

# *In situ* swimming and orientation behavior of spiny lobster (*Panulirus argus*) postlarvae

Andrew S. Kough\*, Claire B. Paris, Erica Staatterman

Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida 33149, USA

**ABSTRACT:** Larval dispersal is common in benthic marine organisms, but the environmental cues guiding the final larval stages to settlement habitat remain largely unknown. Caribbean spiny lobster *Panulirus argus* spend 5 to 12 mo at sea as pelagic phyllosome larvae before transitioning into rapidly swimming and non-feeding puerulus postlarvae. Spiny lobster postlarvae are specialized to seek settlement habitat, making them an ideal model for studying orientation behavior during the transition to benthic environments. We observed the swimming orientation of *P. argus* in the open ocean during all hours of the day and across tidal phases using a circular behavioral arena deployed at sea. Contrary to laboratory observations of only nocturnal activity, swimming and orientation occurred during both the day and the night in open waters ca. 6 to 8 km offshore in the Florida Straits. Individual postlarvae swam directionally with similar accuracy in all hours. The mean orientation direction was significantly different with tidal phase. Postlarvae oriented to the southeast (163.5°) during flood tide, and to the southwest during ebb flow (225.1°), placing them on a shoreward trajectory. Postlarval behavior was circatidal, and during ebb tide, innate swimming behavior beneficial to finding settlement habitat was triggered. Postlarvae also oriented relative to the wind, potentially using the sea breeze to orient towards the coast. A change in behavior tied to ubiquitous coastal signals is a strategy likely used by other pelagic larvae searching for a benthic home.

**KEY WORDS:** Spiny lobster · Orientation · Postlarva · Nocturnal · Tidal · Dispersal · Settlement

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## INTRODUCTION

How, why, when, and where animals move is the focus of the emerging field of movement ecology (Nathan et al. 2008), which also examines how the internal state of the animal and external environmental conditions drive movement. The ocean is underrepresented in studies of movement (Holyoak et al. 2008), perhaps because dispersal within the marine realm is different than most terrestrial systems. Rather than dispersing as adults, many marine organisms have a bipartite lifecycle, where adults are sessile or sedentary, but spawn massive numbers of planktonic larvae that disperse in the sea. Dispersing larvae connect populations of species that live in patches of benthic habitat separated by vast expanses of ocean. Larval behavior can in-

crease the odds of finding discrete settlement habitats, and may mitigate mortality caused by passive advection from ocean currents that move larvae away from desired habitat (Paris et al. 2005, Cowen et al. 2006, Butler et al. 2011). Successful dispersal within an interconnected metapopulation is crucial for species with an 'open' connectivity pattern (Myrberg & Fuiman 2002), yet the behaviors governing how larvae disperse are under-described (Kingsford et al. 2002).

The postlarval stage of the Caribbean spiny lobster *Panulirus argus* is ideal for studying behavior and coastal orientation. The final pelagic stage of the spiny lobster is the puerulus postlarva (hereinafter called postlarva), which is a strikingly different postlarval stage, both morphologically and behaviorally, from earlier phyllosomes. Spiny lobster postlarvae

\*Corresponding author: andrew.kough@gmail.com

do not feed (Lemmens 1994, Jeffs et al. 1999), yet may swim tens to perhaps a hundred kilometers over several weeks to find settlement habitat (Rimmer & Phillips 1979, Jeffs & Holland 2000, Phillips & Melville-Smith 2005, Goldstein et al. 2008, Fitzgibbon et al. 2014). This journey starts near the shelf break, where postlarvae likely metamorphose from phyllosomes (McWilliam & Phillips 2007, Phillips & McWilliam 2009), and ends at a variety of shallow settlement habitats (Butler et al. 2006). In the laboratory, spiny lobster larvae and postlarvae respond to a diverse array of environmental cues, including light (Lecchini et al. 2010, Ziegler et al. 2010), chemical odors (Butler & Herrnkind 1991, Goldstein & Butler 2009), pressure (Goldstein & Butler 2009), and salinity (Field & Butler 1994, Acosta et al. 1997, Goldstein & Butler 2009). Spiny lobsters also support a valuable commercial and recreational fishery in tropical and subtropical oceans around the world (Cruz & Bertelsen 2008, Ehrhardt et al. 2011), giving further significance to research into the behavioral drivers of their recruitment and transition from the pelagic environment.

Linking directional cues with larval orientation behavior *in situ* is logistically challenging, so researchers have relied on studies of larval choice using behavioral chambers or traps in the ocean (Stobutzki & Bellwood 1998, Tolimieri et al. 2000, Radford et al. 2007) and the laboratory (Boudreau et al. 1993, Atema et al. 2002, Goldstein & Butler 2009, Lecchini et al. 2010). However, the binary response in a choice chamber does not demonstrate how larvae use proximate cues to alter their path and does not provide detailed information on individual movements. *In situ* observations made from small boats (Phillips & Olsen 1975, Calinski & Lyons 1983, Cobb et al. 1989) or by SCUBA diving or snorkeling (Shanks 1995, Leis & Carson-Ewart 1998) provide snapshots of larval swimming behavior. Inconspicuous nocturnal studies of behavior are rare (Stobutzki & Bellwood 1998, Fisher & Bellwood 2003), owing to the difficulty of observing the movements of small, often translucent, larvae in an unobtrusive manner in the dark. However, the simultaneous examination of both environmental signals and the larval responses to these signals is now possible using emerging technologies such as the Drifting *In Situ* Chamber (DISC; Paris et al. 2008). The DISC observes and quantifies larval behavior in the open ocean while minimizing any 'observer bias' (Irisson et al. 2009). Observing the behavior of animals *in situ* as they navigate is the next necessary step to describe how they search for appropriate settlement habitat.

The goal of the present study was to determine the directionality of spiny lobster postlarval swimming by observing *in situ* orientation within a DISC deployed off the coast. Crucial to this goal was the development of a new module for the DISC that enabled the first *in situ* nocturnal study of proximate postlarval behavior (see Fig. 1). We focused on behavior across time of the day and tidal phases to determine if postlarvae use these predictable signals to orient towards coastal habitats. We hypothesized that spiny lobster postlarvae would swim only during the night, and that spiny lobster postlarvae would orient shoreward.

## MATERIALS AND METHODS

### The Drifting *In Situ* Chamber

The Drifting *In Situ* Chamber (DISC) is a novel Lagrangian research platform for observing and quantifying the orientation behavior of marine larvae in the open ocean (Paris et al. 2008, 2013; our Fig. 1). The DISC is a cylindrical behavioral framework (1.2 m height × 0.4 m diameter) made of clear acrylic that is transparent to fine-scale turbulence, light, and sound. The DISC is attached to a surface float using low-drag kite line. A clear monofilament bridle centers the line above the DISC. A subsurface buoy attached 1 m beneath the surface acts as a shock absorber and dampens the effect of waves. The DISC can be coupled with environmental sensors to allow simultaneous observation of larvae in conjunction with proximate (sound, temperature, light, wind) and distant (celestial, magnetic) cues in a natural setting. In the present study, a light and temperature pendant (HOBO model UA-002-64) was attached to the DISC, and real-time wind data was obtained from a nearby weather station (FWYF1). The temperature pendant was accurate within 0.53°C, and measured relative light levels, which was appropriate for detecting differences between trials. The DISC was set adrift at sea with an individual postlarva, and postlarval movement was recorded using an imaging system.

Nocturnal observations with the DISC were possible because we rigged the arena with underwater flashlights and a GoPro Hero camera with the infrared (IR) filter removed (Fig. 1). Each flashlight bulb was replaced with a 315 mW LED with a peak wavelength of 850 nm, making the flashlights IR. Four lights were mounted on top of the DISC to illuminate the postlarva, and one pointed up to illuminate a compass.

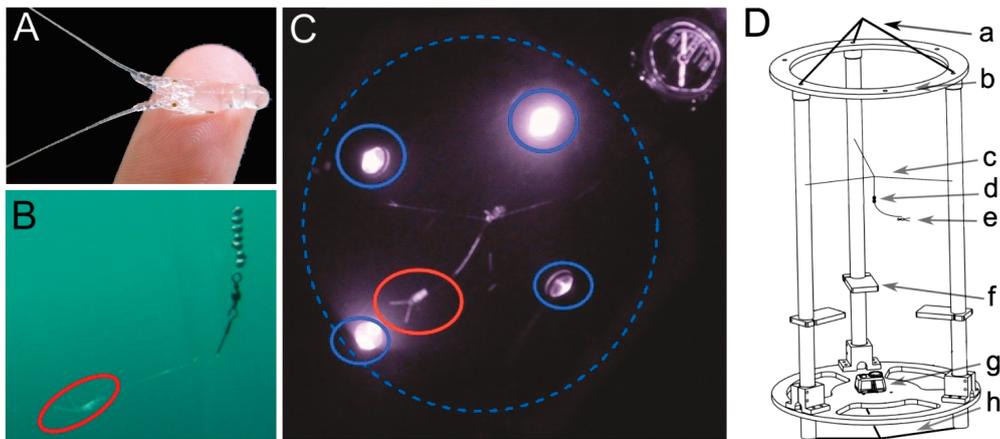


Fig. 1. Tethering *Panulirus argus* postlarvae. (A) A postlarva on a human finger for scale. (B) A tethered postlarva (circled in red) swims forward by beating its pleopods and holding its antennae out in front of it. (C) Sample image from the camera looking up at a tethered postlarva (circled in red) illuminated by the removable infrared lighting rig (lights circled in blue, framework traced with blue dashed circle) during the night. (D) The Drifting *In Situ* Chamber (DISC) is engineered from clear acrylic using an orientation with a 'no frame of reference' design: (a) attachment to surface line; (b) top frame; (c) monofilament between posts; (d) weighted clip at focal point of camera; (e) tethered postlarva; (f) compass; (g) camera and HOBO pendant on bottom frame; (h) clip that attaches to drogue

Data were processed using DISCUS software, which digitizes the location of the postlarva throughout each deployment using the camera images (Irisson et al. 2009). The suite of instruments on the DISC (camera, HOBO temperature and light meter, GPS, electronic tri-axial compass) was synchronized in time for further analysis. The deployment time protocol from earlier studies with the DISC was followed (Irisson et al. 2009, Paris et al. 2013); the first 5 min of each 15 min deployment were treated as acclimation time and were not analyzed.

#### Study site, environmental conditions, and target species

We deployed the DISC in water between 40 and 160 m deep starting ca. 1 km southeast of Fowey Rocks (25.591° N, 80.097° W), which is the northernmost extent of the Florida Keys Reef Tract (Fig. 2). Deployments of the DISC were designed to sample across both the diel cycle and across tides (see Fig. 3). The timing of tides for Fowey Rocks was predicted using the *t\_tide* package for MATLAB and *xtide* harmonics (Pawlowicz et al. 2002). Wind data were available from the NOAA Fowey Rocks Stn FWYF1, at a frequency of once every 10 min (NOAA, National Data Buoy Center, Stennis Space Center, MS, USA).

Spiny lobster postlarval availability varies monthly; lobsters only arrive during certain months of the year in sufficient quantities for our experimental studies (Acosta et al. 1997, Acosta & Butler 1999). The timing

of their arrival, during nocturnal flood tides in the first quarter moon, posed a tradeoff in our sampling. We elected to test animals as soon as possible after collection to minimize any physiological or behavioral changes from confinement. However, this reduced our sample size during nocturnal ebb tide and daytime flood tide conditions due to logistical and temporal constraints.

We collected plankton from Bear Cut, the largest natural tidal inlet into Biscayne Bay, with tidally driven currents in excess of  $100 \text{ cm s}^{-1}$  during flood tide (Fiechter et al. 2006), which are used by incoming postlarvae to travel into the bay (Forward & Tankersley 2001). Spiny lobster postlarvae were caught during nocturnal rising tides using 1 m diameter, 750  $\mu\text{m}$  mesh size, channel nets during the first quarter moons of September 2012, October 2012, and February 2013. Animals were held in static, natural seawater-filled buckets in the laboratory at 16 to 19°C and received a complete water change daily. All animals were used within 72 h of collection from the plankton. Some individuals were held after testing to observe the timing of pigmentation on the edge of the carapace, which did not develop for at least 6 d post-capture ( $n = 14$ ), similar to previous works (Goldstein et al. 2008, Goldstein & Butler 2009).

Postlarval lobsters were attached to tethers before being tested in the DISC. The tether was a 12 cm piece of 1 kg test fly-fishing tippet with a loop tied at one end. To attach the tether, a postlarva was removed from the water and its dorsal carapace was lightly dried with a paper towel. Using a fine point

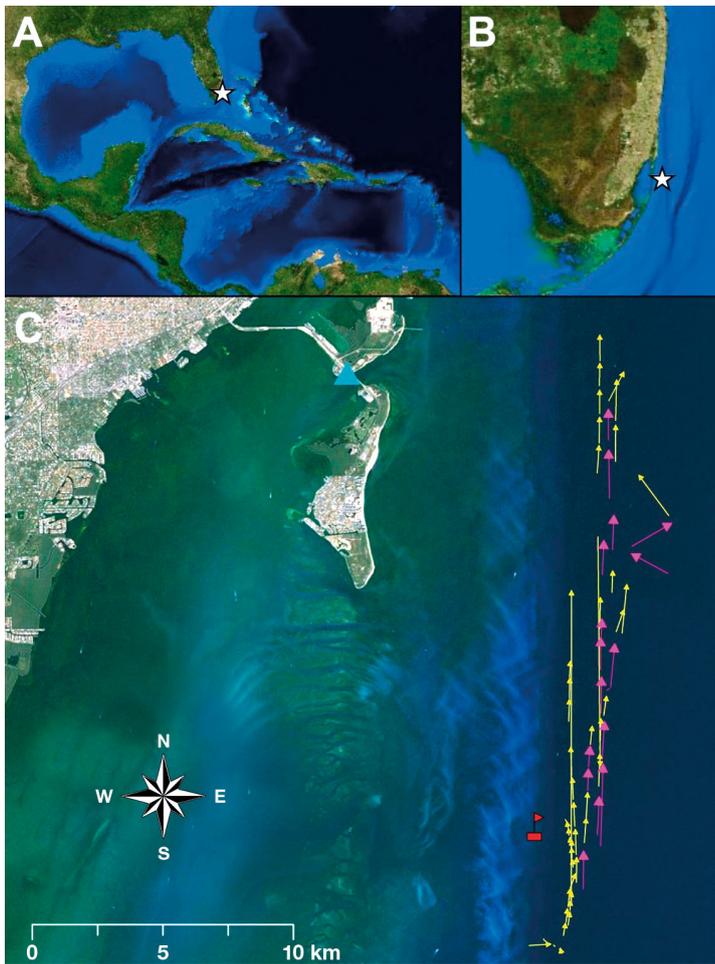


Fig. 2. Study area (white star) for the Drifting *In Situ* Chamber (DISC) deployments in the Caribbean Sea (A), off the coast of Florida (B). (C) Paths of deployments at 25 m ( $n = 18$ ) from the surface are shown in purple, and 3 m ( $n = 55$ ) from the surface in yellow. Fowey Rocks is shown by the red icon, and the location where *Panulirus argus* postlarvae were collected from plankton by the cyan triangle

applicator, a drop of superglue was placed on the center of the dorsal carapace and the tether was attached. The glue was allowed to dry ( $<1$  min), and each postlarva was returned to an individual container of new seawater to prevent tangling. No mortality or noticeable damage was associated with any tethering operations ( $n = 104$ ), and tethered animals retained after use metamorphosed into juveniles without mortality ( $n = 14$ ). After the completion of a trial, the tether was gently removed and the animal was released.

Experiments were carried out in seas forecast to be  $<1.5$  m and wind  $<15$  knots during September 2012, October 2012, and February 2013. During each DISC deployment, a tethered postlarva was attached to a weighted line in the center of the DISC structure at a focal point 42 cm from a GoPro camera (Fig. 1D). The

tether is the only restraint on the postlarva that prevents it from swimming off into the ocean. Attaching the postlarva to a weighted line suspended in the middle of the DISC framework allowed the animal a full range of movement on its tether without being able to physically touch any portion of the DISC. Additionally, the only potentially detectable lateral structures that could influence the physical environment experienced by the postlarvae were the clear acrylic posts of the instrument. We deployed the DISC at 2 distances from the surface: shallow (3 m) and deep (25 m). During September and October 2012, we deployed at 3 m from the surface, and each individual postlarva was used only once. Based on wave theory (Dean & Dalrymple 1991), it is approximated that the influence of the dynamic pressure is  $<1\%$  of the surface wave height at 25 m depth with a wave period of 4 s. Recent work has suggested that Stokes drift decays even more rapidly, and is negligible at a depth on the order of the mean significant wave height (Tamura et al. 2012). Thus we added a second experimental depth of 25 m in February 2013 to deploy the DISC at a depth conservatively beneath most of the orbital wave motion. The same postlarvae were used in both depth treatments in February 2013, with a randomized order between shallow and deep treatments. For all deployments, once the DISC was in the water, the boat was driven upwind and the engine was turned off. Deployments lasted 15 min before the DISC was retrieved.

### Movement analysis

The position of the postlarva relative to the camera and the bearing of the compass relative to the camera were used to create a series of positions for individual larva relative to cardinal directions with a resolution of 1 position every 2 s. The postlarvae alternated between swimming forward to the extent allowed by the tether, and a cessation in swimming causing momentary drifting. Postlarvae actively modified their orientation by swimming, and did so throughout the deployments. If a postlarva was clearly not swimming (the tether was not taut, or the postlarva's antennae were not forward) or not visible in an image, that position was omitted. The DISC rotated slowly throughout each deployment, and custom

software corrected for this rotation (Irisson et al. 2009). The resulting positions were used to describe the mean bearing of each postlarva. A Rayleigh's test was used to test significant directionality (i.e. whether the postlarva was keeping a significant bearing).

Circular statistics were carried out at the individual (first order) and population level (second order). Because each set of postlarval positions (projected as a vector from the center of the behavioral chamber) was unequal in size, due to unique gaps corresponding with occasional picture frames of unclear position or non-swimming behavior, we retained and reported only the mean bearings of significantly directional individuals for use in second-order circular statistics. All movement statistics were performed using the package Circular (Lund & Agostinelli 2011) in R software. Accuracy (the length of the mean vector, Rayleigh's  $r$ ) comparisons were assessed using a Welch's 2-sample  $t$ -test in MATLAB. DISC rotation, temperature, wind speed, current speed, and light intensity during trials were compared using Welch's 2-sample  $t$ -tests in MATLAB to justify pooling data between months and seasons.

## RESULTS

### Accuracy

The accuracy (i.e. the length of the mean vector, Rayleigh's  $r$ ) of postlarval movement represents the strength, or directionality, of individual postlarval swimming. The accuracy was similar across multiple environmental measures, including hour of day, tidal phase, water temperature, wind speed, current speed, and light intensity (Fig. 3). The mean accuracy was not significantly different between ebb and flood tide during shallow (Welch's 2-sample  $t$ -test:  $N1 = 22$ ,  $N2 = 33$ ,  $p = 0.1291$ ) or deep deployments (Welch's 2-sample  $t$ -test:  $N1 = 7$ ,  $N2 = 11$ ,  $p = 0.1291$ ).

### Swimming direction, shallow treatment

Postlarvae swam in a significantly directed manner ( $n = 55$ ; Fig. 4) during deployments 3 m from the surface. During ebb flow, the mean population direction of postlarvae was towards the southwest

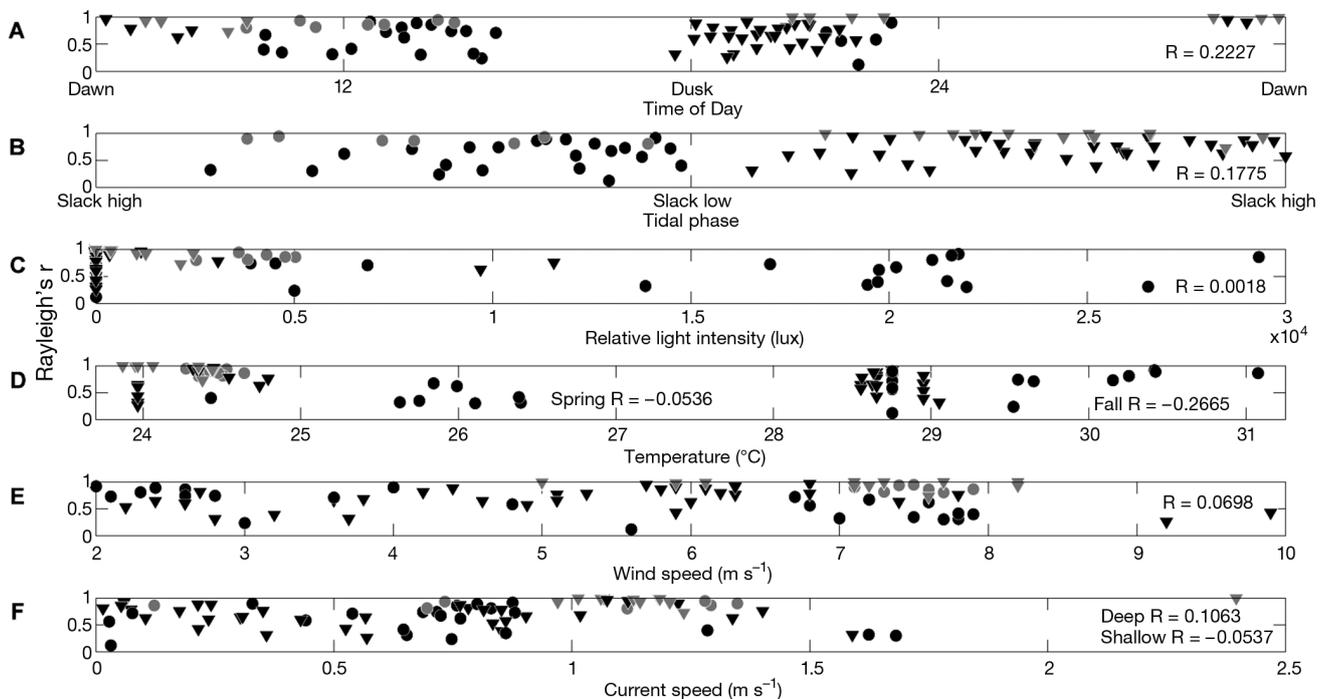


Fig. 3. Accuracy of *Panulirus argus* postlarval swimming direction changing with the environment: (A) time of day, (B) tidal phase, (C) relative light intensity, (D) temperature, (E) wind speed, and (F) current speed, tested in the Drifting *In Situ* Chamber (DISC) at 3 m (black) or 25 m (grey) from the surface. Rayleigh's  $r$  (y-axis) of the mean postlarval swimming direction indicates the strength of the directionality; higher  $r$  values indicate more accuracy. Instances of ebb tide are circles and instances of flood tide are triangles. Spearman's  $R$  was used to test for any correlations across sampled conditions, and no correlation was significant (all  $p > 0.05$ ). Correlations were separated by season in (D) (temperature changed with season), and by depth in (F) (currents were faster deeper)

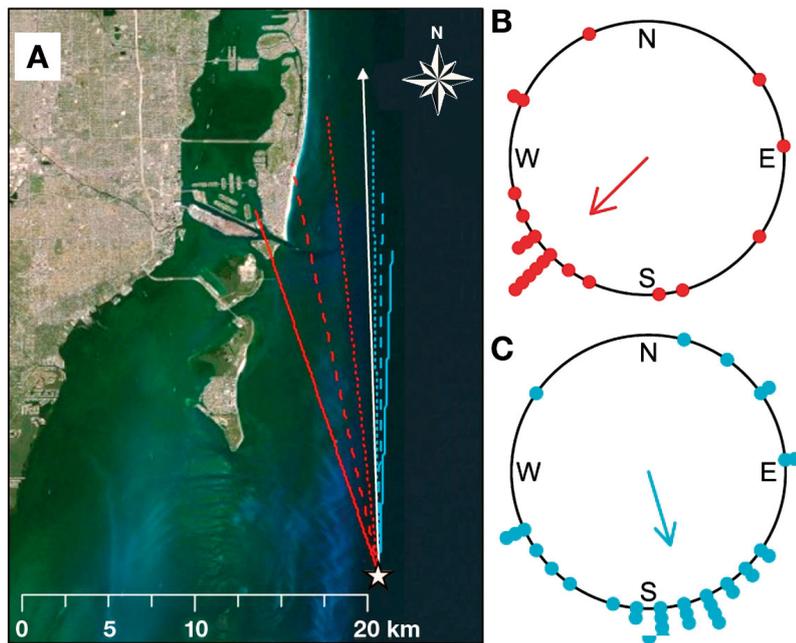


Fig. 4. Consequences of *Panulirus argus* postlarval swimming. (A) 6.5 h (a tidal cycle) of modeled swimming in the mean observed currents (358°N, at a speed of  $0.82 \text{ m s}^{-1}$ ), starting from the mean center of Drifting *In Situ* Chamber (DISC) deployments (white star) at 3 m from the surface. Swimming trajectories were calculated through vector addition of the swimming of the postlarva and the mean observed current speed and direction. The swimming direction is the mean observed in either (B) ebb (red arrow, Rayleigh's  $r = 0.598$ ) or (C) flood tide (cyan arrow, Rayleigh's  $r = 0.560$ ). Each dot corresponds with an individual postlarva's swimming direction. Modeled transport paths in (A) are based on 3 swimming speeds for each tidal direction: 10, 20, and  $30 \text{ cm s}^{-1}$  (dotted, dashed, and solid respectively). Drift without swimming behavior is shown by the white line. If postlarvae continued the swimming behavior observed in the DISC trials, animals orienting with the ebb tide could reach shore

(225.1°) and thus toward coastal environments, whereas during flood tides the mean population direction was towards the southeast (163.5°) and thus toward the open ocean (Table 1, Fig. 4). The mean directions of postlarvae were normally distributed (Watson's test for the von Mises distribution:  $U^2 = 0.0625$ ,  $n = 55$ ,  $\alpha = 0.05$ ,  $U_{\text{crit}} = 0.079$ ), and met the assumptions for parametric statistics. Population orientation was in significantly different directions depending on tidal phase (Watson-Williams test:  $F = 13.0506$ ,  $N_1 = 22$ ,  $N_2 = 33$ ,  $p = 0.000674$ ).

#### Swimming direction, deep treatment

We consider the deep treatment results separately from the shallow results, as a supplement to the main experiment. We observed 18 directional postlarvae in the deep treatment (Table 1, Fig. 5). The direction of postlarval orientation differed with tidal phase (Watson 2-sample test:  $U^2 = 0.2301$ ,  $N_1 = 7$ ,  $N_2 = 11$ ,  $\alpha = 0.05$ ,  $U_{\text{crit}} = 0.187$ ). The mean population direction was heuristically similar to the shallow treatments during ebb tide, but postlarvae did not orient directionally during flood tide. The accuracy of the postlarval swimming direction in the deep treatments did not change with hours of the day, tidal phase, wind speed, current speed, temperature, or relative light (Fig. 3).

#### Swimming direction and current

Postlarvae partially oriented into the prevailing flow during both ebb and flood tide, so we also considered their bearing with respect to the direction of the current (Table 1, Fig. 5A,B,E,F). Swimming directions with respect to current are given in degrees clockwise from the direction that the DISC (a Lagrangian drifter) traveled. The mean directions of postlarvae with respect to drift during shallow deployments swimming were normally distributed (Watson's test for the von Mises distribution:  $U^2 = 0.028$ ,  $n = 55$ ,  $\alpha = 0.05$ ,  $U_{\text{crit}} = 0.079$ ) and significantly different depending on tide (Watson-Williams test:  $F = 16.755$ ,  $N_1 = 22$ ,  $N_2 = 33$ ,  $p = 0.000146$ ). Deep deployments were similar to shallow deployments during ebb tide with respect to the current (Fig. 5A,B), but the animals maintained no significant direction during deep deployments during flood tide (Fig. 5F).

#### Swimming direction and wind

We considered the bearing of swimming postlarvae with respect to concurrent wind direction because the wind is a major force shaping the dynamics of the upper ocean, and detailed empirical data on the wind was available in proximity to our study site. Swimming directions with respect to wind are given in degrees clockwise of the direction from which the

Table 1. Population mean directional data during Drifting *In Situ* Chamber (DISC) deployments of *Panulirus argus* postlarvae. The track of the DISC (a Lagrangian drifter) gave the current direction and the NOAA weather Stn FWYF1 gave wind direction. Postlarval swimming directions are the population means during DISC deployments of different tides and depths. Postlarval swimming directions relative to wind and current are in degrees clockwise of the environmental variable, rather than in a cardinal reference frame. Statistically significant (at  $\alpha = 0.05$ ) population directions are **bold**

Variable	Depth (m)	Tide	n	Rayleigh's r	p	Direction
Current direction	3	Ebb	22	0.9531	<0.0001	<b>355.8°N</b>
	3	Flood	33	0.8866	<0.0001	<b>358.2°N</b>
	25	Ebb	7	0.9975	<0.0001	<b>6.5°N</b>
	25	Flood	11	0.9997	<0.0001	<b>1.7°N</b>
Postlarval swimming direction	3	Ebb	22	0.5983	<0.0001	<b>225.1°SW</b>
	3	Flood	33	0.5596	<0.0001	<b>163.5°SSE</b>
	25	Ebb	7	0.9743	<0.0001	<b>214.4°SW</b>
	25	Flood	11	0.3454	0.053	166.1°SSE
Direction facing wind	3	Ebb	22	0.7502	<0.0001	<b>105.6°E</b>
	3	Flood	33	0.5917	<0.0001	<b>121.9°SE</b>
	25	Ebb	7	0.9969	<0.0001	<b>160.1°SSE</b>
	25	Flood	11	0.3070	0.0761	134.9°SE
Swimming direction relative to current	3	Ebb	22	0.5781	<0.0001	<b>226.4°</b>
	3	Flood	33	0.5353	<0.0001	<b>154.2°</b>
	25	Ebb	7	0.9662	<0.0001	<b>207.9°</b>
	25	Flood	11	0.3439	0.0538	166.5°
Swimming direction relative to wind	3	Ebb	22	0.4352	0.0017	<b>126.1°</b>
	3	Flood	33	0.4326	0.0002	<b>10.3°</b>
	25	Ebb	7	0.9689	<0.0001	<b>54.2°</b>
	25	Flood	11	0.8494	<0.0001	<b>19.9°</b>

wind blew (Table 1, Fig. 5C,D,G,H). The orientation directions of postlarvae with respect to wind during shallow deployments were not normally distributed (Watson's test for the von Mises distribution:  $U^2 = 0.1287$ ,  $n = 55$ ,  $\alpha = 0.05$ ,  $U_{crit} = 0.066$ ), and were significantly different depending on tide (Watson 2-sample test:  $U^2 = 0.3512$ ,  $N_1 = 22$ ,  $N_2 = 33$ ,  $\alpha = 0.05$ ,  $U_{crit} = 0.187$ ). Deep swimming direction with respect to wind was not normally distributed and was not significantly different depending on tide (Watson 2-sample test:  $U^2 = 0.1031$ ,  $N_1 = 7$ ,  $N_2 = 11$ ,  $\alpha = 0.05$ ,  $U_{crit} = 0.187$ ). The only time that postlarvae oriented with the wind was during shallow ebb tide deployments (Fig. 5C); during all other times they oriented upwind.

### Environmental conditions

Having a similar physical environment between tides lets us attribute the changes in orientation direction to circatidal behavior. The DISC was used as a Lagrangian drifter to assess the true current direction and speed. We did not anticipate a change in current direction associated with tide because the tidal current at Fowey Rocks is categorized as weak and variable, indicating a current of <0.25 knots (J. Kent pers. comm., NOAA, Center of Operational

Oceanographic Products and Services). Confirming this, there was no significant difference between the direction of the current during ebb or flood flow during shallow deployments (Watson 2-sample test:  $U^2 = 0.0513$ ,  $N_1 = 22$ ,  $N_2 = 33$ ,  $\alpha = 0.05$ ,  $U_{crit} = 0.187$ ) or deep deployments (Watson 2-sample test:  $U^2 = 0.1579$ ,  $N_1 = 7$ ,  $N_2 = 11$ ,  $\alpha = 0.05$ ,  $U_{crit} = 0.187$ ). The wind direction was onshore and was significantly different between tides during shallow (Watson 2-sample test:  $U^2 = 0.2959$ ,  $N_1 = 22$ ,  $N_2 = 33$ ,  $\alpha = 0.05$ ,  $U_{crit} = 0.187$ ) but not deep deployments (Watson 2-sample test:  $U^2 = 0.1579$ ,  $N_1 = 7$ ,  $N_2 = 11$ ,  $\alpha = 0.05$ ,  $U_{crit} = 0.187$ ), prompting us to also consider orientation relative to the physical environment (Fig. 5). The wind speed was not significantly different between tides during shallow (Welch's 2-sample  $t$ -test:  $N_1 = 22$ ,  $N_2 = 33$ ,  $p = 0.6619$ ) or deep (Welch's 2-sample  $t$ -test:  $N_1 = 7$ ,  $N_2 = 11$ ,  $p = 0.2496$ ) deployments, nor was the current speed different between tides during shallow (Welch's 2-sample  $t$ -test:  $N_1 = 22$ ,  $N_2 = 33$ ,  $p = 0.3471$ ) or deep deployments (Welch's 2-sample  $t$ -test:  $N_1 = 7$ ,  $N_2 = 11$ ,  $p = 0.1619$ ).

We pooled postlarval swimming data between 2 seasons to robustly compare across tides. Although temperature differed with season (Table 2), because orientation accuracy did not change with water temperature (Fig. 3D), our decision to pool data between

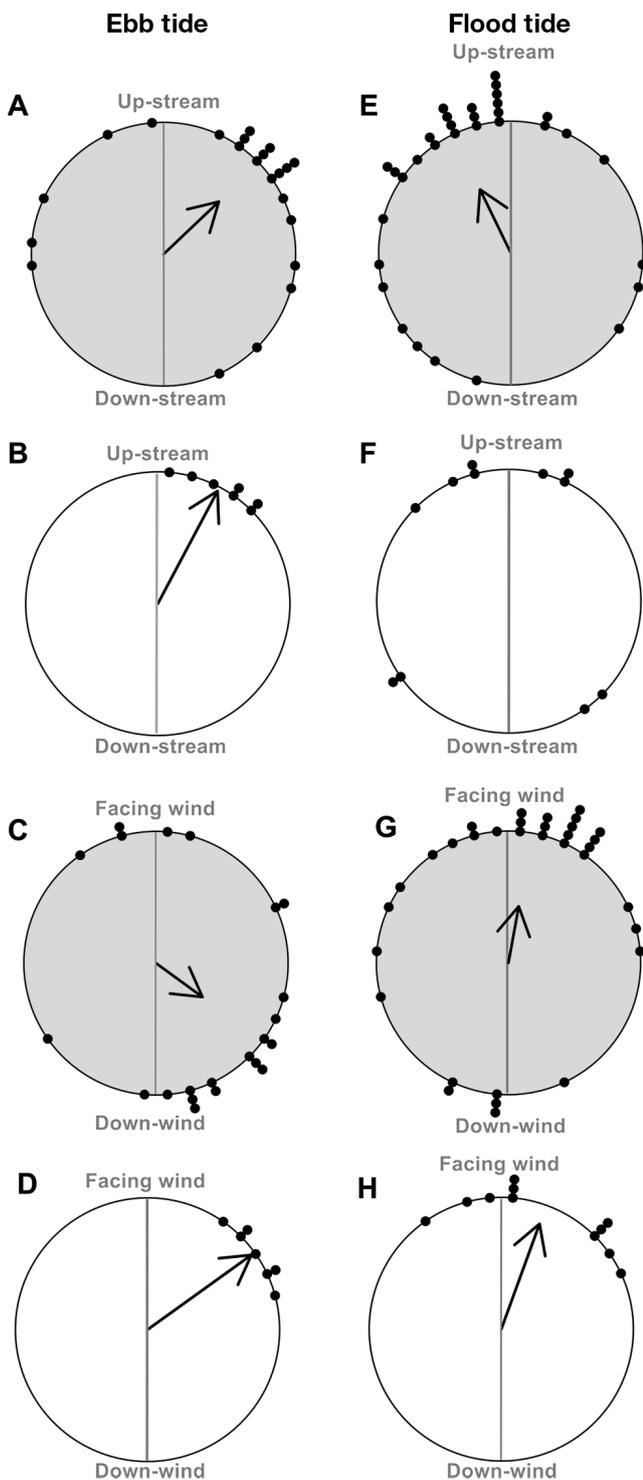


Fig. 5. *Panulirus argus* postlarval *in situ* swimming directions in degrees clockwise facing the current (A,B,E,F) or the wind (C,D,G,H); 3 m (A,C,E,G, shaded gray) or 25 m from the surface (B,D,F,H); and in ebb tide (A–D) or flood tide (E–H). Mean swimming direction of each individual postlarva within the Drifting *In Situ* Chamber (DISC) is indicated by a dot. For significantly directional populations, the length of the arrow indicates Rayleigh's  $r$  value, relative to a maximum of 1

seasons remains appropriate. The relative light level that animals experienced in the DISC during the day was similar (Table 2). The direction from which the wind blew (Watson 2-sample test:  $U^2 = 0.875$ ,  $N1 = 35$ ,  $N2 = 20$ ,  $\alpha = 0.05$ ,  $U_{crit} = 0.187$ ), the wind speed, and the current speed were significantly different between the fall deployments and the spring deployments (Table 2). However, there was no relationship between the current speed and the wind speed (Fig. 6), the current direction remained constant, and the DISC rotated in a similar manner during both seasons, supporting our decision to pool the data. In addition, we compared the orientation of postlarvae relative to the physical environment during each deployment to account for any changes in behavior driven by differences in the season or physical environment (Fig. 5).

## DISCUSSION

Our *in situ* observations of the swimming behavior of spiny lobster postlarvae provide compelling evidence that postlarvae actively orient and swim during both day and night. Previous laboratory work suggested that spiny lobster postlarvae only swam during the night. This difference in swimming behavior between laboratory and field studies demonstrates the enduring merit of *in situ* behavior experiments (Waterman 1988), and is an important piece of information to include in biophysical models of larval lobster transport and settlement (Butler et al. 2011, Kough et al. 2013), since rapid horizontal swimming can alter modeled dispersal patterns (Staaterman et al. 2012). Continuously swimming during the day and the night may reduce the metabolic cost of the larval journey to benthic habitat, and increase available energy stores crucial for surviving the first juvenile molt and successful settlement (Wilkin & Jeffs 2011, Fitzgibbon et al. 2014). In addition, our results show that spiny lobster postlarvae oriented differently and directionally depending on tidal phase, which indicates that pelagic postlarvae adjust their movement towards the coast in response to cues associated with tide. The swimming behavior that we observed during ebb tide would place pelagic postlarvae near the coast and settlement habitat (Fig. 4).

Multimodal cues are associated with tide and could be used by postlarvae. In areas of strong tidal current, such as the channels leading into Biscayne Bay, lobster postlarvae harness flood tide transport at the surface to move further inland (Acosta et al. 1997). However, in our study area, a reaction to the tidal

Table 2. Seasonal differences sampled by the Drifting *In Situ* Chamber (DISC), in fall (September and October 2012;  $n = 35$ ) and spring (February 2013;  $n = 20$ ); means  $\pm$  SD. Temperature and light intensity were sampled with a HOBO probe. Total rotation is the sum of compass movement (path-length of the compass headings) throughout a DISC trial. Maximum displacement is the circular range (minimum arc containing all of the headings) of the compass headings during a DISC trial. Comparisons were made using a Welch's 2-sample *t*-test in MATLAB with  $\alpha = 0.05$ . Significant differences are in **bold**

Variable	Fall	Spring	p
Temperature ( $^{\circ}\text{C}$ )	29.09 $\pm$ 0.65	24.88 $\pm$ 0.91	<b>&lt;0.001</b>
Relative light intensity (lux)	15 810 $\pm$ 9407	15 698 $\pm$ 7880	0.9769
Wind speed ( $\text{m s}^{-1}$ )	4.36 $\pm$ 1.52	6.76 $\pm$ 2.02	<b>&lt;0.001</b>
Current speed ( $\text{m s}^{-1}$ )	0.52 $\pm$ 0.38	0.89 $\pm$ 0.42	<b>&lt;0.01</b>
Total rotation ( $^{\circ}$ )	1011 $\pm$ 319	1114 $\pm$ 167	0.1889
Maximum displacement ( $^{\circ}$ )	140 $\pm$ 92	155 $\pm$ 91	0.5862

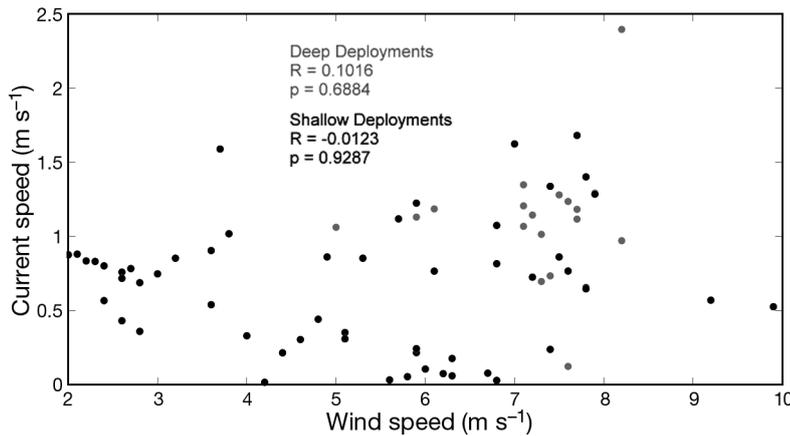


Fig. 6. The Drifting *In Situ* Chamber (DISC) (a Lagrangian drifter) travels independently of the wind. The current speed obtained from the GPS track of the DISC is plotted against the concurrent wind speed obtained from NOAA Stn FWYF1. There is no significant correlation using Spearman's ranked correlations in either deep (gray) or shallow (black) deployments

current is unlikely because the deployments took place in a weak and variable tidal current offshore of the reef tract and at least 8 km from a channel into the bay. In our experiments, the DISC did not drift with respect to tidal phase, but instead drifted with the strong, northward-flowing Gulf Stream (Fig. 2). Additionally, the theory of relativity suggests that tested postlarvae are unable to detect the direction of the current because the DISC is imbedded within the current. Temperature gradients could be established with the tide. Lobster postlarvae arrive into settlement habitat year-round in Florida (Acosta et al. 1997, Yeung et al. 2001), thus swimming behavior towards coastal environments should operate independently of temperature. Supporting this con-

tention, we found no difference in swimming accuracy with temperature (Fig. 3). Salinity gradients may also vary with tide. Spiny lobster postlarvae have been shown to have altered metamorphic responses (Field & Butler 1994) and behavioral aversion (Goldstein & Butler 2009) to extreme salinity changes, but show no significant preference within the moderate gradients (Goldstein & Butler 2009) expected 6 to 8 km offshore. Sound has been suggested as a potential navigational cue for decapod postlarvae (Radford et al. 2007), yet sound from a multi-year study at 2 sites in Florida does not vary with the tide (E. Staaterman unpubl. data). There is an endogenous reaction to the tide. Young (stage I) *Panulirus argus* larvae have a twilight vertical migration pattern mediated by a combination of endogenous rhythm and behavioral response to changing light levels (Ziegler et al. 2010). The periodicity of the endogenous rhythm is imprinted by the hatching location of the larvae, and could be quite different from the local conditions if larvae travel long distances (Briones-Fourzán et al. 2008, Butler et al. 2011, Kough et al. 2013). Additionally, there is no proposed physiological mechanism for how an endogenous cue could become directional, unless the tide acts as a switch, triggering innate behavior (Forward & Tankersley 2001) that requires another cue to act as a compass.

Our results suggest that odor is not followed by spiny lobster postlarvae to find settlement habitat. Previous works suggest that chemical cues may play an important role in postlarval settlement (Butler & Herrnkind 1991, Goldstein & Butler 2009). Additionally, juvenile and adult spiny lobsters can track or avoid chemical signals from food sources (Reidenbach & Koehl 2011), predators (Berger & Butler 2001), and conspecifics, both healthy (Zimmer-Faust et al. 1985, Butler et al. 1999) and diseased (Behringer et al. 2006, Anderson & Behringer 2013), likely by using an infotaxis strategy (Vergassola et al. 2007), since odor is transported more by turbulent advection than by diffusion over scales useful for distant navigation (Atema et al. 2002, Moore & Crimaldi 2004). Such infotaxis is unlikely in our experiments because the DISC was locked into a water parcel, and drifted with

it over the course of a deployment. Thus animals constrained to the DISC are unable to actively map an odor stimulus.

The most plausible response to odor cues in our study is a simple change in swimming behavior with either the presence or absence of an odor. If chemical signals from the tide were responsible for the change in swimming direction, then we would anticipate large variation in the accuracy of the postlarvae over the tide corresponding with changes in the frequency of encountering advectively transported odor. The highest accuracy would be expected when the tidal current is strongest, propelling turbulently advected chemicals offshore, and maximizing encounters with nearshore-flavored eddies. However, we can attribute little variation in accuracy to the time into the tidal phase (Fig. 3B). Still, a chemical cue could trigger another innate behavior beneficial to finding settlement habitat (Paris et al. 2013). Nearshore-specific odors that are advected offshore could activate an internal clock or other instinctive behavior that causes the specific swimming directionality that we observed. We can only speculate on what signal(s) could be resetting or triggering the internal clock, because we collected our experimental animals from a tidal channel, and they were already instilled with circatidal behavior.

Stokes drift, or particle transport due to orbital motion, has been suggested as a mechanism that would enhance onshore transport of spiny lobster postlarvae (Feng et al. 2011). However, the primary evidence suggesting passive hydrodynamic orientation and transport stems from correlations between settlement indices and physical phenomena, and not from observations (Jeffs et al. 2005). It is challenging to relate our findings to Stokes drift, since our vessel was not rigged to collect empirical measurements of the specific wave periodicity, direction, or mean height. However, if the lobster postlarvae were using Stokes drift or orbital motion to ascertain and maintain a bearing, the deeper deployments would have had lower accuracy and no population direction, because wave-related motion rapidly decreases with depth (Tamura et al. 2012). We found that the average accuracy for deep deployments was significantly higher, suggesting that postlarvae are actually better at maintaining a bearing without Stokes drift. We cannot rule out Stokes drift as a compass for orientation, but our deep treatment suggests that other cues are also involved.

We know that animals reliably arrive in Florida Bay using tidal stream transport, but to get far enough onshore to harness the tidal current, using the wind

may be an adaptive strategy. The mean wind during deployments came from the east and southeast, blowing towards shore (Table 1). Our results suggest that while in the top layer of the ocean, where wind-driven currents are at a maximum, lobster postlarvae adjust their bearing relative to the wind and tide. When we consider the bearing of the postlarvae with respect to the wind during deep deployments, there was not a significant difference between tides. However, during the shallow deployments, the bearing of the postlarvae with respect to the wind was significantly different and nearly reversed depending on tidal phase. While within the top 3 m of the ocean during ebb tide, lobster postlarvae oriented with the wind, surfing towards the shore. We do not have a physiological mechanism for how the lobsters could detect the wind, but they are directional with respect to the wind, which suggests that they can detect it.

Our results suggest that the tides act as a proximal cue, possibly via an internal clock mechanism, informing the animal to modify its orientation. Across tidal phases, a southward cardinal orientation would prevent strong advection via the Florida Current, and surfing with the wind would direct postlarvae towards the coast. An analogous situation with respect to the current occurs off Lizard Island in Australia, where populations of reef fish innately swim in a consistent direction during the daytime (Leis & Carson-Ewart 2003). The complex flow patterns in the Caribbean Sea do not contain a single straightforward current system for which a larva such as *P. argus*, with such an extended planktonic stage, could have an adaptive strategy. However, maintaining a bearing could help a postlarva simply keep a course that would increase encounters with settlement habitat. A swimming direction could be maintained by using multimodal cues including celestial, wind, acoustic, or magnetic cues. Our results suggest that the cue that lobster postlarvae use does not change over the course of the day, based on their relatively constant accuracy of swimming direction (Fig. 3). In addition, trials at 25 m depth had similar directional results to shallow deployments at 3 m during ebb tide. This shows that a cue is available further from the surface, which suggests magnetic orientation, as found in adult spiny lobster (Lohmann et al. 1995, Boles & Lohmann 2003). Cue manipulation *in situ* will be necessary to elucidate the nature of the sensory signals. Altering the magnetic field, using speaker playback, or isolating a particular chemical signature from tidal effluent, and then exposing postlarvae in a naturally devoid environment, are approaches possible with the DISC in future experiments.

Observing lobster postlarvae in the open ocean using a novel framework is not without caveats. The use of a tethering system could create unnatural swimming behavior (Peterson & Black 1994), and the depth changes involved with a deployment could trigger barokinesis, as observed in both crustaceans (Tankersley et al. 1995) and fish larvae (Huebert 2008). If postlarvae descend to lower depths during the day, as inferred from observations in the laboratory (Calinski & Lyons 1983, Booth & Phillips 1994, Jeffs & Holland 2000) and rare trawl catches (Ritz 1972, Phillips & Pearce 1997), then the tether and fixed depth of the DISC could prevent them from doing so, forcing them to swim presumably in a descending manner. However, we observed a significant horizontal swimming component. The similar swimming directions for postlarvae at 25 m depth and 3 m depth during ebb tide suggest that the horizontal swimming behavior may be uniform through the top of the water column (Figs. 4 & 5). Also, lobster adults and postlarvae have been successfully used in a variety of tethering experiments examining predation (Acosta & Butler 1999, Mills et al. 2008, Behringer & Butler 2009, Butler & Lear 2009) and orientation (Lohmann et al. 1995, Jeffs & Holland 2000, Lozano-Alvarez et al. 2002, Boles & Lohmann 2003). This body of work suggests that tethering is a valid option for assessing lobster ecology and behavior. For our experiments, this was confirmed by snorkelers observing the behavior of tethered postlarvae in the DISC, noting that postlarvae were swimming forward to the extent allowed by the tether (Fig. 1B).

We observed partially upstream orientation in spiny lobster postlarvae, which is typically only common near the goal of a long-distance journey. This is because the metabolic costs of sustained swimming against flow are considerable (reviewed in Chapman et al. 2011). Animals that demonstrate upstream orientation include those with powerful rheotactic responses, such as salmon, and other diadromous species that use tidal stream transport to transition between habitats (Moore et al. 1998, Forward & Tankersley 2001, Gibson 2003, Trancart et al. 2012). We found that lobster larvae used partial compensation (Chapman et al. 2011), swimming at an angle that could increase their chances of reaching settlement habitat. The metabolic cost of swimming followed by the additional energetic cost of metamorphosis may be a limiting factor in spiny lobster dispersal and survival (Jeffs et al. 1999, 2005, Wilkin & Jeffs 2011). Wilkin & Jeffs (2011) also noted that by swimming continuously throughout the day and night, the postlarvae's metabolic cost would be reduced, although

daytime swimming was not thought to occur, and our study is the first to document it. Comparisons between the projected paths of lobsters orienting during ebb and flood tide demonstrates that lobsters are better positioned to reach nearshore using the ebb flow orientation that we observed (Fig. 4).

The tide is a signal from shallow settlement habitat that is available to dispersing larvae transitioning out of their pelagic phase. A tidally mediated switch in swimming behavior would be beneficial not only to spiny lobster postlarvae, but to a multitude of other pelagic larvae seeking a benthic home. The next step is to discover the cues that larvae can use as a compass to maintain directionality during the day and night, and throughout other variable environmental conditions. Emerging technologies such as the DISC can be used to systematically discover, describe, and quantify both larval behaviors and the environmental cues driving them. Understanding how larvae resolve environmental characteristics to change their orientation during recruitment is fundamental knowledge. If recruiting larvae across taxonomic groups use a compass, it suggests that it is an evolutionary requirement for marine dispersal with a larval phase.

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