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ABSTRACT

Caribbean spiny lobsters are known to undergo migration as adults, but the dispersal and homing ability of subadults and juveniles is not well characterized. Given that settlement habitat for juveniles is inshore seagrass / hardbottom and reproductive habitat is offshore coral reefs, dispersal during ontogeny serves as a bottleneck potentially limiting adult population density. Previous studies have examined factors associated with movement and den selection by juvenile lobsters such as shelter type, predators, and conspecific density. Their attraction to odors of healthy conspecifics plays a significant role in aggregation of lobsters in casitas and traps. But what is unknown is whether juvenile lobsters possess the map and compass orientation found in adults. To examine the ontogeny of homing ability, we conducted multiple mark / displace tracking studies using acoustic telemetry in juvenile hardbottom and subadult coral patch reef habitats. All lobsters regardless of size tend to relocate to new crevice shelters when handled, even if returned to their original shelter. Thus, for non-displaced lobsters tagged and returned to their point of capture, distance and angle travelled appears to be random with distance increasing as function of body size. However, for juvenile and subadult lobsters tagged and displaced away from their point of capture, the distance and angle travelled when released is significantly directed toward the point of capture. Thus, it appears that the map and compass ability of Caribbean spiny lobsters appears early in ontogeny and may allow for individuals to safely explore unfamiliar locations while retaining knowledge of how to return to known shelter. This ability to expand their known habitat map while maintaining knowledge of critical diurnal shelter locations is expected to facilitate their ontogenetic dispersal to adult habitat.

1. Introduction

Many animals have homing abilities on the order of meters to thousands of kilometers (Able, 1980). The proximate causations underlying these remarkable feats of navigation are as diverse as the taxa that employ them, ranging from celestial rotation (Emlen, 1970) to patterns of polarized light (von Frisch, 1993) to changes in the geomagnetic field (Lohmann et al., 2022). Likewise, the ultimate causation of these extraordinary feats of navigation are known to increase survival and reproduction through energy conservation (Weber, 2009), avoidance of disturbance (Mikula et al., 2018), successful return to productive feeding grounds (Acevedo et al., 2022), mating aggregations (Dittman and Quinn, 1996), or nesting sites (Scott et al., 2014). But to what degree are these remarkable homing abilities present early in ontogeny before long distance migrations occur? Here we explore the ontogeny of homing behaviors in the Caribbean spiny lobster *Panulirus argus*, the Caribbean spiny lobster.

Spiny lobsters (Family Palinuridae) are unique among most commercially harvested crustaceans due to two features of their life history. First, members of the family are known to have long larval durations (4–24 months) which assure for a wide dispersal of larvae across hundreds of kilometers leading to settlement in a wide variety of shallow water habitats (Booth and Phillips, 1994). Second, once they settle, palinurid lobsters demonstrate an exceptional ability to travel great distances utilizing different habitats from shallow vegetated shorelines to unvegetated deep water ledges (Herrnkind, 1980). This suite of life history and behavioral traits are exploited by commercial and recreational fisheries around the world by anticipating preferred habitats, local movement patterns, shelter seeking behaviors, and conspecific attraction (Childress, 2007; Briones-Fourzán and Lozano-Álvarez, 2013). Yet, despite years of research, some fundamental questions regarding the movement and sheltering behaviors of palinurid

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lobsters remain a mystery.

Much of what we know about palinurid lobster behavior is due to ground-breaking field research of Professor William F. Herrnkind studying the Caribbean spiny lobster, *Panulirus argus*. Herrnkind first became interested in lobster behavior after observing adult lobsters migrating in single-file formations (Herrnkind and Cummings, 1964; Herrnkind, 1969; Herrnkind et al., 1973). He and his students spent much of the next two decades making direct observations of lobster movement, den-sharing, and migrating queues on SCUBA using mark-recapture and acoustic telemetry to track individuals while saturation diving from the Hydrolab and Tektite Underwater Laboratories (Herrnkind and McLean, 1971; Herrnkind and Redig, 1975; Herrnkind et al., 1975). At the time of this research, no one had previously dissected the complex nature of how lobsters accomplish these amazing feats of animal movement (Herrnkind, 1980). Yet, these studies focus almost exclusively on the largest individuals in the population that had already made their way offshore from their settlement habitat.

In the mid 1980s Herrnkind's attention shifted to the early benthic stages of *P. argus* focusing on the processes of larval recruitment and post-settlement survival (Herrnkind and Butler, 1985). This allowed for an examination of the ontogeny of social behaviors that contribute to the exceptional migratory behaviors of adult lobsters (Childress and Herrnkind, 1996). Postlarval *P. argus* are attracted to nearshore waters containing the chemical cues from red macroalgae (*Laurencia* spp.) and conspecific odors from benthic conspecifics (Butler and Herrnkind, 1991; Zito-Livingston and Childress, 2009; Baeza et al., 2018). Newly settled first stage benthic juveniles are not found in dense aggregations but within a few months they transition from algae to sharing crevice shelters (Marx and Herrnkind, 1985). This transition from solitary to gregarious association is clearly facilitated by the juvenile lobster's ability to detect conspecific cues which significantly reduces exposure time when searching for a suitable shelter from predators (Childress and Herrnkind, 2001).

As juvenile *P. argus* grow larger, so does their ability to move further and further distances from their initial settlement habitat (personal observation). In the Florida Keys spiny lobster nursery, the shallow waters of Florida Bay are a mixture of sponge-soft coral hardbottom and soft sediment seagrass habitats (Butler and Herrnkind, 1992). Here juvenile lobsters utilize crevices under large sponges, solitary coral heads, and holes in the limestone veneer moving to larger and larger crevices as required by their body size (Childress and Herrnkind, 1997). As a result, juvenile lobsters alternate between periods of returning to a familiar diurnal den each dawn versus moving on to a new den closer to their adult habitat. Do these juvenile lobsters possess homing abilities to guide them back to familiar dens after each nocturnal foray?

Upon the discovery of homing, subsequent research into the potential mechanisms by which lobsters navigate has indicated that nonvisual mechanisms such as hydrodynamic (Nevitt et al., 1995), olfactory (Nevitt et al., 2000), and magnetic (Lohmann et al., 1995) cues may play a role. Caribbean spiny lobsters have been found to possess true navigational abilities (Boles and Lohmann, 2003). This study showed that lobsters have a magnetic map because, when they were exposed to magnetic fields that exist at distant locations, they behaved as if they have been displaced there. (Lohmann and Ernst, 2014). Furthermore, evidence pointing to the avoidance of strong magnetic anomalies by adult lobsters provides strengthening evidence for magnetoreception (Ernst and Lohmann, 2018).

Other studies observing adult lobster movement have utilized the development of a novel tracking technology called acoustic telemetry. Acoustic telemetry serves as an efficient method for tracking the behavioral patterns of lobsters and other marine species over large distances (Hussey et al., 2015). In tracking the movement of *P. argus*, acoustic telemetry is particularly useful due to the nighttime activity of this species that would otherwise deem direct observation far less efficient. Instead of relying on visual observations requiring the presence of light, acoustic telemetry utilizes sound transmission to determine the geographic locations of the subjects involved. In a 2009 pioneer study, fixed-array acoustic telemetry was utilized to observe the movement patterns of *P. argus* for the first time (Bertelsen and Hornbeck, 2009). The setup involved capturing lobster subjects by divers, placing acoustic tags on the carapace of lobster subjects, laying out acoustic receptors in a grid shape on the ground throughout the study area, and releasing lobster subjects to allow for sound transmission by the tags and reception by receivers in triangulating locations during the study period (Bertelsen and Hornbeck, 2009). The new technology confirmed previous studies that found evidence pointing to homing behavior in this species (Herrnkind and Redig, 1975). Specifically, this study found evidence supporting homing behavior in both short-term movement, such as nightly foraging, and long-term movement, such as reproductive migrations (Bertelsen and Hornbeck, 2009). In a similar follow-up study, Bertelsen used acoustic telemetry to track longer movements in addition to daily movement (Bertelsen, 2013). The study found evidence of reproductive migrations in females and pointed to the importance of the outlier reef subregion for conservation in the study location, the Western Sambo Ecological Reserve (Bertelsen, 2013).

With the advent of smaller and smaller acoustic tags, the opportunity to study homing behaviors in juveniles and subadult lobster during their ontogenetic transition to adult habitat has become a reality. This study aims to determine if juvenile and subadult lobsters possess the ability for directed movements when displaced from home dens that would suggest a map and compass ability seen in adults. Furthermore, we explore how displacement distance and lobster size are related to the average distance traveled per nocturnal movement bout.

2. Materials and methods

2.1. Study sites and setup

The field portion of this study took place in June 2015, 2018, 2019, and 2020. We selected two locations in the middle Florida Keys within the Florida Keys National Marine Sanctuary known to have resident juvenile and subadult spiny lobsters (Fig. 1). The first study location is 100 m from shore on the Florida Bay side of Lower Matecumbe Key, hereafter referred to as "Matecumbe" (Fig. 1). Matecumbe is a shallow water (1.5–2.5 m depth) hard bottom habitat with a mixed bottom composed of sand, seagrass, *Laurencia* spp. algae, and limestone substrate with living and dead hard corals, loggerhead sponges, and solution holes as the primary dens utilized by juvenile lobsters (15–60 mm carapace length = CL). This habitat is considered an example post-larval lobster settlement habitat where the transition from post-larval stage (PL) to early benthic juvenile stage (EBJ) occurs (Butler and Herrnkind 1997). Two 7-day mark-resight deployments were conducted at this site in June of 2019 and 2020.

The second study location is 2 km from shore on the ocean side of Lower Matecumbe Key, hereafter referenced as "Coral Gardens" (Fig. 1). This habitat is a hardbottom patch reef (3.5–4.5 m depth) with a mixed bottom composed of sand, seagrass, *Laurencia* spp. algae, and limestone (Smith et al., 2023). Coral Gardens contains large live and dead boulder corals fused into patch reefs (100–500 m circumference, 2.0–2.5 m height above substrate) and smaller isolated hard corals (1–3 m circumference, 0.5–1.0 m height) scattered between the larger patch reefs. Subadult lobsters (30–90 mm carapace length = CL) were found more commonly in the smaller isolated coral heads but were also found occasionally in large crevices under the edge of the larger boulder coral patch reefs. This habitat is considered a transitional habitat for subadult lobsters midway between their settlement habitat in Florida Bay and their reproductive habitat along the Florida Reef tract. Three 7-day mark-resight deployments were conducted in Coral Gardens in June of 2015, 2018, and 2020.

At each location, a grid of stationary acoustic telemetry Vemco VR2 receivers was arranged in a hexagonal grid pattern sufficient to cover the entire hardbottom / patch reef habitats extending to the seagrass edge.

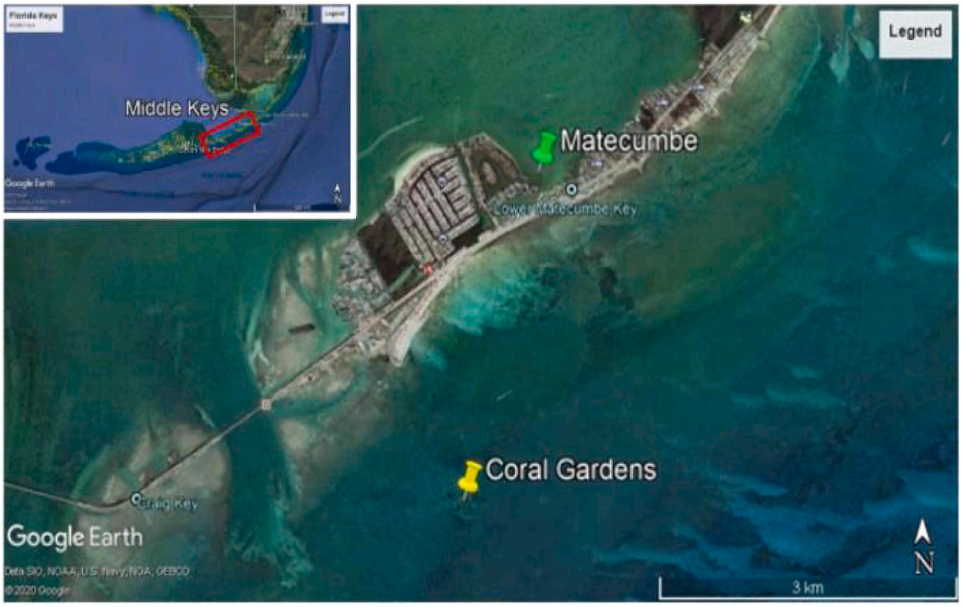

Fig. 1. Map derived from Google Earth visualizing the location of the Middle Florida Keys indicated by a red rectangle (top left) and the relative locations of the two study sites within the Middle Keys. Matecumbe is indicated by a green pin on the Florida Bay side of Lower Matecumbe Key and Coral Gardens by a yellow pin on the ocean/Florida Reef Tract side.

Each receiver was secured within a PVC pipe anchored to a cement base. In the Matecumbe studies, 22 Vemco VR2 receivers, each on stands 30 cm tall, were arranged 60 m apart into a hexagon. In the Coral Gardens studies, 23 Vemco VR2 receivers, on stands 100 cm tall, were arranged approximately 100 m apart into a hexagon. Some of the receivers at Coral Gardens were not spaced exactly 100 m apart into a perfect grid because of constraints due to the location of hard coral patch reefs. To compensate, additional VR2 receivers were placed in the middle of the array at distances of 50 m apart to ensure adequate acoustic tag signal detection (Fig. 2).

2.2. Lobster selection and experimental manipulation

Lobsters were collected from their shelters by SCUBA divers using hand nets (Heldt et al., 2015). Shelters were selected that contained two or more lobsters and were marked with a den ID tag. Surface buoys above each shelter allowed us to get an exact GPS location for every marked shelter. Either two or four intermolt lobsters within the target size range (24–90 mm CL) were then selected from each den. Even numbers were selected to maintain equal numbers of non-displaced and displaced lobsters and we selected individuals to match sizes such that each treatment had similar sized individuals. We recorded lobster size (carapace length measured in mm), sex, molt condition (pre-, intermolt, post-), injuries (number and type), and evidence of PaV1 infection by visual inspection. Non-intermolt (soft or those with a excess fouling with algae), sick (those with milky hemolymph) and injured (those missing antennae or more than one walking leg) lobsters, as well as those not meeting the target size range (25–80 mm CL) were returned to the water and excluded from the study. We tagged 22 lobsters (11 female, 11 male) at Matecumbe (median CL = 31.5 mm, range 24.1–40.6 mm) for which 11 were displaced and 11 were not displaced from their point of capture. We tagged 24 lobsters (11 female, 13 male) at Coral Gardens (median CL = 44.6 mm, range 35.1–89.4 mm) for which 14 were displaced and 10 were not displaced from their point of capture. Sex was not found to influence any of our behavioral measures so sexes were combined for all further analyses.

We attached a Vemco acoustic tag transmitter to the back of each lobster's carapace using cyanoacrylate adhesive (Super Glue) (Fig. 3). Vemco V9 tags were used for smaller lobsters with sizes ranging from 24 to 50 mm CL, and V13 tags were used for larger lobsters with sizes ranging from 50 to 90 mm CL. Lobsters were held on board a minimum of 10 minutes to assure the glue had set before divers returned and release them into a shelter.

Each lobster was randomly assigned to one of two treatments, non-displaced or displaced. Non-displaced lobsters were returned and released into the shelter where they were captured. Displaced lobsters were returned and released into a known lobster shelter other than the one where they were captured (Fig. 4). At Matecumbe, the average

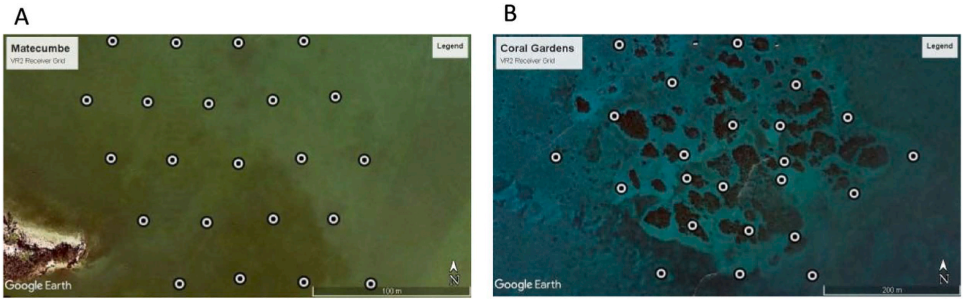

Fig. 2. Google Earth images visualizing the Vemco VR2 receiver grid setups in (A) Matecumbe and (B) Coral Gardens. Each circular white icon represents a VR2 receiver.

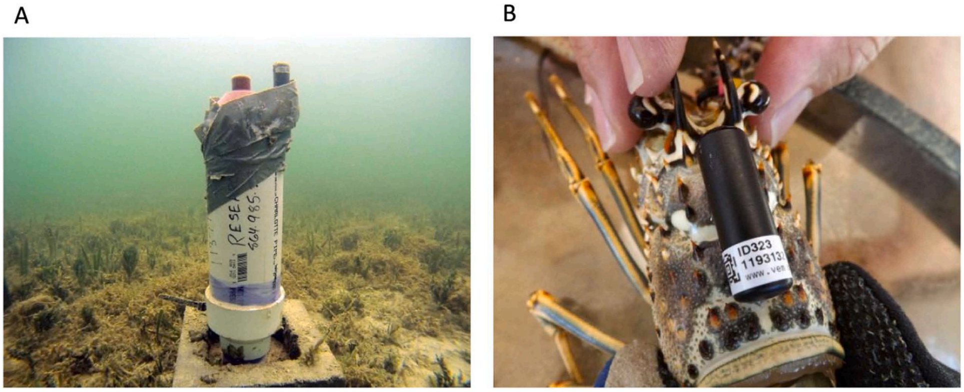

Fig. 3. Photographs captured during the field studies depicting (A) one of the VR2 receivers attached to a concrete block stand and (B) one of the lobster subjects being tagged.

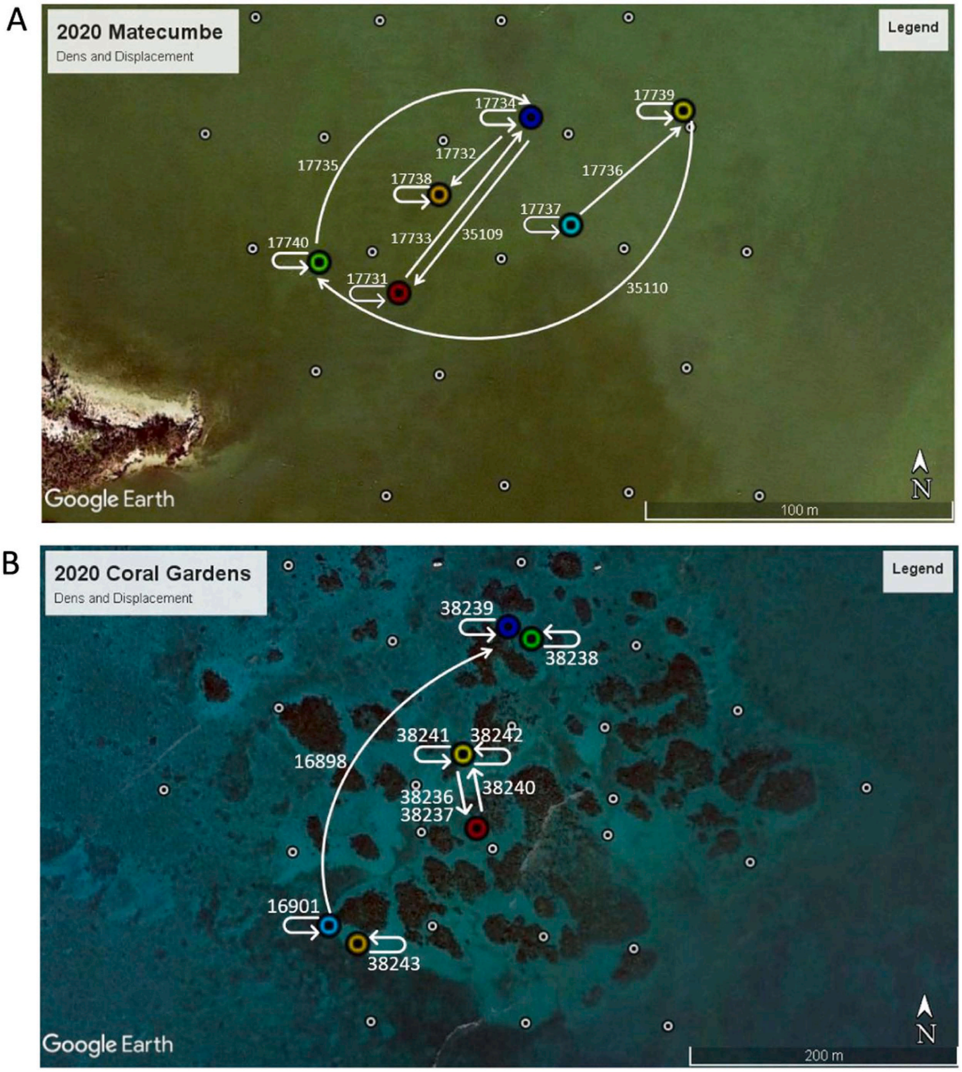

Fig. 4. Google Earth images visualizing the den locations (colored dots) and displacements (curved arrows) in A) Matecumbe and B) Coral Gardens for the field studies conducted in 2020. Numbers represent the Vemco tag number for each lobster released. Arrows that return to the same den represent control (non-displaced) lobsters and those arrows that point from one den to another den represent displaced lobsters.

distance displaced was 64.9 m (range = 34.8–130.5 m), and at Coral Gardens, the average distance displaced was 120.3 m (range = 65.2–390.1 m). All lobsters were released during the day between the hours of 1000 and 1500. Day 1 movement was estimated beginning at 2200 hours the same day as the release until 1000 hours the following day. Day 2 movement was estimated the following day from 2200 to 1000 hours. Receivers were retrieved and downloaded after a minimum of 7 days.

2.3. *Estimating homing using acoustic telemetry location estimates*

The acoustic tags, both the V9 used for smaller lobsters and V13 used for larger lobsters, were set to transmit a coded signal once every 60, 90 or 120 seconds +/- 20–60 seconds. The range of the V9 tags was a minimum 200 m radius, sufficient to reach between 3 and 21 receivers at Matecumbe and between 3 and 9 receivers at Coral Gardens. The range of the V13 tags was a minimum 400 m radius, sufficient to reach between 3 and 15 receivers at Coral Gardens. The acoustic receivers at Matecumbe were in the field and collecting data from tagged lobsters from June 11–19 in 2019 and June 24–30 in 2020. The acoustic receivers at Coral Gardens were in the field and collecting data from tagged lobsters from June 16–22 in 2015, June 16–22 in 2018, and August 4–10 in 2020. We found no effects of date or year for either location so the data was pooled for all remaining analyses.

After downloading the receivers, all acoustic receptions were aligned to a single clock reference from a centrally mounted high output V16 reference tag (180 second +/- 60 second periodicity). Then the adjusted number of receptions per receiver were summed for a 30-minute interval with a sliding window interval of 15 minutes. All receptions received during this 30-minute interval were averaged for receiver latitude and longitude weighted by the number of receptions. This weighted average location was then used to estimate lobster position every 15 minutes (Bertelsen and Hornbeck, 2009, Bertelsen, 2013). The weighted average location values were filtered by the time of day, excluding daytime location data, defined as prior to 2200 hours and after 1000 hours, as lobsters are mostly active only at night. The data was further filtered by excluding any 15-minute interval with fewer than 3 receivers or 10 total receptions as these values are considered insufficient to indicate a reliable position indicative of lobster movement outside of their shelter (Bertelsen and Hornbeck, 2009, Bertelsen, 2013).

Then, the data was separated by tag number and by day, yielding nocturnal activity ranges for each day for each lobster. Day 1 was defined as the first 2200–1000 hour period immediately following lobster release at 1000–1500 hours. Day 2 was defined as the night following Day 1 from 2200 to 1000, and so on. The starting position of movement on Day 1 was assumed to be the point of lobster release. The starting position of movement on Day 2, and thereafter, was assumed to be the first location after 2200 in the period defined as that day meeting the requirements for the minimum number of receptions (minimum of 3 receivers and 10 receptions). The ending position of movement on Day 1, and thereafter, was assumed to be the last location prior to 1000 in the period defined as that day meeting the requirements for the minimum number of receptions.

Every latitude and longitude at 15-minute intervals for each lobster was uploaded into Google Earth along with the receiver locations and the shelter locations. We noted the starting and ending position for each individual for each day of the trial so we could estimate the distance and direction travelled from during their nocturnal activity period. From each daily location map, we estimated the linear distance and summed bearing of movement between the first and last activity point using ImageJ software with a scale set from the Google Earth scale bar.

2.4. *Representation and analysis of daily movements*

Distance and orientation measurements were represented as a vector diagram with the common central point as the shelter on Day 1 and the shelter on Day 2. Each diagram contains arrows radiating from a central point that indicated distance and direction of movement on days 1 and 2 for both non-displaced and displaced individuals. The size of the reference circle is approximately the average distance the displaced lobsters were moved and thus, serves as visual reference for whether the movement was greater or less than the average distance displaced from their original shelter (Matecumbe Fig. 5, Coral Gardens Fig. 6).

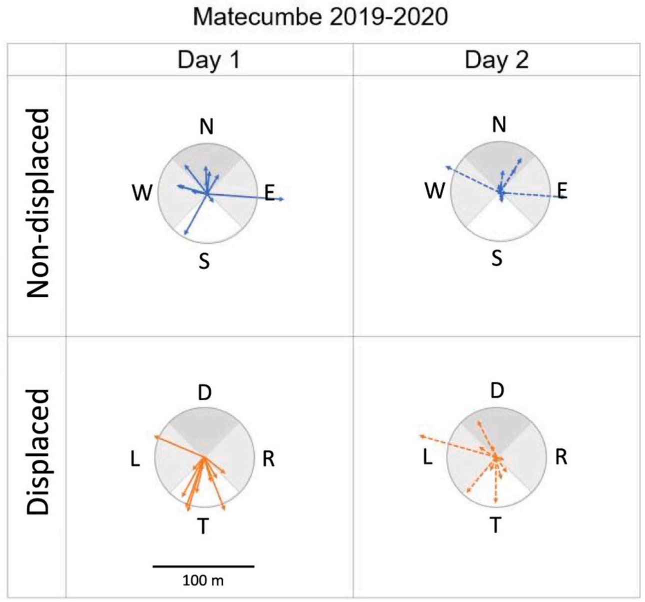

Fig. 5. Composite vector diagrams for the Matecumbe studies conducted in 2019 and 2020. Each arrow represents the movement of one of the lobsters in the indicated experimental group (non-displaced or displaced) on day 1 and on day 2. The circle radius is equal to the average distance that the displaced lobsters were relocated from their point of capture. The circle for the non-displaced lobsters is a true compass rosette with the dark gray sector (N) representing angles from 315° to 45° and the white sector (S) representing angles from 135° to 225°. The light gray sectors (E, W) represent the remaining sectors of possible angles. The circle for the displaced lobsters is not a true compass rosette but instead represents the adjusted angle of travel relative to the angle initially displaced from the point of capture equal to 0°. Thus, the gray sector (D) represents angles −45° to 45° in the same direction that displaced lobster was relocated from its point of capture. The white sector (T) is the target sector and represents angles from −135° to 135° toward the target point of capture (180°). The light gray sectors (L, R) are simply the remaining sectors of angles neither toward the target or away from the target.

The reference angle (0 degrees) is different between the non-displaced and displaced lobsters in Fig. 5 & 6. For the non-displaced lobster vectors, the 0° reference is true North and thus, the four shaded sectors are just visual references dividing the circle into four equal sectors centered on the four cardinal directions (i.e. dark gray = 315° to 45°, white = 135° to 215°). However, for the displaced lobster vectors, the 0 degree reference is the orientation from the release point back to the original shelter. Thus, vectors that orient in the white sector (T = target sector) are heading in the expected direction (+/- 45°) which would take the lobster toward its original shelter when it was captured. Light gray (L = left sector, R = right sector) and dark gray sectors (D = displacement sector) indicate orientation away from the original shelter. We represent these sectors using the same shades of gray and labels in the stacked column chart in Fig. 7.

Analysis of the distance travelled on each day were compared by t-test and ANOVA. The direction travelled on each day was compared by chi-square contingency table analysis, dividing up the compass into four 90-degree sectors. The analysis vector orientations were tested against a null distribution of random angles. Watson’s U circular statistical analysis were performed to test for non-random clustering of angles.

3. Results

3.1. *Average daily movement*

Average day 1 distances (mean +/- SE) moved were not statistically different for non-displaced (33.3 +/- 5.4 m) versus displaced (37.9 +/- 5.0 m) lobsters at Matecumbe ($t = 0.62$, $p = 0.271$). While average day 1 distances were higher at Coral Gardens, distances moved on day 1 were

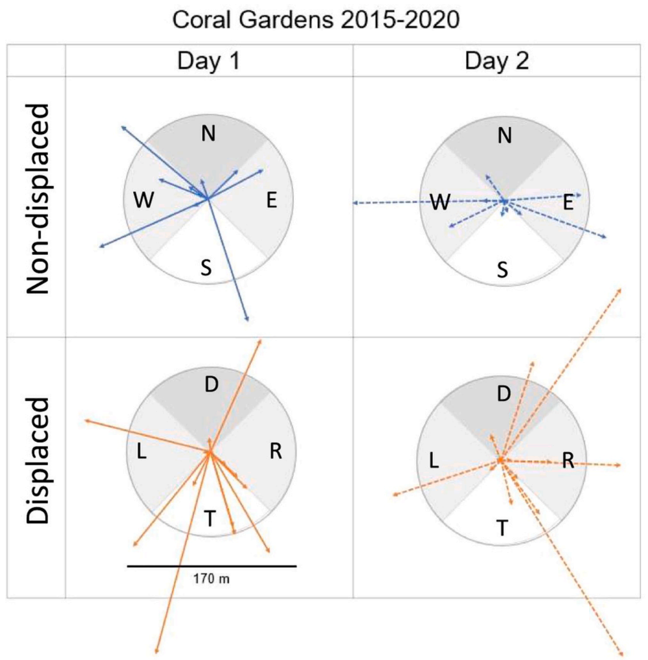

Fig. 6. Composite vector diagrams for the Coral Gardens studies conducted in 2015, 2018, and 2020. Each arrow represents the movement of one of the lobsters in the indicated experimental group (non-displaced or displaced) on day 1 and on day 2. The circle radius is equal to the average distance that the displaced lobsters were relocated from their point of capture. The circle for the non-displaced lobsters is a true compass rosette with the dark gray sector (N) representing angles from 315° to 45° and the white sector (S) representing angles from 135° to 225°. The light gray sectors (E, W) represent the remaining sectors of possible angles. The circle for the displaced lobsters is not a true compass rosette but instead represents the adjusted angle of travel relative to the angle initially displaced from the point of capture equal to 0°. Thus, the gray sector (D) represents angles −45° to 45° in the same direction that displaced lobster was relocated from its point of capture. The white sector (T) is the target sector and represents angles from −135° to 135° toward the target point of capture (180°). The light gray sectors (L, R) are simply the remaining sectors of angles neither toward the target or away from the target.

not significantly different for non-displaced (59.5 +/- 14.4 m) versus displaced (74.4 +/- 16.3 m) (t = 0.685, p = 0.250). The large variance in movement distances appears to be related more to lobster size than whether they were displaced or not (Table 1). Furthermore, day 2 distances moved do not show dramatic differences from day 1 distances suggesting that day 1 distances are not just the result of handling stress from being captured and tagged.

3.2. *Orientation of movement after displacement*

Visual representations of movement distance and orientation on day 1 and 2 (vector diagrams) show apparent differences in the angle of movement between the two experimental groups, particularly on day 1. At the Matecumbe site, non-displaced lobster vectors appear to point in random directions regardless of distance (Fig. 5). The displaced lobster vectors significantly cluster in the target sector (T) opposite the direction initially displaced (D) (Watson's $U^2 = 0.3885$, $p < 0.005$). On day 2, both treatment groups appear to move in random directions for similar distances.

At the Coral Gardens site, the control lobster vectors on day 1 appear to point in random directions regardless of distance, similar to observations at Matecumbe (Fig. 6). The displaced lobster vectors cluster in the target sector (T) opposite the direction initially displaced (D) (Watson's $U^2 = 0.1471$, $p < 0.100$). Similarly on day 2, both treatment groups appear to be moving in random directions for similar distances.

Haphazard selection of displacement dens resulted in a random distribution of initial displacement angles across the two study locations (Fig. 7). On day 1 non-displaced lobsters showed a random distribution of orientation angles but displaced lobsters showed significant non-random orientation angles in the direction opposite of their initial displacement ($\chi^2 = 14.72$, $p = 0.0021$). By day 2, whatever differences there were initially between non-displaced and displaced were gone leading to no significant differences in orientation angles by treatment groups ($\chi^2 = 1.59$, $p = 0.6596$), with both moving in random directions (Fig. 7).

3.3. *Movement pattern differences due to location / lobster size*

Differences were also found between the two study locations, Matecumbe and Coral Gardens. For example, a significant relationship was present between angle of displacement and angle of travel on day 1 in the displaced group in Matecumbe (r = −0.926, p=0.0001), but not for Coral Gardens (Fig. 8A). On day 2, there was a significant relationship found between distance displaced and distance traveled in Coral Gardens (r = 0.578, p=0.01) but not Matecumbe (Fig. 8D). Lastly, it appears that the increased movement distances for Coral Gardens lobsters over those from Matacumbe may be due to differences in lobster size between the study sites (Figs. 8C and 8D).

3.4. *Unplanned measures of long distance lobster movement*

Three tagged lobsters from Coral Gardens were recaptured by fishermen outside of the acoustic array and were reported to the Florida Marine Research Institute in the summer of 2020 (Appendix A, Figure S1A). A male displaced lobster (89.4 mm CL) was captured in a lobster trap at a distance 7.74 km west of the Coral Gardens five days after release (Figure S1B). A male control lobster (78.9 mm CL) was captured by recreational divers at a distance 2.24 km northwest of the Coral Gardens five days after release (Figure S1C). A female displaced lobster (37.4 mm CL) was captured in a lobster trap at a distance 0.40 km west of Coral Gardens 4 weeks after release (Figure S1C).

4. Discussion

Our results demonstrate that juvenile Caribbean spiny lobsters show homing ability as has been demonstrated for adults using both displacement direct observation studies (Herrnkind and Redig, 1975) and acoustic telemetry (Bertelsen, 2013). When displaced from a familiar shelter, juvenile *Panulirus argus* immediately begin a return trip toward their original shelter regardless of the initial distance and direction displaced. This movement does not appear to be any faster than for non-displaced individuals handled and returned to their original shelter, nor is it significantly slower on day 2 after the effect of the initial handling has begun to wane. It does, however, support the notion that juvenile Caribbean spiny lobsters may have a homing ability (Herrnkind, 1980; Vannini and Cannicci, 1995) which has been demonstrated in previous studies on other lobster species (Lozano-Álvarez et al., 2002 – *Panuirus guttatus*, Scopel and Watson, 2021 – *Homarus americanus*).

Perhaps what is most surprising is that smaller juvenile lobsters in Florida Bay (Matacumbe) seemed to show higher accuracy once displaced than did larger subadults in coral patch reefs (Coral Gardens). The relationship between initial dispersal angle and the angle of day 1 movement for these small juveniles was nearly a perfect −1 slope of exact opposite directions whereas subadult lobsters showed a much lower accuracy of return movement on day 1. This may be due to the heterogeneous nature of the Coral Gardens coral heads, preventing direct line-of-sight return vectors due to physical obstructions. Alternatively, larger lobsters may be at less risk from predation or may have higher frequency of suitable alternative shelters (Childress and Jury, 2006). Previous research studying the patterns of den use by juvenile

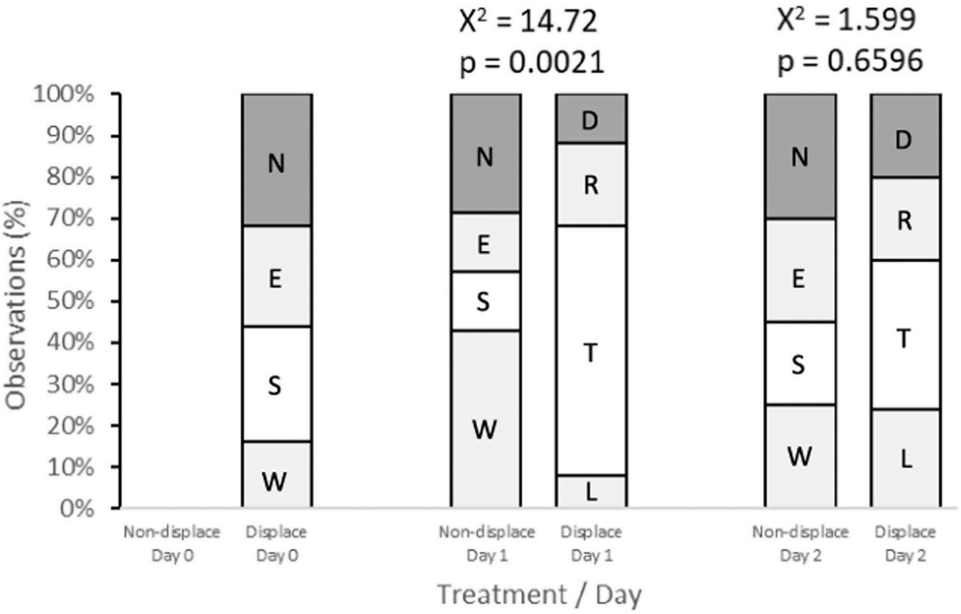

Fig. 7. Stacked bar graphs depicting the proportion of angles displaced (Day 0) and lobster movements (Days 1 and 2)in sectors of 90° each. Day 0 is the day of experimental manipulation, including capture, tag, and release. This shows that displacement angles of were in all four sectors in roughly equal numbers. The graph represents the percent of observed angles in each sector as defined in the Figs. 5–6 captions. N = north, E = east, S = south, W = west, D = displacement sector, T = target sector toward point of capture, L and R = left and right sectors neither toward or away from the point of capture. Displaced and non-displaced lobsters on day 1 differed significantly as displaced lobsters showed highly oriented movements back toward their point of capture (T sector). By day 2, both displaced and non-displaced lobsters showed random orientation angles and were not significantly different in their distributions.

Table 1
Movement distances for lobsters on day 1 and day 2 after tagging and displacement at two locations.

Location	Treatment	Day 1 distance (m)	Day 2 distance (m)	Day 1 student t-test			Day 2 student t-test		
		Mean +/- SEM	Mean +/- SEM	df	t	p	df	t	p
Matecumbe	Non-displaced	33.3 +/- 5.4	24.4 +/- 6.7	20	0.620	0.271	20	0.442	0.331
	Displaced	37.0 +/- 5.0	28.7 +/- 6.8						
Coral Gard	Non-displaced	59.5 +/- 14.4	56.5 +/- 16.1	20	0.685	0.250	20	0.701	0.245
	Displaced	74.4 +/- 16.3	74.4 +/- 19.7						

spiny lobsters indicate that only one third of tagged early benthic juveniles (25–45 mm CL) remain in the same shelter from one day to the next. Another third tends to move to an adjacent shelter, while the final third are not found in the area (Childress and Herrnkind, 1997). When there is a sudden and unexpected loss of shelters, it is the larger juveniles (> 40 mm CL) that choose to leave the crowded shelters and elevate movement levels presumably to disperse from the area (Heldt et al., 2015). Thus, it is possible that the innate homing ability of *P. argus* wanes through ontogeny to facilitate the necessary long-distance movements required to alternately reach spawning and larval release habitats (Bertelsen, 2013).

Our incidental observations of long-distance movements (see Appendix A) by lobsters larger than 74 mm CL suggests there may be some other cue that shifts large lobsters from local nomadism to emigration. One of our acoustic tagged lobsters traveled over 7.4 km in five days until its migration was halted by entering a lobster trap. We have known about these long-distance lobster movements in the Keys since the pioneering mark-recapture fisheries studies of Davis and Dodrill (1989). Juvenile lobsters tagged in Florida Bay were recaptured all along the Florida Keys having travelled 1–100 km. Unfortunately, our study can't unravel the mystery when and why lobsters shift from local nomadism to directional dispersion mode. More work is needed in this area.

While tracking lobsters with acoustic telemetry does give us a much more refined look at patterns of movement and even microhabitat associations, it cannot help us to identify the proximate cues an individual is sensing while moving through the environment. We know that spiny lobsters can detect the odor cues of conspecifics (Zimmer-Faust and Spanier, 1987) which can influence both the time it takes to find shelter (Childress and Herrnkind, 2001) and the actual decision to choose one shelter over another (Nevitt et al., 2000). However, in this study we were unable to evaluate how these cues may have influenced the homing behavior of tagged lobsters. It is very likely that lobsters only home to the general vicinity of their original shelter or until they reached a local area where they are familiar with crevice shelters. Mesocosm studies suggest that lobsters can use odor cues to reduce the time required to find a shelter (Childress and Herrnkind, 2001), but that lobsters rarely remain in the exact same shelter over many days when multiple shelters are available in close proximity (Heldt et al., 2015).

Various organisms possess the ability to utilize earth's magnetic field for directional information, including migratory birds (Able and Able, 1995), molluscs (Cain, 2005), sea turtles (Cain, 2005; Lohmann et al., 2008), salmon (Lohmann et al., 2008) and Caribbean spiny lobsters (Lohmann et al., 1995; Boles and Lohmann, 2003). Some of these species formulate "magnetic maps" that allow them to use magnetic topography to determine position relative to specific goals (Cain, 2005; Lohmann and Lohmann, 2019). There is growing evidence to suggest that Caribbean spiny lobsters possess this ability. A study by Dave Ernst demonstrated that orientation in lobsters is disrupted when pulsed in a strong

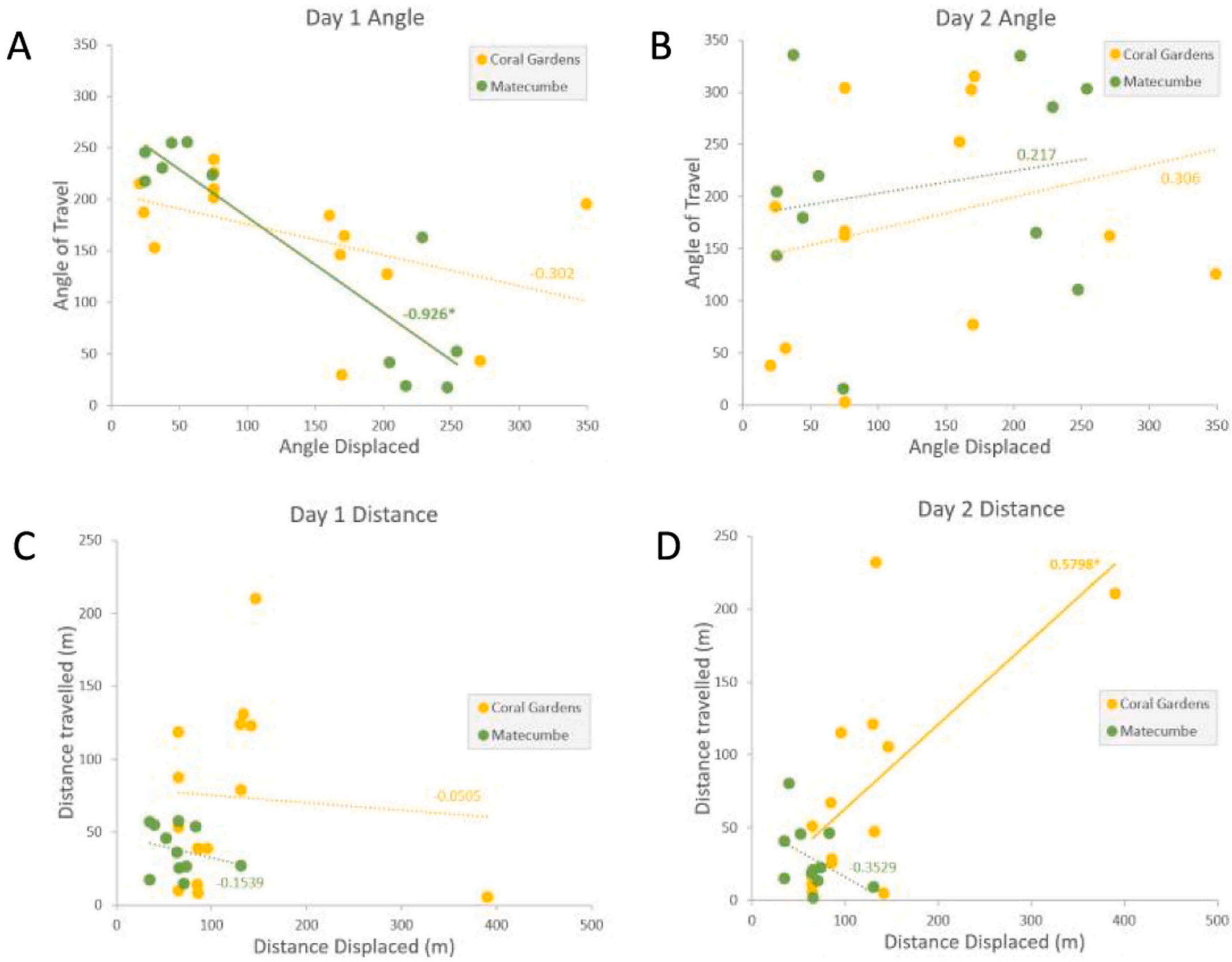

Fig. 8. Scatterplots depicting relationships between (A) angle of displacement and angle of travel on Day 1, (B) angle of displacement and angle of travel on Day 2, (C) distance of displacement and distance of travel on Day 1, and (D) distance of displacement and distance of travel on Day 2, in the displaced experimental group. The data is separated between the two study locations. Trendlines are included for reference, with slopes included adjacent and significant relationships indicated with solid trendlines, bold numbers, and asterisks. Note the distance axes on Figs. 8C and 8D are not exactly the same scale for ease of viewing the data.

electromagnet (Ernst and Lohmann, 2016) and that lobsters avoided sheltering under strong magnetic anomalies (Ernst and Lohmann, 2018). We directly observed that four adult lobsters pulsed with a strong electromagnet and fitted with acoustic tags immediately emigrated from our Coral Gardens array while the four control lobsters handed identically by not pulsed by the magnet remained on site for more than week (Ernst, Bertelsen, Childress personal observation).

While we may never know the exact mechanism underlying spiny lobster homing ability, the evidence is strong that this lobster does indeed possess this ability which emerges very early in their ontogeny, reduces the time to find shelter, facilitates the transition between local habitat patches, and eventually leads to long distance reproductive migrations. This confirms what Professor William F. Herrnkind summarized about the behavior of the Caribbean spiny lobster in 1980 is still very true today:

> "The general picture that emerged from these observations shows adult *P. argus* to be selective of their feeding and home sites regions, gregarious in their residential habitat, selective of – and for long periods, attached to – certain crevices, temporally organized, and spatially oriented in their movements to and from their dens."

CRediT authorship contribution statement

Michael J Childress: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Rodney D Bertelsen:** Writing – review & editing, Visualization, Validation, Software, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Coral Holt:** Writing – original draft, Visualization, Validation, Software, Investigation, Funding acquisition, Formal analysis.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Michael Childress reports financial support was provided by Clemson University. Rodney Bertelsen reports financial support was provided by Florida Marine Research Institute. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

Data Availability

Data will be made available on request.

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Supplemental materials

In the summer of 2020, three tagged lobsters released at Coral Gardens left the study area and were subsequently caught by recreational or commercial fishers (Figure S1). We learned about these recaptures when the fishers contacted the Florida Marine Research Institute. Lobster 38240 (pink), a 37.4 mm female was captured in a lobster trap 30 days after being released (Figure S1 A). The movement vector was 0.43 km at a heading of 223 degrees. Lobster 16901 (blue), a 78.9 mm male was captured by hand net under the Channel Two bridge 5 days after being released (Figure S1 B). The movement vector was 2.24 km at a heading of 291 degrees. Lobster 16898 (green), a 89.4 mm male was captured in a lobster trap 5 days after being released (Figure S1 C). The movement vector was 7.42 km at a heading of 225 degrees.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2024.107132.

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