PERSPECTIVE / PERSPECTIVE

The growing degree-day and fish size-at-age: the overlooked metric

Anna B. Neuheimer and Christopher T. Taggart

Abstract: Growth rate in ectotherms, including most fish, is a function of temperature. For decades, agriculturalists (270+ years) and entomologists (45+ years) have recognized the thermal integral, known as the growing degree-day (GDD, °C·day), to be a reliable predictor of growth and development. Fish and fisheries researchers have yet to widely acknowledge the power of the GDD in explaining growth and development among fishes. We demonstrate that fish length-at-day (LaD), in most cases prior to maturation, is a strong linear function of the GDD metric that can explain >92% of the variation in LaD among 41 data sets representing nine fish species drawn from marine and freshwater environments, temperate and tropical climes, constant and variable temperature regimes, and laboratory and field studies. The GDD demonstrates explanatory power across large spatial scales, e.g., 93% of the variation in LaD for age-2 to -4 Atlantic cod (*Gadus morhua*) across their entire range (17 stocks) is explained by one simple GDD function. Moreover, GDD can explain much of the variation in fish egg development time and in aquatic invertebrate (crab) size-at-age. Our analysis extends the well-established and physiologically relevant GDD metric to fish where, relative to conventional time-based methods, it provides greater explanatory power.

Résumé : Le taux de croissance des ectothermes, dont celui de la plupart des poissons, est fonction de la température. Depuis des décennies, les spécialistes l'agriculture (270+ ans) et de l'entomologie (45+ ans) reconnaissent que la sommation thermique, connue sous le nom de degré-jour de croissance (GDD, °C·jour), permet de prédire de façon fiable la croissance et le développement. Les chercheurs en ichtyologie et en pêcheries tardent à reconnaître à grande échelle la puissance de GDD pour expliquer la croissance et le développement chez les poissons. Nous démontrons que la longueur en fonction du jour (LaD), la plupart des cas avant la maturation, est une solide fonction linéaire de la métrique GDD qui peut expliquer >92 % de la variation de LaD dans 41 séries de données représentant neuf espèces de poissons et tirées de milieux marins et d'eau douce, de climats tempérés et tropicaux, de régimes thermiques constants et variables et d'études de laboratoire et de terrain. La métrique GDD possède une pouvoir d'explication qui s'étend sur de grandes échelles spatiales; par exemple, une simple fonction GDD rend compte de 93 % de la variation de LaD chez des morues franches (*Gadus morhua*) d'âges 2–4 sur l'ensemble de leur répartition (17 stocks). De plus, GDD peut expliquer une grande partie de la variation du temps de développement des oeufs de poissons et de la taille en fonction de l'âge chez les invertébrés aquatiques (crabes). Notre analyse étend aux poissons l'utilisation de la métrique GDD, déjà bien établie et d'intérêt physiologique; cette métrique possède d'ailleurs un pouvoir explicatif plus important que les autres méthodes basées sur le temps.

[Traduit par la Rédaction]

Introduction

The physiological processes that determine growth (e.g., metabolic rate, gas exchange, risk of desiccation in terrestrial organisms, and oxygen supply in aquatic animals) are directly influenced by temperature (Atkinson 1994; van der Have and de Jong 1996). Accordingly, time-dependent variations in temperature are reflected in time-dependent variations in development and in size-at-age where the latter is frequently used to infer growth rate. Within limits, and in general, higher temperatures result in higher enzymatic reaction rates that govern growth (Higley et al. 1986). Diffusion of substrates or enzymes or both increases, resulting in a greater number of enzyme–substrate complexes and more energy to meet reaction demands. This physiological response, greatly simplified in terms of the complex processes involved, is generally linear over a midrange of temperatures approaching the optimum and nonlinear at extreme tempera-

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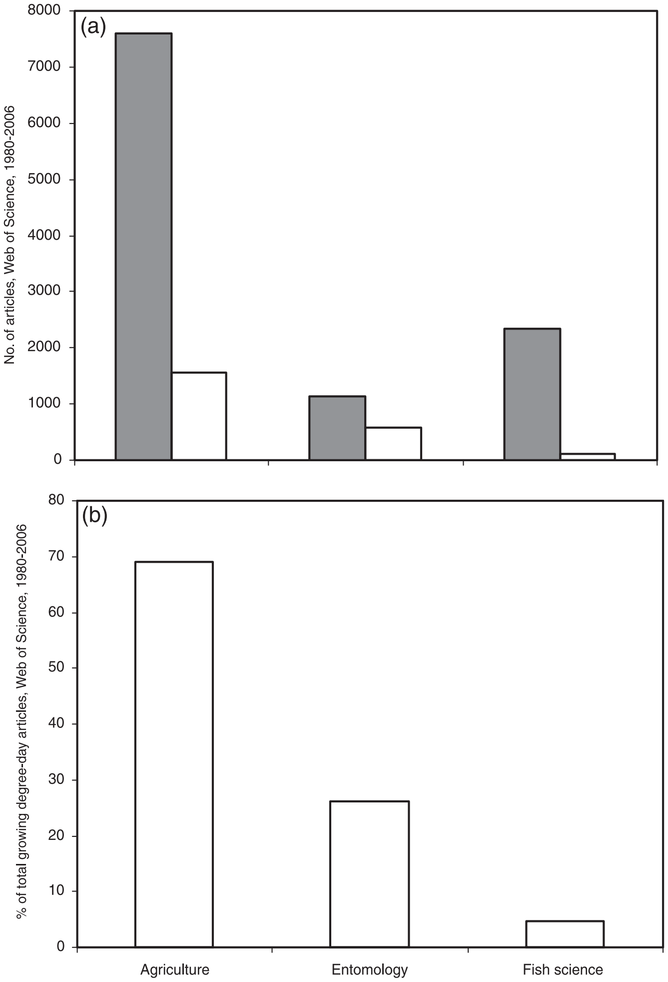
tures where control enzyme(s) are inactivated by conformational change (Sharpe and DeMichele 1977) or where enzymes or substrates are destroyed more rapidly than they are sequestered (Howe 1967). This appears to be true for all ectotherms including plants, insects, aquatic invertebrates, and most reptiles, amphibians, and fish.

In fish, variation in size influences predator–prey interactions, maturation, reproduction and recruitment potential, and vulnerability to size-selective fishing. Thus, explaining or predicting growth variation through size-at-age is often essential to population and ecosystem studies and nutrient/energy pathway explorations (food webs) as well as in determining fishing pressures suitable for sustainable fisheries. The greatest impediment to most fish growth models, including the pervasive von Bertalanffy growth function (VBGF) (von Bertalanffy 1938), is their dependence on calendar time to explain length variation (i.e., length-at-age). Such dependence explicitly ignores time-dependent and physiologically meaningful variables such as temperature. Some growth models do attempt to incorporate temperature, usually instantaneous measures of temperature (Francis 1994; Mallet et al. 1999; Dion and Hughes 2004). However, instantaneous local temperature estimates (e.g., daily mean) do not necessarily reflect the phenotypic expression of the growth integral (i.e., length-at-age) in an equally instantaneous manner. For over 270 years in agriculture and for at least 45 years in entomology, the time-based integral of the heat available for growth — heat transferred from the environment to the ectotherm — has been employed with remarkable success in explaining and predicting growth and development (e.g., Seamster 1950; Atkinson 1994; Bonhomme 2000). The most prevalent parameterization of the heat integral is the growing degree-day (GDD, °C·day), the time integral of the daily temperature measured above some temperature threshold (T_{Th}). The GDD method allows growth and development to be correctly scaled to the physiology that drives ectotherm growth and development. Simply stated, growth and development are proportional to the time spent at temperature (thermal time; Trudgill et al. 2005) within the range where metabolic reaction rates are near-linear functions of temperature. The thermal integral concept should be applicable to most fish simply because they are ectotherms; their metabolic rate is largely determined by the heat transferred from the environment during the period of growth and development (e.g., Leggett et al. 1984; Hamel et al. 1997; Kjellman et al. 2001). However, relative to agriculture and entomology, our examination of the primary literature (Fig. 1) demonstrates that only a handful (4.6%) of studies that address temperature and growth in fishes refer to the GDD metric (e.g., Mills 1988; Mills et al. 1989; Kjellman et al. 2001). Although several fish studies address the combination of time and temperature (e.g., Iwama and Tautz 1981; Brander 1995), none appear to follow through on the implications of the thermal integral or explore its generality. To paraphrase Reaumur (1735, cited in Bonhomme 2000): "The same [fish] are harvested in very different climates; it would be interesting to compare the sums of heat degrees over the months during which the [fish] does most of its growing and reaches complete maturity in hot countries, like Spain or Africa...in temperate countries like France and in the colder countries of the North."

Fig. 1. Histograms of (*a*) the number of articles listed by Web of Science® for the period 1980–2006 referring in title, keywords, or abstracts to temperature and growth (gray bars, key words: "temperature" AND ("development" OR "growth")) or GDD (open bars, key words: "degree day*" OR "thermal sum" OR "day degree*" OR "growing degree day*" OR "thermal time") in agriculture, entomology, and fish science and (*b*) the percent total number of articles listed by the Web of Science® for the period 1980–2006 referring in title, keywords, or abstracts to GDD (key words: "degree day*" OR "thermal sum" OR "day degree*" OR "growing degree day*" OR "thermal time") in agriculture, entomology, and fish science.



Data mining and analyses

We examined 41 data sets (Supplemental Tables S1 and S2)[2] representing nine fish species and different life history stages (most prior to maturation) among subtropical, temperate, freshwater, and marine environments, including control experiments with constant and variable temperature and field

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[2] Supplementary data for this article are available on our Web site (http://cjfas.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5139. For more information on obtaining material, refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

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studies. Across these data, we are able to show that variation in length-at-day (LaD, mm) is a strong linear function ($r^2 \geq 0.92$, $P < 0.05$) of the variation in GDD. Further, our analyses show that GDD is able to explain variation in LaD within and among data sets, something that calendar time cannot do in environments where there are temporal variations in temperature within or among trials or field studies.

GDD in the laboratory

Among constant-temperature growth trials (Folkvord et al. 2004) with Atlantic herring (*Clupea harengus*), calendar time explains most of the variation in LaD within a given trial (Fig. 2*a*), but each trial requires a different parameterization (analysis of covariance (ANCOVA): different slopes, $P = 0.0003$). In contrast, the thermal integral (i.e., GDD) explains the LaD variation within and among trials (Fig. 2*b*) using a single parameterization (ANCOVA: similar slopes, $P = 0.74$; similar intercepts, $P = 0.59$; LaD = 0.033GDD + 10.4; $r^2 = 0.99$, $P < 0.0001$). Other growth trials with herring (Folkvord et al. 2004), now employing a time-varying temperature, show that although calendar time again explains much of the LaD variation within a given trial (Fig. 2*c*), the explanatory power is less than under constant temperature (Fig. 2*a*). Further, and more importantly, each trial requires a different parameterization (ANCOVA: different slopes, $P = 0.0032$). In contrast, GDD explains a greater degree of variation in LaD within and among trials (Fig. 2*d*) and a single parameterization is sufficient (ANCOVA: similar slopes, $P = 0.55$; similar intercepts, $P = 0.064$; *LaD* = 0.035GDD + 10.1; $r^2 = 0.98$, $P < 0.0001$). The strength of the GDD metric becomes readily apparent when one recognizes that there are no differences among the above parameterizations of LaD as a function of GDD in the constant-temperature (Fig. 2*b*) and in the time-varying temperature (Fig. 2*d*) growth trials (Fig. 2*f*) (ANCOVA: similar slopes, $P = 0.91$; similar intercepts, $P = 0.19$; LaD = 0.034GDD + 10.3; $r^2 = 0.98$, $P < 0.0001$). In summary, a single parameterization of LaD as a function of physiological time is sufficient to explain size-at-age variation, with considerable accuracy, among any of the above temperature growth trials that require four different parameterizations when LaD is expressed as a function of calendar time.

A further example of the strength of the GDD metric in assessing fish size-at-age can be demonstrated using the Malzahn et al. (2003) laboratory-rearing of larval houting (*Coregonus oxyrhynchus*). Here, two different parameterizations of LaD as a function of calendar time are required for each trial (Fig. 2*g*) (ANCOVA: different slopes, $P = 0.0001$), although they, like the herring above, collapse to a simpler parameterization when GDD is used (Fig. 2*h*) (ANCOVA: similar slopes, $P = 0.10$; different intercepts, $P < 0.0001$).

When GDD is unable to explain the variation in LaD among trials, it is an indication that other factors (e.g., food availability, genetic composition) are contributing to the size-at-age variation (or the thermal record is incorrect, see below). How much of that size-at-age variation is due to temperature versus other factors can only be teased apart once the trials are compared on the same physiological timescale, i.e., with GDD. When size-at-age is assessed in the same larval houting as above (Malzahn et al. 2003) but now under food limitation, there is no relation (i.e., no growth) between LaD and either calendar time or GDD. (Figs. 2*g* and 2*h*) (linear regression; $0.11 \leq P \leq 0.13$). However, when calendar time is used as the predictor, it is not clear how much of the variation in LaD is a function of temperature and how much is a function of food. As we have shown above, when the GDD metric is employed, the variation in size-at-age owing to temperature can be explained and more so than by calendar time. Consequently, with GDD, any variation related to food limitation (and presumably other variables independent of temperature-dependent physiology) becomes readily apparent. The GDD appears to explain the variation in size-at-age owing to variation in thermal histories of fish and thus can be used to identify the remaining size-at-age variation that can be explored (e.g., other factors). In addition, laboratory growth studies need not control for temperature (within limits) if GDD is employed in the analyses because the GDD can account for the temperature variation through integration as described above (Figs. 2*e* and 2*f*) and below (Figs. 2*i* and 2*j*).

GDD in the field

The strength of the GDD is also demonstrated among field studies (Dion and Hughes 2004) where, for example, the nonlinear evolution in GDD is able to explain the nonlinear evolution of LaD in two different year-classes of age-0+ Arctic grayling (*Thymallus thymallus*) in consecutive years in the same habitat (Fig. 3) and does so in a linear manner (Figs. 2*i* and 2*j*). The original study (Dion and Hughes 2004) used the growth model of Mallet et al. (1999) that was developed for grayling to incorporate seasonal size-at-age variation in the VBGF through a “coefficient of temperature”, a coefficient requiring estimates of the minimum, maximum, and optimum growth temperatures for grayling based on “expert opinion”. A comparison of the residuals resulting from the GDD metric applied to the grayling and those obtained using the modified VBGF (Dion and Hughes 2004) reveals that the residuals (Supplemental Fig. S1)[2] from the former are smaller, more uniform, and trend-free relative to the modified VBGF (although both are autocorrelated, as are most variables of this nature). Thus, consistent with all above, the GDD method provides a simpler metric with greater explanatory power and obviates the five parameters required by the modified VBGF (Dion and Hughes 2004) and by analogues used elsewhere that incorporate asymptotic length, growth coefficient, optimum temperatures, seasonal amplitudes and phases, etc.

The GDD not only explains the variation in LaD among different year-classes in different years (above), it can also explain size-at-age variation among year-classes across multiple years as shown (Figs. 2*k* and 2*l*) by the freshwater minnow in a north-temperate environment (Mills 1988). Here, calendar time explains much of the evolution of LaD with a similar slope among year-classes, but the intercepts are different (Fig. 2*k*) (ANCOVA: similar slopes, $P = 0.85$; different intercepts, $P = 0.0014$). The common slope result (Mills 1988) is most likely related to the fact that there were limited differences in the GDD among years (coefficient of variation (CV) = 16%), i.e., limited differences in the ther-

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Fig. 2. Length-at-day as a function of calendar time (left panels) and as a function of GDD (right panels) for Atlantic herring (Folkvord et al. 2004) (*a*, *b*, *e*, and *f*) for 4 °C constant trial (solid circles) and 12 °C constant trial (crosses), (*c*, *d*, *e*, and *f*) for 4, 8, and 4 °C variable trial (open circles), and (*c*, *d*, *e*, and *f*) for 12, 8, and 12 °C variable trial (squares), houting (Malzahn et al. 2003) (*g* and *h*) for 8.4 °C constant and fed (open circles), 17.5 °C constant and fed (solid circles), 8.4 °C constant and starved (squares), and 17.5 °C constant and starved (crosses), Arctic grayling (Dion and Hughes 2004) (*i* and *j*) for 2000 year-class (solid circles) and 2001 year-class (open circles), and minnow (Mills 1988) (*k* and *l*) for 1978 year-class (solid circles), 1979 year-class (open circles), 1980 year-class (crosses), and 1981 year-class (squares). Also shown is carapace width in spider crab (Penha-Lopes et al. 2006) (*m* and *n*) for 25 °C constant (solid circles) and 28 °C constant (open circles). The linear regression (solid line) and 95% prediction intervals (broken lines) are provided for each relation (see Supplemental Table S2 for details)^2 except where not significant.

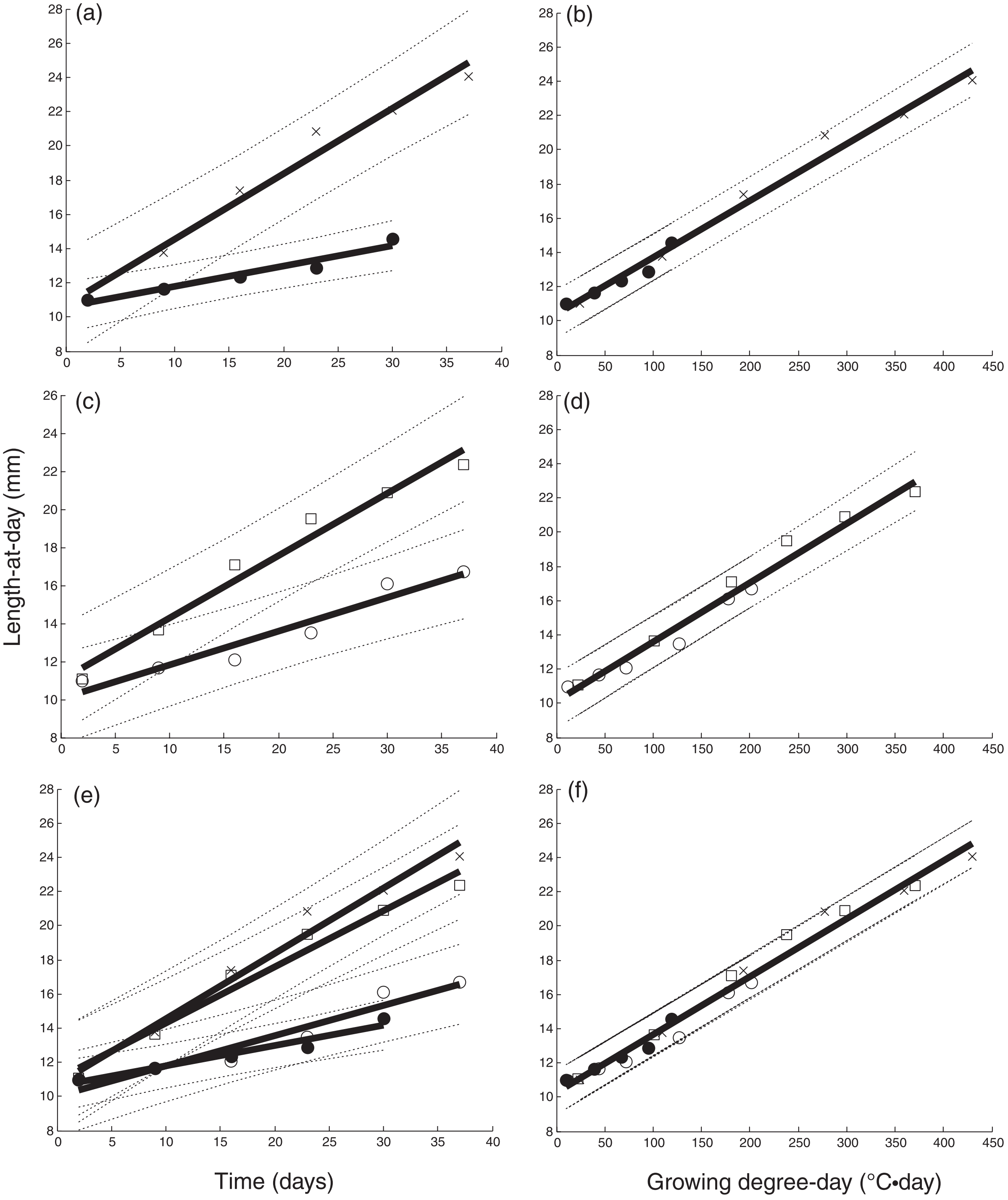
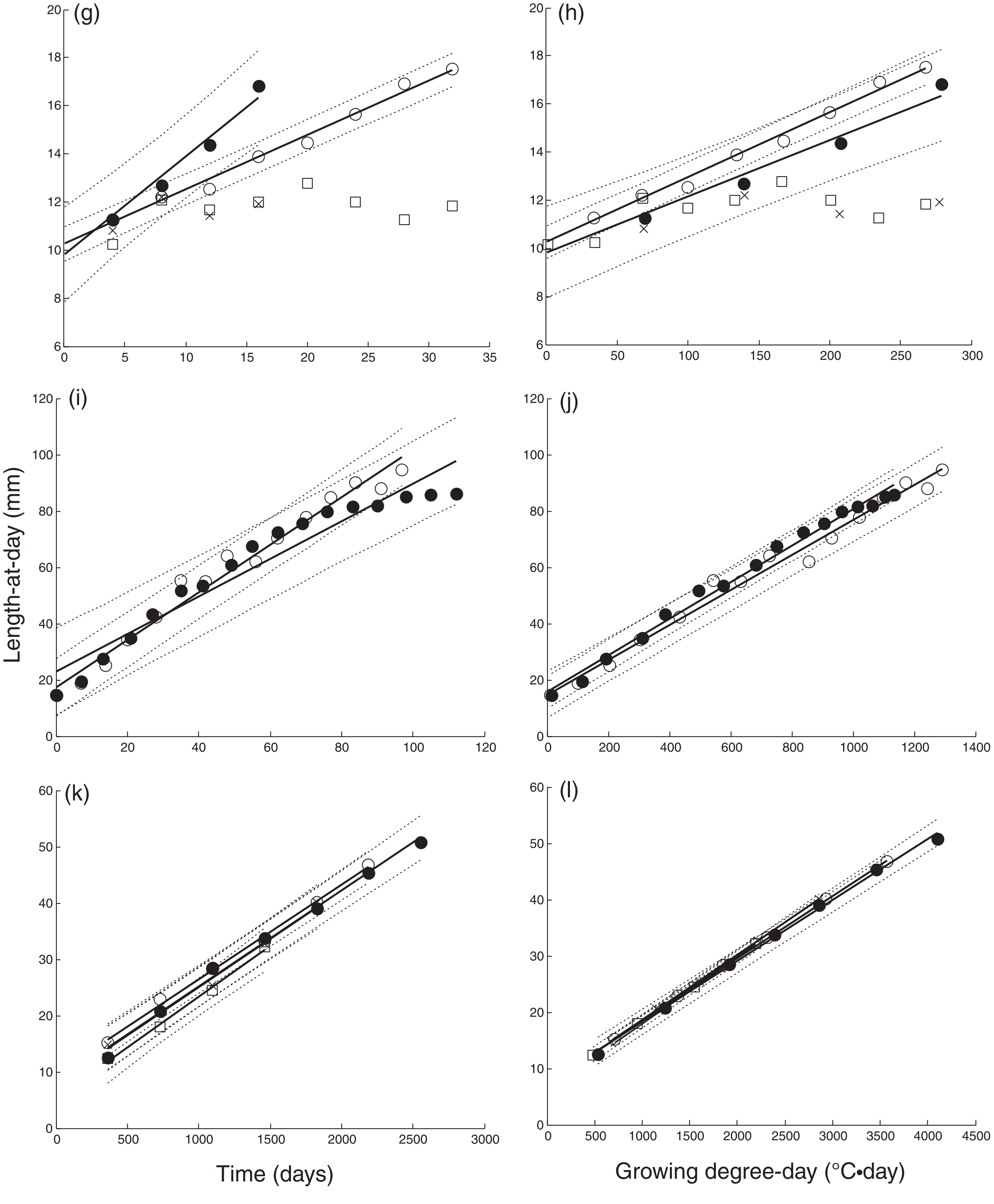


Fig. 2 (*continued*).



mal histories (thermal integrals) of the four year-classes over the 4- to 7-year-period. The disparate intercepts may be related to the first sampling dates among year-classes in relation to the thermal histories of the fish. When the same fish are assessed in terms of their year-class (cohort) and GDD, a single relation holds (Fig. 2*l*) (ANCOVA: similar slopes, $P = 0.19$; marginally similar intercepts, $P = 0.032$) (Supplemental Table S2).[2] In summary, where the thermal environment varies little from one year to the next, calendar time can be expected to explain much of the variation in LaD among year-classes, although in this case, the GDD metric delivers slightly better explanatory power.

GDD in general

The above demonstrations of the ability of the GDD method to explain LaD variation in fishes is mirrored among the other data sets that we examined (41 in all, including those detailed above and below; Supplemental Tables S1 and S2)[2] where the CV (51%) in slopes derived from LaD-at-GDD relations is

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Fig. 2 (*concluded*).

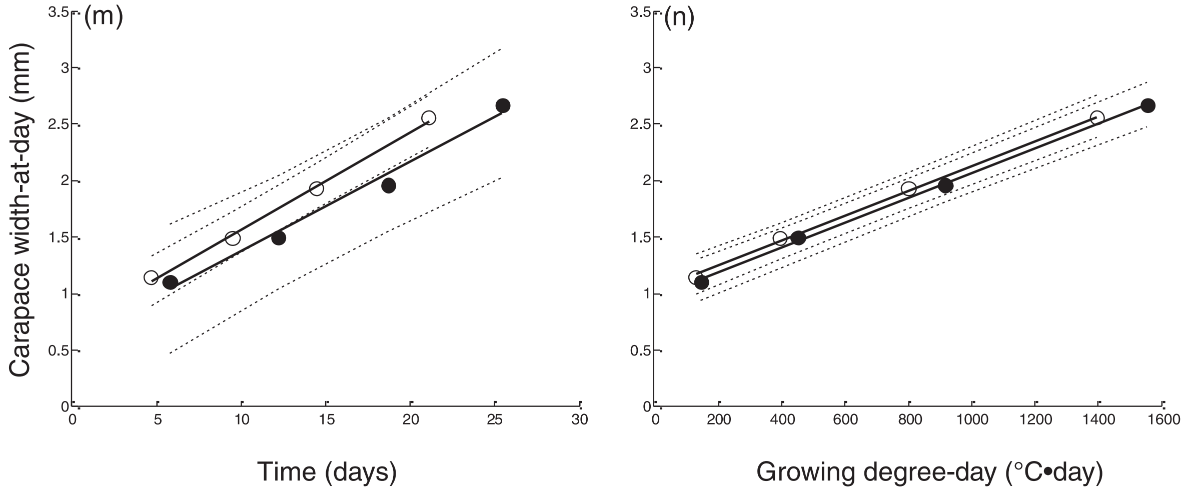
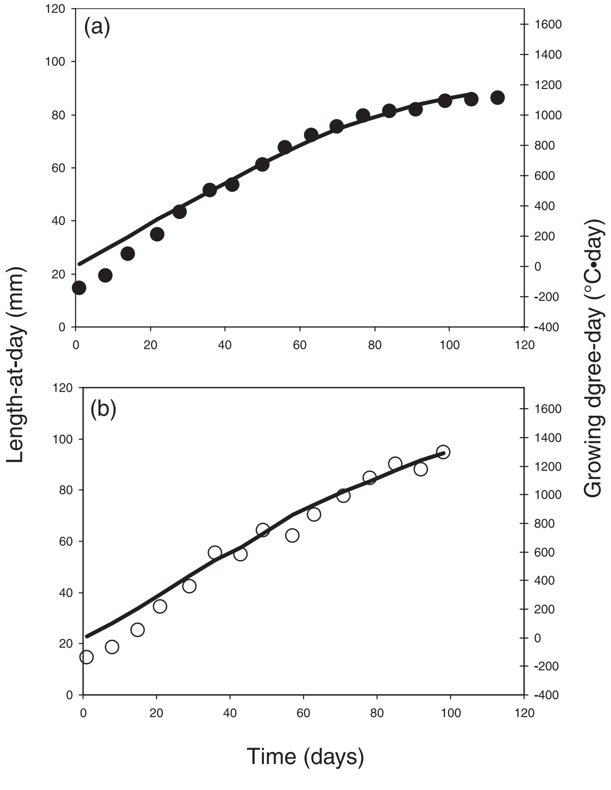


Fig. 3. Nonlinear evolution of length-at-day for (*a*) 2000 year-class (circles) and (*b*) 2001 year-class (circles) of age 0+ Arctic grayling (Dion and Hughes 2004) and the parallel and nonlinear evolution of growing degree-day (line) in time for each year and year-class.



smaller than that derived from the LaD-at-calendar-time relations (63%), demonstrating that physiological time is able to explain more of the variation in size-at-age in fishes among studies (temperatures, year-classes, species, etc.) than does calendar time.

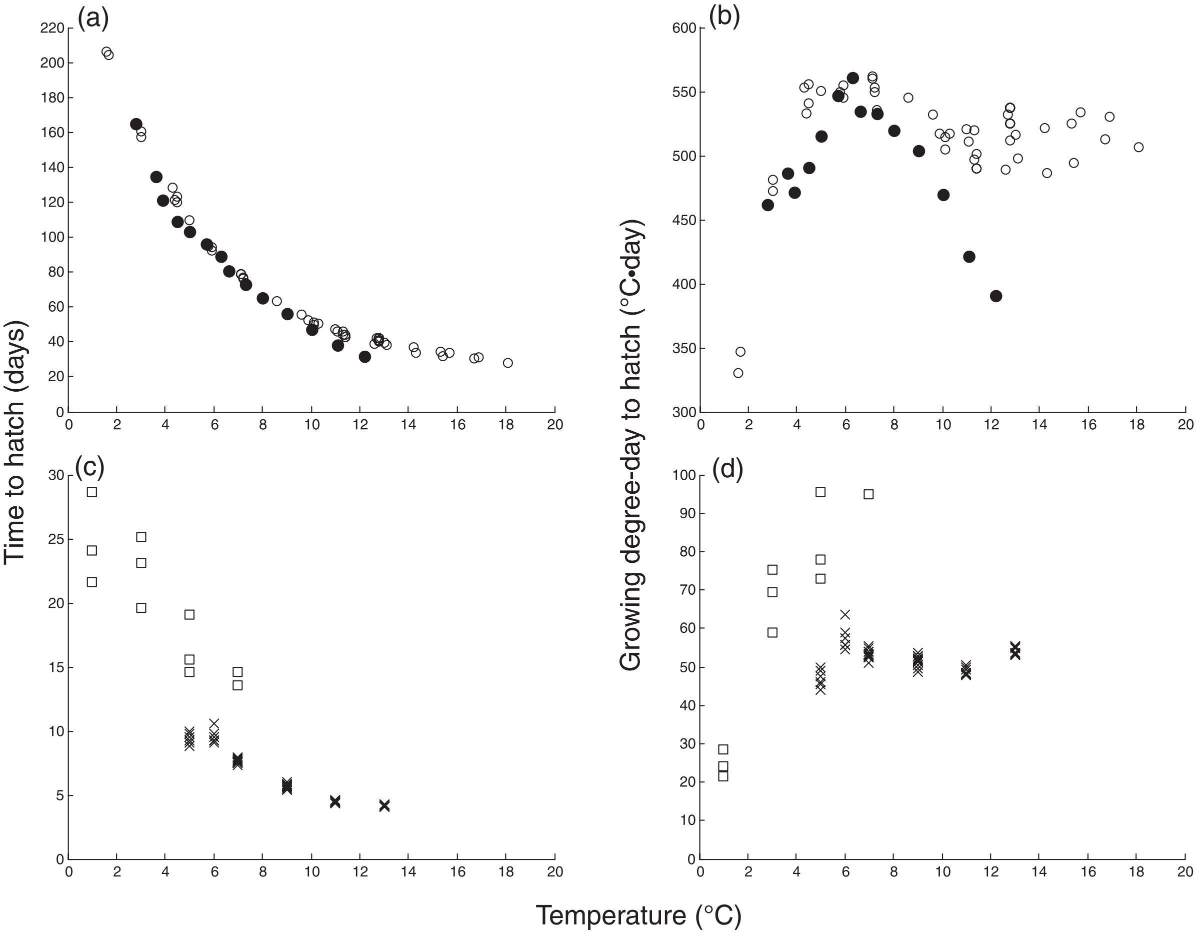
GDD in other aquatic ectotherms

The explanatory power of the GDD appears to hold for other aquatic ectotherms. For example, and as shown above for herring and houting, spider crab (*Mithraculus forceps*) constant-temperature (25 and 28 °C) growth trials (Penha-Lopes et al. 2006) demonstrate that calendar time explains much of the variation in carapace width (mm) within a given trial (Fig. 2*m*) but each trial requires a different parameterization, at least in the intercept (ANCOVA: similar slopes, $P = 0.41$; different intercepts, $P = 0.01$). However, when physiological time is employed, size-at-age relations between temperature trials are identical in slope and the intercepts are marginally the same (ANCOVA: similar slopes, $P = 0.86$; marginally similar intercepts, $P = 0.031$). The GDD method (Stevens 1990) also proves useful for assessing size-at-age in the red king crab (*Paralithodes camtschatics*) where 92% of the variation in carapace length-at-age is a simple linear function of GDD (linear regression, $P < 0.0001$) (Supplemental Fig. S2).[2]

GDD and development

A corollary to the GDD is the thermal constant — the degree-days achieved to advance a given developmental stage — routinely used in agriculture and entomology to determine developmental time to stages such as emergence or maturation (Trudgill et al. 2005). This concept is applicable to fish (Lange and Greve 1997) including, for example, the development and hatching of chinook salmon (*Oncorhynchus tshawytscha*) eggs (Alderdice and Velsen 1978) incubated across a 16 °C temperature range (Fig. 4*a*). Here, the GDD achieved for hatching to occur is 516 ± 40 °C·days regardless of incubation temperature (Fig. 4*b*; Supplemental Table S2),[2] thus reducing the CV in time-to-hatch from 65% (calendar time) to 7.8% (physiological time), although there are some outliers in the thermal constant estimates (see below). Time-to-hatch as a thermal constant is also noted in trout (*Salmo fario*) eggs (Gray 1928) (Fig. 4*a*) near 493 ± 48 °C·days (Fig. 4*b*) and yellowtail flounder (*Limanda ferruginea*, formerly *Pleuronectes ferrugineus*) eggs (Benoit and Pepin 1999) (Fig. 4*c*) near 52 ± 3 °C·days (Fig. 4*d*) where the CV in time-to-hatch is reduced from 44% to 9.7% and from 32% to 6.4%, respectively, when GDD is used instead of calendar time. Again, there are some outliers. The anomalously low thermal constants (outliers) generally appear at the extremes in the incubation temperature ranges, possibly

Fig. 4. Egg development in calendar time to hatch (left panels) and in GDD to hatch (right panels) for incubation at constant temperatures for (*a* and *b*) trout (solid circles) (Gray 1928) and chinook salmon (open circles) (Alderdice and Velsen 1978) and (*c* and *d*) Atlantic cod (squares) (Pepin et al. 1997) and yellowtail flounder (crosses) (Benoit and Pepin 1999).



indicating that the eggs are being incubated outside of the temperature range normally experienced by the organism where the metabolic response to changing temperature is expected to be near-linear. This may explain our examination of Atlantic cod (*Gadus morhua*) eggs (Pepin et al. 1997) (Fig. 4*c*) reared between 1 and 7 °C where the thermal constant appears to be near 66 ± 29 °C·days with anomalously low estimates at the low end of the incubation temperature range (demonstrating an increase in CV from 25% to 44% for calendar time (Fig. 4*c*) and GDD (Fig. 4*d*), respectively), again suggesting incubation outside of temperature ranges within that that the organism has evolved or that some other low-temperature physiology is involved (Valerio et al. 1992). Nevertheless, these examples (Figs. 4*b* and 4*d*) illustrate that the GDD thermal constant may be useful in predicting the timing of life history development and transformation in fish. The substantial variation in thermal constants over large ranges in egg incubation temperatures for some species found in our study, and in that of Reibisch (1902), indicates that our greatly simplified assumptions regarding the physiological responses to temperature may not explain all of the variation stemming from the complex processes involved.

In fish, life history transformations (e.g., smoltification, maturation) are marked by changes in energy allocation from growth to other physiological demands and thus a discontinuity in LaD as a function of GDD is to be expected. Such discontinuities are observed in some of the multiyear data thst we examined (e.g., Atlantic salmon (*Salmo salar*) and threespine stickleback (*Gasterosteus aculeatus*)) and they appear to identify thermal constants that define the physiological time for life history transformation. For example, a discontinuity at approximately 1600 °C·days is apparent (Supplemental Fig. S3)[2] in Atlantic salmon growth trials (based on data from Jones et al. 2002) corresponding to an average LaD of approximately 114 mm, well within the standard deviation of the average LaD (124 ± 14 mm; Hutchings and Jones 1998) reported for smoltification in the study area. Smoltification is associated with physiological changes involving salinity tolerance, hormone titre (thyroid activity), and olfaction (Specker et al. 2000), each presumably associated with a changing energy budget and thus a change in the LaD-at-GDD relation.

GDD at large spatial scales

To test the generality of the GDD measure in explaining size-at-age for fish over large spatial and temperature scales, we examined age-2 to -4 Atlantic cod and their associated long-term mean ocean temperature across their North Atlantic range using Brander's (1995) compilation. In doing so, we explicitly assume that the variation in temperature among

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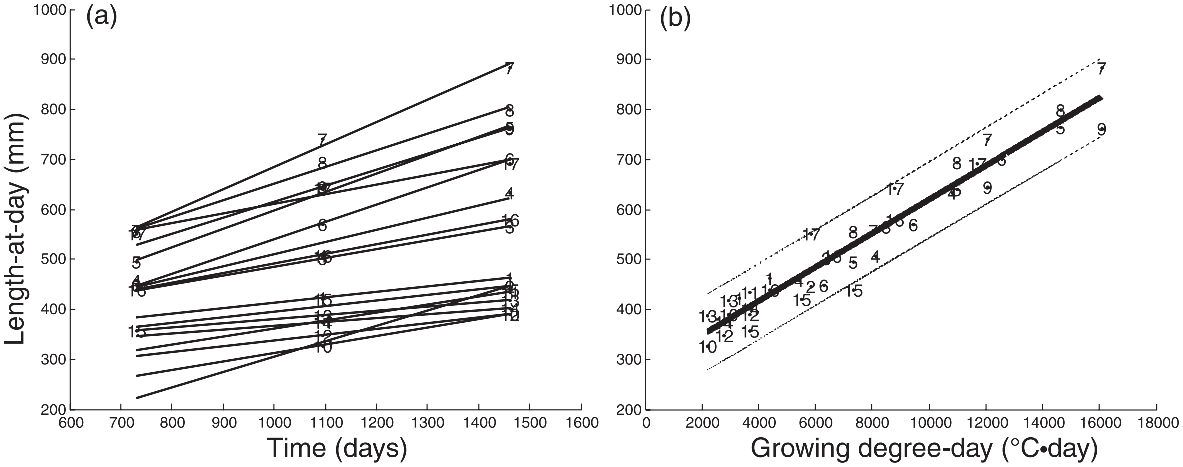
Fig. 5. Length-at-day (LaD) for 17 stocks of age-2 to -4 North Atlantic cod (Brander 1995) as a function of (*a*) calendar time (no significant relation among stocks, linear regression, $P = 0.097$) and (*b*) growing degree-day (GDD) (significant relation among stocks: LaD = 0.034GDD + 280; $r^2 = 0.93$, $P < 0.0001$ with 95% confidence intervals for the prediction (broken lines)). Data labels are stock identifiers (cf. Brander 1995): East and West Greenland (1), Northeast Arctic (2), Iceland (3), Faroe (4), West Scotland (5), North Sea (6), Celtic Sea (7), Irish Sea (8), Eastern Channel (9), Labrador/Grand Bank (10), Southern Grand Bank (11), Northern Gulf of St. Lawrence (12), St. Pierre Bank (13), Southern Gulf of St. Lawrence (14), Eastern Scotian Shelf (15), Western Scotian Shelf (16), and Georges Bank (17).



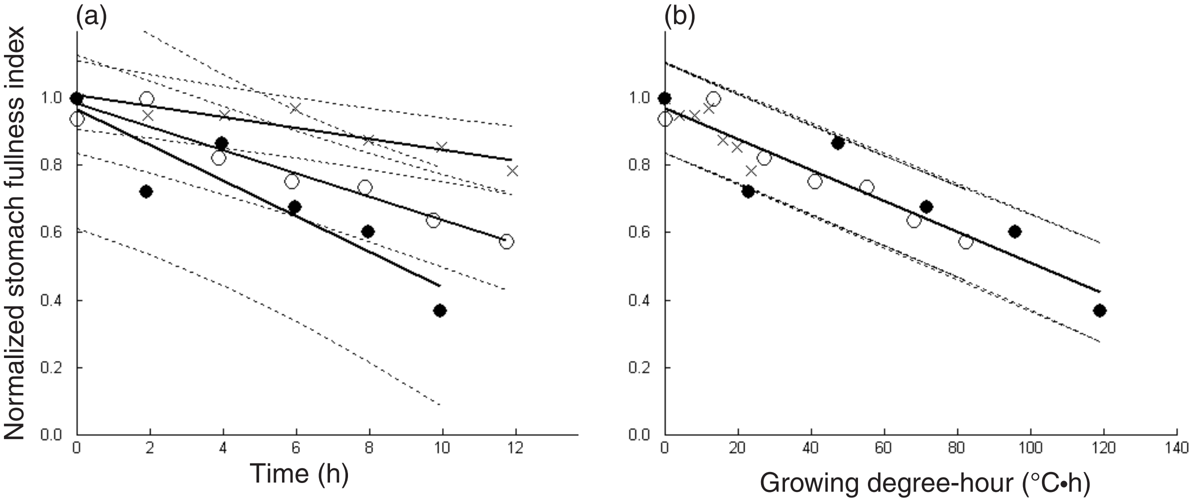
stocks is greater than that within. We are able to demonstrate that although there is a well known and nearly threefold range in length-at-age across the 17 stocks examined — a range attributable to differences in habitat temperature among the stocks (Brander 1995) — fully 93% of the variation in LaD is explained as a single linear function of GDD, i.e., the length of any cod, no matter its stock and habitat–temperature association, is very predictable (±19% being the 95% prediction interval; Fig. 5) from the GDD metric, despite the fact that each stock has its own size-at-age (calendar time) relation owing to differences in their thermally controlled growth rate. Such stock-specific length-at-age relations for many species abound in the literature.

Critical assumptions and unresolved questions

The temperature measures used to estimate GDD must be representative of that experienced by the organism. This ideally requires measurements at a sufficiently high frequency in the locale where the organism is growing. Much literature involving the application of the GDD metric to plant species has focused on microclimates near the plant (Wang 1960). Owing to the high heat capacity of the aquatic environment, the time and space decorrelation scales are typically large relative to terrestrial locales, allowing temperature to be less-frequently estimated and at a larger spatial scale. Further, the thermal acclimation limits of most aquatic ectotherms compromise their ability to move across thermal gradients. Nevertheless, evidence for the necessity of reliable local temperature estimates is found in a study (Kjellman et al. 2001) on European perch (*Perca fluviatilis*) and zander (*Sander lucioperca*, formerly *Stizostedion lucioperca*). There, differences in size-at-age among bay-specific populations disappear within species when a bay-specific GDD is used in place of bay-specific parameterizations based on local air temperature (Kjellman et al. 2001). Further, representative GDD must include the entire thermal history of the organism up to the point of interest (Trudgill et al. 2005), e.g., from hatch or spawning date to a given size or development stage. The more complete the temperature time series, the more the variation in LaD will be explained, as it is the complete (i.e., integrated) thermal history of the fish that contributes to the size-at-age. For example, the New Zealand snapper (*Pagrus auratus*) data (Francis 1994) begin with a hatch date (1 January) near the maximum spawning period and we are able to determine LaD as a strong function of GDD ($0.97 < r^2 < 0.98$) with statistically similar relations among year-classes (ANCOVA: similar slopes, $P = 0.26$; similar intercepts, $P = 0.78$). However, the burbot (*Lota lota*) data (Kjellman and Eloranta 2002) begin at arbitrary starting points in relation to the thermal history of the fish, and although the strength of the LaD-at-GDD relation is maintained ($0.98 < r^2 < 0.99$), the relations between the two year-classes are marginally different (ANCOVA: slopes, $P = 0.058$; intercepts, $P = 0.035$). It is difficult to know if the contrast between the snapper and the burbot examples is due simply to the choice of start date relative to the entire thermal history. It seems that the GDD method maintains strength in the face of temperature data that may be compromised by location, frequency, or completeness of measurement. However, when care is made to optimize these criteria, the GDD is frequently able to explain variation in LaD within as well as among different groups (e.g., locations, year-classes), something that calendar time cannot achieve unless the fish grow in a constant thermal environment. It is here that the increasing amount of archival tag data (e.g., Palsson and Thorsteinsson 2003) may provide unequivocal substantiation of the utility of the GDD measure owing to the relatively high-frequency temperature measures provided over the recorded thermal history of the tagged fish, although getting a comparable length-at-age series may be challenging; we offer microscale accelerometry as a possible avenue of exploration and such development is now underway (D. King, VEMCO Ltd., 77 Chain Lake Drive, Halifax, Nova Scotia, personal communication).

We stress the importance of measuring the length of the fish in studies where the intent is to use a thermal integral. Al-

Fig. 6. Normalized stomach fullness index (nSFI) as a function of (*a*) calendar time and (*b*) growing degree-hour (GDH, °C·h) for freshwater sculpin held at 2 °C (crosses), 7 °C (open circles), and 12 °C (solid circles). Stomach fullness index (SFI) was calculated by Miyasaka et al. (2005) with SFI = $\log_e\{[1000(\text{dry mass of stomach contents})/(\text{dry mass of fish body})] + 1\}$. We have normalized the SFI within temperature trials where nSFI = SFI/(maximum SFI). The linear regression (solid line) and 95% prediction intervals (broken lines) are provided for each (see Supplemental Table S3 for details).[2]



though weight, as a function of length, should, in general, be explained by GDD, seasonal variations in weight-at-age compromise the size measure in contrast with length-at-age that is relatively invariant on a seasonal basis. The latter case is the reason that we converted Brander's (1995) cod weight-at-age to length-at-age (see Supplementary Appendix).[2]

Summary and future directions

Each of the above examples demonstrates that, with basic information on variation in the thermal environment, the physiological time-scaling provided by the GDD explains most of the temperature-related variation in length-at-age (inferred growth) prior to maturation and perhaps beyond. This appears to apply within and among stocks and populations of a given fish species, something that cannot be achieved using calendar time unless the thermal histories are very similar. It appears that the GDD has similar utility in explaining variation in life history development and stage transitions through the thermal constant. Thus, the GDD appears as an essential metric to explain a large amount of variation that is observed in fish growth and development, variation that is frequently attributed to temperature, but often with limited success or in an overly complicated manner, simply because a physiologically scaled temperature measure was not used. Such physiological scaling via GDD could be incorporated into fish simulation models and likely advance such models by avoiding the complications that result from different responses to time-varying and time-constant temperature environments (e.g., Neill et al. 2004). Indeed, identifying a correct physiological timescale through the use of GDD may advance many aspects of aquatic ectotherm research from population-wide studies (e.g., timing of coral bleaching; Berkelmans 2002) to physiological timing within an individual. An example of the latter is the temperature-related variation in the rate of gastric evacuation associated with fish food consumption. In evacuation trials, the fish can be held at different trial-specific constant temperatures, and following the cessation of feeding, the reduction in stomach content (e.g., fullness index) over time is used as an estimate of evacuation. Miyasaka et al. (2005) used this method to determine gastric evacuation in freshwater sculpin (*Cottus nozawae*) held at constant temperatures of 2, 7, and 12 °C. As with our size-at-age analyses above, we show, in accord with Miyasaka et al. (2005), that calendar time requires three separate parameterizations, one for each trial (Fig. 6*a*) (ANCOVA: different slopes, $P = 0.0081$). When assessed using the thermal integral (here using growing - degree-hour (GDH)), we can explain the variation in the normalized stomach fullness index (nSFI) within and among trials using a single parameterization (ANCOVA: similar slopes, $P = 0.49$; similar intercepts, $P = 0.92$; nSFI = –0.0046GDH + 0.97; $r^2 = 0.88$, $P < 0.0001$). We offer this example simply to demonstrate that when the physiologically relevant and short timescale GDH is employed, it clearly explains the different rates in the physiological processes (digestion and evacuation) at the time and temperature scales at which they are occurring.

The implications of not using a physiologically scaled temperature become apparent when we examine the effect of a small increase in daily temperature on a predicted LaD. By example, when the daily temperatures for the 2000 year-class of age-0+ Arctic grayling (Figs. 2*i* and 2*j*) are uniformly raised by 0.6 °C or less, we cannot statistically detect a significant difference between the means of the original and elevated temperature series (neither normal, Wilcoxon rank sum, $P = 0.096$) (Fig. 7) because the variance within is greater than between. However, the GDD method predicts a significant ~5% increase (89–93 mm) in the length-at-day of the grayling at the end of their first growing season based on the elevated temperature record, a change in size that cannot be explained by the change (not significant) in the mean temperature. The LaD estimates from the two series diverge because original and adjusted temperature-based GDD series diverge as the heat transferred from the environment to the fish accumulates. The effect (expected LaD) will magnify

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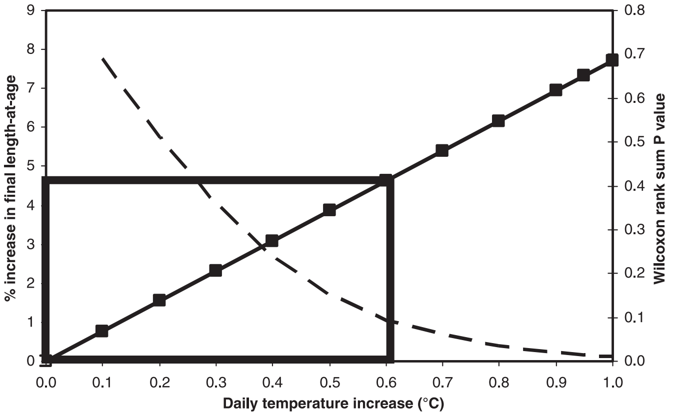
Fig. 7. Percent increase in predicted final length-at-age (mm) (squares and solid line) for the 2000 year-class of age 0+ Arctic grayling (Dion and Hughes 2004) as a function of growing degree-day when the daily temperature series is uniformly increased between 0.1 and 1.0 °C in 0.1 °C increments. The broken line defines the *P* value of a Wilcoxon rank sum test assessing the difference between the mean temperature of each elevated series relative to the original series. The boxed region indicates the predicted increase in length-at-age that cannot be predicted from differences (not significant) in the mean temperature (i.e., mean temperature of original and perturbed temperature series are statistically similar at a conservative *P* > 0.09).



with time (age). Therefore, this physiologically relevant measure of temperature (heat integral) is essential in predicting the response of fish size-at-age to even small changes in temperature, simply because the changes are integrated by the fish over time. Thus, the GDD metric may prove relevant in resolving size-at-age changes in relation to small changes in ocean temperature (e.g., 0.3 °C increase in the 0–300 m ocean stratum from the 1950s to 1990s; Levitus et al. 2000) being reported as a result of global warming.

Although the GDD method has a proven record in explaining growth and development variation among ecototherms for some considerable time (decades to centuries), we know of no previous demonstrations that show GDD to be equally and generally applicable in explaining growth variation (size-at-age) in a variety of fish species and environments, in control and field studies, over large and small spatial and temporal scales.

The GDD appears to have greater explanatory power than contemporary fish growth models. Clearly, “If the life-table, or population model, is to predict the population dynamics correctly, it must work on the correct time-scale. In the case of homeotherms, the correct time-scale is, clearly, calendar time.... If we base [a fish] population model on calendar time, we must allow for the effect of temperature. But it is much simpler to base the model on the [fish’s] own ‘physiological’ time-scale, which is a combination of calendar time and temperature.” (Gilbert et al. 1976, pp. 15–16). Thus, we challenge others to test the GDD metric in all aspects of fish and aquatic invertebrate physiology, growth, and development. We set this challenge because most ectotherms use similar chemical constituents and thermally controlled reaction rates to create an amazing variety of forms across large time and temperature scales. The question has been asked: “Do biological phenomena obey underlying universal laws of life that can be [parameterized] so that biology can be formulated as a predictive, quantitative science?”(West and Brown 2004). Perhaps a convergence of fish physiology, growth, and development, under the scaling of physiological time as provided by the GDD, with that already established in agricultural and entomological research will provide a significant step toward such an underlying law for ectotherm growth and development.

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