



Orientation behavior in fish larvae: A missing piece to Hjort's critical period hypothesis

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ABSTRACT

Larval reef fish possess considerable swimming and sensory abilities, which could enable navigation towards settlement habitat from the open ocean. Due to their small size and relatively low survival, tagging individual larvae is not a viable option, but numerical modeling studies have proven useful for understanding the role of orientation throughout ontogeny. Here we combined the theoretical framework of the biased correlated random walk model with a very high resolution three-dimensional coupled biophysical model to investigate the role of orientation behavior in fish larvae. Virtual larvae of the bicolor damselfish (*Stegastes partitus*) were released daily during their peak spawning period from two locations in the Florida Keys Reef Tract, a region of complex eddy fields bounded by the strong Florida Current. The larvae began orientation behavior either before or during flexion, and only larvae that were within a given maximum detection distance from the reef were allowed to orient. They were subjected to ontogenetic vertical migration, increased their swimming speed during ontogeny, and settled on reefs within a flexible window of 24 to 32 days of pelagic duration. Early orientation, as well as a large maximum detection distance, increased settlement, implying that the early use of large-scale cues increases survival. Orientation behavior also increased the number of larvae that settled near their home reef, providing evidence that orientation is a mechanism driving self-recruitment. This study demonstrates that despite the low swimming abilities of the earliest larval stages, orientation during this "critical period" would have remarkable demographic consequences.

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1. Introduction

For many reef fish, adults are relatively sedentary, but larvae have the potential of dispersing over long distances. Recent studies have demonstrated that fish larvae are strong swimmers that possess considerable sensory capabilities (Fisher, 2005; Kingsford et al., 2002; Leis, 2006). These capabilities allow fish to migrate vertically in the water column and also to navigate towards reefs, thus influencing their dispersal paths (Paris and Cowen, 2004; Vikebø et al., 2007). It has been further hypothesized that orientation behavior in fish larvae may be a significant determinant of the structure of reef fish populations (Leis, 2006; Paris and Cowen, 2004; Vikebø et al., 2007; Doherty and Williams, 1988). We suggest that this orientation behavior is a missing component of Hjort's critical period hypothesis, which focused on the necessity of early feeding behavior for survival (Hjort, 1914). We now know that recruitment variability results from a suite of physical and biological processes (Houde, 2008);

here we add another piece to this puzzle by illustrating the critical role of orientation behavior.

Techniques for tracking larval orientation in situ by following individual larvae (Leis et al., 1996) or using a drifting behavioral chamber (Paris et al., 2008) are valid over short time periods, but cannot be used to track larvae from birth to settlement. Alternatively, it is possible to test hypotheses about the relative importance of behavior through numerical modeling techniques (Paris et al., 2007a; Fiksen et al., 2007). Previous modeling studies that include swimming behavior found that swimming can affect dispersal patterns as well as the number of successful recruits (Fiksen et al., 2007; Wolanski et al., 1997; Porch, 1998). In these studies, however, all larvae either swam directly towards their target or had no target, and had no variability in sensory capabilities or the strength of cues. On the other hand, studies that do include stochastic components are primarily theoretical, testing the importance of parameters without using real ocean currents (Codling et al., 2004). The novel contribution of this paper is the fusion of a theoretical framework (Codling et al., 2004; Armsworth, 2000) with an existing coupled biophysical model that uses "real world" complex hydrodynamics and habitat data (Paris et al., 2007a). Fiksen et al., 2007 emphasized the

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importance of linking hydrodynamic models with rule-based behavioral models in order to understand why and how certain larval traits have prevailed, revealing optimal strategies as well as broader scale ecological processes controlling fish populations (Vikebø et al., 2007; Fiksen et al., 2007).

Beyond demonstrating the proof-of-concept for this new orientation module, we examined the effects of maximum detection distance, the strength of habitat cues, and the timing of orientation behavior on settlement and dispersal patterns. Larval reef fish may be able to navigate towards reefs using a suite of behavioral modalities at a range of distances (i.e., magnetic, 10 km–1000 km; olfactory, 0 km–50 km; acoustic, 0 km–10 km; visual, 0 m–100 m (Kingsford et al., 2002; Atema, 2012). To disentangle the potential utility of these modalities, we used a range of detection distances. Although the development of sensory abilities throughout ontogeny is not well-studied, we allowed orientation behavior to begin either immediately post-hatching or during the flexion period to examine potential consequences of orientation capabilities during the “critical period” of the larval stage (Hjort, 1914).

Specific objectives were to (1) create an orientation module to simulate the behavior of fish larvae in realistic turbulent flow conditions, (2) to examine the effects of orientation behavior on settlement and dispersal patterns and (3) to test for differences between early and late orientation, cue strengths, and so different sensory abilities.

2. Methods

2.1. The connectivity modeling system

The Connectivity Modeling System (CMS, (Helgers and Paris, 2011)) is a coupled biophysical individual-based model that combines physical parameters such as ocean currents, bathymetry, and turbulence, with biological parameters such as spawning production, pelagic larval duration, ontogenetic vertical migration, mortality, and settlement. The “virtual larvae” are released at given locations and times, and are subjected to physical and biological forcing at each time step until settlement occurs. In previous versions of the CMS where orientation was not explicitly modeled, potential settlement locations were represented by polygons which typically included the reef habitat as well as buffer for a sensory zone. In these cases, the boundary of each polygon represented the edge of the edge of the larva’s sensory zone and if a competent larva crossed this boundary, its trajectory was terminated and it was considered to have settled on the reef. In a 2005 study, Paris et al. manipulated the size of this sensory zone and found that a larger sensory zone increased settlement (Paris et al., 2005a). However, little is known of the effects that short-range orientation behaviors (those that take place between the edge of the sensory zone and the reef) have on settlement. Therefore, a more realistic scenario would model the paths of larvae within this near-field region of the reef (Armsworth, 2000), which is the purpose of the orientation module developed here.

The CMS has an ontogenetic vertical migration algorithm which moves larvae in the water column following observed stage-specific distributions (Paris and Cowen, 2004; Irisson and Lecchini, 2008; Irisson et al., 2010). This behavior has been shown to increase local retention (Paris and Cowen, 2004), yet before this behavior begins (usually during the flexion period), larvae are subjected to advection from surface currents. Here our goal was to examine the effect of an additional type of larval movement: horizontal swimming behavior. Therefore, we included vertical migration in all of our simulations, and tested the effect of adding

oriented horizontal swimming behavior to the existing CMS framework.

2.2. The orientation module

The theoretical framework for the new Orientation Module (OM) is based on the biased correlated random walk described in Codling et al. (2004). From any given position in space, there is a target destination which the larva is “seeking,” represented by the centroid of a reef location. The larva’s ability to reach the target destination depends on the (1) strength of the cue (or combination of cues, in the real world) emanating from the target, (2) the maximum detection distance, β , (3) the swimming speed, S , of the animal, and (4) its ability to navigate in a turbulent flow. The equations and framework used to develop this orientation module are summarized below, following the notation of Codling et al. (2004):

The direction in which the larva will travel in the present time step, θ , is picked from the von Mises distribution, $f(\theta)$:

$$f(\theta) = \frac{1}{2\pi I_0(k)} e^{k \cos(\theta - \theta' - \mu_\delta)} \quad (1)$$

where θ' is the current direction the larva is facing (based on travel from previous time step to current time step), $I_0(k)$ is the modified Bessel function (Batchelet, 1981) based on k , a parameter representing the strength of a cue from the habitat. The mean turning angle, μ_δ , is given by:

$$\mu_\delta = -d_T(\theta' - \theta_o) \quad (2)$$

here θ_o is the preferred direction, which is the angle between the current position and the center of the reef (the target destination). The sensing ability of the larva, d_T , is given by:

$$d_T(x) = 1 - \frac{C}{\beta} \quad (3)$$

where C is the distance to the center of the nearest reef, and β is a parameter representing the maximum distance at which the animal can detect the reef (Codling et al., 2004). No orientation behavior takes place when larvae are beyond their maximum detection distance (when $C > \beta$) (see further explanation in Sections 2.3, 2.5.5, and 2.5.6).

Thus, with orientation behavior, each larva at any given time has a choice of possible bearings from the von Mises distribution. We transform the von Mises distribution into its cumulative density function and draw a bearing angle, θ , at random. Using this directional angle, θ , and the swimming speed, S , we calculate:

$$u_{\text{orient}} = S \cos \theta \quad (4)$$

and

$$v_{\text{orient}} = S \sin \theta \quad (5)$$

It is important to remember that this is a biased correlated random walk — biased because it includes a preferred direction, correlated because it remembers its previous direction, and random because the angle is drawn randomly from a distribution.

2.3. Fusion of the orientation module and the connectivity modeling system

The displacement of individual larvae is computed by integrating the total horizontal velocity components, U and V , at each time step. Without orientation behavior, U and V are estimated by interpolating the horizontal velocity components of the ocean currents, u and v , at the larva’s location, while also including u_{turb} and v_{turb} terms for the stochastic velocity due to unresolved subgrid-scale turbulence, i.e., $U = u + u_{\text{turb}}$ and $V = v + v_{\text{turb}}$ (for further detail see Section 2.5.5). Instead, with orientation, larval

movement is directed by $\mathbf{U}=u+u_{\text{orient}}$ and $\mathbf{V}=v+v_{\text{orient}}$, where the terms u_{orient} and v_{orient} , represent the orientation of the larva and include a stochastic component as previously described in the Orientation Module (Section 2.2).

2.4. Simulation scenarios

We conducted an ensemble of simulations to test the effects of orientation behavior on larval settlement to all reefs, the number of larvae that settled within their home region, the length of the pelagic larval duration, and the distance from release location to settlement location. We changed the maximum detection distance β , the strength of the habitat cue k , as well as the day that orientation began, to examine effects on the above mentioned measures. The focal region was the Florida Keys Reef Tract, FL, USA, for which a very high resolution, data-assimilated hydrodynamic model has been developed to resolve the meso- and sub-mesoscale eddy circulation in the region (Kourafalou et al., 2009). The focal species was the bicolor damselfish, *Stegastes partitus*, due to extended knowledge of the reproductive strategy, larval traits, and larval behavior of this species (Paris and Cowen, 2004; Sponaugle and Cowen, 1994; Paris-Limouzy, 2001; Paris et al., 2005b). Velocity fields were obtained from nested simulations of the HYbrid Coordinate Ocean Model for 2007 (HYCOM, www.hycom.org, (Bleck, 2002)). To maximize the resolution of the current fields, two nested oceanographic models were used. For the child grid we used the very high resolution SoFLA-HYCOM 1/100 degree (~900 m) grid resolution model (Kourafalou et al., 2009), extending over a domain encompassing the Florida Keys and the Straits of Florida (Fig. 1, 23–26°N, 79.5–83.3°W). The parent grid covered a larger domain including most of the coast of Florida (21–35°N,

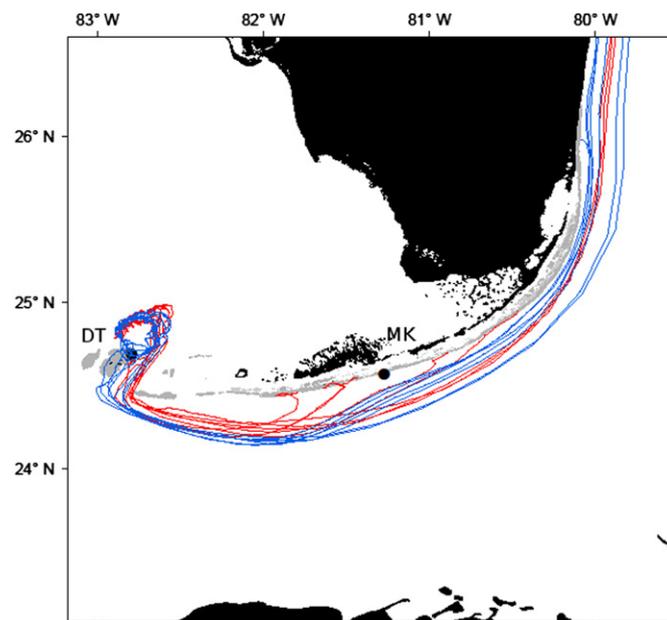


Fig. 1. The FL KEYS–HYCOM domain included the Straits of Florida and the Florida Keys. Gray regions depict the (2 km × 2 km) reef habitats, black regions depict land. Larvae oriented towards the nearest reef polygon once they passed within their maximum detection distance, β . The black dots show the two release locations: the Dry Tortugas (DT) and Middle Keys (MK). Blue lines depict a subset ($n=8$) of larval trajectories released in the Dry Tortugas that did not possess orientation behavior. Most of these larvae were advected into a gyre and were eventually swept past the reefs to the north. The red lines show trajectories ($n=8$) of larvae with orientation behavior, with a maximum detection distance of 10 km. Once the larvae passed within 10 km of a reef, they began to swim towards the reefs and most were able to settle. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

75–87°W) and was represented by the HYCOM-Global 1/12 degree model (Chassignet et al., 2003). Simulations were run offline, with data available every 6 h for the child grid and once daily for the parent grid. The CMS utilizes a zero-order stochastic Lagrangian process and operates with a 4th-order Runge-Kutta integration scheme; integration time steps ranged from 6 min to 1 h, depending on the particular simulation (Table 1).

After each simulation, we calculated the percent of the 1000 released larvae that settled to reef habitat, for each monthly cohort. These percentages were then averaged across months and compared with Kruskal–Wallis tests. We also calculated the average number of larvae that settled each day throughout the entire 5-month period and the average pelagic larval duration (PLD) for the settling larvae. The distance between each larva's starting location to its settlement location was determined; dispersal kernels for each scenario were calculated as the normalized probability of each dispersal distance. To provide measures of self-recruitment, we counted the number of larvae that settled into reef polygons within either 4 km or 15 km of their release location.

2.5. Initial conditions and parameters used

See Table 1.

2.5.1. Locations of release sites, settlement sites, and orientation targets

The release location used for the majority of simulations was upstream of the Florida Keys, in the Dry Tortugas (82.795°W, 24.686°N), but some simulations were repeated with a release in the Middle Keys (81.274°W, 24.571°N). Settlement sites were depicted by 2 km × 2 km reef polygons which were created by overlaying a grid onto larger reef polygons derived from the Coral Reef Millennium Mapping Project (Andrefouet, 2006) (Fig. 1). Any areas of the grid that contained reef habitat were included as potential settlement sites following Paris et al., 2005a (Paris et al., 2005a). These polygons were smaller than those used in previous studies (Paris et al., 2005a; Cowen et al., 2006; Kool et al., 2010) and more accurately represented reef habitat without including a sensory zone. The centroids of these 2 km × 2 km polygons were used as target destinations for the larvae.

2.5.2. Timing of release

Larvae were released throughout five lunar cycles, from April to August of 2007. One thousand larvae were released in each

Table 1

Summary of scenarios performed. Release patterns were similar for all scenarios. Virtual larvae were released over 5 lunar cycles, from April to August 2007; the number of larvae released each day was scaled with observed spawning production and ranged from 5 to 126; a total of 1000 particles were released in each lunar cycle. *Stegastes partitus* life history traits were modeled following (Paris and Cowen, 2004; Sponaugle and Cowen, 1994; Paris-Limouzy, 2001; Paris et al., 2005b). β =maximum distance at which larvae could detect the reef, Δt =integration time of the model, k =cue strength.

Release location	Orientation type	β	Δt	k
Dry Tortugas	No orientation	N/A	1 h	N/A
Dry Tortugas	Early orientation	1 km	6 min	2.5/4.5
Dry Tortugas	Late orientation	1 km	6 min	2.5/4.5
Dry Tortugas	Early orientation	5 km	30 min	2.5/4.5
Dry Tortugas	Late orientation	5 km	30 min	2.5/4.5
Dry Tortugas	Early orientation	10 km	1 h	2.5/4.5
Dry Tortugas	Late orientation	10 km	1 h	2.5/4.5
Middle Keys	No orientation	N/A	1 h	N/A
Middle Keys	Early orientation	10 km	1 h	4.5
Middle Keys	Late orientation	10 km	1 h	4.5

lunar cycle; the number released each day was scaled by the lunar cyclic spawning patterns observed in collections and otolith aging studies of *S. partitus* larvae in this region (D'Alessandro et al., 2007).

2.5.3. Timing of orientation

For each lunar cycle, we simulated 3 scenarios: (1) no orientation, (2) orientation begins the first day after hatching (“early orientation”), and (3) orientation begins during the flexion period (day 6, “late orientation,”) (Paris, 2001).

2.5.4. Timing of settlement

The larvae were allowed to settle any time between the 24th day and the 32nd day after hatching (Paris and Cowen, 2004). If a larva reached a reef before it was competent (before day 24), it continued to travel. If a larva failed to settle by the end of this competency period, its trajectory was terminated and excluded from further analysis.

2.5.5. Turbulence value

For non-orienting scenarios in the CMS, turbulence was simulated by adding a random kick (i.e., u_{turb} and v_{turb}) to the horizontal and vertical velocity vectors at each time step (as described in Section 2.3) to represent turbulent diffusion (Okubo, 1971) unresolved within the 900 m grid of the hydrodynamic model. The random displacement assumes that turbulence is isotropic in the horizontal direction, which is recommended for oceanographic applications (Brickman et al., 2007). In the orientation scenarios, when the larvae were beyond their maximum detection distance, β , the stochastic component of movement was also modeled by this turbulent random kick (see Section 2.5.6). The magnitude of the random kick was given by:

$$n\sqrt{\frac{2K}{\Delta t}} \quad (6)$$

where n is a uniform random number between 0 and 1, Δt is the integration time, and K is the horizontal diffusivity coefficient. Based on the resolution of the FL KEYS–HYCOM model, a value of $K=0.7 \text{ m}^2 \text{ s}^{-1}$ was used (Okubo, 1971).

2.5.6. Maximum detection distance, β

This value represented the maximum distance at which a larva could detect its target. Armsworth (Armsworth, 2000) defines “current-independent cues” as those which propagate radially from the reef center, which is what we modeled here. We tested for differences between three maximum detection distances: 1 km, 5 km, and 10 km, using 6 min, 30 min, and 1 h integration times, respectively (Table 1). When larvae were within β , their movement was directed by $U=u+u_{\text{orient}}$ and $V=v+v_{\text{orient}}$. When larvae were beyond β (i.e., $C > \beta$), then the u_{orient} and v_{orient} terms were replaced with u_{turb} and v_{turb} ; the stochastic component of movement was represented by the usual turbulent random kick used in the CMS for sub-grid scale motion (see Section 2.5.5).

2.5.7. Vertical migration

A probability matrix for the vertical distribution of larvae over time was used to depict the patterns observed from plankton sampling efforts around Barbados, West Indies, where *S. partitus* is also common (Table 2) (Paris and Cowen, 2004). The matrix placed larvae in 20-m depth bins depending on their developmental stage (hatching, pre-flexion, flexion, post-flexion, (Paris et al., 2005b)). The distribution of larvae was dictated by this probability matrix, and individual larvae could move at random between two adjacent depth bins once per day.

Table 2

Probability matrix of depths and times driving the ontogenetic vertical migration of *Stegastes partitus* larvae. Numbers represent the fraction of larvae distributed in each depth bin based on empirical data from Paris and Cowen (2004).

Depth (m)	Hatching (day 0)	Pre-flexion (day 1–day 5)	Flexion (day 6–day 7)	Post-flexion (day 8–day 32)
3	0.80	0.05	0.05	0.01
10	0.20	0.55	0.35	0.19
30		0.30	0.32	0.33
50		0.06	0.16	0.25
70		0.03	0.09	0.18
90		0.01	0.03	0.04

2.5.8. Cue strength, k

This dimensionless parameter represents the strength of a cue emanating from a reef, which relates to habitat quality (Codling et al., 2004). For most of the simulations conducted here, we chose $k=4.5$, a value close to the maximum, $k=5$. We did not repeat the well-developed sensitivity analysis for this parameter conducted by Codling et al. (2004), but we did test the effects of k by running a sub-set of simulations with a smaller value, $k=2.5$. The relationship between the values of k and real measures of habitat quality must be validated with empirical data.

2.5.9. Swimming speed, S

Swimming speed in coral reef fish larvae increases throughout ontogeny (Fisher and Bellwood, 2003; Fisher et al., 2000), thus, we used the nearly-linear equation relating swimming speed to age post-hatching from Fisher (2005) given by:

$$S(\text{age}) = S_{\text{hatch}} + 10^{\frac{\log_{10} \text{age}}{\log_{10}(\text{PLD})}} \log_{10}(S_{\text{settle}} - S_{\text{hatch}}) \quad (7)$$

where S_{hatch} (1.9 cm s^{-1}) was estimated from (Fisher, 2005) and S_{settle} was the published U_{crit} value (42 cm s^{-1} , (Fisher et al., 2005)).

3. Results

3.1. Dry Tortugas

Orientation behavior increased settlement in all months, and larvae that oriented early were more likely to settle than those that oriented late (Figs. 2–4). The average number of daily arrivals was highly variable, yet early and late orientation from both 5 km to 10 km significantly increased daily settlement compared to no orientation (Kruskal–Wallis test, $df=6$, $\text{chisquare}=255.3$, $p < 0.001$). When percent settlement was averaged across months, only the scenarios with a maximum distance of 10 km resulted in significantly higher settlement for both low and high values of k used (Kruskal–Wallis test, $df=6$, for $k=4.5$, $\text{chisquare}=27.02$, $p < 0.001$; for $k=2.5$, $\text{chisquare}=25.3$, $p < 0.001$, Figs. 3 and 4). Larvae that did not orient arrived at settlement habitat significantly later than orienting larvae (Kruskal–Wallis test, $df=6$, $\text{chisquare}=1665.1$, $p < 0.0001$), and larvae that oriented from 5 km to 10 km distance settled significantly earlier than those that oriented from 1 km. Despite a high degree of variability between monthly cohorts (Figs. 2 and 3), the trends were robust: larger maximum detection distances, early orientation, and larger cue strengths increased the likelihood of settlement (Figs. 2–4). Yet, a larger detection distance, β , had a greater effect on settlement than did cue strength, k (Fig. 4).

In all months, early orientation, together with a larger maximum detection distance, resulted in a higher number of self-recruiting larvae (Fig. 5). When the home region was defined as

15 km, these differences were only significant for early and late orientation from a maximum distance of 10 km (Fig. 5(A), Kruskal–Wallis test, $df=6$, $chisquare=21.75$, $p < 0.001$). However, when the home region was limited to 4 km, none of the orientation scenarios resulted in a higher number of self-recruiting larvae (Fig. 5(B), Kruskal–Wallis test, $df=6$, $chisquare=0.58$, $p < 0.99$).

Orientation behavior from all distances significantly decreased the mean dispersal distance of settling larvae for both values of cue strength (k) that were tested (Kruskal–Wallis test, $df=6$: $chisquare=334.2$, $p < 0.001$ for $k=4.5$; $chisquare=197.6$, $p < 0.001$ for $k=2.5$), shifting the peak of the dispersal kernels

closer to the release location (Fig. 6). Early orientation behavior caused larvae to travel smaller distances than late orientation behavior for orientation from 5 km to 10 km.

3.2. Middle Keys

Similarly, for larvae released from the Middle Keys, early orientation behavior increased settlement for all months. Early and late orientation significantly increased the number of daily settlers (Kruskal–Wallis test, $df=2$, $chisquare=66.73$, $p < 0.001$). Yet, when averaged across months, only the early orientation scenario had a significantly greater percent settlement than no orientation (Kruskal–Wallis test, $df=2$, $chisquare=11.18$, $p < 0.005$, Fig. 3).

Self-recruitment for the Middle Keys was highly variable from month to month; there was no significant difference in self-recruitment between the three scenarios when the home region was defined as 15 km (Kruskal–Wallis test, $df=2$, $chisquare=3.46$, $p < 0.177$) or when it was defined as 4 km (Fig. 5, Kruskal–Wallis

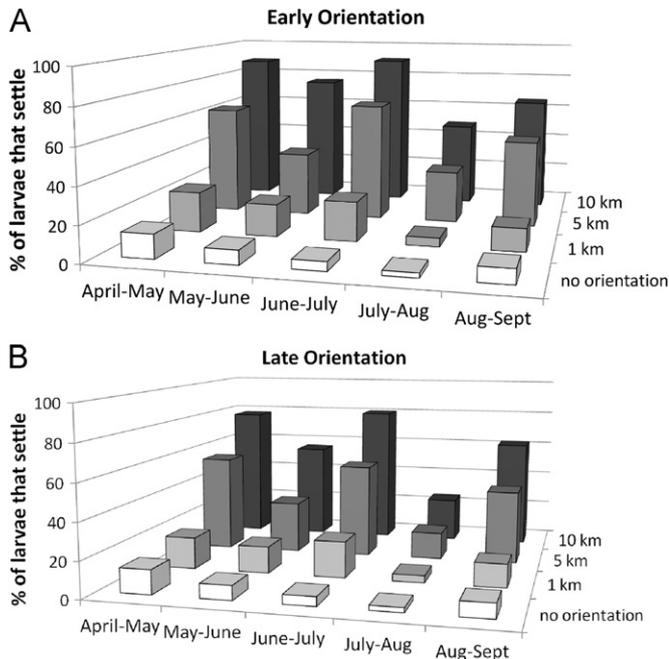


Fig. 2. Monthly settlement for early orientation (A) and late orientation (B) behavior for larvae released in the Dry Tortugas with cue strength, $k=4.5$. In each lunar cycle, 1000 larvae were released for each scenario. Although the magnitude of differences in settlement was variable between months, the trends are consistent: both a larger maximum detection distance and early orientation behavior increased the likelihood of settlement.

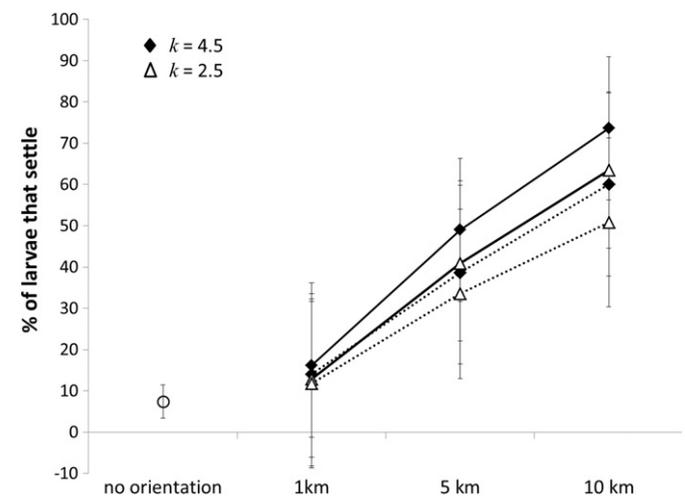


Fig. 4. Sensitivity analysis for the cue strength, k . The mean and standard deviation of the percent of larvae that were released from the Dry Tortugas site that settled. Open circle: no orientation scenario, solid line=early orientation, dotted line=late orientation. A larger detection distance and early orientation had a greater effect on settlement than did cue strength, k .

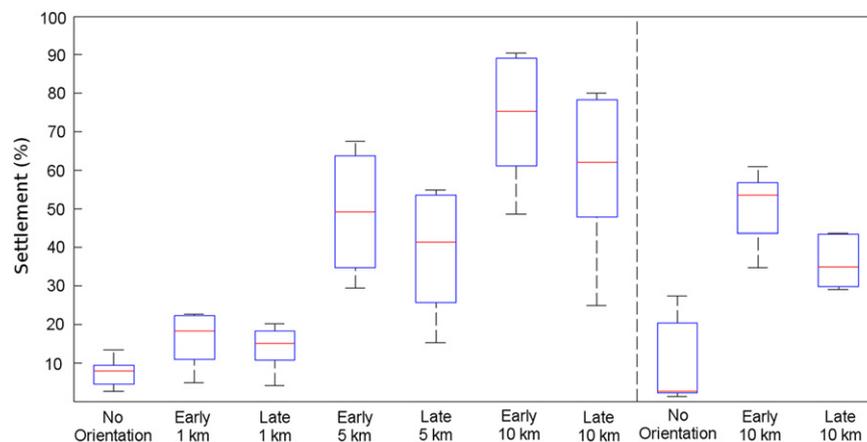


Fig. 3. Sensitivity analysis on the onset of orientation behavior (early/late) and the maximum detection distance, β . The baseline comparison is the percent of non-orienting larvae that settled on any of the 582 2 km \times 2 km reef polygons along the Florida Keys. At total of 1000 larvae were released in each month in each scenario from the Dry Tortugas (left panel) and Middle Keys (right panel), with cue strength, $k=4.5$. Red line depicts median, blue box shows the 25th–75th percentiles, black bars depict the edge of range. Simulated larvae were competent to settle between 24 and 32 day after hatching. A larger maximum detection distance, as well as early orientation behavior, generally increased settlement. This trend is evident, but the large ranges reflect the high degree of variability between monthly cohorts (as shown in Fig. 2). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

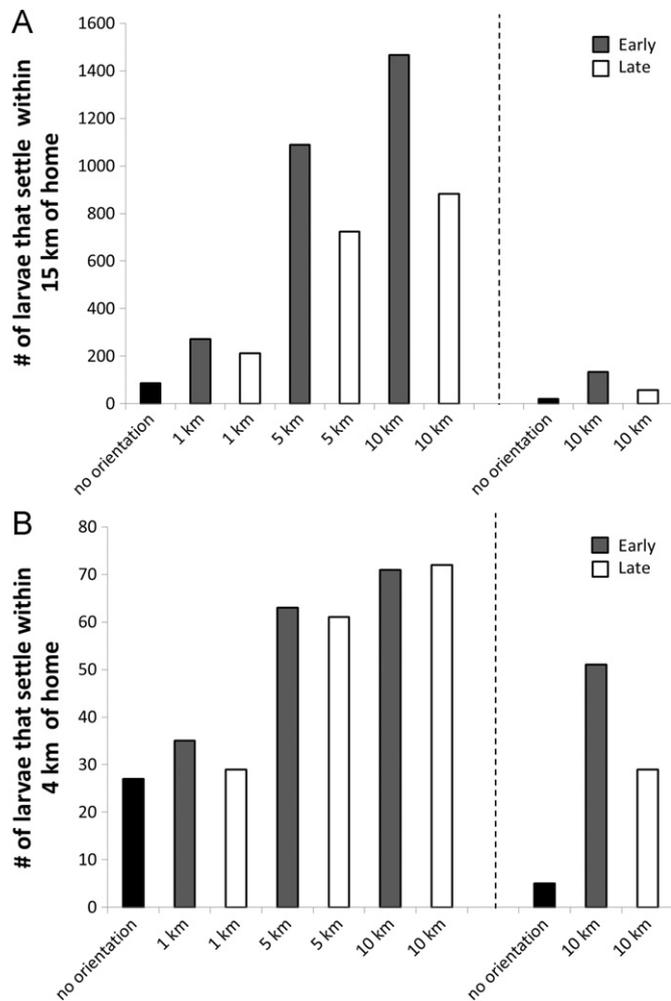


Fig. 5. Sensitivity analysis of orientation behaviors on homing. Number of larvae that settled to reefs within 15 km of home (A) and 4 km of home (B) throughout the five-month spawning period (April–September 2007), with cue strength, $k=4.5$. Results from larvae released in the Dry Tortugas appear on the left panel; results from Middle Keys on the right. In general, a larger detection distance and earlier orientation behavior increased self-recruitment. Large site-specific differences in larval settlement may result from a combination of oceanographic processes and geomorphological characteristics. The dispersal kernels for several of these scenarios are shown in Fig. 6.

test, $df=2$, $\text{chisquare}=3.35$, $p < 0.187$). Yet the total number of larvae that settled near home throughout the 5-month spawning period was greater for early orientation compared to no orientation (Fig. 5).

The dispersal distances of larvae released from the Middle Keys site were highly variable. Orientation increased dispersal in some months, and decreased it in other months. Unlike the Tortugas site, when averaged across months, larvae released in the Middle Keys under both early and late orientation scenarios had significantly longer dispersal distances than non-orienting larvae (Kruskal–Wallis test, $df=2$, $\text{chisquare}=201.6$, $p < 0.001$).

4. Discussion

Our study demonstrates that orientation behavior increases settlement, decreases dispersal distances, and increases the number of larvae that settle close to home. This study builds upon the theoretical framework developed by others (Codling et al., 2004; Armsworth, 2000; Irisson et al., 2004) but utilizes more realistic

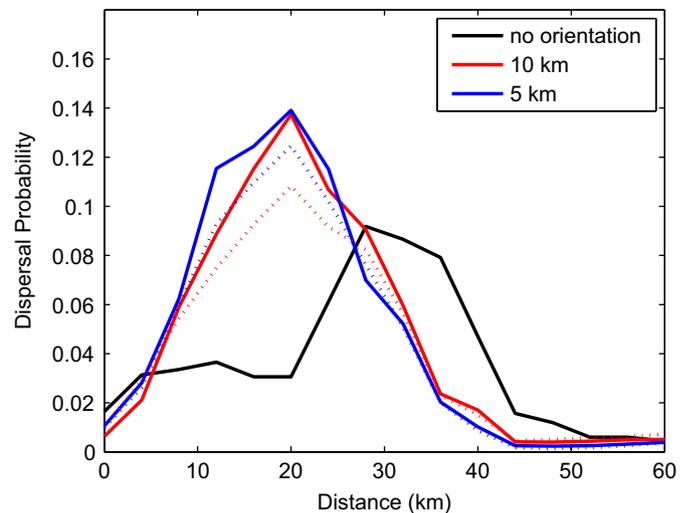


Fig. 6. Dispersal kernels and orientation: probability density functions of dispersal distances for larvae released from the Dry Tortugas. Values represent the normalized probability for each distance, in 4 km bins. Black line: no orientation; solid lines: $k=4.5$; dotted lines: $k=2.5$. Orientation behavior shifted the dispersal kernel closer to the source, returning more larvae to their home region and increasing the probability of settlers (area below the curve). A lower cue strength k decreased the probability of settling without changing the modal distance of the kernel.

ocean circulation conditions, thus demonstrating that in the real world, fish larvae are able to significantly influence their dispersal paths through orientation behavior.

Previous studies have shown that after the onset of vertical migration, most larvae can be retained near their home reef (Paris and Cowen, 2004; Vikebø et al., 2007). Before flexion, however, larvae are vulnerable to advection from the currents, especially in the Florida Keys where the Florida Current is strong and currents are highly variable (Fig. S1). Larvae may be retained if the currents are favorable during this critical period, but because currents are highly variable from month to month, the settlement success of larvae will be highly variable too (Paris and Cowen, 2004). This is supported by our data from the no orientation scenarios; in some months nearly 14% of larvae reached reef habitat, while in other months less than 3% settled in viable habitat. With orientation, larval movement was driven by a combination of swimming speed and ambient ocean currents; this interplay led to considerable variability in settlement. Orienting larvae were not guaranteed to reach a reef — the likelihood of settlement depended on the larva's ability to effectively use the ambient current conditions. This variability is reflected in the average number of larvae that settled each day as well as in the monthly settlement levels.

Despite varying daily and monthly levels of settlement, by adding orientation behavior during this critical pre-flexion period, the likelihood of settlement increased tremendously. We showed that although swimming speeds before flexion were extremely slow ($1.9\text{--}7.5 \text{ cm s}^{-1}$), larvae that oriented early had the highest chance of reaching a suitable reef after ca. four weeks of larval duration (Supplementary material Video S1). Other modeling studies have found similar results, using different mechanisms. For example, Irisson et al. (2004) used an optimization model to demonstrate that the most successful larvae were those that oriented and swam early in their development. In a study by Paris et al. (2005a), “retention zones” around reef habitats represented orientation behavior — if a larva crossed into a retention zone, it was retained. When this behavior occurred earlier, a higher percentage of fish larvae settled within their natal region. The results of our more realistic modeling study corroborated these findings; early orientation limited dispersal (Figs. 6 and 7).

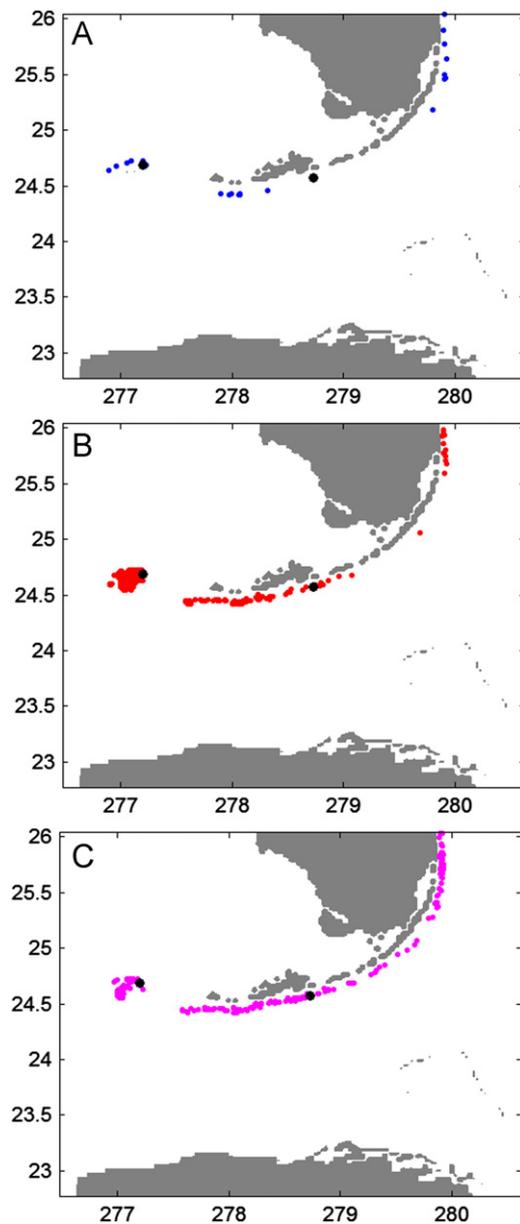


Fig. 7. Settlement patterns and orientation: for larvae with no orientation (A); with early orientation and a detection distance, β , of 10 km and cue strength, $k=4.5$ (B); and with late orientation with $\beta = 10$ km and cue strength, $k=4.5$ (C). Each dot represents the settlement location of one larva released from the Dry Tortugas site from July to August 2007. Larvae only settled to reefs (see Fig. 1 for location of reef polygons). Larvae typically settled closer to home with early orientation behavior.

The condition of a larva upon its arrival on a reef may be closely tied to the length of time that it spends in the pelagic zone (Searcy and Sponaugle, 2001). On average, orienting larvae settled on reefs two days earlier than those that did not orient. These two days can make quite a difference — not only because the fish larvae will be less exhausted upon settlement, but also because those are two fewer days when they are vulnerable to predation (Paris, 2009; Kang and Kourafalou, 2008). Here we did not include mortality, but predation-induced mortality could be added, and we expect that orienting larvae would experience lower mortality levels because they settle earlier. Furthermore, by including growth rates and metabolic activity, the trade-offs between high swimming activity and early settlement compared to lower swimming activity and later settlement could be investigated. An analysis of the condition of settling larvae would allow a

thorough understanding of the benefits of certain behavioral strategies (Fiksen et al., 2007).

The magnitude of difference in levels of self-recruitment between the orientation and no-orientation scenarios for the Dry Tortugas and Middle Keys was markedly different, and it varied depending on the size of the “home region,” (Fig. 5). When home was defined as reefs within 15 km from the natal reef, early orientation with a 10 km detection distance increased the total number of self-recruiting larvae to the Dry Tortugas by nearly one order of magnitude (i.e., 17 times), whereas in the Middle Keys the increase was 7-fold (Fig. 5). However, when home was limited to a 4 km region, orientation in the Middle Keys led to an order of magnitude increase in self-recruitment, while in the Dry Tortugas it led to only a 6-fold increase. Therefore, for larvae in the Middle Keys, where the current is more unidirectional, orientation behavior is absolutely critical in order to settle within a small region of the home reef, whereas in the Dry Tortugas, the benefits of orientation on self-recruitment are less important.

These results reflected the differences in the current regimes and geomorphology at the two sites. In the Dry Tortugas region, larvae were often entrained into a semi-permanent gyre (Kang and Kourafalou, 2008) which means that they passed their home region a second time, once they were older and had stronger swimming abilities (see Appendix A and Supplementary material Video S1). This gyre allowed more larvae to be retained in this region, resulting in higher self-recruitment (Fig. 5) and overall smaller dispersal distances (Figs. 6 and 7). This corroborates previous work on the relative influence of physical and biological processes to larval fish dispersion (Fiksen et al., 2007; Paris et al., 2007b). Paris et al. (2007) showed a sequential shrinkage of larval dispersal kernels and an increase in self-recruitment with eddy activity and deep vertical migrations (Paris et al., 2007b). In addition, the reef habitats are highly patchy in this region, which increased the chance of settlement within the larger 15 km region, but not necessarily within the 4 km region. This is because the model dictated that when they reached settlement age, larvae oriented towards the nearest reef they could detect, without a special preference for their natal reef. In the Middle Keys, the meandering Florida Current quickly advected the larvae to the north (Kang and Kourafalou, 2008), making early orientation behavior even more critical, especially to reach the reefs within 4 km of home. Because the reefs in the Middle Keys are aligned on a straight line and are thus more fragmented, there are fewer dispersal paths that can lead to settlement habitat, so the probability that larvae settled without orientation behavior was low. Furthermore, many larvae were advected beyond the northern edge of the reef tract before they had the chance to orient and move towards the reefs, which explains why it was only the early orientation scenario that increased overall settlement for larvae released in the Middle Keys. In sum, our results indicate that it is a combination of oceanographic conditions, geomorphology, and orientation behavior that explains the site-specific differences in larval recruitment levels.

When examining the effect that maximum detection distance had on larvae released in the Dry Tortugas, we found that larger detection distances led to an increase in settlement (Figs. 2–4) and self-recruitment (Fig. 5). This trend was consistent for each month (Fig. 2). When larvae sensed the reef from farther away, they were able to influence their path and were more likely to find suitable habitat. Interestingly, the change from a 5 km to 10 km detection distance made little difference, suggesting that the most advantageous cues in this model operate on a 1 km–5 km scale, making acoustic cues a likely orientation mechanism. Indeed, these results match the orientation method modeled here, i.e., detection of current-independent cues radiating from a central habitat (Armsworth, 2000). In the future this module

could be adapted for use with “current-dependent” (i.e., olfactory) cues, or large-scale (i.e., solar or magnetic compass) cues, as empirical data become available.

In these simulations we used a range of 1 km–10 km to represent the possible distances at which a fish larva could detect a reef using short-range cues (Kingsford et al., 2002). More empirical data are needed to validate the maximum detection distances used here. In particular, it is important to test the response of fish larvae to these short-range cues in situ (Paris et al., 2008), in realistic flow regimes such as those used in these simulations. Finally, an understanding of the sensitivity of larval fish to various cues throughout ontogeny is of critical importance, as the timing of orientation was a key factor influencing settlement success and dispersal patterns.

Our results raise further questions regarding the abilities of larvae to detect and orient towards reef habitats from a distance. In the simulations described here, a relatively strong habitat cue ($k=4.5$) was used, representative of a healthy reef, as well as a weaker habitat cue ($k=2.5$), representing a mediocre reef habitat. The trends were consistent across k -values; but the most important parameters affecting larval settlement were the maximum detection distance and, to a lesser extent, the timing of orientation (Fig. 4). Here, all reefs were assigned the same k -value. But because the quality of reef habitats varies spatially, an improvement of the Orientation Module should include the ability to parameterize k for individual reefs. This development would allow a more thorough analysis of “homing” behavior, as home reefs could be assigned a very large k -value compared to other reefs. This would allow investigators to determine whether larvae are able to return home with attraction to a strong imprinted cue.

In addition, it is important to assess critical thresholds as well as the real meaning of “habitat cue strength.” Codling et al. (2004) found that it was possible to miss the reef with a small value of k . In the case of more realistic settings with a series of reefs to choose from and highly variable current fields (Fig. S1), we found a similar effect: the arrival of larvae to settlement habitat was diminished with a weaker habitat cue. In the future, it would be useful to determine the cue strength threshold in the context of real oceanographic and habitat data (e.g., barrier reefs, oceanic atolls, etc.). Finally, calibration of this parameter by matching the arbitrary scale of $k=0.5$ – 5 (established by Codling et al. (2004)) to meaningful empirical data on the quality of the habitat is critical. For example, if fish larvae are indeed attracted to reef sounds (Kingsford et al., 2002), a reef with higher biologically-relevant sound levels could be assigned a larger k -value, while a quieter reef would have a lower k -value. With these developments, along with improved empirical data on sensory abilities and behavior, this module could be used to evaluate the critical threshold levels required for fish to detect and orient towards reefs. This Orientation Module could be applied to further investigate the effects of orientation on spatial patterns of settlement and population connectivity.

5. Conclusions

The long-standing assumption that larval fish are passive particles is being overturned. Recent empirical studies have elucidated the sensory and swimming capabilities of these organisms. Using a modeling approach, we showed the demographic consequences of larval navigation. We demonstrated that even with weak swimming speeds, fish larvae that possess strong sensory abilities can influence their dispersal paths and are more likely to successfully find reef habitat, especially when orientation behavior happens early in the pelagic phase. Our results provide a missing piece to Hjort’s critical period hypothesis: orientation

behavior during the “critical period” increases the likelihood that larvae will survive the pelagic phase.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.jtbi.2012.03.016>.

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