorgonians at the FGB, since it seems that biological conditions (i.e., physiological and behavioral) are the limiting factor in this case, given the availability of routes to reach the FGB. Another example of stepping or hopping, most probably, from the Caribbean Sea is the presence of the black coral *P. pennacea* in deep waters of the northern Gulf of Mexico (Boland and Sammarco, 2005). This expansion could have been accomplished following Route 3 and transported by Loop Current eddies since this species has limited dispersal capabilities.

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