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Abstract: Growing degree-days (GDD, °C·days) are an index of ambient thermal energy that relates directly to an ectotherm's cumulative metabolism but is rarely used to describe growth and development in fish. We applied GDD to length and maturity data from 416 populations of walleye (*Sander vitreus*) from Ontario and Quebec, Canada (mean annual GDD = 1200 to 2300 °C·days). On average, males matured after they had experienced 6900 °C·days and reached 350 mm total length (*L*) (*n* = 77 populations), and females matured after 10 000 °C·days and at 450 mm *L* (*n* = 70). Across 143 populations, GDD accounted for up to 96% of the variation in the length of immature walleye but also revealed a twofold difference in growth rate that was indicative of variation in food availability. When applied to data from eight populations in which walleye abundances have changed dramatically over time, GDD revealed a 1.3-fold increase in immature growth rate when abundance was low compared with when it was high. Our results both demonstrate the explanatory power of GDD with respect to fish growth and maturity and inform the development of regional management strategies for walleye.

Résumé : Bien que les degrés-jours de croissance (GDD, °C-jours) soient un indice d'énergie thermale directement relié au cumulatif métabolisme chez les ectothermes, cet indicateur a rarement été considéré pour décrire la croissance et le développement des poissons. Nous avons utilisé l'indice GDD dans l'analyse de données de taille et de maturité provenant de 416 populations de dorés jaunes (*Sander vitreus*) de l'Ontario et du Québec, Canada (moyenne annuelle GDD = 1200 à 2300 °C-jours). En moyenne, les mâles ont atteint la maturité à 6900 °C-jours, correspondant à une longueur totale de 350 mm (n = 77 populations), et les femelles à 10 000 °C-jours, correspondant à une longueur totale de 450 mm (n = 70). Dans une analyse comprenant 143 populations, l'indicateur GDD a permis d'expliquer jusqu'à 96 % de la variabilité dans la taille des individus immatures, en plus de révéler que la variabilité dans l'abondance des proies peut conduire à des différences du taux de croissance allant jusqu'au double. En utilisant les données de huit populations au sein desquelles une grande variation de l'abondance des dorés avait vraisemblablement causé de grands changements dans l'abondance des proies, l'indice GDD a montré que le taux de croissance des individus immatures bénéficiant d'une forte disponibilité de proies était de 1,3 fois supérieur à celui d'individus subissant une faible disponibilité de proies. Nos résultats démontrent le pouvoir de l'indicateur GDD pour expliquer la variabilité dans la croissance et la maturité et seront utiles au développement de stratégies régionales de gestion des populations de dorés jaunes.

Introduction

Fish growth and development are primarily functions of food and temperature (Fry 1971; Kitchell et al. 1977; Palo-

heimo and Dickie 1966). Recently, Neuheimer and Taggart (2007) showed that growing degree-days (GDD, °C·days; an index of ambient thermal energy that relates directly to an ectotherm's cumulative metabolism but is rarely used in

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fish science) could account for much of the variation in length ($r^2 \ge 0.92$) among species and populations of fish.

A corollary of the GDD approach is that variation in growth, over and above that associated with variation in GDD, may be attributable to factors other than temperature (e.g., food availability; Neuheimer and Taggart 2007). For decades, fisheries scientists at the Ontario Ministry of Natural Resources (OMNR), Canada, have used GDD to describe fish length and maturity (e.g., Colby and Nepszy 1981). Although Neuheimer and Taggart (2007) found that a single GDD function was sufficient to explain 93% of the variation in immature length among 17 stocks of Atlantic cod (Gadus *morhua*), we hypothesize that when both GDD and density vary strongly over time or across space, GDD will be associated with a broad range of immature lengths. Immature growth rate and length are important determinants of early survival (see reviews by Cowan et al. (2000), Miller et al. (1988), and Sogard (1997)) and significant life history parameters (e.g., age at maturity, size at age, adult size and longevity; Beverton and Holt 1959). Therefore, quantifying the temperature-independent effect of density on the growth of immature fish across numerous populations is important to understanding the reproductive biology and population dynamics of harvestable species that are distributed over large spatial scales.

In this study, we respond to Neuheimer and Taggart's (2007, p. 384) challenge to "test the GDD metric in all aspects of fish and aquatic invertebrate physiology, growth, and development" by first showing that GDD is a strong predictor of the length and maturity of walleye (*Sander vitreus*) — an economically important freshwater species that is a research and management priority throughout much of its North American range. Using data from eight populations in which walleye abundances have changed dramatically over time, we then use the GDD approach in a combined within- and among-population analysis to quantify a general effect of density on immature growth rate.

Materials and methods

Survey data

Walleye data were obtained from 416 water bodies in Ontario and Quebec (44°N to 53°N latitude). These water bodies were surveyed at least once in fall (surface water 10–15 °C; Morgan 2002) between 1988 and 2002 by either the OMNR or the Ministère des Ressources Naturelles et de la Faune du Québec. Typically, each survey represented eight or more depth-stratified, random, overnight sets of multimesh gill nets (for details, see Morgan 2002). Walleye total length (*L*), maturity, and sex were determined in the field, and age at capture was assigned in the lab using otoliths.

For each walleye population in Ontario, we generated a unique time series of annual growing degree-days (GDD_a) above an air temperature threshold of 5 °C. We based GDD_a on air temperature because water temperature data are not broadly available and because walleye prefer to be above the thermocline (20–25 °C; Colby et al. 1979), where air and water temperatures are strongly correlated over a

broad range of lake morphologies (Livingstone and Lotter 1998; Livingstone and Padisak 2007; Shuter et al. 1983). We used 5 °C as a base temperature because (*i*) it defines the walleye growing season in terms of both ice cover (Shuter et al. 1983) and bioenergetics (Kitchell et al. 1977), and (*ii*) an exploratory analysis following Neuheimer and Taggart (2007, see supplementary information) showed that the coefficient of determination of the relation between walleye length and the cumulative annual growing degree-days (GDD_c) that each walleye experienced prior to capture was maximized for temperature thresholds in the range of 0 °C to 10 °C (Supplemental Fig. S1⁴).

To calculate GDD_a for a given population and year of interest, we (*i*) obtained daily air temperature data from all available Ontario weather stations for that year, (*ii*) calculated a GDD_a for each station (i.e., the difference between the average daily air temperature and 5 °C, summed across all days for which the average daily air temperature was \geq 5 °C), (*iii*) GIS-interpolated these data to produce a province-wide 1 km² GDD_a grid map, and then (*iv*) assigned a unique GDD_a value according to the population's geographic coordinates. Because grid maps of GDD_a were unavailable for Quebec, we estimated the GDD_a for a given population and year directly from nearby temperature stations (i.e., using steps *i* and *ii* above; mean station distance to a lake = 43 km, range 2 to 173 km).

To calculate the GDD_c that each walleye experienced prior to capture, we summed population-specific values of GDD_a across all years in which that walleye was alive. Thus, a 2-year-old walleye from Jessica Lake in fall 2001 experienced three growing seasons (1999, 2000, 2001) prior to capture, each with a specific GDD_a value (1691, 1646, and 1817 °C·days, respectively) that summed to a GDD_c of 5154 °C·days. Because each GDD_a value in a time series was unique, a 2-year-old walleye from the same population but a different year would have experienced a different GDD_c. (A summary of water body (location, surface area, and mean depth), temperature (GDD_a and GDD_c), and walleye data (sex, age, *L*, and maturity) is provided in online Supplemental Table S1⁴)

Length, maturity, and GDD_c

The first step in our analysis of survey data was to define a threshold value of GDD_c below which both males and females were likely to be immature. This step was necessary because the allocation of surplus energy towards reproduction (Day and Taylor 1997; Lester et al. 2004) is likely to produce adult- and sex-specific relations between L and GDD_c, and because the point at which walleye in our final analysis matured was unknown (see Immature length, GDD_c, and density). We used two different methods to define this GDD-at-maturity threshold. The first method was based on male and female L at GDD_c . It assumed that if both sexes grow similarly before maturity but differently after (Day and Taylor 1997; Lester et al. 2004), then deviation from a common L-at-GDD_c pattern should indicate maturity in one or both sexes. This method is useful when maturity data are absent. To estimate maturity thresholds from length data, we first calculated the age- and year-

⁴ Supplementary data for this article are available on the Journal web site (http://cjfas.nrc.ca).

specific mean lengths for both males and females in each population ($n \ge 5$ individuals per mean); associated GDD_c values were calculated accordingly. For both sexes separately, we then fitted a cubic regression spline (Schluter 1988) to the relation between mean *L* and GDD_c. Splines were fit using a smoothing parameter that minimized prediction error; the 95% confidence interval (CI) for the spline fit was estimated by bootstrapping the data *n* times (n = 1629 and 1382 for males and females, respectively). We then defined GDD_c and *L* at maturity as the point at which the 95% CIs around male and female regression splines ceased to overlap.

The second method for estimating maturity thresholds was based directly on survey maturity data; this method also served as a check of the accuracy of the first, length-based approach. For each population, we estimated the L and GDD_c at 50% maturity (L_{50} and GDD_{50} , respectively) by probit analysis (Finney 1971; Trippel and Harvey 1991) of the frequency distribution of mature and immature walleye (n = 100 males or females pooled across all sample years)within a population). We used 5 mm length bins when estimating L_{50} ; because individuals of a given cohort and age shared a common thermal history (i.e., GDD_c), binning was not necessary when estimating GDD₅₀. Finally, we estimated maturity thresholds for both sexes by averaging L_{50} and GDD₅₀ estimates across all populations. To further explore the predictive power of GDD with respect to maturity, we regressed values of L_{50} and age at 50% maturity (t_{50}) in each

lake against mean annual growing degree-days ($\overline{\text{GDD}}_a$). Age at 50% maturity was estimated as above.

Immature length and GDD_c

Once we had defined a threshold value of GDD_c below which individual walleye were likely to be immature, we set out to determine how best to describe immature length. Specifically, we were interested in whether GDD_c explained more variation in immature length than age, and whether simple models were better than complex ones. Although Neuheimer and Taggart (2007) found that a single GDD_c function explained 93% of the variation in immature length among 17 stocks of Atlantic cod, residual variation in relations between immature length and GDD_c among surveyed walleye populations might be large enough to justify a more complex model. If total length is defined as

(1)
$$L = L_0 + a \cdot \text{GDD}_c^b$$

where *a* is a parameter ≥ 0 that depends on the energy that is available for growth, the exponent *b* is the rate at which *L* changes with GDD_c, and L_0 is total length at the beginning of the life history stage of interest (e.g., free swimming, exogenous feeding, piscivory, maturity), then the increase in total length (*L'*) over the period used to derive GDD_c is given by

(2)
$$L' = a \cdot \text{GDD}_{c}^{b}$$

or

(3)
$$\log_{10}L' = \log_{10}a + b \cdot \log_{10}\text{GDD}_{c}$$

Note that $L' = L - L_0$. Equation 3 is ideally suited to com-

parative analyses of length data because (*i*) it allows for both linear and nonlinear growth trajectories (Lester et al. 2004; Quince et al. 2008), (*ii*) it implies a common temperature effect when slopes are consistent, and (*iii*) it implies a surplus energy effect when intercepts vary. For our analysis, we set L_0 to 40 mm, the approximate L at which young walleye become piscivorous (reviewed by Galarowicz and Wahl 2005) — with attendant changes in physiology (Braekevelt et al. 1989) and behaviour (Houde and Forney 1970) — and develop ventral scales (Colby et al. 1979).

Our analysis proceeded as follows. First, we used the threshold value of GDD_c to extract from the survey data all individual walleye that were likely to be immature. We then calculated age- and year-specific mean lengths ($n \ge 5$ individuals, sexes combined) for immature walleye in each population; associated values of GDD_c were calculated accordingly. If a population was sampled more than once between 1988 and 2002 (31 of 143 populations in this analysis, only 12 of which were sampled over a period >5 years), mean values were calculated separately for each sampling year and then pooled under the assumption that walleye abundance had not changed dramatically between sampling years. Pooling in this way ensured that each population had equal weight in the subsequent analysis. We then used linear analysis of covariance (ANCOVA) of log-transformed data to develop three models of L' for both predictor variables (GDD_c and age): (i) a complex model in which a unique intercept and unique slope were estimated for each population (Fig. 1a), (ii) a model of intermediate complexity in which a unique intercept but a common slope were estimated for each population (Fig. 1b), and (iii) a simple model in which a common intercept and slope were estimated for all populations (Fig. 1c). To compare the strength of evidence for each of these six models, we then used a small-sample, bias-corrected form of Akaike's information criterion (AIC_c) to calculate model probabilities (w_i) (Anderson 2008; Burnham and Anderson 2002).

Immature length, GDD_c, and density

The purpose of our final analysis was to determine the efficacy of the GDD metric for quantifying an effect of density on immature length among numerous populations of walleye. For this analysis, we focused on eight well-studied populations in which walleye abundances changed at least fourfold as a result of overexploitation, experimental overexploitation, invasive species, and (or) recruitment failure stemming from introduced species, pollution, or the degradation of spawning habitat (Table 1; Supplemental Table $S2^4$). We used either estimates or indices of walleye abundance, together with published accounts of abundance change, to divide data into periods of time when walleye densities were likely to be either relatively high or low. As described in the following paragraphs, we then used ANCOVA to compare immature L' at GDD_c both between density periods and among populations.

We estimated the L at age of individual walleye in each population and year primarily from the back-calculation of scales (Supplemental Tables S2 and S3⁴). We used backcalculation because gear size selectivity among young age groups can bias direct measurements of L towards fastgrowing individuals. Back-calculations followed the MonFig. 1. Hypothetical examples of the linear analysis of covariance (ANCOVA) models that were evaluated in this study. In our analysis of survey data from 416 populations, we compared among the following six models: (a) $\log(\text{mean total length } (L))$ vs. $\log(\text{calen-}$ dar time (age)) and log L vs. log(thermal time (GDD_c)), both with the categorical variable "population"; (b) $\log L$ vs. log age and $\log L$ vs. $\log \text{GDD}_c$, both with no "population \times time" interaction term; and (c) $\log L$ vs. \log age and $\log L$ vs. $\log \text{GDD}_c$, both with no categorical variable. In our analysis of eight collapsed populations, we compared among the following six models: (a), (b), and (c) with only log GDD_c as a covariate; (d) log L vs. log GDD_c with the categorical variables "population" and "density"; $(e) \log L$ vs. log GDD_c with the categorical variables "population" and "density" but no interaction terms; and (f) $\log L$ vs. $\log \text{GDD}_c$ with "density" as a categorical variable but no interaction terms. Continuous and broken lines in models (d), (e), and (f) illustrate change in L during periods of high and low density, respectively.



Log calendar time (age) or thermal time (GDD_c)

astyrsky nonlinear method (see Francis 1990). We derived the requisite slope of the relation between body length and scale size via a year-specific, log-log regression of L on anterior scale radius. If data from more than one year were available to estimate this slope, we used ANCOVA to calculate a common slope. Because confidence in scale ages tends to be low for older fish, we only backcalculated L at age using scales from 4-, 5-, and 6-yearold walleye (sexes combined). For each age and year, our minimum sample size was five fish per age class (e.g., Lat age 1 in 1974 was derived from $n \ge 5$ age-4 walleye that were captured in 1977). When more than one age class contributed to back-calculated L in a year (e.g., both 4- and 5-year-olds were available to back-calculate L at age 1 in 1974), we used a Monte Carlo randomization procedure (up to 10000 combinations) to test the null hypothesis of no difference between mean L at age. If this null hypothesis was rejected (19 of 171 cases in this study), we based L at age on the youngest age class; otherwise, data were pooled. Finally, we averaged across individual walleye within each year to produce annual estimates of L at age.

Some estimates of *L* at age were obtained from the literature as either back-calculations or direct measures (Supplemental Table S2⁴). Estimates were only included if $n \ge 5$ scales (or walleye) per population and year (sexes combined); however, data were not always available to limit back-calculations to scales from 4-, 5-, and 6-year-olds. When necessary, we developed population-specific regression equations to convert fork length to total length.

We obtained GDD_a and GDD_c values for populations in Ontario as described in Survey data. Missing GDD_a values in a time series were either estimated by linear regression of GIS-interpolated data onto data from the nearest weather station or obtained from the literature. For Saginaw Bay, Lake Huron, we estimated GDD_a and GDD_c directly from the nearest weather station (Supplemental Table S2⁴).

To test for an effect of density on length across all populations, we first divided each time series into periods of relatively high and low abundance. Analysis of L data then followed the combined ANCOVA-AICc approach that is described in the previous section, with two important changes. First, we excluded all age-based models by assuming a priori that GDD_c was better than age at explaining variation in L' (recall that L' = L - 40 mm). This change reduced to three our original list of linear ANCOVA models: one complex (Fig. 1a), one intermediate (Fig. 1b), and one simple (Fig. 1c) relation between L' and GDD_c , each with population as a categorical variable. Second, with the addition of abundance (high or low) as a categorical variable, we were able to evaluate three additional linear AN-COVA models: (i) a complex model in which a unique intercept and a unique slope were estimated for each population in both periods of abundance (Fig. 1d), (ii) a model of intermediate complexity in which a unique intercept but a common slope were estimated for each population in both periods of abundance (Fig. 1e), and (iii) a simple model in which a common intercept and a common slope were estimated for all populations in both periods of abundance (Fig. 1f).

Results

GDD_c and maturity

Cubic spline regression of 26 324 males from 1629 age classes across 369 populations in Ontario and Quebec indicated an abrupt change in *L* at GDD_c at ~6000 °C·days and ~340 mm *L* (Fig. 2*a*). The change in the *L* at GDD_c of females was less abrupt (22 077 individuals from 1382 age classes across 341 populations) but was first noticeable at ~7300 °C·days and ~380 mm *L* (Fig. 2*b*). When overlaid (Fig. 2*c*), these regression splines showed that the *L* at GDD_c of males and females was similar prior to maturation, but that the *L* at GDD_c of adults was sexually dimorphic.

Population	ID	Location (latitude, longitude)	Area (ha)	Mean depth (m)	Magnitude of abundance decline ^a	Principal cause(s) of abundance decline
Crooked Pine Lake	1	48°47′N, 91°05′W	1 604	6.1	10.43	Recruitment failure via a species introduction
Lake Erie (west and west-central basins)	2	41°49′N, 82°38′W	1.95×10^{6}	16.6	3319.28	Overexploitation; recruitment failure
Henderson Lake	3	48°49′N, 90°18′W	151	2.5	15.44	Experimental over- exploitation
Lake Huron (Saginaw Bay)	4	43°59′N, 83°29′W	2.96×10 ⁵	10.1	18.45 ^b	Recruitment failure via spawning habitat degradation
Lower Marmion Lake	5	48°53′N, 91°31′W	3 982	6.8	6.04	Recruitment failure via spawning habitat degradation
Lake Ontario (Bay of Quinte)	6	44°05′N, 77°05′W	25 740	10.0	2008.17	Overexploitation; recruitment failure
Savanne Lake	7	48°50′N, 90°06′W	364	2.6	4.47	Experimental over- exploitation
Shoal Lake	8	49°33'N, 95°01'W	25 856	9.1	17.52^{b}	Overexploitation

Table 1. Populations used to relate the immature length of walleye to GDD_c (°C·days) at both high and low numerical abundance.

Note: See Supplemental Table S2 (available on the Journal web site (http://cjfas.nrc.ca)) for source information.

^aDecline in abundance, expressed as the ratio of high to low abundance.

^bRatio based on commercial yield data.

Regression splines diverged at approximately 5900 °C·days and 340 mm *L*, and 95% CI diverged at approximately 6900 °C·days and 370 mm *L* (Fig. 2*d*). Estimates of GDD_c and *L* at maturity based on available maturity data tended to be larger than those based on *L*–GDD_c profiles, especially for females: on average, males matured at 6872 °C·days ± 457 95% CI and 349 ± 9 mm *L*, and females matured at 10 0037 ± 451 °C·days and 450 ± 10 mm *L* (Fig. 3). In terms of elucidating the maturity status of walleye in our eight study populations, we were confident based on these results that mean lengths associated with GDD_c values < 6000 °C·days were not confounded by the allocation of energy towards reproduction.

 $\overline{\text{GDD}}_{a}$ (i.e., the length of an average growing season) did not explain more than 3% of the variation in L_{50} (Fig. 4*a*). However, we found relatively strong support for a negative relation between t_{50} and $\overline{\text{GDD}}_{a}$ (Fig. 4*b*).

Immature length and GDD_c

Across 143 populations and 9° of latitude (mean GDD_a = 1200 to 2300 °C·days), variation in log L' (i.e., L - 40 mm) of walleye that had experienced <6000 °C·days was best explained by the intermediately complex linear ANCOVA model based on log GDD_c (Table 2; Fig. 5a). However, even when temperature was taken into account, the L at GDD_c of immature walleye from different populations ranged between a low of $\log_{10} L' = 0.81 \cdot \log_{10} \text{GDD}_{c} - 0.75$ and a high of $\log_{10} L' = 0.81 \cdot \log_{10} \text{GDD}_{c} - 0.38$), a more than twofold difference in L at GDD_c (Fig. 5a). Empirical support for the remaining five models was negligible; however, the intermediately complex models always outperformed the simple models, which themselves outperformed the complex models (Table 2). Within this hierarchy, log GDD_c was consistently better than log age at explaining variation in $\log L'$. The simple $\log GDD_c$ model (which was similar to the simple, untransformed GDD_c models presented in Neuheimer and Taggart 2007) was ranked third (Table 2) and took the form $\log_{10} L' = 0.78 \cdot \log_{10} \text{GDD}_{c} - 0.45$. For comparative purposes, a plot of log L' versus log age is shown (Fig. 5*b*).

Immature length, GDD_c, and density

For the eight populations in which walleye abundances changed dramatically over time, empirical support was strongest for the intermediately complex linear ANCOVA model, with a common slope for log GDD_c but intercept values that were dependent on abundance (Table 3; Fig. 1*e*). In other words, although the L-at-GDD_c patterns of immature walleye varied among populations, they responded similarly to changes in abundance. On average, the L at GDD_c of immature walleye was described as $log_{10} L' =$ $1.03 \cdot \log_{10} \text{GDD}_{c} - 1.43$ when abundances were high and then increased to $\log_{10} L' = 1.03 \cdot \log_{10} \text{GDD}_{c} - 1.32$ when abundances were low (a 1.3-fold increase; Fig. 6a). Empirical support for the remaining five models was negligible, although models that included the categorical variable "density" tended to outperform models that ignored it (Table 3). The simple log GDD_c model was ranked last (Table 3) and took the form $\log_{10} L' = 1.03 \cdot \log_{10} \text{GDD}_{c}$ – 1.39 (Fig. 6b).

Discussion

Our results demonstrate the efficacy of GDD as a metric for explaining length in fishes (see also Neuheimer and Taggart 2007). We attribute the consistency with which GDD models outperform age-based equivalents to two factors. First, because age data are discrete (age-1, age-2, age-3, etc.), age-based models severely limit the distribution of Ldata along the x axis. For example, when age was used in place of GDD_c in Fig. 4, length data were restricted to five columns, one for each observed age. This change to the structure of the independent variable represents a considerable loss of information with which to explain variation in

Fig. 2. Mean total length (*L*) versus the cumulative annual growing degree-days (GDD_c, °C·days) for (*a*) male (n = 1629 age classes from 369 populations) and (*b*) female walleye (n = 1382 age classes from 341 populations) in Ontario and Quebec. (*c*) and (*d*) Male and female regression lines (*c*) over the full range of total length (*L*) and GDD_a values and (*d*) at the point of divergence. Continuous lines are cubic splines (Schluter 1988), and broken and dotted lines are bootstrapped 95% confidence interval (CI) for males and females, respectively. Open circles in (*b*) were excluded from analysis. Arrows indicate the GDD_c and *L* at which splines appeared to bend (*a* and *b*) or 95% CI ceased to overlap (*d*) early in life. Data are available from Supplemental Table S1⁴.



the dependent variable (Cottingham et al. 2005). Second, Lage relations ignore the fact that aging and growing are distinct processes insofar as a fish that survives over some time interval will age but the extent to which it increases in L depends not only on time, but also on other factors such as temperature. Put another way, unless the thermal energy (e.g., GDD) that fish are experiencing is known, using age to predict when a fish will reach a certain L is as effective as using a stopwatch alone to predict when a pot of water will boil.

Though GDD is clearly superior to age for describing immature length, our results also show that more complex GDD-based models can reveal patterns of L at GDD_c both through time and among populations. For example, our analysis of survey data from 143 populations of walleye suggests strongly that intercepts were population-specific and that changes in L' at GDD_c implied twofold variation in growth rate among populations. Our analysis of L data from eight populations also shows that relations between $\log L'$ and log GDD_c differed between periods of high and low abundance (i.e., density) within a population; however, the magnitude of this difference was relatively consistent across populations and suggested that immature walleye grew 1.3 times faster when population densities were low compared with when population densities were high. Neuheimer et al. (2008) also showed, in a population of haddock (Melanogrammus aeglefinus), that L-GDD_c relations showed a reduction in L at GDD with increasing population density (1965– 1996; Frank et al. 2001) but proposed that these L changes resulted from a gradual removal of fast-growing and latematuring individuals by size-selective fishing mortality. Given that fishing mortality in our eight study lakes was (i) relatively low or absent when densities were high, (ii) relatively high when densities were low, or (iii) altogether **Fig. 3.** Total length at 50% maturity (L_{50}) and GDD at 50% maturity (GDD₅₀) of male (\times , n = 77 populations) and female (\bigcirc , n = 70 populations) walleye in Ontario and Quebec as determined by probit analysis. Solid symbols within each cluster of points are sexspecific means of L_{50} and GDD₅₀ ± 95% confidence interval (CI). L_{50} increased with GDD₅₀ across all populations because ectotherms must accrue thermal energy if they are to grow. Data are available from Supplemental Table S1.



negligible in shaping density patterns, size selectivity is insufficient to explain the observed increase in L at GDD_c in this study.

Density-dependent changes in L at age have been observed in many individual populations of walleye (e.g., Anthony and Jorgensen 1977; Colby and Nepszy 1981; Reid and Momot 1985); however, direct comparisons involving two or more populations are comparatively rare (a trend that is by no means restricted to walleye). To a large extent, individual case studies are common because of a need for detailed information on individual populations in which L at GDD_c is often the result of numerous factors and their interactions. However, it is also a symptom of the age-based approach to describing length, which limits the efficacy or even feasibility of among-population analyses by emphasizing, rather than accounting for, differences among populations. Length models based on GDD, on the other hand, explicitly account for temperature (arguably one of the most important determinants of growth; Fry 1971; Kitchell et al. 1977; Paloheimo and Dickie 1966) and, in doing so, simplify considerably the job of estimating how immature length changes with density. Furthermore, by relating length to a common currency (thermal age), the GDD metric facilitates the comparison or even aggregation of data across populations. For example, our results with respect to L' at GDD_c suggest a consistent, 1.3-fold increase in immature growth rate with large reductions in density, information that is useful for developing management strategies that can be generalized to multiple populations and (or) disturbance scenarios. Sass and Kitchell (2005) found that GDD_a contributed negligibly (partial $R^2 = 0.001$ for males and 0.02 for females) to a multiple regression model ($R^2 = 0.34$ for both sexes) that used seven predictor variables (including walleve density) to explain variation in walleve L across 859 lakes in Wisconsin. Given that this model included no

Fig. 4. Linear regression of (*a*) total length at 50% maturity (L_{50}) and (*b*) age at 50% maturity (t_{50}) on mean annual growing degreedays ($\overline{\text{GDD}}_{a}$, °C·days) for males (×, broken lines) and females (\bigcirc , continuous lines). Regression results are as follows: male L_{50} ($r^2 = 0.03$, n = 77, P = 0.132); female L_{50} ($r^2 < 0.01$, n = 70, P = 0.884); male $t_{50} = 61846 \cdot \overline{\text{GDD}}_{a}^{-1.306}$ ($r^2 = 0.32$, n = 77, P < 0.0001); female $t_{50} = 36666 \cdot \overline{\text{GDD}}_{a}^{-1.175}$ ($r^2 = 0.42$, n = 70, P < 0.0001). Data are available from Supplemental Table S1⁴.



other temperature variables, we suspect that GDD_a performed poorly in this case because it was estimated from a single, central location but then applied to an area that spanned 7.5 × 10⁴ km² and 3° of latitude; ideally, a unique GDD_a time series should be developed for each lake. Furthermore, because they used GDD_a from the most recent growing season to explain variation in age-3 (males) and age-5 (females), these authors did not account for thermal energy that had accumulated in earlier growing seasons. To illustrate these points using our data, we used linear AN-COVA of age-3 *L* versus location-specific GDD_c with density as a categorical variable and then repeated this analysis using a single, central GDD_a time series (Sudbury, Ontario, Canada: 46°38'N, 80°48'W). Whereas the location-specific

< 0.000

< 0.000

0.96

0.95

uata from 145 waneye populations in Ontario and Quebec.											
Model	Predictor variable	Intercept	Slope	п	K	$\log(\widehat{\sigma}^2)$	AIC _c	AIC _c rank	Δ_i	Wi	$r_{\rm adi}^2$
b	log GDD _c	Unique	Common	637	145	-2.999	-1534.464	1	0.000	1.000	0.95
b	log age	Unique	Common	637	145	-2.926	-1487.643	2	46.821	< 0.000	0.94
С	log GDD _c	Common	Common	637	3	-2.317	-1470.912	3	63.552	< 0.000	0.82
С	log age	Common	Common	637	3	-2.113	-1339.879	4	194.585	< 0.000	0.70

287

287

637

637

Unique

Unique

Table 2. The strength of evidence for six linear analysis of covariance (ANCOVA) models of log(immature total length (L')) according to data from 143 walleye populations in Ontario and Quebec.

Note: L' = L - 40 mm. Models correspond to panels in Fig. 1. Models were ranked according to strength of evidence as determined by a small-sample, bias-corrected form of Akaike's information criterion (AIC_c). *n*, sample size (number of data points across all populations); *K*, number of parameters (intercept(s) + slope(s) + error estimate); $\hat{\sigma}^2$, residual variance; Δ_i , AIC_c differences; w_i , Akaike weight; r_{adj}^2 , adjusted coefficient of determination; GDD_c, cumulative annual growing degree-days.

-3.258

-3.157

-1027.573

-963.555

5

6

506.891

570.909

Fig. 5. Linear analysis of covariance (ANCOVA) model of log-transformed (*a*) mean total length (L', mm) and (*b*) age (years) of immature walleye (GDD_c < 6000 °C·days, sexes combined) versus log-transformed cumulative annual growing degree-days (GDD_c, °C·days) in 143 surveyed populations. Broken and continuous lines represent the fastest and slowest predicted growth trajectories, respectively, according to model *b* (Fig. 1*b*); thin lines represent the 95% prediction intervals. Numeric symbols in (*a*) denote age at time of sampling in a population and year. Untransformed data are available from Supplemental Table S1⁴.



Table 3. The strength of evidence for six linear analysis of covariance (ANCOVA) models of log(immature total length (L')) versus log GDD_c according to data from eight walleye populations in which densities have changed dramatically over time.

								AIC _c			
Model	Density	Intercept	Slope	п	Κ	$\log(\widehat{\sigma}^2)$	AICc	rank	Δ_i	Wi	$r_{\rm adj}^2$
е	Included	Unique	Common	339	11	-2.481	-818.377	1	0.000	1.000	0.87
d	Included	Unique	Unique	339	33	-2.273	-697.369	2	121.008	< 0.000	0.89
а	Ignored	Unique	Unique	339	17	-2.040	-655.807	3	162.570	< 0.000	0.82
b	Ignored	Unique	Common	339	10	-1.980	-650.664	4	167.713	< 0.000	0.80
f	Included	Common	Common	339	4	-1.943	-650.540	5	167.837	< 0.000	0.78
С	Ignored	Common	Common	339	3	-1.844	-619.169	6	199.208	< 0.000	0.73

Note: See Table 2 for comments and definitions. The terms "common" and "unique" apply within a density category for models *d* and *e*, but between density categories for model *f*.

 GDD_{c} term in the first model was highly significant ($P = 1.41 \times 10^{-9}$), the single-location GDD_{a} term in the second model was not (P = 0.06). Overall, our results suggest that when thermal history is accurately accounted for, length can be used as a surrogate method for monitoring large changes in abundance.

The density-dependent growth response that is implied by

our results is not trivial. Because growth rate and size are critical to the early survival of fish (see reviews by Cowan et al. (2000), Miller et al. (1988), and Sogard (1997)), even small changes in growth can significantly affect both the timing and number of individuals that recruit into a fishery. For example, the GDD_a for Oneida Lake, New York, is 2180 °C-days (Goddard Institute for Space Studies 2008;

а

а

log GDD_c

log age

Unique

Unique

Fig. 6. Linear analysis of covariance (ANCOVA) models of log-transformed mean total length of immature walleye (L') (sexes combined) versus log-transformed cumulative annual growing degree-days (GDD_c, °C·days) for eight collapsed stocks with data (a) divided into periods of high (+ and continuous line) and low (\bigcirc and broken line) density (Fig. 1e; showing mean relations within a density period) and (b) pooled over the entire time series (Fig. 1c). Thin lines are 95% prediction intervals; 95% confidence intervals in (a) (not shown) did not overlap. Numeric symbols in (b) identify calendar ages in years. Points above the 6000 °C·days threshold were excluded from analysis because of the potentially confounding effects of maturity.



our calculation). If we assume that density-dependent growth responses follow Fig. 6a, then a GDD_a of 2180 °C days predicts that 1- and 3-year-old walleye will grow to 133 mm and 330 mm L, respectively, when density is high, and 162 and 419 mm L, respectfully, when density is low. Given that walleye in Oneida Lake (i) can experience ~ 1.5 times more overwinter mortality at 133 mm L than at 162 mm L (Rose et al. 1999; our calculation), (ii) become vulnerable to the sport fishery at 381 mm (15 in.) L, and (*iii*) produce ~15 billion eggs·year⁻¹ (Forney 1976), and also assuming that instantaneous rates of natural mortality follow Venturelli et al. (2010), these relatively small differences in predicted L at age translate into dramatic differences in both when and how many walleye are predicted to recruit into the fishery: three age-3 walleye when density is relatively high for every one age-4 walleye when density is relatively low. Conversely, this difference represents the extent to which recruitment can be over- or under-estimated if information on density-dependent immature growth is unavailable or ignored.

In addition to immature length, our results bear on the relevance of GDD to other aspects of walleye life history. Relations between L and GDD_c show clearly that adult lengths are sexually dimorphic over broad temporal and spatial scales (Henderson et al. 2003; Rennie et al. 2008; Sass and Kitchell 2005) and, together with relations between L_{50} and GDD₅₀, that females tend to mature later and at a larger size than males. This sexual dimorphism in both maturity and adult length is consistent with life history theory (Charnov 1993; Roff 1992), which predicts that the minimum size threshold that an individual fish must reach before the benefits of maturity outweigh the costs is lower in males than in females. Overall, our application of GDD to data from 416 populations between GDD_a of 1000 °C days and 2200 °C days shows clearly that most walleye delay maturation until they reach ~340 mm L. Thus, ~6000 °C·days represents a thermal constant: the thermal energy that walleye must experience to reach a maturation size threshold of \sim 340 mm *L*.

Furthermore, if the *L* at maturity of walleye and other long-lived species is relatively constant (Beverton 2002; Rochet 1998; this study), then the rate at which an individual can grow each year (i.e., $\overline{\text{GDD}}_a$) should be a stronger predictor of t_{50} than L_{50} because growth rate determines the time that it takes to reach a size threshold, but not that size threshold itself (Roff 1991). Accordingly, we found no support for a relation between L_{50} and $\overline{\text{GDD}}_a$ but strong support for a relation between t_{50} and $\overline{\text{GDD}}_a$ (see also Baccante and Colby 1996). Thus, male and female walleye in our study matured at ~350 and ~450 mm *L*, respectively, but, depending on $\overline{\text{GDD}}_a$, took 2–15 years to do so. The extent to which L_{50} , t_{50} , and their relations to GDD vary with walleye density and how this variation can shape reproductive rates will be addressed in a future publication.

In conclusion, we echo the call by Neuheimer and Taggart (2007) for further research into the GDD metric, the limited use of which in fish science is out of proportion with its demonstrated utility (e.g., Colby and Nepszy 1981; Neuheimer and Taggart 2007; Ridgway et al. 1991). Although the present study shows that GDD can be used to account for variation in temperature when explaining variation in growth and development, it also raises several questions. (i) Are L-GDD relations consistent throughout a species' tolerance limits or geographical range? Evidence from walleye suggests that the effects of temperature on growth vary among phylogeographic lineages (Zhao et al. 2008; see also Conover et al. 2006). (ii) Does GDD predict other aspects of life history? Because maturity depends on cumulative temperature, then perhaps GDD_c at maturity should be used in place of age at maturity. (iii) How does GDD influence predictions of growth and development under future climate scenarios or in other species? For example, the GDD metric might perform poorly for lake trout (*Salvelinus namaycush*), which seek out thermal refugia (Snucins and Gunn 1995).

We support the results of Neuheimer and Taggart (2007) by demonstrating the explanatory power of the GDD metric with respect to variation in maturity- and density-dependent L at age across hundreds of populations and over a large spatial area. We also expand upon this work by emphasizing the importance of identifying other factors that affect growth, to what extent, and under what circumstances. Although the GDD metric is by no means a panacea, this statistically powerful, "common currency" approach has major advantages over relations between length and calendar time, which must be developed separately for each temperature scenario (e.g., population, treatment, period of time) and generally complicate the synthesis of data from unrelated studies (e.g., through meta-analyses). Given these advantages and the relative ease with which GDD data can be obtained, we strongly encourage the widespread use of GDD in place of age when studying growth and development in fish.

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