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Planktonic larval mortality rates are lower than widely expected

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Abstract. Fundamental knowledge of mortality during the planktonic phase of the typical marine life cycle is essential to understanding population dynamics and managing marine resources. However, estimating larval mortality is extremely challenging, because the fate of microscopic larvae cannot be tracked as they develop for weeks in ocean currents. We used a two-pronged approach to provide reliable estimates of larval mortality: (1) frequent, long-term sampling where the combination of larval behaviors and recirculation greatly reduces larval transport to and from the study area, and (2) an improved method of calculating larval mortality that consists of a vertical life table with a negative binomial distribution to account for the notorious patchiness of plankton. Larval mortality rates of our study species (barnacles and crabs) were $\leq$0.14 larvae/d, which produce survivorships over an order of magnitude higher than commonly determined for marine larvae. These estimates are reliable because they were similar for species with similar dispersal patterns. They are conservative because they were conducted in a highly advective upwelling system, and they may be even lower in other systems using our approach. Until other systems can be tested, our improved estimates should be used to inform future models of population dynamics and the evolution of life histories in the sea.

Key words: crustacean larvae; larval mortality; planktonic larvae; population dynamics; spatial patchiness; vertical life table.

Introduction

Population dynamics in the sea are fundamentally different from those on land because marine organisms typically develop for weeks or months as microscopic larvae in the plankton (Marshall and Morgan 2011). The many larvae produced, their poor swimming capabilities, and episodic settlement events have led to the widespread belief that advection by currents, predation, and starvation are overwhelming, resulting in open populations with unpredictable recruitment in time and space (Thorson 1950, Caley et al. 1996). Because the persistence of adult populations requires replacement by larval recruits, both demographic and genetic connectivity within marine metapopulations depend upon the spatial pattern of larval replenishment, which has important consequences for fisheries management, design of reserve networks, spread of invasive species, and adaptation or extinction in the midst of global climate change (Cowen and Sponaugle 2009, Marshall and Morgan 2011). A complete representation of metapopulation dynamics requires an estimate of the fraction of larvae spawned in each subpopulation that successfully disperse to every other subpopulation (Botsford et al. 2009, Burgess et al. 2014). As such, research on the planktonic larval stage of benthic and pelagic organisms (meroplankton) focuses on two central questions in the ecology and evolution of marine life: where do larvae go and how fast do they die?

Major advances have been made in recent years to address the question of how larvae of benthic and pelagic species disperse. It has become increasingly apparent that larvae regulate transport by exploiting circulation patterns and recruit closer to natal habitats than is widely appreciated (Swearer et al. 2002, Cowen and Sponaugle 2009). Characteristic circulation of coastal regions enables larvae to limit cross-shelf and alongshore transport by regulating depth in opposing stratified currents (Peterson 1998, Queiroga and Blanton 2005, Shanks and Eckert 2005, Morgan et al. 2009*c*).

Far less progress has been made on addressing the question of larval mortality rates, even though it is equally important to population dynamics (Cowen et al. 2000, Metaxas and Saunders 2009, Pineda et al. 2009, Vaughn and Allen 2010). This is due primarily to logistical challenges: whereas dispersal patterns can be estimated by computational models or measured post-dispersal using genetic or chemical signatures (Botsford et al. 2009, Cowen and Sponaugle 2009, Burgess et al. 2014), reliable estimates of larval mortality rates can only be obtained from direct estimation in the field (Houde 1989, Rumrill 1990, Morgan 1995, Bailey et al.

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1996, Metaxas and Saunders 2009). Moreover, the inherent patchiness and variability of larval densities in the ocean have produced highly variable estimates of mortality rates, varying by a factor of two or more for the same species (Houde 1989, Rumrill 1990, Morgan 1995, Vaughn and Allen 2010), and calling into question the reliability of any of the published mortality estimates for meroplankton. Depending on the species, published mortality rate estimates range from quite low (0.01 d^{-1}) to incredibly high (1.01 d^{-1}), although most estimates fall in the vicinity of 0.2 d^{-1} (i.e., 0.25% survival over a 30-d larval duration), consistent with the general sense that larval mortality is quite high, if not precisely known (Cowen and Sponaugle 2009, Metaxas and Saunders 2009).

The large variation in estimated larval mortality rates arise for two methodological reasons. First, the previous studies usually were not designed to provide the most reliable estimates of larval mortality. The best estimates will be obtained for larvae that develop in retention zones to reduce advection of larvae into and out of the study area. In addition, estimates will be most reliable for species with larval behaviors that reduce transport. Finally, frequent, long-term sampling along replicate transects is needed to account for patchy larval distributions. Studies possessing all three of these criteria will provide the most reliable estimates of larval mortality, and, concurrently, examining multiple species with similar dispersal patterns will indicate the repeatability of the estimates.

Methods used to calculate larval mortality also introduce uncertainty. There are two general strategies for estimating larval mortality rates from field samples, both of which were originally developed for studying holoplankton, such as copepods. Both are intended for use with stage-structured populations, and so are most easily applied to crustacean larvae with well-defined developmental stages of fixed duration (see Plate 1). The first approach is the so-called horizontal life table method, which parallels the traditional method of estimating mortality in terrestrial populations: a time series of abundances of stages are analyzed to determine the proportion of individuals that survive from one observation to the next (Wood 1994). This approach can accommodate temporal variation in demographic parameters (including the mortality rate) but is very sensitive to advection; that is, it is impossible to distinguish losses due to mortality from losses due to the advection of larvae away from the sampling station (Bailey et al. 1995, Aksnes et al. 1997). Thus, this method is appropriate for populations in enclosed bodies of water or in shelf regions with minimal advection (Ohman et al. 2004) but is generally inappropriate for larvae, the abundance of which can be strongly influenced by advection (Caley et al. 1996). The second estimation approach, the vertical life table (VLT) method, is intended to avoid the potential errors introduced by advection (Aksnes et al. 1997). The VLT approach estimates mortality from the ratio of abundances of adjacent stages on a single sampling date, rather than a time series of abundances of the same stage (Aksnes and Ohman 1996). In this way, day-to-day variation in abundance due to advection does not influence the mortality estimate, provided that adjacent stages are advected in the same way.

The VLT method has been applied successfully to populations of copepods at a range of shelf and estuarine locations (e.g., Ohman et al. 2004, Plourde et al. 2009). However, an important requirement of the method can limit its usefulness in studies of meroplankton: the VLT approach assumes that estimates of abundance are the average of multiple samples aggregated over a large enough spatial scale to correct for small-scale patchiness (Aksnes and Ohman 1996, Aksnes et al. 1997; also see a similar approach developed for anchovy larvae by Hewitt and Methot 1982). Large-scale sampling is especially important to capture all of the developmental stages of species that have extensive rather than restricted distributions, such as larvae of nearshore species that migrate to the edge of the continental shelf (Peterson 1998, Morgan et al. 2009*b*, *c*). Unfortunately, investigations of the larvae of nearshore organisms are typically very limited in spatial scale and are likely to violate this assumption. This limited scale is sometimes due to logistical constraints, but it can also be by design, as there is increasing evidence that larvae of many species complete development in high densities close to shore even in highly advective upwelling systems along the western margins of continents (Morgan et al. 2009*b*, *c*, Shanks and Shearman 2009, Morgan and Fisher 2010, Drake et al. 2013, Nickols et al. 2013, Fisher et al. 2014, Morgan 2014). For example, Tapia and Pineda (2007) used VLT methods to estimate larval mortality rates for two intertidal barnacles in inner shelf waters in southern California, but patchiness in their data set frequently produced biologically implausible estimates (zero or negative) for some developmental stages and sampling dates.

We modified the VLT method to explicitly account for spatial patchiness and used it to estimate larval mortality rates from high-frequency time series of six taxa of crustacean larvae, providing the most reliable larval mortality estimates for meroplankton. Our analyses yielded relatively low estimates of larval mortality rates ($\leq$0.14 d^{-1} or $\geq$1.5% survival during a 30-d larval period) that challenge the traditional perception of extraordinarily high mortality during the larval phase of the life cycle.

Methods

Study system

Larval samples were collected in the lee of Bodega Head, on the coast of northern California, USA (Appendix A). This region is characterized by persistent equatorward winds during the spring and summer,

which produces Ekman transport and a general flow of near-surface waters equatorward and offshore over the shelf (Largier et al. 1993, Dever et al. 2006). However, the coastline topography and shallow depths reduce offshore Ekman transport and slow alongshore currents in a coastal boundary layer that occurs <10 km from shore (Largier et al. 1993, Nickols et al. 2012, 2013). The combination of this boundary layer and the pattern of recirculation in the lee of the headland (Roughan et al. 2005, Mace and Morgan 2006, Morgan et al. 2011) provided an abundant and diverse pool of larvae (Morgan and Fisher 2010, Morgan et al. 2011, 2012) with which to estimate mortality rates.

Larval surveys

A time-series of larval densities was obtained by collecting plankton every other day for two months (7 June to 10 August 2005) along three transects, which were parallel to the shoreline, ~1.5 km long and ~0.75 km apart (Appendix A). During the 33 sampling trips, plankton was collected by taking one oblique tow throughout the water column (10–15 m) on each of the three transects (33 trips × 3 transects = 99 total samples). We used a sled-mounted 0.5 m diameter ring net fitted with 335-μm mesh and a flowmeter (model 2030; General Oceanics, Miami, Florida, USA) to determine the volume of water sampled (45.2 ± 18.6 m^3 [mean ± SD]). Larvae were averaged across the three transects on each sampling date before estimating mortality.

All crustacean larvae were identified to species and stage when possible and counts were standardized to number per volume of water sampled (no./m^3). In some cases, adjacent developmental stages that are difficult to distinguish reliably were combined. Some species were combined to the genus or family level after determining that the abundance and distributions of larval stages were similar. Some pinnotherids could not be reliably identified to species, but they all complete development close to shore with the exception of *Fabia subquadrata*, which were excluded from analyses (Morgan et al. 2009*c*, Morgan and Fisher 2010). A full description of the species collected in this study is given by Morgan and Fisher (2010). We restricted our analysis to barnacle and crab taxa that complete their development on the inner shelf (Table 1; Morgan et al. 2009*b*) to ensure that adjacent larval stages did not undergo differential advection out of the study area. All stages of these larvae feed in the plankton, except the post-larval stage of barnacles. Observations of *Chthamalus* spp. larvae were limited to days 17–59 of the time series, restricting analysis to those dates for that group. The mesh of the net was too coarse to reliably collect early-stage larvae of barnacles, so that stage was excluded from our analysis. We also collected very few post-larval *Chthamalus* spp., *Pagurus* spp., Pinnotheridae or Porcellanidae, or late-stage *Pagurus* spp., so those stages were also excluded.

Vertical life table estimation

Aksnes and Ohman (1996) developed the original VLT approach to estimate mortality from the ratio of abundances of two developmental stages of known duration. For a particular developmental stage i with constant duration α_i, mortality rate θ_i, and daily recruitment rate into the stage ρ_i, the number of individuals of stage i on day t is

$$n_{i,t} = \rho_i[1 - \exp(-\theta_i\alpha_i)]/\theta_i \quad (1)$$

and the recruitment rate into the next stage, ρ_{i+1}, is

$$\rho_{i+1} = \rho_i \exp(-\theta_i\alpha_i) \quad (2)$$

so that the abundance of stage $i + 1$ on day t is

$$n_{i+1,t} = \rho_{i+1}[1 - \exp[(-\theta\alpha_{i+1})]. \quad (3)$$

Then, it is possible to combine Eqs. 1–3 to obtain the ratio of abundances of the two stages

$$n_{i,t}/n_{i+1,t} = [\exp(\theta_i\alpha_i) - 1]/[1 - \exp(-\theta_{i+1}\alpha_{i+1})]. \quad (4)$$

Given a time series of abundances of each stage over successive days, and if one assumes that the mortality rate for a particular developmental stage $\theta_i = \theta_{i+1} = \theta$, or the overall mortality rate, the ratio $n_{i,t}/n_{i+1,t}$ can be used to solve Eq. 4 for an estimate of θ for each day; these daily estimates can then be averaged to obtain an overall estimate and standard deviation for θ (Aksnes and Ohman 1996; alternatively, abundance ratios could be estimated simultaneously at many sampling stations and averaged to estimate θ). Note that this method assumes that the stage durations, α_i, are known constants, that the recruitment rate, ρ_i, is constant over a time scale greater than α_i, and that adjacent stages have equal mortality rates, θ. The first two assumptions are met in our case. For all six taxa, larval durations have already been estimated, the sampling period spanned much of the reproductive and larval development season (Morris et al. 1980, Strathmann 1987, Mace and Morgan 2006, Morgan et al. 2011), and visual inspection of the time series did not reveal any consistent temporal trends.

We obtained estimates for stage durations for each species from published sources (Table 1). The wide ranges of larval durations primarily reflect temperature differences across species' geographical ranges or among years (Table 1), and therefore, we chose temperatures that most resembled those during our sampling period (mean bottom temperature, where most larvae reside, of 11.3°C, ± 1.7°C standard deviation). Because the study region experiences persistent upwelling with infrequent relaxations during the sampling period (Botsford et al. 2006, Vander Woude et al. 2006, Wilkerson et al. 2006), variability in both temperature and productivity would have been low relative to variation over a species' range and unlikely to introduce high variation in development times. Moreover, there is little intrinsic variation in stage duration, because crustacean larvae have relatively fixed developmental times at constant temperatures and food

TABLE 1. Life-history information for species of crustacean larvae analyzed in this study, including number of larval stages, duration of the entire larval period, and cross-shelf larval distributions.

Family	Taxa	Spawning season	Duration (d)	No. stages	Pooled stages
Cirripedia	*Balanus crenatus*	year-round[1,2]	14–21[1]	6	early,† mid, late, postlarval (8, 8, 4, 4)
Cirripedia	*Balanus glandula*	winter–spring[1,2]	11–14[4]	6	early,† mid, late, post-larval (3, 5, 3, 3)
Cirripedia	*Chthamalus* spp.	spring–fall[1,2]	18–30[5]	6	early,† mid, late, post-larval‡ (10, 5, 5, 5)
Paguroidea	*Pagurus* spp.	May–August[1,3]	43–81[6]	5	early, mid, late,‡ post-larval‡ (10, 20, 10, 10)
Pinnotheridae	Pinnotheridae	May–August[1,3]	30–80[6]	6	early, mid, late, post-larval‡ (9, 18, 18, 9)
Porcellanidae	Porcellanidae	May–August[1,3]	32–40[7]	3	early, late, post-larval‡ (16, 16, 16)

Notes: Larval durations were obtained from field and laboratory studies that were conducted at water temperatures that most resembled those of our study region. Values in parentheses under pooled stages are the duration, in days, of each stage.

Sources: 1, Morris et al. (1980); 2, Strathmann (1987); 3, Mace and Morgan (2006); 4, Brown and Roughgarden (1985); 5, Miller et al. (1989); 6, Lough (1975); 7, MacMillan (1972).

† Early-stage larvae are smaller than net mesh and were excluded from analysis.

‡ Stage excluded from analysis because very few observed in samples.

availabilities; either they obtain enough energy to molt within a given time period or they die (e.g., Sulkin and McKeen 1989, 1994). Further, stage durations during larval development are similar (Sulkin and McKeen 1989, 1994). Thus, there is unlikely to be large error in estimating mortality rates introduced by misestimating stage durations, because the effect of a proportional change in stage durations (α_i) depends on the magnitude of the mortality rates θ (Eq. 4), which were low (<0.14 d^{-1}; see Appendix B for additional analysis of sensitivity to stage duration). Because stage durations are approximately equal (Sulkin and McKeen 1989, 1994), we divided the total larval duration by the number of stages to get individual stage durations (for species without published individual stage durations; Table 1). In cases where we had pooled two adjacent, difficult-to-distinguish stages, the combined stage had twice the duration (Table 1).

Importantly, while the VLT method is not affected by the advection of individuals past the sampling station (provided both stages have similar advection rates), it is assumed that $n_{i,t}$ and $n_{i+1,t}$ are estimated over a large enough spatial scale that their ratio is relatively constant and unaffected by small-scale patchiness in the abundance of each stage (Aksnes and Ohman 1996, Aksnes et al. 1997). When this assumption is not met, estimates of θ tend to have high variance or take on biologically unrealistic values (Aksnes and Ohman 1996, Tapia and Pineda 2007).

Incorporating spatial sampling variation

Counts of spatially clumped ("overdispersed") organisms typically follow a negative binomial distribution, such that the probability of observing N individuals is

$$\Pr(n = N) = \binom{k+N-1}{k-1}\left(\frac{m}{k}\right)^N\left(1-\frac{m}{k}\right)^{-(k+N)} \quad (5)$$

where the number of individuals, n, has an expected value of m and a variance of $m+m^2/k$; k is referred to as the overdispersion parameter. This distribution has been used widely to model spatial variation in abundance of clumped organisms. For example, Young et al. (2009) showed that the negative binomial provided a reasonable representation of copepod distributions that were patchy at the scale of 1 km off the coast of Newfoundland, Canada. Hewitt and Methot (1982) also found that trawl samples of anchovy larvae off the California coast were described well by a negative binomial distribution.

We adapted the VLT method so that rather than assuming the ratio $n_{i,t}/n_{i+1,t}$ was a constant, we assumed that both $n_{i,t}$ and $n_{i+1,t}$ were random variables following negative binomial distributions with overdispersion parameter k and means given by Eqs. 1 and 3. Therefore, the ratio of abundances $n_{i,t}/n_{i+1,t}$ is also a random variable distributed as the ratio of two negative binomial variables. Initial efforts revealed that this problem was not amenable to traditional maximum likelihood estimation, because we were unable to derive an analytical expression for the likelihood $L(n_{i,t}, n_{i+1,t} \mid \theta, k)$, and numerical exploration suggested that the likelihood surface tended to be highly multimodal. Therefore, we took a Bayesian approach to the problem and estimated the joint posterior distribution $\Pr(\theta, k \mid n_{i,t}, n_{i+1,t})$ using Markov chain Monte Carlo (MCMC) and an implicit likelihood calculation (Diggle and Graton 1984, Marjoram et al. 2003), which proved to be much more effective. We used MCMC to estimate the posterior distributions of both k and θ for each species, using uninformative prior distributions for both parameters (Appendix B). We also estimated θ using the original VLT approach for comparison. For three of our taxa (*Chthamalus* spp., *Pagurus* spp., and Porcellanidae), only two developmental stages were present in our data set, so we estimated a single value of θ for those stages. For the other taxa (*Balanus crenatus*, *B. glandula*, and Pinnotheridae), three developmental stages were present in our data set, so we estimated separate values of θ for each pair of adjacent stages. A test of our method using simulated data sets revealed that it correctly estimated k and θ when adjacent stages had the same mortality rate; when mortality rates differed between stages, our method estimated an intermediate mortality rate (Appendix B).

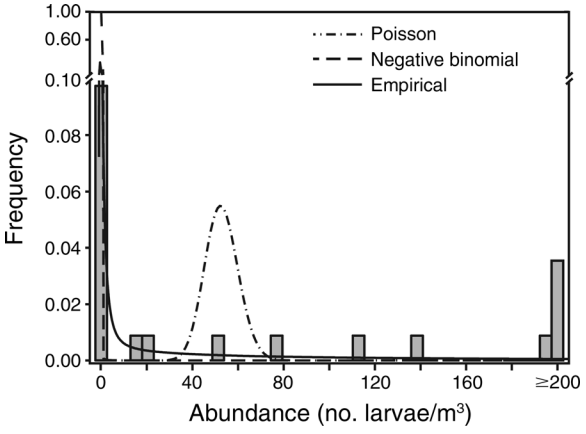

FIG. 1. Frequency distribution of abundance of mid-stage *Chthamalus* spp. larvae in near-shore larval samples. Observations of >200 individuals were pooled into a single bar for clarity. Distributions were fitted with a nonparametric kernel density function (solid curve), Poisson distribution (dot-dashed curve), and negative binomial distribution (dashed curve).

RESULTS

The time series of larval abundances were extremely patchy for all species and stages, with many zero observations and occasional high-density observations. Mid-stage *Chthamalus* spp. provide a representative example, and illustrate how a negative binomial distribution is a better representation of the data (peak at 0 with a long tail, very similar to an empirical kernel density estimate for the distribution) than a Poisson distribution, which is commonly used to approximate non-overdispersed random spatial distributions (Fig. 1).

Estimates of mortality rates using the original VLT method varied widely among species and stages, and standard errors were high relative to the magnitude of the mortality rates. These estimates were based on relatively few observations, as most ratios of daily observations $n_{i,t}/n_{i+1,t}$ contained a zero in either the numerator or denominator and had to be excluded from calculation; consequently, a solution to Eq. 4 was not possible (Table 2). In some cases, the need to exclude illegal ratios meant that replication was much less than the minimum level ($n = 8$) necessary for reliable estimation (Aksnes and Ohman 1996), so those values are highly unreliable.

Estimates of mortality using the modified VLT method revealed several general patterns (Table 2, Fig. 2). First, estimates of the negative binomial parameter k were similar in magnitude across most species, ranging from 1.90 to 9.25 (the exception being *Chthamalus* spp., with a lower value of 0.344). Second, the posterior distributions of the mortality rate, θ, for all taxa fell into one of two patterns. For the mid/late stages of the barnacles *B. crenatus* and *B. glandula* and for the crab taxa *Pagurus* spp., Pinnotheridae (both pairs of developmental stages), and Porcellanidae, there was a distinct mode in the posterior distribution in the vicinity of 0.1 larvae/d and then a long flat tail extending towards $-\infty$ (values were constrained to $>10^{-4}$ d^{-1} during estimation). Median mortality rates for these species were low, ranging from 0.0091 larvae/d to 0.139 larvae/d (Table 2). We have higher confidence in these mortality rate estimates than those for the remaining stages (late/postlarval stages of *B. crenatus* and *B. glandula* and mid/late stage *Chthamalus* spp.). For those latter taxa, the

TABLE 2. Mortality rate estimates using the original vertical life table (VLT) method.

Taxon and stage	Original VLT		Updated VLT		
	Mortality rate, θ (d^{-1})†	n‡	Clumping parameter, k (dimensionless)§	Mortality rate, θ (d^{-1})§	n‡
Balanus crenatus					
Mid/late	0.0559 (0.0334–0.0784)	10	9.25 (4.23–27.41)	0.0091 (0.000169–0.164)	33
Late/postlarva	0.4737 (0.1870–0.7604)	10	1.90 (1.45–2.48)	0.0035 (0.000178–0.0742)	33
Balanus glandula					
Mid/late	0.2611 (0.1345–0.1870)	6	4.22 (2.05–11.72)	0.139 (0.000465–0.871)	33
Late/postlarva	0.2440 (−0.0537–0.5417)	3	2.18 (1.40–3.97)	0.0183 (0.000187–0.745)	33
Chthamalus spp.					
Mid/late	0.0515 (0.0384–0.0646)	3	0.344 (0.133–0.751)	0.0096 (0.0157–0.337)	33
Pagurus spp.					
Early/mid	0.1089 (0.0715–0.1463)	8	5.69 (1.48–22.78)	0.062 (0.000401–0.267)	33
Pinnotheridae					
Early/mid	0.1194 (0.0886–0.1502)	23	6.52 (3.65–12.09)	0.0970 (0.0057–0.1763)	33
Mid/late	0.0450 (0.0364–0.0536)	14	8.00 (4.91–18.39)	0.0699 (0.0185–0.1733)	33
Porcellanidae					
Mid/late	0.1692 (0.1128–0.2256)	6	2.74 (1.30–6.51)	0.0954 (0.000518–0.284)	33

† Values in parentheses are the 95% confidence interval estimated from standard deviation, assuming a normal distribution.

‡ Number of samples used to estimate mortality rates (of 33 possible; note that one estimate is obtained for each pair of adjacent stages).

§ Values in parentheses are the 95% highest posterior density calculated directly from modal region of the Markov chain Monte Carlo-generated posterior distribution.

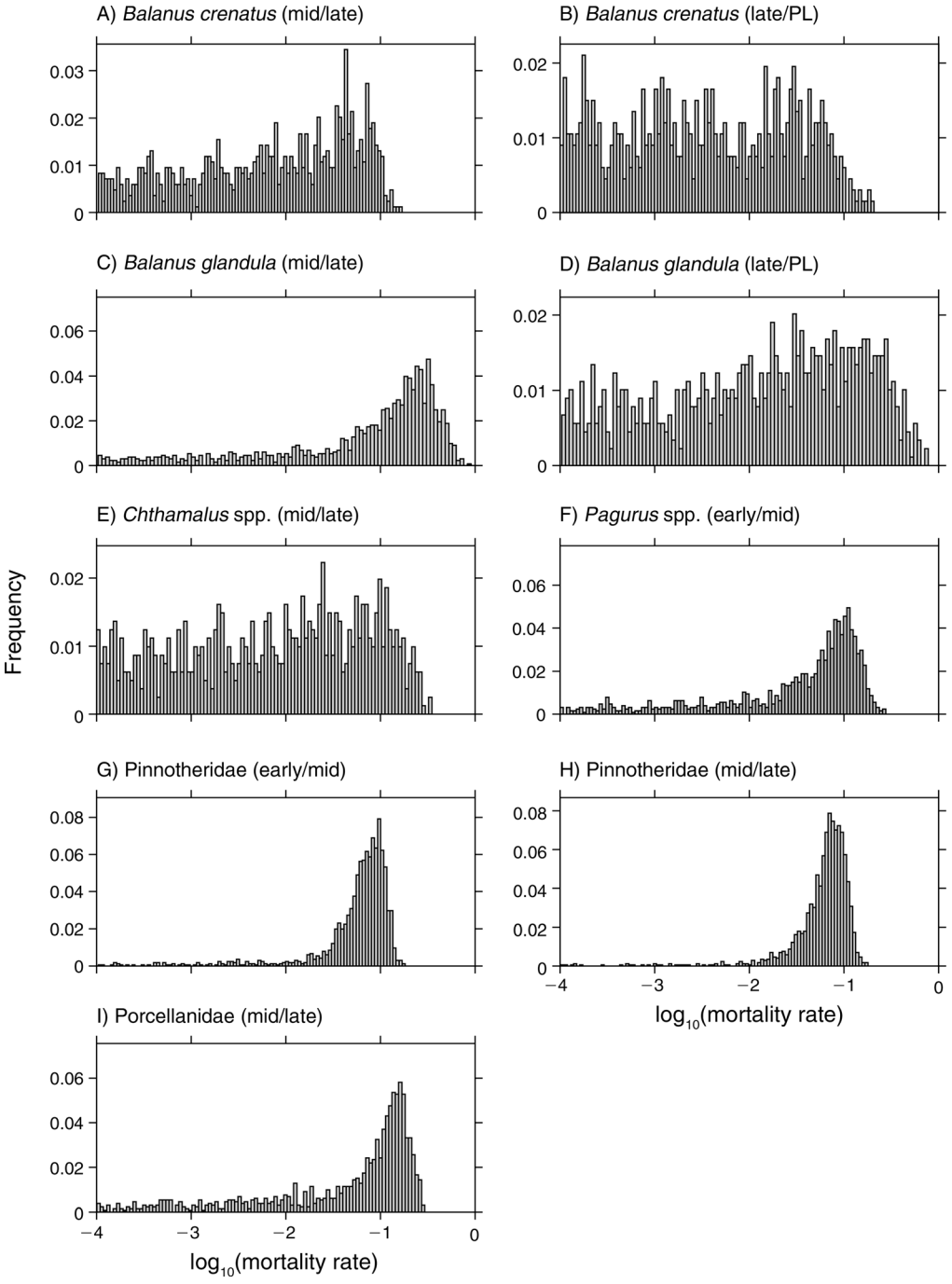

FIG. 2. Posterior distribution of larval mortality rates (θ, d^{-1}) estimated using a modified vertical life table (VLT) method for adjacent pairs of developmental stages of larvae of six taxa of crustaceans. Larvae were sampled on alternate days for two months (7 June to 10 August 2005) in the lee of Bodega Head, California, USA. PL stands for post-larva.

posterior distributions were relatively flat, and the 95% highest posterior density (HPD) regions were very large. However, the posterior estimates of θ were restricted to values $\leq$0.07, 0.75, and 0.34 larvae/d, respectively. Therefore, we have higher confidence in the upper limit of the distribution than in the mean for these stages.

Mortality estimates using the modified VLT method were moderately lower than those obtained using the original method for most taxa and developmental stages, particularly for Pinnotheridae, which had the largest sample sizes for the original method (Table 2). In nearly all cases the 95% HPD region for the updated

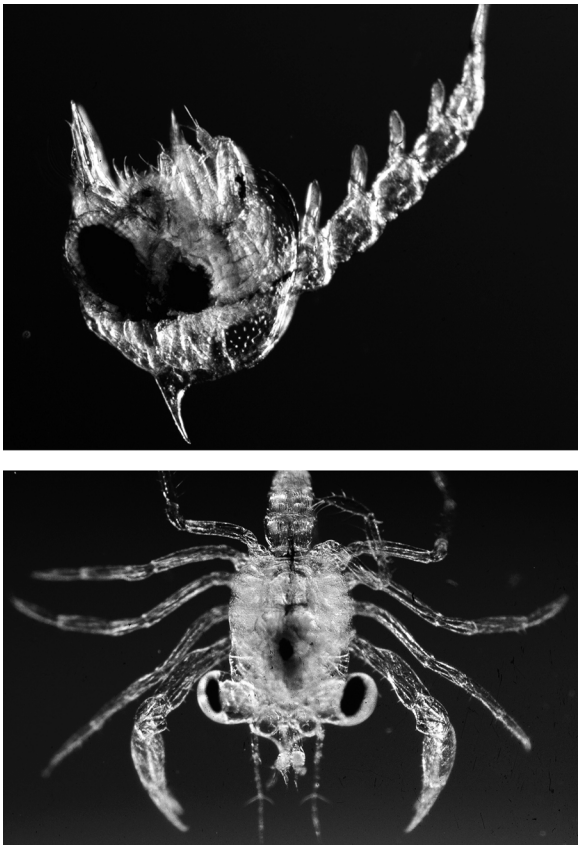

PLATE 1. (Top) Planktonic larval and (bottom) postlarval stages of an unidentified crab similar to the larvae used in this study. Photo credit: Peter Parks.

estimates of θ overlapped the original estimates. The two notable exceptions to this pattern were late/post-larval-stage *B. crenatus* and *B. glandula*, where the original estimates were much higher than the modified estimates. For *B. crenatus* the original estimate (0.47 d^{-1}) was well beyond the upper edge of the 95% HPD region for the modified estimate (0.074 d^{-1}); for *B. glandula* the original estimate (0.244 d^{-1}) was nearly twice the median of the posterior distribution for the modified estimate (0.139 d^{-1}), but it did fall within the broad 95% HPD region of that distribution.

DISCUSSION

We have obtained the first set of reliable estimates of mortality rates for larvae of benthic species by coupling a rigorous, comprehensive, sampling design with an improved method of calculating larval mortality. We did so by minimizing the confounding effects of advection and patchiness on larval mortality estimates by conducting our study (1) in a retention zone, (2) on species with larval behaviors that enhance retention, and (3) with long-term, high-frequency sampling of replicate transects. We also explicitly accounted for spatial patchiness in the resulting data set by modifying the vertical life table (VLT) method (Aksnes and Ohman 1996). This enabled us to successfully analyze a high-temporal-resolution data set collected on a small spatial scale in an advective nearshore environment, where VLT usually fails due to extremely patchy larval distributions and large numbers of zero observations (e.g., Tapia and Pineda 2007). Lastly, studying multiple species with similar dispersal "strategies" yielded similar larval mortality estimates, indicating that our estimates were repeatable, and hence, reliable.

Our analysis revealed relatively low estimates of larval mortality for all three barnacle and three crab taxa: $\leq 0.14\ d^{-1}$. For a species with a 30-d larval duration, this mortality rate would yield a survival rate of 1.5%, an order of magnitude greater than the 0.25% survival rate produced by a mortality rate of 0.2 d^{-1}, which is one of the most commonly reported previous estimates (Cowen et al. 2000, Metaxas and Saunders 2009).

Prior estimates of larval mortality rates range from 0.02 to 1.01 d^{-1} (Dahlberg 1979, Houde 1989, Rumrill 1990, Morgan 1995, Vaughn and Allen 2010), including values that were implausibly high and very divergent for the same species. The values calculated here fall within the lower extreme of that distribution. Many of those earlier estimates were calculated using horizontal life tables (i.e., following a single cohort over time rather than sampling ratios of adjacent cohorts; Wood 1994, Bailey et al. 1996), so they were extremely vulnerable to advection effects and are likely unreliable (Morgan 1995, Metaxas and Saunders 2009). Comparing our revised results to those obtained using the original VLT method (Table 2) shows that the older method typically produces higher mortality estimates, particularly when many zero observations are excluded; this is probably a typical effect of failing to account for patchiness in the data.

In general, our estimates belie the conventional wisdom that larval mortality rates are extremely high. It is important to consider that there are multiple sources of mortality in the larval stage, including starvation, predation, and advection away from suitable benthic habitats, precluding settlement during the competency period (Pineda et al. 2009). However, the mortality rates estimated by VLT methods explicitly exclude losses due to advection. Therefore, our results suggest that the non-advective instantaneous mortality in the plankton is low. This is consistent with observations of extremely low rates of predation on larvae in situ at natural densities (Johnson and Shanks 2003, reviewed by Vaughn and Allen 2010). Mortality from starvation and physiological stress may have been low due to the high productivity and narrow ranges of temperature and salinity in the upwelling regime (Botsford et al. 2006, Vander Woude et al. 2006, Wilkerson et al. 2006). Although our mortality estimates do not include advective losses, that component of mortality also increasingly appears to be lower than previously assumed. Mounting evidence has revealed the

effectiveness of larval behaviors in retaining larvae near adult populations or enabling migrations between adult habitats and larval nursery areas in dynamic upwelling regimes (Morgan et al. 2009*a*, *b*, *c*, Shanks and Shearman 2009, Morgan and Fisher 2010, Drake et al. 2013, Miller and Morgan 2013*a*, *b*, Nickols et al. 2013, Fisher et al. 2014, Morgan 2014) as well as in other marine systems (Swearer et al. 2002, Queiroga and Banton 2005, Cowen and Sponaugle 2009). Hopefully, methodological advances and finer-scale examinations of larval dynamics in the plankton will enable better resolution of the different factors causing mortality in the planktonic stage.

Revised estimates of larval mortality rates have important consequences for our understanding of marine population connectivity. Cowen et al. (2000) demonstrated the importance of using accurate mortality rates in Lagrangian simulations of larval dispersal using ocean circulation models: higher mortality rates drastically decrease connectivity rates among habitat patches. Those model-derived connectivity probabilities are used to elucidate patterns of gene flow and vicariance (e.g., Baums et al. 2006) and population and community dynamics (e.g., Berkley et al. 2010, White et al. 2010), and they are increasingly used to inform the design and analysis of marine protected areas (e.g., Rassweiler et al. 2012, White et al. 2013). To date, larval mortality remains a huge uncertainty in those models (Pineda et al. 2009), and modelers typically rely on the original estimates of mortality from Rumrill (1990) for parameterization (Vaughn and Allen 2010). Our results provide an updated and refined set of estimates for this purpose.

Aksnes and Ohman (1996) validated their original VLT method using individual-based simulations of a larval population. We did not attempt to do this, as it is not straightforward to represent the complex oceanographic processes that produce patchy distributions of larvae (although we did check our method against randomly simulated "dummy" data; Appendix B). Recent results from numerical ocean circulation models produce spatially patchy distributions of larvae that exhibit signatures of eddy circulation and other stochastic processes (Siegel et al. 2008), but these models do not typically resolve spatial patterns at the sub-kilometer scales relevant to the types of larval sampling used in this paper. However, a hypothetical circulation model that resolves meter-scale forces over the inner shelf could be used to validate our approach. In the meantime, we rely on two observations: the negative binomial distribution is (1) extremely flexible for representing patchiness from any number of processes and (2) has previously been found to fit plankton distribution data relatively well (Young et al. 2009). McGurk (1986) suggested that the spatial patchiness of larvae would itself affect the larval mortality rate, because predators would feed more efficiently on larger aggregations of larval prey; he showed a positive correlation between the mortality of fish larvae and their estimated patchiness. We estimated similar levels of patchiness for all of the species in our data set, so we did not attempt a similar comparison.

Our analysis has provided low estimates of larval mortality for a diverse range of intertidal and subtidal crustaceans in a highly advective upwelling system, providing a conservative estimate of larval mortality in other types of systems. We recommend applying our approach to future studies of larval mortality when possible to begin gathering more reliable estimates for diverse taxa and systems. Our approach is best suited to crustaceans and other species with well-defined developmental stages. However, with some adjustment, the approach could also apply to fishes, provided that larval ages are determined from daily otolith annuli as is commonly done (Hewitt and Methot 1982, McGurk 1986). We anticipate that this method will provide a great improvement over the limited estimates of a key demographic rate for marine organisms to inform future models of population dynamics and the evolution of life histories in the sea.

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Supplemental Material

Ecological Archives

Appendices A and B and a Supplement are available online: http://dx.doi.org/10.1890/13-2248.1.sm