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POPULATION ECOLOGY - ORIGINAL RESEARCH

Using post-settlement demography to estimate larval survivorship: a coral reef fish example

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Abstract 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

Introduction

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

For many species (including marine invertebrates and fishes) the youngest stages (e.g., larvae) are small and dispersive. Because these stages can be very difficult to sample directly, estimates of survival through these stages are typically poor. However, the amount of mortality that

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occurs during these early stages can be extremely important to the dynamics of adult populations (e.g., Houde 1987; Grosberg and Levitan 1992; Caley et al. 1996), and to the evolution of life histories (Strathmann 1985; Marshall and Morgan 2011). Moreover, models of dispersal (e.g., coupled biophysical models) are often sensitive to the rate of mortality during the young, dispersive stages (e.g., Cowen et al. 2000, 2006; Largier 2003). Improved estimates of survivorship through these stages are therefore central in efforts to understand many phenomena, including dispersal, genetic connectivity, life history evolution, and dynamics within regional meta-populations (e.g., Pineda et al. 2007; Metaxas and Saunders 2009).

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

Another limitation of field-capture methods is that they necessarily focus on size ranges that are well sampled. Any capture-based estimate of mortality rate is therefore specific to a particular size range. Because mortality rates can change as organisms age and grow, a single field estimate of mortality rate (specific to a particular size range) is therefore unlikely to yield an accurate description of overall survivorship (i.e., survival throughout the entire phase). Such discrepancies are likely to be a common problem for species with complex life cycles in which the young stages are small, dispersive, and abundant. Species with these types of life histories often exhibit type III survivorship (Deevey 1947) in which mortality rates are very high for the youngest ages/sizes and relatively low for older, larger classes (e.g., Peterson and Wroblewski 1984; De Wreede and Klinger 1988; Rumrill 1990; Houde 1997). Accurately estimating survivorship from field estimates of mortality therefore requires (at a minimum) knowledge of both the baseline rate of mortality and how that mortality rate changes over time as organisms age and grow.

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

Materials and methods

Study species

Bicolor damselfish are common, conspicuous, and highly site attached [individuals typically stay within a few meters of their home territory (Myrberg 1972; Schmale 1981)]. These attributes have facilitated thorough, tag-recapture studies that have yielded reliable estimates of post-settlement growth and survival in the field (Carr et al. 2002; Johnson 2008; Johnson and Hixon 2010; Hixon et al. 2012). In addition, males of this species exhibit noticeable reproductive behavior, defend nests of demersal eggs, and readily guard artificial nests (Schmale 1981; Knapp and Warner 1991). These features permit accurate estimation of reproductive rate and age at first reproduction for males

(Johnson et al. 2010; Johnson and Hixon 2011; Hixon et al. 2012). Through our previous studies of this species, we have accumulated data to reliably describe age-specific schedules of mortality and reproduction—key life history traits that determine the lifetime reproductive success of this species.

Estimating larval survivorship

Our approach to estimating average larval survivorship centers on calculating the net reproductive rate (R_0), i.e., the expected number of offspring of the same sex that an average, newborn individual will be replaced with by the end of its life (Caswell 2001). Larval survivorship factors into R_0, and can be calculated if all other aspects of R_0 are known. For *S. partitus* we have detailed estimates of demography from settlement through to reproduction and egg survival until hatching. This information allowed us to estimate larval survivorship as the remaining component of R_0. Because recruitment to local populations will conflate the effects of mortality and dispersal, our calculations of larval survival did not rely on observed patterns of larval settlement and recruitment. Rather, we calculated what the value of larval survivorship must be if per capita production of offspring (in this case, hatched larvae) is to balance per capita mortality during post-settlement life.

To use this approach we make two, related assumptions. First that our demographic data (which were collected at four different locations and across an 8-year time span) are representative of the entire population at large. Second that an average individual will replace itself by producing (on average) one offspring of the same sex that survives to maturity (i.e., $R_0 = 1$). If $R_0 = 1$ (on average), then the average, discrete growth factor will also be 1 and population size will be stable in the long term (e.g., Caswell 2001). Note that if the population is considered to be an open system, the assumption of replacement implies that the study area is neither a net exporter, nor a net importer of larvae in the long term. In other words, we assume that a typical individual replaces itself, even if some offspring may be dispersed to other regions. Our studies of dispersal of bicolor damselfish larvae indicate high gene flow (suggesting that the study region does exchange larvae with other locations), but also higher relatedness among individuals from within the same study region [suggesting that local retention of larvae may be the norm (Christie et al. 2010; Pusack et al. 2014)]. Multigeneration studies of our study species further suggest that the regional population is stable (Hixon et al. 2012). Additionally, we believe that our sample of post-settlement demography is representative of the broader population. We have studied demography of bicolor damselfish at six other sites throughout the Exuma Sound region of the Bahamas. Although sampling was much less frequent in this broad-scale study (three samples per year over 3 years), coarse-scale summary data on survival, growth, and reproduction (number of eggs per nest) suggest that local populations near Lee Stocking Island (i.e., the populations studied in this paper) are average with respect to survival, growth, and reproduction (authors' unpublished data).

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

$$R_{0\mathrm{m}} = \int l_{(x)} p_{(x)} \mathrm{d}x \tag{1}$$

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

$$S_{\mathrm{E}} \times S_{\mathrm{L}} \times \int l_{(t)} p_{(t)} \mathrm{d}t = R_{0\mathrm{m}} = 1 \tag{2}$$

where S_{E} is egg survivorship, S_{L} is larval survivorship, and the term in the integrand describes post-settlement survivorship and paternity. The age schedules of survival and fecundity can be expressed as the combination of component functions and Eq. 2 can be expanded to

$$S_{\mathrm{E}} \times S_{\mathrm{L}} \times \frac{1}{2} \int_{A_{\mathrm{FR}}}^{\infty} S_{\mathrm{s}} \mathrm{e}^{-\int_0^t M_{(t)} \mathrm{d}t} P_{(t)} \theta f_{(t)} \mathrm{d}t = R_{0\mathrm{m}} = 1 \tag{3}$$

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

$$S_{\mathrm{L}} = \frac{2}{S_{\mathrm{E}} \int_{A_{\mathrm{FR}}}^{\infty} S_{\mathrm{s}} \mathrm{e}^{-\int_0^t M_{(t)} dt} P_{(t)} \theta f_{(t)} \mathrm{d}t} \tag{4}$$

where all symbols are as in Eq. 3.

Some of the components on the right-hand side of Eq. 4 are available from published studies (see "Results" for sources). Others can be estimated from our field studies. From 1998 to 2006 we collected extensive field data on individual survival, growth, and reproduction at each of four large reefs near Lee Stocking Island in the Bahamas. Individuals were tagged in situ, and monitored to measure demographic rates. Full details on data collection are reported by Johnson and Hixon (2011) and Hixon et al. (2012). In the paragraphs below, we concentrate on analytical procedures used to estimate functions that describe growth of males, $L_{(t)}$, and post-settlement demography [$M_{(t)}$, $P_{(t)}$, and $f_{(t)}$].

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

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

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

$$L_{(t)} = L_\infty (1 - B\mathrm{e}^{-kt})^{-n} \tag{6}$$

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 (estimated to be 1.5 cm TL). Equation 5 was fit to our data using a nonlinear regression in R (R Development Core Team 2013).

To estimate post-settlement survival, we assigned each individual a value of 1 if it survived >30 days after it was measured and a value of 0 if it disappeared. Because previous studies established that movement of this species away from the study reefs was negligible (Carr et al. 2002; Hixon et al. 2012), and because we exhaustively searched nearby reefs for missing fish, all disappearances were interpreted as mortality. We used a logistic regression to describe survival as a function of size. For fish > 6 cm TL, we used data from males only. Below this size males and females cannot be reliably distinguished, thus mortality was estimated from all tagged fish. Because the data suggested a complex pattern of mortality, we included both squared and cubed body size as predictors of monthly survival. In our final calculations, our equation for monthly survival was converted to one that expressed daily, instantaneous mortality rate [$M_{(t)}$]. We performed this conversion by taking the natural log of our survival expression and dividing it by −30 days.

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

For males that had eggs in their nests, we examined the relationship between ln-transformed egg mass area [directly proportional to egg number (Samhouri 2009; Johnson et al. 2010)], and male size and season. Again, we used a linear, mixed-effects model to describe the data, and both the intercept and the effect of male size were free to vary as random effects. Eggs are laid as a monolayer and females do not lay eggs on top of established egg masses within the nest. Because eggs develop for 3.5 days in the nest (Johnson et al. 2010) and because spawning occurs at dawn, our reproductive censuses measured total egg production within a 4-day window. To convert our estimate of reproductive rate into a daily measure we divided egg mass area by 4.

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

The assumption of population stability (i.e., that a male replaces itself in the next generation) is reasonable for this species, especially given observed, long-term trends in demographic rates and adult population sizes in the region (Hixon et al. 2012). Of course, larval survivorship may vary across seasons, years, regions, etc., but because our demographic data integrated information from four sites and across 8 years at each site, our approach here provides a reasonable average for long-term demography. Nevertheless, it is useful to examine the degree to which our calculations depended on the assumption of population stability. In a second round of our bootstrap procedure, we relaxed the assumption that the population is stable and allowed R_{0m} to vary. Specifically, we calculated larval survival for $R_{0m} = 0.9$ and $R_{0m} = 1.1$. R_0 represents the per generation population growth rate, and these growth rates would result in substantial changes in population size (e.g., if $R_{0m} = 0.9$, population size after ten generations would be $\approx$ 35 % of the original; if $R_{0m} = 1.1$, population size after ten generations would be $\approx$ 260 %). Although these growth rates appear to be outside of what is normally observed for regional, adult population size of bicolor damselfish (Hixon et al. 2012), they do provide a broad test of how sensitive our calculations of larval survivorship are to the assumption that population size is stable. Note that if one considers the population an open system, then changing R_0 values could be conceptualized as a test of how sensitive the estimates of larval survivorship are to the assumption that the study area is neither a net exporter nor a net importer of larvae in the long term. All of the remaining parameters in Eq. 4 were estimated from data, rather than assumed. Variability in these parameter values was quantified and incorporated into our estimate of larval survivorship.

Inferring survivorship from published estimates of larval mortality

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

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

The relationship between larval mortality and SL was reasonably described by an exponential function (see "Results"). We therefore estimated larval survivorship as:

$$S_L^* = \exp\left(-\int_0^{\mathrm{PLD}} \exp(A + B(\exp(L_0 + Kt)))\mathrm{d}t\right), \qquad (7)$$

where A and B are scaling constants estimated from the relationship between SL and larval mortality, and PLD is pelagic larval duration (expressed in days post-hatching). To estimate variability in S_L^*, we used a parametric bootstrap procedure in which we drew 10,000 parameter values at random based on their estimated means and variances [both parameter sets (A and B; L_0 and K) were assumed to be distributed as multivariate normal]. Covariance matrices were estimated among individuals for our growth data. However, because our mortality data were based on an across-species average, we used the variation among species (estimated as the random-effect variation for species identity) as our measure of uncertainty in size-dependent mortality.

Results

Post-settlement demography

Growth of bicolor damselfish males exhibited a pattern typical of fishes in which small individuals grow quickly

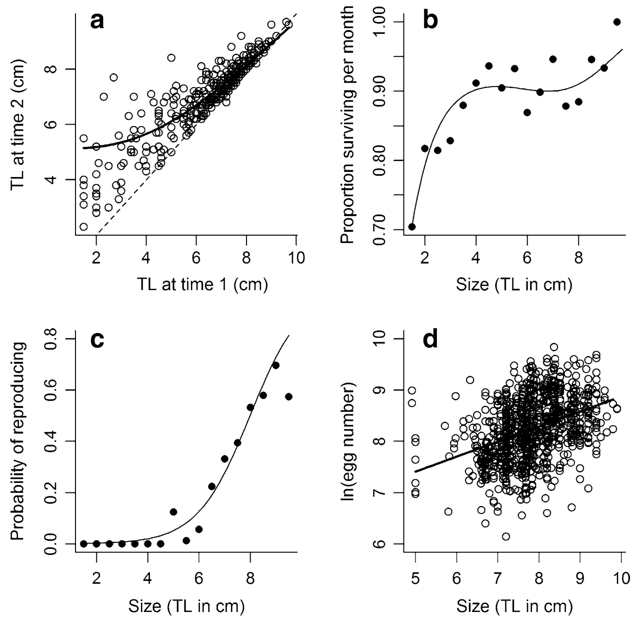

Fig. 1 Summary of post-settlement demography of bicolor damselfish (*Stegastes partitus*). **a** Data used to estimate average growth (size at age) of males. *Data points* represent growth increments [change in total length (*TL*), at various time intervals]. *Solid line* represents the fit of a Richards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

and growth approaches zero at the largest sizes (Fig. 1a). Although there was substantial variability among males, the Richards model is a flexible function that provided a good fit to average size at age. Note that much of the variability in Fig. 1a is due to differences in the interval of time between observations (which is accounted for in the analysis, but not depicted in a two-dimensional graph). The relationship between survival and body size was somewhat complex (Fig. 1b). Monthly survival was lowest for new recruits, increased sharply in the 2- to 4-cm range (TL), plateaued in the 4- to 8-cm range (TL) before increasing at the largest sizes. Probability of reproducing increased sharply with male size (Fig. 1c). Note that the final data point in Fig. 1c represents relatively few observations ($n = 47$ whereas the average sample size within other points was 156) and a simple logistic model was adequate to describe $p_{(t)}$. Finally, the number of eggs in the nest, when eggs were present, increased with male size (Fig. 1d). Although Fig. 1d displays much of the variation that was due to differences among seasons and males, $f_{(t)}$ was well described by an exponential model. Parameter values associated with these demographic functions, as well as the other demographic rates that make up the right hand side of Eq. 4, are summarized in Table 1.

Larval survivorship estimated from post-settlement demography

From our demographic data, we estimated the number of eggs that a newly settled male was expected to father throughout its lifetime [$\int f l_{(t)} p_{(t)} \mathrm{d}t$] to be substantial (median, post-settlement reproductive output = 3,094, 95 % CI 703–1.29×10^4; Fig. 2a). Although observed reproductive rates for males that have survived to maturity can be much higher (e.g., Knapp and Warner 1991; Cole and Sadovy 1995; Johnson and Hixon 2011), this value accounts for the fact that many newly settled males do not survive to reach maturity. Our estimate of reproductive output can be used to calculate survival throughout the larval duration (assuming that $R_{0\mathrm{m}} = 1$). Using Eq. 4, our estimate of the median, larval survivorship was 1.08×10^{-3} (95 % CI 2.55×10^{-4} to 4.84×10^{-3}; Fig. 2b).

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

Larval survivorship estimated from published estimates of larval mortality

Estimates of larval mortality from published literature decreased with body size (Fig. 3). This decrease was well described by an exponential model, i.e., ln(mortality) = −0.231 − 0.143 × SL. Although there was substantial, among-species variation in baseline rates of mortality (Fig. 3a), there was little evidence that the size-dependent scaling of mortality significantly varied among species. Likelihood ratio tests indicated that a simple model in which size scaling was the same among species fit just as well as a more complex model where the scaling relationships differed among species ($P = 0.239$). When considering species that had multiple, yearly estimates of mortality for different sizes of larvae, there was little evidence of negative skewness in the data (i.e., infrequent, very low mortality years). Means tended to match medians, with one exception where the mean was greater than the median, indicating positive skewness (occasional, very high mortality years; Fig. 3b). Combining average, size-dependent

Table 1 Summary of the demographic parameters used to estimate larval survivorship (Eq. 4 in "Estimating larval survivorship" section)

Process	Symbol	Equation	Parameter	Means	(Co)variances	References
Egg survival	S_E	NA	S_E	0.60	1.23×10^{-3}	Johnson et al. (2010)
Pelagic larval duration	PLD	NA	PLD	27.5	0.176	Rankin and Sponaugle (2011)
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} $2.00 \times 10^{-3}, 4.62 \times 10^{-4}$ $-3.33 \times 10^{-5}, -4.04 \times 10^{6}, 5.15 \times 10^{-8}$	This study
Age at first reproduction	A_{FR}	$A_{FR} = a_0 + a_1 L_\infty$	a_0 a_1	−1.12E3 217	9.34×10^{4} $-1.12 \times 10^{4}, 1.37 \times 10^{3}$	This study
Survival during settlement	S_s	e^{μ_s}	μ_S	−1.18	0.34	Almany and Webster (2006)
Post-settlement mortality	$M_{(t)}$	$\frac{-1}{30}\log\left(\frac{\exp(\propto_0+\propto_1 L_{(t)}+\propto_2 L_{(t)}^2+\propto_3 L_{(t)}^3)}{1-\exp(\propto_0+\propto_1 L_{(t)}+\propto_2 L_{(t)}^2+\propto_3 L_{(t)}^3)}\right)$	$\propto_0$ $\propto_1$ $\propto_2$ $\propto_4$	−1.382 1.985 −0.351 0.0201	0.263 −0.230, 0.207 0.0532, −0.0490, 0.012 $-3.60 \times 10^{-3}, 3.36 \times 10^{-3}, -8.33 \times 10^{-4}, 5.97 \times 10^{-5}$	This study
Probability of reproducing	$P_{(t)}$	$P_{(t)} = \frac{\exp(\beta_0+\beta_1 L_{(t)}+\beta_2 \text{Seas})}{(1-\exp(\beta_0+\beta_1 L_{(t)}+\beta_2 \text{Seas}))}$	β_0 β_1 β_2	−13.5 1.69 0.418	1.12 −0.147, 0.0201 $-0.0168, -9.26 \times 10^{-4}, 0.0271$	This study
Conditional fecundity	$F_{(t)}$	$F_{(t)} = \frac{1}{4}\exp(\gamma_0 + \gamma_1 L_{(t)} + \gamma_2 \text{Seas})$	γ_0 γ_1 γ_2	0.428 0.257 0.368	0.0690 $-8.62 \times 10^{-3}, 1.14 \times 10^{-3}$ $-2.62 \times 10^{-3}, -1.15 \times 10^{-4}, 3.94 \times 10^{-3}$	This study
Egg density	θ	NA	θ	229	8.8	Samhouri (2009)

Where appropriate, parameter sets are presented as a vector of mean values and the lower half of a covariance matrix

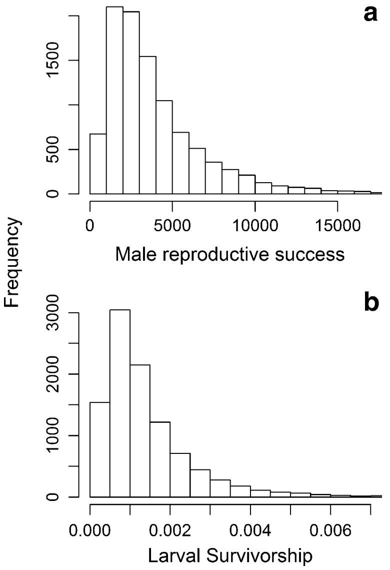

Fig. 2 Uncertainty distributions associated with the estimates of **a** post-settlement reproductive output (expected no. of offspring fathered by an average, newly settled male) and **b** larval survivorship

mortality with estimated growth rates of bicolor damselfish produced an estimate of larval survivorship of 3.70 × 10^{-5}. The uncertainty associated with this estimate was substantial, though highly skewed towards lower survivorship (95 % CI 1.58 × 10^{-9} to 4.60 × 10^{-3}; Fig. 4).

Discussion

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

Our demographic estimate of larval survivorship was approximately two orders of magnitude greater than what would be expected if mortality of bicolor damselfish larvae followed the average, size-dependent scaling relationship observed for a sample of teleost fishes (Houde 1997). Given our demographic data, we regard the latter estimate of larval survivorship as unrealistic for our study species. Based on our calculations, the value of larval survivorship that corresponds to an R_{0m} value of 1 is 1.08 × 10^{-3}. If larval survivorship was 3.70 × 10^{-5} (as calculated from average, size-scaled estimates of mortality), then our estimate of the per generation growth rate would be 0.034.

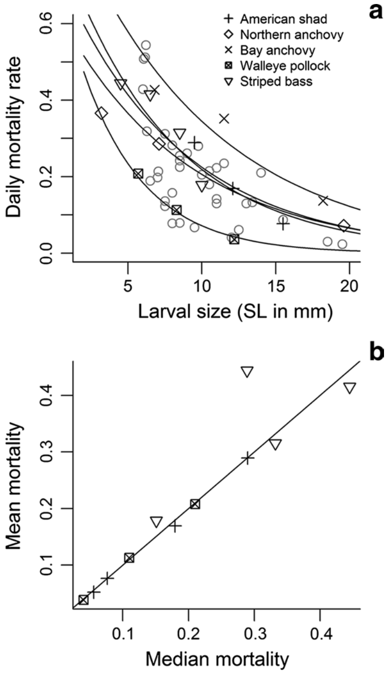

Fig. 3 **a** Relationship between larval size and in situ estimates of mortality across multiple species. *Black symbols* are coded by species and represent average mortality values for a particular size (data from Houde 1997). *Solid lines* describe average mortality as an exponential function of body size and were fit to each species within a mixed-effects model framework. Included are cases where only a single, size-specific estimate of mortality was available for each species [*gray circles* (data from Morse 1989; D'Alessandro et al. 2010, 2011)]. **b** Relationship between means and medians of the distributions of mortality estimates for three of the species in Houde's (1997) review (*triangles* striped bass, $n = 5$ observations per data point; *plus signs* American shad, $n = 6$; *boxes* walleye pollock, $n = 7$). Deviations from the *solid 1:1 line* indicate skew in distribution of mortality values. *SL* Standard length

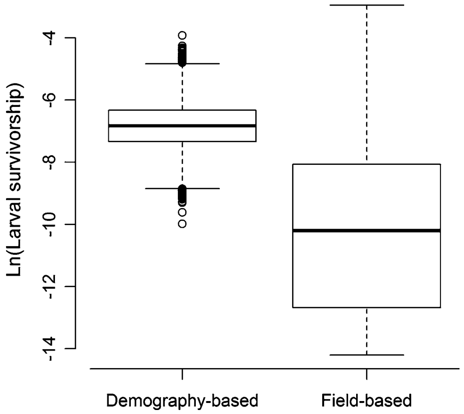

Fig. 4 Comparison of the bootstrapped estimates of larval survivorship generated in this study

This would correspond to a precipitous decline in population size (i.e., <1 % remaining after only two generations), which is clearly not the case for our study species (Hixon et al. 2012).

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

There may be multiple reasons for the discrepancy between our demographic estimate of larval survivorship and the one derived from published estimates of larval mortality. First, bicolor damselfish larvae may follow the same type of size-dependent mortality relationship as observed in Fig. 3 (e.g., an exponential function), but the overall rates of mortality may be among the lowest values observed. Although this explanation is within the realm of possibility, there are no obvious reasons why mortality of bicolor damselfish larvae would be so very low relative to other species. For example, bicolor damselfish larvae do not appear to have any morphological defenses and they inhabit warm waters where mortality rates are hypothesized to be high, on average (Johannes 1978; Houde 1989a). On the other hand, bicolor damselfish larvae are capable swimmers [critical swimming speed was 1.2 SD greater than the size-scaled, all-species average reported in a review by Fisher et al. (2005)], and have been shown to migrate deeper into the water column as they age and grow (Paris and Cowen 2004). These related mechanisms could reduce average mortality rates by decreasing susceptibility to predators and/or advection away from favorable habitat.

Another reason for the discrepancy may be that at the smallest of sizes (2.2–6.0 mm SL), mortality of bicolor damselfish larvae does not scale exponentially with body size. There are very few estimates of larval mortality within this size range, and it is difficult to tell whether scaling relationships are truly exponential, or whether they follow a different pattern. Conceptual models of larval predation suggest that vulnerability to common predators may reflect a balance between detection/encounter rate, which generally increases with larval size, and susceptibility to predation, which decreases with larval size (Bailey and Houde 1989). The result is a dome-shaped relationship between larval size and overall vulnerability to predation. Data from a substantial number of behavioral experiments provide support for dome-shaped relationships between vulnerability and relative sizes of larval prey and their predators (review by Paradis et al. 1996). If throughout the full range of larval sizes the relationship between larval size and mortality is something other than a monotonic decline (e.g., the relationship could be shaped like a parabola or a hockey stick), then the two estimates of larval survivorship may be much closer in magnitude. For example, if we assume that mortality is constant at the smallest of sizes (i.e., mortality stays at the predicted value for a 6-mm larva for sizes 2.2–6.0 mm SL) and then scales according to the observed average, this procedure yields an estimate of 3.07×10^{-4} for larval survivorship—a number closer to our demographic estimate of survivorship. In any case, our results highlight the need to understand mortality during the earliest part of the larval phase more fully.

The distribution of larval mortality rates in natural populations may be skewed such that mortality rates are typically high, but under rare circumstances are very low. This phenomenon is hypothesized to generate patterns of episodic, high-recruitment events for marine species (reviewed by Jennings et al. 2001). If the majority of population replenishment occurs during these events [e.g., a feature of the "storage effect" (Chesson 1983; Warner and Chesson 1985)], then one might expect an estimate of larval survivorship based on the average of in situ samples to be lower than survivorship required to ensure population replacement. However, the importance of skewness in mortality in natural populations remains unclear. High recruitment variability can be driven by variation in reproduction (e.g., Robertson et al. 1988; Rickman et al. 2000), and episodic patterns of recruitment can be produced by subtle, rather than extreme shifts in daily mortality rate (Houde 1987, 1989b). For those few cases where replicate measurements are available for larval mortality at a particular size, there is no evidence that infrequent, low mortality events skew the data (Fig. 3b), though more sampling is required to capture truly rare events.

Finally, spatial patchiness of larvae in the plankton may result in biased estimates of mortality. Estimates of larval mortality from field samples are typically calculated from the ratio of abundances of older individuals to younger individuals, with the accompanying assumption that such ratios are constant and unaffected by spatial patchiness (e.g., Aksnes and Ohman 1996). A recent study by White et al. (2014) relaxed this assumption by treating abundances as random variables that follow a spatially clustered distribution (which was modeled as a negative binomial). Importantly, this method allowed the inclusion of many samples where the abundance of at least one of the older or younger stages was observed to be zero. White et al. (2014) found that by accounting for spatial patchiness, rates of larval mortality (per day) were often orders of magnitude lower than those calculated under traditional assumptions. The differences in larval survivorship they observed between the two methods were comparable to the differences in survivorship that we found when applying two different methods to our study species.

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

Author contribution statement D. W. J. conceived and designed the analysis reported here. All authors collected the data as part of a large-scale study of damselfish population dynamics. D. W. J. wrote the manuscript, and all authors contributed substantially to the revisions.

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