Thermal time explains size-at-age variation in molluscs

Franziska Broell[1,*], J. Scott P. McCain[1,2], Christopher T. Taggart[1]

[1]**Department of Oceanography, Dalhousie University, Halifax, NS B3H 4R2, Canada**
[2]**Department of Biology, Dalhousie University, Halifax, NS B3H 4R2, Canada**

ABSTRACT: Temperature strongly influences growth and development in most ectotherms. The thermal integral, or growing degree day (*GDD*) metric (°C d), has been widely used to characterize plant, insect, and more recently fish growth and development variation. However, the *GDD* has not been widely examined among molluscan species. We examined 42 different sets of data drawn from the literature representing temperature-dependent growth and development variation among a variety of bivalve, cephalopod and gastropod species. We demonstrate that thermal time (*GDD*) is better able to explain temperature-dependent variation in size-at-age and size-at-stage compared to calendar time (d) and conclude that thermal time is the appropriate metric to use when assessing variation in growth and development among molluscs. We also address how thermal time may lead to more accurate comparisons among populations and how it may help diagnose other factors influencing growth variation.

KEY WORDS: Growing degree day · Thermal time · Molluscs · Bivalves · Cephalopods · Gastropods · Growth · Development

INTRODUCTION

Ambient temperature is the primary variable controlling metabolic rate, energy expenditure, most physiological processes, and thus growth and development among ectotherms (Atkinson 1993, van der Have & de Jong 1996). Generally, an increase in ambient temperature results in increased enzymatic reaction rates and therefore increased metabolic rate. Enzymatic reaction rates increase after a given threshold temperature (T_{Th}) is reached, in a generally linear fashion toward a temperature optimum (T_0), above which the rates decrease toward zero at a given maximum temperature (T_{max}) when enzymes are inactivated or denatured (Bonhomme 2000). The influence of temperature on enzymatic reaction rates among ectotherms is near instantaneous. However, when the temperature experienced by the organism is integrated over time, it can directly translate as a phenotypic expression, such as size-at-age and/or size at developmental stage. Size-at-age is often used to infer growth rate.

To date, most growth models (e.g., von Bertalanffy 1934 and its many variants) rely on calendar time (age) as the predictor variable to explain variation in size-at-age among ectotherms. In doing so, such models disregard the relevant time scale experienced by the organism(s): i.e., physiological time or 'thermal time' (Gilbert et al. 1976). Thermal time has been used effectively as a reliable predictor of growth and development in agricultural research for centuries (Reamur 1735 cited in Bonhomme 2000), in entomological research for decades (McMaster & Wilhem 1997, Bonhomme 2000) and more recently for a variety of fish species at the scale of individuals and populations (Neuheimer & Taggart 2007, Ven-

turelli et al. 2010, Neuheimer & Grønkjær 2012, Chezik et al. 2014a,b). The growing-degree-day (*GDD*,°C d) is representative of thermal time and it is a metric used frequently to describe the timing of biological processes (McMaster & Wilhelm 1997). *GDD* relies on the assumption that if the metabolic rate is a near-linear function of temperature (i.e., from T_{Th} to T_{max}), then size-at-age should be a near-linear function of *GDD*, the time spent at temperature (Bonhomme 2000, Trudgill et al. 2005). Therefore, *GDD* is only applicable when growth is near-linear over developmental stanzas (Bonhomme 2000, Trudgill et al. 2005, Neuheimer & Taggart 2007) that include pre- or post-maturation growth (Dumas et al. 2007, Neuheimer & Taggart 2010).

The nature of *GDD* not only allows a more accurate representation of ectotherm growth, it also allows a single species-specific size-at-age relation (i.e., slope) in thermal time across all normally encountered (T_{Th} to T_{max}) temperatures experienced in the lab or in the wild, as opposed to multiple size-at-age relations in calendar time (several citations above). Additionally, *GDD* allows the determination of thermal constants defined by a marked change in slope trajectory; such as time-at-maturity. Therefore, it can be a powerful tool for population modelling (e.g., Neuheimer & Taggart 2007) and it can be used to diagnose other factors that influence size-at-age, such as food limitation or size-selective fishing (e.g., Venturelli et al. 2010, Neuheimer & Taggart 2007, 2010).

The thermal time concept has been applied to many fish species and it should therefore be applicable to other aquatic ectotherms, including molluscs (Huey & Stevenson 1979). With few exceptions (e.g., Bayne & Worrall 1980, Wood & O'Dor 2000, Hoving et al. 2007, Lv et al. 2009, Seuffert et al. 2012, Filgueira et al. 2015), attempts to explain variation in size-at-age among molluscs have relied on calendar time and have generally overlooked the explanatory power of *GDD*. In this paper, we postulate that if *GDD* is appropriate for explaining size-at-age variation in fish and other ectotherms, it should be appropriate for molluscs. Thus, we postulate that under normally encountered growth conditions, and over the ascending stanzas of the growth curve (typically prior to, or following, maturation), size should scale linearly with *GDD*. We explore this postulate by assessing relationships between size-at-age and *GDD* among 3 classes of molluscs: Bivalvia, Cephalopoda, and Gastropoda. Where possible, we also assess developmental stage-at-age as a function of *GDD*.

MATERIALS AND METHODS

Data

We examined 42 datasets (see data files in Supplement 1 and Table S1 in Supplement 2 at www.int-res.com/articles/suppl/m573p157_supp/) derived from 21 publications in the literature (including graduate theses) that represented 25 mollusc species among the Bivalvia, Cephalopoda and Gastropoda classes. Each dataset represents a unique species and the associated experimental treatment(s) for growth trials under various thermal conditions where size-at-age (n = 37) and/or developmental stage-at-age (n = 5) was reported. In all cases data were extracted from figures, using DataThief (Tummers 2006) and/or WebPlotDigitizer (Rohatgi 2015), and/or tables provided by the authors of the original publication. To minimize digitization error, moments of the distributions (mean and variance) and/or regression models were compared to the information provided in the original publication.

Of the 42 datasets examined, 48% included treatments outside the species-specific optimal thermal range; i.e., temperatures $>T_{Max}$ or $<T_{Th}$. As associated thermal stress may lead to physiological processes that exhibit a negative effect on growth (Trudgill et al. 2005), some temperature treatments were excluded from the analyses if the original publication explicitly stated that growth was reduced due to thermal stress or food limitation etc., or that temperature-related mortality occurred. If there were no such statements and/or there was no evidence in the literature to suggest species-specific decreased growth and/or survival at a given temperature, all temperature treatments were included in the analyses. Detailed descriptions of the exclusion criteria, including the literature used to determine species-specific temperature range (if not provided in the original publication) are provided in Table S1. The goal of our analyses was to determine first how size-at-age or size-at-stage was related to the temperature treatments in calendar time, and second how these same metrics were related to the temperature treatments in thermal time.

Statistical analyses

For each of the 42 datasets we used linear regression to assess variation in size, i.e., length (*L*) or weight (*W*), as a function of calendar time (*t*, d) and as a function of thermal time (*GDD*, °C days) among all

temperature (T,°C) treatments. In each case we report (Table S2 in Supplement 2) the slope (β_1), the intercept (β_0), the corresponding standard error and the adjusted coefficient of determination (r^2). We then assessed differences among temperature treatments using an analysis of covariance (ANCOVA) for calendar time with the interaction terms t and temperature T, and for thermal time with the interaction terms GDD and T.

The ANCOVA assessed differences among slopes of the various temperature treatments with distinct temperature treatments as fixed categorical variables. The assumption of linearity and error distribution of the residuals was examined. The significances of the model terms were assessed using reductions in residual sums of squares via analysis of variance tables involving the sequential addition of model terms beginning with the null model. If the slopes among the various temperature treatments were not different we simplified the model by removing the interaction term and report the resulting coefficients. All statistical analyses were performed in the R statistical environment (R Development Core Team 2015) using a Type I error rate of 5% significance criterion. All R scripts for analyses and graphical presentations are provided online (https://github.com/jspmccain/GDD-Mollusc).

Size measurements

The importance of using L, as opposed to W, when assessing size-at-age relations has been addressed for fish (Neuheimer & Taggart 2007). Similarly to fish, among molluscs GDD is expected to scale linearly with L but not with W, as W is typically a power function of L (e.g., Froese 2006). Therefore, where required, W was transformed to L using species-specific $W \approx aL^b$ relations found in the literature. Where such relations were not available, they were drawn from comparable species of the same genus (e.g., the $W \approx aL^b$ relation for *Haliotis varia* was used for *H. midae*). For one species (*Bulinus nyassanus*) we were unable to

find a reliable $W \approx aL^b$ relation and weight was not transformed. The original data and all transformations and corresponding literature are provided in Supplement 1 and Table S1.

RESULTS

For most mollusc species differences in size-at-age among different temperature growth trials (Fig. 1) converged to one linear function of thermal time (GDD) in contrast to the several different tem-
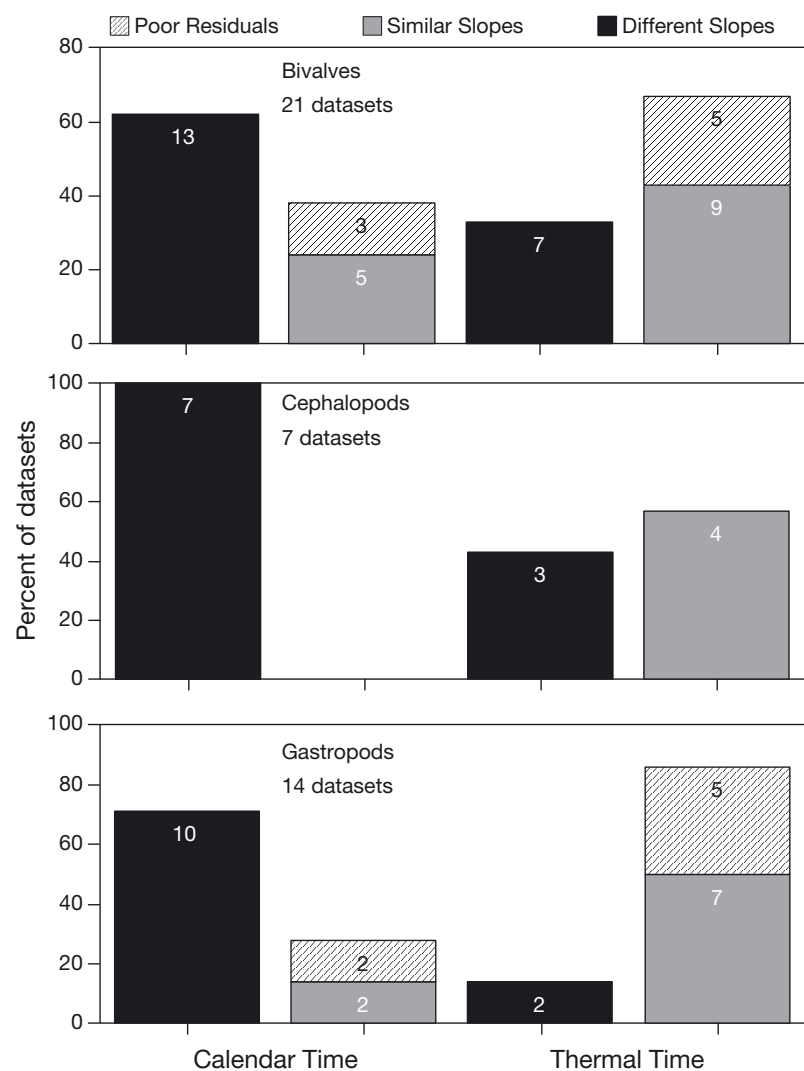

Fig. 1. Comparison of use of calendar time (d) and thermal time (growing degree day, GDD) to explain temperature-dependent variation in size-at-age and size-at-stage in molluscs: results of linear regression analyses across temperature treatments of bivalve (top panel), cephalopod (middle) and gastropod (bottom panel) datasets (total n = 42), showing proportion (%) of regression models with different slopes (black), similar slopes (dark grey), and similar slopes with poor residuals (hatching)

perature-dependent functions of calendar time (d). For bivalves, 38% of the trials (n = 21) had similar slopes in calendar time. In contrast, 67% collapsed to a similar slope in thermal time, although 24% of these exhibited poor residuals. For cephalopods (n = 7), 57% of the trials converged to similar slopes in thermal time and none had similar slopes in calendar time. For gastropods (n = 14), only 28% had similar slopes in calendar time while 86% converged to similar slopes in thermal time, although 36% of these exhibited poor residuals. Across all phyla, poor residuals (n = 10) were attributed to the presence of an apparent thermal constant (n = 6), or an apparent suboptimal thermal condition (n = 1) or apparent mortality (n = 1) or the size-at-age metric used (n = 2).

Below we highlight a subset of the species examined and they represent at least one example for each phylogenetic class. Subsets were chosen to demonstrate the power of *GDD* in explaining size-at-age in adult (*Haliotis midae*, *Sepia officinalis*, *Octopus bimaculoides*, *Crepidula fornicata*) and an early developing mollusc (*Bulinus nyassanus*). The other examples were chosen to demonstrate how *GDD* models with poor residuals may be diagnostic of growth-limiting factors including environmental conditions such as salinity (*Ostrea edulis*) or suboptimal temperature (*Mytilus edulis* embryo). The detailed results of the analyses for each set of data are provided in Table S2. Unless otherwise stated, adjusted r^2 values are reported.

GDD across phyla

Size-at-age in the South African abalone (*H. midae*, Bivalvia; Britz et al. 1997), expressed as a function of calendar time varied across temperature treatments (12 to 20°C: different slopes, p < 0.05; Fig. 2a). When size-at-age was expressed as a function of *GDD*, the temperature treatments showed different slopes (p = 0.018; Fig. 2b) though the *GDD* size-at-age model explained most of the variation (r^2 = 0.997).

Size-at-age in the cuttlefish (*S. officinalis*, Cephalopoda; Domingues et al. 2002) expressed as a function of calendar time differed between temperature treatments (15 and 27°C: different slopes, p < 0.05; Fig. 2c). The temperature treatments had similar slopes (p = 0.46) when growth was assessed as a function of *GDD*, though with different intercepts (p = 0.016), while thermal time explained almost all variation (r^2 = 0.97) in size-at-age (Fig. 2d).

Size-at-age in female octopus (*O. bimaculoides*, Cephalopoda; Forsythe & Hanlon 1988) expressed as a function of calendar time was different between temperature treatments (18 and 23°C: different slopes, p = 0.004; Fig. 2e). When growth was expressed as a function of thermal time the temperature treatments had similar slopes (p = 0.17; Fig. 2f), different intercepts (p = 0.043) and virtually all variation (r^2 = 0.99) in size-at-age was explained.

Size-at-age in slipper snails (*C. fornicata*, Gastropoda; Pechenik 1984) as a function of calendar time was different between temperature treatments (18 and 24°C: different slopes, p < 0.05; Fig. 2g), while having similar slopes (p = 0.70), but different intercepts (p < 0.001) in thermal time. Again, when growth was expressed as a function of thermal time, *GDD* explained almost all variation with both treatments combined (r^2 = 0.97; Fig. 2h).

Embryo size-at-age in the freshwater snail (*Bulinus nyassanus*, Gastropoda; Kubiriza et al. 2010) expressed as a function of calendar time was different among temperature treatments (22 to 31°C: different slopes, p < 0.001; Fig. 2i) while all 4 treatments had similar slopes (p = 0.112; Fig. 2j), though with different intercepts (p < 0.001) when growth was expressed as a function of thermal time, and again *GDD* explained most of the variation in size-at-age across treatments (r^2 = 0.95).

GDD and growth limitation

Size-at-age in oyster (*Ostrea edulis*, Bivalvia; Robert et al. 1988) expressed as a function of calendar time varied across temperature treatments (15 to 30°C) at all levels of salinity (20, 25, 30 and 35‰) and had different slopes (p < 0.01; Fig. 3). As a function of *GDD* the different temperature treatments had similar slopes for the 20, 30 and 35‰ salinities (p = 0.138, 0.595 and 0.149, respectively) and similar intercepts for the 20 and 30‰ treatments (p = 0.141 and 0.113, respectively). Across treatments, *GDD* explained most of the variation in size-at-age (r^2 = 0.86, 0.97, and 0.96 for 20, 30 and 35‰ salinity respectively).

Changes in developmental stage for the blue mussel (*Mytilus edulis*, Bivalvia; Hayhurst 1997) expressed as a function of calendar time varied across 4 temperature treatments (5 to 20°C, p = 0.005; Fig. 4a). As a function of *GDD* the temperature treatments had similar slopes (p = 0.37; Fig. 4b) and intercepts (p = 0.074) and explained most of the variation in developmental stage (r^2 = 0.82), though with poor residuals.
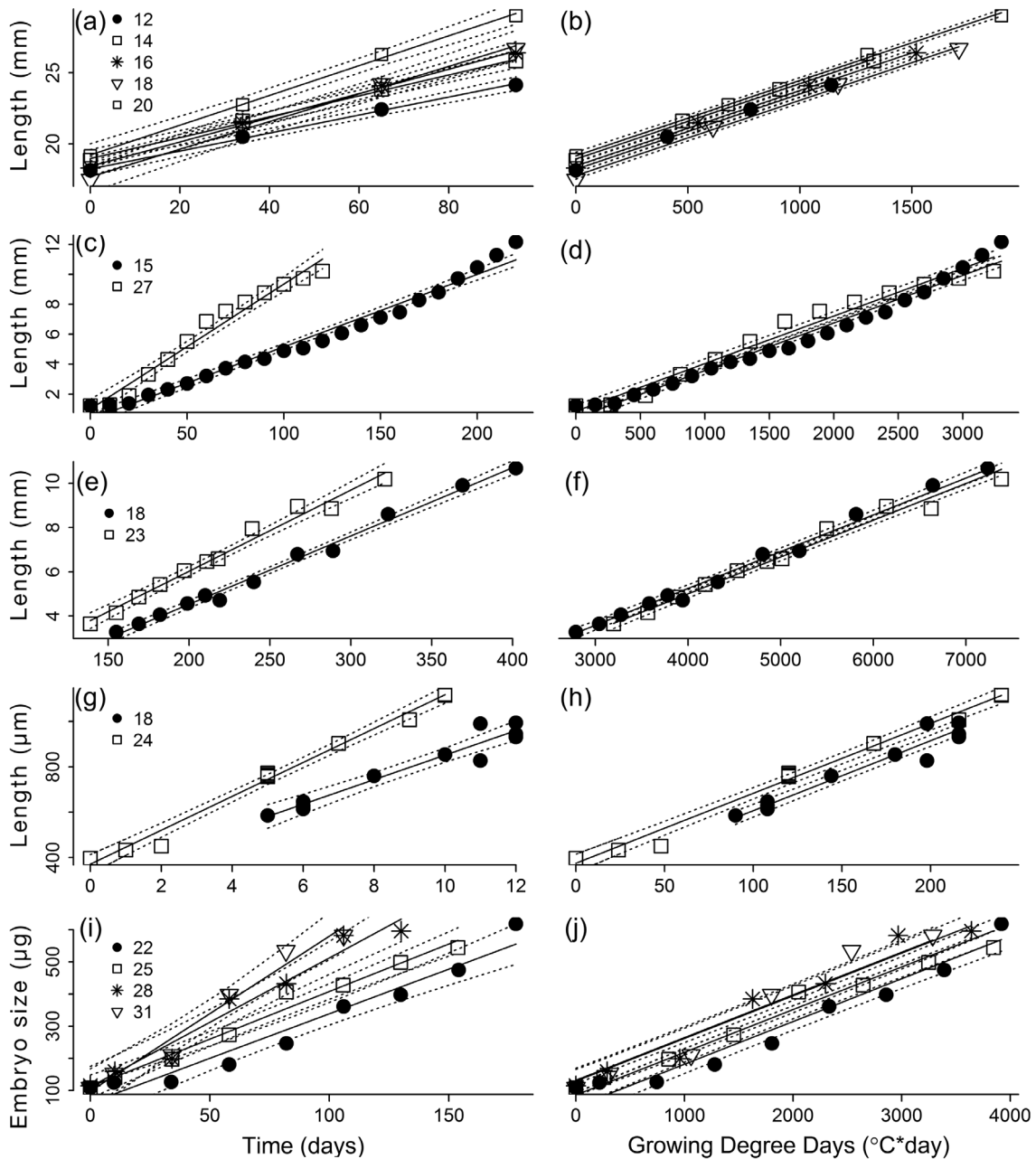
Fig. 2. Size-at-age as a function of calendar time (days) (left panels) and thermal time (*GDD*) (right panels) for different molluscan species under various temperature treatments (various symbols, °C): (a,b) *Haliotis midae* (Britz et al. 1997); (c,d) *Sepia officinalis* (Domingues et al. 2002); (e,f) *Octopus bimaculoides* (Forsythe & Hanlon 1988); (g,h) *Crepidula fornicata* (Pechenik 1984); (i,j) *Bulinus nyassanus* (Kubiriza et al. 2010). The linear regression models (solid lines) and 95% confidence intervals (dotted lines) are provided for each case where the relation is significant (see Table S2 for details)

DISCUSSION

As far as we know this is the first study to address the utility of the *GDD* method in explaining size-at-age or size-at-stage variation in thermal time among a variety of molluscan species. Approximately 70% of the datasets examined among 25 species across the 3

phylogenetic classes illustrated that *GDD* was the most appropriate metric for explaining temperature-dependent size-at-age variation. An overall average 85% of the variation was explained by *GDD* using a single size-at-age relation. Further, our analyses indicate that *GDD* may also be most appropriate for explaining variation in developmental stage transitions.
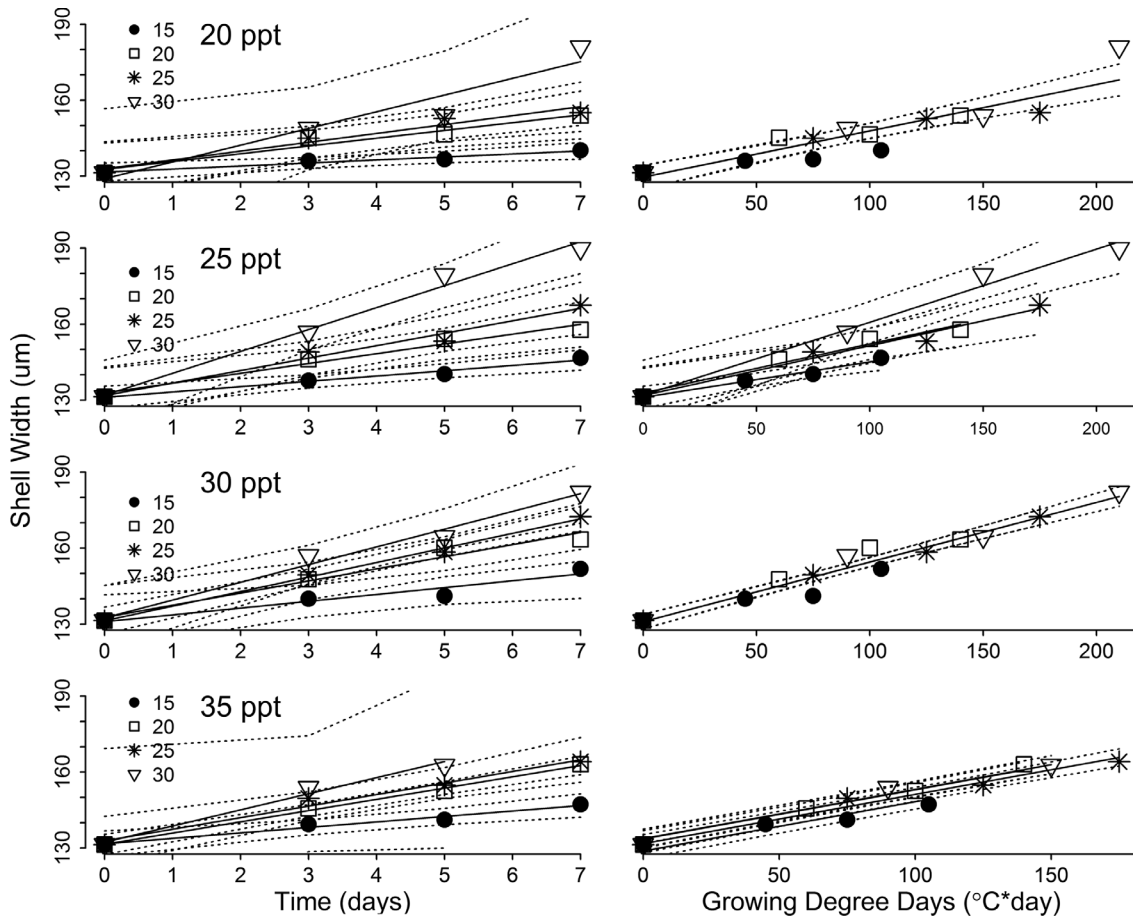
Fig. 3. Size-at-age as a function of calendar time (days) (left column) and thermal time (*GDD*) (right column) for *Ostrea edulis* (Robert et al. 1988) grown under different temperature (various symbols,°C) and salinity ('ppt' labels, ‰) treatments. The linear regression models (solid lines) and 95% confidence intervals (dotted lines) are provided for each case (single or multiple temperature treatments) where the relation is significant (see Table S2 for details)
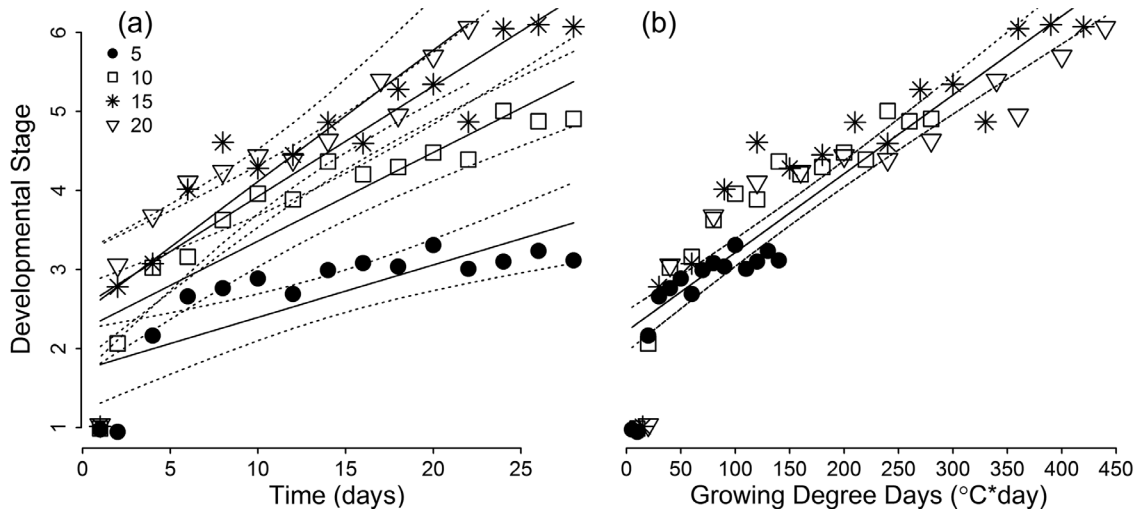

Fig. 4. Developmental stage as a function of (a) calendar time (days) and (b) thermal time (*GDD*) for *Mytilus edulis* (Hayhurst 1997) under different temperature treatments (various symbols,°C) during larval development. The linear regression models (solid lines) and 95% confidence intervals (dotted lines) are provided for each case (single or multiple temperature treatments) where the relation is significant (see Table S2 for details)

The use of *GDD* in explaining size-at-stage varied across species and the developmental metric used. While *GDD* explained temporal development variation in some post-hatching octopus species (e.g., *Octopus bimaculoides*; Forsythe & Hanlon 1988), pre-hatching egg development in the snail (*Bulinus nyassanus*; Kubiriza et al. 2010) was not sufficiently explained in thermal time. The deficiency is likely related to either the growth metric used; i.e., an ordinal scale (i.e., 1st, 2nd, 3rd stage etc.) as opposed to an interval scale (e.g., *W* or *L*) and/or suboptimal thermal conditions and/or the presence of a thermal constant (e.g., the mussel, *Mytilus edulis*; Hayhurst 1997).

Determining an appropriate growth metric is particularly challenging for some molluscs, such as bivalves, as their growth is not principally along one body axis. Further, resource allocation toward shell growth may be mismatched by resource allocation toward an increase in weight, as shell and soft-tissue growth is loosely coupled (Hilbish 1986, Borrero & Hilbish 1988). Additionally, shell and soft-tissue growth may be limited by different environmental conditions such as calcium concentration (Beeby & Richmond 2007). Any non-linear increase in *L* along each body axis may therefore result in a non-linear relation between length-at-age and thermal time. We suspect that a different size metric, such as shell volume, may prove to be more appropriate.

It is also challenging that the metrics used for determining growth within and among molluscan taxa vary across the literature (e.g., Moltschaniwskyj & Martínez 1998). In such instances the *GDD* could be used to identify the optimal size-at-age variable. For example, if a series of metrics (shell length, width, volume, weight, etc.) were measured across temperature treatments and were expressed as a function of the *GDD*, such metrics (or a combination thereof) with similar slopes may provide a better standard for explaining temperature-dependent size-at-age variation.

Limitations and advances

In general, the *GDD* has 2 primary limitations: it applies only for a species-specific optimal range of temperatures (Bonhomme 2000, Trudgill et al. 2005) and for the linear stanzas apparent in the size-at-age curve. First, outside the species-specific thermal range growth may be non-linear and limited by metabolic processes (Trudgill et al. 2005) and that may result in lower growth rates (e.g., snails, *Haliotis midae or H. duryi*) and/or higher mortality (e.g., mussels, *Mytilus galloprovincialis*). When variations in size-at-age are not explained by thermal time they may be diagnostic of a suboptimal conditions in terms of temperature or another environmental variable (e.g., salinity) and *GDD* may thus prove useful in diagnosing physiologically optimal or suboptimal ranges. For example, the poor residuals associated with the *GDD* in the development of *M. edulis* (Hayhurst 1997) indicate that 5°C is a suboptimal temperature, while results for *O. edulis* (Robert et al. 1988) indicate a suboptimal salinity at a lower temperature.

The second limitation of the *GDD* is that it is only applicable during the developmental stanzas for which growth is near-linear (Bonhomme 2000, Trudgill et al. 2005, Neuheimer & Taggart 2007). Once an organism has reached a thermal constant, such as maturity, the growth trajectory changes, though it may still be a linear function of thermal time thereafter. This is generally interpreted as a biphasic growth trajectory (Trudgill et al. 2005, Venturelli et al. 2010). In turn, determining the thermal constants (i.e., where the trajectory changes such as at the time of maturation or smoltification in salmon) can be useful in population modelling (Neuheimer & Taggart 2007). For example, the timing of mollusc time-at-maturity expressed in thermal time could be used to optimize mollusc growth and rearing in an aquaculture environment (e.g., Filgueira et al. 2015).

It is important to note that we used a 'mechanistic' linear model for explaining size-at-age as a function of thermal time. That is, we expect that the relationship between size and thermal time across all temperatures will be linear until some thermal constant is reached. In some cases, the assumption of normality in the error distribution of our analyses was violated as exhibited by patterns in the residuals. In 24% of the datasets analysed (Fig. 1) the linear thermal time model had poor residuals. In these cases, even though the assumptions of the ordinary least squares model were violated, a large proportion of the variation was explained by thermal time ($r^2 > 0.80$). Causes of the poor residuals included very small sample sizes, a change in the inferred growth trajectory when the organisms reached a thermal constant (e.g., Fig. 4; Neuheimer & Taggart 2007) and apparently suboptimal thermal conditions. Poor residuals in these cases were therefore indicative of an underlying physiological process.

To rigorously identify a thermal constant, a non-linear model may be required with the assumption of logarithmic growth. Given that typical mollusc-growth studies, including those used in this study, rarely continue beyond the point where a thermal constant may

have been reached, it is difficult or impossible to identify such constants. We acknowledge the limitations of the assumption of linearity, but also recognize the power this simple mechanistic but statistical approach has, especially given the physiological underpinnings.

Conclusions

We have demonstrated that thermal time expressed as *GDD* is better able to explain temperature-dependent variation in size-at-age and -stage compared to calendar time across a diverse suite of molluscan species. Though the simple linear approach has some limitations when identifying thermal constants, our results suggest that thermal time is most appropriate when assessing variation in growth and development in molluscs among laboratory studies and likely also among natural populations.

LITERATURE CITED

Atkinson D (1993) Temperature and organism size — a biological law for ectotherms? Adv Ecol Res 25:1–58

Bayne BL, Worrall CM (1980) Growth and production of mussels *Mytilus edulis* from two populations. Mar Ecol Prog Ser 3:317–328

Beeby A, Richmond L (2007) Differential growth rates and calcium-allocation strategies in the garden snail *Cantareus aspersus.* J Molluscan Stud 73:105–112

Bonhomme R (2000) Bases and limits to using 'degree.day' units. Eur J Agron 13:1–10

Borrero FJ, Hilbish TJ (1988) Temporal variation in shell and soft tissue growth of the mussel *Geukensia demissa.* Mar Ecol Prog Ser 42:9–15

Britz PJ, Hecht T, Mangold S (1997) Effect of temperature on growth, feed consumption and nutritional indices of *Haliotis midae* fed a formulated diet. Aquaculture 152:191–203

Chezik KA, Lester NP, Venturelli PA (2014a) Fish growth and degree-days I: selecting a base temperature for a within-population study. Can J Fish Aquat Sci 71:47–55

Chezik KA, Lester NP, Venturelli PA (2014b) Fish growth and degree-days II: selecting a base temperature for an among-population study. Can J Fish Aquat Sci 71:1303–1311

Domingues PM, Sykes A, Andrade J (2002) The effects of temperature in the life cycle of two consecutive generations of the cuttlefish *Sepia officinalis* (Linnaeus, 1758), cultured in the Algarve (South Portugal). Aquacult Int 10:207–220

Dumas A, France J, Bureau DP (2007) Evidence of three growth stanzas in rainbow trout (*Oncorhynchus mykiss*)

across life stages and adaptation of the thermal-unit growth coefficient. Aquaculture 267:139–146

Filgueira R, Brown MS, Comeau LA, Grant J (2015) Predicting the timing of the pediveliger stage of *Mytilus edulis* based on ocean temperature. J Molluscan Stud 81:269–273

Forsythe JW, Hanlon RT (1988) Effect of temperature on laboratory growth, reproduction and life span of *Octopus bimaculoides.* Mar Biol 98:369–379

Froese R (2006) Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. J Appl Ichthyology 22:241–253

Gilbert N, Gutierrez AP, Frazer BD, Jones RE (1976) Ecological relationships. Freeman, San Francisco

Hayhurst S (1997) The effects of temperature on the survival, growth and development of larvae of two blue mussel species (*Mytilus edulis* and *Mytilus trossulus*). MSc Thesis, University of Maine, Orono, ME

Hilbish TJ (1986) Growth trajectories of shell and soft tissue in bivalves seasonal variation in *Mytilus edulis* L. J Exp Mar Bio Ecol 96:103–113

Hoving HJT, Lipinski MR, Roeleveld MAC, Durholtz MD (2007) Growth and mating of southern African *Lycoteuthis lorigera* (Steenstrup, 1875) (Cephalopoda; Lycoteuthidae). Rev Fish Biol Fish 17:259–270

Huey RB, Stevenson RD (1979) Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. Integr Comp Biol 19:357–366

Kubiriza GK, Madsen H, Likongwe JS, Sfauffer JR, Ombe JK, Kapute F (2010) Effect of temperature on growth, survival and reproduction of *Bulinus nyassanus* (Smith, 1877) (Mollusca: Gastropoda) from Lake Malawi. Afr Zool 45:315–320

Lv S, Zhang Y, Liu HX, Hu L and others (2009) Invasive snails and an emerging infectious disease: results from the first national survey on *Angiostrongylus cantonensis* in China. PLOS Negl Trop Dis 3:e368

McMaster GS, Wilhelm W (1997) Growing degree days: one equation, two interpretations. Agric Meteorol 87:291–300

Moltschaniwskyj NA, Martínez P (1998) Effect of temperature and food levels on the growth and condition of juvenile *Sepia elliptica* (Hoyle 1885): an experimental approach. J Exp Mar Biol Ecol 229:289–302

Neuheimer AB, Grønkjær P (2012) Climate effects on size-at-age: growth in warming waters compensates for earlier maturity in an exploited marine fish. Glob Change Biol 18:1812–1822

Neuheimer AB, Taggart CT (2007) The growing degree-day and fish size-at-age: the overlooked metric. Can J Fish Aquat Sci 64:375–385

Neuheimer AB, Taggart CT (2010) Can changes in length-at-age and maturation timing in Scotian Shelf haddock (*Melanogrammus aeglefinus*) be explained by fishing? Can J Fish Aquat Sci 67:854–865

Pechenik J (1984) The relationship between temperature, growth rate, and duration of planktonic life for larvae of the gastropod *Crepidula fornicata* (L.). J Exp Mar Biol Ecol 74:241–257

R Development Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Robert R, His E, Dinet A (1988) Combined effects of temperature and salinity on fed and starved larvae of the European flat oyster *Ostrea edulis.* Mar Biol 97:95

Rohatgi A (2015) WebPlotDigitizer, Ver 3.9. http://arohatgi. info/WebPlotDigitizer

Seuffert ME, Saveanu L, Martín PR (2012) Threshold temperatures and degree-day estimates for embryonic development of the invasive apple snail *Pomacea canaliculata* (Caenogastropoda: Ampullariidae). Malacologia 55: 209−217

Trudgill DL, Honek A, Li D, Van Straalen NM and others (2005) Thermal time — concepts and utility. Ann Appl Biol 146:1−14

Tummers B (2006) DataThief III. http://datathief.org

Van der Have TM, de Jong G (1996) Adult size in ectotherms: temperature effects on growth and differentiation. J Theor Biol 183:329−340

Venturelli PA, Lester NP, Marshall TR, Shuter BJ (2010) Consistent patterns of maturity and density-dependent growth among populations of walleye (*Sander vitreus*): application of the growing degree-day metric. Can J Fish Aquat Sci 67:1057−1067

Von Bertalanffy L (1938) A quantitative theory of organic growth (inquiries on growth laws. II). Human Biol 10: 181−213

Wood JB, O'Dor RK (2000) Do larger cephalopods live longer? Effects of temperature and phylogeny on interspecific comparisons of age and size at maturity. Mar Biol 136:91−99