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.

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 Akaiake 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. 1A 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. 1B and SI Appendix). We then fit a universal temperature dependence model with random intercepts but fixed linear and quadratic coefficients for the remaining species (Fig. 2B).


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

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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). 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. (A) Caterpillar plot for species-level residuals $u_0$ 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. spirobidz, S. banaloides, 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 $u_0$. Because the majority (46 of 72) of the confidence intervals fail to include 0, we conclude that the species-specific intercept parameters $\beta_0$ are significantly different from the population-averaged value $\beta_0$ for most species. No adjustments for multiple testing were made.

2.4) 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. 2B).

We find that PLD shows essentially the same relationship with temperature across species (Fig. 1A) and differs only in how the curve is scaled (as determined by the factor $\beta_0$ in Eq. 2; Fig. 1B). Individual intercept values ($\beta_0$) are highly species-specific and most are not well represented by the population-averaged estimate (Figs. 1B and 2B). 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 $\sim$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...
analyses (5, 8). Gillooly et al. (5) predicted that the average activation energy (i.e., temperature scaling) for metabolic processes in ectotherms is \( \approx 0.62 \) 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 PLDs (lower values of \( \beta_0 \)) 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 PLDs 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 \( \beta_0 \) in Eq. 4; Figs. 1B and 4), (ii) variation among species in the scaling effect of temperature (parameters \( \beta_1 \) and \( \beta_2 \) 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 PLDs 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. 2A; 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. tyrrena. A common species in the warm-temperate eastern Atlantic Ocean, adult C. tyrrena 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 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. 5A). 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. 2B), 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 geography 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. 5B). Some sources 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 PLDs in colder climates than expected based on temperature (Fig. 4) (17). There are two adaptive explanations for shorter than expected cold water PLDs: 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

![Temperature vs. Dispersal Distance](image-url)
management of marine populations and ecosystems. Effective management requires knowledge of population size, genetic diversity, and connectivity; these properties depend on propa-
gule 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, popu-
lation connectivity and effective population size should, in
general, be inversely related to ocean temperature. Conse-
quently, 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 connectiv-
ity. The degree of connectivity and openness also affects local
and landscape-scale processes, including predator–prey interac-
tions, local community composition, and metacommunity dy-
namics (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 vari-
tion (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 ac-
counted 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 tempera-
ture 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 uni-
versal temperature dependence of metabolism previously doc-
umented 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 evolu-
tionary 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 macroevolution-
ary processes that take place over geological time scales.

**Methods**

**Data Transformation.** The temperature dependence of larval de-
velopment 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/Tc), where T is tempera-
ture (°C) and Tc = 15°C. This is equivalent to subtracting ln(Tc)
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 hierar-
chical model (13)]. Because observations are nested within species,
we treat this as a two-stage model 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,
β0 is the intercept, and β1 and β2 are linear and quadratic
parameters, respectively. T = temperature (°C) and Tc = 15°C.

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

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

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

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

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

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

We assumed that individual observations were realizations
from a normal distribution with constant variance $\sigma^2$ 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 condi-
tions, to compare nested models that differed in the number of
random effects they contained (SI Table 8 and SI Appendix).

Holding 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 tem-
perature term (Eq. 2) best approximates the relationship be-
tween temperature and PLD. Based on model diagnostics (SI
Appendix) we identified those species not well described by our
chosen model (Figs. 1A and 2A). With these outliers removed,
the model requires random effects only for the intercept ($\beta_0$)
(Eq. 4). Our final model written in statistical form, where $i$
indexes species and $j$ indexes observations, is the following:

Level 1: $\ln(PLD_{ij}) = \beta_{0i} + \beta_1 \times (\ln(T_{ij}/T_c)) + \beta_2$
$$\times (\ln(T_{ij}/T_c))^2 + e_{ij}$$ $[4]$
Level 2: $\beta_{0i} = \beta_0 + u_{0i} \sim N(0, \tau^2), \quad \varepsilon_{ij} \sim N(0, \sigma^2)$.

$\beta_1$ and $\beta_2$ are fixed for all species (Fig. 2B). $u_{0i}$ is a random effect that allows $\beta_{0i}$ to vary across species.

**Variation in PLD with Climate.** We estimated species’ normal temperature range by calculating the mean of the In(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. 5A 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. 1B (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:

$$S_C = S_0^{PLD}. \quad [6]$$

Terms are the percent of a cohort surviving through metamorphosis ($S_0$), 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. 2B (PLD in days).

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