This is the author-created version of the following work:

Graham, Erin M., Baird, Andrew H., Willis, Bette L., and Connolly, Sean R. (2013) *Effects of delayed settlement on post-settlement growth and survival of scleractinian coral larvae.* **Oecologia, 173 (2) pp. 431-438.**

Access to this file is available from:

https://researchonline.jcu.edu.au/29301/

Please refer to the original source for the final version of this work:

http://dx.doi.org/10.1007/s00442%2D013%2D2635%2D6

Population ecology - Original research

Effects of delayed settlement on post-settlement growth and survival of scleractinian coral larvae

Erin M. Graham • Andrew H. Baird • Bette L. Willis • Sean R. Connolly

E.M. Graham • B.L. Willis • S.R. Connolly

School of Marine and Tropical Biology, James Cook University, Townsville, QLD 4811, Australia

A.H. Baird • B.L. Willis • S.R. Connolly

ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia

Corresponding author: E.M. Graham

E-mail: erin.graham@my.jcu.edu.au; Telephone: +61 7 4781 5725; Fax: +61 7 4725 1570

1   **Abstract**   Demographic connectivity requires both the dispersal of individuals between sub-

2   populations, and their subsequent contribution to population dynamics. For planktonic, non-

3   feeding marine larvae, the capacity to delay settlement enables greater dispersal distances, but

4   the energetic cost of delayed settlement has been shown to adversely impact post-settlement

5   fitness in several taxa. Here, we assess whether delayed settlement influences mortality rates or

6   growth rates for the first six weeks following settlement of the scleractinian coral, *Acropora*

7   *tenuis*. Coral larvae that were settled at two, four, and six weeks after spawning, and then

8   deployed in the field, showed negligible effects of delayed settlement on post-settlement survival

9   and time to initial budding for colony formation. Between-cohort differences in budding rate

10   appeared to be explained by temporal variation in the post-settlement acquisition of

11   zooxanthellae. The potential for coral larvae to remain in the pelagic zone for increased periods

12   of time with little to no effect on post-settlement survival and growth suggests that the capacity

13   for delayed settlement is likely to have meaningful demographic consequences in reef-building

14   corals, and that the predicted trade-off between delayed settlement and post-settlement fitness is

15   less applicable to reef-building scleractinian corals than other taxa with non-feeding larvae.

16

17   **Keywords** coral reefs • dispersal • connectivity • population dynamics • post-settlement

18   processes

19

20   **Introduction**

21   Dispersal affects many aspects of a species ecology and life history evolution, including

22   metapopulation dynamics, biogeography, and the genetic structure of populations. Benefits of

23   dispersal include escape from density-dependent competition and predation, colonization of new

24   habitats, and recolonization of previously-occupied habitats (Bowler and Benton 2005).

25   Increased gene flow resulting from dispersal can reduce inbreeding depression, increase genetic

26   variability, and reduce extinction rates (Clobert et al. 2001). However, to be effective, dispersal

27   requires more than just movement of propagules; propagules must also successfully establish

28   themselves in their new environment long enough to contribute to the new population

29   ("effective" or "realized" dispersal: Kinlan and Gaines 2003). A trade-off exists between the

30   benefits of an extended dispersal period and increased population connectivity, and the potential

31   for post-settlement fitness costs, including reduced survival and reproductive success (Bonte et

32   al. 2011). Understanding the consequences of delays in settlement (or an extended period in the

33   plankton) is therefore essential to our understanding of a species' ecology and evolution

34   (Marshall and Morgan 2011). Moreover, improved understanding of realized dispersal is

35   required to assess the evolutionary benefits of dispersal and regulation of populations (Travis et

36   al. 2012).

37   In the marine environment, most invertebrate species have a complex life cycle with a

38   benthic, relatively sedentary or sessile, adult phase and a dispersive larval stage. Dispersal times

39   can range from hours to months, but generally there is a minimum amount of time that must

40   elapse before a marine larva is competent to settle. Some larvae can delay settlement beyond this

41   obligate pre-competent stage, which increases the likelihood of encountering suitable habitat and

42   can enhance population connectivity (Pechenik 1999). However, increased time in the plankton

43   also has costs. Energy expended during dispersal is unavailable for use post-settlement, so in

44   addition to the risk of starvation during dispersal, propagules that delay settlement are likely to

45   have lower energy reserves at settlement than those that settle immediately after competence is

46   acquired. For non-feeding species, the effects of delayed dispersal on larval energetics are

47   expected to be more severe than for planktotrophic species (Miller 1993). Most studies on non-

48   feeding larvae have examined species with short larval durations lasting only hours to days, such

49   as bryozans, ascidians, and sponges. In most cases, delayed settlement caused a decrease in post-

50   settlement survival and growth (Wendt 1998; Maldonado and Young 1999; Marshall et al. 2003;

51   but see Hunter et al. 1999; Marshall et al. 2003 for exceptions). Much less is known about the

52   effect of delaying settlement on non-feeding larvae with longer larval durations. A delay of two

53   to three weeks resulted in a 25-50% decrease in survival and a 20-30% decrease in post-

54   settlement growth for abalone (Roberts and Lapworth 2001; Takami et al. 2002; Onitsuka et al.

55   2010), which suggests that the energetic costs of dispersal may be larger and more

56   demographically significant for taxa with longer-lived, non-feeding larvae.

57   Scleractinian corals are the primary architects of coral reefs, which are among the most

58   productive ecosystems in the world. Most reef-building coral species are broadcast spawners,

59   releasing their gametes into the water column where fertilization and embryogenesis occur

60   externally (Baird et al. 2009). Initially, coral larvae pass through an obligate pre-competent

61   period, during which larvae undergo rapid morphological and physiological changes. This is

62   followed by a competent period, in which the larvae are capable of metamorphosis into juvenile

63   corals. Competence can be acquired as soon as 2-3 days after spawning for some species

64   (Nozawa and Harrison 2005), but peak competence, when the majority of a cohort is capable of

65   settling, does not generally occur until 4-13 days after spawning (Connolly and Baird 2010).

66   Coral larvae have unusually long competence periods, with some species capable of delaying

67   settlement for over 100 days (Connolly and Baird 2010). Most broadcast-spawned larvae are

68   non-feeding and derive all of their energetic requirements during dispersal from the yolk (Baird

69   et al. 2009).

70   The extended periods of competency found for coral larvae suggest the potential for

71   considerable variation in age at settlement. Recent work has shown that there are costs associated

72   with increased time in the plankton. Connolly and Baird (2010) showed that the proportion of the

73   cohort that is competent to settle declines markedly after peak competence is achieved 1-2 weeks

74   after spawning. Similarly, survivorship also decreases after peak competence is attained (Graham

75   et al. 2008). However, there have, as yet, been no studies of the possible post-settlement costs of

76   delayed settlement for non-feeding coral larvae, such as effects of depletion of energy reserves

77   during dispersal on post-settlement growth and survival. In particular, the acquisition of

78   zooxanthellae is an important event in the life cycle of corals because the majority of a coral's

79   energy needs post-settlement are met by the translocation of carbon from the photosynthesizing

80   zooxanthellae (Muscatine et al. 1981). Although some coral larvae inherit zooxanthellae

81   maternally and can supplement their energy reserves (Richmond 1987), the majority of species

82   must acquire zooxanthellae from the environment. Thus the rate at which zooxanthellae are

83   acquired after propagules arrive at the settlement site also has important implications for post-

84   settlement survival and growth.

85   Here, we examine the effects of delayed settlement on the post-settlement success of the

86   common, broadcast-spawning reef coral, *Acropora tenuis*. Our aim was to determine if coral

87   larvae that delay settlement have higher post-settlement mortality than larvae that settle without a

88   delay, and whether or not the process of colony growth, which occurs in corals through

89   replication of module polyps by a process known as budding, is hindered by a delay. We also

90   quantify the timing of zooxanthellae acquisition, to assess the extent to which it may provide an

91   alternative explanation for patterns in survival or growth. Demographic costs of delayed

92   settlement, if significant, could mean that the apparently high dispersal potential of corals, which

93 has been identified in studies of coral larvae, is unlikely to translate into realized dispersal that

94 provides meaningful demographic connectivity over large distances.

95

96 **Materials and methods**

97 The study took place at Orpheus Island Research Station (OIRS), on Orpheus Island in the

98 central Great Barrier Reef (18° 61'S 146° 48'E) from Nov-2009 to Jan-2010. *Acropora tenuis* is

99 a locally abundant, broadcast spawning species with non-feeding larvae that lack zooxanthellae

100 when released. Larvae become competent to settle after ~4 days but have been observed to settle

101 as late as 69 days after spawning (Nishikawa et al. 2003).

102   Larvae were cultured from *A. tenuis* colonies collected from Pioneer and Cattle Bays as

103 follows. Six adult, gravid colonies were collected 2-3 days prior to the full moon and maintained

104 in outdoor aquaria. On 26-Nov-2009, spawned gametes from all colonies were collected,

105 combined, and left for two hours to fertilize. After fertilization, the developing embryos were

106 transferred to 500 L aquaria containing 0.2 μm filtered seawater (FSW), where swimming larvae

107 developed between 36-48 h later. The aquaria were continuously supplied with fresh FSW, at a

108 flow rate of approximately 1.5 L/min, and air stones were provided to increase oxygenation. The

109 aquaria were maintained for 40 days in a temperature controlled room at 29°C with a 12:12 h

110 light:dark cycle.

111   At 12 days after spawning (DAS), when most larvae were competent to settle, ~ 2,000

112 larvae were transferred into 70 L settlement tanks containing 150mm x 15mm Petri dishes that

113 had been drilled with a hole through the centre, roughened with sandpaper and soaked in FSW

114 for 24 h. The dishes were also sprinkled with crushed crustose coralline algae, a known

115 settlement inducer for *Acropora* species (Morse et al. 1996). To maximize the number of settlers,

116 larvae were left in the settlement tanks for 48 h. Water was changed after 24 hours and ~2,000

117 more larvae then introduced. After 48 h, a census of the number of successfully attached, solitary

118 juveniles on the settlement surfaces was completed. Within 24 h of the first census, the 40 dishes

119 with the greatest number of settled juveniles were randomly distributed onto four racks (10

120 dishes each) and transported to Cattle Bay. The racks were suspended from star pickets at 3 m

121 depth in habitat containing adult colonies of *A. tenuis*. Censuses were then made weekly, with

122 the dishes collected from Cattle Bay, taken to OIRS for the census, and then returned to the field

123 within 24-36 h. Additional batches of larvae were settled after both a two-week (26 DAS) and

124 four-week delay (40 DAS), deployed to Cattle Bay, and censused weekly in the same manner as

125 described above. At each census, the number of living juveniles was recorded for survival

126 analysis and a digital photograph of each juvenile was taken for the determination of size at

127 settlement, number of secondary polyps, and onset of zooxanthellae infection. Size was

128 measured using ImageJ software (Abramoff et al. 2004) and calculated as the average of the

129 longest diameter through the mouth of the settler and the diameter perpendicular to the first

130 measurement. Zooxanthellae infection was defined as the first time zooxanthellae were observed

131 inside the tissue of the settler using a stereo dissecting microscope. Censusing continued until 55

132 DAS. The study was terminated by Cyclone Yasi in Feb-2011, which destroyed most of the

133 racks and dishes. The three cohorts of juveniles will be referred to as 2 wk, 4 wk, and 6 wk

134 settlers in the following sections.

135   We used mixed effects models to determine if delayed settlement had an effect on the

136 size at settlement, survival, time to bud secondary polyps, or time to acquire zooxanthellae. The

137 mixed-effects approach allowed us to explicitly account for random variation associated with

138 settlement dish, or (where appropriate) with the deployment rack to which the settlement dish

139   was affixed in the field. All analyses were done using R 2.13.0 (R Development Core Team

140   2011). Specifically, to determine if delayed settlement had an effect on size at settlement, we fit

141   a linear mixed effects (LME) model with age at settlement, measured as DAS, as a fixed effect,

142   and settlement dish as a random effect using the function "lme" in package "nlme" (Pinheiro et

143   al. 2011). To determine whether delayed settlement had an effect on post-settlement survival,

144   time to bud, or acquisition of zooxanthellae after deployment in the field, we used a mixed

145   effects Cox Proportional Hazards (CPH) model ("coxme" package; Therneau 2011). The CPH

146   model is a time-to-event analysis, which is designed for data that record when a defined event

147   occurs (Muenchow 1986). CPH models allow for the hazard rate (the stochastic rate at which an

148   event occurs) to vary over time in arbitrary fashion, but make a "proportional hazards

149   assumption" that the relative effect of any treatment (i.e., the ratio of hazards between two

150   treatments) is consistent over time. For each CPH analysis, we first tested the proportional

151   hazards assumption using the "cox.zph" function in the "survival" package in R (Therneau and

152   Lumley 2011), which fits a least-squares regression to Schoenfeld's partial residuals to diagnose

153   nonproportionality (Grambsch and Therneau 1994). Provided the assumption was met, we then

154   fit a series of models with and without the fixed effect of age at settlement, and all possible

155   combinations of the random effects of deployment rack and settlement dish (rack effect only,

156   dish effect only, dish effect nested within rack). To select the best model for the data, we used

157   Akaike's Information Criterion (AIC). We calculated Akaike weights for each model, which are

158   estimates of the relative likelihood of a model, given the data, compared to the other models

159   being considered (Burnham and Anderson 2002). We also used Akaike weights to calculate

160   model-averaged parameter estimates of the fixed effect for each analysis. This is essentially an

161   average effect size across all models, weighted by the models' relative likelihood, given the data.

162   This approach yields more robust estimates of effect size than inference based solely on the best-

163   fitting model (Burnham and Anderson 2002).

164

165   **Results**

166   Delayed settlement had a negative effect on the initial size of settlers. The estimated mean size of

167   larvae that settled at 2 weeks (1139 $\pm$10.97 µm) was significantly greater than that of 4 wk

168   settlers (944 $\pm$ 14.56 µm), which, in turn, was greater than that of 6 wk settlers (895 $\pm$ 14.58 µm)

169   (LME model, effect of DAS: $F_{2, 102}$=151.41, p < 0.001).

170   In contrast to the initial size of settlers, delayed settlement had no detectable effect on

171   survival of *A. tenuis* juveniles (Fig. 1A; electronic supplementary material, Table S1). An initial

172   analysis using all three cohorts found highly significant violation of the proportional hazards

173   assumption of the Cox model (X^2 = 29.68; *P*<0.001). Inspection of the data suggested that this

174   was due to the 6 wk cohort, which had disproportionately high survival during the first week

175   post-settlement, but not the second week (Fig. 1A). Therefore, we excluded this third cohort and

176   compared only the 2 wk and 4 wk cohorts. For this subset of the data, the proportional hazards

177   assumption was met (X^2 = 0.685; *P*=0.408). The best-fit model included a random effect of dish

178   nested within rack, but no fixed effect of delayed settlement (electronic supplementary material,

179   Table S1). Indeed, survival was virtually indistinguishable between 2 wk and 4 wk cohorts, a

180   result that is apparent in their highly coincident survivorship curves (Fig. 1A), and the fact that

181   confidence intervals on the model-averaged hazard ratio are narrowly centred around one (i.e.,

182   no difference: Table 1)

183   For budding and zooxanthellae acquisition, there was strong evidence for between-cohort

184   differences, but they were contrary to our expectations (Fig. 1B, C). In both analyses, the

185   proportional hazards assumption between groups was met for the analysis with all three cohorts

186   (budding: 4 wk X^2=2.53, P=0.11; 6 wk X^2=0.50, P=0.48; zooxanthellae acquisition: 4 wk

187   X^2=1.71, P=0.19; 6 wk X^2=0.95, P=0.33). Also for both analyses, the best-fitting model included

188   a fixed effect of settlement cohort and a random effect of dish (electronic supplementary

189   material, Table S1). Budding commenced sooner after settlement in the 4 wk cohort, compared

190   to the 2 wk cohort (Table 1). In contrast, time to commence budding in the 2 wk and 6 wk

191   cohorts were not significantly different (i.e., confidence intervals on the model-averaged hazard

192   ratio encompassed 1: Table 1). Zooxanthellae were acquired sooner in both the 4 wk and 6 wk

193   cohorts, compared to the 2 wk cohort (Fig 1C, Table 1).

194
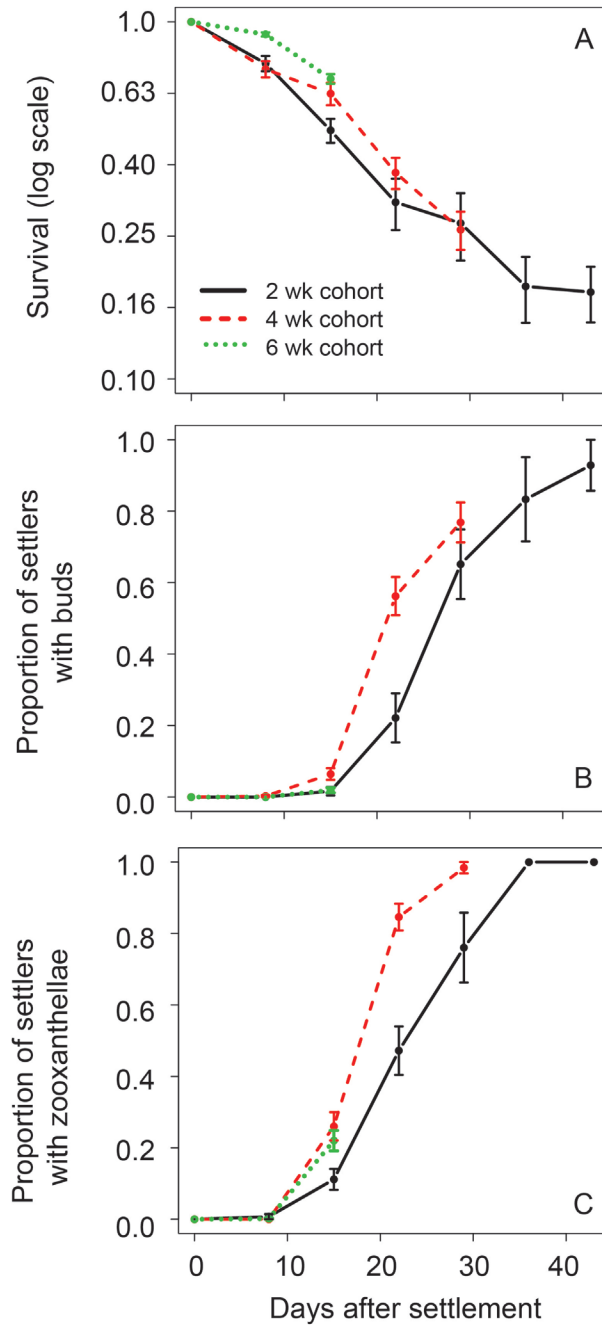
Fig. 1 Effect of delayed settlement on the survival, time to bud, and acquisition of zooxanthellae

of three cohorts of *Acropora tenuis* settlers. The points represent the mean proportion of settlers

on each dish that A) survived, B) budded additional polyps, or C) acquired zooxanthellae. Error

bars represent one standard error.

199   **Table 1** Model averaged estimates of the hazard ratio (with 95% confidence intervals) for the

200   effect of delayed settlement on survival, time to bud, and acquisition of zooxanthellae of three

201   cohorts of *Acropora tenuis* juveniles. "Hazard Ratio" is the rate at which the relevant event

202   occurs (mortality, zooxanthellae acquisition, or budding) for the indicated cohort, relative to the

203   2 wk cohort (e.g., a hazard ratio of 2.5 for the 4 wk cohort indicates that the event occurs at

204   approximately 2.5 times the rate at which it occurs in the 2 wk cohort). Random effects are noted

205   in parentheses in the "Best Model" column, with the forward slash (/) indicating nesting. Note

206   that there is no parameter estimate for the 6 wk cohort in the survival analysis because the

207   proportional hazards assumption was violated

208

| Analysis	Best Model	Fixed Effect	Hazard Ratio Estimate	P
Survival	(rack/dish)	4 wk	0.99 (0.93-1.04)	--
Budding	cohort + (dish)	4 wk	2.06 (1.28-3.33)	<0.01
		6 wk	0.64 (0.29-1.40)	0.27
Zooxanthellae	cohort + (dish)	4 wk	2.59 (1.59-4.24)	<0.001
Acquisition		6 wk	2.39 (1.41-4.05)	<0.001

209

210   **Discussion**

211   Survival and settlement competence of larval cohorts are known to decline substantially after

212   peak competence (typically 1-2 weeks after spawning for *Acropora* species: Graham et al. 2008;

213   Connolly and Baird 2010). However, for those larvae that do survive and successfully settle, we

214   found no evidence that the delay deleteriously affected the post-settlement processes measured in

215 this study, despite the fact that newly settled lecithotrophic larvae were smaller when settlement

216 was delayed. Larval energetics are often invoked to explain the costs of delayed settlement on

217 non-feeding invertebrate larvae (e.g., Jaeckle 1994; Marshall et al. 2003); long larval durations

218 cause larvae to expend more energy, which leaves fewer reserves for post-settlement survival

219 and growth. Our results suggest that *A. tenuis* larvae have ample energy reserves to sustain at

220 least a four-week delay in settlement, with no appreciable adverse effects on three critical post-

221 settlement processes: survival, budding, and the acquisition of zooxanthellae.

222   Contrary to our expectation, 4 wk settlers began budding more quickly after settlement

223 than 2 wk settlers, although 6 wk settlers did not. Presently, little is known about the initial

224 period of growth after settlement for corals, as they are difficult to track and usually not studied

225 in the field until they are large enough to be seen with the naked eye. Although growth of marine

226 invertebrates (including colonial organisms) generally increases with warmer water temperatures

227 and increased food availability (Hunter and Hughes 1993; Lambert 2005; Saunders and Metaxas

228 2009), temperature is an unlikely explanation for the more rapid growth of the 4 wk settlers.

229 Average water temperature during the second week after settlement, when differences in budding

230 rate first became apparent, differed by $<0.1^0$C between the 2 wk (28.76^0C) and 4 wk (28.73^0C)

231 settlers, and was actually highest for the 6 wk settlers (29.74^0C) (AIMS 2011).

232   One possible explanation for the lack of a negative effect of delayed settlement on polyp

233 budding is that this process might be more strongly dependent on the uptake of zooxanthellae

234 than on energy reserves at settlement, and that zooxanthellae uptake itself might not be affected

235 by delayed settlement. Corals derive the majority of their carbon from their endosymbionts

236 (Muscatine et al. 1981), so the acquisition of zooxanthellae is a key event in the life cycle of a

237 coral. Budding may well be sufficiently energetically expensive for a newly-settled coral that it

238   is strongly dependent on the successful establishment of symbiosis. Consistent with this, the

239   proportion of juveniles with zooxanthellae increased slightly faster than the proportion with buds

240   (Fig. 1B, C), and, of the 190 settlers that produced secondary polyps during the study, only one

241   of these lacked zooxanthellae. To examine this possibility more quantitatively, we used a

242   generalized linear mixed model with a binomial response (success or failure to bud), fit only to

243   the subset of settlers that had acquired zooxanthellae, on each day separately ("glmer" function,

244   "lme4" package; Bates et al. 2011). This analysis suggests that, once the presence of

245   zooxanthellae is accounted for, budding responds nearly identically in all three cohorts (Fig. 2).

246   Consequently, the variation in time to budding between cohorts appears likely to be explained, at

247   least in part, by the timing of zooxanthellae acquisition.

248
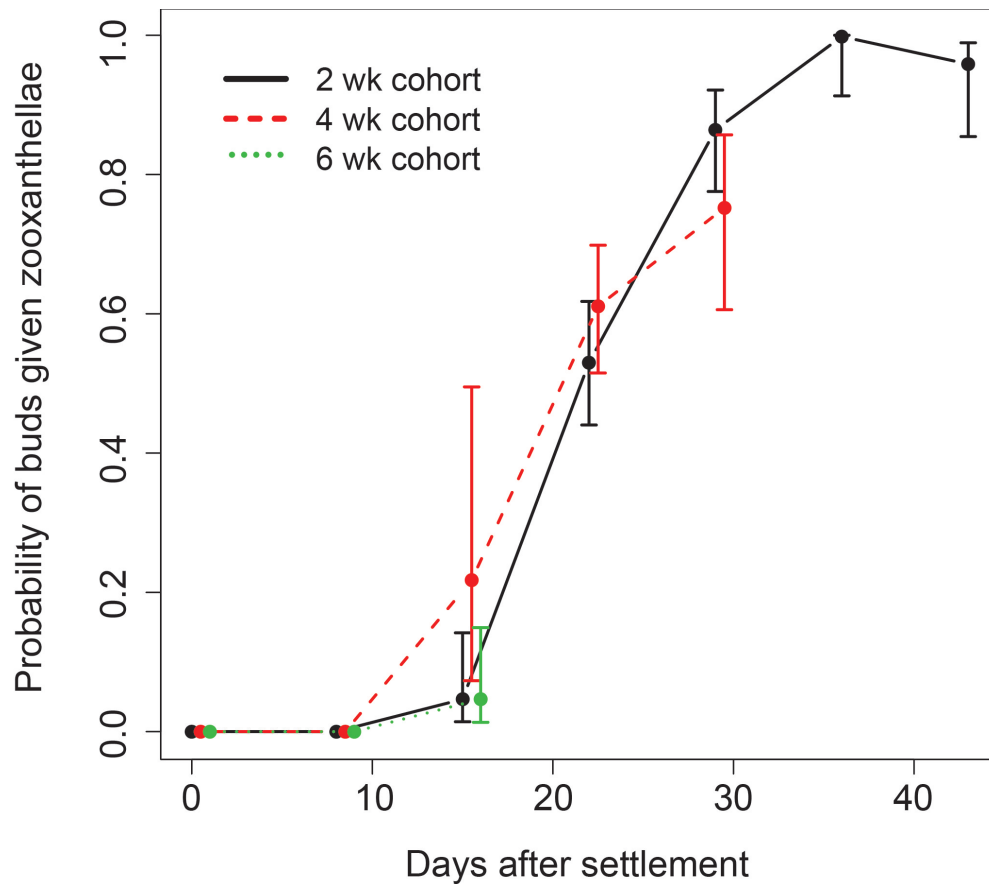
Fig. 2 Proportion of juveniles with zooxanthellae that also have buds for the three cohorts of

Acropora tenuis settlers. Error bars represent the standard error of the estimated proportion,

obtained from a generalized linear mixed effects model fit to each day, with a random effect of

dish and binomial error. Note that standard errors are asymmetric because they have been back-

transformed from an inverse logistic scale.

254

255

There are two possible explanations for the temporal pattern of zooxanthellae acquisition.

The higher rate of acquisition in the 4 wk cohort could, in principle, be due to developmental

constraints on how soon after fertilization corals can acquire zooxanthellae, i.e., the age of the

individual rather than the time since settlement. However, this seems unlikely: in experiments

260   where zooxanthellae were artificially supplied in the laboratory, several *Acropora* species

261   acquired zooxanthellae as early as 5 DAS, with the proportion infected approaching 100% by 7

262   DAS (Harii et al. 2009). This suggests that temporal variation in prevailing environmental

263   conditions that influence zooxanthellae availability or uptake is a more likely explanation.

264   Unfortunately, virtually nothing is known about the ecology of free-living zooxanthellae in reef

265   habitats. Regardless of the mechanism driving the observed variation in time to acquire

266   zooxanthellae, however, the onset of symbiosis appears to provide a much better explanation for

267   the among-cohort variation in budding rate than the length of delay prior to settlement.

268   The ability to delay settlement for a period of time after competence is achieved, without

269   suffering major deleterious post-settlement effects, supports the hypothesis that the long pelagic

270   larval durations and extended competence periods of corals enhance their potential for realized

271   dispersal. This is not to say that delayed settlement has no deleterious effects. Mortality in the

272   water column, though difficult to measure, is presumed to be quite high (Thorson 1950).

273   Moreover, the proportion of a cohort that survives and is capable of successfully

274   metamorphosing declines by 3-100-fold between two and six weeks in three *Acropora* species

275   (Connolly and Baird 2010). However, previous work has shown that, for some taxa, species with

276   non-feeding larvae are more likely to suffer physiological costs of dispersal after settlement,

277   compared to species with planktotrophic larvae, and thus costs of delayed settlement may

278   constitute a greater barrier to population connectivity in non-feeding larvae (Pechenik 2006). Our

279   results suggest that the trade-off between extended dispersal periods and post-settlement fitness

280   for *A. tenuis* is less severe than expected, with post-settlement costs close to zero, and thus that

281   the overwhelming majority of the cost of delayed settlement accrues during the planktonic phase

282   (due to larval mortality and loss of settlement competence), rather than after settlement. While

283 our results are obviously specific to our study species, recent work shows that depletion of

284 energy reserves by non-feeding coral larvae declines to near zero within the first two weeks after

285 spawning across a range of species (including *A. tenuis*), such that two and six week-old larvae

286 have very similar levels of energy reserves (Graham et al., in review). This offers a mechanism

287 underpinning the lack of effects of delayed settlement in *A. tenuis*, and suggests that low post-

288 settlement costs of delayed settlement may be similarly muted in other scleractinian coral

289 species.

290

294   **References**

295   Abramoff MD, Magalhaes PJ, Ram SJ (2004) Image processing with ImageJ. Biophotonics

296   International 11:36-42

297   AIMS (Australian Institute of Marine Science). 2011. Table generated 12th December 2011

298   using Reef Weather, Orpheus Island. Long Term Monitoring and Data Centre, AIMS.

299   http://data.aims.gov.au/aimsrtds/station_data.xhtml?station=9.

300   Baird AH, Guest JR, Willis BL (2009) Systematic and biogeographical patterns in the

301   reproductive biology of scleractinian corals. Annu Rev Ecol Evol Syst 40:551-571 doi:

302   10.1146/annurev.ecolsys.110308.120220

303   Bates D, Maechler M, Bolker B (2011) lme4: Linear mixed-effects models using S4 classes. R

304   package version 0.999375-41.

305   Bonte D et al. (2012) Costs of dispersal. Biol Rev 87:290-312 doi: 10.1111/j.1469-

306   185X.2011.00201.x

307   Bowler DE, Benton TG (2005) Causes and consequences of animal dispersal strategies: relating

308   individual behaviour to spatial dynamics. Biol Rev 80:205-225 doi:

309   10.1017/S1464793104006645

310   Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical

311   information-theoretic approach, 2nd edn. Springer, New York

312   Clobert J, Danchin E, Dhondt AA, Nichols JD (eds) (2001) Dispersal. Oxford University Press,

313   New York

314   Connolly SR, Baird AH (2010) Estimating dispersal potential for marine larvae: dynamic models

315   applied to scleractinian corals. Ecology 91:3572-3583 doi: 10.1890/10-0143.1

316   Graham EM, Baird AH, Connolly SR (2008) Survival dynamics of scleractinian coral larvae and

317   implications for dispersal. Coral Reefs 27:529-539 doi 10.1007/s00338-008-0361-z

318   Grambsch PM, Therneau TM (1994) Proportional hazards tests and diagnostics based on

319   weighted residuals. Biometrika 81:515-526 doi: 10.1093/biomet/81.3.515

320   Harii S, Yasuda N, Rodriguez-Lanetty M, Irie T, Hidaka M (2009) Onset of symbiosis and

321   distribution patterns of symbiotic dinoflagellates in the larvae of scleractinian corals. Mar

322   Biol 156:1203-1212 doi: 10.1007/s00227-009-1162-9

323   Hunter E, Hughes RN (1993) Effects of diet on life-history parameters of the marine bryozoan,

324   *Celleporella hyalina* (L). J Exp Mar Biol Ecol 167:163-177 doi: 10.1016/0022-

325   0981(93)90029-N

326   Hunter E, Shimizu K, Fusetani N (1999) Role of protein in larval swimming and metamorphosis

327   of *Bugula neritina* (Bryozoa: Cheilostomatida). Mar Biol 133:701-707 doi:

328   10.1007/s002270050511

329   Jaeckle WB (1994) Rates of energy-consumption and acquisition by lecithotrophic larvae of

330   *Bugula neritina* (Bryozoa, Cheilostomata). Mar Biol 119:517-523 doi: 10.1007/BF00354313

331   Kinlan BP, Gaines SD (2003) Propagule dispersal in marine and terrestrial environments: A

332   community perspective. Ecology 84:2007-2020

333   Lambert G (2005) Ecology and natural history of the protochordates. Can J Zool 83:34-50 doi:

334   doi: 10.1139/Z04-156

335   Maldonado M, Young CM (1999) Effects of the duration of larval life on postlarval stages of the

336   demosponge *Sigmadocia caerulea*. J Exp Mar Biol Ecol 232:9-21 doi: 10.1016/S0022-

337   0981(98)00076-8

338   Marshall DJ, Morgan SG (2011) Ecological and evolutionary consequences of linked life-history

339   stages in the sea. Curr Biol 21:R718-R725 doi: 10.1111/j.1461-0248.2009.01408.x

340   Marshall DJ, Pechenik JA, Keough MJ (2003) Larval activity levels and delayed metamorphosis

341   affect post-larval performance in the colonial, ascidian *Diplosoma listerianum*. Mar Ecol

342   Prog Ser 246:153-162 doi: 10.3354/meps246153

343   Miller SE (1993) Larval period and its influence on postlarval life-history - Comparison of

344   lecithotrophy and facultative planktotrophy in the aeolid nudibranch *Phestilla sibogae*. Mar

345   Biol 117:635-645 doi:10.1007/BF00349776

346   Morse ANC, Iwao K, Baba M, Shimoike K, Hayashibara T, Omori M (1996) An ancient

347   chemosensory mechanism brings new life to coral reefs. Biological Bulletin 191:149-154

348   doi: 10.2307/1542917

349   Muenchow G (1986) Ecological use of failure time analysis. Ecology 67:246-250

350   Muscatine L, McCloskey LR, Marian RE (1981) Estimating the daily contribution of carbon

351   from zooxanthellae to coral animal respiration. Limnol Oceanogr 26:601-611 doi:

352   10.4319/lo.1981.26.4.0601

353   Nishikawa A, Katoh M, Sakai K (2003) Larval settlement rates and gene flow of broadcast-

354   spawning (*Acropora tenuis*) and planula-brooding (*Stylophora pistillata*) corals. Mar

355   Ecol Prog Ser 256:87-97 doi: 10.3354/meps256087

356   Nozawa Y, Harrison PL (2005) Temporal settlement patterns of larvae of the broadcast spawning

357   reef coral *Favites chinensis* and the broadcast spawning and brooding reef coral *Goniastrea*

358   *aspera* from Okinawa, Japan. Coral Reefs 24:274-282 doi:10.1007/s00338-005-0476-4

359   Onitsuka T, Kawamura T, Ohashi S, Iwanaga S, Horii T, Watanabe Y (2010) Effects of delayed

360   metamorphosis and delayed post-settlement feeding on post-larval survival and growth of

361   the abalone *Haliotis diversicolor*. Aquaculture 298:239-244 doi:

362   10.1016/j.aquaculture.2009.11.009

363   Pechenik JA (1999) On the advantages and disadvantages of larval stages in benthic marine

364   invertebrate life cycles. Mar Ecol Prog Ser 177:269-297 doi: 10.3354/meps177269

365   Pechenik JA (2006) Larval experience and latent effects - metamorphosis is not a new beginning.

366   Integr Comp Biol 46:323-333 doi: 10.1093/icb/icj028

367   Pinheiro JC, Bates MD, DebRoy S, Sarkar D, R Development Core Team (2011) nlme: Linear

368   and nonlinear mixed effects models. R package version 3.1-100.

369   R Development Core Team (2011) R: A language and environment for statistical computing. R

370   Foundation for Statistical Computing, Vienna, Austria.

371   Richmond RH (1987) Energetics, competence, and long-distance dispersal of planula larvae of

372   the coral *Pocillopora damicornis*. Mar Biol 93:527-533 doi: 10.1007/BF00392790

373   Roberts RD, Lapworth C (2001) Effect of delayed metamorphosis on larval competence, and

374   post-larval survival and growth, in the abalone *Haliotis iris* Gmelin. J Exp Mar Biol Ecol

375   258:1-13 doi: 10.1016/S0022-0981(00)00346-4

376   Saunders MI, Metaxas A (2009) Effects of temperature, size, and food on the growth of

377   *Membranipora membranacea* in laboratory and field studies. Mar Biol 156:2267-2276 doi:

378   10.1007/s00227-009-1254-6

379   Takami H, Kawamura T, Yamashita Y (2002) Effects of delayed metamorphosis on larval

380   competence, and postlarval survival and growth of abalone *Haliotis discus hannai*.

381   Aquaculture 213:311-322 doi: 10.1016/S0044-8486(02)00338-1

382   Therneau T (2011) coxme: Mixed Effects Cox Models. R package version 2.2-1.

383   Therneau T, Lumley T (2011) survival: Survival analysis, including penalised likelihood. R

384   package version 2.36-5.

385   Thorson G (1950) Reproductive and larval ecology of marine bottom invertebrates. Biol Rev

386   Camb Philos Soc 25:1-45 doi: 10.1111/j.1469-185X.1950.tb00585.x

387   Travis JMJ et al. (in press) Modelling dispersal: an eco-evolutionary framework incorporating

388   emigration, movement, settlement behaviour and the multiple costs involved. Methods in

389   Ecology and Evolution doi: 10.1111/j.2041-210X.2012.00193.x.

390   Wendt DE (1996) Effect of larval swimming duration on success of metamorphosis and size of

391   the ancestrular lophophore in *Bugula neritina* (Bryozoa). Biol Bull 191:224-233

392

393 **Effects of delayed settlement on post-settlement growth and survival of scleractinian coral**

394 **larvae**

395 Oecologia

396 Erin M. Graham, Andrew H. Baird, Bette L. Willis, and Sean R. Connolly

397

398 Corresponding author:

399 E.M. Graham

400 School of Marine and Tropical Biology, James Cook University, Townsville, QLD 4811,

401 Australia

402 E-mail: erin.graham@my.jcu.edu.au

403

404   **Electronic Supplementary Material** Time-to-Event Model Selection Results

405

406   **Table S1**.   Model selection results for time-to-event analyses of three cohorts of *Acropora*

407   *tenuis* juveniles. "NULL" is the simplest model with no fixed or random effects. Random effects

408   are noted in parentheses, with the forward slash (/) indicating nesting. "Cohort" refers to a fixed

409   effect associated with when settlement occurred (2 wk, 4 wk, or 6 wk). ΔAIC is the difference

410   between the AIC of the indicated model and the best-fitting model, which is indicated in bold

411   type. w_i indicates the Akaike weight (the estimated probability that the model is the best in the

412   model set).

413

Model	Survival		Budding		Zooxanthellae Acquisition	
	ΔAIC	w_i	ΔAIC	w_i	ΔAIC	w_i
1) NULL	213.68	0.00	20.50	0.00	76.49	0.00
2) (rack)	122.28	0.00	12.12	0.00	49.07	0.00
3) (dish)	7.63	0.02	14.11	0.00	16.14	0.00
4) (rack/dish)	**0.00**	**0.71**	9.62	0.01	7.14	0.02
5) cohort	214.07	0.00	4.30	0.08	48.85	0.00
6) cohort + (rack)	124.27	0.00	5.96	0.03	42.12	0.00
7) cohort + (dish)	9.59	0.01	**0.00**	**0.65**	**0.00**	**0.57**
8) cohort + (rack/dish)	1.99	0.26	2.01	0.24	0.65	0.41

414

415