Born at the right time? A conceptual framework linking reproduction, development, and settlement in reef fish

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Abstract. Parents are expected to make decisions about reproductive timing and investment that maximize their own fitness, even if this does not maximize the fitness of each individual offspring. When offspring survival is uncertain, selection typically favors iteroparity, which means that offspring born at some times can be disadvantaged, while others get lucky. The eventual fate of offspring may be further modified by their own decisions. Are fates of offspring set by birthdates (i.e., determined by parents), or can offspring improve upon the cards they've been dealt? If so, do we see adaptive plasticity in the developmental timing of offspring? We evaluate these questions for a coral reef fish (the sixbar wrasse, *Thalassoma hardwicke*) that is characterized by extreme iteroparity and flexible larval development. Specifically, we monitored larval settlement to 192 small reefs over 11 lunar months and found that most fish settled during new moons of a lunar cycle (consistent with preferential settlement on dark nights). Settlement was significantly lower than expected by chance during the full moon and last quarter of the lunar cycle (consistent with avoidance of bright nights). Survival after settlement was greatest for fish that settled during times of decreasing lunar illumination (from last quarter to new moon). Fish that settled on the last quarter of the lunar cycle were ~10% larger than fish that settled during other periods, suggesting larvae delay settlement to avoid the full moon. These results are consistent with a numerical model that predicts plasticity in larval development time that enables avoidance of settlement during bright periods. Collectively, our results suggest that fish with inauspicious birthdates may alter their developmental trajectories to settle at better times. We speculate that such interactions between parent and offspring strategies may reinforce the evolution of extreme iteroparity and drive population dynamics, by increasing the survival of offspring born at the "wrong" time by allowing them to avoid the riskiest times of settlement.

Key words: developmental delay; life history; lunar periodicity; nocturnal illumination; phenology; post-settlement processes; recruitment; reef fish; size at settlement.

Introduction

"Timing is everything," or so the saying goes. Birth order and timing of reproduction can determine survival, shape personalities, and influence other opportunities for offspring (Altus 1966, Semlitsch et al. 1988, Thomas et al. 2001, Platt et al. 2003, Verdu and Traveset 2005, Duckworth et al. 2015). Parents choose when to reproduce, and offspring may be left to play the hand they've been dealt. Thus, we may ask, can offspring alter their developmental rates and trajectories to compensate for a poorly timed birth? If so, how does this plasticity affect patterns of population replenishment and subsequent dynamics?

These are important and relatively unexplored questions for many marine reef organisms that have complex life cycles (Caley et al. 1996). In marine reef ecosystems, adults are often iteroparous and produce many offspring (eggs, larvae) that develop, disperse, and mostly die (White et al. 2014) in offshore waters before survivors settle back to reef habitats. The process of settlement is also risky (Doherty et al. 2004). Thus, many species have larvae that settle at a higher rate during new moons of a lunar cycle (e.g., Rankin and Sponaugle 2014) when peak tidal amplitudes can enhance transport to settlement destinations (Forward and Tankersley 2001), and cover of darkness reduces predation rates (Acosta and Butler 1999). Dark periods of a lunar cycle may represent a good settlement window (sensu Pineda et al. 2006) for larvae of many marine reef organisms (see Todd and Doyle 1981 for an analogous example involving prey resources).

Adults should make decisions about reproductive timing and investment that maximize their own fitness, even if this does not maximize the fitness of each offspring (Warner 1998). Environmental uncertainty often selects

for iteroparity as a diversified bet-hedging strategy (Wilbur and Rudolf 2006). Adults of many reef fish are highly iteroparous, spawning on a fairly continuous basis (Claydon et al. 2014) to produce larvae with a wide range of birthdates. Larvae spawned at certain times may have better odds of survival (e.g., well-timed to hit a favorable settlement window; Fig 1a) than others that were spawned at less advantageous times. However, larvae of many reef organisms also have plastic developmental rates (Victor 1986, Sponaugle and Cowen 1996, Robertson et al. 1999), excellent sensory and locomotory capabilities (Leis 2006), and are therefore well equipped to change where and when they settle (Shima 2001a). A high degree of plasticity could enhance larval survival and concentrate settlement compared to what would be predicted based upon birthdate alone. Both increased survival and synchrony could enhance the strength of density dependence and thus alter spatial and temporal population dynamics and regulation.

Here, we investigate patterns of larval settlement for a coral reef fish (the sixbar wrasse, *Thalassoma hardwicke*) that exhibits life-history traits common to many reef organisms: adults are highly iteroparous (Claydon et al. 2014), and they produce larvae with flexible developmental durations (Victor 1986, Fig 1a). First, we evaluate the hypothesis that sixbars settle non-randomly across the lunar cycle, with greatest settlement during the new moon (indicative of a good settlement window; e.g., Sponaugle and Cowen 1996, Robertson et al. 1999). Second, we ask whether the distribution of sizes of settlers (arriving across the lunar cycle) is consistent with a hypothesis that individuals adjust their developmental rates to target new moons and/or avoid full moons (e.g., Sponaugle and Cowen 1996, Robertson et al. 1999). Third, we explore post-settlement survival and growth of sixbars that settled during different periods of the lunar cycle. Finally, we use a simple mathematical model to explore fitness payoffs to larvae that can change their development times. We evaluate empirical results against the optimal developmental durations predicted by this simulation. Collectively, our results support a conceptual model in which flexible development and associated demographic consequences likely contribute to a type of eco-evolutionary feedback (sensu Schoener 2011) that should reinforce iteroparity, as adaptive plasticity in the timing of settlement by larvae will reduce a potential cost of adult iteroparity by increasing the survival of offspring born at the "wrong" time.
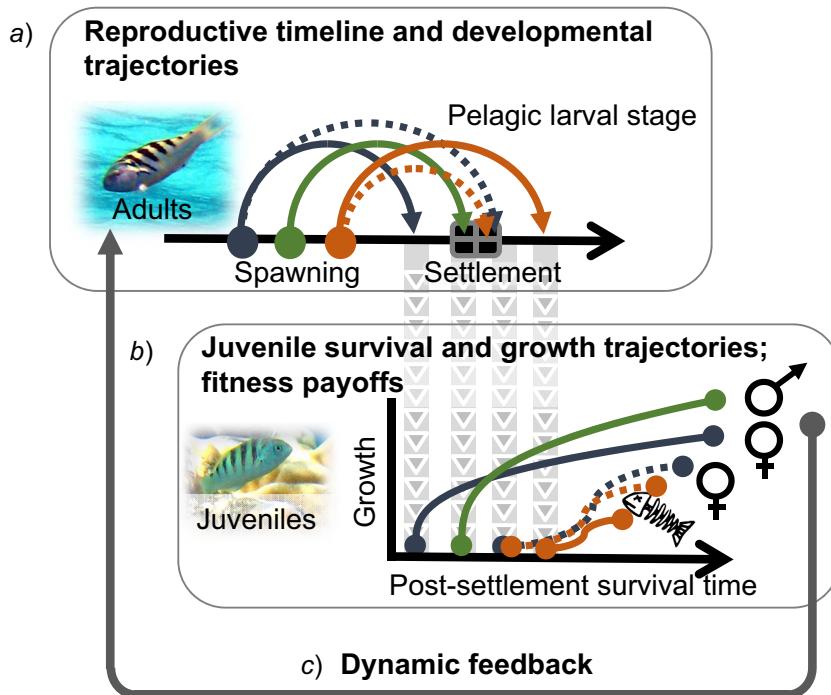

Fig. 1. Iteroparity, developmental plasticity, and good/bad times to settle. Conceptual framework: (a) Daily spawning and a characteristic developmental time means some individuals will hit a favorable settlement window (e.g., green trajectory is well timed to hit a settlement window corresponding to a new moon period). Others will settle early (solid blue trajectory), late (solid orange trajectory), or alter their development (dashed trajectories) to settle at a good time. (b) Birthdates and/or developmental trajectories may affect subsequent survival (length of lines), growth (curves), and maturation (e.g., pattern and timing of sex differentiation in a protogynous hermaphrodite), with fitness consequences. Fitness consequences resulting from different developmental trajectories may drive a dynamic (i.e., eco-evolutionary) feedback that reinforces extreme iteroparity as a reproductive strategy.

METHODS

Study system

We evaluated settlement of a coral reef fish (sixbar wrasse, *Thalassoma hardwicke*) to small patch reefs on the island of Moorea, French Polynesia (17°30′ S, 149°50′ W). Sixbars are small-bodied fish that inhabit shallow coral reefs across much of the Indo-Pacific region, and are particularly common within the lagoon system of Moorea (Galzin 1987). In general, they exhibit life history patterns common to many marine organisms; e.g., they are highly iteroparous, with spawning occurring on most days of a lunar cycle and across much of the year (Claydon et al. 2014). On Moorea, we typically observe spawning activity along reef edges and during outgoing tides, consistent with a parental strategy that maximizes advection of propagules off the reef (Johannes 1978, Claydon 2004). Larvae develop in the pelagic environment and appear to have flexible developmental durations (range 39–63 d; Victor 1986). Late-stage larvae reenter the lagoon system of Moorea by traversing across the offshore barrier reef crest (Dufour and Galzin 1993, Lecchini et al. 2007) and settle to small patch reefs that are typically interspersed amid sand, pavement, or cobble substrate (Shima 1999, 2001a,b, Shima and Osenberg 2003, Shima et al. 2008). In addition, and like many other wrasses (Kazancioglu and Alonzo 2010), sixbars are sequential protogynous hermaphrodites.

Periodicity in settlement

We estimated settlement of sixbars onto 192 small patch reefs over six lunar cycles (January–July) in 2004, and five lunar cycles (February–June) in 2005. Sampled reefs were evenly distributed among 12 sites (16 patch reefs per site). Reefs varied in size (mean surface area = 12.38 ± 5.96 m [mean ± SD]) and composition (mean live coral cover = 64% ± 20%; turf algae = 16% ± 21%; macroalgae = 6% ± 9%; bare substrate = 9% ± 11%; see Shima et al. 2008 for further methodological details). We estimated the numbers and sizes (standard lengths, to nearest millimeter, aided by photographic references in situ) of all juvenile sixbars on each reef, approximately every 3–5 d (mean interval between censuses = 3.96 ± 2.55 d), over all 11 months of observation. We differentiated newly settled sixbars by their small size (9–13 mm), lack of full pigmentation (mostly transparent), characteristic behavior patterns (typically sheltering in small colonies of branching corals or clumps of macroalgae), and absence from previous censuses (see Shima et al. 2008). Surveys were conducted by multiple observers in 2004, and by a single observer in 2005.

We categorized new settlers to (1) a lunar month and (2) a quarter of the lunar month (i.e., centered on first quarter, full moon, last quarter, and new moon) based upon observed settlement dates. We distributed settlement observations over the days between sampling events (i.e., to correct for variable sampling effort), to derive an estimate of the number of settlers for each day for each reef. We summed these estimates of daily settlement across reefs, and then calculated the average proportion (and 95% CI) of sixbars that settled during each quarter ($n = 11$ lunar months). We compared the observed distribution to a null expectation of homogeneous settlement (i.e., equal settlement to each quarter: proportions = 0.25).

Size at settlement

Because our visual estimates of size of young sixbars varied among observers by 1–3 mm in 2004, we evaluated variation in size at settlement using data only from 2005, when a single observer made all of the observations. These estimates of size have high precision (correlation between visual estimates and size of collected fish, 0.96) and low bias (average error = 0.02 mm; Geange 2010). We evaluated variation in size at settlement using a generalized linear mixed effects model (Proc Glimmix, SAS 9.3; SAS Institute, Cary, North Carolina, USA) with a Poisson distribution (because the response variable comprised a small set of integers, e.g.,: 9, 10, 11, 12, 13). Specifically, we modeled size at settlement as a function of lunar quarter (first quarter, full moon, last quarter, or new moon; treated as a fixed effect), lunar month (included as a block to control for potential seasonal variation; fixed effect), and reef (to accommodate potential non-independence of different fish settling to common reefs; random effect). We also evaluated an interaction term (between lunar quarter and lunar month); this was not significant, so we excluded it from our final model.

Survival and growth after settlement

We estimated post-settlement survival of all newly settled sixbars from surveys made at 3–5 d intervals. The relatively small number of fish on reefs, and linear relationship between body length and age over this size range (Shima 1999), enabled us to discern survival and growth trajectories of individuals (or groups of individuals that settled at the same size and time). We estimated death dates of individuals from the disappearances of appropriately sized fish in a survey interval (for more details, see Shima and Osenberg [2003], Shima et al. [2008]). We calculated survival time as the difference between death date and settlement date. We evaluated variation in survival time as a function of the lunar quarter and lunar month when settlement occurred, using a survival analysis (Proc Lifereg, SAS 9.3). We used a Weibull distribution, which allows the hazard function to vary with post-settlement age. We also evaluated the interaction term (between lunar quarter and lunar month); this was not significant, so we excluded it from our final model. We estimated mean survival times for lunar months and quarters by taking the product of

the exponentiated intercept parameter and the factorial of the SAS scale parameter (after Shima et al. 2008).

Because the analyses described above suggested (1) size at settlement varied among lunar quarters and (2) survival also varied with lunar phase at settlement, we conducted a secondary analysis to distinguish between effects of size and lunar quarter. In addition, we also tested the hypothesis that survival depended upon lunar illumination, i.e., that the probability of death was greater during full moons, independent of the lunar quarter during which the fish settled. Specifically, we evaluated variation in survival as a function of the lunar quarter and lunar month when settlement occurred, size at settlement, and an index of lunar illumination. We estimated lunar illumination as the fraction of the moon illuminated (http://aa. usno.navy.mil/data/docs/MoonFraction.php) on the date that individuals went missing; for fish that survived beyond the end of our survey period (i.e., censored observations in our survival analysis), lunar illumination was assigned as a missing value. As above, we used a survival analysis (Proc Lifereg, SAS 9.3) with a Weibull distribution, and we evaluated a full model with all possible interactions; we sequentially removed non-significant higher-order interactions to determine a reduced model.

We estimated post-settlement growth rate for all fish that survived >7 d (i.e., sufficient time to observe an increase in size, given our measurement precision) as the difference between final size and initial size, divided by the time interval separating these two observations. This metric assumes that growth in body length per unit time is constant over the range of fish sizes that we observed (this assumption seems reasonable given a linear relationship between size and age for a similar sample of sixbars [Shima 1999]). We evaluated variation in growth rate using a generalized linear mixed effects model (Proc Glimmix, SAS 9.3), as a function of when and where the fish settled, i.e., lunar quarter (fixed effect), lunar month (fixed effect), and reef (random effect). As above, we evaluated an interaction term (between lunar quarter and lunar month); this was not significant, so we excluded it from our final model.

Modeling developmental decisions

To evaluate how plasticity in offspring development might evolve in response to variation in the timing of spawning over the lunar cycle, we modeled the fitness payoff to larval sixbars that (1) were born at particular times determined by the spawning decisions of parents and (2) could choose when to settle. We assumed continuous and aperiodic spawning by parents and allowed for the possibility of plasticity in the duration of the developmental period in larvae. Our motivation was to provide a simple representation of our system, and to address the question, "what should a larva do?" with respect to settlement decisions. The model is a thought experiment to explore whether, under extreme iteroparity, variation in the fitness consequences of different

settlement decisions are (1) sufficient to drive the expression of developmental plasticity and (2) consistent with observed patterns in settlement and settler size/age.

In our model, the fitness payoff for a larva with a given birth date and pelagic larval duration is represented by the probability of surviving through the larval stage to the post-settlement stage, which we represent as the product of two functions. The first, $d(x)$, describes the effect of larval duration (x) on the probability of surviving from birth to settlement. The second, $p(s)$, describes the additional effect of the lunar phase on the probability of survival, where $p(s)$ is periodic on the day of settlement, s. Thus, survival from birth to settlement for a larva with birth date b and settlement date s is $d(x) p(s)$, where pelagic larval duration is $x = s - b$.

First, we assume that larval survival is a unimodal function of larval duration (e.g., Peterson and Wroblewski 1984), which initially increases with duration due to the positive effects of increasing larval competence (i.e., attainment of sufficient energetic reserves to settle and metamorphose into the juvenile form), but then declines due to the negative effects of staying too long in the pelagic environment (Anderson 1988, Leggett and DeBlois 1994, Hare and Cowen 1997). We capture this general biological scenario using the function

$$d(x) = e^{-ax} \frac{e^{kx-c}}{1 + e^{kx-c}} \qquad (1)$$

where x = age at settlement (pelagic larval duration, in d) and a, k, c are parameters that specify the shape of $d(x)$. For a, k, $c > 0$ and $k > a$, the resulting function $d(x)$ is unimodal with a maximum at $x^* = \frac{1}{k} \left(c - \ln\left(\frac{a}{k-a}\right) \right)$. Thus, the three parameters collectively determine the optimal age at settlement. In our numerical solutions, we set $c = 47k + \ln\left(\frac{a}{k-a}\right)$ such that $x^* = 47$ d, the approximate average age of sixbar settlers (Victor 1986). Although Eq. 1 allows a positive probability of survival for any $x \geq 0$, the function $d(x)$ can be parameterized to obtain an arbitrarily narrow range of possible ages at settlement; i.e., $d(x)$ approaches 0 for large deviations from x^* (Fig. 2a–c). The strength of selection against flexibility in age at settlement depends on the slope of $d(x)$ around x^*. If k is large (Fig. 2a), $d(x)$ is steep for $x < x^*$, representing rapid onset of larval competence and low survival for larvae that settle before the optimal age. If a is large (Fig. 2c), $d(x)$ falls off rapidly from the peak, representing a severe survival penalty for delayed settlement. If both a and k are small (Fig. 2b), $d(x)$ is approximately symmetric, representing similar survival penalties for early and late settlement.

Next, we assume that survival of settlers depends on the lunar phase during which settlement occurs. In particular, we assume that predation risk varies in proportion to lunar illumination, which is greatest during a full moon. This predation risk primarily occurs as the settler traverses the reef crest, but the lunar effect may also include predation risk immediately after settlement. We
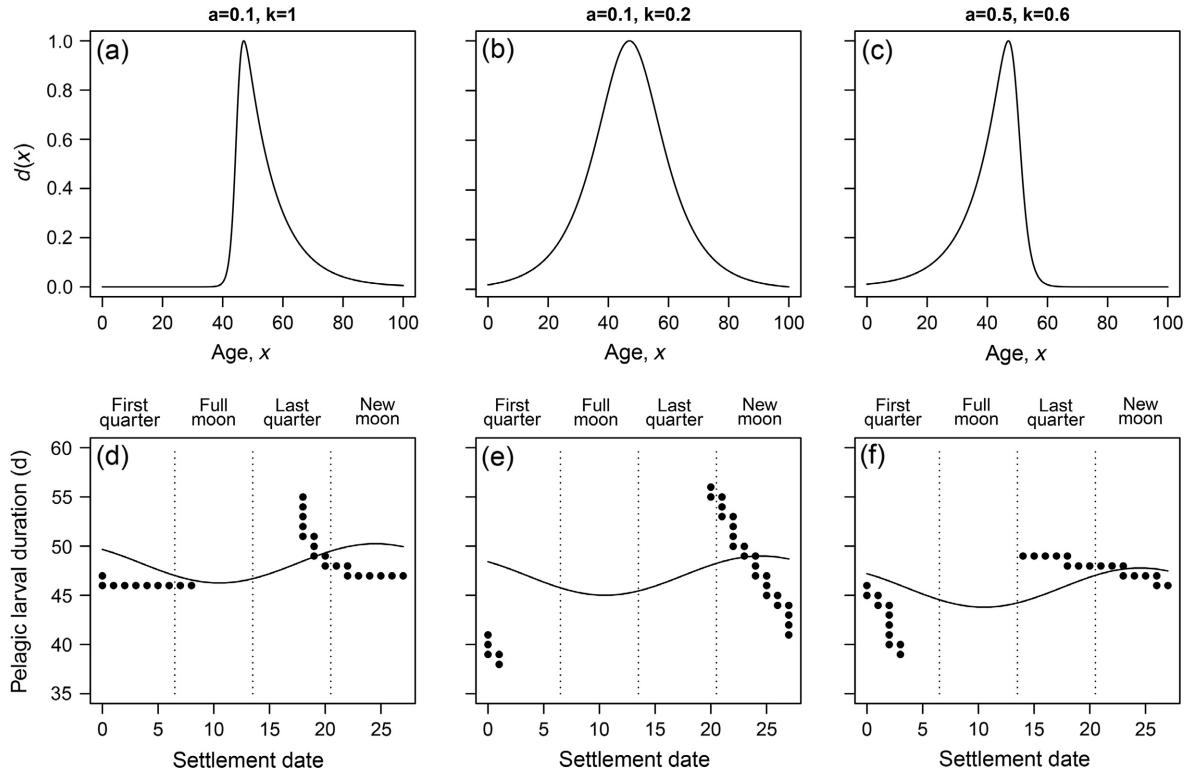
FIG. 2. (a–c) Survival to settlement, $d(x)$, as a function of pelagic larval duration, x. In all three cases, $c = 47k + \ln\left(\frac{a}{k-a}\right)$ such that approximate average age of sixbar settlers $x^* = 47$ d, where a, k, c are parameters that specify the shape of $d(x)$. The function $d(x)$ is scaled by its maximum value to make the curves comparable for each combination of a and k. This scaling (multiplication by a constant) has no effect on the optimum settlement times. (d–f) Optimal developmental durations for larval sixbars that settle across a lunar month. Each point is the optimal pelagic larval duration for larvae that settle on a particular date in the lunar cycle. Multiple points on the same settlement date, indicate that fishes with different birth dates all choose to settle on that same day. The absence of a point indicates that no larvae are predicted to settle on that date. Ages >47 d indicate that larvae should delay settlement relative to x^*, whereas smaller ages indicate that larvae initiated earlier than expected settlement, to avoid the full moon (i.e., the environmental suboptimum centered around day 10.5). Survival through the predator gauntlet (solid line = $p(s)$; where $p(s)$ is the additional effect of the lunar phase on the probability of survival with a mean of m with a total amplitude of $2h$) is superimposed to illustrate the lunar cycle, with parameters $m = 0.2$ and $h = 0.1$ ($p(s)$ has been scaled to be visible in the plot).

represent this as a sinusoidal function with a period of 28 d

$$p(s) = h\left(\cos\left(\frac{2\pi}{28}(s - L)\right)\right) + m \qquad (2)$$

where s = settlement date and $p(s)$ has a mean of m with a total amplitude of $2h$ (with h and m specified such that $0 < p(s) < 1$). The phase is offset by L days, where L determines the day of the lunar cycle in which survival is maximal. We set $L = 24.5$, under the assumption that survival peaks at the new moon, with the first quarter of the lunar cycle arbitrarily set to begin at $s = 0$.

These two equations capture how adult reproductive timing and larval developmental duration affect the probability of larval survival up to the post-settlement stage. The challenge for larvae then becomes one of timing settlement to coincide with the right general time (found by Eq. 2) subject to the constraint imposed by the larva's birth date, which will usually mean that it will

be a suboptimal age when predation risk is minimal. Each larva must therefore balance the conflicts arising between timing with respect to its age vs. time of settlement. We therefore find the settlement date (s^*) that maximizes total survival for each birthdate over a lunar cycle ($b = 1, 2, \ldots, 28$). We find s^* numerically by calculating $d(x)p(s)$ for all values of larval duration (x) up to 100 d (sufficient for the parameter values used in Fig. 2) and selecting the optimum. We then find the predicted ages of individuals that settle on each day of the lunar cycle under the assumption that spawning is aperiodic and each larva settles on the optimal day for a given birthdate. We present numerical solutions for three sets of parameter values (a, k, h, m) that demonstrate possible outcomes of selection against deviation from the optimum, x^*; i.e., strong selection against settling early (Fig. 2a), equal selection against positive and negative deviations away from the optimum (Fig. 2b), and strong selection against delayed settlement (Fig. 2c). R code for numerical solutions is provided in Data S1.

RESULTS

Periodicity in settlement

We recorded 1038 newly settled sixbars on 192 reefs over 11 lunar months (583 over 6 months in 2004, and 455 over 5 months in 2005). Settlement was unevenly distributed across lunar quarters within lunar months. More than one-half of the settlers (mean = 0.52; 95% CI 0.38–0.68) arrived during the new moon (i.e., significantly more than expected by chance; the 95% CI does not include 0.25; Fig. 3a). The proportion of settlers arriving during the first quarter of the lunar cycle (0.20; 0.1–0.30) was similar to the null expectation of 0.25. The proportions of fish settling during the full moon (0.15; 0.07–0.23) and last quarter of the lunar cycle (0.12; 0.06–0.18) were both significantly lower than expected by chance (Fig. 3a).

Size at settlement

Size (standard length) of settlers observed in 2005 also varied among lunar quarters ($F_{3,323} = 3.44$, $P = 0.0172$). Sixbars that settled during the last quarter were approximately 10% larger than fish that settled during other quarters of the lunar cycle (Fig. 3b). Size at settlement did not vary significantly among blocks (i.e., lunar months; $F_{4,323} = 0.60$, $P = 0.67$).

Survival and growth after settlement

Post-settlement survival of sixbars was dependent upon lunar quarter of settlement (Type III analysis of effects, df = 3, Wald Chi-square = 8.93, $P = 0.03$). Fish that settled during the first quarter (mean survival time = 56.3 d) or during the full moon (mean survival time = 58.7 d) experienced greater mortality than did fish that settled during the last quarter (mean survival time = 90.7 d) or during the new moon (mean survival time = 79.3 d; Fig. 4). Survival of sixbars also varied across lunar months (Type III analysis of effects, df = 4, Wald Chi-square = 17.67, $P = 0.0014$). Mean survival times generally declined across the settlement season, although mean survival time was particularly low for fish that settled in April (mean survival time for lunar months of settlement: February, 137.8 d; March, 84.46 d; April, 48.63 d; May, 80.70 d; June, 79.28 d).

Because both size at settlement and survival varied with respect to lunar quarter of settlement (Figs. 3b, 4), we conducted a secondary analysis to statistically decouple the effects of size and lunar quarter on survival; e.g., was the high survival of fish that settled during the last quarter due to the lunar phase or due to the larger size of these settlers? This analysis also incorporated the effects of post-settlement lunar luminosity on survival. The relationship between post-settlement survival and lunar quarter of settlement remained qualitatively unchanged from our original analysis presented above (Type III analysis of
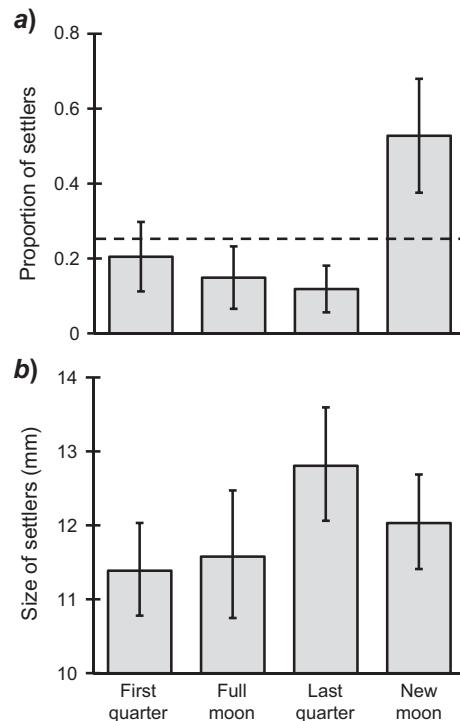

FIG. 3. Variation in settlement of sixbar wrasse across the lunar cycle. (a) Proportion of settlers (mean and 95% CI) arriving in each quarter of the lunar cycle ($n = 11$ lunar months surveyed in 2004 and 2005). Dashed line indicates null hypothesis of even (random) settlement across the lunar cycle. (b) Size (mean standard length and 95% CI) of settlers arriving in each quarter of the lunar cycle ($n = 5$ lunar months surveyed in 2005). [Color figure can be viewed at wileyonlinelibrary.com]

effects, df = 3, Wald chi-square = 10.04, $P = 0.018$), as did the effect of lunar month of settlement (Type III analysis of effects, df = 4, Wald chi-square = 90.30 $P < 0.0001$). Controlling for these lunar effects, size at settlement did not significantly affect post-settlement survival (Type III analysis of effects, df = 1, Wald chi-square = 0.40, $P = 0.53$). Thus, this analysis suggests that variation in size did not confound our interpretation of the effects of lunar quarter on survival. Interestingly, lunar illumination was not a significant predictor of post-settlement survival (Type III analysis of effects, df = 1, Wald chi-square = 2.67, $P = 0.10$). However, we note the non-significant trend was for a 2% reduction in survival for every 10% increase in the fraction of moon illuminated (corresponding to a 20% reduction in survival during the full moon, relative to survival during the new moon).

Post-settlement growth rate of sixbars did not vary as a function of the lunar quarter ($F_{3,240} = 0.94$, $P = 0.42$) or lunar month ($F_{4,240} = 1.34$, $P = 0.26$) of settlement. Fish that settled during the first quarter moon grew 0.14 mm/d (95% CI 0.13–0.16); fish that settled during the full moon grew 0.14 mm/d (0.12–0.16); fish that settled during the last quarter moon grew 0.14 mm/d

(0.12–0.15); and fish that settled during the new moon grew 0.13 mm/d (0.11–0.14). Variation in growth across lunar months was similarly invariant.

Modeling developmental decisions

The combination of developmental plasticity and temporal variation in predation risk results in differences in the age of settlers over the lunar cycle (Fig. 2d–f). Because $x^* = 47$ d for our parameterization, a larva that settles with age $x > 47$ d has delayed settlement relative to the age at which $d(x)$ is maximized, and vice versa. For example, in Fig. 2d, the individual that settled on lunar day 18 with age $x = 55$ delayed settlement by 8 d to avoid the peak of the full moon (which occurred 47 d after the larva was born). The individual that settled on day 8 with age $x = 46$ in Fig. 2d settled 1 d early to avoid the waxing moon (which peaked 48 d after the larva was born).

The particular pattern of early vs. delayed settlement that is predicted depends on the shape of $d(x)$. The empirical results (e.g., Fig. 3) are consistent with the case in which larval competency imposes a relatively sharp constraint on early settlement (Fig. 2a, d). With $a = 0.1$ and $k = 1$, the model predicts an asymmetric response, with larvae more severely delaying their settlement than initiating settlement early. In this case, the greatest decrease in age at settlement is 1 d, i.e., larvae born 51–59 d before a full moon settle with age $x = 46$ d. In contrast, fish whose birth date would dictate that they settle after the full moon, but before new moon (i.e., born 36–47 d before a full moon) should delay settlement by as much as 8 d (an average of 3.67 d: Fig. 2d). This avoidance of peak mortality under the full moon generates a schism in settlement patterns in which settlers that arrive during the last quarter tend to be as much as 9 d older than settlers that arrive during other quarters

of the lunar cycle (c.f., Fig. 3b). If fish delay settlement by approximately 4 d, and assuming that larvae grow at approximately the same rate as small juveniles (i.e., 0.14 mm/d) then we would expect an approximately 0.6 mm difference in the size of settlers in the last quarter. This is approximately what we observed (Fig. 3b).

If the costs of early vs. delayed settlement are reversed (Fig. 2f) then the opposite pattern is observed, with settler ages up to 8 d less than x^* and only slight delays in settlement for fish that expect to settle just after the full moon. On the other hand, if costs are more symmetric (Fig. 2e) then the magnitude of the delayed vs. early settlements are comparable, leading to the greatest disparity in the ages of settlers (i.e., differing by as much as 18 d and about 3 mm difference in length).

DISCUSSION

Iteroparity enables parents to bet-hedge when environmental conditions are uncertain, but this means that some offspring will be disadvantaged. Developmental plasticity may enable offspring to improve their own odds of survival (and increase the fitness of their parents thereby reducing one potential cost of adult iteroparity). Irrespective of developmental plasticity, iteroparity for sixbar wrasse may be favored if there is strong selection for larvae to settle during particular conditions (i.e., dark nights), but parents are unable to predict when these conditions might occur (e.g., because dark nights may depend on stochastic cloud cover, etc.). Similarly, developmental plasticity in sixbars may be favored if pelagic larvae are unable to predict timing of encounters with suitable habitat for settlement. Thus, either iteroparity or developmental plasticity on its own may constitute a risk avoidance strategy. When considered together, developmental plasticity of larvae may reinforce an existing iteroparous strategy in adults because offspring can compensate for an inauspicious birthdate that might otherwise select against iteroparity and more generally variation in the timing of reproduction.

Sixbar wrasse settle in greater numbers during the new moon, a pattern typical of many reef fishes (e.g., Dufour and Galzin 1993, Rankin and Sponaugle 2014) that suggests that new moons may represent better times to settle (i.e., Pineda et al. 2006). Improved odds of larval survival on dark nights (e.g., Acosta and Butler 1999) is one mechanism that almost certainly contributes to this pattern. Settling sixbars must migrate into shallow water and surf over a barrier reef crest; once inside the lagoon, they must drift or swim another ~100–1,000 m to locate suitable reef habitat (e.g., Doherty et al. 2004). We have observed small piscivores actively feeding in these areas of sixbar migration on nights with bright moons (*personal observations*), and we suspect that survival across this predator gauntlet is closely linked with lunar illumination. Hence, perhaps the most obvious explanation for the lunar periodicity in settlement is intense predation (i.e., settlers arrive at equal frequency over the lunar cycle
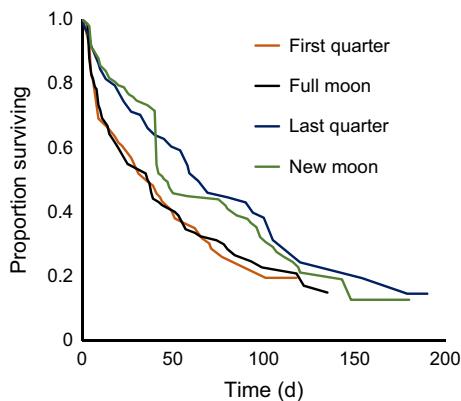

FIG. 4. Post-settlement survival of sixbar wrasse that settled during different quarters of the lunar cycle. Fish that settled during waxing moons (from first quarter to full moon; i.e., times of increasing illumination) had lower rates of survival than fish that settled during waning moons (from last quarter to new moon; i.e., times of decreasing illumination).

but predators eliminate most of the settlers that don't arrive on the new moon). However, this hypothesis alone doesn't predict the observed size differences in settlers over the lunar cycle without invoking a more complex mechanism (e.g., in which size-selective predation varies in a particular way across the lunar cycle: i.e., it cannot adequately account for our empirical observations).

At least two other mechanisms (not mutually exclusive) may contribute to the lunar pattern of settlement that we have observed. First, periodic spawning by adults may drive variation in the number of larvae available to settle during certain portions of the lunar month (e.g., Robertson et al. 1988). Adult sixbars appear to spawn over all days of a lunar month, but available evidence (from another location) indicates that spawning activity is greatest around the new moon (Claydon et al. 2014); this is consistent with Johannes'(1978) hypothesis predicting that adults should spawn at times (and places) that minimize egg predation. However, when combined with the average developmental duration reported for sixbar larvae (47 d; Victor 1986), this suggests that (all else being equal) larval settlement should peak between the full and last quarter moon (i.e., lunar periodicity in spawning cannot explain our empirical observations).

A second potential mechanism that might contribute to the observed peak in sixbar settlement around the new moon is a flexible developmental duration for larvae. Larvae may have the capacity to settle early and/or delay their settlement (relative to a normative developmental duration, i.e., ~47 d for sixbars; Victor 1986). If developmental duration is flexible, and full moons are particularly dangerous, then we would expect larval sixbars to avoid settling during full moons. Using size as a proxy for age, our observation that sixbars settle at a larger size just after the full moon is consistent with this hypothesis. (i.e., many of those fish "should" have settled on the first quarter or the full moon). Though we cannot directly test an alternative hypothesis that growth rates of larvae vary across the lunar cycle (giving rise to fish that settle at the same age but different sizes), this seems unlikely to us as our estimates of post-settlement growth were invariant across the lunar cycle (and larval growth is correlated with post-settlement growth in this system; Shima et al. 2006). We note that an evaluation of otolith microstructure (e.g., Shima and Swearer 2009*a,b*, Rankin and Sponaugle 2014) would enable us to clearly differentiate between these alternatives, and this is a priority for our future work.

Sixbars that settled during waxing moons (from first quarter to full moon; i.e., increasing illumination) suffered substantially greater mortality relative to fish that settled during waning moons (from last quarter to new moon; i.e., decreasing illumination). Waxing and waning moon phases also differ in the timing of moonrise and moonset, with the consequence that waxing phases will tend to illuminate reefs after sunset and waning periods will tend to illuminate reefs before sunrise. We speculate that the difference in survivorship between waxing and waning periods may be attributable to prolonged activity by crepuscular predators, and/or young sixbars may remain active later into the evening (increasing their vulnerability to predators), when illumination occurs at dusk (and this effect may be less important when reefs are illuminated nearer to dawn). The steep decline in survivorship with time for waxing moon phases suggests that early post-settlement mortality may be shaped by the timing and intensity of nocturnal illumination, and this may reinforce selection for flexible developmental durations that enable fish to avoid settling during particular phases of the moon.

For fish that settled during a new moon phase, we noted an anomalously steep decline in survivorship at 41 d after settlement (Fig. 4), and this roughly corresponds to the second full moon period experienced by settled fish (further suggesting that bright periods may be times of heightened risk). We also noted that fish that settled during the last quarter of the lunar month had the highest mean survival time (90.7 d, compared with 79.3 d for fish that settled during the new moon). As a consequence of these observations, we hypothesized that variation in post-settlement survival could be explained by variation in size at settlement and/or lunar illumination. We evaluated these hypotheses with a modified survival analysis that included these additional covariates. This new analysis failed to support the hypothesis that size at settlement influenced post-settlement survival independent of lunar quarter of settlement. Additionally, we evaluated a competing model that substituted size at settlement for lunar quarter and found that this had much less support based upon Akaike's information criterion (AIC), and the effect of size at settlement remained non-significant. Lunar illumination on the estimated death date was also not a significant predictor of survival, though the trend was for a reduction in survival with increasing illumination. As our estimate of lunar illumination (i.e., the fraction of the moon illuminated) doesn't take into account cloud cover or moonrise/moonset times, we are hesitant to conclude that nocturnal illumination, particularly around dusk, is not an important determinant of variation in survival. Additionally, we speculate that the survival advantage accruing to settlers in the last quarter moon phase may be a consequence of density-dependent mortality (Shima 1999, 2001a,b, Shima and Osenberg 2003, Shima et al. 2008) and/or priority effects (Geange and Stier 2009, Geange 2010). Relative to fish settling during the new moon, fish that settled during the last quarter of the lunar month were at lower density on average (Fig. 3a), and preceded a large number of settlers that arrived in the following quarter (i.e., on the new moon). The general decrease in mean survival times from January to June is also consistent with density-dependent mortality and/or priority effects documented elsewhere (Shima 1999, 2001a,b, Shima and Osenberg 2003, Shima et al. 2008, Geange and Stier 2009, Geange 2010), as reefs were comparatively empty at the start of the settlement season.

Our analyses did not detect variation in post-settlement growth rates with respect to lunar periodicity. This is somewhat surprising given (1) variation in settler densities across lunar quarters (and an expectation for density-dependent growth rates; Booth 1995) and (2) variation in survival probabilities as a function of lunar quarter (which suggest heightened risk during waxing moons; we might expect this to result in increased sheltering time and decreased foraging time shortly after settlement, and hence decreased growth rates). Of course, another possibility is that our approach lacked the ability or precision to detect small differences in individual growth rates. Future planned otolith-based demographic reconstructions will enable a more powerful test of these patterns.

Predictions from our simple numerical simulation were consistent with empirical observations of variation in size at settlement across the lunar cycle. Our numerical representation assumed two interacting sources of mortality (an intrinsic mortality rate following a threshold of competency, and an extrinsic mortality rate attributable to lunar illumination). This model predicts optimal larval strategies that vary with individual birthdate and lunar cycle. By extension, iteroparity should be favored (and reinforced) as a reproductive strategy when larval developmental duration is plastic. Given a probable developmental threshold (e.g., Anderson 1988, Leggett and DeBlois 1994, Hare and Cowen 1997), larvae should delay settling to avoid full moons, resulting in variable settlement rates and size asymmetries across the lunar cycle (i.e., consistent with our empirical results). This variation in time and size at settlement will likely have consequences for intraspecific interactions following settlement and may affect other aspects of growth and reproduction in species.

The decisions about "when to settle" may have further consequences for lifetime fitness. Many reef fish species have socially-controlled sex determination (i.e., sex-change capability; Warner and Swearer 1991, Kazancioglu and Alonzo 2010). Some of these species also exhibit plasticity in maturation strategies (Munday et al. 2006). For protogynous hermaphrodites (including sixbars), fish typically mature first as females, with the most dominant fish becoming a male that monopolizes matings with subordinates to achieve a large increase in fitness. However, some individuals mature directly as small males and sneak matings as an alternate strategy. Birthdates and subsequent developmental decision-making may determine order of arrival, relative growth rates, and positions within dominance hierarchies that can profoundly affect future reproductive fitness (Fig. 1b). Environmental variation that may, in part, result from birthdates and developmental decisions, has been shown to alter the life-history trajectories in other fish (Taborsky 2006).

Our results lead us to propose a conceptual framework in which (1) plasticity in larval developmental duration is an adaptive response to iteroparity, (2) this results in a wide range of developmental histories (i.e., "decisions" of larvae in response to birthdates issued by parents), and (3) these developmental histories contribute importantly to variability in future performance (e.g., survival and reproductive potential; Fig. 1). We speculate that the demographic heterogeneity that arises from variable developmental histories has unexplored consequences for population dynamics (e.g., Shima et al. 2008, Noonburg et al. 2015) that may, in turn, shape evolutionary processes (Diekmann et al. 1999, Alonzo and Sinervo 2001, Lof et al. 2012, Holman and Kokko 2013). For the sixbar wrasse, we hypothesize that dynamic feedbacks (i.e., between developmental histories, demographic consequences, and future fitness (e.g., Coulson et al. 2006, Saccheri and Hanski 2006, Pelletier et al. 2009, Post and Palkovacs 2009, Hanski and Mononen 2011, Schoener 2011, Cameron et al. 2013, Smallegange and Coulson 2013, Johnson et al. 2014) may reinforce selection favoring extreme iteroparity by increasing the survival of offspring born at the "wrong" time. More generally, we speculate that interactions between parental reproductive strategies, larval plasticity (and constraints on this), and the demographic consequences that result from this set of "developmental histories" may drive feedbacks that ultimately reinforce different reproductive strategies within and among species.

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