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Larval behavior and settlement dynamics of a ubiquitous Caribbean octocoral and its implications for dispersal

Márcio A. G. Coelho[1,*], Howard R. Lasker[1,2]

[1]Graduate Program in Evolution, Ecology and Behavior, University at Buffalo, Buffalo, New York 14260, USA
[2]Department of Geology, University at Buffalo, Buffalo, New York 14260, USA

ABSTRACT: Biological traits of marine benthic species have important effects on the extent of larval dispersal. Yet, empirical characterizations of many of these traits, which are critical data for parameterizing models of larval dispersal, remain scant for most species, particularly corals. We characterized spawning, larval development, settlement dynamics, survival, and propagule buoyancy and vertical swimming behavior of the Caribbean octocoral *Antillogorgia americana*. Spawning of *A. americana* in the Florida Keys, USA, was associated with the lunar cycle and occurred over 2 separate events following the full moon of November 2014. Despite the rapid larval development (2–3 d) and onset of competency to settle at ~4 d, most larvae delayed settlement for an extended period of time, with 50% of the cohort transitioning to the benthos by 36 d, and 95% by 58 d. Larval mortality in the laboratory was surprisingly low (10% over 58 d). Egg buoyancy and larval swimming behavior were highly variable both within cohorts and over time. In particular, there was a significant decrease in propagule buoyancy during embryogenesis, which was gradually offset by the increase in larval swimming activity (~3–4 d). Most larvae had negative geotactic behavior for up to 20 d. The observed capacity to delay settlement suggests the dispersal potential of *A. americana* is high, which undoubtedly contributes to its broad distribution in the Caribbean. Importantly, our results underline the inherent variation observed in these larval traits, particularly swimming behavior, which has potentially important implications for dispersal and may improve our understanding of connectivity.

KEY WORDS: Larval biology · Pelagic larval duration · Life history traits · Population connectivity · Coral reef · Gorgonian

INTRODUCTION

Dispersal is a key ecological process influencing species' population dynamics and evolution in multiple ways (Dieckmann et al. 1999). Dispersal affects the patterns of population connectivity and stability of metapopulations (Cowen et al. 2000, Gaines et al. 2007, Tromeur et al. 2016); it modulates distribution ranges and potential to re-colonize extirpated areas (Jackson 1986, Almany et al. 2007), and it influences population genetic structure, thereby mediating processes such as local adaptation and speciation (Hedgecock 1986, Jackson 1986). Yet, for many marine species with bipartite life cycles, the extent of larval dispersal and population connectivity are unknown, mostly because of the complexity of the physical and biological processes controlling larval dispersal, and because of the difficulty of directly estimating dispersal of the enormous numbers of minute propagules produced by most species (Cowen & Sponaugle 2009, Jones et al. 2009).

Over the past several years there has been a growing appreciation of the importance of biological traits

*Corresponding author: marcioan@buffalo.edu

in mediating larval dispersal (Kingsford et al. 2002, Sponaugle et al. 2002, Leis 2007, Cowen & Sponaugle 2009, Coelho & Lasker 2016). For example, the role of larval swimming behavior, which can range from strong orientation and navigation skills (e.g. fish: Paris et al. 2013; decapods: Kough et al. 2014) to partial navigation (sensu Kingsford et al. 2002) involving vertical migration (e.g. corals: Szmant & Meadows 2006, Martínez-Quintana et al. 2015), can facilitate either larval retention or dispersal away from natal reefs (Sponaugle et al. 2002). Among marine benthic invertebrates such as corals, recent efforts addressing the recurring paradox of ample self-recruitment despite high dispersal potential have focused on the minimum time to settlement competency, which in several species of broadcast spawners is short enough to allow local retention of larvae in many reef systems (Miller & Mundy 2003, Harrison 2006, Figueiredo et al. 2013). Nonetheless, our understanding of the role of larval biology in controlling dispersal is a glass that is half-full and half-empty. The glass is half-full in the sense that many of the biological traits influencing larval dispersal are now identified, thus offering the necessary framework for characterizing dispersal; but the glass is half-empty because these traits have not been quantified for most benthic species and because little is known about the temporal and spatial scales at which they operate in nature.

Given the limitations of directly observing larval dispersal for most marine benthic species, biophysical models of larval dispersal have become the premier tool for studying dispersal (Werner et al. 2007, reviewed in Miller 2007). While the integration (and understanding) of all physical processes controlling larval transport remains challenging, particularly at small spatial scales (Largier 2003, Gawarkiewicz et al. 2007, Werner et al. 2007), parameterization of these models with biological data is a necessary prerequisite for making realistic inferences about patterns of population connectivity (Sponaugle et al. 2002, Leis 2007, Cowen & Sponaugle 2009, Coelho & Lasker 2016). Notwithstanding how crucial these data are, empirical characterizations of the relevant biological parameters are limited for most species, particularly for corals (Metaxas & Saunders 2009, Coelho & Lasker 2016).

Moreover, for those studies incorporating some component of the larval biology in model simulations, the parameterizations are often simplifications of complex patterns. For instance, pelagic larval duration (PLD) is often bounded by fixed minimum and maximum times to settlement competency during which virtual larvae will 'settle' when settlement substrata become available (e.g. Baums et al. 2006, Galindo et al. 2006, Siegel et al. 2008, Sanvicente-Añorve et al. 2014).This approach, which is commonly used in simulations, does not incorporate the considerable variability among larvae in the time needed to reach competency (Connolly & Baird 2010). Similarly, egg buoyancy and larval swimming behavior, which influence propagules vertical distribution in the water column and may have a substantial impact on dispersal, is rarely considered, particularly among benthic invertebrates with weak swimming abilities such as corals (Baums et al. 2006, Andutta et al. 2012, Foster et al. 2012, Thomas et al. 2015; but see Holstein et al. 2016).

Here, we characterize those biological traits most relevant for dispersal of the broadcast-spawner *Antillogorgia americana*, one of the most common and widespread species of octocorals on shallow-water (<30 m) Caribbean reefs (Kinzie 1973, Lasker & Coffroth 1983, Alcolado et al. 2008, Williams et al. 2015). With recent evidence suggesting that the changes in community structure of Caribbean reefs appear to be favoring octocorals (Ruzicka et al. 2013, Lenz et al. 2015, Edmunds et al. 2016), sound knowledge about their ecology is imperative to our understanding of modern Caribbean reef communities. Specifically, we document the spawning behavior of *A. americana* in the Florida Keys, USA, describe larval development, and quantify the settlement dynamics and ontogenetic variability of propagules' (i.e. eggs, embryos and larvae) buoyancy and vertical swimming behavior. Furthermore, we describe PLD as a function in which the percentage of the larvae leaving the pelagic environment (i.e. settling) changes continuously.

MATERIALS AND METHODS

Adult sample collection

The exact timing of *Antillogorgia americana* spawning in Florida was ascertained in a pilot study conducted in October and November 2013, when spawning was predicted to occur (Fitzsimmons-Sosa et al. 2004). Branches from colonies from the Florida Keys and from reefs in the vicinity of Fort Lauderdale were monitored in outdoor tanks at the Keys Marine Laboratory (KML) and at Nova Southeastern University, respectively. Spawning was observed at both sites during the evening 5 and 6 d after the November full moon. Based on those observations, the ex-

periments were conducted following spawning in November 2014 at KML. At the time of the full moon, branches from forty colonies of *A. americana* were collected from an inshore patch reef (24° 46′ 42″ N, 80° 44′ 9″ W) located ~5 km east of Tennessee Reef in the Middle Keys, Florida. Branches (hereafter colonies) were collected and transported to KML in individual zip-sealed plastic bags filled with seawater. On shore, the colonies were secured to artificial holdfasts and transferred to 2 large outdoor tanks (~265 l) with running seawater, where they were kept for the duration of the study. The sex and maturation state of each colony was determined in the laboratory by dissecting individual polyps of a small branchlet (~5 cm long) using a binocular microscope, and colonies were subsequently redistributed equally between the 2 tanks. In total, 23 females and 17 males were collected. The temperature inside the tanks was recorded every 10 min using temperature loggers (HOBO model H08-001-02).

Spawning and larval rearing

The running seawater in the tanks was temporarily shut off prior to sunset each day and the colonies periodically checked for egg or sperm release until ~00:00–01:30 h of the following day. During that period, aeration was turned on regularly to circulate the seawater within the tanks and minimize the accumulation of mucus on the colonies. Following spawning, the eggs were left in the tanks for 1–2 h to allow fertilization and then transferred to 6 l polycarbonate round containers filled with 4 l of filtered seawater (FSW; 5 µm) using a transfer pipette. The seawater was changed at 4, 12, 24, 36 and 48 h during the first 2 d after spawning, daily for the next 2 d, and every 2–3 d thereafter. Cohorts spawned on different nights were maintained separately. All rearing containers were kept at ambient temperature in the laboratory at KML, which averaged ~24°C. The average ambient seawater temperature in the Florida Keys is ~26°C during November, but 24°C was well within the range of temperature fluctuations for the area in 2014 (Fig. S1 in the Supplement; www.int-res.com/articles/suppl/m561p109_supp.pdf) and during this time of the year in general.

Larval development and survivorship

At 0–2, 4, 8, 12, 24, 48 and 72 h after spawning 15–20 propagules were randomly sampled from one of the rearing containers and fixed in a solution of 10% (v/v) formalin in seawater for scanning electron microscopy. Older planula larvae were also fixed in formalin to examine the potential loss of ciliation occurring at later ages, as observed in some octocorals (Lasker & Kim 1996). A sub-sample of the preserved propagules were later washed in distilled water, dehydrated through a graded series of ethanol, and transferred to a solution of 100% (v/v) hexamethyldisilizane before being air-dried. The preparations were sputter-coated with graphite and photographed at the South Campus Instrument Center, University at Buffalo, using a field emission scanning electron microscope (Hitachi SU70 and S4000).

Larval survival was followed in 5 replicate samples of 100 randomly selected propagules. The propagules, initially a mix of eggs and embryos, were transferred from the rearing containers to 0.95 l clear polypropylene containers filled with FSW (600 ml), and the number surviving was counted daily. After 48 h, only 77.6 ± 2.2% (mean ± SE) of the propagules had survived and developed to larvae, most likely from the decay of unfertilized eggs and abnormal development due to polyspermy; thus, the survivorship censuses were re-started at Day 2 using surviving larvae from the rearing containers (100 larvae per replicate). The number of surviving larvae was counted every day during the first 21 d, and every 3 d subsequently. Water changes were conducted as detailed above for the rearing containers. On December 3, 2014, the replicates were transported to the University at Buffalo (UB), where they were kept in a temperature-controlled environmental chamber (24°C). Artificial seawater (ASW) was used in all experiments conducted at UB.

Competency period, settlement dynamics and pelagic larval duration

The onset and duration of competency to settle was determined from the proportion of larvae settling onto artificial substrata over time in the laboratory. We quantified larval settlement for 2 cohorts of larvae: (1) larvae from the spawning event of November 11, 2014 which were reared at KML starting at 3 d after spawning; and (2) larvae from spawning on November 26, 2014 which were transferred to UB, with observations starting at 8 d after spawning. Larval settlement and metamorphosis are known to be induced by biological cues produced by specific species of crustose coralline algae (CCA) and/or fouling communities associated with their surface in many scler-

actinian corals (e.g. Morse et al. 1988, 1996, Negri et al. 2001). In octocorals, however, although it has been suggested that CCA may play a role in larval settlement (Lasker & Kim 1996), much less is known about the specificity of these processes or exact settlement requirements of the larvae. In the experiment conducted at KML we tested unglazed terracotta tiles that had been conditioned in the flow-through tanks at KML for ~2 mo, tiles that were conditioned in seawater with CCA for 1 wk, and unconditioned tiles. A chip of CCA was added to each replicate in the conditioned treatments. The unknown species of CCA used in the study was obtained from coral rearing tanks at the MOTE Tropical Research Laboratory. Ten replicates of 50 randomly selected larvae were used in each of the treatments. At UB, we used unconditioned tiles and dead gorgonian skeleton with (10 replicates of 50 larvae per treatment) and without (4 replicates of 50 or 24 [1 replicate in the treatment containing gorgonian skeleton] larvae per treatment) CCA chips added to each replicate. All replicates were maintained in 0.95 l clear polypropylene containers filled with 600 ml of FSW/ASW, with partial (~70%) water changes conducted daily during the first 3 d (KML) and every 3–7 d subsequently (KML and UB). The replicates at both KML and UB were kept at ~24°C. However, for the experiment conducted at UB, the seawater temperature in the replicates varied between 24 and 28°C during the first 6 d due to direct overhead illumination, which was subsequently turned off.

Although the usage of the term 'settlement' varies across studies, it is generally restricted to the attachment and metamorphosis of the larvae. In that usage, the stage of searching and testing the substratum that precedes attachment and metamorphosis (Underwood 1979, Keough & Downes 1982, Harrison & Wallace 1990) is independent of settlement per se. Because the 'testing' stage is effectively benthic (i.e. no longer part of the dispersal phase) and occurs at spatial scales that are likely unimportant for population dynamics in terms of dispersal, in this study we distinguish between 2 processes: (1) the transition from the pelagic environment to the benthos, irrespective of whether or not the larvae on the bottom of the containers were attached or metamorphosed, which we refer to as the pelagic–benthic transition (PBT); and (2) settlement and metamorphosis, which we simply refer to as settlement. Planulae that have undergone the PBT include those that were crawling, those attached to the substratum, including larvae that were loosely attached and easily dislodged by gentle agitation of the water (i.e. reversible attachment), as well as those that were metamorphosed. Because unattached and reversibly attached larvae can transition back to the water column, our measure of PBT is a net rate. The onset of reversible attachment was used to infer the onset of competency to settle, and hence, the duration of the pre-competency period.

PLD was inferred from the proportion of larvae in the water column over time. Defining PLD based on a single value (e.g. maximum longevity) is in many cases an ambiguous description of dispersal potential. Instead, we report the points in time at which 25, 50 and 95% of the initial number of larvae were no longer pelagic, designating them PLD_{25}, PLD_{50} and PLD_{95} (Coelho & Lasker 2016). The proportion of larvae in the water column was normalized to the number at the start of the observations. Incorporating mortality into the calculation had no effect on the inferred PLDs due to high survivorship in the laboratory (data not shown). In order to infer the time period at which the transition to the benthos was the highest, we also determined the daily net flux of larvae onto the substratum (hereafter daily PBT).

Egg buoyancy and larval vertical swimming behavior

The ontogenetic changes in *A. americana* egg buoyancy and larval swimming behavior were quantified from video recordings of the propagules in sealed, 2.8 l clear polybutyrate cylinders (5 cm diameter, 36 cm height), which were placed inside a large aquarium tank (106 l) with circulating water at ~24°C. This procedure was designed to minimize temperature differences inside and outside of the cylinder, as even small temperature differences produce convection cells within the cylinder. For each of 2 cohorts spawned 2 nights apart (i.e. differing in age by 2 d), 2 replicates of ~100 propagules were randomly sampled from the rearing containers (containing ~1000–1500 individuals) and placed inside the cylinders. Before each video recording, the propagules were allowed to adjust to the experimental conditions by leaving the cylinders laying horizontally and undisturbed in the aquarium tank for 30 min, after which the cylinders were gently reoriented to a vertical position and the behavior recorded on video for 10 min. As the cylinders were completely full, the change in position did not generate any flow within the cylinder. Video recordings of the propagules were taken at 2–4, 12 and 24 h following spawning, and then daily to a maximum of 20 d. The time at

which the video recordings were taken each day was gradually changed to start earlier in the day (sunset by Day 7). The larvae in each replicate cylinder were recorded separately and the seawater temperature inside the tank recorded. All tests were conducted under illumination provided by overhead fluorescent lights in the laboratory. The field of view in the videos was restricted to the central 10 cm of the cylinder, which was marked with a ruler. The vertical velocities of all the propagules in the field of view of a subset of the videos were subsequently quantified by visual analysis. The procedure consisted of determining the time required for each propagule to move 2 cm in the vertical plane, either upward or downward. The measurements were rounded to the nearest second, which for the overall mean vertical velocity (0.12 cm s^{-1}) represents a measuring error of ~0.01 cm s^{-1}. Larvae that reversed trajectories were not used in the analyses. All videos were recorded using a JVC Everio camcorder (Model GZ-MG330 AU) at 30 frames s^{-1} and 480 p resolution.

Statistical analyses

The effects of the different substratum treatments on larval PBT and settlement were tested using a 2-way analysis of variance (ANOVA) with repeated measures. Proportion data (response variables) were arcsin square root-transformed in order to meet the assumptions of normality and homogeneity of variances. Changes in PBT and settlement over time (UB data only) were tested using a 1-way repeated-measures ANOVA with pairwise multiple comparisons. Significance levels were adjusted using a Bonferroni procedure. The per capita net flux of larvae onto the substratum (i.e. PBT rate) and the per capita net larval settlement (i.e. settlement rate) were treated as response variables and time as a fixed factor. The PBT and settlement rates were calculated as follows:

$$\text{PBT rate} = \frac{1 - \frac{L_{\text{sw}(t)}}{L_{\text{sw}(t-1)} - L_{\text{m}(t)}}}{\Delta t} \quad (1)$$

$$\text{Settlement rate} = \frac{\frac{L_{\text{s}(t)} - L_{\text{s}(t-1)}}{L_{\text{a}(t-1)}}}{\Delta t} \quad (2)$$

where $L_{\text{sw}(t)}$ is the number of larvae swimming at time t; $L_{\text{m}(t)}$ is the number of larvae dying to time t; $L_{\text{s}(t)}$ is the number of larvae settled at time t; $L_{\text{a}(t)}$ is the number of larvae available for settlement at time t (calculated as $L_{\text{sw}(t)}$ plus the number of larvae exploring the substratum); and Δt is the time interval between counts in days. Both PBT and settlement rates were arcsin square root-transformed. The PBT rate, as well as daily PBT (see above), was adjusted for mortality by subtracting the number of larvae that had died during each time interval. Adjusting for mortality in this manner does not differentiate between mortality among swimming larvae and mortality of benthic larvae, a bias that can either under- or overestimate the PBT. However, the overall pattern was not different if mortality was not incorporated in the calculation (Fig. S2 in the Supplement).

The effect of age and cohort on propagule vertical velocities was tested with linear mixed-effects models using the 'nlme' (Pinheiro et al. 2015) package in R (R Core Team 2014). We modeled vertical velocities as a function of 'age' and 'cohort' (fixed factors) with 'replicate cylinder' as a random effect. Model selection was based on hypothesis testing using a combination of *t*-statistics, *F*-statistics and likelihood ratio tests. Because the assumption of homogeneity of variance was not met (after arcsin square root-transformation), we implemented a weighted variance structure to incorporate different variances within levels (i.e. factors) into the model. In addition, we removed 6 influential observations from the analysis, which were detected by visual inspection of a Normal Q-Q plot. Multiple pairwise comparisons (Tukey contrasts) for significant factors were performed with the 'multcomp' package in R (Hothorn et al. 2008) using the coefficients of the optimal model obtained with 'nmle'.

RESULTS

Spawning

Consistent with the preliminary observations made at KML and Nova Southeastern University in 2013, *Antillogorgia americana* spawned shortly after the full moon in November 2014. The colonies maintained in the flow-through tanks spawned in 2 events 2 wk apart, 1 over 3 consecutive nights (5, 6 and 7 d following the full moon) and another one-night event 15 d after the full moon. Both spawning events were preceded and followed by a night in which only a couple dozen eggs were released. Egg release in the tanks was observed as early as 17:45 h and peaked between 20:00 and 22:00 h depending on the night. Spawning by male colonies was never observed directly despite successful fertilization of the eggs collected. No obvious association between timing of spawning and seawater temperature was evident from the temperature logger data (Fig. S1 in the Supplement).

Larval development and survivorship

Fertilized eggs developed into mobile larvae over a 2–3 d period (Fig. S3a–c in the Supplement). Ciliated larvae were first observed 48 h following spawning, concurrent with the onset of swimming activity. By 3 d following spawning most larvae were highly mobile and remained at the surface of the seawater. Mature larvae (Fig. S3d) were ciliated throughout the duration of the larval phase. Surface ciliation was observed on 'demersal' (i.e. crawling) 54 d old larvae that were no longer swimming in the rearing containers, and which exhibited morphologies associated with the onset of attachment (Fig. S3e,f).

Larval survival in the laboratory was high (Fig. 1). Mortality rates were somewhat greater during the first 6 d (monitoring started with 2 d old larvae) and then again when transferred from KML to UB. However, other than those 2 time periods, larval mortality was low and remained stable for several weeks. The mean percentage of larvae (±SE) surviving until 59 d of age was 89.8 ± 2.1%. Variation among replicates was low, with the SD ranging from 1.92 and 4.76% at 18 and 52 d, respectively. Although larvae were kept alive for over 80 d in the survival experiments (without settlement substratum), the great majority of the larvae were no longer swimming at that time and remained at the bottom of the containers, either crawling or partially metamorphosed. Those larvae contained sclerites and exhibited unusual asymmetric forms.

Larval competency and settlement dynamics

The patterns of larval settlement in *A. americana* did not differ significantly between any of the substratum treatments tested ($p > 0.05$); thus, only the pooled data are shown. The minimum time to settlement competency, as inferred from the onset of larval 'testing' behavior in which larvae temporarily (or permanently if suitable habitat was found) attached to the substratum, was first observed 4 d after spawning. However, the duration of the dispersive pelagic phase was much longer. The great majority of the larvae remained in the water column for well over 1 mo, with only 25% of the cohort transitioning to the benthos during the first 25 d (i.e. PLD_{25}) (Fig. 2a). After this period, the proportion of larvae swimming decreased gradually throughout the duration of the experiment (Fig. 2a). The PLD_{50} and PLD_{95} were 36 and 58 d, respectively. In the experiment conducted at KML, the percentage of larvae that transitioned to

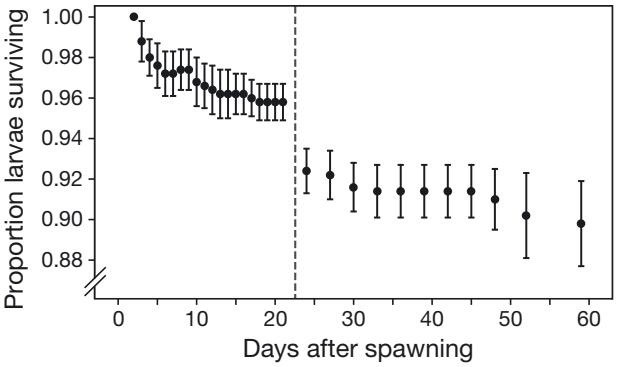

Fig. 1. Larval survival of *Antillogorgia americana* in the laboratory. Data points: mean proportion (±SE) of surviving larvae in 5 replicates (n = 100). Vertical dashed line: time when all replicates were transported from the Keys Marine Laboratory to the University at Buffalo. Monitoring started 2 d after spawning

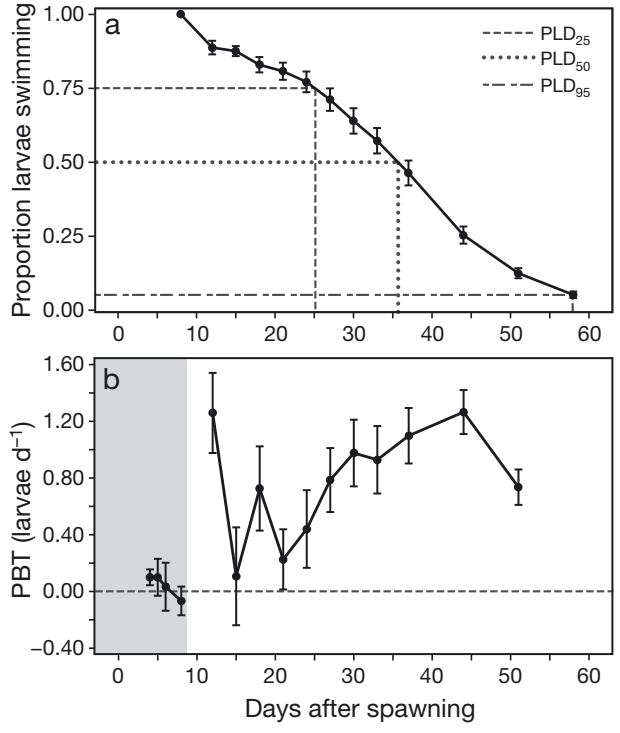

Fig. 2. Larval settlement dynamics in *Antillogorgia americana*. (a) Pelagic larval duration (PLD) plotted as mean proportion (±SE) of larvae in the water column over time normalized to the initial number of larvae in the replicates (n = 28) for all settlement treatments pooled. Points in time at which 25, 50 and 95% of the larvae were no longer pelagic (PLD_{25}, PLD_{50} and PLD_{95}) are shown. Monitoring of larval settlement started 8 d after spawning at the University at Buffalo. (b) Mean daily net flux (±SE) of larvae onto the substratum (i.e. daily pelagic–benthic transition, PBT) over time for each of 2 cohorts of larvae followed at the Keys Marine Laboratory (shaded area) and at the University at Buffalo. Daily PBT calculated using the composite of larvae leaving the water column while accounting for larval mortality (see 'Materials and methods')

the benthos after 3 wk was less than 4% (data not shown). At UB, daily PBT was high at 12 d, which was the first data point in the experiment (Fig. 2b). That rate was calculated based on the 4 d period from the start of the experiment, but it incorporates PBT over 12 d since spawning. Aside from the rates at 12 and 18 d, when the number of larvae crawling on the bottom of the containers was high in a few replicates, the daily PBT was low during the first 21 d, after which time it increased uniformly to a maximum of 1.27 ± 0.16 larva d^{-1} (mean ± SE) at Day 44 (Fig. 2b).

The PBT rate differed significantly over time (F = 6.59, df = 10, $p < 0.05$) and increased steadily (except for peaks at 12 and 18 d) until 51 d after spawning (Fig. 3a). The PBT rates at 44 and 51 d were substantially higher and statistically different from those at Days 15 and 21 (both cases), and at Day 24 (later case only) (Fig. 3a). The settlement rate also differed significantly over time (F = 2.11, df = 10, $p < 0.05$), but peaked at Day 44, after which time it appeared to drop slightly (Fig. 3b). The settlement rates varied considerably among replicates, and pairwise multiple comparisons showed that only the settlement rate at 44 d differed significantly from those observed at other times (12, 15 and 18 d).

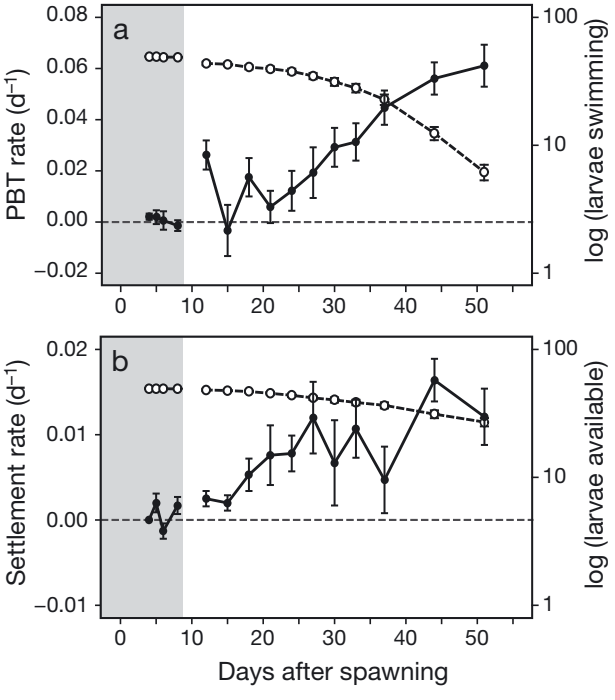

Fig. 3. Larval pelagic–benthic transition (PBT) and settlement rates in *Antillogorgia americana* for each of 2 cohorts of larvae at the Keys Marine Laboratory (shaded area) and University at Buffalo. (a) Mean (±SE) per capita net flux of larvae onto the substratum, i.e. PBT rate, over time (●). PBT rate was calculated using the composite of larvae leaving the water column while accounting for larval mortality (see 'Materials and methods'). Number of larvae swimming over time (○). (b) Mean (±SE) per capita net larval settlement, i.e. settlement rate, over time (●). Negative values reflect post-settlement mortality. Number of larvae available for settlement (○)

Egg buoyancy and larval vertical swimming behavior

All 3 approaches used to select the optimal model for the vertical velocity data supported the same preferred model: 2 factors (age and cohort) with a significant interaction term; for reasons of clarity, we only show the results of the likelihood ratio tests (L). Overall, age had a strong effect on the vertical velocities of *A. americana* eggs/embryos (buoyancy) and larvae (composite of buoyancy and swimming) (L = 39.32; df = 9; $p < 0.001$), but not cohort (L = 0.65; df = 1; $p = 0.418$). Because the interaction 'age × cohort' was statistically significant (L = 45.05; df = 9; $p < 0.001$), the effect of one factor at each level of the other was explored by decomposing main effects and interaction effects (i.e. data sweeping), as well as with an interaction plot (following Quinn & Keough 2002). Both approaches suggested that with the exception of a few cases the interaction effects were relatively small and did not swamp main effects despite a statistically significant interaction term (Fig. S4, Table S1 in the Supplement). Moreover, the age effects were much stronger than those of cohort (Table S1 in the Supplement), and the output of the optimal model suggested that the inter-dependence of age and cohort was only statistically significant at Day 18 (t = 3.562; df = 16; $p = 0.003$), though it was close to significance at Day 3 as well ($p = 0.091$).

The eggs of *A. americana* were positively buoyant. The 2–4 h old eggs rapidly ascended to the top of the cylinders at an average vertical velocity (±SE) of 0.17 ± 0.01 cm s^{-1} in both Cohorts 1 (n = 93) and 2 (n = 125) (Fig. 4). There was a statistically significant decrease in the vertical velocities 12 h following spawning (Tukey's test, $p < 0.05$; Fig. 4). Despite this decrease, the great majority of the propagules had positive (i.e. rising) vertical velocities, although a small proportion were observed to sink. This phase of lower vertical velocities appeared to last until ca. Days 3 and 4 in Cohorts 1 and 2, respectively, when the velocities increased again coincident with the increasing number of larvae that were swimming (Fig. 4). This pattern is more evident when analyzing the median velocities. Although some larvae were observed to swim vertically in an undulating motion, the great

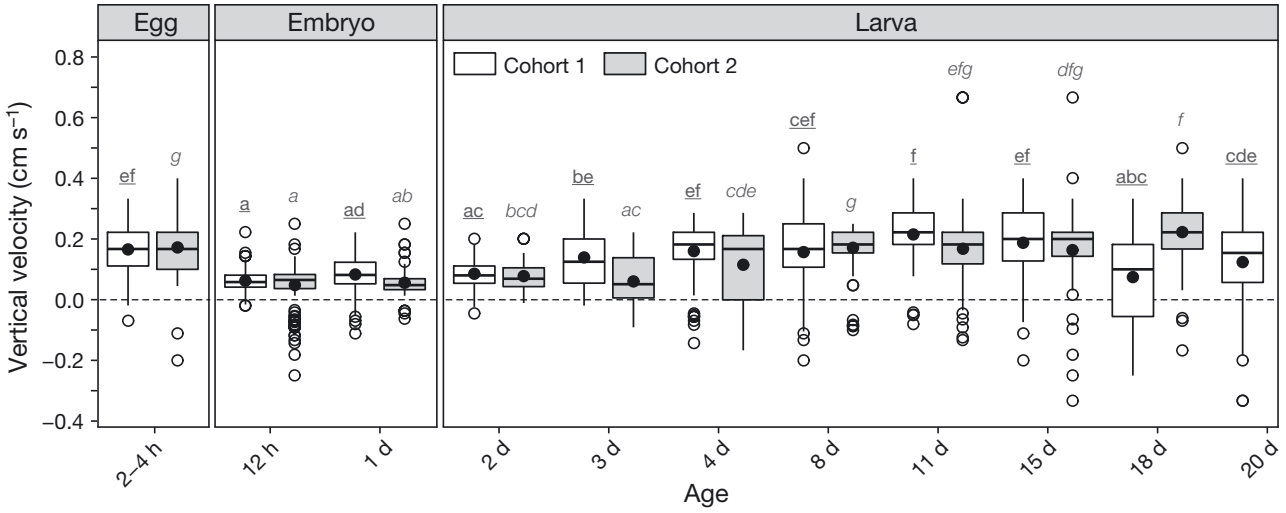

Fig. 4. Ontogenetic changes in *Antillogorgia americana* propagule vertical velocities during the first 20 d of pelagic larval duration. Cohort 1 from spawning on November 11, 2014 (48 < n < 118) (open boxes); Cohort 2 from spawning on November 13, 2014 (36 < n < 147) (grey boxes). Mean vertical velocities (●). Lower and upper hinges of the boxplots correspond to the first and third quartiles (i.e. 25th and 75th percentiles), respectively. Horizontal line within the boxplots: median. Upper and lower whiskers extend to highest and lowest measured values within 1.5× inter-quartile range. Outliers plotted as open circles (○). Shared letters above the boxplots: statistically supported homogeneous subsets for Cohort 1 (underlined) and Cohort 2 (italicized) after a Tukey's test using the coefficients of the optimal linear mixed-effects model ($p > 0.05$). Optimal model was fit with maximum likelihood estimation. Note that for Cohort 2 no measurements were taken at Day 20

majority swam linearly along the vertical plane, presumably by means of cilia. The mean vertical velocities of the larvae peaked 11 d after spawning in Cohort 1 (0.22 ± 0.01 cm s^{-1}) and 18 d in Cohort 2 (0.22 ± 0.01 cm s^{-1}) (Fig. 4). In Cohort 1, there was a statistically significant decrease in the mean vertical velocities of 18 d old larvae relative to the maximum mean observed at Day 11 (Tukey's test, $p < 0.05$; Fig. 4), which coincided with an increase in the proportion of larvae that were sinking (33 % of the larvae measured) (Fig. S5 in the Supplement). In general, the onset of larval swimming activity resulted in an increase in the variation and range of vertical velocities (Fig. S5).

DISCUSSION

Spawning

Similar to other Caribbean corals, the time of spawning of *Antillogorgia americana* in the Florida Keys was predictable from year to year and associated with the lunar cycle (Szmant 1986, Wyers et al. 1991, van Veghel 1993, Lasker et al. 1996, Marhaver et al. 2015). In both 2013 and 2014, *A. americana* spawned shortly after the full moon of November, during lunar nights 5–6 and 5–7, respectively. The late autumn spawning corresponds well with the timing of larval release and spawning of several other congeners in the Florida Keys and Bahamas (Gutiérrez Rodríguez & Lasker 2004, Coelho & Lasker 2014). However, there appears to be regional variation in the timing of spawning of *A. americana*, which is reported to occur in August in the southern Caribbean (Bastidas et al. 2005).

In 2014, a one-night spawning event was also observed 2 wk after the first event. While we did not determine if the second spawning event was restricted to specific colonies, multiple spawning events means the initial environmental conditions experienced by the propagules are likely to differ, which may greatly affect the extent of larval transport (Sponaugle et al. 2002, Kough & Paris 2015, Coelho & Lasker 2016). This is particularly relevant for broadcast spawning species with an obligate pre-competent planktonic phase during part of which propagule transport is entirely passive. In fact, the 2 spawning events observed for *A. americana* occurred during markedly different environmental conditions (Fig. S1 in the Supplement) with respect to wind, which affects ocean surface flow and mixing (Garrett 1996), and temperature, which affects the rates of larval development and hence the duration of larval transport (Nozawa & Harrison 2007, Heyward & Negri 2010, Woolsey et al. 2013, Figueiredo et al. 2014). Although multiple spawning events may simply reflect variance in 'reading' environmental cues that control

spawning, the observation is also consistent with a bet-hedging strategy with regard to spawning success and dispersal. This underlines the importance of precise characterizations of spawning behavior for understanding the extent of larval dispersal and population connectivity in corals.

Larval settlement and swimming behavior

Pelagic larval duration, and more recently, the minimum time to settlement competency, are often regarded as the primary biological traits affecting the extent of larval dispersal in marine benthic invertebrates (Scheltema 1968, Sponaugle et al. 2002, Miller & Mundy 2003, Figueiredo et al. 2013; among others). While the maximum and minimum times to settlement competency delimit the extent of larval dispersal, they do not accurately characterize dispersal dynamics in a cohort of larvae (i.e. dispersal kernel), nor do they inform us about which behavioral traits might control how larvae are dispersed. We found that despite a fairly rapid onset of competency to settle (~4 d), a substantial proportion of *A. americana* larvae were able to delay settlement for an extended period of time, with 50 and 95% of the cohort transitioning to the benthos by 36 and 58 d after spawning, respectively (Fig. 2a). The initial delay in PBT was consistent with our observations of larval swimming behavior during the first 20 d, in which most larvae exhibited negative geotactic behavior (Fig. 4). This implies larval swimming behavior may be crucial in promoting long-distance dispersal in *A. americana*. The settlement pattern observed in the laboratory may, however, differ substantially in nature due to larval mortality as an extended period of time in the water column increases the risk of predation and exposure to environmental stressors (Pechenik 1999, Connolly & Baird 2010), which can curtail recruitment to distant populations simply because larvae do not survive (Cowen et al. 2000).

The timing of larval PBT and settlement observed in our study may overestimate *A. americana* PLD due to the absence of appropriate substrata and/or lack of cues for metamorphosis in the experiments. Lecithotrophic larvae of marine invertebrates have been shown to become less stringent about their settlement requirements as energy reserves deplete (the desperate larva hypothesis; Knight-Jones 1953, Marshall & Keough 2003), and it is possible that the settlement patterns observed in *A. americana* simply result from larvae delaying settlement for as long as energetically possible owing to the sub-optimal conditions provided. Nevertheless, the capacity to delay settlement while retaining competency to settle and metamorphose, as observed for *A. americana*, allows for long-distance dispersal and can lead to successful recruitment to distant, down-current sites. This is especially important in settings in which larvae are advected away from reefs. Such a prolonged PLD undoubtedly contributes to the broad distribution range of *A. americana*, which is a major component of coral reef hard ground communities throughout the Caribbean (Bayer 1961, Kinzie 1973, Lasker & Coffroth 1983, Alcolado et al. 2008, Williams et al. 2015).

Long delays in settlement as documented here are not unusual among species of corals with lecithotrophic (i.e. non-feeding) larvae (e.g. Ben-David-Zaslow & Benayahu 1998, Wilson & Harrison 1998, Nishikawa & Sakai 2005, Connolly & Baird 2010). For lecithotrophic larvae, delaying settlement requires the use of energetic reserves, which can adversely affect post-settlement survival and growth (reviewed in Pechenik 1990). While our study was not designed to test the adverse effects of delaying settlement (but see Graham et al. 2013), the observation that a substantial proportion of *A. americana* larvae remained immobile on the bottom of the experimental containers after 44 d suggests that at the least the ability to attach and metamorphose is affected, similar to the scleractinian *Agaricia humilis* (Hartmann et al. 2013). Although we observed new larval settlement at 51 d, the daily PBT and settlement rate appeared to decline after maximums at 44 d (Figs. 2b & 3b), suggesting *A. americana* larvae may have reached a critical point in their competency to attach and metamorphose earlier than 58 d (PLD_{95}).

While not unexpected, one of the most interesting outcomes of this study was the observed ontogenetic change in the vertical velocities of *A. americana* propagules (Fig. 4), particularly the decrease in egg and embryo buoyancy at 12 h following spawning, which appeared to last until larvae were highly mobile (~3–4 d after spawning). These findings are consistent with the temporal decrease in lipid content that occurs in several species of broadcast spawning corals as larvae develop (Harii et al. 2007, Figueiredo et al. 2012), especially wax esters, the primary source of coral propagules' energy and buoyancy (Arai et al. 1993). The pattern of declining buoyancy early in development also occurs in the scleractinian *Orbicella faveolata* (Szmant & Meadows 2006), suggesting it may be common among broadcast spawning corals with aposymbiotic lecithotrophic larvae. The average rising velocity (±SE) of *A. americana* eggs (0.17 ±

0.01 cm s^{-1}) was remarkably similar to that of *O. faveolata* (0.182 cm s^{-1}) (Szmant & Meadows 2006). Overall, these results suggest the distribution of the propagules in the water column, including the passively dispersed egg and embryonic stages, varies throughout development, which has important implications for dispersal. For instance, although the propagules' vertical velocities during the period of lower buoyancy were still positive (i.e. rising), when coupled with hydrodynamic features like wind-driven turbulence, such small changes in rising velocities are likely to affect transport due to vertical displacement of the propagules between different water layers.

The onset of *A. americana* larval swimming behavior appeared to counteract the gradual reduction of buoyancy expected from the consumption of lipid reserves. In general, a large proportion of the larvae rose to the upper-most section of the cylinders during the first 20 d of PLD, suggesting a negative geotactic swimming behavior as observed in several marine invertebrates (e.g. Fadlallah 1983, Park et al. 2004, Larsson et al. 2014, Cohen et al. 2015). However, at any given age, the vertical velocities varied substantially within cohorts and to a lesser extent between cohorts. Such variability has the potential to affect the vertical distribution of the larvae in the water column, thereby increasing the range of hydrodynamic conditions (and dispersal routes) experienced by the larvae. Importantly, much of the observed variation appeared to be driven by the proportion of sinkers and swimmers, which may be purely behavioral, though we did not distinguish between larval buoyancy and swimming behavior as done elsewhere (Martínez-Quintana et al. 2015). Unlike the octocoral *Corallium rubrum* in which the mean larval swimming activity and velocities did not vary with age (up to 12 d) (Martínez-Quintana et al. 2015), we found evidence for ontogenetic differences in the *A. americana* larval vertical velocities (composite of buoyancy and swimming).

CONCLUSIONS

The overall view of dispersal working as a conveyor belt carrying a group of passive larvae to a set location has given way to the notion that larval transport is a complex process (Cowen et al. 2007, Cowen & Sponaugle 2009), in which variability in the seascape and biological traits of the species create an immeasurable variety of routes larvae can take (Coelho & Lasker 2016). Yet, detailed characterizations of the relevant biological traits, as well as incorporation of those data in biophysical models of dispersal, remain scant, especially among corals. Specifically, most current models of larval dispersal use fixed minimum and maximum times to settlement competency in their simulations with no consideration of how these traits vary at the intra-specific level. Similarly, the integration of coral larval swimming behavior is rarely considered (but see Holstein et al. 2016) despite compelling evidence of their ability to move vertically in the water column (e.g. Stake & Sammarco 2003, Szmant & Meadows 2006, Gleason et al. 2009, Martínez-Quintana et al. 2015, present study). In this regard, characterizations of PLD defining specific points in time at which a cohort of larvae have transitioned to the benthos (present study), or instead based on settlement rates as described elsewhere (Connolly & Baird 2010, Figueiredo et al. 2014), provide a better characterization of how these traits vary.

We showed that the PLD of the octocoral *Antillogorgia americana* varied at the intra-cohort level, with most larvae delaying PBT for a long period of time despite developing fairly rapidly. In addition, we documented significant changes in the vertical velocities of propagules throughout the planktonic phase, including during early development when physical processes control transport, thus highlighting the importance of incorporating the often-overlooked swimming capabilities (and variation) of coral larvae in models of dispersal. For instance, most biophysical models of dispersal equate settlement with proximity to the substratum. However, negative geotaxis will retard settlement, even if vertical advection brings the larvae in close proximity to the substratum. Overall, our results attest to the high dispersal potential of *A. americana* and underline the inherent variation observed in these biological traits, especially in egg buoyancy and larval swimming behavior. Consideration of such variation in dispersal models, while largely untested, has the potential to change our estimates of larval retention and dispersal, which may greatly improve our understanding of population connectivity in corals and marine benthic invertebrates in general. The extent to which the inclusion of differences in the vertical velocities of propagules will affect connectivity predicted by biophysical modeling is tightly linked to the scale and magnitude of the simulated flow fields in the oceanographic models used in the simulations. As those oceanographic models improve, quantification of larval behavior and traits such as larval mortality will become increasingly important in developing better characterizations of larval dispersal in marine systems.

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