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Vertical distribution and ontogenetic "migration" in coral reef fish larvae

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Abstract

Vertical distribution patterns were studied in the community of coral reef fish larvae around Tetiaroa (French Polynesia) using vertically stratified net tows within the first 100 m of the water column. These patterns were examined statistically using an approach based on the center of mass of larval patches. Regression trees first highlighted large differences between taxa, followed by an ontogenetic effect within each taxon. Many families displayed a vertical spread during ontogeny that accounted in part for a downward shift in the distribution of centers of mass. The spread suggests that, throughout ontogeny, individuals move within a wider range of depths rather than migrate downward synchronously. Both the spread and the shift were consistent at the community level despite the taxonomic differences. No difference in mean depth or spread was discernible between day and night, except for Serranidae, which were shallower at night. Environmental factors (such as thermocline depth or current shear) usually explained little variance, except for Lethrinidae and Blennidae, which were consistently deeper when the halocline was deeper. Although the overall effect of the observed ontogenetic spread in such a mildly stratified environment is likely to be small, it might still favor exceptional cases of retention, which can be important given the very low recruitment rate of coral reef fishes.

Rhythm is put in the oceans by the regular migration of organisms between depth and surface. Within the mixed surface layer, fish larvae are no exception, and vertical migration is one of the most studied of their behaviors (Leis 2006). Fish larvae migrate vertically at two temporal scales: they accompany most of the rest of the plankton in its diel or subdiel (e.g., tidal) migration, and their mean preferred depth also seems to change as they develop (Fortier and Harris 1989; Paris and Cowen 2004; Leis et al. 2005).

The vertical distribution of planktonic organisms was found to correlate with many environmental factors, such as light intensity (Munk et al. 1989; Job and Bellwood 2000; Guizien et al. 2006), temperature (Annis 2005), or the depth of clines (pycnocline, Munk et al. 1989; thermocline, Boehlert et al. 1992; Annis 2005; chlorophyll maximum, Lampert et al. 2003). In most cases, these correlations relate to diel or subdiel movements and presumably result from a trade-off between reaching high concentrations of food near the surface or around the clines (Munk et al. 1989) and avoiding surface-dwelling visual predators (Fiksen and Giske 1995) cold water at depth, which slows down growth (Lampert et al. 2003). A model including only the balance between swimming toward the food maximum and condition-related sinking was even sufficient to allow Sclafani et al. (1993) to explain a wide range of vertical distributions observed in the field for cod larvae (*Gadus morhua* L.). The most common explanation for diel vertical migration is therefore that organisms stay hidden at depth during daytime and go up to feed only at night, when obscurity keeps them safe from some of the predators (Lampert 1989). Downward ontogenetic vertical migration may also be a longer-term manifestation of this trade-off (Fortier and Harris 1989). For example, as fish larvae develop, the point where light is abundant enough to feed but dim enough to stay hidden from visual predators becomes deeper and deeper because their visual system improves (Job and Bellwood 2000). Temperature, because of its influence on metabolic rates (Brown et al. 2004), could also modulate this trade-off over the course of ontogeny: organisms living in deeper, colder waters have slower metabolism and hence need to find less food but also grow more slowly.

Besides influencing the probability to find food, these vertical movements also affect how larvae are advected by currents. Indeed, a shear is often noticeable between fast surface velocities and moderate flow at depth because of wind stress at the surface and/or bottom friction at depth. Therefore, moving a couple dozen meters vertically may have dramatic consequences on horizontal advection. For example, a model of oysters dispersal in Chesapeake Bay shows that vertical swimming by larvae greatly modifies their dispersal routes (North et al. 2008). On coasts featuring strong tides, synchronization of vertical migration with tides has been recognized as a very efficient means of transport, either inshore or offshore (Forward and Tankersley 2001; Fox et al. 2006). Ontogenetic vertical migration may also favor retention at all scales (Georges Bank, Werner et al. 1993; Banyuls Bay, Guizien et al. 2006; Barbados Island, Paris and Cowen 2004). Finally, more theoretical work suggests that exploiting vertical shears is an efficient strategy

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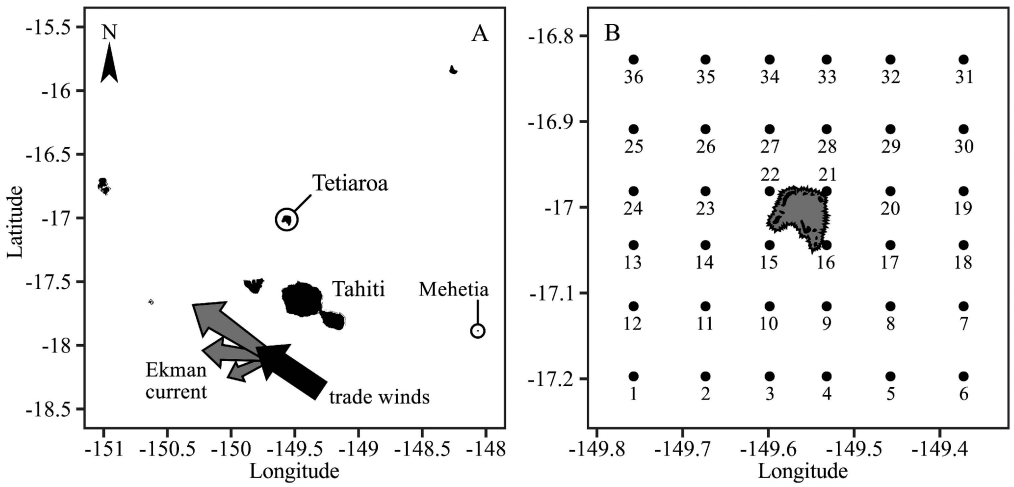

Fig. 1. (A) Map of Tetiaroa in the Society archipelago. The direction of trade winds is represented by a black arrow. The spiraling Ekman current it creates is represented by gray arrows. (B) Close-up on Tetiaroa (7 km across) and sampling stations. Stations were sampled in order, from 1 to 36, in less than 3 d.

to reach a settlement site, especially for larvae not capable of swimming against the flow (Armsworth 2001).

Because vertical migration affects both the survival rate and the trajectories of advection of larvae, it may shape the outcomes of the pelagic larval phase, influencing recruitment levels and connectivity routes (Mora and Sale 2002). However, the generality of the patterns of *ontogenetic* vertical migration in fish larvae as well as its potential causes are currently unknown.

Most of the data on vertical distribution of plankton come from stratified sampling by towed plankton nets (Boehlert et al. 1992; Cowen and Castro 1994; Paris and Cowen 2004). To interpret the results of these methods correctly, it is important to bear in mind that they describe the vertical *distribution* of larvae and do not give direct information on individual *migration* behavior. To relate distributions to behavior, one needs precise information on the causes and mechanisms behind vertical movement (e.g., hunger, swimming speed, buoyancy, distribution of predators, of food; Sclafani et al. 1993). Furthermore, the resolution of vertical movements can only be as fine as the thickness of the layers sampled by each net (usually several dozen meters). So, if individuals move around in a way that does not conspicuously modify the overall distribution of the population at this scale, the range of vertical movement of each larva could be very different from what is inferred from the distribution (Pearre 1979). At the other end of the scale, an ontogenetic shift in distribution toward depth could be the result of selective mortality near the surface, without any movement by larvae. Therefore, caution is advised when interpreting distribution data and trying to infer the movement of individuals, or even patches, from it.

This study seeks to detect and quantify shifts in the vertical distribution of coral reef fish larvae. Repeated, large-scale, vertically stratified sampling is used to describe the structure of the water column and the vertical distribution of larvae around an oceanic island. This approach should help answer the following key questions: Which environmental parameters drive the vertical distribution of larval fish, if any? Is ontogenetic migration detectable, and what is is vertical extent? How widespread is this behavior on a taxonomic level? The results are used to discuss the potential effect of observed vertical shifts on advection in a mildly stratified oceanic environment.

Methods

Sampling protocol—Thirty-six stations were repeatedly sampled around the atoll of Tetiaroa (149.55°W, 17°S; Fig. 1A) on 10–27 May 2006 aboard the NO *Alis*. The currents in the region are fueled by trade winds blowing from the Southeast, which create an Ekman transport toward the Northwest and West in the surface, mixed layer. To sample several different conditions and describe vertical distribution of larvae on a large scale, the stations were placed on a coarse grid around the atoll: 25 km from the atoll coastline to the farthest stations and a minimum of 8 km between stations, which was considered a good trade-off between sampling density and sample area (Fig. 1B). Indeed, 8 km was larger than commonly observed patch sizes (1–2 km, Kingsford and Choat 1989; 6 km, Williams and English 1992; 2–6 km, Paris and Cowen 2004) and therefore should have allowed independent sampling of individual larval patches.

At each station, physical and biological data were sampled simultaneously. A 4-m^2 opening, 800-μm mesh, Multiple Opening-Closing Net and Environmental Sampling System (MOCNESS) allowed stratified sampling of the planktonic fauna. Net 0 was lowered at 9–12 m min^{-1} from surface down to the maximum depth, then nets 1–4 were towed back up and opened sequentially at roughly 25-m intervals. The MOCNESS was towed at about 2.8 km h^{-1}. The speed of hauling by the winch varied within 3–5.5 m min^{-1} and was adjusted to keep the angle of the net close to 45°, which is optimal for fishing. Each depth bin sampled by a net was summarized by its mean depth in further analyses (*see* Statistical Analysis). To spread those means more uniformly and increase the resolution of vertical patterns, depth intervals were shifted

on a four-station cycle. At the first station of the cycle, a new net was opened (and the previous one was closed) at 105, 80, 55, 30 m. At the next station, depths were shifted up 5 m at 100, 75, 50, 25 m and again on the third and fourth stations. However, on the fourth, the last net fished from 20 m (instead of 15 m) to the surface because the volume sampled would have been too low to be representative otherwise. The maximum depth sampled was 105 m because most coral reef fish larvae concentrate in the first 100 m (the thermocline was about 70 m deep around Tetiaroa, and most larvae are above or near the thermocline; Cha et al. 1994). For each new survey, Sta. 1 was shifted to the next state in this four-state cycle to avoid sampling the same stations always at the same depths.

During the tow, net angle, volume filtered, conductivity–temperature–depth (CTD) and fluorescence data were sent to the ship every 4 s through the device's cable. At the end of the tow, the nets were rinsed with seawater, the sample of net 0 was preserved in 90% ethanol (for genetic identification, not detailed here), and sample collected in nets 1–4 were preserved in a solution of 4% buffered formaldehyde and seawater. Following the MOCNESS tow, the ship was stopped, and a 300-kHz Acoustic Doppler Current Profiler (ADCP) was lowered alongside the hull and measured the local flow every 18 s for 4 min, from 6-m down to 100-m depth, in approximately 24 layers (4-m interval). Each station took about 1 h to complete. During this time, the Differential Global Positioning System (DGPS) of the ship provided position at 1-s intervals (hence speed), and meteorological sensors provided wind speed and direction at 30-s intervals.

The grid was sampled continuously, day and night, and the 36 stations were completed in 68 h (2.8 d) on average. Immediately after sampling Sta. 36, the ship was repositioned to Sta.1 and a new sampling survey started. Three surveys were completed in a row, and a fourth one was done after a 4-d break.

Treatment of samples and data—In the laboratory, fish larvae were separated from other plankton in the MOCNESS samples, and reef fishes were identified to the lowest possible taxonomic level under a stereomicroscope using books such as those of Moser (1996), Leis and Carson-Ewart (2004), and Miller and Tsukamoto (2004). When identification was equivocal, several experts were solicited remotely through an online photographic database (http://cbetm.univ-perp.fr/larvae). When morphological characteristics could be identified clearly but not definitively associated with a taxon, morphological groups were defined. The ontogenetic stage of each individual was classified as preflexion (notochord completely straight), flexion (notochord bent but caudal fin not yet fully formed), and postflexion (notochord flexion approaching 90° and all caudal fin rays present). In the first 168 samples, the standard length of larvae was measured to the nearest tenth of a millimeter using the micrometer scale of a stereomicroscope. No correction for shrinkage was made.

Outliers in CTD profiles near the surface (0–50 m) were filtered out using techniques based on the median absolute deviation (Davies and Gather 1993). Then, the thermo-, halo-, and pycnocline depths were detected on smoothed profiles as the depths of maximum rate of variation of temperature, salinity, and density. Similarly, the fluorometry maxima (a proxy for the chlorophyll maxima) were identified on smoothed fluorometry profiles and their depths recorded.

ADCP measurements are highly variable inherently and particularly with the setting used here. To avoid outlying values, the start and end time records were discarded and the intermediate values filtered following the method of Paris et al. (2002). In addition, the ship drifted during the measurement, and its speed needed to be suppressed from the velocity measured by the instrument. Instantaneous ADCP records were taken every 18 s for 4 min. The drift speed of the ship was computed on 22-s intervals centered on each ADCP record, hence introducing a bit of overlap that smoothed instantaneous variability. For each interval, the distance drifted was computed from start and end DGPS positions assuming that the displacement occurred along a straight line. Then the drift vector was subtracted from the velocity measured by the ADCP. Finally, instantaneous measurement were averaged over the 4 min of recording. As the apparatus tended to drop some data at depth, the mean speed of each depth layer was computed only if at least five individual measurements were available for this layer.

Statistical analysis—Given the size of the grid, vertical positions of larvae were supposed to be independent between stations (> 8 km apart), and stations were considered as the statistical unit. At each station, the distribution of larvae in the four nets was summarized by the center of mass (z_{cm}) of the larval patch sampled at this station. While this approach simplified part of the information, it gave access to a wider array of statistical tools to dissect variance afterward.

The z_{cm} is computed as the mean of the depths sampled by each net, weighted by the proportion of larvae captured in those nets:

$$z_{cm} = \sum_i \frac{a_i}{\sum a_i} z_i \quad (1)$$

where z_i is the mean of the depth range sampled by net i and a_i is a measure of the abundance of larvae in net i. Each net does not necessarily sample homogeneously within its depth range of action, so z_i was actually computed from the individual MOCNESS records: for every 4-s interval, the mid-depth of the interval was weighted by the volume sampled during the interval, and the overall mean depth was computed per net. Because the volume sampled usually also varies between nets, captures have to be scaled by the sampling effort per net. Hence, they are first transformed into concentrations and then into *standardized abundances* following Röpke et al. (1993):

$$a_i = a_i^{std} = \frac{a_i^{raw}}{v_i} h_i 1 \quad (2)$$

where the subscript i denotes the net, a^{raw} is the raw abundance, v is the volume sampled in m^3 (a/v is the concentration), h is the depth range sampled by each net in meters, and 1 is a dimensionalization constant in m^2.

Equation 1 justifies the sampling strategy presented above: it provides a more uniform distribution of z_is within 0–100 m than classic constant depth bins, therefore increasing the power of regression-based analyses and the overall resolution.

One z_{cm} was computed per station, using Eq. 1 applied to the concentrations of the whole community or of certain groups (divided taxonomically, ontogenetically, and so on) depending on the question at hand. z_{cm}s of all stations were considered equally informative despite potentially large differences in concentration between stations. Indeed, the interest was in the relative position of larvae along the vertical, not in their absolute abundance. The z_{cm}s were then treated as any numerical data, accounting for the fact that z_{cm}s are bounded at the surface and possibly at depth and hence not normally distributed. The gamma distribution, which is bounded at zero, was used for parametric approaches.

Successive regression trees (Breiman et al. 1984) were constructed to rank the factors influencing the distribution of z_{cm}s and ensure that other sources of variance were not obscuring the effect of ontogeny. Regression trees divide observations into groups depending on the value of one explanatory variable. The divisions maximize intergroup variance relative to intragroup variance. Successive splits explain less and less variance, so the explanatory variables driving the first splits are the ones most structuring for the data set. The explanatory variables considered here, in addition to ontogeny, were taxonomy (family), time of day, geography (latitude, longitude, and location with respect to the atoll, i.e., windward, leeward), and hydrography (depth of thermo-, halo-, pycnoclines and of the fluorometry maximum, mean current speed in the surface layer, and current shear between surface and depth). When variables were obviously correlated (e.g., depths of thermo- and pycnocline, which are linked by the formula used to compute density from temperature, salinity, and depth), they were tested independently, and only the most explanatory was kept in the final tree.

The effect of discrete explanatory variables was investigated by comparing z_{cm}s between groups (by taxon, by ontogenetic stage, and so on) using nonparametric tests for the difference in medians (Wilcoxon–Mann–Whitney and Kruskal–Wallis) and homogeneity of variances (Fligner–Killeen). When variances are different, the α-error risk of the classic nonparametric tests increases (Kasuya 2001; Neuhäuser 2002), and only robust rank procedures can be used (Fligner and Policello 1981) when distributions are symmetric (Zumbo and Coulombe 1997). Distributions were asymmetric here, so the only fallback was to lower the significance level of the Wilcoxon–Mann–Whitney or Kruskal–Wallis tests to 0.01.

The effect of continuous explanatory variables was estimated by regression using generalized linear models (GLMs) with a gamma distribution of errors to account for the bounded distribution of z_{cm}s.

The size of the 3624 coral reef fish larvae that were measured was used as a proxy for development. Indeed, larvae usually reach a particular ontogenetic level at a given size rather than at a given age (Fuiman and Higgs 1997). As size varies greatly among fish taxa, sizes were normalized per taxon: for each of the lowest taxonomic units identified, the size of the smallest fish captured was set to zero, and the size of the largest fish was scaled to one. While the ranges of ontogenetic stages captured probably differed between taxa (i.e., size = 1 did not correspond to the same point in development for all taxa), this still brought sizes on a more comparable scale. Relative sizes were then averaged across taxa and per station, hence smoothing out vertical patchiness and taxonomic differences in order to focus on large-scale, community-level processes. Finally, a regression analysis was used to test whether there was a continuous change in vertical distribution during ontogeny (i.e., along with increasing sizes). Mean relative sizes were regressed against the community z_{cm}s with a GLM featuring gamma errors to account for the bounded distribution of z_{cm}s.

All analyses were performed in R (R Development Core Team 2009), with the additional package mvpart (De'ath 2007) for regression trees.

Table 1. Abundances of the 10 most abundant families of coral reef fishes. Both total abundance and abundance per ontogenetic stage are reported. The most abundant stage is shown in bold. NA = nonavailable ontogenetic stage (usually larvae with a damaged tail).

Family	Total	Preflexion	Flexion	Postflexion	NA
Acanthuridae	2907	**2543**	261	81	22
Labridae	826	30	151	**643**	2
Holocentridae	756	**662**	48	43	3
Lutjanidae	654	**466**	136	42	10
Scaridae	624	19	30	**573**	2
Pomacentridae	541	119	**281**	137	4
Apogonidae	506	78	201	**226**	1
Serranidae	442	**246**	117	75	4
Lethrinidae	428	**312**	94	19	3
Gobiidae	337	1	6	**329**	1

Results

Of the 576 MOCNESS samples, 572 could be used. The mean volume filtered per sample was 1056 m^3 (SD = 302 m^3). They contained an estimated 47,800 fish larvae, comprised of at least 94 families (pelagic or deep-water taxa were not all sorted). Epi- and mesopelagic species were more than twice as abundant as coral reef fish larvae. The two most common orders were the Clupeiformes (mostly Engraulidae) and the Myctophiformes; 10,794 coral reef fish larvae were identified, and the most common, by far, were Acanthuridae (Table 1). The relative abundances of coastal vs. oceanic taxa were comparable to those observed around another isolated atoll in the tropical North Pacific (Boehlert et al. 1992) or in the Florida Keys (Limouzy-Paris et al. 1994). Compared to the Florida Keys, Bregmacerotidae were notably less prominent, and Acanthuridae were particularly abundant. Among these > 10,000 coral reef fish larvae, 3624 were measured, and the median body length was 3.5 mm; 10% and 90% quantiles were 2.47 and 6.3 mm, respectively. Small, young

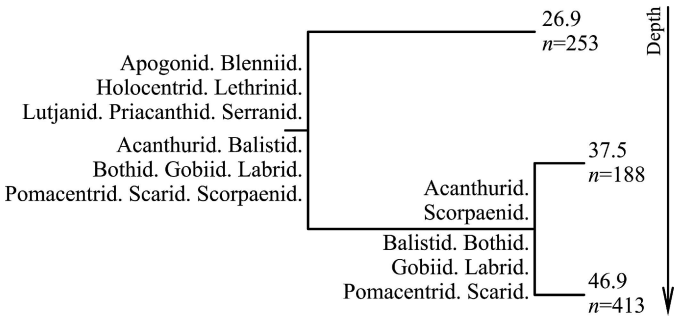

Fig. 2. Univariate regression tree of the z_{cm}s (computed by station, family, and stage) against taxonomic (family), physical (depth of the thermocline and the fluorometry maximum, time of day, geographic location, and current shear), and ontogenetic (flexion stage) factors. Splits separate groups of observations most different from one another. Both splits separate groups of families, hence indicating a strong taxonomic effect. The length of branches is proportional to the variance explained by each split. The numbers at the tip of branches are the average z_{cm} and the number of observations in the group defined by the preceding splits.

larvae dominated the samples in most families (Table 1) probably reflecting both an age structure driven by mortality, where successive ontogenetic stages become rarer and rarer, and avoidance of the net by larger, older, and hence more behaviorally capable larvae. The early ontogenetic stage limited most identifications to family level. Indeed, given the important biodiversity in the region, fin rays and spine counts were often required to identify genera, and they are not fully developed in preflexion- and flexion-stage larvae.

Hierarchy of factors affecting vertical distribution—A univariate regression tree was built to rank the effect of taxonomy, physical variables, and ontogeny on the location of the z_{cm}, computed per family and per stage, at each station. The first splits, robust after cross validation, showed a strong effect of taxonomy (Fig. 2). Some families, such as Lutjanidae, Lethrinidae, and Holocentridae, were systematically higher in the water column than others. These two splits alone accounted for 23% of the variability (residual cross-validated error = 0.77). This result was confirmed by a significant difference between per-family z_{cm}s (Kruskal–Wallis, $\chi^2 = 211.43$, df = 9, $p < 10^{-16}$, but variances were different: Fligner–Killeen, $\chi^2 = 29.7$, df = 9, $p = 0.0005$).

After normalization of the influence of family, a new tree highlighted an effect of ontogeny, whereby preflexion and flexion larvae were higher in the water column than postflexion ones. Besides ontogeny, some geographic (location with respect to the atoll) as well as hydrographic (thermocline depth, current shear) factors appeared, but both were less robust after cross validation. The ontogenetic effect was the only one resisting cross validation and accounted for 7% of the variance in the new, normalized data set.

The taxonomic influence was very strong at the family level, but only a few differences between the distributions of subfamily taxonomic groups were significant. For example, within the Serranidae, Epinephelini were higher in the water column than Grammistini (Fligner–Killeen, $\chi^2 = 1.1$, df = 1, $p = 0.3$; Wilcoxon, $W = 5$, $p = 0.002$). A difference also existed among the five identified genera and morphological groups of Acanthuridae (Fligner–Killeen, $\chi^2 = 16.24$, df = 4, $p = 0.002$; Kruskal–Wallis, $\chi^2 = 83.43$, df = 4, $p < 10^{-16}$). However, the number of larvae involved in these comparisons was, of course, lower than at the family level, and results could have been confounded by non-taxonomic factors, such as ontogeny. For example, most Grammistini were postflexion, while most Epinephelini were preflexion.

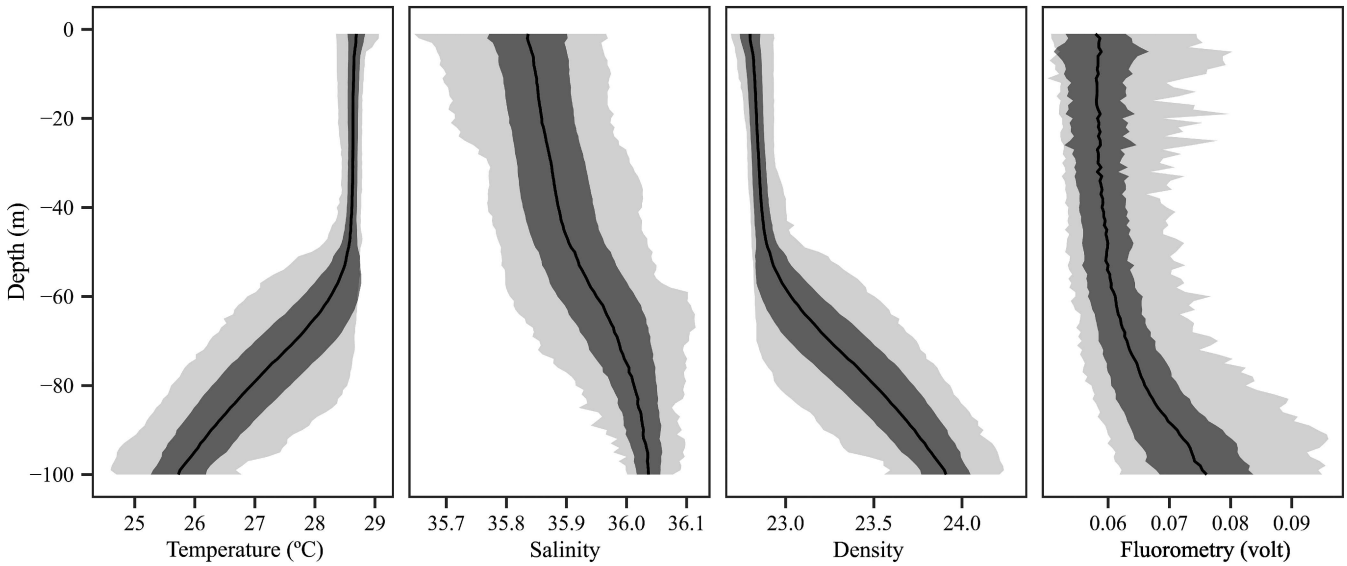

Fig. 3. Temperature, salinity, density, and fluorometry profiles measured by the MOCNESS net on 0–100 m for all stations. The solid line is the mean, the dark gray shape is the standard deviation around the mean, and the light gray shape is the range of the data.

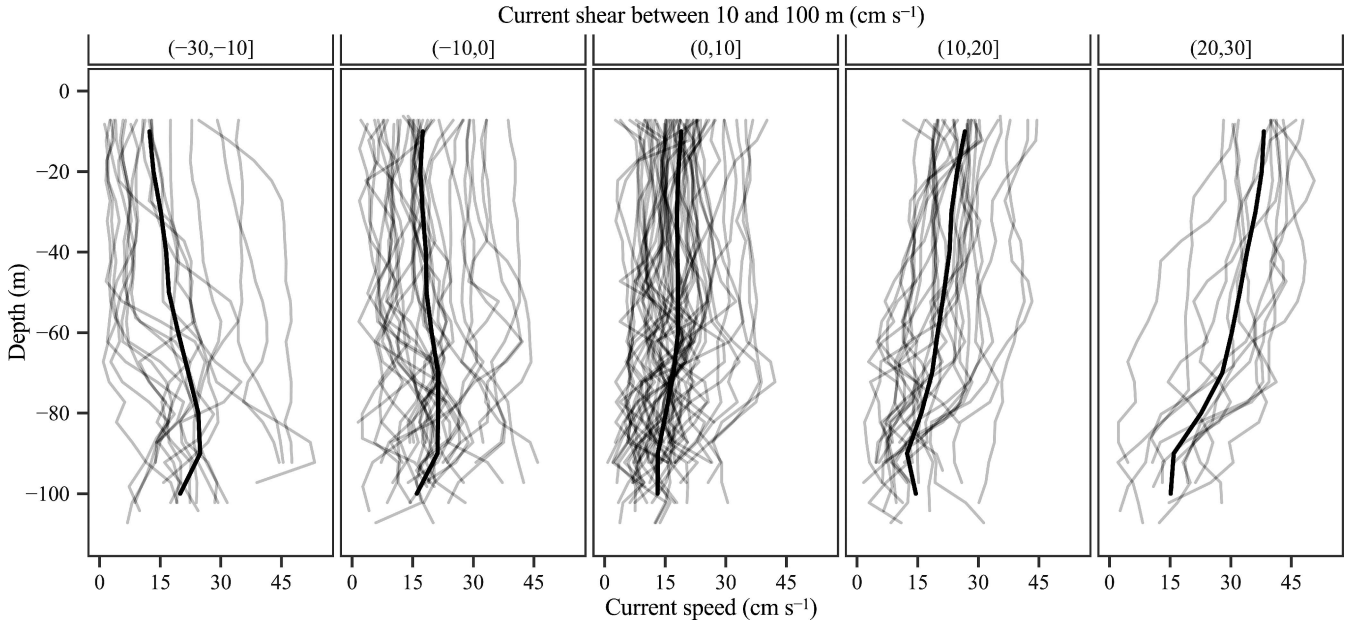

Fig. 4. Profiles of current speed on 0–100 m for all stations, grouped by the amount of shear between current at 10 and 100 m. Shear was computed on profiles smoothed by a spline function to erase local variation and obtain a better representation of the actual slope of the profile. For each shear category, the average profile is plotted as a thicker line.

The influence of geographic location mentioned above was probably caused by differences in physical conditions between these locations. For example, the depth of the bottom of the mixed layer varied between 45 and 75 m, as can be seen on the temperature or density profiles (Fig. 3). No effect was significant in a GLM regression, with a gamma error distribution, of the community-mean z_{cm} on the depth of clines and the fluorometry maximum. Similarly, a multivariate regression of the z_{cm}s of the most abundant families on the same variables was not significant. While there did not seem to be a common trend across taxa, some of the individual GLM regressions were significant. For example, deeper z_{cm}s were associated with deeper thermoclines in Lethrinidae ($p = 0.0005$) and Gobiidae ($p = 0.023$) and with shallower thermoclines in Bleniidae ($p = 0.031$). All the slopes were about $\pm$ 0.5 (a 40-m variation in thermocline was accompanied by a mean shift of 20 m in z_{cm}), but the overall variance explained was low ($\sim$ 5%). The halocline was less consistent overall (Fig. 3), but the GLM regressions, which consider data per station (i.e., per profile), were significant for Lethrinidae ($p = 0.035$), Lutjanidae ($p = 0.011$), and Pomacanthidae ($p = 0.026$). The slopes were about one-third (the depth of the z_{cm} increased with the depth of the halocline), and the variance explained was 16%, 9%, and 25%, respectively.

Current speeds ranged from 1 to 53 cm s^{-1}, with an average of 19.8 cm s^{-1} (SD = 10.5 cm s^{-1}). The vertically averaged current speed per station did not influence z_{cm}s, according to GLM regressions for the total community or per family. Nevertheless, the shear between surface and depth (here computed between 10 and 100 m) might be more related to vertical position than speed averaged over the water column. The absolute value of the shear was < 10 cm s^{-1} for 60% of the stations (panels (−10,0] and (0,10] in Fig. 4), with occasional spikes above 20 cm s^{-1}. In 35% of the stations, current was actually faster at depth than near the surface (i.e., negative shear in Fig. 4). GLM regressions revealed that current shear influenced z_{cm}s in some families (Apogonidae $p = 0.0001$, Blenniidae $p = 0.013$, Chaetodontidae $p = 0.001$, Holocentridae $p = 0.001$, Lethrinidae $p < 10^{-4}$, and Lutjanidae $p = 0.002$) but that its influence was weak. Surprisingly, larvae were higher in the water column when the shear was strong, that is, when diving down would have had the most influence. Stronger shear was not associated with particular stratification (no significant relation between shear and depth or strength of the thermo-, halo-, or pycnocline in a linear regression analysis). However, the effect of shear on z_{cm} seemed driven by only a few stations with shallow z_{cm}s and strong shear. And indeed, when the scope of the analysis was reduced to most common values of the shear (between −20 and 20 cm s^{-1}), no regression was significant. The results were similar when restricted to the more mobile postflexion larvae.

The existence of a diel vertical migration was tested for each family because of its prevalence in the literature. Values of the z_{cm}s revealed a tendency for upward movement at night in all families, but the difference between day and night was significant only for Serranidae (average z_{cm} during the day: 55 m; night: 40 m; Fligner–Killeen, $\chi^2 = 1.1$, df = 1, $p = 0.3$; Wilcoxon, $W = 480$, $p = 0.02$). Late-stage larvae are more mobile and hence more likely to migrate on a daily basis, but the differences were still not significant when the comparisons were restricted to postflexion larvae. In addition, while coral reef fish larvae were found to be more diffused at night when observed in the first 20 m of the water column (Leis 1991, 1993), no difference in spread between day and night was evident here

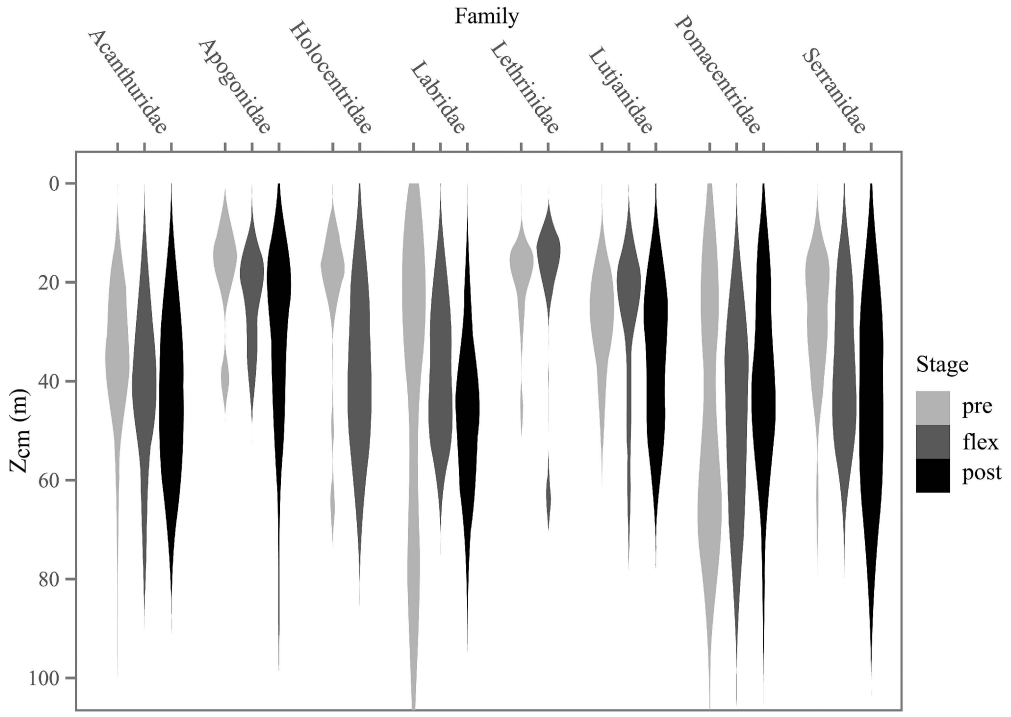

Fig. 5. "Violin" plot of the distribution of z_{cm} by family and ontogenetic stage. Each shape represents the probability density function of z_{cm}s on the range 0–100 m (estimated via kernel density at 512 points). That is, the width of the violins represents the proportion of z_{cm}s in function of depth. The probability density was not estimated for postflexion larvae in Lethrinidae and Holocentridae because catches were too low.

on a 0–100-m scale (Fligner–Killeen, $p > 0.1$, for the 10 most abundant reef fish families).

Ontogenetic shifts in vertical distribution—As taxonomic differences in z_{cm} were prominent, the effect of ontogeny was first tested within each family. Among the ten most abundant families (Table 1), only eight had enough catches in different ontogenetic stages to warrant further analysis (Gobiidae and Scaridae were excluded because almost all larvae were postflexion).

The centers of mass for postflexion larvae were detected throughout the water column, while preflexion larvae were usually more localized (Fig. 5). However, when tested as a difference in variance, this spread was never significant (though very close to significance for Apogonidae; Table 2). The location (i.e., median) of the centers of mass, on the other hand, was significantly different between stages for four families: Acanthuridae, Holocentridae, Labridae, and Serranidae (Table 2). All these families displayed a clear downward ontogenetic shift in vertical distribution, as highlighted in Table 2 and Fig. 5. Pomacentridae, however, seem to display an inverse pattern whereby postflexion larvae are on average shallower than flexion and preflexion larvae, although the differences are not significant. For families in which enough genera were identified (Acanthuridae, Lutjanidae, and Pomacentridae), the behavior in each genus seemed remarkably consistent with the tendencies displayed at the family level. However, at this level, the

Table 2. Tests for differences in variances (Fligner–Killeen) and medians (Kruskal–Wallis) for the z_{cm}s of different ontogenetic stages of eight abundant families of coral reef fishes. For Lethrinidae and Holocentridae, only preflexion and flexion stages were used. For each test, both the test statistic and the *p*-value are reported (values are shown in bold in significant tests and italicized in close-to-significant ones). In the last three columns are the median z_{cm}s (in m) for each family and stage.

	Variance		Median		z_{cm}		
Family	χ^2	*p*	χ^2	*p*	Preflexion	Flex	Postflexion
Serranidae	5.07	0.08	7.86	**0.02**	29	36	45
Pomacentridae	4.02	0.13	2.63	0.27	58	46	41
Lutjanidae	1.16	0.56	2.16	0.34	27	22	31
Lethrinidae	2.66	0.26	3.12	0.21	17	14	—
Labridae	0.63	0.73	7.91	**0.02**	26	38	47
Holocentridae	3.12	0.21	6.10	**0.047**	17	40	—
Apogonidae	6.07	*0.05*	5.88	*0.053*	15	20	24
Acanthuridae	1.38	0.5	6.44	**0.04**	35	41	43

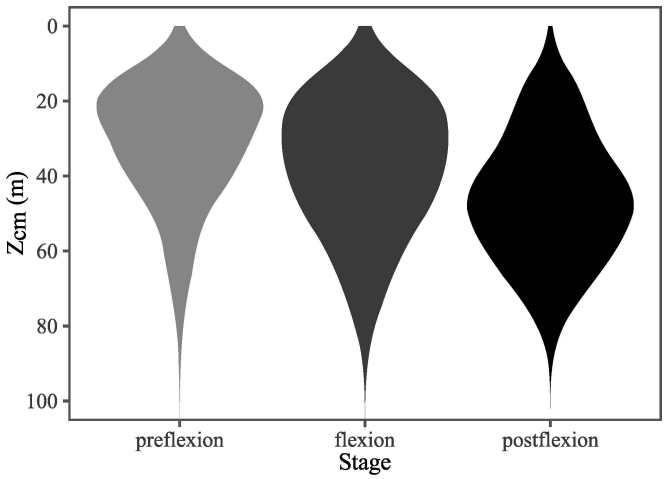

Fig. 6. Violin plot of the vertical distribution of z_{cm} computed for the global community (all families) at three ontogenetic stages.

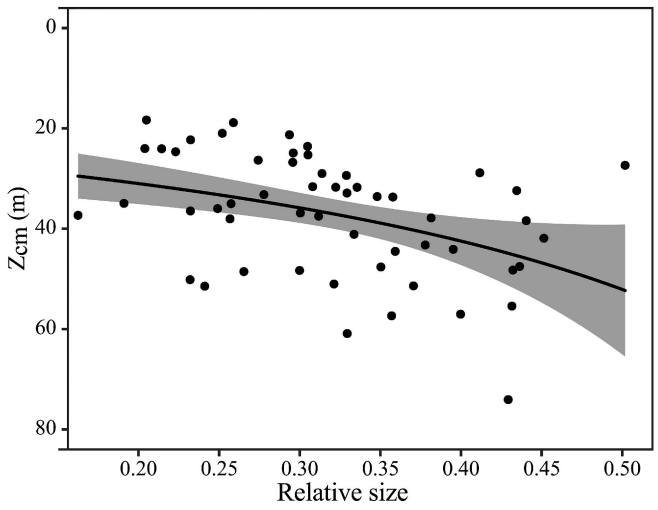

Fig. 7. Z_{cm} per station for the global coral reef fish community in function of mean relative size of larvae at the corresponding station (size information was available for 55 stations). Dots are data points (i.e., stations), the solid line is the fit from a GLM model with a gamma error distribution, and the shaded area is the 95% confidence interval around the fit.

number of z_{cm} per group was often low, and the tests were not conclusive.

In all cases in which a shift in distribution was significant, it occurred in the same direction: from surface toward deep water. This effect was already suggested by the second regression tree once z_{cm}s were normalized by family. This suggested the existence of a global ontogenetic trend beyond taxonomic differences. Indeed, at the community level, the ontogenetic shift toward depth was significant (Kruskal–Wallis, $\chi^2 = 111.4$, df = 2, $p < 10^{-15}$; variances were homogeneous: Fligner–Killeen, $\chi^2 = 4.2$, df = 2, $p = 0.12$). All stages were distributed differently from one another (Wilcoxon, with Holm's correction for multiple testing: preflexion–flexion, $p < 10^{-5}$; flexion–postflexion, $p < 10^{-8}$; preflexion–postflexion, $p < 10^{-15}$), and postflexion larvae were on average 25 m lower in the water column than preflexion stages (Fig. 6).

Similarly, the regression between mean relative size (a proxy for the advancement of development) and z_{cm}, computed at the level of the whole community, was significant (GLM with gamma errors, $p = 0.0023$) and explained 16.3% of the variance in z_{cm}s. As shown in Fig. 7, z_{cm}s were deeper at stations where larvae were larger (i.e., older) on average.

Discussion

Factors shaping the vertical distribution—The z_{cm} analysis first highlighted that different families had contrasting vertical distributions and that taxonomy was the most important factor determining the vertical assemblages of coral reef fish larvae. Analyses were mostly inconclusive when conducted at taxonomic levels under family, probably because of the small sample sizes imposed by the difficulty of identifying larvae to genus. Only more extensive sampling or other identification techniques (such as genetic barcoding; Hebert et al. 2003) could have overcome this limitation. When these analyses were possible, however, they highlighted possible intrafamily differences in vertical distribution (for Acanthuridae and Serranidae). The only documented cause of taxonomic differences in vertical positioning are family-level differences in the minimum intensity of light required to feed and hence in the maximum sustainable depth (Job and Bellwood 2000). Based on those requirements, Apogonidae should be deeper in the water column than Pomacentridae because they have a more sensitive visual system. However, the opposite was observed here (Fig. 5), even though Apogonidae were on average older than Pomacentridae (45% and 26% of larvae in the postflexion stage, respectively) and therefore had even better vision. In the clear waters bathing Tetiaroa, light intensity in the first 100 m may not be as limiting as it might be in other environments. In such an oligotrophic environment, another possibility is that the distribution of larvae relates to the distribution of their scarce zooplanktonic prey, even more than in temperate systems (Munk et al. 1989). The diet of coral reef fish larvae appears to be quite specific, and different taxa are not likely to eat the same prey (Llopiz and Cowen 2009). If those prey are distributed differently, fish larvae would probably tend to concentrate where their respective prey are most abundant. Finally, swimming abilities are also species specific (Fisher et al. 2005), and both horizontal swimming and vertical placement influence dispersal trajectories (Werner et al. 1993; Irisson et al. 2004; Paris and Cowen 2004). In fact, their interaction might be of prime importance because slow swimmers or larvae with little energetic resources would benefit more from staying deeper in the water column, in usually slower currents, than fast swimmers would (Armsworth 2001). Overall, those differences in vertical position are likely to exemplify the array of ecological strategies displayed by different taxa: they are distinct solutions to the trade-offs between feeding,

growing, and surviving that larvae face during their pelagic phase.

The absence of significance in diel distribution patterns is intriguing given the prevalence of diel vertical migration in the literature and textbooks (Lampert 1989; Kaiser et al. 2005). The sampling strategy was not designed to capture daily migration of a specific group of individuals—it would have been more appropriate to follow and sample repeatedly a single patch throughout several days. So the results may have been obscured by interpatch variability. Yet this source of variability did not prevent the detection of the ontogenetic signal. Furthermore, diel vertical migration has often been described for late-stage larvae or juvenile fishes (Leis 1993; Brodeur and Rugen 1994) and may be more obvious in larvae older than those caught here. Here, it was still not detected more clearly in postflexion larvae than in the total population. In this data set, the distribution of the population of larvae suggests the existence of upward movement at night but does not allow one to actually detect diel vertical migration.

The effect of the depth of clines was only significant for a few taxa and generally explained little variance (notable exceptions were Lethrinidae and Bleniidae, which followed the halocline). The top of the thermocline was usually below 60 m within the sampling domain (Fig. 3), and many families were distributed mostly above it (Fig. 5). With such little overlap, there was no room for variations in temperature to influence the distribution of larval fish. Furthermore, clines were quite diffuse. For example, three deeper CTD casts suggested that the temperature decline observed between 60 and 100 m continued steadily down to at least 300 m, while salinity stabilized. So, in this region, the thermo- and haloclines were not the sharp boundaries they can be in temperate ecosystems. They were therefore less likely to be limiting the bottom of the distribution of fish larvae.

Local current conditions also seemed to have little influence on the vertical placement of larvae. When they had, larvae of all ages were found to be most abundant near the surface where the current was fast, which is contrary to the usual hypothesis that larvae exploit vertical heterogeneity to avoid advection (Paris and Cowen 2004). However, these correlations may be artifacts caused by a few shallow nets that sampled a fast surface current and had above-average captures. Those could either be very local events or be the result of sampling bias because larvae are less capable of escaping the net when they face a strong current. In any case, the general pattern was that larvae of all ages did not react to local shear. Larvae are embedded within the moving water mass, and, without a geostatic reference, there is no basis for them to sense its large-scale movement (Montgomery et al. 2001). While they might be able to sense small-scale shears by moving along the vertical, they might not react to shear on the 10–100-m scale typically measured in oceanography.

Ontogenetic vertical ''migration''?—Old larvae were found to be significantly deeper in the water column than young ones, either in the total community or in some abundant families (Acanthuridae, Holocentridae, Labridae, and Serranidae). The fact that population-level ontogenetic shifts were significant and consistent across families despite interpatch variability underlines the importance and universality of this process. Notable exceptions were Pomacentridae, which showed a tendency for an upward ontogenetic shift. This is consistent with observations from Atlantic coral reef fish communities, suggesting that some genera of Pomacentridae, but not all, display an inverse ontogenetic shift (Cowen 2002). Such heterogeneity of behaviors within the Pomacentridae are likely to obfuscate the patterns at the family level and, together with limited sample sizes, explain the nonsignificance of results here.

As noted in the introduction, the description of shifts in the *distributions* might in fact not relate directly to individual *migration* behavior. A possible source of artifacts would be differential mortality. First, within a family, if two species were distributed differently and one suffered higher mortality than the other, the patterns at the family level would change through time, without this being related to ontogenetic vertical migration. However, ontogenetic shifts, when significant, were consistent across families. It seems very unlikely that all were confounded in the same way by differences at lower taxonomic levels. Second, if larvae suffer higher predation in the surface layer (e.g., because predators are more abundant or larvae are more visible; Lampert 1989) or faster advection out of the sampling domain because of stronger surface currents (Paris and Cowen 2004), the relative abundance of deep-dwelling larvae would increase, and distributions would give the false impression of a vertical movement. However, Apogonidae, for example, were still very abundant near the surface after flexion. In fact, in most families, many postflexion larvae were present in the surface layer. The only difference with preflexion larvae is that they were *also* abundant at depth (Fig. 5).

This vertical spread throughout ontogeny could explain, at least in part, the downward shift of the median z_{cm}. Here also, the downward shift in the descriptor of the distribution of the population might not relate to a consistent downward movement of all individuals. Indeed, the spread suggests only that young larvae were somehow restricted to shallow depths. A restricting factor for young larvae could have been light (Job and Bellwood 2000), but it was remarked above that light did not seem to be limiting in this system. Another explanation for the spread could be that diel vertical migration did occur in postflexion larvae but was not necessarily synchronized for all individuals of the population. Indeed, migration is often considered to be determined by an energetic balance (Lampert 1989; Fiksen and Giske 1995) that is specific to each individual. Differences in feeding histories and energetic reserves would translate into differences in the timing of the migration (Kristiansen et al. 2009). Overall, larvae could therefore be captured at different moments in their diel cycle, the diel signal would be blurred, and the vertical extent of the blur would increase during ontogeny as larvae become more mobile. In any case, the amount of movement at the level of the individual would not necessarily relate to what is measured on the distribution of the population.

Beyond taxonomic differences, the vertical spread and downward shift of the mean z_{cm} during ontogeny were widespread and clearly showed at community level (Fig. 6). They may represent a common strategy to increase self-recruitment because downward movement has been shown to increase retention (Werner et al. 1993; Paris and Cowen 2004). Yet the bulk of dispersal trajectories in the population is still likely to be unaffected because few larvae reach the postflexion stage (Table 1), only some of them would spend significant time at depth because larvae seem to spread rather than all migrate down (Fig. 5), and current shear around Tetiaroa was on average mild (Fig. 4). However, only 1 in 10^5 larvae finally recruits (Doherty 1983), so it may well be that this common ontogenetic strategy "fails" in many cases but participates in the few exceptional recruitment events that eventually sustain local populations.

The confusion between individual migration behavior and population-level distribution highlights how little is currently known about the behavior of larvae and how important its details can be for the outcome of the larval phase. The consistency of the ontogenetic spread and shift across families and at the community level would ease their necessary inclusion in models. Indeed, large-scale field studies, such as this one, can help in identifying the processes at play during the larval phase but cannot single out exceptions that might be essential to recruitment. For those, the implementation of said processes in numerical models, calibrated with empirical data, can be more effective. It requires, however, to explicitly explore rare events in simulations and, despite their probabilistic nature, not limit the analysis by focusing only on the mean.

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