Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation

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Temperature controls the rate of fundamental biochemical processes and thereby regulates organismal attributes including development rate and survival. The increase in metabolic rate with temperature explains substantial among-species variation in life-history traits, population dynamics, and ecosystem processes. Temperature can also cause variability in metabolic rate within species. Here, we compare the effect of temperature on a key component of marine life cycles among a geographically and taxonomically diverse group of marine fish and invertebrates. Although innumerable lab studies document the negative effect of temperature on larval development time, little is known about the generality versus taxon-dependence of this relationship. We present a unified, parameterized model for the temperature dependence of larval development in marine animals. Because the duration of the larval period is known to influence larval dispersal distance and survival, changes in ocean temperature could have a direct and predictable influence on population connectivity, community structure, and regional-to-global scale patterns of biodiversity.

metabolic scaling | population connectivity | temperature dependence | larval development | survival

Through a general effect on metabolic rate, variation in environmental temperature can influence population, species, and community-level processes (1–3). Recently, evidence for a universal temperature dependence has linked individual metabolism to community-wide productivity, which in turn leads to predictable rates of population growth, carbon flux, and patterns of regional diversity (4–7). Although less appreciated in this context, the universal temperature dependence of metabolism implies an inverse relationship between temperature and life-stage duration (8). For marine animals whose offspring develop in the water column, the duration of the larval life stage determines the length of time that larvae are subject to movement by currents and exposed to sources of mortality. Therefore, a general and quantitative influence of temperature on larval duration potentially implies a mechanistic link between ocean temperature and the biogeographic patterns mediated by the ecological processes of larval dispersal and survival.

Two aspects of the influence of temperature on larval duration are well documented. First, Thorson's rule describes the latitudinal gradient of a decreasing proportion of marine species with planktonic larval development toward the poles (9, 10). Second, temperature is known to cause among-species variation in larval development and duration (10, 11). Studies in this vein have emphasized between-species comparisons without accounting for within-species relationships between temperature and planktonic larval duration (*PLD*); therefore, these studies report strong relationships only within narrower taxonomic groupings. Numerous other studies have documented the temperature dependence of the larval development period within species. Typically this relationship has been described as exponential (e.g., ref. 12) with species-specific parameter values. Therefore, the generality of the temperature-dependence of larval duration remains untested. If general for a wide variety of animals, a quantitative model of the effect of temperature on planktonic larval duration could enhance hypotheses and existing models to evaluate the ecological and evolutionary consequences of temperature change in the ocean.

We tested the generality of the temperature-dependence of planktonic larval duration for 72 species of marine animals [see supporting information (SI) Tables 3 and 4]. We synthesized the effect of temperature on *PLD* by comparing results from 62 laboratory experiments in which vertebrate and invertebrate larvae were reared at multiple, nonlethal temperatures (*SI Text* 1 and SI Table 4). We used a multilevel model to estimate parameter values that describe the influence of temperature on development of marine larvae (*SI Appendix*) (13). We then used our results to formulate models of the effect of temperature on dispersal and survival.

Results

The quantitative relationship between planktonic larval duration and temperature is highly predictable across taxa, latitudes, and oceans (Figs. 1 and 2). Using Akaike Information Criteria (AIC) for model selection, we determined that an exponential model quadratic in temperature on a log–log scale, hereafter called the exponential-quadratic model (methods: Eq. **2**), best describes the general temperature dependence of *PLD* within species (SI Table 5 and *SI Appendix*).

An analysis of species-level (level-2) residuals using caterpillar plots (14) suggests that a species-specific model with random intercepts but constant linear and quadratic coefficients fits nearly all species under consideration (Fig. 1 and *SI Appendix*). However, a few species deviate significantly from this overall pattern (Fig. 1*A* and *SI Appendix*). We identified these species by constructing 95% confidence intervals for species-level residuals of the model parameters (Fig. 1). Sequential removal of the most deviant species reveals that only three species (*Limulus polyphemus*, *Laqueus californianus*, and *Callianassa tyrrhena*, Fig.

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Abbreviations: *PLD*, planktonic larval duration; UTD, universal temperature dependence.

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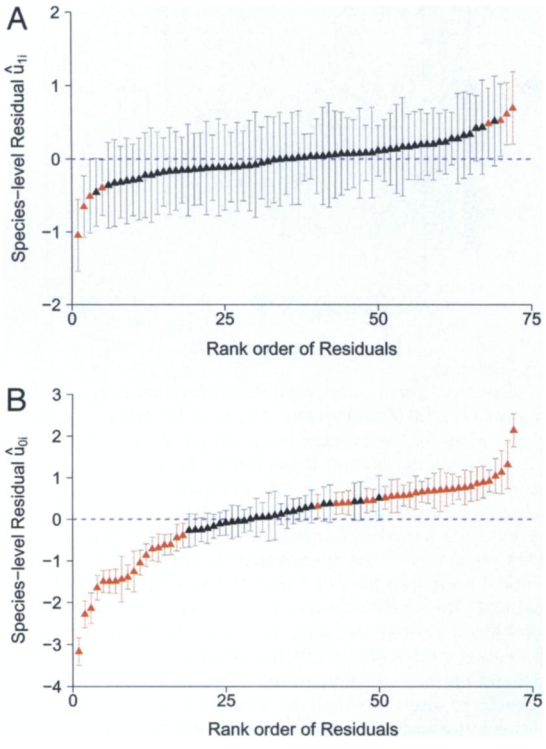

Fig. 1. Caterpillar plots comparing ranked species-level residuals (random effects) for 72 species along with 95% confidence intervals, for two of the three level-1 parameters. Confidence intervals that do not intersect zero identify species whose species-specific value for that parameter is significantly different from the corresponding population-averaged value. The caterpillar plot graphically identifies those species poorly represented by the population-averaged model (see *SI Appendix*). (*A*) Predictions and 95% confidence intervals (black triangles and gray error bars) for the random effect component (u_{1i}) of the linear scaling parameter β_{1i} for each species (Eq. **15**). Confidence intervals do not include 0 for seven species (red points): *L. polyphemus*, *C. tyrrhena*, *H. americanus*, *G. morhua*, *S. spirorbis*, *S. balanoides*, and *L. californianus*. After removing the three most-deviant outliers, *L. polyphemus*, *L. californianus*, and *C. tyrrhena*, there is no longer a need for random effects for the linear and quadratic scaling parameters. (*B*) Caterpillar plot for species-level residuals u_{0i}. Because the majority (46 of 72) of the confidence intervals fail to include 0, we conclude that the species-specific intercept parameters β_{0i} are significantly different from the population-averaged value β_0 for most species. No adjustments for multiple testing were made.

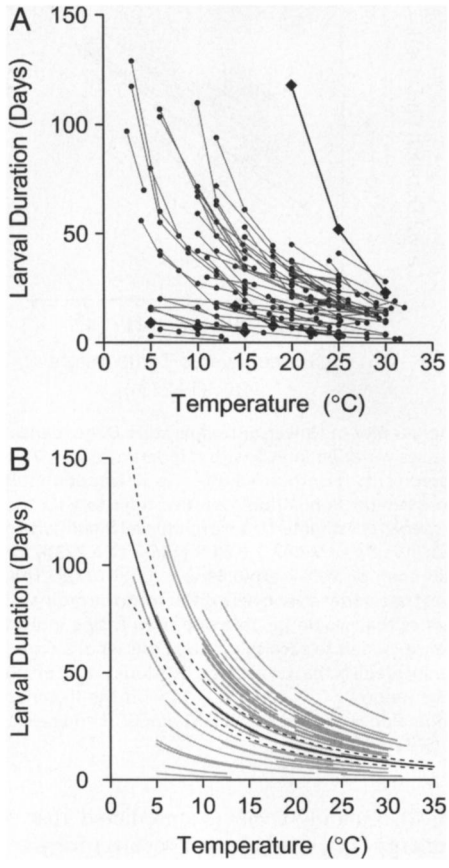

Fig. 2. The relationship between water temperature and PLD based on results from published experimental laboratory studies on the effect of temperature on larval duration for 72 species (six phyla: 6 fish, 66 invertebrates; SI Tables 3 and 4). (*A*) Mean recorded larval duration at each temperature for each species; two to six data points per species connected by gray lines. Subsequent analyses identified three outliers (black diamonds). (*B*) Population-averaged (black) and species-specific (gray) trajectories obtained from a multilevel exponential model quadratic in temperature on a log–log scale with random intercepts displayed here on an arithmetic scale. Estimated population-averaged curve: $\ln(PLD) = 3.17 - 1.34 \times \ln(T/T_c) - 0.28 \times (\ln(T/T_c))^2$, which yields the plotted estimated geometric mean curve: $PLD = \exp(3.17) \times (T/T_c)^{(-1.40-0.27\times\ln(T/Tc))}$, $T_c = 15°C$ (*SI Appendix*). The parameter estimates $\beta_1 = -1.34$ and $\beta_2 = -0.28$ adequately describe 69 species, whereas β_0 is highly variable among species (see *SI Text* for model application). Shown here is the population-averaged trajectory for *PLD* about which individual species-level trajectories are assumed to vary randomly. $\beta_0 = 3.17$ is interpretable as the value of $\ln(PLD)$ at 15°C. Three outliers were excluded in estimating the model (data not shown); dashed lines represent the 95% confidence band for the population-averaged trajectory.

2*A*) are driving the need for random linear and quadratic terms in the log–linear formulation of the model. When these three species are removed from the analysis, a multilevel model with only random intercepts adequately fits the remaining 69 species. Therefore, we present a population-averaged model for a data set that excludes the three outliers (Fig. 2*B*).

We find that *PLD* shows essentially the same relationship with temperature across species (Fig. 1*A*) and differs only in how the curve is scaled (as determined by the factor β_0 in Eq. **2**; Fig. 1*B*). Individual intercept values (β_{0i}) are highly species-specific and most are not well represented by the population-averaged estimate (Figs. 1*B* and 2*B*). Thus, most of the variation among species is with respect to the magnitude of the larval duration at a given temperature but not its relationship to changing temperature.

The nearly uniform temperature sensitivity of larval-development time is consistent with a model derived from first principles of physics and biology (2, 5) (Fig. 3 and SI Fig. 7). Gillooly *et al.* (5) described the universal temperature dependence (UTD) of biological processes, a mechanistic theory that links whole-organism metabolic rates to the effects of temperature on biochemical processes. Although the UTD model was not the best fit of the models we tested (SI Table 5), the functional forms of the mechanistic UTD model (Eq. **3**) and the purely descriptive exponential–quadratic model (Eq. **2**) are similar over most of the temperature range (SI Fig. 8). The primary difference is that the exponential model predicts a steeper slope to the temperature dependence below ≈7°C. This similarity suggests that the mechanistic basis of the UTD model may be relevant to the temperature dependence of *PLD*. Another important difference between the two models is their treatment of larval mass: the UTD model assumes mass-normalized development durations (8), whereas the exponential–quadratic model (Eq. **2**) does not. Although sufficient larval mass data were not available for this analysis, the omission of mass could explain why Eq. **2** is a better fit for these data.

The within-species temperature dependence of *PLD* matches the predicted effect of temperature based on among-species

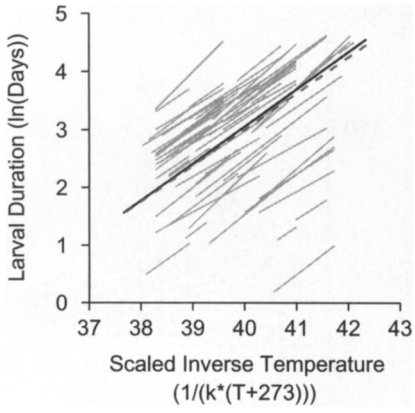

Fig. 3. Arrhenius plot of Universal Temperature Dependence model (Eq. 3) for within-species variation in PLD with temperature (n = 72). Temperature (°C) is expressed as its reciprocal adjusted to Kelvin and multiplied by the Boltzmann constant (k). Population-averaged trajectory for the temperature effect within species as estimated from a multilevel model with random slopes and intercepts: $\ln(PLD) = -22.47 + 0.64 \times (1/(k \times (T + 273)))$ for temperature (T) in °C (solid line), or $PLD \propto \exp(0.64/(k \times (T + 273)))$. The model-based empirical Bayes trajectories shown here differ from the ordinary least-squares-fitted trajectories that would be obtained from fitting individual temperature-dependence models to each species one species at a time (*SI Appendix*). Metabolic theory predicts that on average the slope is 0.62 eV (5) (dashed line) and within the range 0.60–0.70 eV (2). As with the linearized power law model, a random slopes and intercepts UTD model is required for this data set of 72 species (SI Table 9).

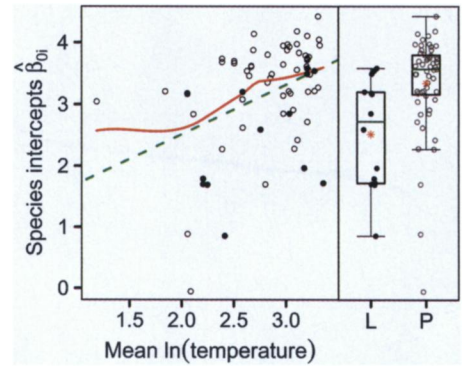

Fig. 4. Effect of climate and developmental mode on the temperature dependence of *PLD* for 69 species. We used mean ln(test temperature) for each species as a proxy for the average temperature in each species' geographic range. The best model among those we examined was one in which the random intercepts model (Eq. 4) was extended to allow ln(*PLD*) to vary additively with mean ln(test temperature) and developmental mode (SI Table 6). In the multilevel modeling framework, these two species-level variables are considered predictors of the species-specific intercept, β_{0i}. In the centered level-1 model presented here (SI Table 7), this intercept is interpretable as ln(*PLD*) at 15°C. The predicted intercepts from a random intercepts multilevel model (Eq. 4) are plotted here against mean ln(test temperature) (*Left*) and developmental mode (*Right*). (*Left*) The lowess (solid curve) and linear trend (dashed line) suggest that larvae tested at colder temperatures tend to have smaller predicted intercepts than do larvae tested at warmer temperatures. (*Right*) Schematic boxplots, following standard conventions for such graphs, of predicted intercepts for each developmental mode are displayed, with means indicated by asterisks. Lecithotrophs (L, filled circles) tend to have smaller predicted intercepts than do planktrophs (P, open circles).

analyses (5, 8). Gillooly *et al.* (5) predicted that the average activation energy (i.e., temperature scaling) for metabolic processes in ectotherms is ≈0.62 eV, which matches our estimate for developing larvae that used the UTD model (95% CI: 0.59–0.69, Fig. 3 and SI Fig. 7). To date, the UTD hypothesis has generally been tested by making among-species comparisons of mass-normalized resting metabolic rates (5, 15). In contrast, our estimate of the temperature sensitivity of *PLD* focuses on within-species temperature dependence. This similarity between the within- and among-species patterns (Fig. 3 and SI Fig. 7) suggests that the effect of temperature on larval development is universal and not species-specific. Our result is consistent with the only other test of this hypothesis (16).

In colder water, increased temperature dependence and generally longer development times (Fig. 2) may affect the evolution of molecular processes and life history traits. Because high cumulative mortality rates are associated with very long larval duration, there may be selection to reduce planktonic larval duration in animals that evolve in cold climates (17). We tested whether home-range temperature could explain variation in *PLD* among species by adding a species-level regional temperature variable to the multilevel model (Fig. 4; Eq. 7). The addition of this variable significantly improved the ability of the model to predict species-specific *PLD* (SI Table 6) and explains 17% of the variation in intercepts among species (*SI Text*). Species from colder climates tend to have shorter *PLD*s (lower values of β_{0i}) compared with species from warmer regions (Fig. 4). Adding a variable for developmental mode (lecithotrophic vs. planktotrophic) to the model increases the explained variance in intercepts to 27%; planktotrophs tend to have longer *PLD*s than lecithotrophs (Fig. 4).

Discussion

Our results demonstrate a strong effect of temperature on planktonic larval duration that is quantitatively constant across nearly all species tested. A single, parameterized model describes the temperature dependence of the planktonic larval period for a diverse group of species from six phyla over a range of body sizes and habitats. A general temperature dependence of larval duration implies common and predictable effects of ocean temperature on larval dispersal distance and survival.

The universal form of the temperature dependence emerges despite enormous differences in larval size and other life-history traits among species. Conceptually, the remaining variation in PLD among species can be thought of as partitioning into three categories: (*i*) variation in *PLD* among species at any particular temperature (the intercept parameter β_{0i} in Eq. 4; Figs. 1*B* and 4), (*ii*) variation among species in the scaling effect of temperature (parameters β_{1i} and β_{2i} in Eq. 4; *SI Appendix*), and (*iii*) scatter of measured *PLD* around the individual regression lines because of measurement error or other unmeasured variation (*SI Text*). Variation among species in *PLD* at any given temperature (variation type 1), as observed in Figs. 1 and 2, could be due to life-history traits such as development mode, larval size at hatching or competency, or assimilation efficiency. For example, lecithotrophic (nonfeeding) larvae tend to be larger and generally have shorter *PLD*s than planktotrophic (feeding) larvae (18) (Fig. 4). There are contrasting predictions for how larval size affects planktonic duration. Large eggs and larvae can result from increased parental investment before release, allowing for shorter planktonic periods (19–21). Alternatively, metabolic ecological theory predicts that development time and body size should be positively correlated such that species with larger larvae require longer larval durations (2, 8). Metabolic theory might accommodate this apparent contradiction. Part of the solution may lie in appropriately separating the disparate effects of variation in larval size at hatching from larval size at competency. In addition, lecithotrophs may have higher food quality than planktotrophs, or may be more efficient at assimilating energy. Food quality and assimilation efficiency are held constant in the general metabolic scaling model (8)

but may, in fact, vary systematically among lecithotrophs and planktotrophs.

We observed very little variation among species in the scaling effect of temperature (type 2 variance above). Residual analysis suggests that a single model fits 69 of 72 species (Fig. 2*A*; and see *SI Appendix*). We suggest three hypotheses for the species with unique temperature dependence: (*i*) unique evolutionary history, (*ii*) unique selective environments, or (*iii*) metabolic cold adaptation. Regarding hypothesis *i*, two of the species are the sole representatives of their taxonomic order in this data set (the brachiopod *L. californianus* and the horseshoe crab *L. polyphemus*). Because the temperature dependence parameter estimates for these species deviate in different directions, their selective environment may have driven their unique temperature dependence (hypothesis *ii*). These hypotheses do not appear to explain the third outlier, the ghost shrimp *C. tyrrhena.* A common species in the warm-temperate eastern Atlantic Ocean, adult *C. tyrrhena* are widely distributed among shallow sand flat environments, and larvae are commonly found in the plankton (22).

Common and predictable temperature control of larval duration may have important implications for many ecological processes and applied issues, including larval dispersal, larval mortality, population connectivity, and recruitment dynamics. For many marine species, the planktonic larval phase is the only life stage in which individuals disperse away from the parental population. Unless oceanographic retention processes or larval behaviors change radically in concert with water temperature (23), an increased development rate effectively shortens the duration of the planktonic larval phase (24). Syntheses of marine dispersal data show that *PLD* is, in turn, positively correlated with larval dispersal distance (25, 26). Although a variety of other factors may also influence realized dispersal distances, including active larval behavior and complex oceanography (27), on average, the more time larvae spend in the planktonic phase, the farther they tend to travel before they settle (25).

To illustrate the potential influence of water temperature on larval dispersal, we used a simple, idealized model of the relationship between *PLD* and passive larval dispersal distance (25). This "null model" of larval dispersal predicts the average dispersal distance of passive larvae along a linear coastline as a function of two-dimensional near-shore current velocity statistics and the larval competency period. Despite its simplicity, predictions of this model correspond well with available empirical measures of marine larval dispersal for currents typical of coastal oceans (25). Our results suggest that water temperature may have a striking effect on the dispersal distance of marine larvae (Fig. 5*A*). Because dispersal distance scales nonlinearly with *PLD*, maximum predicted dispersal distances for larvae in colder water are much greater than those in warmer water. Using the temperature-*PLD* model (Fig. 2*B*), we predict that, all else being equal, mean dispersal distance should vary by over an order of magnitude (20 versus 225 km) as temperature varies from warm tropical conditions (30°C) to cold temperate waters (5°C). More detailed numerical models tailored to the oceanography of particular regions and investigations into how larval behavior and life history traits may modulate the temperature effect on dispersal will lead to further insight on the impacts of changing temperature on connectivity in actual populations.

By controlling larval duration, temperature also mediates the duration of exposure to important sources of larval mortality (10, 28). Larval survival is generally very low, often <1% (28, 29), and decreases exponentially with time when mortality sources such as predation or the likelihood of encountering harsh environmental conditions are relatively constant over the lifespan of a larva (28, 29). Assuming that mortality remains constant with temperature, the exponential loss of larvae with increasing *PLD* (30) should lead to much lower cumulative larval survival rates in cold water than in warmer water (Fig. 5*B*). Some sources

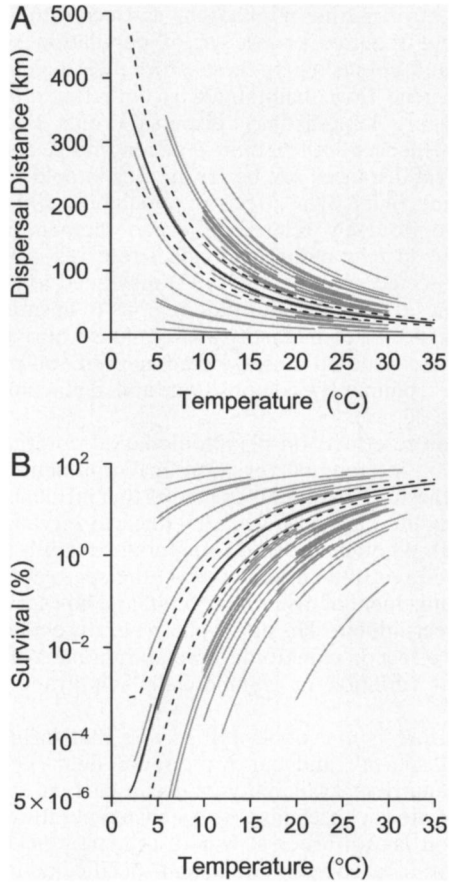

Fig. 5. The predicted effects of ocean temperature on two important ecological and evolutionary parameters: larval dispersal distance (*A*) and larval survival (*B*). The predicted effect on dispersal distance is based on our population-averaged temperature-PLD model (Fig. 1*B*) and on a published model relating PLD to dispersal (25) that used mean current velocity (*U*) = 0 cm/s and with standard deviation (*s*) = 15 cm/s to reflect typical near-shore coastal ocean currents. Species-specific projections are shown (gray lines) to convey the range of variability. Confidence band (95%) is for prediction of mean temperature effect on *PLD*, as in Fig. 1*B*. Predicted effects on cumulative survival assume a constant density- and temperature-independent daily mortality rate of 15% (18).

of mortality, however, such as starvation, oxygen limitation, or predation, are not constant through the larval development period and may change either with larval density, age (31), or temperature (24). Survival of a larval cohort reflects mortality due to both these temperature sensitive factors and to constant factors.

Reduced survival over long larval periods may select for shorter *PLD*s in colder climates than expected based on temperature (Fig. 4) (17). There are two adaptive explanations for shorter than expected cold water *PLD*s: either organisms have adapted life history traits that reduce time spent in the plankton, or molecular processes have evolved to be faster at cold temperatures (32). Within some taxa, life-history traits correlated with reduced *PLD* are more common in cold regions. There is a greater proportion of species with either lecithotrophic or nonplanktonic development in polar regions for some taxa (17, 28, 30, 31), consistent with Thorson's rule (17, 33). Because we observe declining *PLD* with home-range ocean temperature in both lecithotrophs and planktotrophs (Fig. 4), we suggest that lecithotrophy and larval size are two distinct strategies for reducing *PLD* that can occur separately or together.

The general influence of temperature on marine larval dispersal has fundamental implications for the understanding and

management of marine populations and ecosystems. Effective management requires knowledge of population size, genetic diversity, and connectivity; these properties depend on propagule and gene flow maintained by both frequent, medium-range, and rare, long-distance, dispersal events. Because larval duration influences both medium- and long-range dispersal (34), and dispersal distances can be far greater in cold water, population connectivity and effective population size should, in general, be inversely related to ocean temperature. Consequently, the spacing among individual reserves in networks of marine protected areas (MPAs) (35) may need to be far closer in the tropics than in high-latitude regions to ensure connectivity. The degree of connectivity and openness also affects local and landscape-scale processes, including predator–prey interactions, local community composition, and metacommunity dynamics (24, 36, 37).

Temperature effects on planktonic larval duration may also explain some interannual variation in recruitment. It has long been hypothesized that events or factors that influence vital rates during early life-history stages are linked to recruitment variation (24, 38). Whether increased temperature results in increased or decreased recruitment depends on the species' ecology, the spatial arrangement of essential habitat, and how larval duration relates to recruitment. The effect of temperature on recruitment through its effect on planktonic larval duration may help explain recruitment variation in commercially important or invasive species.

Temperature is one of several factors that influence larval duration, dispersal, and survival in the field. For example, changes in nutrient availability or ocean current dynamics are often associated with change in ocean temperature, and their influence on larval dispersal would ultimately need to be accounted for in a species- or system-specific model of larval dispersal and recruitment. Nonetheless, two lines of evidence suggest that the temperature-dependent dispersal model we present here will be a useful tool for dispersal models: (*i*) most laboratory studies that factorially tested the effect of temperature and another environmental variable, such as salinity or food availability, found temperature to have the greatest effect on development time (e.g., ref. 39), and (*ii*) the quantitative model we present here is applicable to nearly all species and so can either serve as a null model for the effects of changing ocean temperature, or can be combined with other quantified effects.

This research provides a context for understanding the effect of environmental temperature on the patterns and processes that influence population dynamics and species diversity. The universal temperature dependence of metabolism previously documented extends to the larval development of ectothermic marine organisms and, hence, to their PLD. Recognition that this temperature effect is common to the most motile life stage of many marine organisms will improve our ability to predict the effects of variation in temperature on demographic and evolutionary processes and to incorporate the effects of temperature into marine species and ecosystem management. Our results suggest that a fundamental constraint of enzyme kinetics can explain a remarkable degree of variation in local, regional, and global patterns and processes and possibly even macroevolutionary processes that take place over geological time scales.

Methods

Data Transformation. The temperature dependence of larval development time typically follows a power law (9, 24). To linearize this relationship and satisfy statistical assumptions, both *PLD* and temperature were ln-transformed (*SI Appendix*, Section II). To aid interpretation and improve numerical stability of the model, we express temperature as $\ln(T/\mathrm{T_c})$, where T is temperature (°C) and $\mathrm{T_c} = 15$°C. This is equivalent to subtracting $\ln(\mathrm{T_c})$ from each temperature observation on a log scale and thus is a form of centering (*SI Appendix*). Statistical results from centered and uncentered models are identical (*SI Appendix*). All statistical analyses were performed in R 2.4.0 (40).

Statistical Analyses. To estimate the relationship between *PLD* and temperature and to compare that effect among species, we used a random-effects (multilevel) model [also called a hierarchical model (13)]. Because observations are nested within species, we treat this as a two-stage sample and fit a random-effects model in which parameters are allowed to vary across species. A multilevel model allowed us to explore intra- and interspecific patterns while respecting the inherent structure of the data. Different models were possible depending on which parameters were allowed to vary across species. We treated model parameters for each species as random effects at the species level, treating these species as random representatives of all species. Because the analysis fits the model to all species at once, we were able to include in the analysis even those species that provided only two data points. See *SI Appendix* for a more detailed description of statistical methods.

Model Selection. We compared ln-transformed versions of three theoretical models of temperature effects on *PLD*. In each model, β_0 is the intercept, and β_1 and β_2 are linear and quadratic scaling parameters, respectively. T = temperature (°C) and $\mathrm{T_c} = 15$°C.

(*i*) A linearized power law model that has traditionally been used to approximate the effect of temperature on *PLD* (41):

$$\ln(PLD) = \beta_0 + \beta_1 \times \ln(T/\mathrm{T_c}); \qquad [1]$$

(*ii*) A linearized power law model that is quadratic in temperature (42). We are calling this the exponential-quadratic model:

$$\ln(PLD) = \beta_0 + \beta_1 \times \ln(T/\mathrm{T_c}) + \beta_2 \times (\ln(T/\mathrm{T_c}))^2; \qquad [2]$$

(*iii*) The UTD equation (5), where k is the Boltzmann constant (8.62×10^{-5} eV $\mathrm{K^{-1}}$), and (T (°C) + 273) is absolute temperature (K):

$$\ln(PLD) = \beta_0 + \beta_1/(k \times (T + 273)). \qquad [3]$$

We assumed that individual observations were realizations from a normal distribution with constant variance σ^2 and that conditional mean was given by the respective theoretical models. Within each model type (Eqs. **1–3**), we first investigated the need for including random effects that allow the intercepts, slopes, and/or quadratic coefficients to vary among species. We used modified likelihood ratio tests, adjusted for boundary conditions, to compare nested models that differed in the number of random effects they contained (SI Table 8 and *SI Appendix*). Having chosen the best random-effects model of each type (e.g., Eq. **1**, **2**, or **3**), the winners were then compared by using Akaike's Information Criterion (AIC) (43) (SI Table 5). We conclude that a multilevel linearized power-law model with a quadratic temperature term (Eq. **2**) best approximates the relationship between temperature and *PLD*. Based on model diagnostics (*SI Appendix*) we identified those species not well described by our chosen model (Figs. 1*A* and 2*A*). With these outliers removed, the model requires random effects only for the intercept (β_{0i}) (Eq. **4**). Our final model written in statistical form, where i indexes species and j indexes observations, is the following:

$$\text{Level 1: } \ln(PLD_{ij}) = \beta_{0i} + \beta_1 \times (\ln(T_{ij}/\mathrm{T_c})) + \beta_2 \times (\ln(T_{ij}/\mathrm{T_c}))^2 + \varepsilon_{ij} \qquad [4]$$

Level 2: $\beta_{0i} = \beta_0 + u_{0i}$; $u_{0i} \sim N(0,\tau^2)$, $\varepsilon_{ij} \sim N(0, \sigma^2)$.

β_1 and β_2 are fixed for all species (Fig. 2*B*). u_{0i} is a random effect that allows β_{0i} to vary across species.

Variation in PLD with Climate. We estimated species' normal temperature range by calculating the mean of the ln(temperatures) tested for each species, and considered this value to be a proxy for the average temperature in the species' normal geographic range. In the majority of studies, test temperatures spanned the range of temperatures experienced by the organism during most of the year.

Projection of Temperature Scaling of Dispersal Distance and Survival. We used a model linking nearshore current velocity and flow patterns to average passive larval dispersal distance. The model projects larval movement in coastal surface currents and accounts for serial correlation in larval trajectories introduced by large turbulent eddies. See Kinlan *et al.* (34) for further discussion of this use of the Siegel *et al.* (25) model. The model presented in Fig. 5*A* is:

$$D_d = 0.695 \times (PLD) \times U + 0.234 \times (PLD) \times s. \quad [5]$$

Terms are the current velocity (U in km/d), its standard deviation (s in km/d), and the temperature-dependent larval duration model presented in Fig. 1*B* (*PLD* in days). Numeric constants in Eq. **5** are fit parameters for dispersal kernels as functions of the flow parameters for near-shore coastal environments (25).

To calculate the survival of a cohort based on temperature effects on PLD, we used the exponential decay model:

$$S_c = S_d^{PLD}. \quad [6]$$

Terms are the percent of a cohort surviving through metamorphosis (S_c), daily survival rate ($S_d = 1 - M_d$, where M_d is the daily mortality rate), and the temperature-dependent larval duration model presented in Fig. 2*B* (*PLD* in days).

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