

Patterns of spawning and settlement of reef fishes as strategic responses to post-settlement competition

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ARTICLE INFO

Keywords:

Coral reefs
Early life history
Lunar periodicity
Priority effects
Recruitment
Reproductive phenology

ABSTRACT

Settlement is a critical transition in the life history of reef fish, and the timing of this event can have a strong effect on fitness. Key factors that influence settlement timing are predictable lunar cyclic variation in tidal currents, moonlight, and nocturnal predation risk as larvae transition from pelagic to benthic environments. However, populations typically display wide variation in the arrival of settlers over the lunar cycle. This variation is often hypothesized to result from unpredictable conditions in the pelagic environment and bet-hedging by spawning adults. Here, we consider the hypothesis that the timing of spawning and settlement is a strategic response to post-settlement competition. We use a game theoretic model to predict spawning and settlement distributions when fish face a tradeoff between minimizing density-independent predation risk while crossing the reef crest vs. avoiding high competitor density on settlement habitat. In general, we expect competition to spread spawning over time such that settlement is distributed around the lunar phase with the lowest predation risk, similar to an ideal free distribution in which competition spreads competitors across space. We examine the effects of overcompensating density dependence, age-dependent competition, and competition among daily settler cohorts. Our model predicts that even in the absence of stochastic variation in the larval environment, competition can result in qualitative divergence between spawning and settlement distributions. Furthermore, we show that if competitive strength increases with settler age, competition results in covariation between settler age and settlement date, with older larvae settling when predation risk is minimal. We predict that competition between daily cohorts delays peak settlement, with priority effects potentially selecting for a multimodal settlement distribution.

1. Introduction

The timing of life-history events, such as reproduction and migration, often coincide with seasonally varying environmental conditions (e.g., food availability, temperature). The fitness consequences of these events depend on how closely the timing of the events matches favorable conditions (e.g., Cushing 1990, Thomas et al., 2001, Beaugrand et al. 2003, Bradshaw et al. 2004). However, fitness also depends on the actions of others. For example, synchronized reproduction within a population can lead to even greater benefits than expected if the high production of young swamps predators (e.g., masting in trees:

Silvertown 1980), but may reduce fitness if synchronized reproduction exacerbates future competitive interactions. If density-dependent interactions are concentrated among similarly aged offspring, these deleterious effects can be even more pronounced and may negate the benefits of good timing. Organisms must therefore strike a balance between matching favorable environmental conditions while also minimizing competition. This balancing act may explain the timing of arrival of birds on their breeding grounds (Johansson and Jonzen 2012), seed germination (ten Brink et al. 2020), and insect emergence patterns (Poethke et al. 2016). Thus, variation in phenologies within a population may reflect a tradeoff between matching environmental cues and

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<https://doi.org/10.1016/j.tpb.2024.08.001>

Received 24 October 2023; Received in revised form 10 August 2024; Accepted 14 August 2024

Available online 23 August 2024

0040-5809/© 2024 Published by Elsevier Inc.

avoiding or pre-empting competitors.

Most coral reef fish species spawn pelagic larvae that settle back to the reef on characteristic schedules. Settlement is a particularly critical life-history transition, and larvae experience high mortality risk as they transition from pelagic to benthic environments and seek suitable juvenile habitat (Sale and Ferrell 1988; Carr and Hixon 1995; Frederick 1997; Caselle 1999; Doherty et al. 2004; Almany and Webster 2006). For many species that inhabit backreef/lagoon habitats, transiting the reef crest can be a particularly vulnerable time. Settlement often follows a lunar cycle, with peaks that appear to minimize predation risk, with many species settling at night, on or near new moons, when low illumination minimizes the risk from visual predators (Robertson 1992; Milicich and Doherty 1994; Acosta and Butler 1999; Robertson et al. 1999; Shima 2001; Sponaugle et al. 2006; D'Alessandro et al. 2007; Sponaugle et al. 2012; Rankin and Sponaugle 2014, Besson et al. 2017). Settlement coincident with new or full moons may also capitalize on high tidal flows that allow rapid transit across the reef, to further minimize exposure to reef-associated predators.

Nevertheless, empirical studies of species with lunar cyclic settlement patterns typically reveal wide variation around peak settlement times (e.g., Robertson 1992, Robertson et al. 1999, D'Alessandro et al. 2007, Besson et al. 2017). Attempts to explain this variation have focused on density-independent factors that affect larvae prior to their arrival on a reef. In particular, unfavorable conditions in the pelagic environment may contribute to variation in survival (Cushing 1990) and/or prevent larvae from arriving on reefs at the optimal time (Sponaugle and Pinkard 2004; Sponaugle et al. 2012). The unpredictability of currents and other sources of variation may select for bet-hedging reproductive strategies, in which adults spread spawning over time. In some cases, larvae with developmental plasticity may be able to modify their pelagic larval duration to settle close to the optimal lunar phase even if they were spawned at the wrong time (Sponaugle and Cowen 1994; Shima et al. 2018, 2020). However, not all species appear to have this developmental flexibility.

After larval fish successfully settle, they must survive and grow in the reef environment. Numerous studies have demonstrated that juvenile survival declines as the number of settling conspecifics increases (see reviews by Osenberg et al. 2002, Hixon and Jones 2005, Bonin et al. 2015). Similarly, high conspecific density can reduce post-settlement growth rate, which also slows the maturation rate (Jones 1987; Forrester 1990; Booth 1995). Thus, reproduction that is well-timed with environmental conditions that benefit larvae might lead to intense competition later in the life history. What then are the consequences of variation in reproduction for future competitive interactions and, furthermore, how might these interactions drive the evolution of life histories?

In this paper, we use a game theoretic model to explore these questions and examine the hypothesis that variation in settlement timing is a strategic response to post-settlement competition. To isolate the effects of post-settlement competition, we ignore other variables that might affect the timing of spawning and settlement (e.g., stochastic variation in currents, lunar periodicity in larval growth and survival). In the absence of competition, we therefore expect highest settlement to occur when predation risk for larvae crossing the reef crest is predictably lowest (e.g., at the new moon). Consequently, peak spawning should occur prior to peak settlement with a delay equal to the pelagic larval duration.

Our primary interest is in the effects of several features of post-settlement competition on this prediction. First, we consider the case in which competition only occurs among fish that settle on the same day. We vary the strength of competition and examine how predictions differ with compensating vs. overcompensating density dependence. Next, we derive predictions for the case in which more time spent growing in the pelagic stage confers an advantage in post-settlement competition (Shima et al. 2020). In this context, we ask how variation in larval age (and thus size) at settlement affects the spawning distribution and the

distribution of settler age classes over the lunar cycle. Finally, we explore the effects of competition among fish that settle on different days. Here, we ask how arrival and mortality of successive daily cohorts affect the predicted settlement timing. We also model a priority effect such that earlier arrivals have a competitive advantage over settlers that arrive in subsequent daily cohorts (Geange and Stier 2010). By sequentially adding individual features of competition to the basic model, we elucidate the effects of each on the predicted patterns of spawning and settlement. Although our goal is primarily heuristic, we highlight predictions that potentially distinguish the effects of competition from density independent processes such as random variation in larval dispersal.

2. Model

We consider a population in which adults on an arbitrary unit area of reef spawn a total of L larvae over a lunar cycle. Lunar day varies over $d = 0, 1, \dots, 28$, with new moon on $d = 0$ and full moon on $d = 14.5$ (i.e., equal lunar illumination on days 14 and 15) to approximate the 29.5d lunar cycle. We constrain larval age at settlement, a , between minimum (a_{min}) and maximum (a_{max}) values. A larva spawned on day d that survives to its target age a settles on lunar day $d_s = d + a$. All arithmetic with d is modulo 29, e.g., a larva born on $d = 25$ with settlement age $a = 10$ settles on $d_s = 6$.

Each female has a finite number of eggs that she can spawn over one lunar cycle. A female distributes her spawning over each lunar cycle according to her spawning strategy, $R(d, a)$, defined as the proportion of offspring born on each lunar date d with settlement age a (were they to survive). The spawning strategy $R(d, a)$ therefore consists of $a_{max} - a_{min} + 1$ values ≥ 0 for each of the 29 values of d , and the values of $R(d, a)$ must sum to 1.

We make three key assumptions in the model. First, as stated above, we ignore stochastic variation in the pelagic environment. Hence, the best value(s) of a can be determined at birth, and we do not need to consider developmental flexibility in larvae. Second, we assume the population is large, such that each female makes an infinitesimal contribution to the total number of larvae spawned, and we can ignore potential competition among siblings. Third, we assume that the population is neither growing nor declining; hence, we do not consider discounting for time when evaluating spawning strategies.

2.1. Payoff function

We seek an evolutionary stable strategy (ESS, Maynard Smith 1982) for $R(d, a)$. The ESS is a strategy such that, when it is adopted by the entire population, no individual can obtain a greater payoff by switching to another strategy. With the assumptions stated above, the payoff from a strategy is the expected fraction of larvae that survive from birth through post-settlement competition. For a larva spawned on day d with target settlement age a , the probability of survival from birth through post-settlement competition is the product $s_1(a)s_2(d_s)s_3(d_s, a)$, where

$$\begin{aligned} s_1(a) &= \text{probability of survival from birth to arrival at the reef at age } a \\ s_2(d_s) &= \text{probability of survival over the reef crest on lunar day } d_s \\ s_3(d_s, a) &= \text{probability of survival through post-settlement competition} \end{aligned}$$

The payoff to an individual with strategy $R(d, a)$ is then

$$F(d, a) = \sum_{d=0}^{28} \sum_{a=a_{min}}^{a_{max}} R(d, a) s_1(a) s_2(d_s) s_3(d_s, a) \quad (1)$$

We assume $s_1(a)$ and $s_2(d_s)$ are density independent and depend only on time spent in the pelagic dispersal stage (a) and lunar date of settlement (d_s), respectively. Survival through post-settlement competition depends on the density of competitors, which is determined by d_s and a

as we describe in the following.

Assuming daily mortality rate during the pelagic stage (m) is constant,

$$s_1(a) = e^{-ma} \quad (2)$$

We assume survival over the reef crest follows a sinusoidal curve corresponding to lunar illumination, with maximum survival on the new moon and minimum survival on the full moon:

$$s_2(d_s) = b \sin\left(\frac{2\pi}{29}\left(d_s + \frac{29}{4}\right)\right) + c \quad (3)$$

where c is the mean survival and b is the amplitude of the cycle. This assumption is based on the hypothesis that lunar illumination increases the vulnerability of larvae to visual predators on the reef.

The density of settlers that arrive on day d_s with age a is $n(d_s, a)$. If the population adopts strategy $R(d, a)$, settler density is

$$n(d_s, a) = LR(d, a)s_1(a)s_2(d_s) \quad (4)$$

The product $LR(d, a)$ is the number of larvae spawned per unit of reef area on day d with a larval duration of a , and $s_1(a)s_2(d_s)$ is their survival from birth to settlement.

Density affects the post-settlement survival probability, $s_3(d_s, a)$. We assume a settler must survive through a “competition window” of fixed duration that includes its settlement day and the following w days. Survival through this period is the product of $w + 1$ daily survival probabilities:

$$s_3(d_s, a) = \prod_{i=0}^w p_{d_s, a}(d_s + i) \quad (5)$$

where $p_{d_s, a}(d_s + i)$ is the probability of survival through one day, $d_s + i$, for a settler that arrives on day d_s with settlement age a . For example, $p_{d_s, a}(d_s + 3)$ is the probability of survival from the end of $d_s + 2$ to the end of $d_s + 3$ (not the probability of survival from d_s to $d_s + 3$). Fish that survive $w + 1$ days (from settlement to the end of day $d_s + w$) transition out of the population of competitors and no longer affect or are affected by other recently settled fish.

The one-day survival probability $p_{d_s, a}(d_s + i)$ depends on the density

of competitors present on day $d_s + i$. The potential competitors consist of new settlers that arrived on $d_s + i$ as well as larvae that settled on the previous w days and survived to $d_s + i$, i.e., all surviving fish that have not yet completed their competition windows. For example, if $w = 1$, the density of potential competitors that settled with age a' and are still alive on d_s is $n(d_s, a') + n(d_s - 1, a')p_{d_s - 1, a'}(d_s - 1)$. For $w = 1$, the probability of survival through day $d_s - 1$, $p_{d_s - 1, a'}(d_s - 1)$, depends on the total number of larvae (of all ages, a) that settled on $d_s - 1$ and survivors from $d_s - 2$. An example with $w = 2$ is diagrammed in Fig. 1.

Potential competitors may have stronger or weaker effects on other settlers. Because differences in settlement age and day may influence the strength of competition, we weight competitor densities with two factors. First, we allow settlers that spent longer in the pelagic stage to have a greater effect on the survival of fish that settled with smaller a . This simulates the possibility that more time spent in the pelagic results in greater size and competitive strength at settlement (e.g., Shima et al. 2020). The relative effect of competitors that settled with age a' on settlers that arrived with age a is $g(a, a')$, which is an increasing function of a' with $g(a, a') = 1$ for $a' = a$, $0 \leq g(a, a') < 1$ for $a' < a$, and $g(a, a') > 1$ for $a' > a$.

Second, we vary the relative effect of competitors that arrived closer vs. further in time from a settler. We weight the relative effect of competitors that settled on d_s' with a factor h_δ , where $\delta = d_s' - d_s$ varies from $-w$ to w . For example, h_{-2} wt the effect of competitors that arrived two days before a given cohort, and h_1 wt the effect of competitors that settle one day after d_s . We use these weights to model two scenarios. First, we suppose interactions decrease among settlers that arrive at increasingly disparate dates (h_δ decreases with increasing $|\delta|$). This might occur if, e.g., interactions occur primarily among similar-sized fish, and post-settlement growth therefore reduces interactions with new settlers (Shima 1999). Second, we model priority effects, in which fish that settled earlier have a stronger effect on fish that settle later, and vice versa (maximum h_δ for some $\delta < 0$; Geange and Stier 2010). For example, fish that settle at the beginning of a pulse might exclude future settlers from the best refuge habitat on a reef. Continuing the example with $w = 1$ above, the weighted density of competitors that settled with age a' and are still alive on d_s is $h_0 g(a, a') n(d_s, a') + h_{-1} g(a, a') n(d_s - 1, a') p_{d_s - 1, a'}(d_s - 1)$. This expression must be summed over all possible competitor ages

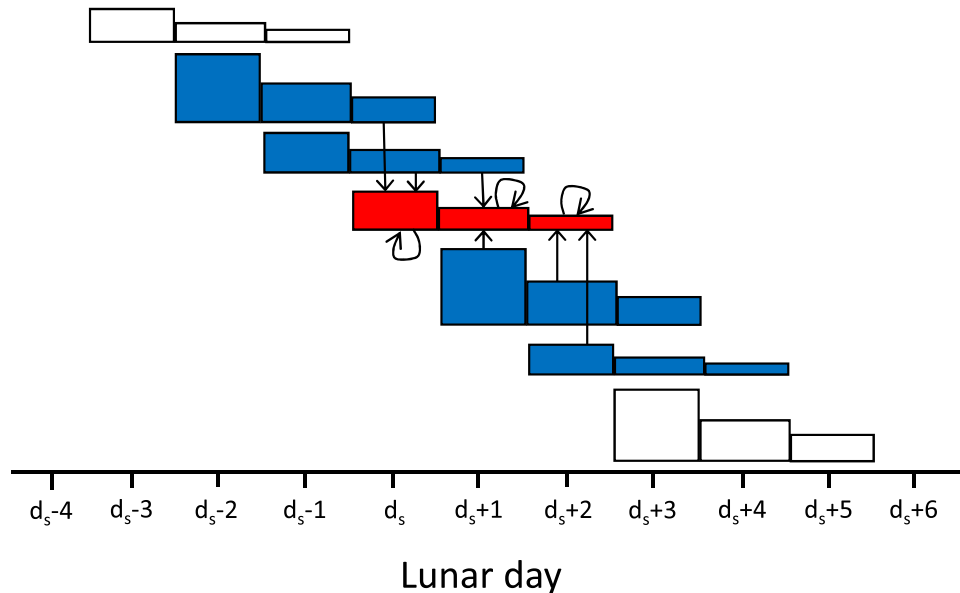


Fig. 1. Post-settlement competition for a focal cohort that arrived on d_s (red bars) for $w = 2$. Additional competitors are indicated by blue bars (those that settled within two days of the focal cohort (between $d_s - 2$ and $d_s + 2$), while earlier and later cohorts (white bars) never interact directly with the focal cohort. Densities of survivors in each cohort (indicated by the height of bars) decline each day due to mortality, and each cohort transitions out of the population of competitors after 3 days. Straight arrows indicate intercohort competitive effects and the curved arrows indicate intracohort effects. For example, on day $d_s + 1$, the focal cohort competes with survivors from the cohort that arrived on $d_s - 1$, the new cohort that settled on $d_s + 1$, and its own cohort.

($a_{min} \leq a' \leq a_{max}$) to obtain the total weighted competitor density.

In general, for an individual that settled on day d_s with age a , the weighted competitor density on d_s+i is

$$N_{d_s,a}(d_s+i) = \sum_{a'=a_{min}}^{a_{max}} \left(h_0 g(a', a') n(d_s+i, a') + \sum_{j=1}^w h_{i-j} g(a', a') n(d_s+i-j, a') \prod_{k=1}^j p_{d_s+i-j,a'}(d_s+i-k) \right) \tag{6}$$

where the first term inside the summation over a' is the weighted density of settlers that arrived on d_s+i with any age a' , and the second term is the weighted density of survivors from the previous w days. For the case in which $w = 0$ (settlers only compete within each cohort on their settlement day), we drop the second term and set $N_{d_s,a}(d_s) = \sum_{a'=a_{min}}^{a_{max}} h_0 g(a', a') n(d_s, a')$.

The one-day survival probability for any day d_s+i is a decreasing function $f(N_{d_s,a}(d_s+i))$ of weighted competitor density:

$$p_{d_s,a}(d_s+i) = f(N_{d_s,a}(d_s+i)) \tag{7}$$

The particular form of the function f depends on the underlying mechanism of competition (Brännström and Sumpter 2005). We compare the predictions for two competition functions that have been fit to empirical data (Shima and Osenberg 2003; Johnson 2007),

$$\text{Beverton – Holt : } f_{BH}(N_{d_s,a}(d_s+i)) = r_0 (1 + r_1 N_{d_s,a}(d_s+i))^{-1} \tag{8}$$

$$\text{Ricker : } f_R(N_{d_s,a}(d_s+i)) = r_0 e^{-r_1 N_{d_s,a}(d_s+i)} \tag{9}$$

To examine the effect of compensating (Beverton-Holt) and overcompensating (Ricker) density dependence. Because overcompensating density dependence can invert the relationship between density of settlers and density of survivors, we hypothesize that Beverton-Holt and Ricker models can produce qualitatively distinct results. In both models, the parameter r_0 is the maximum probability of survival in the absence of competitors and r_1 specifies the rate at which survival decreases with increasing weighted competitor density.

2.2. ESS solution

For any strategy $R(d,a)$, the payoff (Eq. (1)) is a weighted sum of offspring survival probabilities $s_1(a)s_2(d_s)s_3(d_s,a)$ for each combination of d and a , where the weights are the values of $R(d,a)$. At an ESS, each combination of d and a for which $R(d,a) > 0$ must have equal offspring survival (otherwise, an invader that weights more successful combinations more heavily would achieve a greater payoff). For all numerical results presented below, we use the default parameter values (Table 1) and the solution procedure described by McNamara et al. (1997) to find an ESS for the spawning strategy (code is provided at <https://figshare.com/s/7346f65b6a91cde21034>). In all of the examples that we present, the numerical solutions met conditions for an ESS; however, the solution procedure does not guarantee that the ESS is convergent stable.

We use the ESS spawning strategy to derive predictions for four distributions, which we define here. These distributions are potentially observable in the field and allow us to link our model predictions to empirical patterns. First, the spawning strategy ($R(d,a)$) is also the predicted spawning distribution, i.e., the proportion of offspring with each value of spawning day and age at settlement, predicted at birth assuming $s_1(a)s_2(d_s)=1$. We also examine the distribution of offspring that survive to each stage in a population that adopts the ESS spawning strategy. The distribution of offspring immediately prior to crossing the reef crest (the arrival distribution) is

$$P_1(d_s, a) = \frac{R(d_s - a, a)s_1(a)}{\sum_{d_s=0}^{28} \sum_{a=a_{min}}^{a_{max}} R(d_s - a, a)s_1(a)} \tag{10}$$

The distribution of settlers immediately after crossing the reef crest (the settlement distribution) is

$$P_2(d_s, a) = \frac{R(d_s - a, a)s_1(a)s_2(d_s)}{\sum_{d_s=0}^{28} \sum_{a=a_{min}}^{a_{max}} R(d_s - a, a)s_1(a)s_2(d_s)} \tag{11}$$

The distribution of settlers that survive all three stages (the total survivor distribution) is

$$P_3(d_s, a) = \frac{R(d_s - a, a)s_1(a)s_2(d_s)s_3(d_s, a)}{\sum_{d_s=0}^{28} \sum_{a=a_{min}}^{a_{max}} R(d_s - a, a)s_1(a)s_2(d_s)s_3(d_s, a)}$$

Each of these three distributions is the proportion of survivors that settled on day d_s with age a .

Because offspring survival probabilities $s_1(a)s_2(d_s)s_3(d_s,a)$ must be equal for all $R(d,a) > 0$ at an ESS and the values of $R(d,a)$ must sum to 1,

$$P_3(d_s, a) = \frac{R(d_s - a, a)}{\sum_{d_s=0}^{28} \sum_{a=a_{min}}^{a_{max}} R(d_s - a, a)} = R(d_s - a, a) \tag{12}$$

i.e., the total survivor distribution must be identical to the ESS spawning

Table 1
Notation and default parameter values used in the model*.

Parameter/ function	Default value	Definition
a		Age at settlement
a_{min}	29	Minimum age at settlement
a_{max}		Maximum age at settlement
b	0.1	Amplitude of variation in survival over the reef crest
c	0.2	Mean survival over the reef crest
d		Spawning date
d_s		Settlement date
g_0		Exponent in age-dependent competition function
h_s		Competitive weight of settlers that arrive δ days before/after d_s
L	50	Number of larvae spawned per unit reef area
m	0.01	Mortality rate in the pelagic stage
r_0	0.9	Maximum post-settlement survival
r_1		Rate of decrease in post-settlement survival with increasing weighted competitor density
w		Duration of post-settlement competition
α		Shape parameter 1 in competitive weights
β		Shape parameter 2 in competitive weights
$f(N_{d_s,a}(d_s+i))$		Competition function
$F(d,a)$		Payoff function
$g(a,a')$		Age-dependent competitive weight function
$n(d_s,a)$		Settler density
$N_{d_s,a}(d_s+i)$		Weighted competitor density
$p_{d_s,a}(d_s+i)$		Post-settlement daily survival probability
$P_1(d_s,a)$		Arrival distribution
$P_2(d_s,a)$		Settlement distribution
$P_3(d_s,a)$		Total survivor distribution
$R(d,a)$		Spawning distribution
$s_1(a)$		Survival from birth to arrival at the reef
$s_2(d_s)$		Survival over the reef crest
$s_3(d_s,a)$		Survival through post-settlement competition

* Default values are used in all numerical solutions. Parameters with no default value listed here take different values as specified in the Results section.

strategy. For example, suppose half of all spawning occurs on the new moon and those larvae settle after 50 days. If those larvae comprise more than half of all survivors, then an adult would benefit from increasing its spawning on the new moon. Hence, at an ESS, the total survivor distribution must equal the spawning strategy.

As a baseline, we start with the simplest case in which there is no competition (competitive weights for all fish are $h_s=0$). In this case, a larva does not benefit from avoiding other settlers and the optimal settlement date for all larvae is on the new moon ($d_s=0$), i.e., when predation risk on the reef crest is minimal. Similarly, in the absence of competition there is no advantage to spending extra time in the pelagic environment, which only incurs greater mortality risk; thus the optimal age at settlement is a_{min} . Hence, all spawning should occur on day $0-a_{min}$. We use this baseline as a point of comparison for our models with competition, with the general expectation that post-settlement competition will select for more varied spawning and settlement strategies.

We add individual features of competition (described above) to examine the consequences of each. We begin with the next simplest case in which each individual only competes with settlers that arrive on the same day ($w = 0, h_o=1$). We use this case to explore the effects of increasing the strength of competition, changing the type of competition (compensating vs. overcompensating), and age-dependent competition. We then proceed to the case in which settlers compete over a wider competition window ($w > 0$). Due to the relative complexity of this case ($w > 0$), we focus on the effects of competition among daily settlement cohorts and the introduction of priority effects. (In many cases with both $w > 0$ and age-dependent competition, the numerical algorithm failed to converge to an ESS. We were unable to determine whether this was due to the best response method used to find ESS solutions or the absence of

an ESS in these cases.)

In all of the numerical examples we set the minimum age at settlement to $a_{min}=29$ days. If competition does not depend on age at settlement, mortality during the pelagic stage selects for settlement at $a=a_{min}$. As a consequence, lunar date of settlement is equal to lunar date of spawning ($d_s=d + 29=d$): i.e., the 29-day duration of the pelagic phase shifts the arrival distribution exactly one lunar cycle later than the spawning distribution. Hence, in the absence of age-dependent competition, $P_1(d_s,a)=R(d,a)$ at the ESS. This equality facilitates comparisons in the case with age-dependent competition, in which some larvae have $a \neq a_{min}$ at the ESS. The particular value of a_{min} does not affect the qualitative results, because daily mortality risk in the pelagic stage is constant. For example, if we used a larger value of a_{min} , we could recover identical results by using a smaller value of μ .

3. Results

3.1. Competition within settlement days ($w=0$)

3.1.1. Age-independent competition

We start with the case in which the effects of competition are restricted to fish that settle on the same day ($w = 0$) and independent of the age of those settlers: $g(a,a')=1$ for any competitor age a' . As expected, post-settlement competition selects for spreading settlement over multiple days. For example, with Beverton-Holt competition, the settlement distribution is symmetric with a peak at the new moon (Fig. 2, bars). This is achieved by spreading spawning around a peak a_{min} days prior to the new moon (Fig. 2, magenta points). Because the duration of the pelagic stage is identical for all larvae (because there is

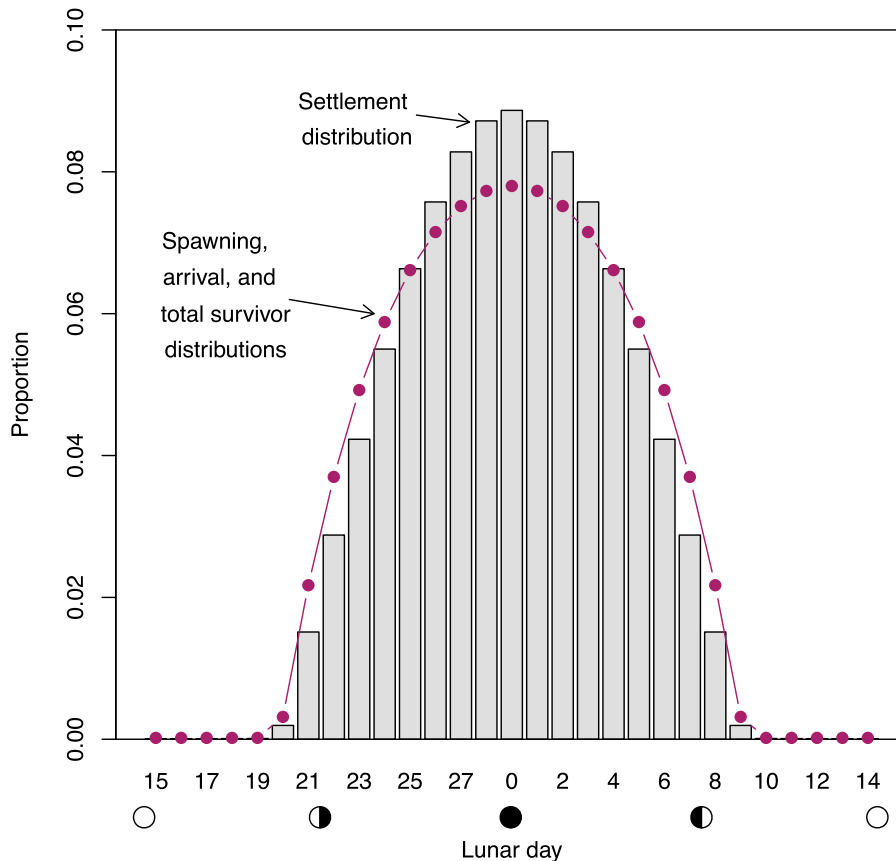


Fig. 2. ESS spawning, arrival, and total survivor distributions (magenta circles, $R(d,a) = P_1(d_s,a)=P_3(d_s,a)$), and settlement distribution (bars, $P_2(d_s,a)$) for the Beverton-Holt competition model with $r_1=1.0$. Competition is age-independent and only occurs within the settlement day ($w = 0$). Lunar phases are indicated by circles under the X axis: filled circle=new moon, open circle=full moon, and half-filled circles=first and third quarters. Lines connecting points are for clarity of presentation and do not imply continuous distributions.

no advantage to being older), mortality during the pelagic stage lowers the density of larvae that arrive at the reef crest on each day but does not change the shape of the arrival distribution, $P_1(d_s, a)$. Hence, the arrival distribution is identical to the spawning distribution, shifted by a_{min} days: $P_1(d_s, a) = R(d_s - a_{min}, a)$.

On the other hand, lunar variation in survival over the reef crest ($s_2(d_s)$) does modify the settlement distribution ($P_2(d_s, a)$) relative to the arrival distribution. The density of arrivals is greatest on the new moon, but greater pre-settlement mortality before and after the new moon narrows the distribution further so that the settlement distribution is narrower than the arrival distribution (Fig. 2, gray bars with taller peak and shorter tails). This narrowing of the settlement distribution is a general prediction that will be true of any process that increases the penalty for arriving further from the new moon. In contrast, post-settlement competition (which transforms the settler distribution to the total survivor distribution, $P_3(d_s, a)$), cancels out the benefits of settling at the new moon and generates a settlement distribution that matches the spawning distribution (i.e., $P_3(d_s, a) = R(d_s - a_{min}, a)$). In this case, lower competitor density offsets lower survival over the reef crest for larvae that settle further from the new moon. Increasing the strength of post-settlement competition (increasing r_1 in Eq. (8)) widens the spawning distribution (Fig. 3) such that settlers are more widely dispersed around the new moon ($P_2(d_s, a)$, not shown).

The prediction that settler density peaks at the new moon (maximum $P_2(d_s, a)$ at $d_s = 0$) is true for any decreasing competition function (e.g., the Beverton-Holt and Ricker functions, Eqs (8) and 9), and does not depend on whether density dependence is compensating or overcompensating. With $w = 0$ and $g(a, a') = 1$, the weighted competitor density on lunar day d_s is

$$N_{d_s, a_{min}}(d_s) = h_0 n(d_s, a_{min}) \tag{13}$$

At the ESS spawning strategy, the payoffs must be equal for any two days d_s and d'_s :

$$s_2(d_s) f(h_0 n(d_s, a_{min})) = s_2(d'_s) f(h_0 n(d'_s, a_{min})) \tag{14}$$

If d_s is closer to the new moon than d'_s , then survival over the reef crest is greater ($s_2(d_s) > s_2(d'_s)$, Eq. (3)) and $n(d_s, a_{min}) > n(d'_s, a_{min})$ because $f(N_{d_s, a}(d_s))$ is a decreasing function. Hence, settler density must decrease (possibly to 0) on either side of the new moon. Note that this prediction does not necessarily hold with competition that is age-dependent ($g(a, a') \neq 1$) or that occurs over multiple days ($w > 0$).

Although peak settlement is predicted to occur on the new moon for compensating and overcompensating competition functions, the ESS spawning distribution does not necessarily peak a_{min} days prior to peak settlement. For the Ricker model (Eq. (9)) with sufficiently strong overcompensating density dependence, the ESS spawning distribution ($R(d, a)$) can have a minimum at the new moon. This is the case for large values of r_1 (Fig. 4, magenta points) or L (not shown). As a result, larval density immediately prior to crossing the reef crest is greatest on the full moon and lowest on the new moon. However, lunar variation in survival over the reef crest ($s_2(d_s)$) reverses this pattern, such that settler density prior to competition peaks on the new moon (Fig. 4, bars). With strong overcompensating density dependence, post-settlement competition reverses this pattern again, and the distribution of birth dates among survivors peaks at the full moon ($P_3(d_s, a) = R(d, a)$).

3.1.2. Age-dependent competition

We now suppose that settlers that spent longer in the pelagic stage have a greater effect on survival of settlers that spent less time in the pelagic stage and vice versa: $g(a, a') > 1$ and $g(a', a) < 1$ for $a' > a$. This scenario potentially selects for an ESS that includes variation in age at

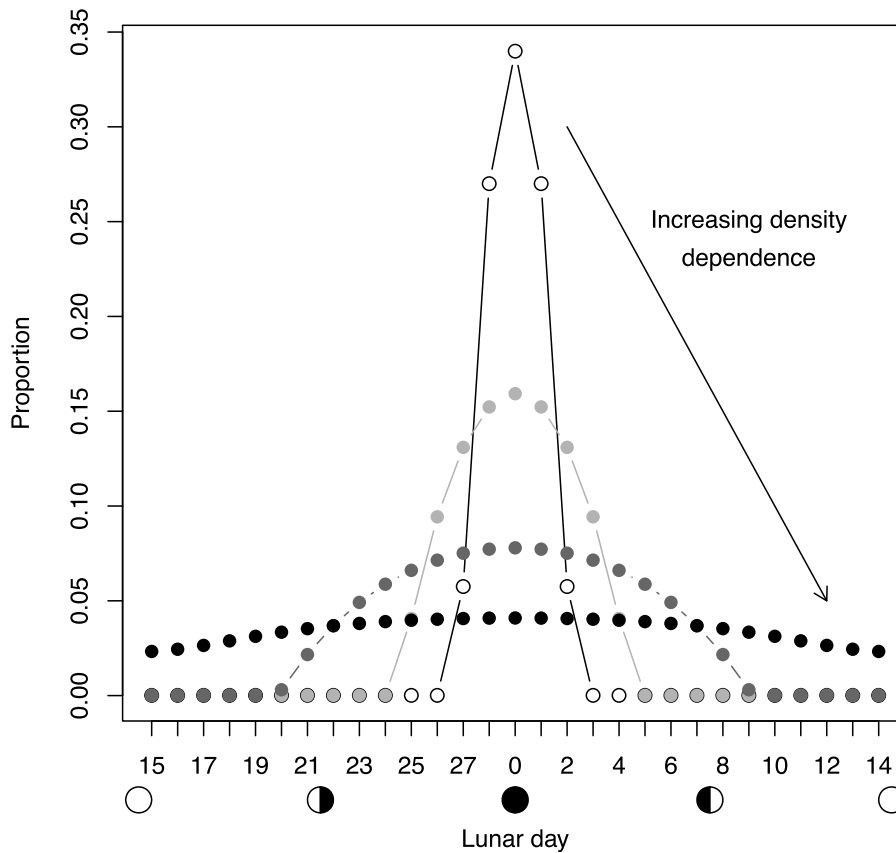


Fig. 3. ESS spawning distributions, $R(d, a_{min})$, with increasing strength of density dependence in the Beverton-Holt competition model: $r_1 = 0.01$ (white points), $r_1 = 0.1$ (light grey points), $r_1 = 1.0$ (dark grey points), and $r_1 = 10$ (black points). Competition is age-independent and only occurs within the settlement day ($w = 0$). Lines connecting points are for clarity of presentation and do not imply continuous distributions.

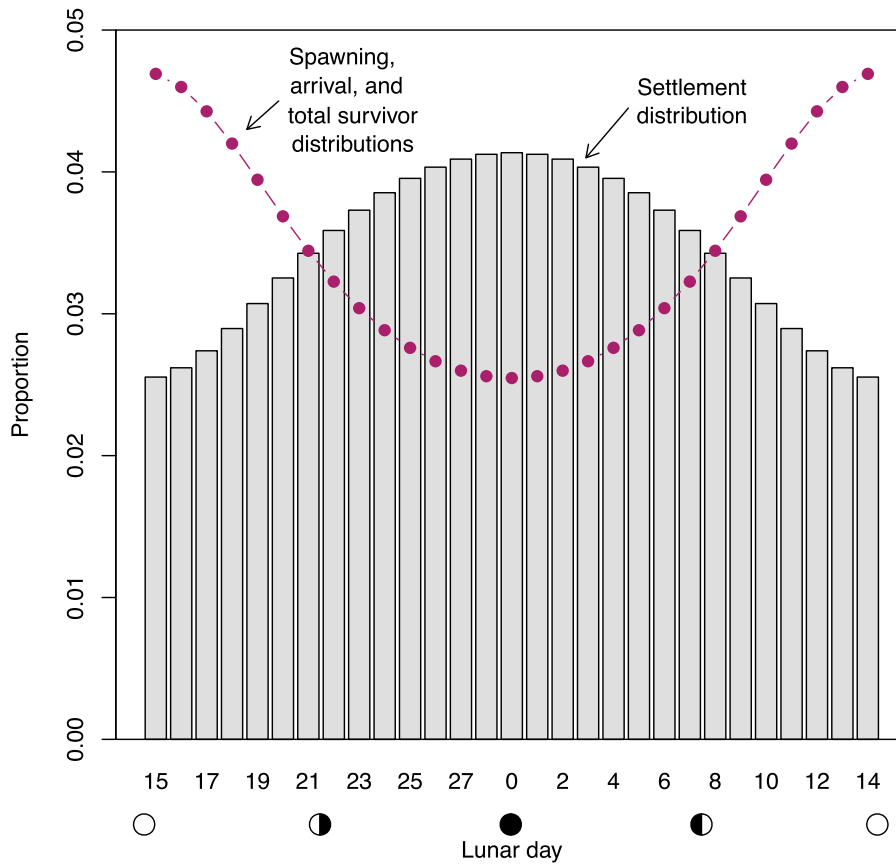


Fig. 4. ESS spawning, arrival, and total survivor distributions (magenta circles, $R(d_s, a) = P_1(d_s, a) = P_3(d_s, a)$), and settlement distribution (bars, $P_2(d_s, a)$) for the Ricker competition model with strong overcompensating density dependence ($r_1 = 10$). Competition is age-independent and only occurs within the settlement day ($w = 0$). Lunar phases are indicated by circles under the X axis: filled circle=new moon, open circle=full moon, and half-filled circles=first and third quarters. Lines connecting points are for clarity of presentation and do not imply continuous distributions.

settlement and coadaptation between settlement date and age. Selection for greater age at settlement depends on the costs and benefits of spending longer in the pelagic stage. For example, if the population adopts a strategy with settlement age a on lunar day d_s , an invader with settlement age $a' > a$ on day d_s can invade if it receives a greater payoff:

$$s_1(a')s_2(d_s)f(h_0g(a', a)n(d_s, a)) > s_1(a)s_2(d_s)f(h_0n(d_s, a)) \quad (15)$$

or

$$\frac{s_1(a')}{s_1(a)} < \frac{f(h_0g(a', a)n(d_s, a))}{f(h_0n(d_s, a))} \quad (16)$$

This condition simply implies that the greater risk of mortality during the longer pelagic stage ($s_1(a') < s_1(a)$) must be more than offset by increased post-settlement survival due to the reduced competitive effect of the residents on the invader ($g(a', a) < 1$).

For example, suppose

$$g(a, a') = \left(\frac{a'}{a}\right)^{g_0} \quad (17)$$

i.e., the effect of competition from settlers with age a' on survival of a settler with age a is a power function of the ratio a'/a with exponent g_0 . Older settlers have greater competitive strength than younger settlers if $g_0 > 0$.

The shapes of the predicted arrival distribution ($P_1(d_s, a)$) summed over values of a is nearly identical to the result without age-dependent competition (Fig. 5, compared to Fig. 2). However, the spawning distribution differs considerably (Fig. 5, magenta points). The differences are the result of variation in age at settlement (shaded bars in Fig. 5): e.

g., the early peak in spawning includes many larvae that settle with $a > a_{min}$ around the new moon. The ESS spawning distribution also includes multiple values of a for some birth dates (not shown). Hence, the ESS predicts some larvae born on the same day will settle on different days with different ages.

Another prediction from this example is that older larvae tend to settle closer to the new moon (darker bars in Fig. 5). This is a general prediction for both Beverton-Holt and Ricker competition. If the invasion condition in Eq. (16) is true for any day d_s , it must be true for any other day on which the density of settlers is greater, because the right-hand side of Eq. (16) increases with increasing $n(d_s, a)$. As noted above, the number of settlers increases with $s_2(d_s)$, i.e., closer to the new moon. Hence, at an ESS that includes a mix of settler ages, older larvae settle around the new moon, when survival over the reef crest is greatest, and younger larvae settle further from the new moon (and thus avoid severe competition with older fish but incur greater predation as they cross the reef crest). This is similar to a competition-colonization tradeoff, in that larvae that delay settlement attain greater competitive strength upon arrival in the reef habitat, whereas larvae that settle with lower age have lower mortality risk while dispersing to the reef. Hence, the tradeoff is between mortality risk during dispersal vs. mortality risk post-dispersal.

3.2. Competition across settlement days ($w > 0$)

We now relax the assumption that settlers only compete with other settlers that arrive on the same day. Instead, we allow the competition window to extend beyond the settlement day ($w > 0$). The strength of competition between fish that settle within w days of one another

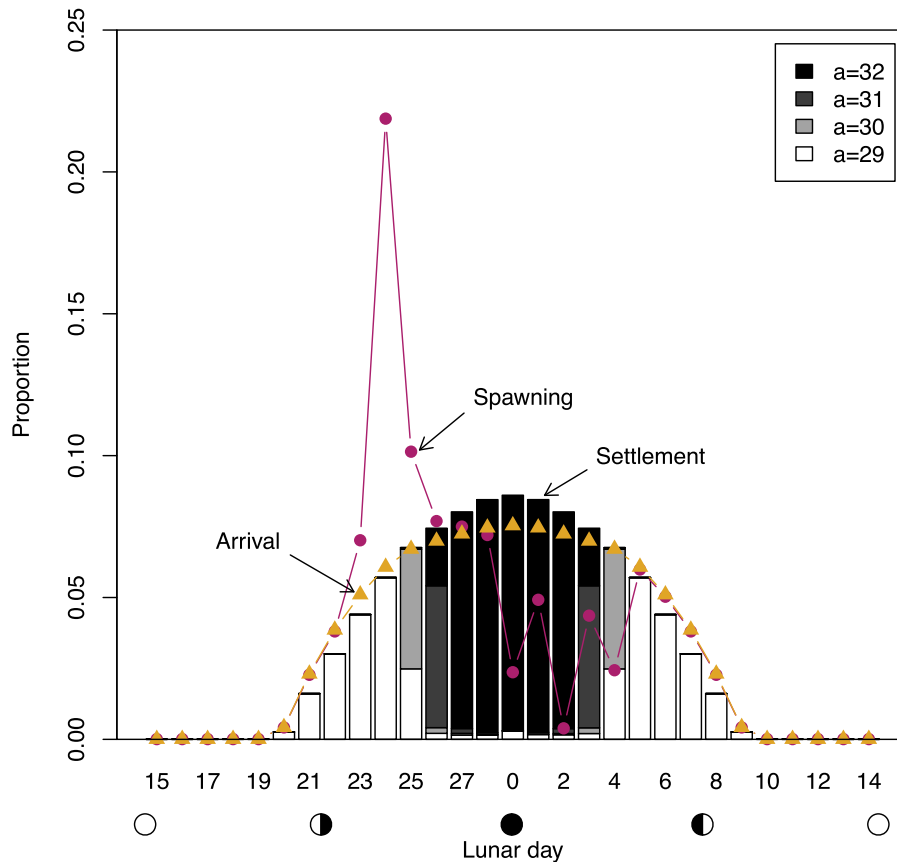


Fig. 5. ESS spawning distribution (magenta circles, $R(d,a)$), arrival distribution (orange triangles, $P_1(d_s,a)$), and settlement distribution (bars, $P_2(d_s,a)$) for age-dependent competition ($a_{min}=29$, $a_{max}=32$, $g_0=0.75$). Age at settlement is indicated in the settlement distribution by shading. The spawning and arrival distributions are summed over all values of a for clarity of presentation. Competition is restricted to fish that settled on the same day ($w = 0$) and follows the Beverton-Holt model with $r_1=1.0$. Lines connecting points are for clarity of presentation and do not imply continuous distributions.

depends on the difference in settlement date, δ , where $-w \leq \delta \leq w$.

In the simplest case, which we consider first, competition is strongest among fish that settled on the same day and tapers off symmetrically with increasing δ (Fig. 6, white points) This would be appropriate if, e.g., fish tend to interact with others of similar size and post-settlement growth reduces interactions with new, smaller settlers. In this case, there is no priority effect, i.e., a fish interacts with competitors that arrived δ days earlier in the same way that it interacts with competitors that arrive δ days later. Next, we model priority effects in competition. In this case, a fish has a stronger competitive effect on fish that settle later, and vice versa. This assumption implies that $h_{\delta} > h_{-\delta}$ for at least some small values of δ (Fig. 6, filled points).

In the numerical examples presented in this section, we assume Beverton-Holt competition (Eq. (8)) and we set the competition window to span one lunar cycle ($w = 14$). We focus on the effects of competition on the ESS spawning distributions, $R(d,a)$, and the settlement distributions, $P_2(d_s,a)$. We assume competitive effects are independent of age, which implies $a=a_{min}$ in all cases. Hence, the arrival distribution is identical to the spawning distribution shifted by a_{min} : $P_1(d_s,a)=R(d+a_{min},a)$. To simplify presentation of results, we do not plot $P_1(d_s,a)$ in the figures.

3.2.1. Symmetric competitive effects

We examine the effect of competition over a range of values of r_1 , which determines the overall strength of density dependence (Eq. (8)). Because settlers must survive w days post-settlement, an individual that settles on any day d_s competes with fish that settled and survived over the previous w days as well as those that settle on d_s and the following w days. In general, stronger density dependence tends to spread the

spawning distribution (Fig. 7, magenta points), as when competition only occurred among larvae that settled on the same day (Fig. 3). However, although the competitive weights are symmetric around h_0 , the effects of competitors that arrive earlier vs. later differ because post-settlement mortality eliminates some of the earlier arrivals each day.

For example, settlement peaks on the new moon if density dependence is weak (Fig. 7a, bars). Settlers can avoid some competitors by arriving before or afterward, trading off reduced competition for increased mortality over the reef crest (lower $s_2(d_s)$). At the ESS, a greater proportion settle after the new moon because many of the potential competitors that settled on the new moon will have died. Alternatively, a smaller proportion settle before the new moon. Early arrivals experience a relatively low initial competitor density, but these individuals must compete with all settlers that subsequently arrive on the new moon and afterward (for at least one day, before some die). No larvae settle more than one day before or after the new moon because density dependence is too weak to counteract lower survival over the reef crest.

Stronger density dependence pushes peak settlement later in the lunar cycle due to selection to avoid competition with earlier arrivals (Fig. 7b-d, bars). Initially, there is a smaller peak prior to the new moon (Fig. 7b), because density dependence is too weak to select for settlement when survival over the reef crest is extremely low (even earlier relative to the new moon). Further increases in the strength of density dependence spread settlement over the entire lunar cycle. Stronger density dependence also causes the settlement distribution to diverge from the spawning distribution, as a greater proportion of larvae arrive further from peak $s_2(d_s,a)$ on the new moon.

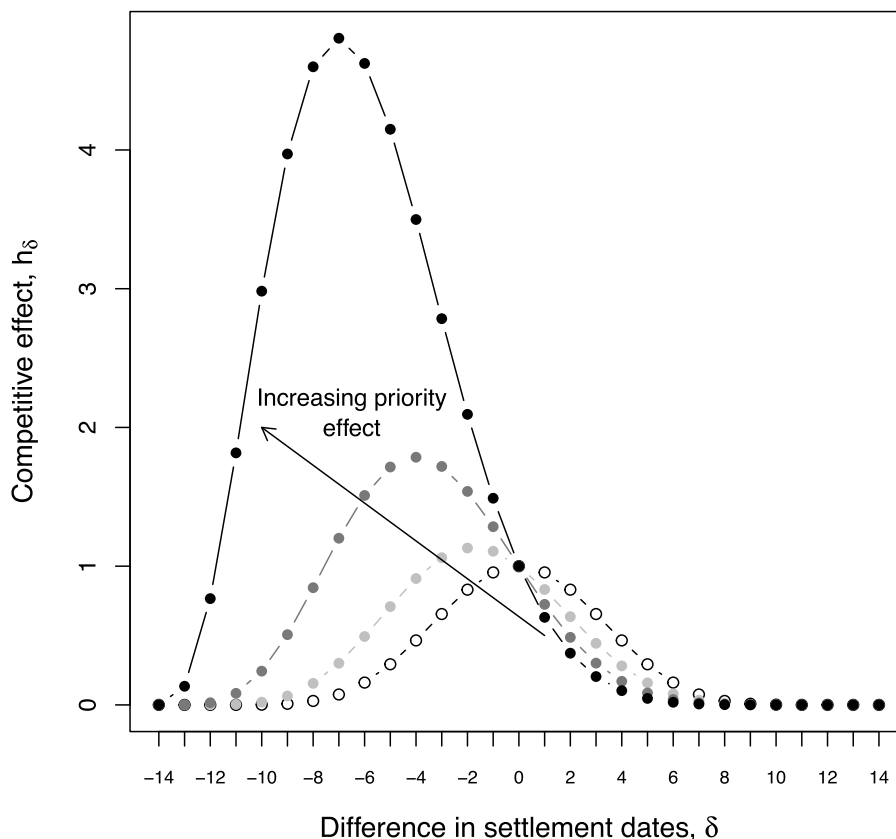


Fig. 6. Values of competitive weights, h_{δ} , used to model competition among settlement days. The h_{δ} are values of the beta probability density function at 29 evenly spaced points (i.e., for $w = 14$), scaled such that $h_0=1$. This is simply a convenient function with symmetric and asymmetric forms, specified by two shape parameters (α and β). Symmetric competitive weights (white points) are scaled values of the beta distribution function with $\alpha=\beta=10$. The remaining three curves show competitive weights for the priority ($\alpha<\beta$). The strength of the priority effect increases with decreasing α : $\alpha=8$ (light grey), $\alpha=6$ (dark grey), $\alpha=4$ (black). Lines connecting points are for clarity of presentation and do not imply continuous distributions.

3.2.2. Priority effects

In general, a priority effect (in which earlier arriving fish have larger competitive effects and are less affected by competition) tends to counteract the delaying effect of competition with earlier arrivals described above (Fig. 8). The priority effect not only increases the competitive weight of earlier arrivals, but also decreases the weight of later arrivals. This favors avoiding competition by arriving earlier.

If the priority effect is sufficiently strong, the ESS settlement distribution consists of multiple peaks separated by large drops in settlement (Fig. 8d). These peaks are generated by the combined effects of delaying to avoid competition from survivors of the previous peak and arriving earlier than the next peak to take advantage of the priority effect.

4. Discussion

Our model predictions confirm our expectation that post-settlement competition can select for a settlement strategy that is widely distributed around the optimal lunar date. This resembles empirical patterns of settlement of many species with lunar periodicity (Robertson 1992; Robertson et al. 1999; D'Alessandro et al. 2007; Besson et al. 2015). In our model this result is a consequence of trading off survival through transit over the reef crest (mediated by reef predators) with survival after settlement (mediated by competition). This mechanism distinguishes our model from hypotheses based on density independent pre-settlement processes such as stochasticity in the larval environment.

We derived several novel and counterintuitive predictions for spawning and settlement patterns that could be observed in empirical data as signals of post-settlement competition. In general, the spawning distribution may not be simply related to the arrival distribution (i.e.,

shifted by larval age, a), and spawning and settlement may not peak on the lunar date with minimal predation risk. For example, with competition only within settlement days, strong overcompensating density dependence selects for a spawning distribution that peaks a days before the lunar date with minimal settlement (Fig. 4). This implies that most settlers are born on days when spawning is minimal, and relatively few of the larvae born at peak spawning survive to settlement. Alternatively, if settlers compete across settlement days with symmetric competitive weights, peak settlement is delayed relative to the lunar date with minimal predation risk (Fig. 7), i.e., a disproportionate fraction of larvae arrive on dates with sub-optimal survival across the reef crest. Although a priority effect can counteract this delay, it can also result in multimodal spawning and settlement distributions (Fig. 8). Consequently, the particular nature of competitive interactions alone can qualitatively change patterns of spawning and/or settlement, from a lunar rhythm to a semi-lunar or tri-lunar rhythm (e.g., Seymour et al. 2018).

Inclusion of age-dependent competition results in additional predictions regarding spawning and settlement distributions. If competitive strength increases with larval age, older settlers are predicted to arrive closer to the new moon. This coadaptation between age and settlement date obscures the relationship between spawning and arrival distributions (Fig. 5). Furthermore, the non-random association between larval age and settlement date would not be expected if the distribution of settlement dates around the new moon were simply the consequence of stochastic variation in the pelagic environment.

Post-settlement competition, as well as priority effects are often examined in field experiments (e.g., Geange and Stier 2010, Poulos and McCormick 2014, 2015). The intensity of cohort effects on survival (the strength of density dependence) varies greatly among studies (Osenberg

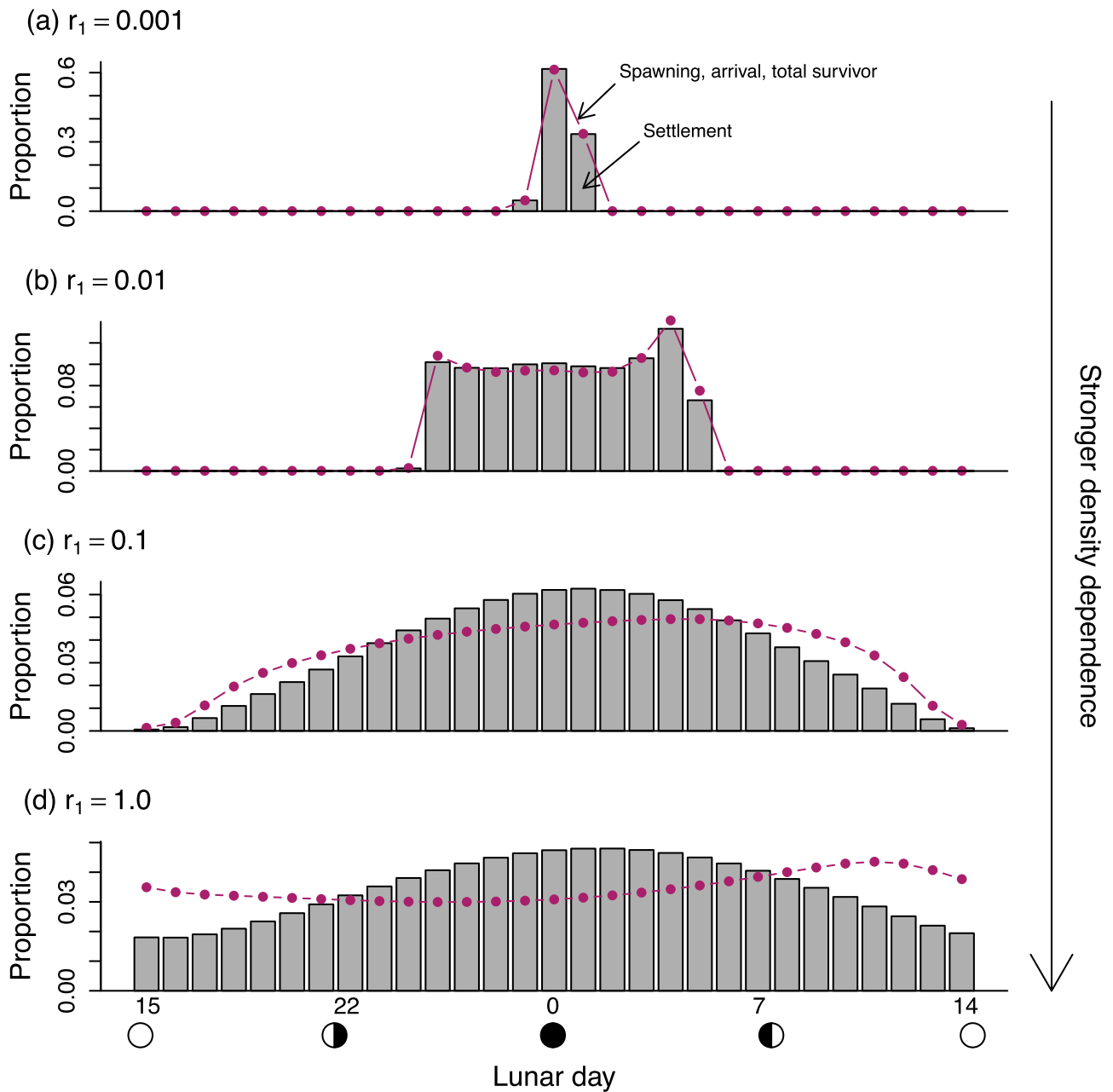


Fig. 7. ESS spawning, arrival, and total survivor distributions (magenta circles, $R(d,a) = P_1(d_s,a) = P_3(d_s,a)$), and settlement distributions ($P_2(d_s,a)$, bars) with competition among settlement days ($w = 14$) and symmetric competitive weights ($\alpha = \beta = 10$, no priority effect; see Fig. 6). Strength of density dependence (r_1 in the Beverton-Holt model) increases from top to bottom. Competition is age-independent. Lines connecting points are for clarity of presentation and do not imply continuous distributions.

et al. 2002). Although Shima and Osenberg (2003), using an extensive dataset on post-settlement density-dependent survival in a tropical wrasse, found that the Beverton-Holt formulation outperformed the Ricker, Johnson (2007) found better support for the Ricker in several temperate fishes. Our model predictions demonstrate that the difference between these two forms of density dependence can invert the relationship between spawning and settlement distributions (compare Fig. 2 and Fig. 4). Hence, variation in the form and intensity of post-settlement competition could play a key role in driving empirical variation in spawning and settlement patterns. Future comparative work should strive to integrate data on spawning and settlement with post-settlement processes. Yet, to date, attempts to explain spawning and settlement patterns have focused, not on post-settlement competition, but predation during the settlement process, as well as effects associated with tidal

delivery of larvae (e.g., Sponaugle and Cowen 1996, Robertson et al. 1999, Doherty et al. 2004, Sponaugle and Pinkard 2004, Sponaugle et al. 2005, D'Alessandro et al. 2007).

This modelling was, in part, motivated by previous empirical observations of the sixbar wrasse, which spawns across the lunar cycle (Shima et al. 2020; Mitterwallner and Shima 2022a, 2022b), exhibits plasticity in PLD (Shima et al. 2020), settles at the new moon (Shima et al. 2018), and incurs density-dependent post-settlement mortality (Shima 2001; Shima and Osenberg 2003) and size-based competition and priority effects (Geange and Stier 2010). We observed peak spawning on new moons—that, when coupled with developmental plasticity—resulted in (1) lower larval survival (Shima et al. 2020) but, (2) larger settlers that tended to arrive prior to peak settlement on the new moon (Shima et al. 2018, 2020). Our previous focus was on parental

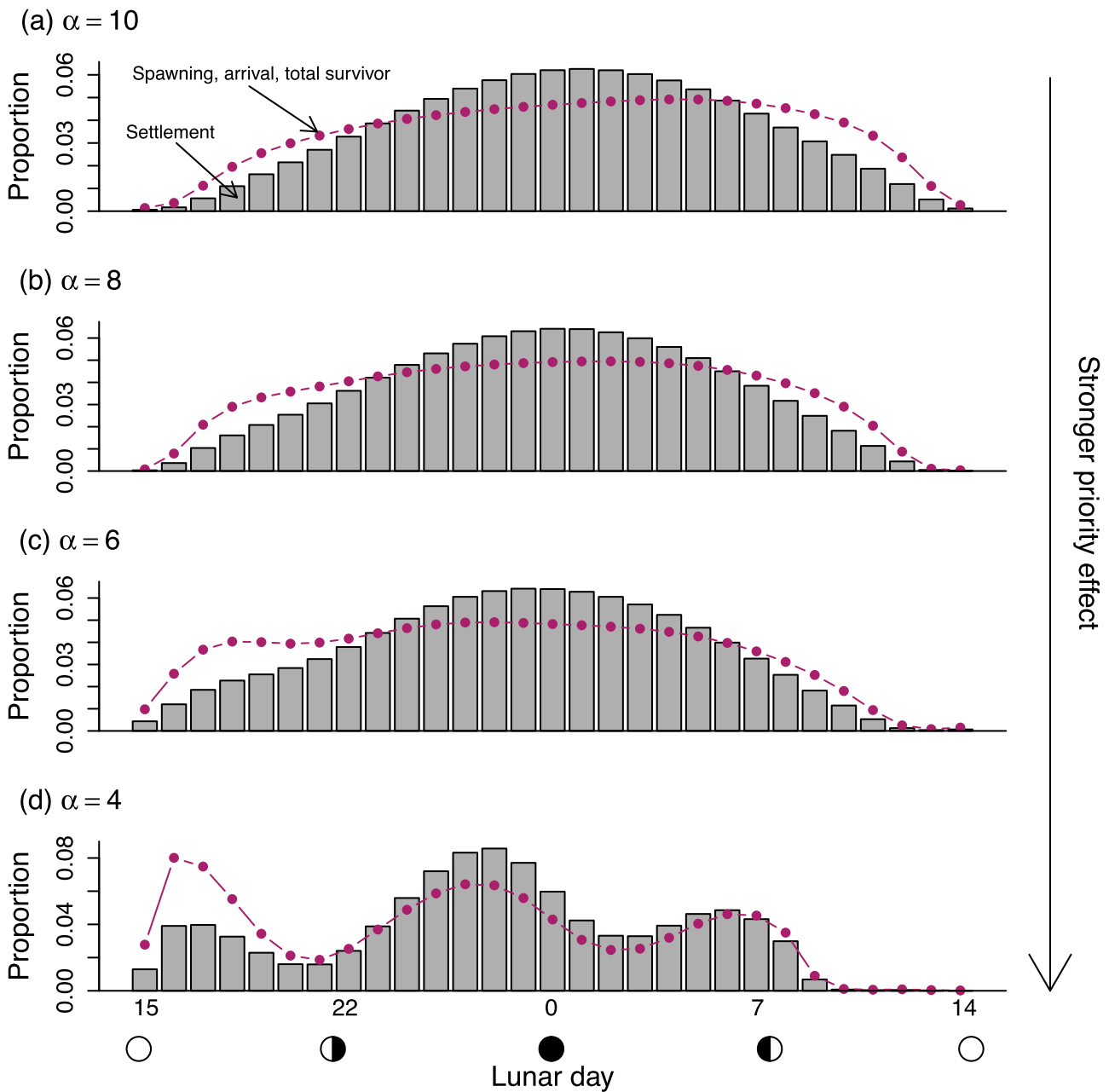


Fig. 8. ESS spawning, arrival, and total survivor distributions (magenta circles, $R(d,a) = P_1(d_s,a) = P_3(d_s,a)$), and settlement distributions ($P_2(d_s,a)$, bars) with competition among days ($w = 14$) and the priority effect. The strength of the priority effect increases with decreasing α , from none ($\alpha = \beta = 10$) to strong ($\alpha = 4$) with decreasing α (top to bottom, see Fig. 6). The shape parameter $\beta = 10$ in all cases. Competition is age-independent and follows the Beverton-Holt model with $r_1 = 0.1$. Lines connecting points are for clarity of presentation and do not imply continuous distributions.

decisions, and we speculated that adults may spawn at times that trade-off poorer larval survival for improved post-settlement competitive ability. Here, we explore the (non-mutually exclusive) hypothesis that variation in *settlement timing* is a strategic response to post-settlement competition. We conclude that settlement timing, modulated by different forms of post-settlement competitive interactions, is sufficient to drive much of the life history variation that we observe in sixbars and many other species.

We have also observed lunar rhythms in larval growth of sixbar wrasse (Shima et al. 2021). In particular, sixbars that were spawned close to the new moon experienced increased opportunities for growth during the pelagic stage, and settled at a time of accelerating growth. Growth advantages accrued across the larval stage may improve survival probabilities on the reef, and further help to explain adult

spawning patterns, settlement timing, and post-settlement competition. The observation of older and larger settlers arriving prior to the new moon may not be consistent with our model predictions here because the current version of this model does not include variable growth and plasticity in larval development. Our model also did not consider the possibility that predation risk changes with larval size, or that growth and predation risk may continue to depend on lunar illumination after settlement. Future modelling should explore this further.

The distribution of settlers over time is conceptually similar to the distribution of competitors over space, i.e., a lunar day is equivalent to a habitat patch. Indeed, our model predictions for the case in which competition occurs only within settlement days (Fig. 2, Fig. 3, Fig. 4) are comparable to the classic result from habitat selection theory, the ideal free distribution (Fretwell and Lucas 1969). However, this direct

comparison breaks down when we consider competition among days. The explicit temporal dynamic—settlers that survive compete with new arrivals over successive days—leads to novel predictions that do not arise from treating settlement as an ideal free distribution in time (Fig. 7, Fig. 8).

Competition and density-independent processes are not mutually exclusive hypotheses to explain empirical patterns, and we expect both to influence reef fish dynamics. We have not addressed the question of how a density-dependent strategy might evolve if, e.g., environmental stochasticity hinders a spawning female's ability to predict offspring arrival date. Furthermore, the ESS is a predicted distribution at the population level. The prediction does not specify how individuals spread their spawning over time, as long as their combined spawning results in the ESS distribution. At the individual level, the spawning distribution may be influenced by, e.g., constraints on clutch size and frequency. The effects of such limitations remain to be explored.

Nonetheless, here, we have shown that post-settlement competition alone can drive diversity in spawning and settlement tactics. More generally, density dependence at one stage can have important consequences for timing of events at multiple points in the life history. This interplay makes interpretation of phenological patterns observed in life histories particularly challenging.

CRedit authorship contribution statement

Erik G. Noonburg: Conceptualization, Formal analysis, Software, Writing – original draft. **Suzanne H. Alonzo:** Conceptualization, Writing – original draft. **Craig W. Osenberg:** Conceptualization, Writing – original draft. **Stephen E. Swearer:** Conceptualization, Writing – original draft. **Jeffrey S. Shima:** Conceptualization, Writing – original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

This submission uses code which is provided as private-for-peer review via : <https://figshare.com/s/7346f65b6a91cde21034>. Upon publication, this code will be permanently archived at Figshare.

Funding

This work was supported by the Royal Society of New Zealand–Marsden Fund (VUW1503), the U.S. National Science Foundation (OCE-1851032), and Victoria University of Wellington.

Acknowledgements

J. Brown and W. White provided helpful feedback on the manuscript.

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