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Born at the right time? A conceptual framework linking reproduction, development, and

settlement in reef fish

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Running Head: *Born at the right time?*

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31

32   **Abstract**

33   Parents are expected to make decisions about reproductive timing and investment that

34 maximize their own fitness, even if this does not maximize the fitness of each individual

35 offspring. When offspring survival is uncertain, selection typically favors iteroparity, which

36 means that offspring born at some times can be disadvantaged, while others get lucky. The

37 eventual fate of offspring may be further modified by their own decisions. Are fates of offspring

38 set by birthdates (i.e., determined by parents), or can offspring improve upon the cards they've

39 been dealt? If so, do we see adaptive plasticity in the developmental timing of offspring? We

40 evaluate these questions for a coral reef fish (the sixbar wrasse, *Thalassoma hardwicke*) that is

41 characterized by extreme iteroparity and flexible larval development. Specifically, we monitored

42 larval settlement to 192 small reefs over 11 lunar months and found that most fish settled during

43 new moons of a lunar cycle (consistent with preferential settlement on dark nights). Settlement

44 was significantly lower than expected by chance during the full moon and last quarter of the lunar

45 cycle (consistent with avoidance of bright nights). Survival after settlement was greatest for fish

46 that settled during times of decreasing lunar illumination (from last quarter to new moon). Fish

47 that settled on the last quarter of the lunar cycle were ~10% larger than fish that settled during

48 other periods, suggesting larvae delay settlement to avoid the full moon. These results are

49 consistent with a numerical model that predicts plasticity in larval development time that enables

50 avoidance of settlement during bright periods. Collectively, our results suggest that fish with

51 inauspicious birthdates may alter their developmental trajectories to settle at better times. We

52 speculate that such interactions between parent and offspring strategies may reinforce the

53 evolution of extreme iteroparity and drive population dynamics, by increasing the survival of

54 offspring born at the "wrong" time by allowing them to avoid the riskiest times of settlement.

55 *Keywords:* reef fish; lunar periodicity; size-at-settlement; developmental delay; life history;

56 recruitment; nocturnal illumination; post-settlement processes, phenology

57

58   **Introduction**

59   "Timing is everything", or so the saying goes. Birth order and timing of reproduction can

60 determine survival, shape personalities and influence other opportunities for offspring (Altus

61 1966, Semlitsch et al. 1988, Thomas et al. 2001, Platt et al. 2003, Verdu and Traveset 2005,

62 Duckworth et al. 2015). Parents choose when to reproduce, and offspring may be left to play the

63 hand they've been dealt. Thus, we may ask: can offspring alter their developmental rates and

64 trajectories to compensate for a poorly-timed birth? If so, how does this plasticity affect patterns

65 of population replenishment and subsequent dynamics?

66   These are important and relatively unexplored questions for many marine reef organisms

67 that have complex life-cycles (Caley et al. 1996). In marine reef ecosystems, adults are often

68 iteroparous and produce many offspring (eggs, larvae) that develop, disperse, and mostly die

69 (White et al. 2014) in offshore waters before survivors settle back to reef habitats. The process of

70 settlement is also risky (Doherty et al. 2004). Thus, many species have larvae that settle at a

71 higher rate during new moons of a lunar cycle (e.g., Rankin and Sponaugle 2014) when peak tidal

72 amplitudes can enhance transport to settlement destinations (Forward and Tankersley 2001), and

73 cover of darkness reduces predation rates (Acosta and Butler 1999). Dark periods of a lunar

74 cycle may represent a good settlement window (*sensu* Pineda et al. 2006) for larvae of many

75 marine reef organisms (*see* Todd and Doyle 1981 for an analogous example involving prey

76 resources).

77   Adults should make decisions about reproductive timing and investment that maximize

78 their own fitness, even if this does not maximize the fitness of each offspring (Warner 1998).

79 Environmental uncertainty often selects for iteroparity as a diversified bet-hedging strategy

80 (Wilbur and Rudolf 2006). Adults of many reef fish are highly iteroparous, spawning on a fairly

81 continuous basis (Claydon et al. 2014) to produce larvae with a wide range of birthdates. Larvae

82 spawned at certain times may have better odds of survival (e.g., well-timed to hit a favorable

83 settlement window; Fig 1a) than others that were spawned at less advantageous times. However,

84 larvae of many reef organisms also have plastic developmental rates (Victor 1986, Sponaugle and

85 Cowen 1996, Robertson et al. 1999), excellent sensory and locomotory capabilities (Leis 2006),

86 and are therefore well equipped to change where and when they settle (Shima 2001). A high

87 degree of plasticity could enhance larval survival and concentrate settlement compared to what

88 would be predicted based upon birthdate alone. Both increased survival and synchrony could

89 enhance the strength of density-dependence and thus alter spatial and temporal population

90 dynamics and regulation.

91   Here, we investigate patterns of larval settlement for a coral reef fish (the sixbar wrasse,

92   *Thalassoma hardwicke*) that exhibits life-history traits common to many reef organisms: adults

93   are highly iteroparous (Claydon et al 2014), and they produce larvae with flexible developmental

94   durations (Victor 1986; Fig 1a). First, we evaluate the hypothesis that sixbars settle non-

95   randomly across the lunar cycle, with greatest settlement during the new moon (indicative of a

96   good settlement window; e.g., Sponaugle and Cowen 1996, Robertson et al. 1999). Second, we

97   ask whether the distribution of sizes of settlers (arriving across the lunar cycle) is consistent with

98   a hypothesis that individuals adjust their developmental rates to target new moons and/or avoid

99   full moons (e.g., Sponaugle and Cowen 1996, Robertson et al. 1999). Third, we explore post-

100 settlement survival and growth of sixbars that settled during different periods of the lunar cycle.

101 Finally, we use a simple mathematical model to explore fitness payoffs to larvae that can change

102 their development times. We evaluate empirical results against the optimal developmental

103 durations predicted by this simulation. Collectively, our results support a conceptual model in

104 which flexible development and associated demographic consequences likely contribute to a type

105 of eco-evolutionary feedback (*sensu* Schoener 2011) that should reinforce iteroparity, as adaptive

106 plasticity in the timing of settlement by larvae will reduce a potential cost of adult iteroparity by

107 increasing the survival of offspring born at the "wrong" time.

108

109   **Methods**

110 *Study System*

111   We evaluated settlement of a coral reef fish (sixbar wrasse, *Thalassoma hardwicke*) to

112 small patch reefs on the island of Moorea, French Polynesia (17° 30' S, 149° 50' W). Sixbars are

113 small-bodied fish that inhabit shallow coral reefs across much of the Indo-Pacific region, and are

114 particularly common within the lagoon system of Moorea (Galzin 1987). In general, they exhibit

115 life history patterns common to many marine organisms: e.g., they are highly iteroparous, with

116 spawning occurring on most days of a lunar cycle and across much of the year (Claydon et al.

117 2014). On Moorea, we typically observe spawning activity along reef edges and during outgoing

118 tides, consistent with a parental strategy that maximizes advection of propagules off the reef

119 (Johannes 1978, Claydon 2004). Larvae develop in the pelagic environment and appear to have

120 flexible developmental durations (range: 39 to 63 days; Victor 1986). Late-stage larvae re-enter

121 the lagoon system of Moorea by traversing across the offshore barrier reef crest (Dufour and

122   Galzin 1993, Lecchini et al 2007) and settle to small patch reefs that are typically interspersed

123   amid sand, pavement, or cobble substrate (Shima 1999, 2001, Shima and Osenberg 2003, Shima

124   et al 2008). In addition, and like many other wrasses (Kazancioglu and Alonzo 2010), sixbars are

125   sequential protogynous hermaphrodites.

126

127   *Periodicity in Settlement*

128   We estimated settlement of sixbars onto 192 small patch reefs over 6 lunar cycles

129   (January-July) in 2004, and 5 lunar cycles (February-June) in 2005. Sampled reefs were evenly

130   distributed among 12 sites (16 patch reefs per site). Reefs varied in size (mean surface area =

131   12.38 m, SD = 5.96) and composition (mean live coral cover = 64% [SD = 20]; turf algae = 16%

132   [SD = 21]; macroalgae 6% [SD = 9]; bare substrate = 9% [SD=11]; see Shima et al. 2008 for

133   further methodological details). We estimated the numbers and sizes (standard lengths, to nearest

134   mm, aided by photographic references *in situ*) of all juvenile sixbars on each reef, approximately

135   every 3-5 days (mean interval between censuses= 3.96 d; SD=2.55), over all 11 months of

136   observation. We differentiated newly settled sixbars by their small size (9-13 mm), lack of full

137   pigmentation (mostly transparent), characteristic behavior patterns (typically sheltering in small

138   colonies of branching corals or clumps of macroalgae), and absence from previous censuses (see

139   Shima et al 2008). Surveys were conducted by multiple observers in 2004, and by a single

140   observer in 2005.

141   We categorized new settlers to (1) a lunar month, and (2) a quarter of the lunar month

142   (i.e., centered on first quarter, full moon, last quarter, and new moon) based upon observed

143   settlement dates. We distributed settlement observations over the days between sampling events

144   (i.e., to correct for variable sampling effort), to derive an estimate of the number of settlers for

145   each day for each reef. We summed these estimates of daily settlement across reefs, and then

146   calculated the average proportion (± 95% CI) of sixbars that settled during each quarter (n=11

147   lunar months). We compared the observed distribution to a null expectation of homogeneous

148   settlement (i.e., equal settlement to each quarter: proportions = 0.25).

149

150   *Size-at-settlement*

151   Because our visual estimates of size of young sixbars varied among observers by 1-3 mm

152   in 2004, we evaluated variation in size-at-settlement using data only from 2005, when a single

153   observer made all of the observations. These estimates of size have high precision (correlation

154   between visual estimates and size of collected fish: 0.96) and low bias (average error = 0.02mm;

155   Geange 2010). We evaluated variation in size-at-settlement using a generalized linear mixed

156   effects model (Proc Glimmix, SAS 9.3) with a Poisson distribution (because the response

157   variable comprised a small set of integers, e.g., : 9, 10, 11, 12, 13) . Specifically, we modelled

158   size-at-settlement as a function of lunar quarter (first quarter, full moon, last quarter, or new

159   moon; treated as a fixed effect), lunar month (included as a block to control for potential seasonal

160   variation; fixed effect), and reef (to accommodate potential non-independence of different fish

161   settling to common reefs; random effect). We also evaluated an interaction term (between lunar

162   quarter and lunar month); this was not significant, so we excluded it from our final model.

163

164   *Survival and growth after settlement*

165   We estimated post-settlement survival of all newly settled sixbars from surveys made at

166   3-5d intervals (described above). The relatively small number of fish on reefs, and linear

167   relationship between body length and age over this size range (Shima 1999), enabled us to

168   discern survival and growth trajectories of individuals (or groups of individuals that settled at the

169   same size and time). We estimated death dates of individuals from the disappearances of

170   appropriately sized fish in a survey interval (*for more details, see* Shima and Osenberg 2003,

171   Shima et al 2008).   We calculated survival time as the difference between death date and

172   settlement date. We evaluated variation in survival time as a function of the lunar quarter and

173   lunar month when settlement occurred, using a survival analysis (Proc Lifereg, SAS 9.3). We

174   used a Weibull distribution, which allows the hazard function to vary with post-settlement age.

175   We also evaluated the interaction term (between lunar quarter and lunar month); this was not

176   significant, so we excluded it from our final model. We estimated mean survival times for lunar

177   months and quarters by taking the product of the exponentiated intercept parameter and the

178   factorial of the SAS scale parameter (*after* Shima et al. 2008).

179   Because the analyses described above suggested (1) size-at settlement varied among lunar

180   quarters, and (2) survival also varied with lunar phase at settlement, we conducted a secondary

181   analysis to distinguish between effects of size and lunar quarter. In addition, we also tested the

182   hypothesis that survival depended upon lunar illumination: i.e., that the probability of death was

183   greater during full moons, independent of the lunar quarter during which the fish settled.

184   Specifically, we evaluated variation in survival as a function of the lunar quarter and lunar month

185   when settlement occurred, size-at-settlement, and an index of lunar illumination. We estimated

186   lunar illumination as the fraction of the moon illuminated

187   (http://aa.usno.navy.mil/data/docs/MoonFraction.php) on the date that individuals went missing;

188   for fish that survived beyond the end of our survey period (i.e., censored observations in our

189   survival analysis), lunar illumination was assigned as a missing value. As above, we used a

190   survival analysis (Proc Lifereg, SAS 9.3) with a Weibull distribution, and we evaluated a full

191   model with all possible interactions; we sequentially removed non-significant higher-order

192   interactions to determine a reduced model.

193   We estimated post-settlement growth rate for all fish that survived >7 d (i.e., sufficient

194   time to observe an increase in size, given our measurement precision) as the difference between

195   final size and initial size, divided by the time interval separating these two observations. This

196   metric assumes that growth in body length per unit time is constant over the range of fish sizes

197   that we observed (this assumption seems reasonable given a linear relationship between size and

198   age for a similar sample of sixbars; Shima 1999). We evaluated variation in growth rate using a

199   generalized linear mixed effects model (Proc Glimmix, SAS 9.3), as a function of when and

200   where the fish settled: i.e., lunar quarter (fixed effect), lunar month (fixed effect), and reef

201   (random effect). As above, we evaluated an interaction term (between lunar quarter and lunar

202   month); this was not significant, so we excluded it from our final model.

203

204   *Modelling developmental decisions*

205   To evaluate how plasticity in offspring development might evolve in response to variation

206   in the timing of spawning over the lunar cycle, we modelled the fitness payoff to larval sixbars

207   that (1) were born at particular times determined by the spawning decisions of parents and (2)

208   could choose when to settle. We assumed continuous and aperiodic spawning by parents and

209   allowed for the possibility of plasticity in the duration of the developmental period in larvae. Our

210   motivation was to provide a simple representation of our system, and to address the question:

211   "what should a larva do?" with respect to settlement decisions. The model is a thought

212   experiment to explore whether, under extreme iteroparity, variation in the fitness consequences of

213   different settlement decisions are (1) sufficient to drive the expression of developmental plasticity

214   and (2) consistent with observed patterns in settlement and settler size/age.

215   In our model, the fitness payoff for a larva with a given birth date and pelagic larval

216 duration is represented by the probability of surviving through the larval stage to the post-

217 settlement stage, which we represent as the product of two functions. The first, $d(x)$, describes the

218 effect of larval duration (x) on the probability of surviving from birth to settlement. The second,

219 $p(s)$, describes the additional effect of the lunar phase on the probability of survival, where $p(s)$ is

220 periodic on the day of settlement, s. Thus, survival from birth to settlement for a larva with birth

221 date b and settlement date s is $d(x)p(s)$, where pelagic larval duration is $x = s - b$.

222   First, we assume that larval survival is a unimodal function of larval duration (e.g.,

223 Peterson and Wroblewski 1984), which initially increases with duration due to the positive

224 effects of increasing larval competence (i.e., attainment of sufficient energetic reserves to settle

225 and metamorphose into the juvenile form), but then declines due to the negative effects of staying

226 too long in the pelagic environment (Anderson 1988, Leggett and DeBlois 1994, Hare and

227 Cowen 1997). We capture this general biological scenario using the function:

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

229 where $x =$ age at settlement (= pelagic larval duration, in days) and a, k, c are parameters that

230 specify the shape of $d(x)$. For $a,k,c>0$ and $k>a$, the resulting function $d(x)$ is unimodal with a

231 maximum at $x^* = \frac{1}{k}\left(c - ln\left(\frac{a}{k-a}\right)\right)$. Thus, the three parameters collectively determine the

232 optimal age at settlement. In our numerical solutions we set $c = 47k + ln\left(\frac{a}{k-a}\right)$ such that $x^*=47$

233 days, the approximate average age of sixbar settlers (Victor 1986). Although Eq. 1 allows a

234 positive probability of survival for any $x\geq0$, the function $d(x)$ can be parameterized to obtain an

235 arbitrarily narrow range of possible ages at settlement: i.e., $d(x)$ approaches 0 for large deviations

236 from x^* (Fig 4a-c). The strength of selection against flexibility in age at settlement depends on

237 the slope of $d(x)$ around x^*. If k is large (Fig 4a), $d(x)$ is steep for $x<x^*$, representing rapid onset

238 of larval competence and low survival for larvae that settle before the optimal age. If a is large

239 (Fig 4c), $d(x)$ falls off rapidly from the peak, representing a severe survival penalty for delayed

240 settlement. If both a and k are small (Fig 4b), $d(x)$ is approximately symmetric, representing

241 similar survival penalties for early and late settlement.

242   Next, we assume that survival of settlers depends on the lunar phase during which

243 settlement occurs. In particular, we assume that predation risk varies in proportion to lunar

244 illumination, which is greatest during a full moon. This predation risk primarily occurs as the

245   settler traverses the reef crest, but the lunar effect may also include predation risk immediately

246   after settlement. We represent this as a sinusoidal function with a period of 28 days:

247
$$p(s) = h\left(\cos\left(\tfrac{2\pi}{28}(s - L)\right)\right) + m \qquad (2)$$

248   where s = settlement date and $p(s)$ has a mean of m with a total amplitude of $2h$ (with h and m

249   specified such that $0<p(s)<1$). The phase is offset by L days, where L determines the day of the

250   lunar cycle in which survival is maximal. We set $L=24.5$, under the assumption that survival

251   peaks at the new moon, with the first quarter of the lunar cycle arbitrarily set to begin at $s=0$.

252   These two equations capture how adult reproductive timing and larval developmental

253   duration affect the probability of larval survival up to the post-settlement stage. The challenge

254   for larvae then becomes one of timing settlement to coincide with the right general time (found

255   by equation 2) subject to the constraint imposed by the larva's birth date, which will usually mean

256   that it will be a suboptimal age when predation risk is minimal. Each larva must therefore

257   balance the conflicts arising between timing with respect to its age vs. time of settlement. We

258   therefore find the settlement date ($s*$) that maximizes total survival for each birthdate over a lunar

259   cycle ($b = 1,2,…,28$). We find $s*$ numerically by calculating $d(x)p(s)$ for all values of larval

260   duration (x) up to 100 days (sufficient for the parameter values used in Fig. 4) and selecting the

261   optimum. We then find the predicted ages of individuals that settle on each day of the lunar cycle

262   under the assumption that spawning is aperiodic and each larva settles on the optimal day for a

263   given birthdate. We present numerical solutions for three sets of parameter values (a,k,h,m) that

264   demonstrate possible outcomes of selection against deviation from the optimum, $x*$: i.e., strong

265   selection against settling early (Fig 4a), equal selection against positive and negative deviations

266   away from the optimum (Fig 4b), and strong selection against delayed settlement (Fig 4c). R

267   code for numerical solutions is provided in electronic supplementary material.

268

269   **Results**

270   *Periodicity in Settlement*

271   We recorded 1038 newly settled sixbars on 192 reefs over 11 lunar months (583 over 6

272   months in 2004, and 455 over 5 months in 2005). Settlement was unevenly distributed across

273   lunar quarters within lunar months. More than half of the settlers (mean = 0.52; 95% CI = 0.38-

274   0.68) arrived during the new moon (i.e., significantly more than expected by chance; the 95% CI

275   does not include 0.25; Fig 2a). The proportion of settlers arriving during the first quarter of the

276   lunar cycle (0.20; 0.11-0.30) was similar to the null expectation of 0.25. The proportions of fish

277   settling during the full moon (0.15; 0.07-0.23) and last quarter of the lunar cycle (0.12; 0.06-0.18)

278   were both significantly lower than expected by chance (Fig 2a).

279

280   *Size-at-settlement*

281   Size (standard length) of settlers observed in 2005 also varied among lunar quarters ($F_{3,323}$

282     $= 3.44$, $p = 0.0172$). Sixbars that settled during the last quarter were approximately 10% larger

283   than fish that settled during other quarters of the lunar cycle (Fig 2b). Size-at-settlement did not

284   vary significantly among blocks (i.e., lunar months; $F_{4,323} = 0.60$, $p = 0.67$).

285

286   *Survival and growth after settlement*

287   Post-settlement survival of sixbars was dependent upon lunar quarter of settlement (Type

288   III analysis of effects, df $= 3$, *Wald Chi-square* $= 8.93$, $p = 0.03$). Fish that settled during the first

289   quarter (mean survival time $= 56.3$ d) or during the full moon (mean survival time $= 58.7$ d)

290   experienced greater mortality than did fish that settled during the last quarter (mean survival time

291     $= 90.7$ d) or during the new moon (mean survival time $= 79.3$ d; Fig 3). Survival of sixbars also

292   varied across lunar months (Type III analysis of effects, df $= 4$, *Wald Chi-square* $= 17.67$, $p =$

293   0.0014). Mean survival times generally declined across the settlement season, although mean

294   survival time was particularly low for fish that settled in April (mean survival time for lunar

295   months of settlement: Feb $= 137.8$ d; Mar $= 84.46$ d; Apr $= 48.63$ d; May $= 80.70$ d; Jun $= 79.28$

296   d).

297   Because both size-at-settlement and survival varied with respect to lunar quarter of

298   settlement (Fig 2b, 3), we conducted a secondary analysis to statistically decouple the effects of

299   size and lunar quarter on survival: e.g., was the high survival of fish that settled during the last

300   quarter due to the lunar phase or due to the larger size of these settlers? This analysis also

301   incorporated the effects of post-settlement lunar luminosity on survival. The relationship

302   between post-settlement survival and lunar quarter of settlement remained qualitatively

303   unchanged from our original analysis presented above (Type III analysis of effects, df $= 3$, *Wald*

304   *Chi-square* $= 10.04$, $p = 0.018$), as did the effect of lunar month of settlement (Type III analysis

305   of effects, df $= 4$, *Wald Chi-square* $= 90.30$ $p < 0.0001$). Controlling for these lunar effects, size-

306   at-settlement did not significantly affect post-settlement survival (Type III analysis of effects, df

307   = 1, *Wald Chi-square* = 0.40, *p* = 0.53). Thus, this analysis suggests that variation in size did not

308   confound our interpretation of the effects of lunar quarter on survival. Interestingly, lunar

309   illumination was not a significant predictor of post-settlement survival (Type III analysis of

310   effects, df = 1, *Wald Chi-square* = 2.67, *p* = 0.10). However, we note the non-significant trend

311   was for a 2% reduction in survival for every 10% increase in the fraction of moon illuminated

312   (corresponding to a 20% reduction in survival during the full moon, relative to survival during

313   the new moon).

314   Post-settlement growth rate of sixbars did not vary as a function of the lunar quarter

315   ($F_{3,240}$= 0.94, *p* = 0.42) or lunar month ($F_{4,240}$ = 1.34, *p* = 0.26) of settlement. Fish that settled

316   during the first quarter moon grew 0.14 mm · d^{-1} (95% CI: 0.13-0.16); fish that settled during the

317   full moon grew 0.14 mm · d^{-1} (0.12-0.16); fish that settled during the last quarter moon grew 0.14

318   mm · d^{-1} (0.12-0.15); and fish that settled during the new moon grew 0.13 mm · d^{-1} (0.11-0.14).

319   Variation in growth across lunar months was similarly invariant.

320

321   *Modelling developmental decisions*

322   The combination of developmental plasticity and temporal variation in predation risk

323   results in differences in the age of settlers over the lunar cycle (Fig 4d-f). Because x^*=47 days for

324   our parameterization, a larva that settles with age x>47 days has delayed settlement relative to the

325   age at which $d(x)$ is maximized, and vice versa. For example, in Fig 4d, the individual that settled

326   on lunar day 18 with age x=55 delayed settlement by 8 days to avoid the peak of the full moon

327   (which occurred 47 days after the larva was born). The individual that settled on day 8 with age

328   x=46 in Fig 4d settled 1 day early to avoid the waxing moon (which peaked 48 days after the

329   larva was born).

330   The particular pattern of early vs. delayed settlement that is predicted depends on the

331   shape of $d(x)$. The empirical results (e.g., Fig 2) are consistent with the case in which larval

332   competency imposes a relatively sharp constraint on early settlement (Fig 4a,d). With a=0.1 and

333   k=1, the model predicts an asymmetric response, with larvae more severely delaying their

334   settlement than initiating settlement early. In this case, the greatest decrease in age at settlement

335   is 1 day, i.e., larvae born 51-59 days before a full moon settle with age x=46 days. In contrast,

336   fish whose birth date would dictate that they settle after the full moon, but before new moon (i.e.,

337   born 36-47 days before a full moon) should delay settlement by as much as 8 days (an average of

338   3.67 days: Fig 4d). This avoidance of peak mortality under the full moon generates a schism in

339   settlement patterns in which settlers that arrive during the last quarter tend to be as much as 9

340   days older than settlers that arrive during other quarters of the lunar cycle (*c.f.,* Fig 2b). If fish

341   delay settlement by approximately 4 days, and assuming that larvae grow at approximately the

342   same rate as small juveniles (i.e., 0.14 mm · d^{-1}) then we would expect an approximately 0.6mm

343   difference in the size of settlers in the last quarter. This is approximately what we observed (Fig

344   2b).

345   If the costs of early vs. delayed settlement are reversed (Fig 4f) then the opposite pattern

346   is observed, with settler ages up to 8 days less than x^* and only slight delays in settlement for fish

347   that expect to settle just after the full moon. On the other hand, if costs are more symmetric (Fig

348   4e) then the magnitude of the delayed vs. early settlements are comparable, leading to the greatest

349   disparity in the ages of settlers (i.e., differing by as much as 18 days and about 3mm difference in

350   length).

351

352   **Discussion**

353   Iteroparity enables parents to bet-hedge when environmental conditions are uncertain, but

354   this means that some offspring will be disadvantaged. Developmental plasticity may enable

355   offspring to improve their own odds of survival (and increase the fitness of their parents thereby

356   reducing one potential cost of adult iteroparity). Irrespective of developmental plasticity,

357   iteroparity for sixbar wrasse may be favored if there is strong selection for larvae to settle during

358   particular conditions (i.e., dark nights), but parents are unable to predict when these conditions

359   might occur (e.g., because dark nights may depend on stochastic cloud cover, etc). Similarly,

360   developmental plasticity in sixbars may be favored if pelagic larvae are unable to predict timing

361   of encounters with suitable habitat for settlement. Thus, either iteroparity or developmental

362   plasticity on its own may constitute a risk avoidance strategy. When considered together,

363   developmental plasticity of larvae may reinforce an existing iteroparous strategy in adults

364   because offspring can compensate for an inauspicious birthdate which might otherwise select

365   against iteroparity and more generally variation in the timing of reproduction.

366   Sixbar wrasse settle in greater numbers during the new moon, a pattern typical of many

367   reef fishes (e.g., Rankin and Sponaugle 2014, Dufour and Galzin 1993) which suggests that new

368   moons may represent better times to settle (i.e., Pineda et al. 2006). Improved odds of larval

369   survival on dark nights (e.g., Acosta and Butler 1999) is one mechanism that almost certainly

370   contributes to this pattern. Settling sixbars must migrate into shallow water and surf over a

371   barrier reef crest; once inside the lagoon, they must drift or swim another ~100-1000 m to locate

372   suitable reef habitat (e.g., Doherty et al. 2004). We have observed small piscivores actively

373   feeding in these areas of sixbar migration on nights with bright moons (personal observations),

374   and we suspect that survival across this predator gauntlet is closely linked with lunar

375   illumination. Hence, perhaps the most obvious explanation for the lunar periodicity in settlement

376   is intense predation (i.e., settlers arrive at equal frequency over the lunar cycle but predators

377   eliminate most of the settlers that don't arrive on the new moon). However, this hypothesis alone

378   doesn't predict the observed size differences in settlers over the lunar cycle without invoking a

379   more complex mechanism (e.g., in which size-selective predation varies in a particular way

380   across the lunar cycle: i.e., it cannot adequately account for our empirical observations).

381   At least two other mechanisms (not mutually exclusive) may contribute to the lunar

382   pattern of settlement that we have observed. First, periodic spawning by adults may drive

383   variation in the number of larvae available to settle during certain portions of the lunar month

384   (e.g., Robertson et al. 1988). Adult sixbars appear to spawn over all days of a lunar month, but

385   available evidence (from another location) indicates that spawning activity is greatest around the

386   new moon (Claydon et al. 2014); this is consistent with Johannes'(1978) hypothesis predicting

387   that adults should spawn at times (and places) that minimize egg predation. However, when

388   combined with the average developmental duration reported for sixbar larvae (47 d, Victor 1986),

389   this suggests that (all else being equal) larval settlement should peak between the full and last

390   quarter moon (i.e., lunar periodicity in spawning cannot explain our empirical observations).

391   A second potential mechanism that might contribute to the observed peak in sixbar

392   settlement around the new moon is a flexible developmental duration for larvae. Larvae may

393   have the capacity to settle early and/or delay their settlement (relative to a normative

394   developmental duration, i.e., ~47 d for sixbars, Victor 1986). If developmental duration is

395   flexible—and full moons are particularly dangerous—then we would expect larval sixbars to

396   avoid settling during full moons. Using size as a proxy for age, our observation that sixbars settle

397   at a larger size just after the full moon is consistent with this hypothesis. (i.e., many of those fish

398   "should" have settled on the first quarter or the full moon). Though we cannot directly test an

399   alternative hypothesis that growth rates of larvae vary across the lunar cycle (giving rise to fish

400 that settle at the same age but different sizes), this seems unlikely to us as our estimates of post-

401 settlement growth were invariant across the lunar cycle (and larval growth is correlated with post-

402 settlement growth in this system; Shima et al. 2006). We note that an evaluation of otolith

403 microstructure (e.g., Shima and Swearer 2009a,b, Rankin and Sponaugle 2014) would enable us

404 to clearly differentiate between these alternatives, and this is a priority for our future work.

405 Sixbars that settled during waxing moons (from first quarter to full moon; i.e., increasing

406 illumination) suffered substantially greater mortality relative to fish that settled during waning

407 moons (from last quarter to new moon; i.e., decreasing illumination). Waxing and waning moon

408 phases also differ in the timing of moonrise and moonset, with the consequence that waxing

409 phases will tend to illuminate reefs after sunset and waning periods will tend to illuminate reefs

410 before sunrise. We speculate that the difference in survivorship between waxing and waning

411 periods may be attributable to prolonged activity by crepuscular predators, and/or young sixbars

412 may remain active later into the evening (increasing their vulnerability to predators), when

413 illumination occurs at dusk (and this effect may be less important when reefs are illuminated

414 nearer to dawn). The steep decline in survivorship with time for waxing moon phases suggests

415 that early post-settlement mortality may be shaped by the timing and intensity of nocturnal

416 illumination, and this may reinforce selection for flexible developmental durations that enable

417 fish to avoid settling during particular phases of the moon.

418 For fish that settled during a new moon phase, we noted an anomalously steep decline in

419 survivorship at 41 d after settlement (Fig. 3), and this roughly corresponds to the second full

420 moon period experienced by settled fish (further suggesting that bright periods may be times of

421 heightened risk). We also noted that fish that settled during the last quarter of the lunar month

422 had the highest mean survival time (90.7 d, compared with 79.3 d for fish that settled during the

423 new moon). As a consequence of these observations, we hypothesized that variation in post-

424 settlement survival could be explained by variation in size-at-settlement and/or lunar

425 illumination. We evaluated these hypotheses with a modified survival analysis that included

426 these additional covariates. This new analysis failed to support the hypothesis that size-at-

427 settlement influenced post-settlement survival independent of lunar quarter of settlement.

428 Additionally, we evaluated a competing model that substituted size-at-settlement for lunar quarter

429 and found that this had much less support based upon AIC, and the effect of size-at-settlement

430 remained non-significant. Lunar illumination on the estimated death date was also not a

431   significant predictor of survival, though the trend was for a reduction in survival with increasing

432   illumination. As our estimate of lunar illumination (i.e., the fraction of the moon illuminated)

433   doesn't take into account cloud cover or moonrise/moonset times, we are hesitant to conclude

434   that nocturnal illumination, particularly around dusk, is not an important determinant of variation

435   in survival. Additionally, we speculate that the survival advantage accruing to settlers in the last

436   quarter moon phase may be a consequence of density-dependent mortality (Shima 1999, 2001,

437   Shima and Osenberg 2003, Shima et al 2008) and/or priority effects (Geange and Stier 2009,

438   Geange 2010). Relative to fish settling during the new moon, fish that settled during the last

439   quarter of the lunar month were at lower density on average (Fig 2a), and preceded a large

440   number of settlers that arrived in the following quarter (i.e., on the new moon). The general

441   decrease in mean survival times from January to June is also consistent with density-dependent

442   mortality and/or priority effects documented elsewhere (Shima 1999, 2001, Shima and Osenberg

443   2003, Shima et al 2008, Geange and Stier 2009, Geange 2010), as reefs were comparatively

444   empty at the start of the settlement season.

445   Our analyses did not detect variation in post-settlement growth rates with respect to lunar

446   periodicity. This is somewhat surprising given (1) variation in settler densities across lunar

447   quarters (and an expectation for density-dependent growth rates; Booth 1995) and (2) variation in

448   survival probabilities as a function of lunar quarter (which suggest heightened risk during waxing

449   moons; we might expect this to result in increased sheltering time and decreased foraging time

450   shortly after settlement, and hence decreased growth rates). Of course, another possibility is that

451   our approach lacked the ability or precision to detect small differences in individual growth rates.

452   Future planned otolith-based demographic reconstructions will enable a more powerful test of

453   these patterns.

454   Predictions from our simple numerical simulation were consistent with empirical

455   observations of variation in size-at-settlement across the lunar cycle. Our numerical

456   representation assumed two interacting sources of mortality (an intrinsic mortality rate following

457   a threshold of competency, and an extrinsic mortality rate attributable to lunar illumination). This

458   model predicts optimal larval strategies that vary with individual birthdate and lunar cycle. By

459   extension, iteroparity should be favored (and reinforced) as a reproductive strategy when larval

460   developmental duration is plastic. Given a probable developmental threshold (e.g., Anderson

461   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, Smallengange and Coulson 2013 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

493 demographic consequences that result from this set of 'developmental histories' may drive

494 feedbacks that ultimately reinforce different reproductive strategies within and among species.

495

506

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644

645

Figure 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.

657

Figure 2. Variation in settlement of sixbar wrasse across the lunar cycle. (*a*) Proportion of

settlers (mean ± 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 ± 95% CI) of settlers arriving in each

quarter of the lunar cycle (n = 5 lunar months surveyed in 2005).

663

Figure 3. 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).

668

Figure 4. 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 x^*=47 days. 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

676   choose to settle on that same day. The absence of a point indicates that no larvae are predicted to

677   settle on that date. Ages greater than 47 indicate that larvae should delay settlement relative to x^*,

678   whereas smaller ages indicate that larvae initiated earlier than expected settlement, to avoid the

679   full moon (i.e., the environmental suboptimum centered around day 10.5). Survival through the

680   predator gauntlet (solid line=$p(s)$) is superimposed to illustrate the lunar cycle, with parameters

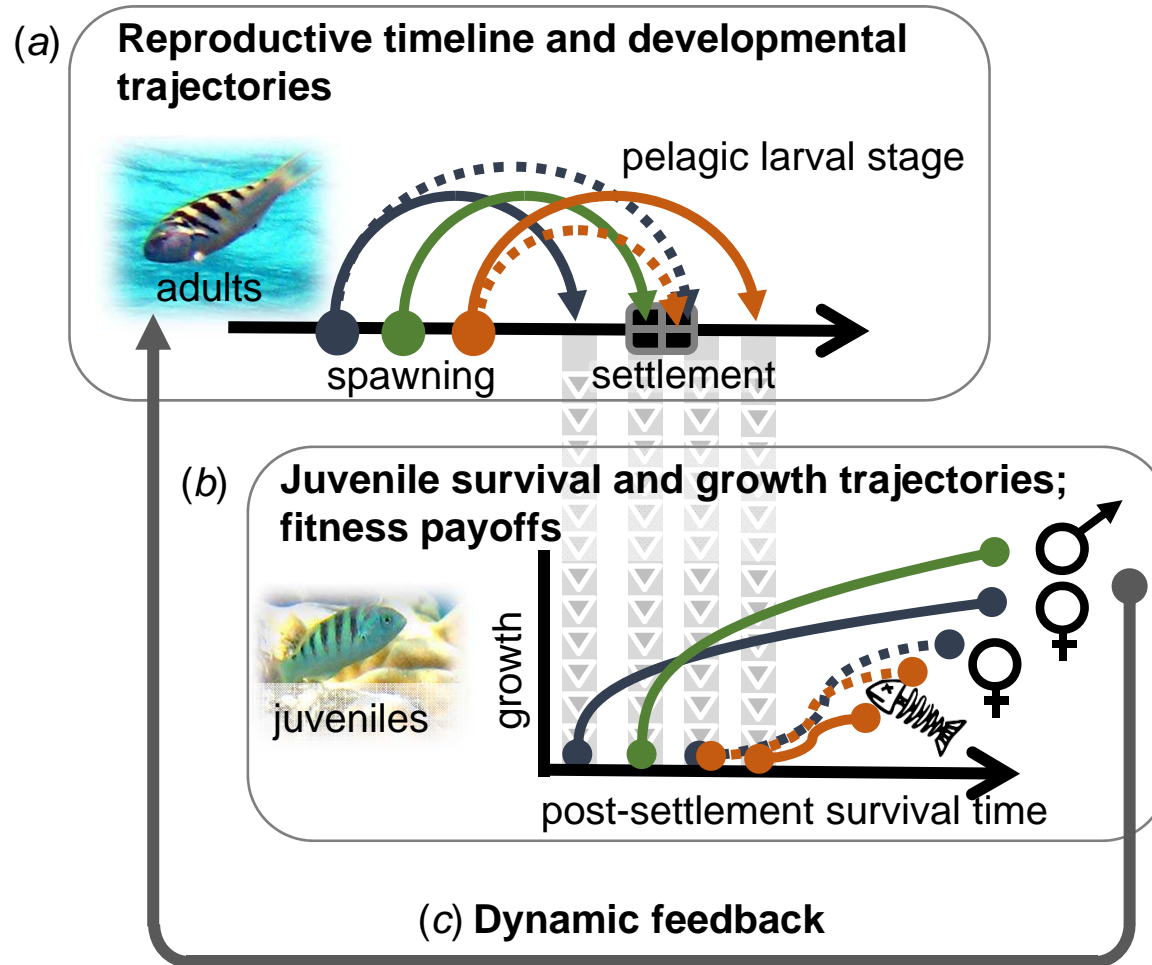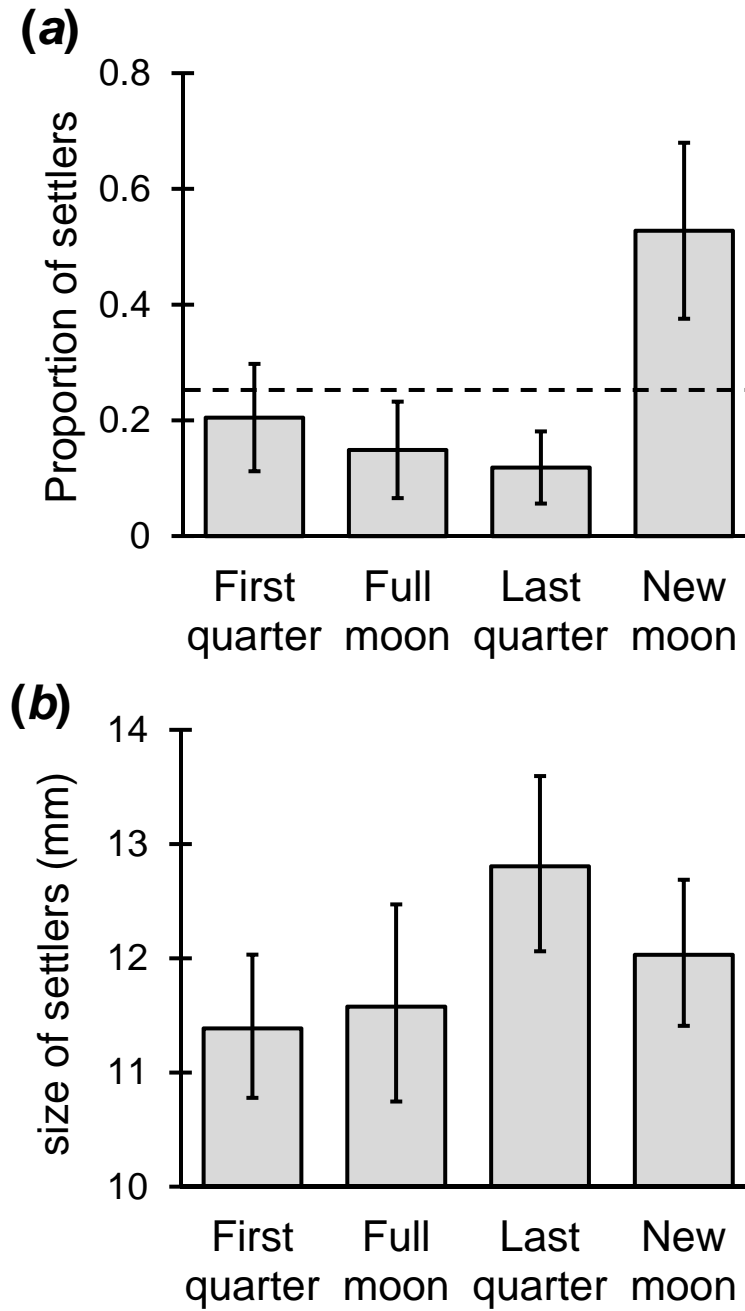681 m=0.2 and h=0.1 ($p(s)$ has been scaled to be visible in the plot).

(a) **Reproductive timeline and developmental trajectories**

pelagic larval stage

adults

spawning   settlement

(b) **Juvenile survival and growth trajectories; fitness payoffs**

juveniles

growth

post-settlement survival time

(c) **Dynamic feedback**

Fig 1

Fig 2

Fig 3

a=0.1, k=1   **a=0.1, k=0.2**   **a=0.5, k=0.6**
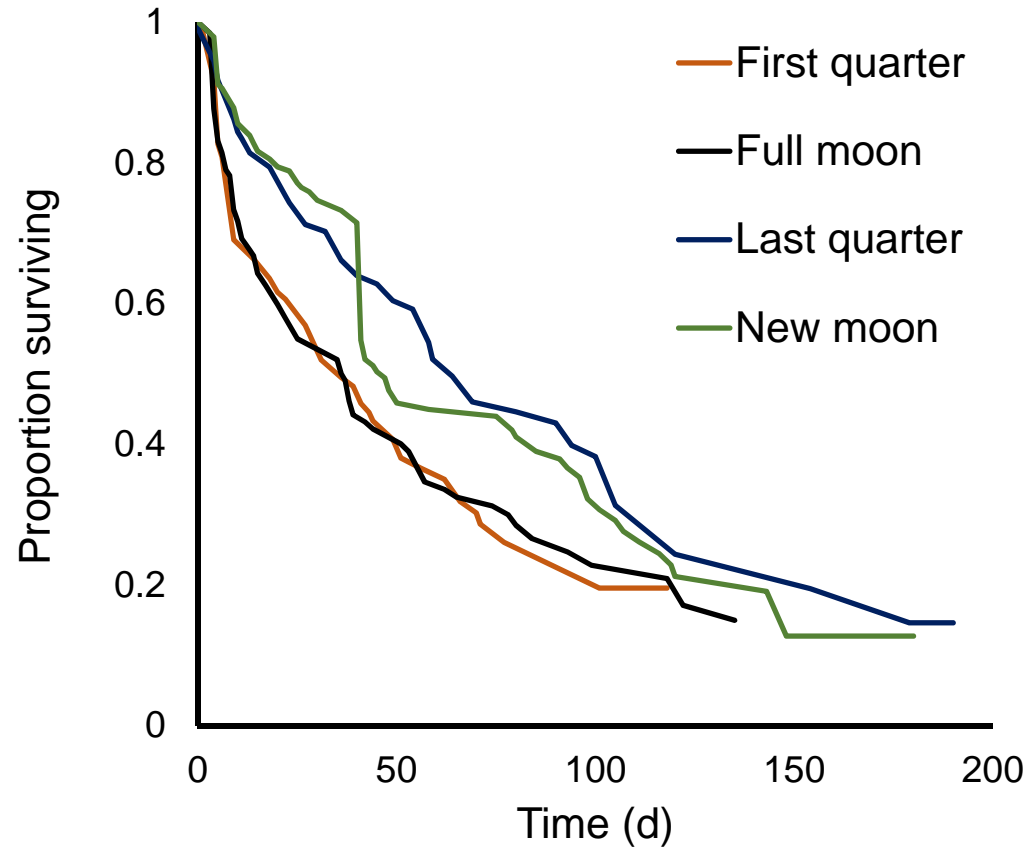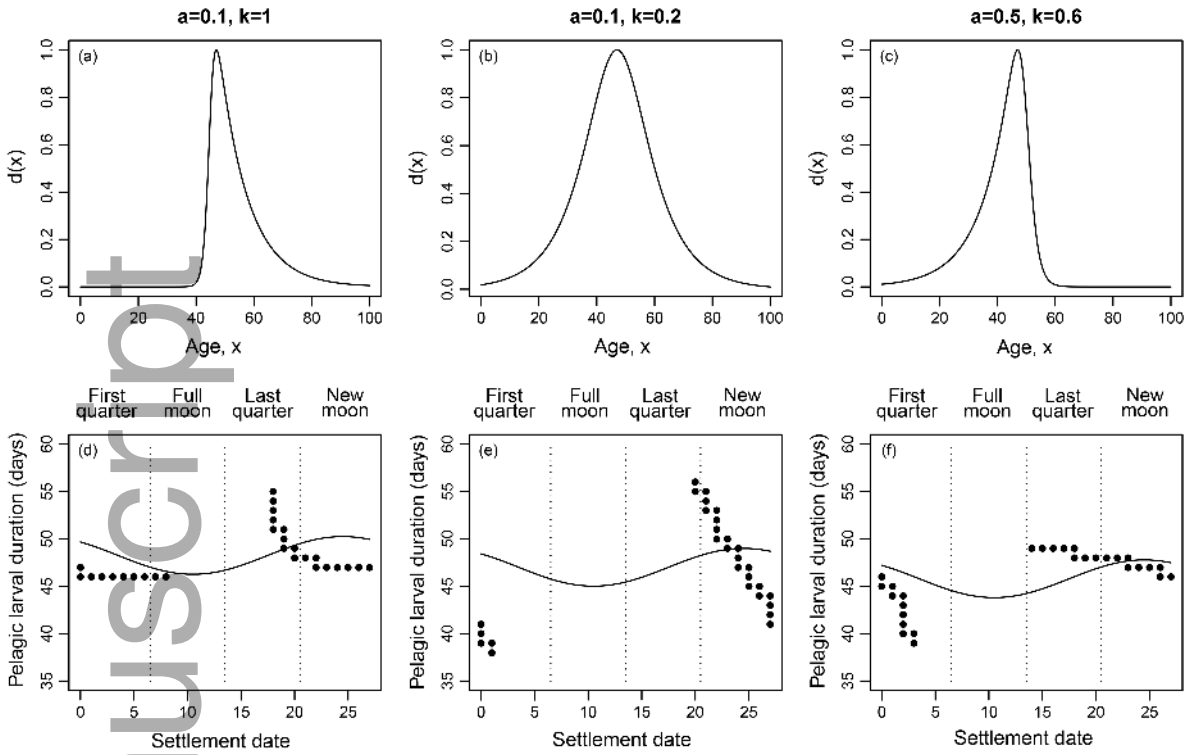
ecy_2048_f4.tif

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