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ARTICLE

Fish growth and degree-days I: selecting a base temperature for a within-population study

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Abstract: Degree-days (DD) are an increasingly popular method for explaining variation in fish growth and development. By including a base temperature (T_o) the DD formula limits calculations to temperatures that are relevant to growth. However, our review of growth studies shows multiple T_o values in use for a given fish species. To determine how T_o affects the ability of DD to explain within-population growth variation, we first show that the ability of DD to describe a growing season is robust to low values of T_o. We then analyze immature length data from eight species and 85 water bodies in North America to show that there is a broad range of T_o values that effectively explain growth variation. Based on these results, we argue that precise T_o estimates are unwarranted for most single-population studies and recommend standard T_o values (0, 5, 10, 15 °C). Standardization facilitates comparative studies and promotes the use of DD in future research. To this end, we provide equations for converting annual DD at a given T_o to annual DD at a standard T_o.

Résumé : Les degrés-jours (DJ) constituent une méthode de plus en plus usitée pour expliquer les variations associées à la croissance et au développement des poissons. L'incorporation d'une température de base (T_o) dans la formule des DJ limite les calculs aux températures pertinentes pour la croissance. Un examen des études sur la croissance indique toutefois que de multiples valeurs de T_o sont utilisées pour des espèces de poissons données. Afin de déterminer l'incidence de T_o sur l'adéquation des DJ pour expliquer les variations de croissance au sein d'une population, nous démontrons d'abord l'adéquation des DJ pour décrire une période de croissance jusqu'à de faibles valeurs de T_o. Nous analysons ensuite des données sur la longueur de poissons immatures pour huit espèces et 85 plans d'eau en Amérique du Nord pour démontrer qu'il existe une grande fourchette de valeurs de T_o qui permettent d'expliquer adéquatement les variations de croissance. À la lumière de ces résultats, nous postulons que des estimations précises de T_o ne sont pas nécessaires pour la plupart des études sur des populations individuelles et recommandons l'utilisation de valeurs de T_o normalisées (0, 5, 10, 15 °C). Une telle normalisation facilite les études comparatives et favorisera l'utilisation de DJ dans des travaux futurs. Nous présentons à cet effet des équations pour la conversion de DJ annuels pour une T_o quelconque en DJ annuels pour une T_o normalisée. [Traduit par la Rédaction]

Introduction

The metabolic rate of fish and other ectotherms is largely determined by the ambient temperature of their environment (Hazel and Prosser 1974) and increases linearly over a midrange of temperatures (Sharpe and DeMichele 1977). The amount of midrange ambient thermal energy that an ectotherm has experienced can be quantified using a degree-day approach (also known as thermal time, e.g., Trudgill et al. 2005). The degree-day for a single day (DD; °C·days) is calculated as

$$(1)\qquad \mathrm{DD} = \left(\frac{T_{\mathrm{Max}} + T_{\mathrm{Min}}}{2}\right) - T_o$$

where T_{Max} and T_{Min} are the maximum and minimum daily ambient temperatures, respectively, and T_o (often referred to as the base or threshold temperature) is the temperature below which growth or development is nonlinear and effectively zero. When non-negative DD values are summed over some period of interest, the resultant cumulative degree-days at a given T_o (CDD_{T_o}; °C·days) is an index of the metabolically relevant thermal energy that was experienced over that period. This index is useful for describing concurrent patterns of growth and development (e.g., Neuheimer and Grønkjær 2012; Venturelli et al. 2010).

Although DDs have been used for decades to describe growth and development in plants (e.g., Reaumur 1735, cited in Bonhomme 2000) and insects (e.g., Seamster 1950; Thorup 1963), this approach is rare in fish science, accounting for only 5% of all temperature-related growth studies between 1980 and 2006 (Neuheimer and Taggart 2007). Relationships between temperature and development in fish are well understood (e.g., Morrow and Mauro 1950; Paloheimo and Dickie 1966; Fry 1971; Kitchell et al. 1977), but for decades the DD approach was limited to egg development (e.g., Wallich 1901). DDs were first applied to growth by Le Cren (1958), but it was not until the late 1970s that this application began to increase in popularity (Chezik 2013). This increase appears to have been facilitated by the use of air temperatures as a surrogate for surface water temperatures (e.g., Ney and Smith 1975; Colby and Nepszy 1981). Air temperatures are highly correlated with surface water temperatures (e.g., Macan and Maudsley 1966; Reuter et al. 2009), and air temperature records are typically more extensive and complete. Therefore, air temperatures permit growth studies

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Table 1. A summary of published T_o values used in growth studies of freshwater fishes within a single water body or localized region.

Scientific name	Common name	Age (s)^a	T_o (°C)	Temp.^{b}	Just.^{c}	Reference	Adoption frequency
Abramis brama	Common bream	0	12.8	W	1	Mooij et al. 1994	2
Aplodinotus grunniens	Freshwater drum	1–10	9.0	W	2	Braaten and Guy 2002	0
Barbus barbus	Barbel	0	13.5	W	3	Baras and Philippart 1999	0
Carassius carassius	Crucian carp	0–2	12.0	W	4	Copp et al. 2008	1
Carpiodes carpio	River carpsucker	1–8	10	W	2	Braaten and Guy 2002	0
Coregonus clupeaformis	Lake whitefish	2–3	5	A	9	Rennie et al. 2009	0
Esox lucius	Northern pike	Juvenile	7	W	2	Bry et al. 1991	0
		Unknown	10	W	5	Frost and Kipling 1967	3
Gobio gobio	Gudgeon	0	12	W	9	Cowx 2000	0
Gymnocephalus cernua	Ruffe	0	7.6	W	1	Mooij et al. 1994	0
Lepomis gibbosus	Pumpkinseed	0	14	W	2	Murphy et al. 2012	0
Lepomis macrochirus	Bluegill	0	14	W	2	Murphy et al. 2011	0
Leuciscus leuciscus	Common dace	0	12	W	9	Cowx 2000	0
		0	12	W	3	Mills and Mann 1985	4
Lota lota	Burbot	1–3	0^d	W	9	Kjellman and Eloranta 2002	0
Macrhybopsis meeki	Sicklefin chub	1–2	10	W	2	Braaten and Guy 2002	0
Micropterus salmoides	Largemouth bass	0	0	W	9	Schlosser et al. 2000	0
Morone americana	White perch	0	15	W	2	O'Gorman and Burnett 2001	0
Notropis atherinoides	Emerald shiner	1–2	7	W	2	Braaten and Guy 2002	0
Oncorhynchus clarkii	Cutthroat trout	0	5	W	2	Coleman and Fausch 2007	1
Osmerus eperlanus	European smelt	0	–3.6	W	1	Mooij et al. 1994	1
		1–2	5	A	7	Power and Attrill 2007	0
Perca flavescens	Yellow perch	0	0	W	2	Mills et al. 1989	0
		0	4.4	A	9	Ney and Smith 1975	0
		0	10	A	9	Ney and Smith 1975	0
		2–4	14	W	5	Henderson 1985	0
		0	13.5	W	5	Tardif et al. 2005	0
Perca fluviatilis	European perch	1	0^d	W	9	Borcherding and Magnhagen 2007	1
		0	9.8	W	1	Mooij et al. 1994	4
		0	14	W	9	Griffiths and Kirkwood 1995	0
		1–14	14	W	2	Le Cren 1958	8
Rhodeus amarus	European bitterling	0	12	W	2	Konečná et al. 2009	0
Rutilus rutilus	Roach	0	10.2	W	1	Mooij et al. 1994	1
		0	11.5	W	1	Mooij and van Tongeren 1990	1
		0	12	W	9	Cowx 2000	0
		0	12	W	4	Grenouillet et al. 2001	0
		0	12	W	4	Nunn et al. 2003	3
		1–5	13	W	3	Müller and Meng 1986	0
		0	14	W	3	Broughton and Jones 1978	0
		0	14	W	9	Griffiths and Kirkwood 1995	0
		0	16	W	3	Kempe 1962	0
		0	17.5	W	1	Mooij et al. 1994	1
Salmo salar	Atlantic salmon	1	0^d	W	9	Jonsson et al. 2005	0
		Unknown	0^d	W	9	Skinner et al. 2008	0
Salmo trutta	Brown trout	0–1	0^d	W	8	Baglinière and Maisse 1990	0
		0	0^d	W	9	Ojanguren and Braña 2003	0
Sander canadensis	Sauger	1–6	5	W	2	Braaten and Guy 2002	0
Sander lucioperca	Pikeperch (i.e., zander)	0	10	W	1	Mooij et al. 1994	2
Sander vitreus	Walleye	0	5	A	10	Uphoff et al. 2013	0
Semotilus atromaculatus	Creek chub	0	0	W	9	Schlosser et al. 2000	0
Squalius cephalus	European chub	0	12	W	2	Mann 1976	1
		0	12	W	4	Nunn et al. 2003	2
Thymallus thymallus	Grayling	0	0^d	W	9	Haugen 2000	1
Multiple species	—	0–1	12	W	4	Wolter 2007	0

Note: Adoption frequency refers to the number of times that an estimated T_o value was adopted in later studies involving the same species.

^{a}Age-0 refers to young of the year; all other values are age classes.

^{b}Temperature: W = water; A = air.

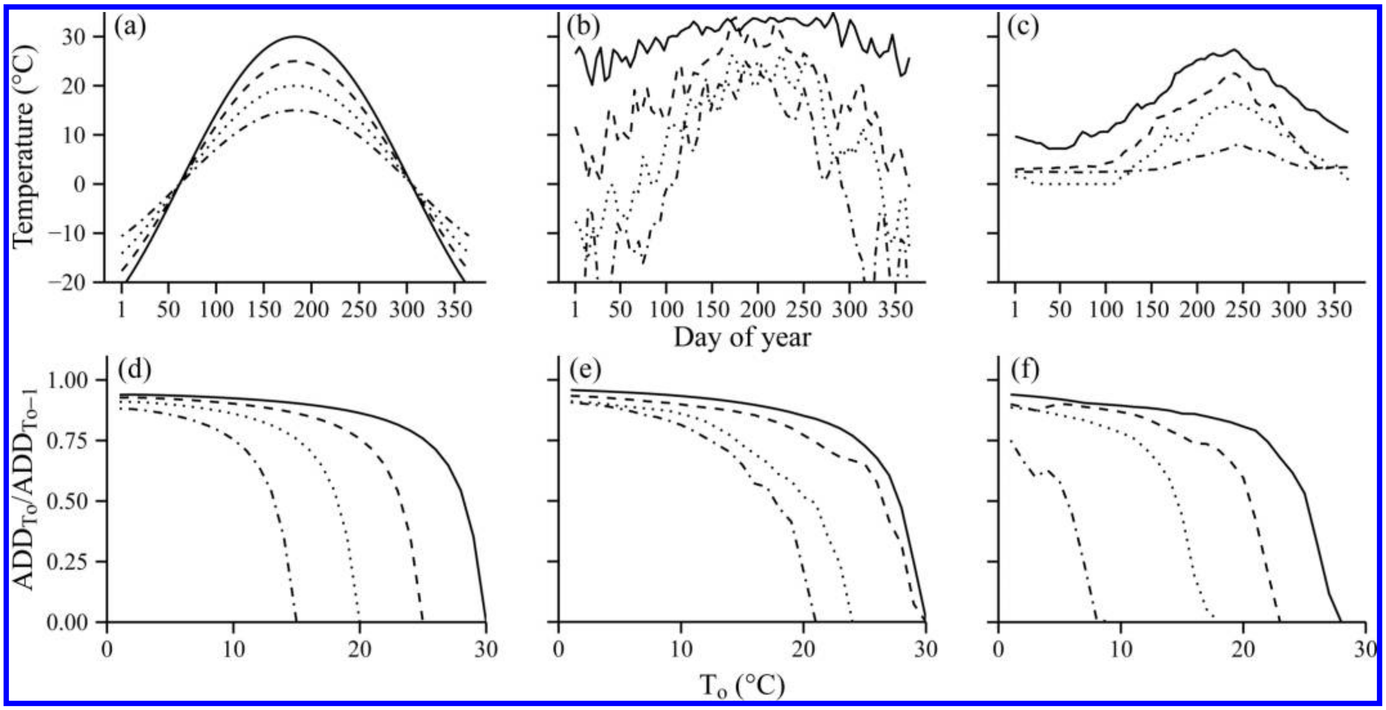
^{c}Justification (why the study chose the given T_o value): 1 = fit a growth model (e.g. bioenergetics model), 2 = minimum temperature for physiological process, 3 = goodness of fit (e.g., T_o that maximizes r^2), 4 = used for common dace (Mills and Mann 1985), 5 = used for European perch (Le Cren 1958), 6 = commonly used in plant studies, 7 = physiologically relevant to *O. mordax*, 8 = used for Atlantic salmon egg survival (Ketola et al. 2000), 9 = none given, 10 = used in Shuter et al.'s 1983 among-population study.

$^d T_o$ not reported; assumed to be 0 °C.

over large spatial and temporal scales (e.g., Purchase et al. 2005; Wagner et al. 2007; Latta et al. 2008) and when local time series of water temperature are incomplete or unavailable (e.g., Rennie et al. 2009; David 2012; Rypel 2012).

The DD approach to describing fish growth is increasing in popularity, but a review of the freshwater literature shows a diversity of methods for estimating T_o and a diversity of T_o values in use for a given species (Table 1). More often than not, T_o values

Fig. 1. Annual temperature curves and associated values of ADD_{T_o} expressed as a proportion of ADD_{T_o-1}. Data in panels (*a*) and (*d*) are from a sine curve (eq. 2) with *w* values of 15 °C (dot-dashed line), 20 °C (dotted line), 25 °C (solid line), and 30 °C (dashed line). Data in panels (*b*) and (*e*) are from daily 2009 T_{Min} and T_{Max} values at weather stations (NOAA, unpublished data, National Climatic Data Center) in Bettles, Alaska (dot-dashed line), Duluth, Minnesota (dotted line), Springfield, Missouri (solid line), and Everglade City, Florida (dashed line). Data in panels (*c*) and (*f*) are from daily mean temperature values taken above the thermocline within Shadow Bay of Lake Chaeukuktuli, Alaska, 2008 (dot-dashed line) (Darrell S. Kaufman, unpublished data, climatic records from lakes in southern Alaska), Lake Superior, Minnesota, 1992 (NOAA, unpublished data, index of publications and tech reports) (dotted line), Pillager Lake, Minnesota, 2011 (Andrew Carlson, MNDNR, unpublished data, 1601 Minnesota Drive, Brainerd, MN 56401, USA) (solid line) and Lake Powell, Utah, 2011 (dashed line) (Wayne Gustaveson, unpublished data, http://lakepowell.water-data.com/).



are used without justification. When justification is provided, it is usually that T_o was (*i*) based on the minimum temperature for some physiological process (growth, feeding, spawning, etc.), (*ii*) estimated via model fitting (e.g., bioenergetics, regression), or (*iii*) taken from other (sometimes unrelated) fishes or even plants (Table 1). Among freshwater species, reported values of T_o range from –3.6 °C for European smelt (*Osmerus eperlanus*) to 18 °C for spotted gar (*Lepisosteus oculatus*). Within species, T_o can range from 0 to 14 °C (yellow perch (*Perca flavescens*); European perch (*Perca fluviatilis*)) and take as many as seven different values (roach (*Rutilus rutilus*); Table 1). This diversity appears to be due, in part, to a tendency to estimate T_o anew rather than to adopt an existing estimate (Table 1).

There are at least four potential reasons to be concerned about the inconsistency with which T_o values for fish growth are being estimated (or simply adopted). First, different approaches to estimating or justifying T_o are likely to lead to different values, even for the same population. For example, T_o for roach in a Dutch lake was 11.5 °C in the lab, 10.2 °C when fitting a growth model to field data, and 17.5 °C when using this model to predict growth in the field (Table 1). Second, the same estimation method can yield different T_o values for different populations (e.g., goodness of fit applied to roach; Table 1), which suggests that we must estimate T_o for every population. Third, different T_o values can lead to differences in the ability of DDs to explain or predict growth. These differences arise because T_o determines the extent to which DDs integrate thermal energy that is relevant to growth. This point argues for the adoption of a single, robust estimation method across studies and cautions against adopting T_o values from different species. Finally, variation in T_o hinders the comparison and interpretation of DDs and growth rates among populations and studies. For example, whereas Abbey and Mackay (1991) reported a yellow perch growth rate of 0.02 mm·(°C·day)$^{-1}$ using T_0, Power and van den Heuvel (1999) reported 0.09 mm·(°C·day)$^{-1}$ when using $T_{13.5}$.

In this study we address potential concerns over variation in T_o among within-lake studies of DDs and growth. Specifically, we use simulated and empirical data to (*i*) determine how variation in T_o affects the ability of DDs to account for within-lake variation in immature growth and (*ii*) identify the scope for standardized T_o values in future within-lake growth studies. Our interest is in T_o from an applied rather than a theoretical perspective. In theory, there is a precise, species- or population-specific temperature below which growth rate is effectively zero (Charnov and Gillooly 2003), and it is therefore appropriate to set T_o to this value. However, if the ability of DDs to explain growth is robust to T_o, then from an applied perspective, it is appropriate to abandon precise T_o estimates in favour of a standardized value or set of values.

The effect of T_o on degree-days

A logical first step in determining how the ability of DDs to explain growth changes with T_o is to determine how DDs themselves change with T_o. To this end, we assumed that annual temperature cycles are well approximated by a sine curve (Arnold 1959; Shuter et al. 1983). Annual degree-days above some T_o (ADD_{T_o}; °C·days) are then given by the area under this curve (Baskerville and Emin 1969):

$$(2) \qquad \mathrm{ADD}_{T_o} = \frac{365}{\pi}\left[w\int_{\theta}^{\frac{\pi}{2}} \sin t\, dt - \int_{\theta}^{\frac{\pi}{2}} (T_o - T_{\mathrm{Mean}})dt\right]$$

where *t* is day in year, 365 is the cycle period, $w = \dfrac{T_{\mathrm{Max}} - T_{\mathrm{Min}}}{2}$, T_{Mean} is mean annual temperature, and $\theta = \dfrac{T_o - T_{\mathrm{Mean}}}{w}$ (Fig. 1*a*). To determine

Table 2. Species-specific summary of fish data from both the OMNR and MNDNR.

Scientific name	Common name	Water bodies	ADD_0 range	Cohorts	Fish
Catostomus commersonii	White sucker	1	2523–3083	6	54
Coregonus artedi	Cisco	1	2617–3132	5	135
Esox lucius	Northern pike	1	2482–3084	5	113
Lepomis macrochirus	Bluegill	2	2584–3637	11	116
Morone chrysops	White bass	1	3153–3863	6	62
Perca flavescens	Yellow perch	8	2517–3567	93	3 652
Sander canadensis	Sauger	6	2295–4110	86	2 680
Sander vitreus	Walleye	81	1886–4110	976	40 674

Note: ADD_0 range is the observed range of annual degree-days above 0 °C across all cohorts and water bodies, and cohorts refer to the number of unique age classes in a given sampling year summed across all sampling years and water bodies. OMNR, Ontario Ministry of Natural Resources; MNDNR, Minnesota Department of Natural Resources.

the effect of T_o on ADD_{T_o}, we used eq. 2 to calculate ADD_{T_o} for all integer values of T_o in the range 0 to 30 °C and for four values of w (15, 20, 25, and 30 °C). Increasing the threshold (T_o) decreased the summable area under the curve (i.e., ADD_{T_o}), and increasing w increased available thermal energy (i.e., decreased latitude). For each w, we then expressed each value of ADD_{T_o} as a proportion of ADD_{T_o-1} (Fig. 1*d*). Results suggest that $\text{ADD}_{T_o} \approx \text{ADD}_{T_o-1}$ for a range of T_o values ≥1 °C and that the extent of this plateau increases with w (Fig. 1*d*). In other words, a 1 °C change at low T_o results in relatively similar ADD_{T_o} values, while a 1 °C change at high T_o results in relatively different ADD_{T_o} values. We observed a similar pattern in both air (Figs. 1*b* and 1*e*) and water (Figs. 1*c* and 1*f*) temperature data from the Gulf Coast to Alaska. Overall, these results suggest that our ability to describe a growing season using DDs is largely robust to T_o regardless of medium, provided that T_o is not too large (or w is not too small).

The effect of T_o on explained variation in growth

If our ability to describe a growing season using DDs is robust to T_o, then our ability to use DDs to explain growth within a population should also be robust to T_o. To test this hypothesis, we compiled fish and temperature data from Ontario, Canada, and Minnesota, USA, and regressed cohort length-at-age of each population against cumulative DDs for a range of T_o values. We used the coefficient of determination (r^2) of each length|DD regression as a measure of the effect of T_o on explained variation in species-specific growth within a water body. This method has been developed independently by Baras and Philippart (1999) and Neuheimer and Taggart (2007) and was applied to a population of walleye (*Sander vitreus*) by Venturelli et al. (2010). We used the goodness of fit (r^2) approach and empirical rather than simulated growth data to test our hypothesis because (*i*) the r^2 approach allowed us to both identify and evaluate the performance of each T_o value, (*ii*) empirical growth data integrate both direct (i.e., metabolic) and indirect (i.e., productivity-based) temperature effects, and (*iii*) we are ultimately interested in the ability of DDs to explain growth in natural environments.

Methods

Fish data

We created a database of individual fish records that combined the Ontario Ministry of Natural Resources (OMNR) fall walleye index netting database (1993–2008) with the Minnesota Department of Natural Resources (MNDNR) statewide database (2001–2011) and supplemental data (2001–2011) from Minnesota's ten large lakes (Winnibigoshish, Rainy, Vermillion, Leech, Cass, Pepin, Mille Lacs, Kabetogama, Lake of the Woods, and Upper Red Lake). Minnesota data were collected between March and December using a variety of methods (e.g., electrofishing, gillnetting, trap-netting, trawling, trot-lining, seining, angling). Ontario data were collected between September and November using multimesh gillnets set overnight at multiple depths (Morgan 2002).

For each fish we were interested in the following information: water body, sample date (day, month, and year), species, age (years), total length (L; mm), maturity, and aging structure. We focused on immature fish so that our analyses of somatic growth were not confounded by the allocation of surplus energy to reproduction. This approach can create a small bias in the growth trajectory if it removes the fast-growing (i.e., early-maturing) fish from the oldest cohort(s). We also focused on fish that were aged using a reliable aging structure or sampled at the start or end of the growing season. We avoided unreliable aging structures because the accuracy of the DD assignment depended on the accuracy of age estimates (see next section). We assigned reliability to different aging structures using a combination of expert opinion (Mike McInerny, MNDNR, 23070 N. Lakeshore Drive, Glenwood, MN 55041, USA; Susan Mann, OMNR, 479 Government Road, P.O. Box 730, Dryden, ON P8N 2Z4, Canada) and the literature (Campbell and Babaluk 1979; Graeb et al. 2010; Schneider 2001; Soupir et al. 1997; Trippel and Harvey 1991). For example, we assumed that only age-0 fish were accurately aged in the field and that only walleye ≤age-5 were accurately aged using scales. We also used expert opinion (MNDNR) to define the growing season as June through August, inclusive. We avoided records that were sampled during this period because there is currently no validated protocol for combining whole- and partial-season DDs in a single analysis.

Our final database contained 47 486 fish records representing eight species from 64 water bodies in Ontario, Canada, and 21 water bodies in Minnesota, USA (Table 2). Walleye comprised the majority of the database (86% of all fish), followed by other percid species (14%).

Temperature data

We assigned CDD_{T_o} values to each fish by summing the annual DDs that each fish experienced prior to capture. This approach required time series estimates of ADD_{T_o} for each water body. For water bodies in Minnesota, we calculated ADD_{T_o} time series (2001–2011) using 100 km² resolution maps of kriging-interpolated air temperature data (T_{Min} and T_{Max}). These data were collected from automated weather stations owned and operated by the National Weather Service and assembled and processed by the Minnesota State Climatology Office–MNDNR. We calculated ADD_{T_o} by applying eq. 1 to daily T_{Min} and T_{Max} values from the grid point closest to the centroid of the water body of interest and then summing across non-negative DD values in that year. Because our objective was to determine the effect of T_o on explained variation in growth, we repeated these DD calculations for each integer value of T_o in the range 0–30 °C (the range of water temperatures that a temperate, freshwater fish is likely to experience in a given growing season). Thus, we generated a unique time series of ADD_{T_o} values for all water bodies and T_o values. For water bodies in Ontario, we obtained ADD_{T_o} time series (1981–2008) using the Historical Climate Analysis Tool (Cross et al. 2012), which automatically applied the above protocol to 1 km² resolution maps of kriging-interpolated T_{Min} and T_{Max} data.

We used age, together with capture year and month, to determine the CDD_{T_o} that each fish experienced prior to capture. Because fish are aged to a January 1 birthday (Holden and Raitt 1974), we used different summation rules for different capture months. For fish captured during the period January to May (i.e., after their common birthday but before the start of a growing season), we summed ADD_{T_o} across the previous n growing seasons, where n is the age of the fish in years. Thus, if a 2-year-old fish was captured in January 2005, we calculated CDD_{T_o} as the sum of ADD_{T_o} values from 2003 to 2004. For fish captured during the period September to December (i.e., before their common birthday but after the previous growing season), we calculated CDD_{T_o} by summing ADD_{T_o} across the previous $n + 1$ growing seasons, beginning with the current year of capture. Thus, if a 2-year-old fish was captured in September 2005, we summed ADD_{T_o} values from 2003 to 2005.

Statistical analyses

Our analyses included populations for which we had ≥5 cohorts distributed over ≥3 age classes that each contained ≥5 individuals (sexes combined). We set these minima to ensure that growth was accurately described and not unduly influenced by outliers. For each population, we calculated mean length-at-age for each cohort. Here "cohort" refers to an age class observed during a sampling event rather than a group of fish that hatched in the same year. This means if we had multiple years of data for a given population, a single age class typically had several mean length estimates (e.g., Fig. 2). We assumed the length (L) of immature fish could be described by a linear model

$$L = m \cdot \mathrm{CDD}_{T_o} + b \tag{3}$$

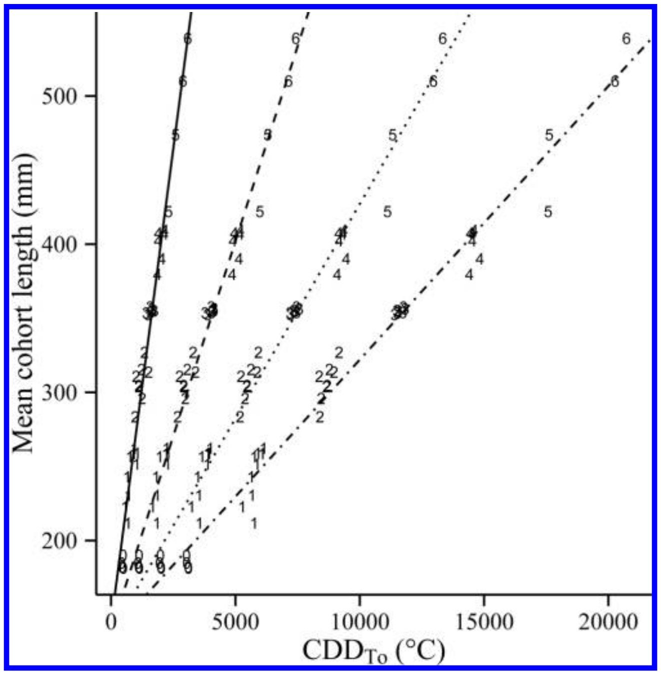
where CDD_{T_o} is the thermal age for a given T_o. We used ordinary least squares to estimate parameters m and b and the coefficient of determination (r^2) for a range of T_o values (0 to 30 °C) — see example in Fig. 2. We then plotted r^2 against T_o to examine how goodness of fit varied with temperature threshold.

Statistically speaking, the relative goodness of fit of different models should be evaluated using AIC because (*i*) r^2 is an inappropriate method for comparing models when the range of the explanatory variable varies among models (which was the case in our study), and (*ii*) r^2 is biased towards models with large ranges in the explanatory variable (Maindonald and Braun 2007). However, whereas both approaches produced qualitatively (and almost quantitatively) identical results, r^2 also quantifies the strength of the relationship and there is precedence for this approach (Baras and Philippart 1999; Neuheimer and Taggart 2007; Venturelli et al. 2010).

Results

Across species and water bodies (Fig. 3), the r^2 method revealed a wide range of T_o values that were effective at describing growth. For all eight species in our database, r^2 values were similar for small values of T_o. Beyond this plateau, r^2 dropped off quickly or became erratic. Erratic behaviour at high T_o was common for species or water bodies that had low sample sizes (i.e., few cohorts or fish per cohort). This plateau in r^2 was evident in all 81 walleye populations in our analysis and had a median value of 14 °C (range 6–21 °C; Fig. 4). Although Fig. 1 suggests that the length of the r^2 plateau increases with the length of the growing season and w in eq. 2, we found no evidence in walleye that the r^2 plateau increased with mean ADD_0 ranging from 2157 to 3733 °C·days (df = 79, $r^2 = 0.04$, p value = 0.062). Visual inspection of each regression and associated diagnostic plots indicated the assumptions of the linear model were met.

Fig. 2. Example mean cohort length-at-age given CDD_{T_o} regression analysis at $T_o = 0$ °C (dot-dashed line), 5 °C (dotted line), 10 °C (solid line), and 15 °C (dashed line). Data are from walleye in Cass Lake, Minnesota. Number points show the age in years of each cohort. Each regression had 36 degrees of freedom, p values < 0.05, and r^2 values ≥ 0.97.



Discussion

In the Introduction, we described four concerns over the inconsistency with which T_o values are being estimated (or adopted) in within-lake growth studies: (*i*) different approaches applied to the same population are likely to lead to different T_o values, (*ii*) identical approaches applied to different populations are likely to lead to different T_o values, (*iii*) different T_o values can lead to differences in the ability of DDs to explain or predict growth, and (*iv*) variation in T_o hinders the comparison and interpretation of DDs and growth rates among populations and studies. Our results suggest that, from an applied perspective, concerns *i*–*iii* are largely unfounded; within a given water body, there is a broad range of T_o values that are almost equally effective at explaining variation in growth. This pattern was consistent across the eight freshwater species (Fig. 3) and among the 81 walleye populations in this study (Fig. 4). It was also apparent in 21 other freshwater and marine species (Baras and Philippart 1999; supplemental material for Neuheimer and Taggart 2007). This broad range of effective T_o values has little to do with limitations on growth at temperatures approaching 0 °C. Rather, it stems from an inherent property of the DD approach, namely that ADD_{T_o} values become increasingly similar as T_o approaches 0 °C (Fig. 1). These results suggest that there is little benefit in precisely estimating T_o when describing growth within a water body. Indeed, given that T_o estimates are likely to vary across methods, populations, and species (Table 1), increased precision is costly in that it complicates comparisons across populations and studies (concern *iv*).

The lack of a need to precisely estimate T_o for a given water body and the benefit of being able to compare results across populations and studies provides ample scope for adopting standard T_o values when describing fish growth. To this end, we recommend standardized T_o values of 0, 5, 10, and 15 °C for growth studies involving freshwater fishes in temperate and Arctic water bodies. These standards are widely used in agronomy and entomology (Pruess 1983) and are common in engineering (e.g., heating and

Fig. 3. The coefficient of determination (r^2) for the relationship between total length (mm) and CDD_{T_o} over a range of T_o values for (*a*) white sucker in Lake of the Woods, Ontario (see Table 2), (*b*) cisco in Leech Lake, Minnesota (see Table 2), (*c*), northern pike in La Cloche Lake, Ontario (see Table 2), (*d*) bluegill in Pumushe Lake, Minnesota (63 individuals across six cohorts), (*e*) white bass in Lac Qui Parle, Minnesota (see Table 2), (*f*) yellow perch in Lake Mille Lacs, Minnesota (2299 individuals, 26 cohorts), (*g*) sauger in Lake Pepin, Minnesota (859 individuals, 21 cohorts), and (*h*) walleye in Lake Pepin, Minnesota (616 individuals, 26 cohorts). Black circles show the approximate extent of each r^2 plateau.

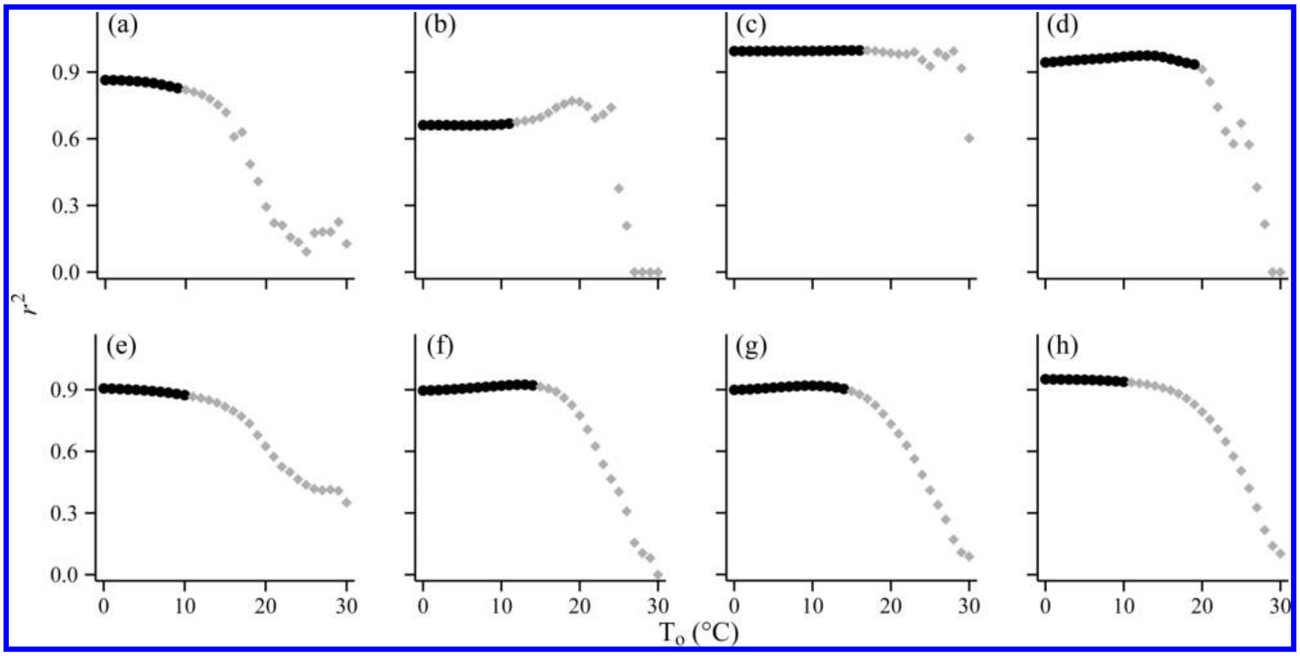
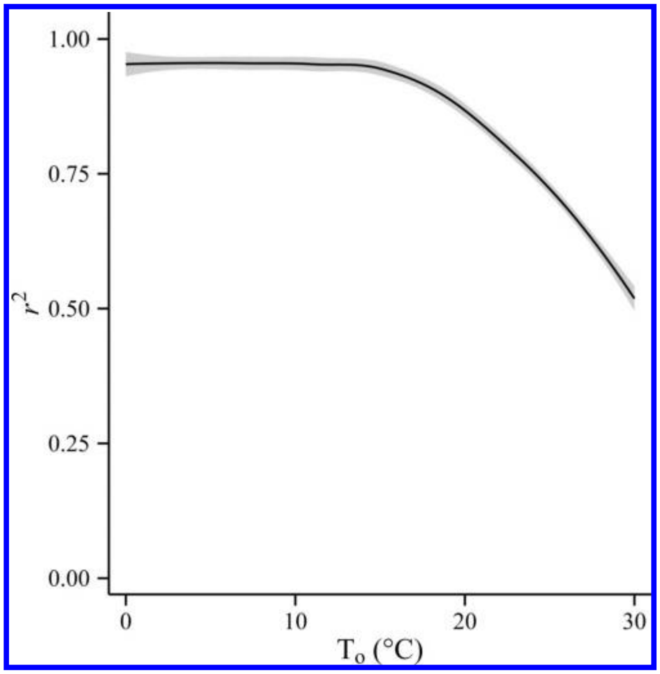


Fig. 4. The coefficient of determination (r^2) for the relationship between total length (mm) and CDD_{T_o} over a range of T_o values, averaged over 81 walleye populations in Minnesota (n = 20) and Ontario (n = 61). The solid line is a LOESS fit (α = 0.65) to all data combined, and the shaded area is the 95% confidence interval.



cooling DDs). As such, air temperature-based DD data for each of these standards are widely available. These standards should apply equally well to marine fishes (at least in temperate and Arctic waters; supplemental material for Neuheimer and Taggart 2007) and processes other than growth (e.g., maturation) because the correlation between ADD_{T_o} values is an inherent property of the DD.

Standardization does not imply that a single threshold model is the best way to account for variation in growth. The bioenergetics literature clearly shows that growth in fish is a complex function of temperature, rather than the simple step function that is assumed by the DD approach; growth rate typically increases as temperature approaches an optimal value and then declines as temperature exceeds the optimum (e.g., Kitchell et al. 1977; Hanson et al. 1997 — Wisconsin Bioenergetics model). Although a single threshold model can approximate the rise in growth with temperature, it does not account for a reduction at high temperature. Thus, the single threshold DD approach assumes that more heat is always better. However, standardization is appropriate for the DD approach because there is a range of T_o values that effectively explain growth in a given species, and these ranges of values overlap considerably among species (Fig. 3). We provide multiple standardized values so as to accommodate the disparate thermal preferences among species (e.g., cold-, cool-, and warm-water species; Magnuson et al. 1979) and simplify the task of assigning a single T_o to a given species or community.

To facilitate the use of 0, 5, 10, and 15 °C as T_o standards in fish science, we used air-based annual DD data from 303 water bodies in Ontario for the period 1981–2008 (n = 8484 water body years) to derive the following linear conversion equation:

$$\mathrm{ADD}_{T_{o,y}} = i + s \cdot \mathrm{ADD}_{T_{o,x}} \tag{4}$$

where

$$i = a_1 \cdot T_{o,x} + a_2 \tag{5}$$

and

Table 3. Parameter values and range limits for using eq. 4 to convert annual degree-days at a given T_o ($\mathrm{ADD}_{T_{o,x}}$) to annual degree-days at one of four T_o standards ($\mathrm{ADD}_{T_{o,y}}$).

	Intercept parameter values		Slope parameter values					
Standard T_o (°C)	a_1	a_2	a_3	a_4	a_5	$T_{o,x}$ range limit (°C)	$\mathrm{ADD}_{T_{o,y}}$ range limit (°C·days)	$\mathrm{ADD}_{T_{o,y}}$ $\overline{\overline{\mathrm{SE}}}$ and ($\sigma_{\overline{\overline{\mathrm{SE}}}}$)
0	126.00	–32.44	0.05	0.99	—	0–8	1809–3725	46 (0.61)
5	96.04	–446.21	1.31	–0.08	0.81	0–12	922–2425	37 (0.32)
10	68.61	–681.79	1.66	–0.05	1.13	2–16	45–1464	26 (0.36)
15	35.98	–544.76	3.77	–0.36	0.75	8–19	43–743	17 (0.24)

Note: Parameter values were estimated for each standard T_o by fitting curves to describe how the slope and intercept of the $\mathrm{ADD}_{T_{o,y}} | \mathrm{ADD}_{T_{o,x}}$ relationship changed with T_o (CurveExpert Professional 1.6.5). Only $\mathrm{ADD}_{T_{o,y}} | \mathrm{ADD}_{T_{o,x}}$ regressions with an $r^2 > 0.90$ were included when describing these relationships. The $T_{o,x}$ range limit indicates the range of T_o values from which conversion is appropriate, and the $\mathrm{ADD}_{T_{o,y}}$ range limit indicates the range of ADD values to which conversion is appropriate. Conversion outside of either of these ranges is likely to result in greater prediction error ($\mathrm{ADD}_{T_{o,y}}$ $\overline{\overline{\mathrm{SE}}}$). We estimated prediction error and its standard deviation via bootstrap validation of eq. 4 (1×10^4 iterations).

$$s = \begin{cases} a_3 \cdot T_{o,x} + a_4, & T_{o,y} = 0 \\ \dfrac{1}{a_3 + a_4 \cdot T_{o,x}^{a_5}}, & T_{o,y} > 0 \end{cases} \tag{6}$$

and where $\mathrm{ADD}_{T_{o,x}}$ is observed annual degree-days, $T_{o,x}$ is the T_o value being converted, $\mathrm{ADD}_{T_{o,y}}$ is predicted annual degree-days at the $T_{o,y}$ standard of interest (0, 5, 10, or 15 °C), and a_1–a_5 are constants (Table 3). Because we estimated parameter values using of $\mathrm{ADD}_{T_{o,y}} | \mathrm{ADD}_{T_{o,x}}$ relationships for which $r^2 \geq 0.90$, each standard $T_{o,y}$ model has an $\widehat{\mathrm{ADD}_{T_{o,y}}} | \mathrm{ADD}_{T_{o,y}}$ r^2 value of 0.91 ± 0.006 provided that $T_{o,x}$ and $\mathrm{ADD}_{T_{o,y}}$ are within prescribed range limits (see Table 3). Without further study, we recommend against using eq. 4 to convert among DDs based on water temperatures. Although air and water temperatures are both highly correlated at a given location and well approximated by a sine curve (Fig. 1), these sine curves and the ADD_{T_o} values that result from them are different because annual air and water profiles do not share the same T_{Mean}, w, or cycle period.

The argument for adopting standardized base temperatures when applying DDs to fish growth is essentially this: if one is interested in using DDs to describe growth, and the ability of DDs to describe growth is robust to T_o (as we have shown), then the benefits of standardizing T_o far outweigh the costs. We acknowledge that standardization can result in a marginal reduction in explanatory and predictive power and will certainly preclude certain types of analyses (e.g., among-species comparisons of the extent to which DDs explain growth). However, standardization eliminates the need to identify T_o values for each population and study, facilitates comparative studies, and promotes the use of DDs in future research. When the use of a standard T_o value is untenable, our advice is to follow published precedent. Following precedent for identifying T_o values relevant to growth should ensure a modicum of standardization. If T_o must be estimated with precision, then we recommend setting T_o to the minimum temperature for growth. Methods for estimating T_o in this way are described in relevant references in Table 1; see also Charnov and Gillooly (2003), Gagné and Rodríguez (2008), and Legg et al. (1998).

In this study, we showed that the ability to describe fish growth in a single population is robust to T_o and that there is scope for adopting standard T_o values that are already in use in agronomy and entomology. However, it remains to be tested whether these results hold when describing fish growth in multiple populations or over large spatial scales (e.g., marine stocks). Until this work is complete, we caution that precise T_o might be necessary in certain studies. We also encourage research to determine the extent to which our results hold at more southern latitudes and under what circumstances we should include thermal maxima in DD calculations. Similarly, further research is needed to determine if cisco (*Coregonus artedi*) growth in Leech Lake was best explained using a T_o of ~20 °C (Fig. 3*b*). Given that cisco exhibit optimal growth at 18.1 °C and prefer 8.7 to 16.1 °C (Hasnain et al. 2013), this result is likely a statistical anomaly stemming from a relatively small sample size. Regardless, it appears that growth in this population is relatively poorly described by air temperature-derived DDs, and we wonder if this trend is evident in other populations and coldwater species. In general, there is also a need to develop protocols for combining whole- and partial-season DDs in a single analysis and for converting among T_o values when DDs are based on water temperature. Clearly, there is still much to learn about the use of DDs in fish science, and we encourage more research to address these and other questions.

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