Relationships between spawning date and larval development time for benthic marine invertebrates: a modeling approach

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ABSTRACT: Marine larval biologists frequently assume that selection to shorten larval duration drives the evolution of reproductive strategies (e.g. egg size). If this assumption is correct, we would also expect larval duration to influence when adults spawn, because adult spawning time can influence the amount of food and temperatures larvae experience, and thus larval duration. Here we develop a simple model to predict development times for marine invertebrates with lecithotrophic larvae as a function of spawning date and sea-surface temperature for the NE Pacific Ocean. We focus on species with non-feeding (lecithotrophic) larvae because the duration of larval life is most influenced by seawater temperature alone. Because there are few empirical data on the relationship between larval development rate and temperature of lecithotrophic species, we used several different functions that represented a range of shapes. Our primary result reveals that the shape of the relationship of development rate to temperature has a pronounced influence on which spawning dates result in the shortest larval duration. For an increasing decelerating relationship, there is a broad range of spawning dates that minimize larval duration. This relationship did overlap with the empirical spawning data for lecithotrophic species in the region. However, for a linear and an increasing accelerating relationship, there is a narrower range of time that results in the shortest larval duration, and for these 2 relationships, observed spawning times did not match as well. Our model also predicted substantial inter-annual variation in development times for all relationships. In addition, we compared spawning times for species with planktotrophic and brooded larval development and found reproductive periods for species with planktotrophic larvae to be similar to those for lecithotrophic larvae, while species with brooded larvae are reproductive over broader periods. Our results suggest that earlier reproductive periods may be favored for reasons independent of development time, potentially including decreased larval predation and increased recruitment success.

KEY WORDS: Development time · Lecithotrophy · Larva · Spawning time · Temperature

INTRODUCTION

The time larvae spend in the plankton is considered to be a major determinant in shaping life history characters (e.g. maternal investment; Vance 1973, Christiansen & Fenchel 1979, Roughgarden 1989, McEdward 1997, review by Havenhand 1995), because the major mortality risks for pelagic larvae, such as preda-

tion, starvation, offshore transport, and exposure to intolerable physical conditions are time-dependent and can be severe. Support for this assumption comes from empirical studies in the field that report high rates of mortality for planktonic larvae (15% d[−1]: Rumrill 1990; 16.4% d[−1]: Lamare & Barker 1999). Based on the apparent importance of larval duration, we can extend a similar argument to predict when adults should

spawn their gametes. If there is strong selection to reduce the duration of time larvae spend in the plankton, then it is reasonable to assume that adults will spawn at times that allow larvae to develop the fastest (Olive 1992).

Most theoretical and empirical work investigating the relationship of adult reproductive strategies and environmental variables have focused on the development of feeding (planktotrophic) larvae (e.g. theoretical: Vance 1973, McEdward 1997; empirical: Morgan 1987, 1990, Starr et al. 1993, Morgan & Christy 1994). For planktotrophic larvae there are 2 primary variables, food and temperature, that strongly influence planktonic larval duration. The interactive effects of both food and temperature make predictions about adult reproductive periods and environmental variables difficult. These confounding effects can be avoided by investigating non-feeding (lecithotrophic) larvae. Lecithotrophic larvae develop from eggs with sufficient energy to complete development and metamorphose without exogenous food intake. With food-dependent development excluded, development time for lecithotrophic larvae is likely influenced by temperature alone.

The general relationship of temperature to developmental rate for non-feeding larvae is a positive correlation whereby increasing temperatures will increase developmental rate, but the specific shape of this relationship is unclear. Most research relating temperature to development in other organisms has measured how temperature influences development time (Gillooly & Dodsom 2000, Gillooly et al. 2002). We found only 1 study for marine invertebrates with lecithotrophic larvae that reported enough data to determine a functional relationship between development time and

temperature; this supported a decreasing decelerating functional relationship of temperature and development time for the ascidian *Ciona savignyi* (Nomaguchi et al. 1997). Additional research has reported reduction in development time at higher temperatures, although the precise relationship is difficult to resolve (e.g. a chiton: Pechenik 1984; asteroids: Hoegh-Guldberg & Pearse 1995). Several studies have also investigated the relationship of developmental rate and temperature during embryogenesis with similar results (e.g. copepods: Corkett 1972; an echinoid: Fujisawa & Shigei 1990). These particular studies have thus far supported a positive curvilinear relationship between development rate and temperature that is, in part, species specific. Variation in the response of development rate to temperature may have significant influence on adult spawning periods (Olive 1992).

In this paper we address 3 questions. (1) When should an adult spawn to minimize larval duration? (2) How does the relationship of development time to temperature influence the predicted dates adults should spawn? To answer these first 2 questions we developed a simple model. (3) Do observed spawning times of lecithotrophic species match the predictions of our model? For this third question, we compared empirical data for reproductive periods to our predicted spawning times. In addition, we compared species with other reproductive strategies (i.e. planktotrophic larvae and brooded larvae) to evaluate general relationships of reproductive periods.

MATERIALS AND METHODS

Our model calculates the development time of offspring (egg to juvenile) as a function of seawater temperature. We have focused on the NW Pacific Ocean in our analysis due to an abundance of sea temperature data and the rich empirical data on benthic marine invertebrate reproduction for this region. We downloaded sea-surface temperature data from the NOAA website (http://www.ndbc.noaa.gov). Our model converted these temperature files into predicted development times for lecithotrophic larvae spawned on different dates; we then compared these predictions with species data.

Seawater temperature data. Temperature files from 1987 to 1998 were downloaded from the NOAA website for Cape Elizabeth, Washington, Buoy #46041. The Cape Elizabeth buoy is located on the outer coast of Washington State near the entrance to Puget Sound (47° 20′ 24″ N, 124° 45′00″ W), and was chosen because its data on sea-surface temperature in this geographic area were the most complete and extensive. Files provided sea-surface temperature (°C) every hour. For
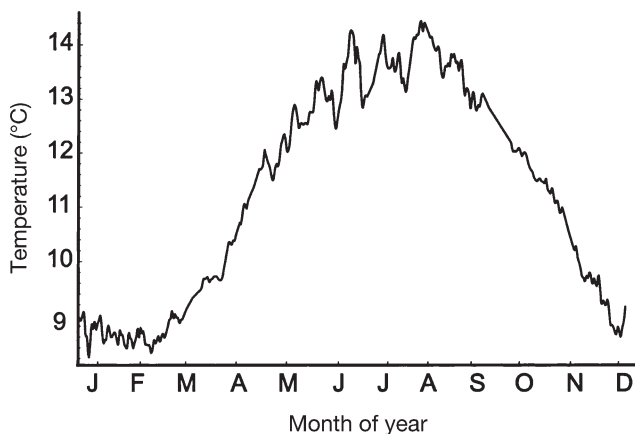

Fig. 1. Mean seawater temperature of outer coast of Washington, USA. Buoy data, average of 10 yr data set (1988–1998). Peak daily seawater temperatures occur between middle-June and September

files with missing temperatures, the missing data were assumed to be the same as on the nearest preceding date. Model output was generated for the individual years 1988, 1990, 1992, 1993 and 1996; these were selected because they had the most complete data sets. In addition, we generated predictions from the average temperature per calendar day from 1988 to 1998 (Fig. 1).

Development time model. We wrote the program for our model in Mathematica 4.0 (Wolfram). Because data were discrete, we fitted a complex function to each data file (1988, 1990, 1992, 1993, 1996, and the 1988 to 1998 average) in order to predict temperatures at any time during the year. In Mathematica 4.0, the 'interpolation function' estimated the mathematical relationship between temperature and date. We used these temperature–date relationships to calculate the development time for larvae spawned on different dates.

In order to calculate larval duration for each day of a calendar year, we specified the relationship of rate of development to temperature. Development rate increases with increasing temperature; however the shape of the relationship between development rate and temperature is unclear. Since this relationship is rarely studied and probably variable among species (see 'Introduction'), we investigated 6 possible relationships (Fig. 2). The relationships represent 2 stages of how a developing organism would respond to temperature: minimal temperature threshold to optimal temperature and optimal temperature, to maximum temperature threshold. Development rate from the minimum temperature to the optimal temperature for development can be linear, decelerating, or accelerating. Beyond this optimal temperature to a maximum tolerable temperature defined in the parameters, development rate can then either be maintained at the maximum development rate or the development rate can decrease linearly to zero. The model incorporated 2 developmental attributes with respect to temperature: optimal temperature for development and minimum time to complete development to metamorphosis. Optimal temperature for development is defined as the temperature at which the development rate of the offspring is maximum (1.0). The optimal temperature for development was tested from 10 to 25°C by 1°C increments. These values were selected to include the observed temperatures for this area as well as additional larger values to analyze their effects. The minimum time to development represents the shortest period of time the offspring will take to develop when the development rate is at a maximum for the entire developmental period. We simulated minimum development time at 10 and 20 d to represent a range of lecithotroph development times consistent with literature data (Strathmann 1987). Development was restric-

ted to a 12°C temperature range—10°C below, and 2°C above the optimal temperature. If experienced temperatures exceeded these values throughout the course of the individual's development, the organism died and a development time of 0 d was recorded.

The model predicted the larval duration for each day of the year. We simulated all the combinations of optimal temperature, minimum development time, growth function, and temperature file for each individual year as well as the mean temperature for all years. The model output displays development time as a function of adult spawning date for a 1 yr cycle. Because we only used temperature data for a year, we were not able to calculate development times for larvae that had not completed development by the end of year. However, adults that spawned during the winter months are expected to have the longest development times and therefore present no problem for estimating the date that minimizes development time.

We have assumed that all development of larvae occurs in the plankton. This is a reasonable assumption for benthic spawning marine invertebrates with pelagic larvae, although some species with lecithotrophic larvae may brood initial embryonic stages (Strathmann 1987). We have also assumed that neither adult ecology (e.g. habitat, food preference) nor egg size would affect predictions on development for lecithotrophic larvae.

Empirically observed spawning times. We compiled a database for spawning dates for marine invertebrates of the NE Pacific Ocean from Strathmann (1987). We required 2 types of information in order to include a species in our analysis: reproductive dates and development mode (i.e. planktonic feeding, planktonic nonfeeding, or brooding) for each species. We eliminated
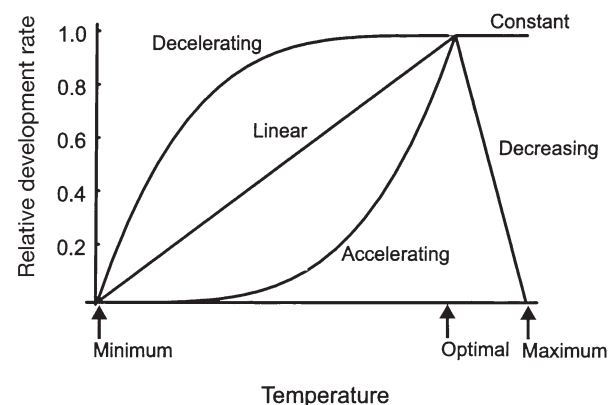

Fig. 2. Development rate functions used to model development time as a function of spawning date for a hypothetical marine invertebrate: accelerating constant; accelerating decreasing; linear constant; linear decreasing; decelerating constant; decelerating decreasing

Table 1. Species data used for assessing reproductive periods in relation to temperature. All data from Strathmann (1987)

Species	Spawning season	Reproductive mode
Annelida		
Nereis pelagica	Summer	Lecithotroph
Nereis procera	July–August	Lecithotroph
Platynereis bicanaliculata	June–September	Lecithotroph
Mesochaetopterus taylori	April–May	Planktotroph
Armandia brevis	May–September	Planktotroph
Harmothoe imbricata	June–August	Planktotroph
Lepidonotus squamatus	Spring–summer	Planktotroph
Sabellaria cementarium	April–June	Planktotroph
Crucigera irregularis	Spring	Planktotroph
Crucigera zygophora	Spring	Planktotroph
Serpula vermicularis	April–September	Planktotroph
Abarenicola pacifica	January–April	Brooder
Lumbrineris zonata	Early summer	Brooder
Axiothella rubrocincta	April–December	Brooder
Micronereis nanaimoensis	Late spring–early summer	Brooder
Sabella media	June–September	Brooder
Polydora (*Boccardia*) *hamata*	Summer	Brooder
Polydora (*Boccardia*) *proboscidea*	Late spring–summer	Brooder
Polydora (*Polydora*) *commensalis*	Spring	Brooder
Pygospio elegans	November–December	Brooder
Protolaeospira eximia	Year-round	Brooder
Paradexiospira vitrea	Year-round	Brooder
Circeis spirillum	Year-round	Brooder
Autolytus sp.	Spring–summer	Brooder
Exogone sp.	November–February	Brooder
Arthropoda		
Pollicipes polymerus	April–October	Planktotroph
Balanus glandula	December–January	Planktotroph
Semibalanus cariosus	Winter–spring	Planktotroph
Acartia clausi	Year-round	Planktotroph
Calanus pacificus	May, September	Planktotroph
Epilabidocera longiedata	April–September	Planktotroph
Pollicipes polymerus	April–October	Brooder
Balanus glandula	February–December	Brooder
Semibalanus cariosus	Winter–spring	Brooder
Euchaeta elongata	June–July	Brooder
Pseudocalanus sp.	Spring–summer	Brooder
Diarthrodes cystoecus	Spring–summer	Brooder
Harpacticus uniremis	December–April	Brooder
Tigriopus californicus	Year-round	Brooder
Tisbe cucumariae	Year-round	Brooder
Brachiopoda		
Terebratulina unguicula	February–March	Brooder
Hemithyris psittacea	December–January	Brooder
Bryozoa		
Bowerbankia gracilis	May–June, September–October	Lecithotroph
Bugula pacifica	February–November	Lecithotroph
Crisia elongata	Spring–summer	Lecithotroph
Hippodiplosia insculpta	Summer–fall	Lecithotroph
Membranipora membranacea	April, September–October	Planktotroph
Cnidaria		
Stomphia didemon	April–May	Lecithotroph
Urticina crassicornis	April–May	Lecithotroph
Urticina lofotensis	October–February	Lecithotroph
Anthopleura elegantissima	September–October	Planktotroph
Anthopleura xanthogrammica	August–October	Planktotroph
Metridium sp.	May–August	Planktotroph
Peachia quinquecapitata	March–November	Planktotroph

Table 1. (continued)

Species	Spawning season	Reproductive mode
Cnidaria		
Cribrinopsis fernaldi	March–May	Brooder
Epiactis lisbethae	Spring–summer	Brooder
Epiactis prolifera	Year-round	Brooder
Echinodermata		
Crossaster papposus	March–April	Lecithotroph
Mediaster aequalis	April–May	Lecithotroph
Solaster dawsoni	April	Lecithotroph
Solaster endeca	April	Lecithotroph
Solaster stimpsoni	April	Lecithotroph
Gorgonocephalus eucnemis	October–February	Lecithotroph
Cucumaria miniata	March–April	Lecithotroph
Cucumaria piperata	March–April	Lecithotroph
Cucumaria fallax	March–May	Lecithotroph
Eupentacta quinquesemita	March–May	Lecithotroph
Pentamera populifera	February–March	Lecithotroph
Psolidium bullatum	March–May	Lecithotroph
Psolus chinitonoides	March–May	Lecithotroph
Molpadia intermedia	November–December	Lecithotroph
Florometra serratissima	June	Lecithotroph
Evasterias troschelii	April–June	Planktotroph
Patiria miniata	May–July	Planktotroph
Pisaster ochraceus	May–June	Planktotroph
Pycnopodia helianthoides	May–June	Planktotroph
Allocentrotus fragilis	Late spring	Planktotroph
Strongylocentrotus droebachiensis	March–April	Planktotroph
Strongylocentrotus franciscanus	April–June	Planktotroph
Strongylocentrotus pallidus	March	Planktotroph
Strongylocentrotus purpuratus	December–April	Planktotroph
Brisaster latifrons	Spring	Planktotroph
Dendraster excentricus	April–July	Planktotroph
Ophiopholis aculeate	April–September	Planktotroph
Ophiura sarsi	March–June	Planktotroph
Parastichopus californicus	May–July	Planktotroph
Leptasterias hexactis	January–March	Brooder
Amphipholis squamata	Year-round	Brooder
Cucumaria lubrica	November–December	Brooder
Cucumaria pseudocurata	December–January	Brooder
Leptosynapta clarki	November–December	Brooder
Mollusca		
Cryptochiton stelleri	April–May	Lecithotroph
Katharina tunicata	June	Lecithotroph
Lepidochitona dentiens	April–May	Lecithotroph
Mopalia ciliata	April–June	Lecithotroph
Mopalia hindsii	February–April	Lecithotroph
Mopalia laevior	March–April	Lecithotroph
Mopalia lignosa	June–July	Lecithotroph
Mopalia muscosa	May–June	Lecithotroph
Tonicella insignis	April	Lecithotroph
Tonicella lineata	April–June	Lecithotroph
Haliotis kamschatkana	April–June	Lecithotroph
Lottia digitalis	Spring–summer	Lecithotroph
Calliostoma ligatum	February–July	Lecithotroph
Mytilus californianus	June–July	Planktotroph
Mytilus edulis	April–May	Planktotroph
Crassostrea gigas	June–September	Planktotroph
Chalmys hastate	Spring	Planktotroph
Podoesmus cepio	June–August	Planktotroph
Clinocardium nattallii	July–August	Planktotroph

Table 1. (continued)

Species	Spawning season	Reproductive mode
Mollusca (continued)		
Tresus capax	March–May	Planktotroph
Mya arenaria	April–July	Planktotroph
Panope abrupta	April–July	Planktotroph
Littorina plena	Spring–summer	Planktotroph
Littorina scutulata	May–September	Planktotroph
Alia gausapata	January–April	Planktotroph
Ilyanassa obsolete	Spring–summer	Planktotroph
Kurtziella plumbea	March–May	Planktotroph
Oenopota levidensis	February–July	Planktotroph
Ophiodermella inermis	October–July	Planktotroph
Petaloconchus compactus	Year-round	Brooder
Hipponix cranioides	Spring–summer	Brooder
Crepidula adunca	Winter–summer	Brooder
Lasaea subviridis	Year-round	Brooder
Transennella tantilla	Year-round	Brooder
Kellia suborbicularis	Summer	Brooder
Mysella tumida	February–May	Brooder
Pseudopythina rugifera	March–April	Brooder
Nemertea		
Micrura alaskensis	May–July	Planktotroph
Phoronida		
Phoronopsis harmeri	April–June	Planktotroph
Phoronis ovalis	Winter	Brooder
Phoronis vancouverensis	March–September	Brooder
Sipuncula		
Golfingia pugettensis	October–February	Lecithotroph
Golfingia vulgaris	December	Lecithotroph
Phascolosoma agassizii	June	Planktotroph
Urochordata		
Distaplia occidentalis	Spring–summer	Brooder
Diplosoma macdonaldi	Summer–fall	Brooder
Corella inflata	Year-round	Brooder

any species for which data were incomplete or ambiguous in any of these 2 criteria. The total data set included a total of 139 species, of which 40 species were planktonic non-feeders (lecithotrophs), 52 were planktonic feeders, and 47 were brooders (Table 1). These species represented a total of 11 phyla.

RESULTS

Predicted spawning times

We report output for 3 temperatures (10, 15 and 20°C), which represent the range of patterns generated for the range of temperatures tested (Fig. 3). Our results were insensitive to the minimum development time, thus only results for 10 d as the minimum development time are given.

The model predictions for an optimal temperature of 10°C suggest that only organisms that spawn from November to early April will produce offspring that survive. Temperatures during the summer months exceed the prescribed maximum thermotolerance, resulting in the death of larvae spawned at this time. Individuals that spawn in the winter months would produce viable larvae, which would need approximately 15 d to develop. The minimum development time is nearly identical (±1 to 2 d) across these spawning times, indicating that reproductive success is equal on these dates. The 6 development-rate functions also have no predicted influence on development time (continuous line in Fig. 3).

When the model was run for the optimal temperature of 15°C, adults could spawn at any time of the year and offspring would survive to metamorphosis. Planktonic development time ranged from 15 to 200 d depending on spawning date. The linear and accelerating functions (Fig. 3) generated similar curves indicating that whether an animal responds to temperature in a linear or accelerating fashion would not influence spawning behavior. Adults that spawned in July/August would have larvae with the shortest time in the plankton. The decelerating
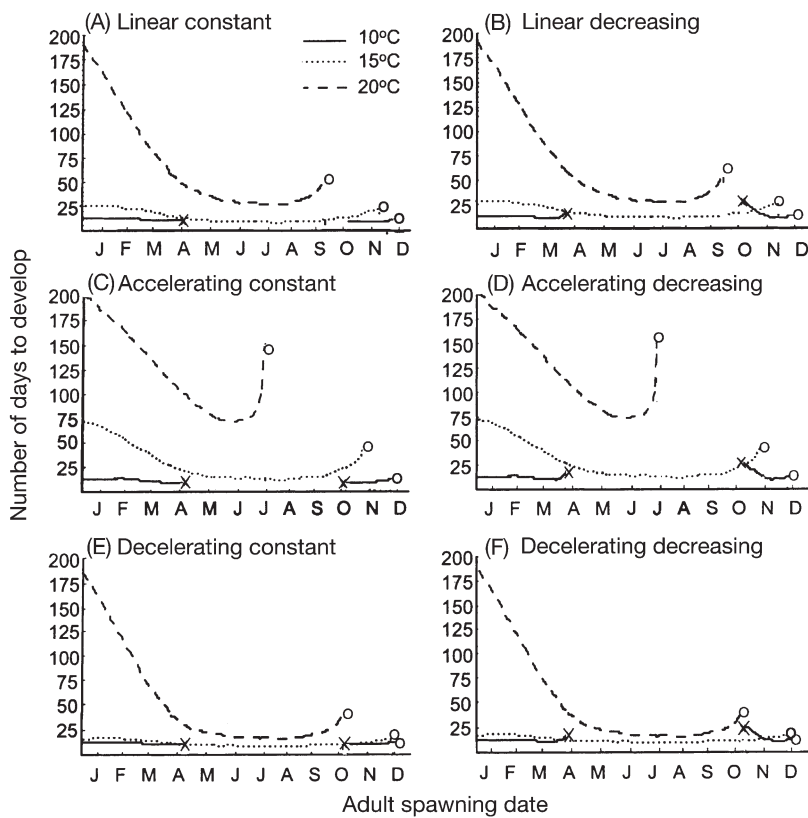
Fig. 3. Predicted development times for spawning dates throughout 1 yr based on mean temperature of 10 yr. The 6 plots correspond to the 6 development rate functions, and each plot shows output for 3 optimal temperatures. Output representing death of larvae when thermotolerance conditions were exceeded (✗). Output extended beyond 1 yr period represented by model (○)

sents the most flexible pattern by allowing for the shortest development time over a broad period of the year (June to early September: Fig. 3E,F).

All the above simulations were run with the mean temperature for the 10 yr data set. We also compared the output from individual years to address how temperature variation between years would affect the predictions of our model. When model simulations were run for temperatures from individual years, we observed that inter-annual temperature variation had a significant effect on predictions (Fig. 4). Temperatures in different years would have dramatic effects on when an adult would spawn to minimize development time. The same date in one year would result in the shortest time for planktonic development (e.g. Fig. 4: 1996, Day 250, mid-September), while in another year it would exceed the thermotolerance, resulting in death of the larvae (e.g. 1990, Day 250, mid-September).

Observed spawning times

Spawning time for marine invertebrate species with lecithotrophic larvae is generally in April to June, corresponding to late spring to early summer

relationship produces a distinctly different pattern. The dates an adult could spawn with reduced development time is extended over a wider time period (cf. Fig. 3A, E). Thus, the decelerating function predicts a potential for an extended spawning season (many months) with similar lengths of planktonic development.

The results of simulations from the model run at 20°C for optimal temperature differed from those for the cooler temperatures. Organisms displaying a linear response to temperature should spawn from July to early August in order to have the shortest development time (35 d, Fig. 3A). Organisms with an accelerating pattern would have a much narrower optimal spawning time (June to early July) and still have a comparatively prolonged development time of 75 d (Fig. 3C,D). As was observed with the 15°C simulations, the decelerating pattern repre-
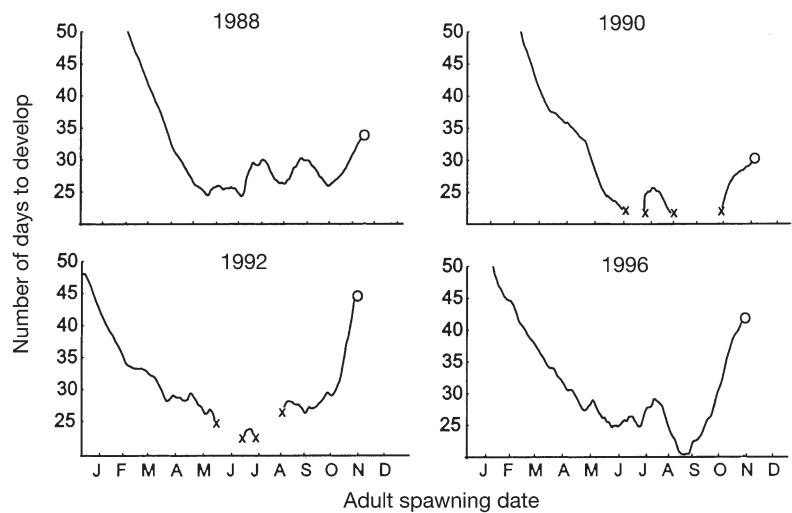

Fig. 4. Predicted development times for spawning dates based on temperature for different years. Simulations ran at optimal temperature of 15°C and minimum development time of 20 d. Symbols as in Fig. 3
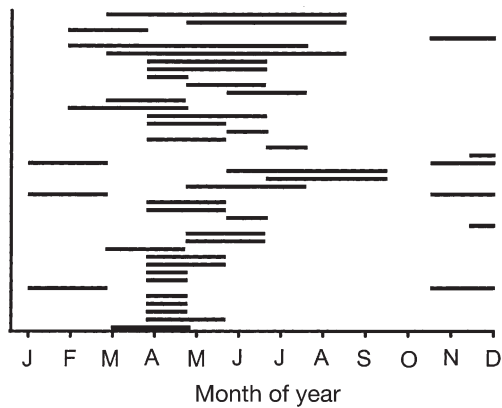
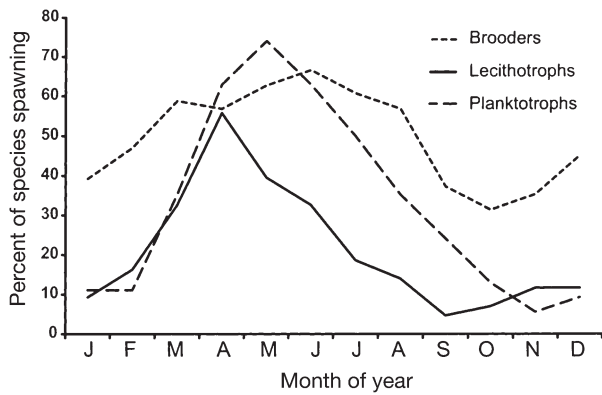Fig. 5. Reproductive seasons for 40 species with lecithotrophic larvae from the NE Pacific Ocean

Fig. 6. Percentage of surveyed species (40 lecithotrophs, 50 planktotrophs, 52 brooders) that are reproductive during each month of any given year

for this geographic area (Figs. 5 & 6). The distribution of spawning times for all animals with planktotrophic and lecithotrophic development is similar, with a peak in the late spring to early summer (Fig. 6). Compiling data across phyla, reproductive periods for both planktotrophs and lecithotrophs would on average begin in April, and would last approximately 1.4 mo longer in planktotrophs (3.8 mo as opposed to 2.4 mo for lecithotrophs). This pattern is distinct from that of brooders who are reproductive throughout the year, with slightly more reproduction from May to August. Most of the invertebrates for which spawning periods were observed belonged to 1 of 3 phyla: Echinodermata, Annelida, or Mollusca. Within-phylum data show how development mode and spawning season are related in more similar organisms (Fig. 7). The trends are similar for each phylum (peak reproduction from March to June), with the exception of lecithotrophic annelids, which spawn

later in the summer months. Again, species that brood their larvae usually have year-round or fall–winter reproductive periods.

DISCUSSION

Our model has shown that the relationship of temperature and development rate for lecithotrophic lar-
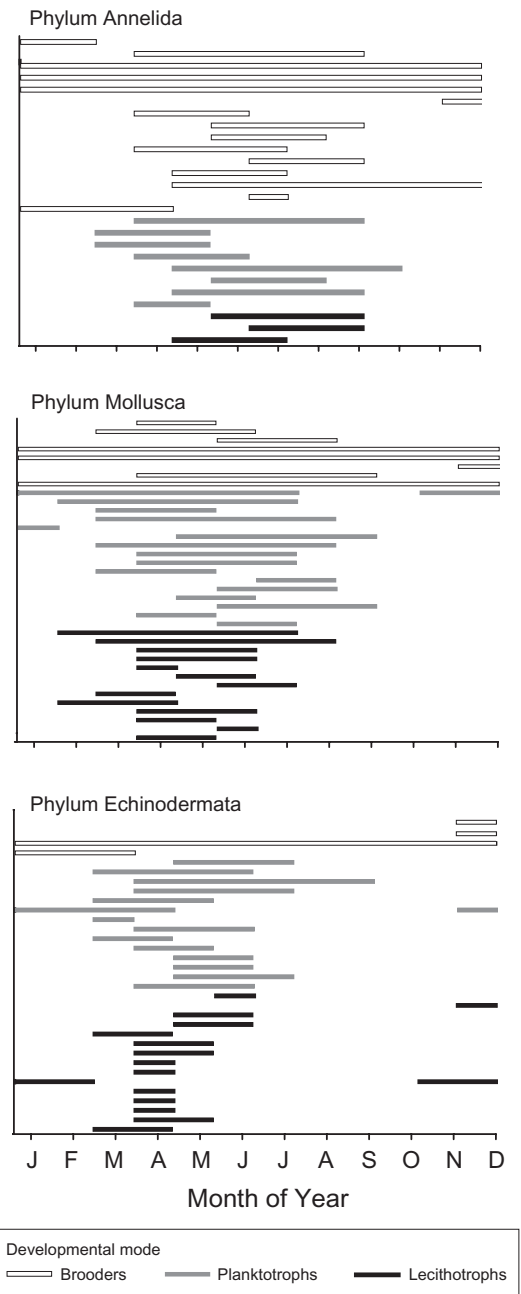

Fig. 7. Reproductive periods for 3 phyla (Annelida, Mollusca, and Echinodermata) with 3 different developmental modes

vae has profound impacts on predictions as to when marine organisms will spawn. The range of dates that results in the shortest offspring development time is variable, and is dependent on the shape of the temperature–development rate relationship. Species with offspring displaying a decelerating relationship would appear to have the 2-fold advantage of (1) highest fitness for offspring due to short development times, and (2) the most flexible spawning time, allowing adults to respond to other environmental factors (e.g. predators, other abiotic conditions). Compared with either the linear or accelerating relationships, the decelerating relationship would be the most flexible relationship for marine invertebrate development.

As stated in the 'Introduction', we know little empirically about the relationship of development time and temperature. Our compiled data set of reproductive periods for marine invertebrates with lecithotrophic larvae shows that the greatest proportion of species are reproductive in April, many months before peak seawater temperatures in the NE Pacific Ocean. Himmelmann (1975) made similar observations, reporting that species with lecithotrophic larvae spawn during the spring phytoplankton bloom, again prior to peak seawater temperatures. Our model supports the observations of Himmelmann (1975), since species with lecithotrophic and planktotrophic larvae have similar reproductive periods. The concordance between these observations could imply that adults with lecithotrophic larvae may at times refrain from spawning in order to reduce the pelagic development time — but why? If adults can assess environmental temperature reasonably accurately (e.g. Fujisawa & Shigei 1990), then we suggest 3 hypotheses to explain this.

Our first hypothesis, derived from the model results, is that species with lecithotrophic larvae have a decelerating developmental rate relationship with temperature. If the decelerating function most accurately represents how development rate is related to temperature for these species, spawning periods prior to peak seawater temperatures would be consistent with selection for minimizing development time. The decelerating function predicts that a broader reproductive period would result in an identical planktonic development time, such that spawning would not have to occur around the peak temperature for the year. Species might then spawn in the earlier portion of this period (i.e. spring) due to other factors that also influence spawning season such as adult feeding, fertilization success, or aspects directly affecting offspring survival, such as predation (Olive 1995).

Our second hypothesis is that spawning at the warmest time of the year is detrimental to the offspring's survival. The general hypothesis of temperature limits to development and associated effects (e.g.

limited reproductive periods, geographic range) was initially proposed by Orton (1920). Empirical data have supported the idea that small changes in temperature can significantly change faunal distributions. A survey of zooplankton and intertidal organisms over 70 yr in the western English Channel has suggested that small increases in the annual mean temperature (0.5°C) have dramatic influences on population structures and species' distribution (Southward et al. 1995). Some data have supported lethal effects of environmental temperature on marine invertebrate development. Work by Chen & Chen (1992) has shown that development at higher temperatures in a planktotrophic species, *Arachnoides placenta*, results in higher mortality in the larval stage. Similarly, Fujisawa (1989) reported limited spawning seasons in many echinoid species dependent on species-specific embryonic thermotolerance. Thus, there may be trade-offs associated with spawning at higher temperatures in order to minimize development time. A 'temperature-limited' explanation for our observations is likely to be of limited applicability (e.g. Thorson 1950, Sewell & Young 1999); additional empirical study would help quantify the generality of such hypothesis. The impacts could be easily assayed empirically by measuring embryonic and larval thermotolerance for the species surveyed to test for effects on survival and juvenile quality (e.g. competitive ability, size-specific predation).

Our third hypothesis to explain the difference between reported and predicted spawning times is that minimizing development time is not of primary importance for marine invertebrate life history strategies. This hypothesis is diametrically opposite to the conclusions derived from models supporting selection to reduce development time in order to increase fitness (e.g. Vance 1973). Although the evidence we present is indirect, if development rate for most species shows a linear or accelerating relationship with increasing temperature, species would spawn at times that would prolong, not reduce, their pelagic development. If this hypothesis is supported by further empirical studies, factors that favor longer development time (such as dispersal or juvenile size of feeding larvae) or that directly influence spawning season (such as adult feeding or intensity of pelagic predation) may exert a strong influence on the life histories of marine benthic invertebrates. For example, depending on the severity of pelagic predation, development time may have little influence on the predictions of models of marine invertebrate life histories (McEdward 1997). Zooplankton density is lowest during the spring phytoplankton bloom, presumably due to absence of food (Legendre & Demers 1984). This reduction in zooplankton density would probably lower predation on larvae and possibly result in higher overall offspring survival despite

prolonged pelagic development. Similarly, earlier reproduction might permit a larger probability of successful benthic recruitment due to reduced competition for space (Connell 1985). Lecithotrophic larvae will typically have much shorter pelagic periods than planktotrophic larvae, and thus recruit to the benthos at an earlier date. Thus, timing of reproduction as a function of predation or benthic recruitment, and not of temperature, may be a more significant selection pressure for individual fitness and ultimately life history evolution (Himmelmann 1975, Starr et al. 1990, Morgan & Christy 1994). This particular predation hypothesis seems to be indirectly supported by the almost year-round reproductive periods of brooders.

The above hypotheses all assume adaptive evolution of reproductive periods for the marine invertebrates surveyed (Olive 1992). One nonadaptive explanation for the observed reproductive times could be the influence of shared phylogenetic history. Lecithotrophic and brooding life history strategies are commonly assumed to be unidirectionally derived from planktotrophic life histories (Strathmann 1985, Hart et al. 1997). Thus, similarities in reproductive periods for planktotrophs and lecithotrophs may simply be the result of shared evolutionary history, unrelated to current selection pressures (Harvey & Pagel 1991, Miles & Dunham 1993). The impact of shared history is difficult to evaluate without better phylogenies, but we do not feel it to be a reasonable global explanation for our data. Eckelbarger & Watling (1995) have discussed supported cases where phylogenetic relationships have had a discernible impact on spawning periods of deep-sea species. In the data we examined, brooders displayed dramatic differences in reproductive periods from either of the other 2 development modes, suggesting that the independent evolution of reproductive periods is labile. We know of no indication that brooding species have a consistently wider divergence from planktotrophic ancestors that allows more time for change in reproductive periods than lecithotrophic species. Consequently, we argue that the observed reproductive periods of lecithotrophic species are evolutionarily maintained by current selective pressures, and are not the result of their shared history with planktotrophic ancestors.

Our model creates testable hypotheses indicating that marine invertebrates spawn at times of the year that minimize development time of their offspring. The results of our model show that the interrelationship of temperature and development rate has dramatic effects on the development time of planktonic larvae and the periods at which spawning adults could achieve the shortest development time. There has been little work addressing how larval development rates are influenced by temperature. Relationships are potentially similar for both lecithotrophic and planktotrophic species (Hoegh-Guldberg & Pearse 1995) and we observed reproductive periods to be similar for species with both larval types (Figs. 6 & 7). Whether larvae from different populations experiencing different temperature dynamics can compensate for temperature influences on development is unclear. Intraspecific geographic or seasonal variation in developmental temperature responses for invertebrate larvae has been reported (Stephens 1972, Johnson & Babcock 1994, Palmer 1994, Bingham et al. 1997, Nomaguchi et al. 1997). Conversely, larvae of other species have been shown not to regulate their ontogenetic timing to compensate for cooler temperatures by quicker development. This has been particularly well-documented for Antarctic echinoderm larvae (Bosch et al. 1987, Pearse et al. 1991, Pearse 1994). The mechanisms, if any, for the evolution of norms for temperature–development rate reactions are unclear, but the evolution of these mechanisms and their effect on the relationship of temperature and development time may have significant influences on adult spawning behavior and the evolution of life histories.

Understanding the interrelationship of environmental temperature and reproductive periods for marine invertebrates is imperative for predicting organismal responses to global warming. As detailed by Bhaud et al. (1995), global warming influences not only the mean annual temperature, but also average summer maxim and winter minima and interannual variations. One suggestion arising from our model is that the shape of the development rate function can have dramatic influences on optimal as well as permissive periods for successful reproduction. Therefore, an empirical understanding of the relationship of development and temperature could help the biological interpretation of changes in species distributions as a function of global warming.

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