

1 **Using post-settlement demography to estimate larval survivorship:**

2 **a coral-reef fish example**

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Abstract

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Many species have multi-stage life cycles in which the youngest stages (e.g., larvae) are small, dispersive, and abundant, whereas later stages are sessile or sedentary. Quantifying survival throughout such early stages is critical for understanding dispersal, population dynamics, and life-history evolution. However, dispersive stages can be very difficult to sample *in situ*, and estimates of survival through the entire duration of these stages are typically poor. Here we describe how demographic information from juveniles and adults can be used to estimate survival throughout a dispersive larval stage that was not sampled directly. Using field measurements of demography, we show that detailed information on post-settlement growth, survival, and reproduction can be used to estimate average larval survivorship under the assumption that a typical individual replaces itself over its lifetime. Applying this approach to a common coral-reef fish (bicolor damselfish, *Stegastes partitus*), we estimated average larval survivorship to be 0.108% (95% CI: 0.025% – 0.484%). We next compared this demography-based estimate to an expected value derived from published estimates of larval mortality rates. Our estimate of larval survivorship for bicolor damselfish was approximately two orders of magnitude greater than what would be expected if larval mortality of this species followed the average, size-dependent pattern of mortality inferred from a published sample of marine fishes. Our results highlight the importance of understanding mortality during the earliest phases of larval life, which are typically not sampled, as well as the need to understand the details of how larval mortality scales with body size.

Keywords: allometry, larval mortality, net reproductive rate, recruitment, size-dependent mortality

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Introduction

40 Many organisms have complex life cycles in which the various stages of development occupy
41 different ecological niches (reviewed by Wilbur 1980). Developmental stages are often found in
42 different habitats, can perform specialized functions (e.g., dispersal, mating, diapause), and can
43 be subjected to different sets of evolutionary pressures (Istock 1967, Moran 1994). These
44 features ultimately shape the life histories of species and the dynamics of their populations. It is
45 often difficult to study all stages of a complex life cycle, yet demographic information from each
46 stage is critical to understanding dynamics of populations (e.g., Roughgarden et al. 1988, Vonesh
47 & De la Cruz 2002).

48 For many species (including marine invertebrates and fishes) the youngest stages (e.g., larvae)
49 are small and dispersive. Because these stages can be very difficult to sample directly, estimates
50 of survival through these stages are typically poor. However, the amount of mortality that occurs
51 during these early stages can be extremely important to the dynamics of adult populations (e.g.,
52 Houde 1987, Grosberg & Levitan 1992, Caley et al. 1996), and to the evolution of life histories
53 (Strathmann 1985, Marshall and Morgan 2011). Moreover, models of dispersal (e.g., coupled
54 biophysical models) are often sensitive to the rate of mortality during the young, dispersive
55 stages (e.g., Cowen et al. 2000, 2006, Largier 2003). Improved estimates of survivorship
56 through these stages are therefore central in efforts to understand many phenomena, including
57 dispersal, genetic connectivity, life history evolution, and dynamics within regional meta-
58 populations (e.g., Pineda et al. 2007, Metaxas & Saunders 2009).

59 When larvae can be sampled directly in the field (i.e., field-capture methods), there are two
60 general approaches that can be used to estimate mortality rates: cross-sectional and cohort-based

61 (also called annual or cohort-based catch curves). With cross-sectional approaches, mortality
62 rates can be inferred by comparing abundances of different sizes and/or ages within a single
63 sample. In such approaches, the decline in abundance with age/size can be used to estimate
64 mortality rates, given the (usually strong) assumptions that that input of each size and/or age
65 class was similar, and if size-based, that transition times between sizes are known (Ricker 1975,
66 Aksnes & Ohman 1996). Cohort-based approaches estimate mortality by sampling the
67 abundance of a cohort over time. Although this approach is more direct, it does assume that
68 changes in abundance are due to mortality, rather than dispersal away from the study area. Both
69 cross-sectional and cohort-based approaches assume that all ages/sizes are sampled with the
70 same efficacy. Field capture methods are also influenced by the spatial patchiness of organisms,
71 a phenomenon that often necessitates a large sampling effort to average the effects of sampling a
72 patchy population (e.g., McGurk 1986). If the scale of sampling is insufficient to account for
73 patchiness, then estimates of larval mortality may be biased. For example, a recent study by
74 White et al. (2014) improved upon a cross-sectional approach to estimating mortality (vertical
75 life tables; Asknes and Ohman 1996) by assuming that the abundance of larvae (sampled in
76 plankton tows) followed a clustered distribution (negative binomial) rather than a randomly-
77 dispersed one. By explicitly accounting for patchiness, these authors found that improved
78 estimates of larval mortality may be orders of magnitude lower than traditionally-calculated
79 estimates (White et al. 2014).

80 Another limitation of field-capture methods is that they necessarily focus on size ranges that
81 are well sampled. Any capture-based estimate of mortality rate is therefore specific to a
82 particular size range. Because mortality rates can change as organisms age and grow, a single
83 field estimate of mortality rate (specific to a particular size range) is therefore unlikely to yield

84 an accurate description of overall survivorship (i.e., survival throughout the entire phase). Such
85 discrepancies are likely to be a common problem for species with complex life cycles in which
86 the young stages are small, dispersive, and abundant. Species with these types of life histories
87 often exhibit type III survivorship (Deevy 1947) in which mortality rates are very high for the
88 youngest ages/sizes and relatively low for older, larger classes (e.g., Peterson & Wroblewski
89 1984, De Wreede & Klinger 1988, Rumrill 1990, Houde 1997). Accurately estimating
90 survivorship from field estimates of mortality therefore requires (at a minimum) knowledge of
91 both the baseline rate of mortality and how that mortality rate changes over time as organisms
92 age and grow.

93 Here we describe a different approach to estimating survivorship that is not limited by the
94 same processes and assumptions as field-capture methods. We show that detailed information on
95 post-settlement growth, survival, and reproduction can be used to estimate average pre-
96 settlement larval survivorship under the assumption that a typical individual replaces itself over
97 its lifetime. Using extensive field measurements of demography for a common coral-reef fish
98 (bicolor damselfish, *Stegastes partitus*), we obtain a robust estimate of average total larval
99 survivorship. Because our method is an unconventional one, we wanted to compare our estimate
100 of larval mortality with one derived from more traditional means. We compared our
101 demography-based estimate of larval survivorship to one inferred using *in situ* estimates of larval
102 mortality from a sample of marine fishes (no direct, field estimates of mortality were available
103 for our study species). Our results highlight the importance of more accurately measuring
104 mortality that occurs during the earliest larval phases, which are typically not sampled, as well as
105 the need to understand how movement of larvae and spatial patchiness may bias estimates of
106 survivorship.

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Methods

108 *Study species*

109 Bicolor damselfish are common, conspicuous, and highly site-attached (individuals typically
110 stay within a few meters of their home territory; Myrberg 1972, Schmale 1981). These attributes
111 have facilitated thorough, tag-recapture studies that have yielded reliable estimates of post-
112 settlement growth and survival in the field (Carr et al. 2002, Johnson 2008, Johnson & Hixon
113 2010, Hixon et al. 2012). In addition, males of this species exhibit noticeable reproductive
114 behavior, defend nests of demersal eggs, and readily guard artificial nests (Schmale 1981, Knapp
115 & Warner 1991). These features permit accurate estimation of reproductive rate and age at first
116 reproduction for males (Johnson et al. 2010, Johnson & Hixon 2011, Hixon et al. 2012).
117 Through our previous studies of this species, we have accumulated data to reliably describe age-
118 specific schedules of mortality and reproduction -- key life history traits that determine the
119 lifetime reproductive success of this species.

120 *Estimating larval survivorship*

121 Our approach to estimating average larval survivorship centers on calculating the net
122 reproductive rate (R_0), i.e., the expected number of offspring of the same sex that an average,
123 newborn individual will be replaced with by the end of its life (Caswell 2001). Larval
124 survivorship factors into R_0 , and can be calculated if all other aspects of R_0 are known. For *S.*
125 *partitus* we have detailed estimates of demography from settlement through to reproduction and
126 egg survival until hatching. This information allowed us to estimate larval survivorship as the
127 remaining component of R_0 . Because recruitment to local populations will conflate the effects of
128 mortality and dispersal, our calculations of larval survival did not rely on observed patterns of

129 larval settlement and recruitment. Rather, we calculated what the value of larval survivorship
130 must be if per capita production of offspring (in this case, hatched larvae) is to balance per capita
131 mortality during post-settlement life.

132 To use this approach we make two, related assumptions. First is that our demographic data
133 (which were collected at four different locations and across an eight year time span) are
134 representative of the entire population at large. Second is that an average individual will replace
135 itself by producing (on average) one offspring of the same sex that survives to maturity (i.e., $R_0 =$
136 1). If $R_0 = 1$ (on average), then the average, discrete growth factor will also be 1 and population
137 size will be stable in the long term (e.g., Caswell 2001). Note that if the population is considered
138 to be an open system, the assumption of replacement implies that the study area is neither a net
139 exporter, nor a net importer of larvae in the long term. In other words, we assume that a typical
140 individual replaces itself, even if some offspring may be dispersed to other regions. Our studies
141 of dispersal of bicolor damselfish larvae indicate high gene flow (suggesting that the study
142 region does exchange larvae with other locations), but also higher relatedness among individuals
143 from within the same study region (suggesting that local retention of larvae may be the norm;
144 Christie et al. 2010, Pusack et al. 2014). Multigeneration studies of our study species further
145 suggest that the regional population is stable (Hixon et al. 2012). Additionally, we believe that
146 our sample of post-settlement demography is representative of the broader population. We have
147 studied demography of bicolor damselfish at six other sites throughout the Exuma Sound region
148 of the Bahamas. Although sampling was much less frequent in this broad-scale study (3 samples
149 per year over 3 years), coarse-scale summary data on survival, growth, and reproduction (number
150 of eggs per nest) suggest that local populations near Lee Stocking Island (i.e., the populations

151 studied in this paper) are average with respect to survival, growth, and reproduction (*authors'*
152 *unpublished data*).

153 Although R_0 is most often calculated for females, the biology of *S. partitus* and our sampling
154 protocol made it possible to measure for R_0 for males only. We therefore calculated net
155 reproductive rate of males (R_{0m}) as:

$$156 \quad R_{0m} = \int l_{(x)}p_{(x)}dx \quad (1)$$

157 Where $l_{(x)}$ is the age-schedule of survival and $p_{(x)}$ is the age-schedule of paternity (measured as
158 number of eggs sequestered and fertilized by a male and somewhat analogous to fecundity [$m_{(x)}$]
159 in conventional demography). Because R_0 describes the number of offspring (of the same sex
160 and stage) that replace an individual, R_0 also provides an appropriate measure of fitness (Roff
161 2002). We do not believe that studying males instead of females introduces any bias in our
162 estimates of larval survivorship. Although it is somewhat unconventional to measure
163 demography of males instead of females, note that because every individual has one mother and
164 one father, *average* fitness of males and females is the same. The key is that one must consider
165 the entire life cycle (as we do here) and the sample must be representative of the entire
166 population (Fisher 1930, Grafen 1988). If we assume that the population is stable such that a
167 male will, on average, replace himself in the next generation, then $R_{0m} = 1$. Also note that if we
168 express survival and paternity as functions of post-settlement age (t), then we can separate egg
169 and larval survivorship from post settlement demography:

$$170 \quad S_E \times S_L \times \int l_{(t)}p_{(t)} dt = R_{0m} = 1 \quad (2)$$

171 where S_E is egg survivorship, S_L is larval survivorship, and the term in the integrand describes
 172 post-settlement survivorship and paternity. The age-schedules of survival and fecundity can be
 173 expressed as the combination of component functions and equation 2 can be expanded to

$$174 \quad S_E \times S_L \times \frac{1}{2} \int_{A_{FR}}^{\infty} S_s e^{-\int_0^t M(t) dt} P_{(t)} \theta f_{(t)} dt = R_{0m} = 1 \quad (3)$$

175 where A_{FR} is age at first reproduction (in days post settlement), S_s is survival through settlement,
 176 and θ is egg density (number per square centimeter). $M_{(t)}$ is a function describing post-settlement
 177 mortality over time (t) as fish age and grow. $P_{(t)}$ is a function describing the average, daily
 178 probability that a male of age t has eggs in the nest (this quantity increases as males age and
 179 grow). $f_{(t)}$ describes the average, daily number of offspring produced by a male of age t , given
 180 that it has eggs in the nest. Age t is expressed as days post settlement. Size-based demographic
 181 rates can be combined with growth functions to express demographic rates as a function of post-
 182 settlement age. Multiplying the integrand by a value of $\frac{1}{2}$ accounts for the fact that $f_{(t)}$ measures
 183 offspring of both sexes, and assumes a 1:1 sex ratio of offspring. Because we wish to estimate
 184 larval survivorship, we can rearrange equation 3 as follows:

$$185 \quad S_L = \frac{2}{S_E \int_{A_{FR}}^{\infty} S_s e^{-\int_0^t M(t) dt} P_{(t)} \theta f_{(t)} dt} \quad (4)$$

186 where all symbols are as in equation 3.

187 Some of the components on the right hand side of equation 4 are available from published
 188 studies (see *Results* section for sources). Others can be estimated from our field studies. From
 189 1998 to 2006 we collected extensive field data on individual survival, growth, and reproduction
 190 at each of four large reefs near Lee Stocking Island in the Bahamas. Individuals were tagged *in*
 191 *situ*, and monitored to measure demographic rates. Full details on data collection are reported by

192 Johnson & Hixon (2011) and Hixon et al. (2012). In the paragraphs below, we concentrate on
193 analytical procedures used to estimate functions that describe growth of males, $L_{(t)}$, and post-
194 settlement demography ($M_{(t)}$, $P_{(t)}$, and $f_{(t)}$).

195 To describe growth (total length at age) we fit a Richards function to our size-at-recapture
196 data. The Richards function describes an asymptotic growth pattern in which small fish grow
197 quickly and growth approaches zero at the largest sizes. The mark-recapture version of this
198 equation (Ebert 1980) describes size at recapture (L_{t2}) as a function of size at previous capture
199 (L_{t1}), time interval (Δt), asymptotic size (L_{∞}), a growth constant (k), and a scaling exponent (n),
200 i.e.,

$$201 \quad L_{t2} = [L_{\infty}^{(-1/n)}(1 - e^{-k\Delta t}) + L_{t1}^{(-1/n)}e^{-k\Delta t}]^{-n} \quad (5)$$

202 Equation 5 can be rearranged to describe size-at-age $L_{(t)}$

$$203 \quad L_{(t)} = L_{\infty}(1 - Be^{-kt})^{-n} \quad (6)$$

204 where B is a scaling parameter equal to $(L_{\infty}^{(-1/n)} - L_0^{(-1/n)})/L_{\infty}^{(-1/n)}$, and L_0 is size at settlement
205 (estimated to be 1.5cm TL). Equation 5 was fit to our data using a nonlinear regression in R (R
206 development core team 2013).

207 To estimate post-settlement survival, we assigned each individual a value of 1 if it survived >
208 30 days after it was measured and a value of 0 if it disappeared. Because previous studies
209 established that movement of this species away from the study reefs was negligible (Carr et al.
210 2002, Hixon et al. 2012), and because we exhaustively searched nearby reefs for missing fish, all
211 disappearances were interpreted as mortality. We used a logistic regression to describe survival
212 as a function of size. For fish > 6cm TL, we used data from males only. Below this size males

213 and females cannot be reliably distinguished, thus mortality was estimated from all tagged fish.
214 Because the data suggested a complex pattern of mortality, we included both squared and cubed
215 body size as predictors of monthly survival. In our final calculations, our equation for monthly
216 survival was converted to one that expressed daily, instantaneous mortality rate ($M_{(t)}$). We
217 performed this conversion by taking the natural log of our survival expression and dividing it by
218 -30 days.

219 The age-schedule of paternity was described by two functions. First, we estimated the
220 probability that a male had eggs in the nest during weekly censuses. Observations were assigned
221 a value of 1 if the male had eggs and a 0 otherwise. Because many observations were made for
222 each male, we used a generalized linear mixed model with a binomial link to describe the
223 probability of a male having eggs as a function of both its total length and an indicator variable
224 for season (winter=0, summer=1, spring/fall=0.5). Both the intercept and the effect of male size
225 were free to vary as random effects. Because we were interested in reproductive rates for the
226 average male, we report only the fixed effects here (though among-male variation was taken into
227 account when estimating variability). Models were fit using the *lme4* package in R (Bates et al.
228 2013).

229 For males that had eggs in their nests, we examined the relationship between ln-transformed
230 egg mass area (directly proportional to egg number; Samhoury 2009, Johnson et al. 2010), and
231 male size and season. Again, we used a linear, mixed effects model to describe the data, and
232 both the intercept and the effect of male size were free to vary as random effects. Eggs are laid
233 as a monolayer and females do not lay eggs on top of established egg masses within the nest.
234 Because eggs develop for 3.5 days in the nest (Johnson et al. 2010) and because spawning occurs

235 at dawn, our reproductive censuses measured total egg production within a 4-day window. To
236 convert our estimate of reproductive rate into a daily measure we divided egg mass area by 4.

237 Once we obtained estimates of the demographic rates, we used equation 4 to calculate larval
238 survivorship. Moreover, we used our estimates of the variability in demographic rates to
239 describe the uncertainty in our estimate of larval survivorship. In our calculations, we used a
240 parametric bootstrap procedure in which we drew 10 000 values of each parameter at random
241 from their estimated distributions. All parameter values were assumed to come from normal
242 distributions described by their estimated means and (co)variances (summarized in the *Results*
243 section). Seasonal effects were evaluated at their average value (i.e., the indicator variable was
244 fixed at 0.5). For each of the 10 000 parameter draws we calculated two quantities: (1) the post-
245 settlement reproductive success (i.e., the expected number of offspring produced by males that
246 had survived to the post-settlement stage); and (2) larval survivorship (S_L). This procedure
247 produced distributions describing the uncertainty about our estimates of these two quantities.

248 The assumption of population stability (i.e., that a male replaces itself in the next generation)
249 is reasonable for this species, especially given observed, long-term trends in demographic rates
250 and adult population sizes in the region (Hixon et al. 2012). Of course, larval survivorship may
251 vary across seasons, years, regions, etc., but because our demographic data integrated
252 information from four sites and across eight years at each site, our approach here provides a
253 reasonable average for long-term demography. Nevertheless, it is useful to examine the degree
254 to which our calculations depended on the assumption of population stability. In a second round
255 of our bootstrap procedure, we relaxed the assumption that the population is stable and allowed
256 R_{0m} to vary. Specifically, we calculated larval survival for $R_{0m} = 0.9$ and $R_{0m} = 1.1$. R_0
257 represents the per-generation population growth rate, and these growth rates would result in

258 substantial changes in population size (e.g., if $R_{0m} = 0.9$, population size after 10 generations
259 would be $\approx 35\%$ of the original; if $R_{0m} = 1.1$, population size after 10 generations would be \approx
260 260%). Although these growth rates appear to be outside of what is normally observed for
261 regional, adult population size of bicolor damselfish (Hixon et al. 2012), they do provide a broad
262 test of how sensitive our calculations of larval survivorship are to the assumption that population
263 size is stable. Note that if one considers the population an open system, then changing R_0 values
264 could be conceptualized as a test of how sensitive the estimates of larval survivorship are to the
265 assumption that the study area is neither a net exporter nor a net importer of larvae in the long
266 term. All of the remaining parameters in equation 4 were estimated from data, rather than
267 assumed. Variability in these parameter values was quantified and incorporated into our estimate
268 of larval survivorship.

269 *Inferring survivorship from published estimates of larval mortality*

270 No direct, field estimates are available for larval mortality of bicolor damselfish. However, in
271 the absence of more direct information, one way to estimate larval survivorship is to rely on
272 averages of *in situ* estimates of larval mortality for other fishes. By assuming that larval mortality
273 for a particular species of interest is similar to the among-species average, one may generate an
274 approximate estimate of larval survivorship (e.g., Kool et al. 2011, Diamond et al. 2013,
275 Johnston & Purkis 2013). Larval mortality rates generally decline with body size (e.g., Peterson
276 & Wroblewski 1984, Lorenzen 1996), and Houde (1997) provides the most recent review of how
277 larval mortality scales with body size within species. We therefore estimated larval survivorship
278 by combining growth rates of bicolor damselfish with an estimate of average, size-dependent
279 mortality derived from Houde's (1997) review. We then compared this estimate of larval
280 survivorship with the one obtained from our demographic study.

281 For bicolor damselfish, the average size at hatching is 2.17 mm SL (SE = 0.08) and near our
 282 study sites individuals settle at an average size of 13.2 mm SL (SE = 0.42), calculated from
 283 Rankin & Sponaugle (2011) using the otolith size to standard length conversion provided by
 284 Nemeth (2005). Assuming that larval size-at-age ($L(t)$) follows an exponential form (e.g.,
 285 Vigliola et al. 2007), we can approximate larval growth as $L(t) = \exp(L_0 + Kt)$, where L_0 is size
 286 at hatching, K is a growth constant (fit to the data on size at hatching and settlement), and t is
 287 time in days post hatching. Size-dependent mortality was estimated from the data in Houde's
 288 (1997) review. We used a linear mixed-effects model to describe how the natural log of
 289 mortality depended on both standard length (treated as a fixed effect of slope) and species
 290 identity (treated as a random effect that manifests as differences in intercept values). We also fit
 291 a model in which the effects of standard length on mortality varied with species (i.e., both the
 292 slope and intercept varied as random effects). We used a likelihood ratio test to compare the fits
 293 of these two models.

294 The relationship between larval mortality and standard length was reasonably described by an
 295 exponential function (see *Results* section). We therefore estimated larval survivorship as:

$$296 \quad S_L^* = \exp\left(-\int_0^{\text{PLD}} \exp(A + B(\exp(L_0 + Kt)))dt\right), \quad (7)$$

297 where A and B are scaling constants estimated from the relationship between standard length and
 298 larval mortality, and PLD is pelagic larval duration (expressed in days post hatching). To
 299 estimate variability in S_L^* , we used a parametric bootstrap procedure in which we drew 10 000
 300 parameter values at random based on their estimated means and variances (both parameter sets
 301 [A and B ; L_0 and K] were assumed to be distributed as multivariate normal). Covariance
 302 matrices were estimated among individuals for our growth data. However, because our mortality

303 data were based on an across-species average, we used the variation among species (estimated as
304 the random-effect variation for species identity) as our measure of uncertainty in size-dependent
305 mortality.

306 **Results**

307 *Post-settlement demography*

308 Growth of bicolor damselfish males exhibited a pattern typical of fishes in which small
309 individuals grow quickly and growth approaches zero at the largest sizes (Fig. 1A). Although
310 there was substantial variability among males, the Richards model is a flexible function that
311 provided a good fit to average size-at-age. Note that much of the variability in Fig. 1A is due to
312 differences in the interval of time between observations (which is accounted for in the analysis,
313 but not depicted in a 2-D graph). The relationship between survival and body size was
314 somewhat complex (Fig. 1B). Monthly survival was lowest for new recruits, increased sharply
315 in the 2-4cm range (TL), plateaued in the 4-8cm range (TL) before increasing at the largest sizes.
316 Probability of reproducing increased sharply with male size (Fig. 1C). Note that the final data
317 point in Fig. 1C represents relatively few observations (n=47 whereas the average sample size
318 within other points was 156) and a simple logistic model was adequate to describe $p_{(t)}$. Finally,
319 the number of eggs in the nest, when eggs were present increased with male size (Fig. 1D).
320 Although Fig. 1D displays much of the variation that was due to differences among seasons and
321 males, $f_{(t)}$ was well described by an exponential model. Parameter values associated with these
322 demographic functions, as well as the other demographic rates that make up the right hand side
323 of equation 4 are summarized in Table 1.

324 *Larval survivorship estimated from post-settlement demography*

325 From our demographic data, we estimated the number of eggs that a newly settled male was
326 expected to father throughout its lifetime ($\int l_{(t)}p_{(t)}dt$) to be substantial (median, post-settlement
327 reproductive output = 3094, 95% CI: 703 - 1.29×10^4 , Fig. 2A). Although observed
328 reproductive rates for males that have survived to maturity can be much higher (e.g., Knapp &
329 Warner 1991, Cole & Sadovy 1995, Johnson & Hixon 2011), this value accounts for the fact that
330 many newly settled males do not survive to reach maturity. Our estimate of reproductive output
331 can be used to calculate survival throughout the larval duration (assuming that $R_{0m} = 1$). Using
332 equation 4, our estimate of the median, larval survivorship was 1.08×10^{-3} (95% CI: $2.55 \times 10^{-4} -$
333 4.84×10^{-3} , Fig. 2B).

334 Varying R_{0m} resulted in moderate changes in larval survivorship. For an R_{0m} value of 1.1,
335 larval survivorship was 1.12×10^{-3} (95% CI: $2.81 \times 10^{-4} - 5.31 \times 10^{-3}$). For an R_{0m} value of 0.9,
336 larval survivorship was 9.62×10^{-4} (95% CI: $2.22 \times 10^{-4} - 4.22 \times 10^{-3}$). Because the R_{0m} values
337 chosen for these calculations represent large differences in the per-generation population growth
338 rates, these results suggest that our calculation of larval survivorship is only modestly sensitive
339 to the assumption that population size is stable.

340 *Larval survivorship estimated from published estimates of larval mortality*

341 Estimates of larval mortality from published literature decreased with body size (Fig. 3).
342 This decrease was well described by an exponential model, i.e., $\ln(\text{mortality}) = -0.231 -$
343 $0.143 \cdot \text{SL}$, where SL is standard length. Although there was substantial, among-species variation
344 in baseline rates of mortality (Fig. 3A), there was little evidence that the size-dependent scaling
345 of mortality significantly varied among species. Likelihood ratio tests indicated that a simple
346 model in which size-scaling was the same among species fit just as well as a more complex

347 model where the scaling relationships differed among species ($P = 0.239$). When considering
348 species that had multiple, yearly estimates of mortality for different sizes of larvae, there was
349 little evidence of negative skewness in the data (i.e., infrequent, very low mortality years).
350 Means tended to match medians, with one exception where the mean was greater than the
351 median, indicating positive skewness (occasional, very high mortality years; Fig. 3B).
352 Combining average, size-dependent mortality with estimated growth rates of bicolor damselfish
353 produced an estimate of larval survivorship of 3.70×10^{-5} . The uncertainty associated with this
354 estimate was substantial, though highly skewed towards lower survivorship (95% CI: 1.58×10^{-9}
355 $- 4.60 \times 10^{-3}$; Fig. 4).

356 Discussion

357 By using high-resolution data on post-settlement demography and life history, we estimated
358 larval survivorship in an indirect, yet robust way. This demographic estimate of larval
359 survivorship is valuable for two major reasons. First, it is complete in the sense that it estimates
360 survival throughout the entire larval phase. Models of the dynamics of populations typically
361 require information on larval survivorship, which is often inferred from less complete point
362 estimates of larval mortality rates (e.g., Caddy 1991, Eckman 1996, Cowen et al. 2000). Second,
363 comparing multiple estimates of larval survivorship can shed light on how predictable larval
364 survivorship is across species, and how larval mortality scales with body size.

365 Our demographic estimate of larval survivorship was approximately two orders of magnitude
366 greater than what would be expected if mortality of bicolor damselfish larvae followed the
367 average, size-dependent scaling relationship observed for a sample of teleost fishes (Houde
368 1997). Given our demographic data, we regard the latter estimate of larval survivorship as

369 unrealistic for our study species. Based on our calculations, the value of larval survivorship that
370 corresponds to an R_{0m} value of 1 is 1.08×10^{-3} . If larval survivorship was 3.70×10^{-5} (as
371 calculated from average, size-scaled estimates of mortality), then our estimate of the per-
372 generation growth rate would be 0.034. This would correspond to a precipitous decline in
373 population size (i.e., < 1% remaining after only 2 generations), which is clearly not the case for
374 our study species (Hixon et al. 2012).

375 These results suggest that larval survivorship for a particular species may not be very
376 predictable based on average estimates of larval mortality (gathered across species). Estimates
377 of larval mortality are unavailable for most species, yet there is often a pressing need to model
378 the dynamics of populations. For example, investigators often need to understand the efficacy of
379 no-take reserve networks (e.g., Crowder et al. 2000, Gerber et al. 2003), forecast the spread of
380 invasive species (e.g., deRivera et al. 2007, Gallien et al. 2010, Morris et al. 2011), and
381 anticipate the effects of climate change on species' abundances and ranges (e.g., Clark et al.
382 2003, Findlay et al. 2010). In such cases, an estimate of larval survivorship is required, and
383 deriving survivorship estimates from among-species, average values of mortality may seem like
384 a reasonable start. However, our results show that at least for bicolor damselfish, estimates of
385 survivorship based on the all-species average of mortality rates estimated in the plankton may be
386 inaccurate, even when the among-species variation in size-specific mortality rates is accounted
387 for.

388 There may be multiple reasons for the discrepancy between our demographic estimate of
389 larval survivorship and the one derived from published estimates of larval mortality. First,
390 bicolor damselfish larvae may follow the same type of size-dependent mortality relationship as
391 observed in Fig. 3 (e.g., an exponential function), but the overall rates of mortality may be

392 among the lowest values observed. Although this explanation is within the realm of possibility,
393 there are no obvious reasons why mortality of bicolor damselfish larvae would be so very low
394 relative to other species. For example, bicolor damselfish larvae do not appear to have any
395 morphological defenses and they inhabit warm waters where mortality rates are hypothesized to
396 be high, on average (Johannes 1978, Houde 1989). On the other hand, bicolor damselfish larvae
397 are capable swimmers (critical swimming speed was 1.2 SD greater than the size-scaled, all-
398 species average reported in a review by Fisher et al. 2005), and have been shown to migrate
399 deeper into the water column as they age and grow (Paris & Cowen 2004). These related
400 mechanisms could reduce average mortality rates by decreasing susceptibility to predators and/or
401 advection away from favorable habitat.

402 Another reason for the discrepancy may be that at the smallest of sizes (2.2 – 6.0mm SL),
403 mortality of bicolor damselfish larvae does not scale exponentially with body size. There are
404 very few estimates of larval mortality within this size range, and it is difficult to tell whether
405 scaling relationships are truly exponential, or whether they follow a different pattern.

406 Conceptual models of larval predation suggest that vulnerability to common predators may
407 reflect a balance between detection/encounter rate, which generally increases with larval size,
408 and susceptibility to predation, which decreases with larval size (Bailey & Houde 1989). The
409 result is a dome-shaped relationship between larval size and overall vulnerability to predation.
410 Data from a substantial number of behavioral experiments provide support for dome-shaped
411 relationships between vulnerability and relative sizes of larval prey and their predators (review
412 by Paradis et al. 1996). If throughout the full range of larval sizes the relationship between larval
413 size and mortality is something other than a monotonic decline (e.g., the relationship could be
414 shaped like a parabola or a hockey stick), then the two estimates of larval survivorship may be

415 much closer in magnitude. For example, if we assume that mortality is constant at the smallest
416 of sizes (i.e., mortality stays at the predicted value for a 6-mm larva for sizes 2.2 – 6.0mm SL)
417 and then scales according to the observed average, this procedure yields an estimate of $3.07 \times$
418 10^{-4} for larval survivorship – a number closer to our demographic estimate of survivorship. In
419 any case, our results highlight the need to understand mortality during the earliest part of the
420 larval phase more fully.

421 The distribution of larval mortality rates in natural populations may be skewed such that
422 mortality rates are typically high, but under rare circumstances are very low. This phenomenon
423 is hypothesized to generate patterns of episodic, high-recruitment events for marine species
424 (reviewed by Jennings et al. 2001). If the majority of population replenishment occurs during
425 these events (e.g., a feature of the “storage effect”; Chesson & Warner 1981, Warner & Chesson
426 1985), then one might expect an estimate of larval survivorship based on the average of *in situ*
427 samples to be lower than survivorship required to ensure population replacement. However, the
428 importance of skewness in mortality in natural populations remains unclear. High recruitment
429 variability can be driven by variation in reproduction (e.g., Robertson et al. 1988, Rickman et al.
430 2000), and episodic patterns of recruitment can be produced by subtle, rather than extreme shifts
431 in daily mortality rate (Houde 1987, 1989). For those few cases where replicate measurements
432 are available for larval mortality at a particular size, there is no evidence that infrequent, low
433 mortality events skew the data (Fig. 3B), though more sampling is required to capture truly rare
434 events.

435 Finally, spatial patchiness of larvae in the plankton may result in biased estimates of
436 mortality. Estimates of larval mortality from field samples are typically calculated from the ratio
437 of abundances of older individuals to younger individuals, with the accompanying assumption

438 that such ratios are constant and unaffected by spatial patchiness (e.g., Aksnes and Ohman 1996,
439 others). A recent study by White et al. (2014) relaxed this assumption by treating abundances as
440 random variables that follow a spatially-clustered distribution (which was modeled as a negative
441 binomial). Importantly, this method allowed the inclusion of many samples where the
442 abundance of at least one of the older or younger stages was observed to be zero. White et al.
443 (2014) found that by accounting for spatial patchiness, rates of larval mortality (per day) were
444 often orders of magnitude lower than those calculated under traditional assumptions. The
445 differences in larval survivorship they observed between the two methods were comparable to
446 the differences in survivorship that we found when applying two different methods to our study
447 species.

448 Because marine larvae and dispersive stages of many other species are so difficult to study in
449 the field, there is a considerable gap in our knowledge of their demography. To help fill this gap,
450 investigators may need to rely on multiple sources of information, even if single sources are
451 indirect and/or incomplete. Here we have illustrated that a comprehensive understanding of a
452 species' post-settlement demography and life-history can provide useful information on pre-
453 settlement larval survivorship. Future studies that combine such demography-based approaches
454 with other methods of investigating larval survival and growth (e.g., field-capture studies,
455 behavioral experiments) may be especially successful at illuminating larval demography and
456 improving our understanding of the population dynamics of species with complex life cycles.

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464 **Literature Cited**

465 Aksnes DL, Ohman MD (1996) A vertical life table approach to zooplankton mortality
466 estimation. *Limnology and Oceanography* 41:1461–1469.

467 Almany GR, Webster MS (2006) The predation gauntlet: early post-settlement mortality in reef
468 fishes. *Coral reefs* 25:19–22.

469 Bailey KM (1989) Predation on eggs and larvae of marine fishes and the recruitment problem.
470 *Adv Mar Biol* 25:1–83.

471 Caddy JF (1991) Death rates and time intervals: is there an alternative to the constant natural
472 mortality axiom? *Reviews in Fish Biology and Fisheries* 1:109–138.

473 Caley MJ, Carr MH, Hixon MA, et al (1996) Recruitment and the local dynamics of open marine
474 populations. *Annual Review of Ecology and Systematics* 477–500.

475 Carr MH, Anderson TW, Hixon MA (2002) Biodiversity, population regulation, and the stability
476 of coral-reef fish communities. *Proceedings of the National Academy of Sciences*
477 99:11241–11245.

478 Caswell H (2001) *Matrix population models*. Sinauer, Sunderland MA

479 Chesson PL (1983) Coexistence of competitors in a stochastic environment: the storage effect. In
480 *Population Biology: Lecture Notes in Biomathematics*. Springer, pp 188–198

481 Christie MC, Johnson DW, Stallings CD, Hixon MA (2010) Self-recruitment and sweepstakes
482 reproduction amid extensive gene flow in a coral-reef fish. *Molecular Ecology*, 19: 1042-
483 1057.

484 Clark RA, Fox CJ, Viner D, Livermore M (2003) North Sea cod and climate change—modelling
485 the effects of temperature on population dynamics. *Global Change Biology* 9:1669–1680.

486 Cole KS, Sadovy Y (1995) Evaluating the use of spawning success to estimate reproductive
487 success in a Caribbean reef fish. *Journal of Fish Biology* 47:181–191.

488 Cowen RK, Lwiza KM, Sponaugle S, et al (2000) Connectivity of marine populations: open or
489 closed? *Science* 287:857–859.

490 Cowen RK, Paris CB, Srinivasan A (2006) Scaling of connectivity in marine populations.
491 *Science* 311:522–527.

492 Crowder LB, Lyman SJ, Figueira WF, Priddy J (2000) Source-sink population dynamics and the
493 problem of siting marine reserves. *Bulletin of Marine Science* 66:799–820.

494 D’Alessandro EK, Sponaugle S, Llopiz JK, Cowen RK (2011) Larval ecology of the great
495 barracuda, *Sphyraena barracuda*, and other sphyraenids in the Straits of Florida. *Marine*
496 *biology* 158:2625–2638.

497 D’Alessandro EK, Sponaugle S, Serafy JE (2010) Larval ecology of a suite of snappers (family:
498 Lutjanidae) in the Straits of Florida, western Atlantic Ocean. *Marine Ecology Progress*
499 *Series* 410:159–175.

500 Deevey ES (1947) Life tables for natural populations of animals. *The Quarterly Review of*
501 *Biology* 22:283–314.

502 De Wreede RE, Klinger T (1988) Reproductive strategies in algae. Oxford University Press, New
503 York

504 Diamond SL, Murphy CA, Rose KA (2013) Simulating the effects of global climate change on
505 Atlantic croaker population dynamics in the mid-Atlantic Region. *Ecological Modelling*
506 264:98–114.

507 Ebert TA (1980) Estimating parameters in a flexible growth equation, the Richards function.
508 *Canadian Journal of Fisheries and Aquatic Sciences* 37:687–692.

509 Eckman JE (1996) Closing the larval loop: linking larval ecology to the population dynamics of
510 marine benthic invertebrates. *Journal of Experimental Marine Biology and Ecology*
511 200:207–237.

512 Findlay HS, Burrows MT, Kendall MA, et al (2010) Can ocean acidification affect population
513 dynamics of the barnacle *Semibalanus balanoides* at its southern range edge? *Ecology*
514 91:2931–2940.

515 Fisher RA (1930) The genetical theory of natural selection. Oxford University Press, Oxford.

516 Fisher R, Leis JM, Clark DL, Wilson SK (2005) Critical swimming speeds of late-stage coral reef
517 fish larvae: variation within species, among species and between locations. *Marine Biology*
518 147:1201–1212.

519 Gallien L, Münkemüller T, Albert CH, et al (2010) Predicting potential distributions of invasive
520 species: where to go from here? *Diversity and Distributions* 16:331–342.

521 Gerber LR, Botsford LW, Hastings A, et al (2003) Population models for marine reserve design:
522 a retrospective and prospective synthesis. *Ecological Applications* 13:47–64.

523 Grafen A (1988) On the uses of data on lifetime reproductive success. In *Reproductive success*
524 (ed. T.H. Clutton-Brock). pp. 454-471. University of Chicago Press.

525 Grosberg RK, Levitan DR (1992) For adults only? Supply-side ecology and the history of larval
526 biology. *Trends in Ecology & Evolution* 7:130–133.

527 Heath M, Gallego A (1997) From the biology of the individual to the dynamics of the population:
528 bridging the gap in fish early life studies. *Journal of Fish Biology* 51:1–29.

529 Hitchcock NG, Teck SJ, Steves BP, et al (2007) Larval development rate predicts range
530 expansion of an introduced crab. *Marine Biology* 150:1275–1288.

531 Hixon MA, Anderson TW, Buch KL, et al (2012) Density dependence and population regulation
532 in marine fish: a large-scale, long-term field manipulation. *Ecological Monographs* 82:467–
533 489.

534 Houde ED (1989a) Subtleties and episodes in the early life of fishes. *Journal of Fish Biology*
535 35:29–38.

536 Houde ED (1997) Patterns and trends in larval-stage growth and mortality of teleost fish. *Journal*
537 *of Fish Biology* 51:52–83.

538 Houde ED (1989b) Comparative growth, mortality, and energetics of marine fish larvae:
539 temperature and implied latitudinal effects. *Fishery Bulletin* 87:471–495.

540 Houde ED (1987) Fish early life dynamics and recruitment variability. *American Fisheries*
541 *Society Symposium*

542 Istock CA (1967) The evolution of complex life cycle phenomena: an ecological perspective.
543 Evolution 592–605.

544 Jennings S, Kaiser M, Reynolds JD (2001) Marine fisheries ecology. Blackwell

545 Johannes RE (1978) Reproductive strategies of coastal marine fishes in the tropics.
546 Environmental Biology of Fishes 3:65–84.

547 Johnson DW (2008) Combined effects of condition and density on post-settlement survival and
548 growth of a marine fish. Oecologia 155:43–52.

549 Johnson DW, Christie MR, Moyer J (2010) Quantifying evolutionary potential of marine fish
550 larvae: heritability, selection, and evolutionary constraints. Evolution 64:2614–2628.

551 Johnson DW, Hixon MA (2010) Ontogenetic and spatial variation in size-selective mortality of a
552 marine fish. Journal of Evolutionary Biology 23:724–737.

553 Johnson DW, Hixon MA (2011) Sexual and lifetime selection on body size in a marine fish: the
554 importance of life-history trade-offs. Journal of Evolutionary Biology 24:1653–1663.

555 Johnston MW, Purkis SJ (2013) Modeling the potential spread of the recently identified non-
556 native panther grouper (*Chromileptes altivelis*) in the Atlantic using a cellular automaton
557 approach. PloS one 8:e73023.

558 Knapp RA, Warner RR (1991) Male parental care and female choice in the bicolor damselfish,
559 *Stegastes partitus*: bigger is not always better. Animal Behaviour 41:747–756.

560 Kool JT, Paris CB, Barber PH, Cowen RK (2011) Connectivity and the development of
561 population genetic structure in Indo-West Pacific coral reef communities. *Global Ecology*
562 and *Biogeography* 20:695–706.

563 Largier JL (2003) Considerations in estimating larval dispersal distances from oceanographic
564 data. *Ecological Applications* 13:71–89.

565 Lorenzen K (1996) The relationship between body weight and natural mortality in juvenile and
566 adult fish: a comparison of natural ecosystems and aquaculture. *Journal of Fish Biology*
567 49:627–642.

568 Marshall DJ, Morgan SG (2011) Ecological and evolutionary consequences of linked life-history
569 stages in the sea. *Current Biology* 21:R718–R725.

570 McGurk MD (1986) Natural mortality of marine pelagic fish eggs and larvae: role of spatial
571 patchiness. *Marine Ecology Progress Series* 34:227–242.

572 Metaxas A, Saunders M (2009) Quantifying the “bio-” components in biophysical models of
573 larval transport in marine benthic invertebrates: advances and pitfalls. *The Biological*
574 *Bulletin* 216:257–272.

575 Moran NA (1994) Adaptation and constraint in the complex life cycles of animals. *Annual*
576 *Review of Ecology and Systematics* 573–600.

577 Morris Jr JA, Shertzer KW, Rice JA (2011) A stage-based matrix population model of invasive
578 lionfish with implications for control. *Biological Invasions* 13:7–12.

579 Morse WW (1989) Catchability, growth, and mortality of larval fishes. *Fishery Bulletin* 87:417–
580 446.

581 Myrberg Jr AA (1972) Social dominance and territoriality in the bicolor damselfish,
582 *Eupomacentrus partitus* (Poey) (Pisces: Pomacentridae). Behaviour 207–231.

583 Nemeth RS (2005) Linking larval history to juvenile demography in the bicolor damselfish
584 *Stegastes partitus* (Perciformes: Pomacentridae). Revista de Biología Tropical 53:155–163.

585 Paradis AR, Pepin P, Brown JA (1996) Vulnerability of fish eggs and larvae to predation: review
586 of the influence of the relative size of prey and predator. Canadian Journal of Fisheries and
587 Aquatic Sciences 53:1226–1235.

588 Paris CB, Cowen RK (2004) Direct evidence of a biophysical retention mechanism for coral reef
589 fish larvae. Limnology and Oceanography 49:1964–1979.

590 Peterson I, Wroblewski JS (1984) Mortality rate of fishes in the pelagic ecosystem. Canadian
591 Journal of Fisheries and Aquatic Sciences 41:1117–1120.

592 Pineda J, Hare JA, Sponaugle S (2007) Larval transport and dispersal in the coastal ocean and
593 consequences for population connectivity.

594 Pusack TJ, Christie MR, Johnson DW et al. (2014) Spatial and temporal patterns of larval
595 dispersal in a coral-reef fish metapopulation: evidence of variable reproductive success.
596 Molecular Ecology 23: 3396-3408.

597 Rankin TL, Sponaugle S (2011) Temperature influences selective mortality during the early life
598 stages of a coral reef fish. PloS one 6:e16814.

599 Ricker W (1975) Computation and interpretation of biological statistics of fish populations. Bull
600 Fish Res Board Can 191:382.

601 Rickman SJ, Dulvy NK, Jennings S, Reynolds JD (2000) Recruitment variation related to
602 fecundity in marine fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 57:116–124.

603 Robertson DR, Green DG, Victor BC (1988) Temporal coupling of production and recruitment of
604 larvae of a Caribbean reef fish. *Ecology* 370–381.

605 Roughgarden J, Gaines S, Possingham H (1988) Recruitment dynamics in complex life cycles.
606 *Science* 241:1460–1466.

607 Rumrill SS (1990) Natural mortality of marine invertebrate larvae. *Ophelia* 32:163–198.

608 Samhuri JF (2009) Food supply influences offspring provisioning but not density-dependent
609 fecundity in a marine fish. *Ecology* 90:3478–3488.

610 Schmale MC (1981) Sexual selection and reproductive success in males of the bicolor
611 damselfish, *Eupomacentrus partitus* (Pisces: Pomacentridae). *Animal Behaviour* 29:1172–
612 1184.

613 Strathmann RR (1985) Feeding and nonfeeding larval development and life-history evolution in
614 marine invertebrates. *Annual Review of Ecology and Systematics* 339–361.

615 Vigliola L, Doherty PJ, Meekan MG, et al (2007) Genetic identity determines risk of post-
616 settlement mortality of a marine fish. *Ecology* 88:1263–1277.

617 Vonesh JR, De la Cruz O (2002) Complex life cycles and density dependence: assessing the
618 contribution of egg mortality to amphibian declines. *Oecologia* 133:325–333.

619 Warner RR, Chesson PL (1985) Coexistence mediated by recruitment fluctuations: a field guide
620 to the storage effect. *American Naturalist* 769–787.

621 White JW, Morgan SG, Fisher JL (2014) Planktonic larval mortality rates are lower than widely
622 expected. *Ecology* 95: 3344-3353.

623 Wilbur HM (1980) Complex life cycles. *Annual review of Ecology and Systematics* 67–93.

624

625 Table 1. Summary of the demographic parameters used to estimate larval survivorship (equation 4 in the main text). Where
626 appropriate, parameter sets are presented as a vector of mean values and the lower half of a covariance matrix. Data sources are
627 ¹Johnson et al. 2010, ²Rankin and Sponaugle 2011, ³This study, ⁴Almany and Webster 2006, ⁵Samhuri 2009.

Process	Symbol	Equation	Param.	Means	(Co)variances	Ref.
Egg survival	S_E	NA	S_E	0.60	1.23×10^{-3}	1
Pelagic larval duration	PLD	NA	PLD	27.5	0.176	2
Length-at-age	$L_{(t)}$	$L_{(t)} = L_{\infty}(1 - Be^{-Kt})^{-n}$	L_{∞} K n	8.58 1.48×10^{-3} -0.320	2.78×10^{-2} 2.00×10^{-3} 4.62×10^{-4} -3.33×10^{-5} -4.04×10^{-6} 5.15×10^{-8}	3
Age at first reproduction	A_{FR}	$A_{FR} = a_0 + a_1 L_{\infty}$	a_0 a_1	$-1.12E^3$ 217	9.34×10^4 -1.12×10^4 1.37×10^3	3
Survival during settlement	S_s	e^{μ_s}	μ_s	-1.18	0.34	4
Post-settlement mortality	$M_{(t)}$	$\frac{-1}{30} \log\left(\frac{\exp(\alpha_0 + \alpha_1 L_{(t)} + \alpha_2 L_{(t)}^2 + \alpha_3 L_{(t)}^3)}{1 - \exp(\alpha_0 + \alpha_1 L_{(t)} + \alpha_2 L_{(t)}^2 + \alpha_3 L_{(t)}^3)}\right)$	α_0 α_1 α_2 α_3 α_4	-1.382 1.985 -0.351 0.0201	0.263 -0.230 0.207 0.0532 -0.0490 0.012 -3.60×10^{-3} 3.36×10^{-3} -8.33×10^{-4} 5.97×10^{-5}	3
Probability of reproducing	$P_{(t)}$	$P_{(t)} = \frac{\exp(\beta_0 + \beta_1 L_{(t)} + \beta_2 Seas)}{(1 - \exp(\beta_0 + \beta_1 L_{(t)} + \beta_2 Seas))}$	β_0 β_1 β_2	-13.5 1.69 0.418	1.12 -0.147 0.0201 -0.0168 -9.26×10^{-4} 0.0271	3
Conditional fecundity	$F_{(t)}$	$F_{(t)} = \frac{1}{4} \exp(\gamma_0 + \gamma_1 L_{(t)} + \gamma_2 Seas)$	γ_0 γ_1 γ_2	0.428 0.257 0.368	0.0690 -8.62×10^{-3} 1.14×10^{-3} -2.62×10^{-3} -1.15×10^{-4} 3.94×10^{-3}	3
Egg density	θ	NA	θ	229	8.8	5

628

629

630

Figure Captions

631 **Fig. 1. Summary of post-settlement demography of bicolor damselfish (*Stegastes***
632 ***partitus*). (A) Data used to estimate average growth (size-at-age) of males. Data points**
633 **represent growth increments (change in total length, TL, at various time intervals). Solid**
634 **line represents the fit of a Richards growth equation, and describes expected change in size**
635 **over the average time interval. (B) Monthly survival rates as a function of size. Data**
636 **points represent average survival values of fish within 0.5-cm size bins (average no. of**
637 **observations per bin = 173). (C) Probability of a male having eggs in the nest, as a function**
638 **of size. Data points represent average probability of reproducing for fish within 0.5-cm**
639 **size bins (average no. of observations per bin = 156). (D) Given that eggs were present,**
640 **number of eggs within the nest as a function of male body size**

641

642 **Fig. 2. Uncertainty distributions associated with the estimates of (A) post-settlement**
643 **reproductive output (expected number of offspring fathered by an average, newly-settled**
644 **male) and (B) larval survivorship**

645

646 **Fig. 3. (A) Relationship between larval size and *in situ* estimates of mortality across**
647 **multiple species. Black symbols are coded by species and represent average mortality**
648 **values for a particular size (data from Houde 1997). Solid lines describe average mortality**
649 **as an exponential function of body size and were fit to each species within a mixed-effects**
650 **model framework. Included are cases where only a single, size-specific estimate of**
651 **mortality was available for each species (gray circles; data from Morse 1989, D'Alessandro**

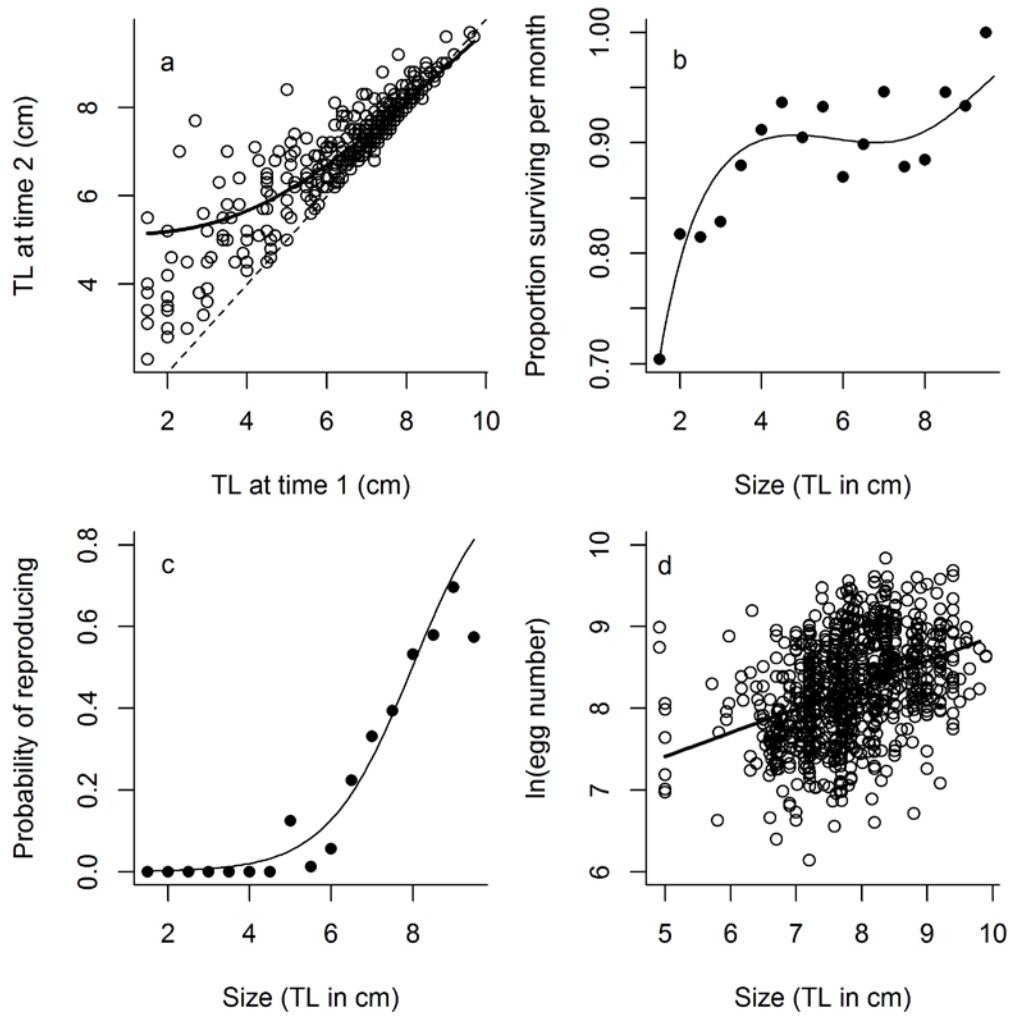
652 et al. 2010, 2011). (B) Relationship between means and medians of the distributions of
653 mortality estimates for three of the species in Houde's (1997) review (triangles = Striped
654 bass, n=5 observations per data point; plus signs = American shad, n = 6; boxes = Walleye
655 pollock, n = 7). Deviations from the solid, 1:1 line indicate skew in distribution of mortality
656 values

657

658 **Fig. 4. Comparison of the bootstrapped estimates of larval survivorship generated in this**
659 **study**

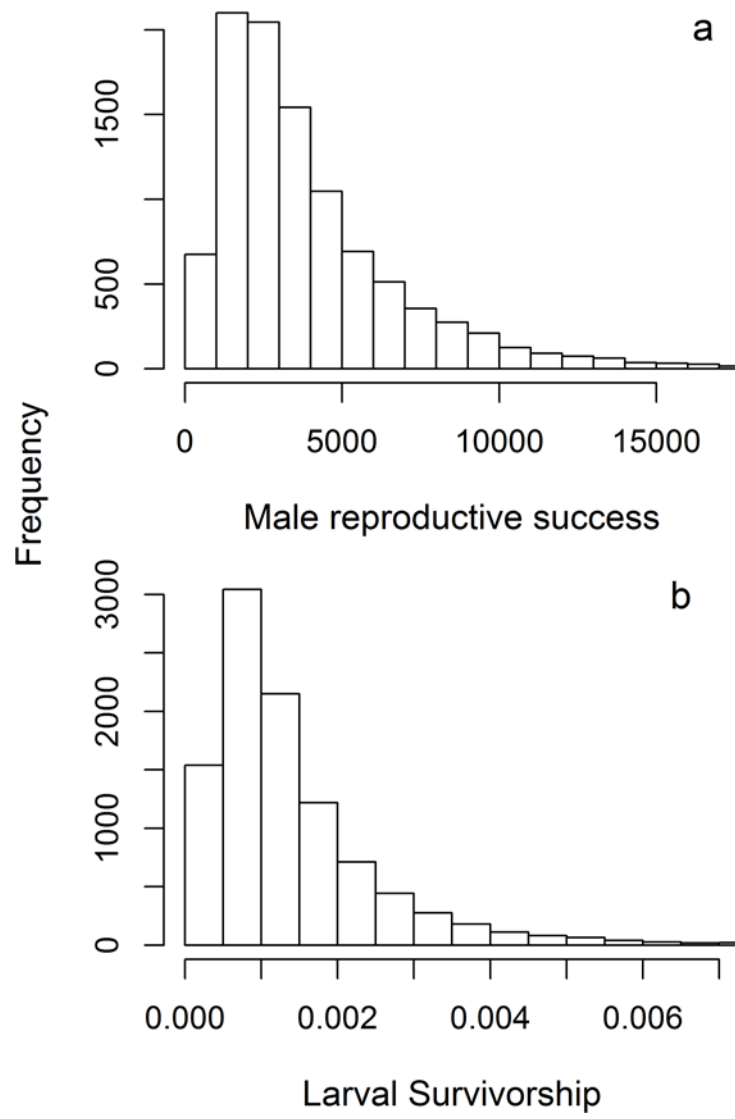
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Fig. 1



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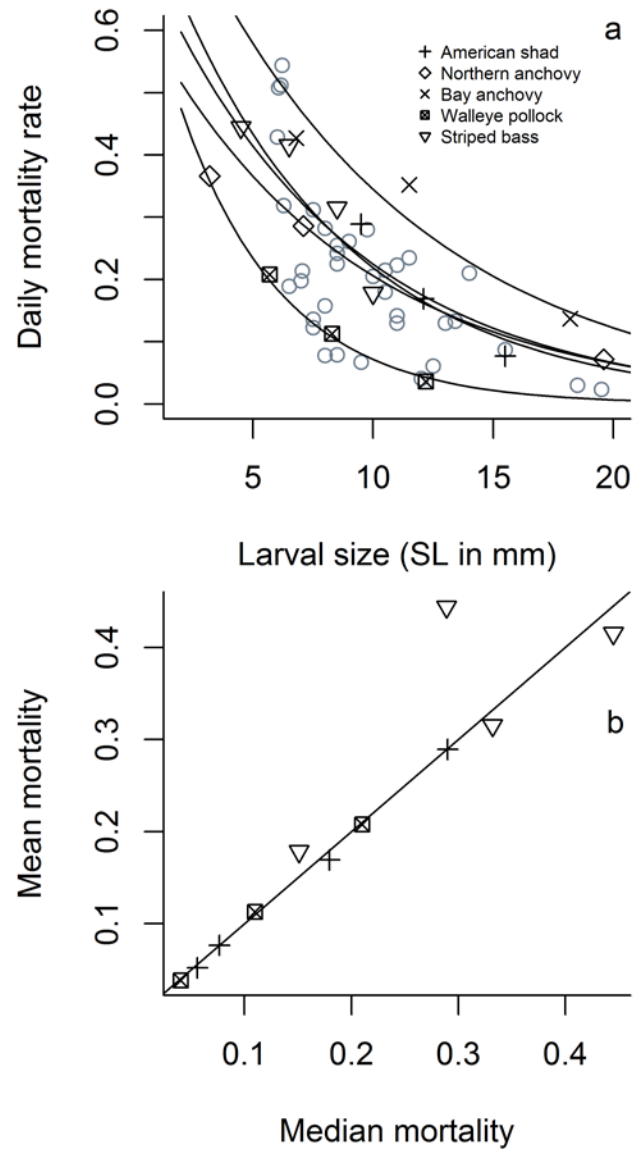
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666 Fig. 3.



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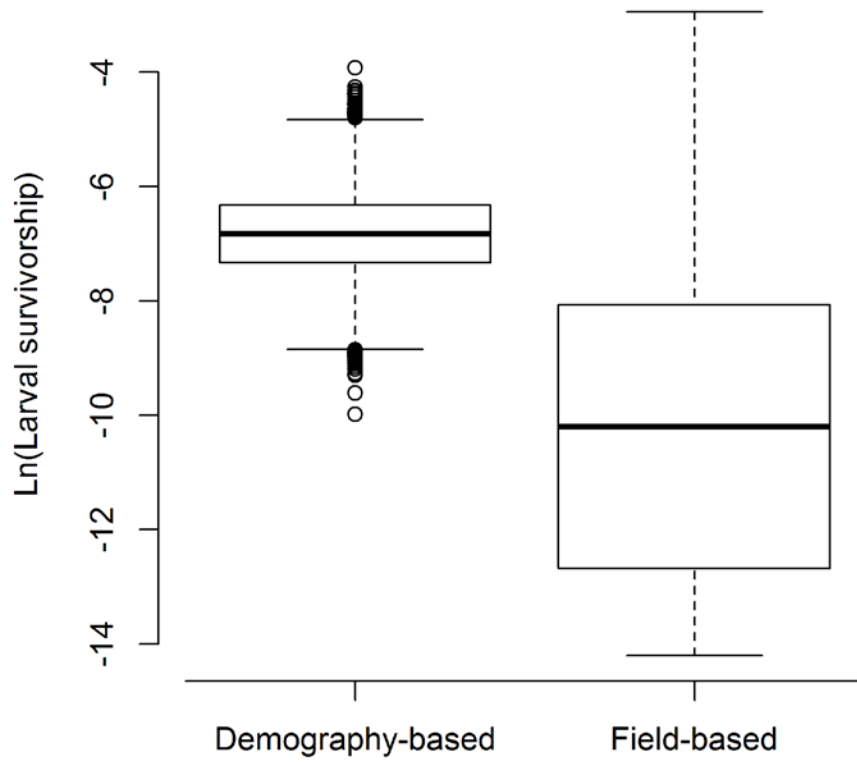
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Fig. 4.

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