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STÉPHANIE GAGNÉ

MODÉLISATION DE LA CROISSANCE SAISONNIÈRE POUR
DÉTERMINER LE DÉBUT DE LA CROISSANCE ANNUELLE CHEZ LES
POISSONS

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RÉSUMÉ

Une nouvelle méthode basée sur la modélisation de la croissance saisonnière est présentée pour estimer la date du début de la saison de croissance chez les poissons. La croissance saisonnière est mesurée par l'augmentation de la taille de l'individu depuis le début de la saison de croissance. Différents modèles ont été utilisés dans la présente étude pour décrire les patrons de croissance chez 16 espèces de poissons du lac St-Pierre. Les modèles polynomiaux (variantes linéaire et quadratique) étaient les meilleurs modèles ou équivalents au meilleur modèle pour décrire la croissance saisonnière pour toutes les espèces. L'estimation de la date du début de la croissance était similaire pour les deux années d'échantillonnage et entre les classes d'âge. Le début de la croissance était également synchronisé entre plusieurs espèces à l'intérieur d'une petite fenêtre de deux semaines entre le 18 mai et le 2 juin, ce qui correspondait à une température de l'eau entre 16.1 et 17.3 °C. Il a toutefois été impossible de relier la température de l'eau avec le préférendum thermique de chaque espèce. La méthode présentée comporte des avantages par rapport aux méthodes conventionnelles basées sur la croissance marginale proportionnelle puisqu'elle permet d'obtenir une estimation ponctuelle du début de la saison de croissance et peut être utilisée pour toutes les classes d'âge simultanément.

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AVANT-PROPOS

Ce mémoire comprend deux chapitres. Le premier chapitre est une synthèse en français du projet de maîtrise. Le second chapitre est un article soumis pour publication dans le périodique *Journal of Fish Biology* et qui présente les résultats essentiels de mon projet de maîtrise.

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CHAPITRE 1. MODÉLISATION DE LA CROISSANCE SAISONNIÈRE POUR DÉTERMINER LE DÉBUT DE LA CROISSANCE ANNUELLE CHEZ LES POISSONS

Introduction

L'étude de la croissance est un aspect fondamental pour la recherche et la gestion des populations de poissons. La durée de la saison de croissance et la somme des degrés-jours sont reconnues pour être des éléments majeurs influençant le taux de croissance (Conover, 1990; Power & van den Heuvel, 1999; Neuheimer & Taggart, 2007). La croissance et la taille des individus déterminent plusieurs caractéristiques écologiques des populations comme les interactions prédateurs-proies, la maturation, les potentiels de reproduction et de recrutement, et la mortalité (Neuheimer & Taggart, 2007).

La croissance marginale mesurée sur les structures rigides (après la formation du dernier annulus) est souvent utilisée pour valider le moment et la périodicité de la formation des annuli. Cette analyse comporte cependant de nombreuses limites, dont une faible précision quant à l'estimation de la date du début de la croissance (détermination du mois ou de la saison; Chung & Woo, 1999; Harada & Ozawa, 2002). De plus, cette méthode ne peut s'appliquer que sur les individus d'âge 1+ et plus, puisque chez les 0+, une année complète de croissance n'est pas disponible pour mesurer la croissance relative depuis le dernier annulus par rapport à un incrément annuel complet (Cailliet *et*

al., 2006). Chez ces derniers, les incréments journaliers mesurés sur les otolithes peuvent être utilisés pour estimer la date d'éclosion.

Cette étude présente une nouvelle méthode pour estimer le début de la saison de croissance chez les poissons. Cette méthode est basée sur la modélisation de la croissance saisonnière et a été appliquée à 16 espèces de poisson d'un lac fluvial tempéré. Puisque la température influence directement les processus physiologiques déterminant la croissance chez les poissons (Brett, 1979) et qu'elle est ainsi susceptible d'initier la croissance saisonnière, la relation entre la température de l'eau présente au début de la saison de croissance et le préférendum thermique de chaque espèce a également été examinée.

Méthodes

Aire d'étude et échantillonnage

Le lac Saint-Pierre est le plus grand lac fluvial du fleuve Saint-Laurent, Québec, Canada. Il possède la plus grande plaine inondable en eau douce du Québec, alors que sa superficie peut varier entre 387 et 501 km² selon le niveau de l'eau (Hudon, 1997). Environ 50 espèces de poissons résidents composent la communauté ichtyologique.

L'échantillonnage s'est fait à l'aide d'un bateau de pêche électrique (Smith-Root, Cataraft SR-17) sur 80 transects parallèles à la rive dans la zone littorale du lac Saint-Pierre aux étés 2003 et 2004. Tous les individus capturés ont été identifiés, mesurés et

pesés. Un sous échantillon a été sacrifié et emporté au laboratoire pour le prélèvement des structures rigides servant à la détermination de l'âge. La température de l'eau a été calculée par une régression multiple à partir de la température moyenne journalière de l'air mesurée à la station du lac Saint-Pierre par Environnement Canada. La variation saisonnière de la température de l'eau était similaire au cours des deux années d'étude (Figure 2.1).

Détermination de l'âge et rétro-calcul

Un total de 1066 poissons réparti en 16 espèces et de classes d'âge de 0+ à 5+ était disponible pour les analyses (Tableau 2.1). Les structures utilisées pour la détermination de l'âge sont présentées au Tableau 2.1. Les lectures d'âge et la mesure de la longueur des incréments entre chaque annulus ont été faites à l'aide d'un système d'analyse d'images. Pour chaque structure, la longueur totale a été mesurée du noyau à la marge antérieure, et chaque incrément annuel a été mesuré du noyau au premier annulus, puis entre chaque annulus.

La validation de l'âge a été faite selon la technique de Petersen (DeVries & Frie, 1996). L'équation de Fraser-Lee (Francis, 1990) a été utilisée pour déterminer la taille des individus à chaque âge antérieur. La croissance saisonnière, une mesure de l'accroissement en longueur du corps depuis le début de la saison de croissance, a été calculée par la différence entre la taille à la capture et la taille rétro-calculée à partir du dernier annulus.

Modèles de croissance

Six modèles de croissance ont été examinés afin de sélectionner le meilleur modèle de base : deux fonctions polynomiales, soit la variante linéaire et la variante quadratique (Figure 2.2), le modèle de von Bertalanffy, et les fonctions modifiées de Farazdaghi et Harris, Freundlich et Chapman-Richards. Une variable d correspondant au nombre de jours entre le 1^{er} mars et la date de capture a été inscrite pour chaque poisson. Tous les paramètres, sauf le paramètre d_0 qui correspond à la date du début de la croissance, étaient variables selon la classe d'âge. La fonction *nls* du logiciel R, version 2.3.1 (R Development Core Team, 2006) a été utilisée pour estimer les paramètres des différents modèles appliqués aux données de croissance saisonnière de chaque espèce. La comparaison des modèles a été basée sur l'AIC (Akaike's information criterion; Burnham & Anderson, 2002). Une fois le modèle de base sélectionné, l'effet de l'année et de la classe d'âge sur l'estimation de d_0 a été testé par comparaison de l'AIC.

Préférendum thermique

Les données de préférenda thermiques ont été tirées des revues effectuées par Coutant (1977), Jobling (1981) et Wismer & Christie (1987). Lorsque c'était possible, chaque étude a été notée comme ayant été réalisée en nature ou en laboratoire, à quelle saison et dans quel habitat (lac ou rivière). Une régression linéaire de type II (Systat 10.2; SPSS Inc., 2002) a été utilisée pour relier le préférendum thermique et la température de l'eau au début de la saison de croissance. Une classe de température a également été assignée à chaque espèce selon Coker *et al.* (2001).

Résultats

Les modèles polynomiaux étaient les meilleurs modèles pour 13 des 16 espèces (Tableau 2.2). Le modèle quadratique était équivalent au meilleur modèle pour les trois autres espèces ($|\Delta AIC| < 2$ unités; Burnham & Anderson 2002). L'estimation des paramètres a convergé pour le modèle linéaire pour toutes les espèces, ce qui n'a pas été le cas pour les autres modèles. La comparaison entre le modèle polynomial (modèle de base) et le modèle avec effet de l'année ou avec effet de l'âge n'a pas détecté de différence pour d_0 entre les années et les classes d'âge pour les espèces ayant suffisamment de données disponibles (Tableau 2.3), sauf dans un seul cas où l'AIC du modèle avec effet de l'année était inférieur à l'AIC du modèle de base (-9.8 unités). Un exemple de courbes de croissance linéaires et quadratiques appliquées à nos données est présenté à la Figure 2.3.

La date du début de la saison de croissance a été déterminée à l'aide des modèles de base polynomiaux pour toutes les espèces (Tableau 2.4). À l'exception de *N. heterolepis* pour qui l'estimation était très imprécise, la date du début de la saison de croissance a été estimée entre le 2 mai et le 11 juin. L'estimation de d_0 pour 8 des 16 espèces était comprise dans un petit intervalle entre le 18 mai et le 2 juin, intervalle rejoignant également l'intervalle de confiance de toutes les espèces (Figure 2.4a). Le début de la saison de croissance pour toutes les espèces a eu lieu au moment où la température de l'eau se situe entre 16.1 et 17.3 °C, intervalle contenant l'estimation pour 8 des 16 espèces et l'intervalle de confiance pour l'ensemble des espèces (Figure 2.4b). Aucune relation n'a pu être établie entre la température de l'eau à la date du début de la

saison de croissance et la classification thermique de Coker *et al.* (2001), ni avec le préférendum thermique issue des différentes études.

L'imprécision dans l'estimation du paramètre d_0 est le résultat de deux facteurs, soit le nombre de poissons dans la classe d'âge avec le moins d'individus et le nombre de classes d'âge utilisées pour l'estimation (Figure 2.5).

Discussion

Les modèles polynomiaux étaient les meilleures fonctions pour modéliser la croissance saisonnière chez les 16 espèces de poissons du lac Saint-Pierre. Considérant que la forme fonctionnelle d'une courbe de croissance peut varier selon les espèces et les périodes étudiées, le choix d'un modèle de croissance devrait toujours être précédé par l'application de différentes fonctions afin de sélectionner le meilleur modèle pour les données sous étude (Cailliet *et al.*, 2006).

La date du début de la croissance était similaire pour les deux années d'échantillonnage et pour toutes les classes d'âge d'une même espèce. Aucune méthode indépendante n'a été utilisée pour corroborer l'estimation de la date du début de la saison de croissance. Toutefois, la concordance de l'estimation du paramètre d_0 entre toutes les classes d'âge, même si ce paramètre était variable à travers celles-ci, confirme son estimation.

Il n'a pas été possible de relier la température de l'eau au début de la saison de croissance avec les préférences thermiques de chaque espèce. D'autres facteurs tels que la période de crue (apport de nourriture) ou la photopériode pourraient jouer un rôle dans l'initiation de la croissance, mais ces facteurs varient de façon graduelle contrairement à la température qui est connue pour influencer la croissance au-dessus d'un certain seuil (Keast, 1985; McNerny & Held, 1995). La difficulté à mettre en évidence la relation entre la température de l'eau et les préférences thermiques pourrait être causée par la faible variation dans la classification thermique entre les espèces étudiées.

Une importante amélioration de la méthode proposée dans cette étude est la possibilité d'inclure toutes les classes d'âge simultanément dans la même analyse, incluant les 0+. De plus, la modélisation de la croissance saisonnière permet d'obtenir une estimation ponctuelle de la date du début de la croissance, contrairement à une estimation du mois ou de la saison du début de la croissance obtenue avec l'analyse de la croissance marginale proportionnelle sur les structures rigides. La date du début et la durée de la saison de croissance sont particulièrement cruciaux pour les 0+ qui doivent atteindre rapidement une certaine taille afin de diminuer les risques de mortalité par prédation ou durant l'hiver. La période de reproduction est également parfois utilisée pour déterminer le début de la saison de croissance, mais cette méthode est une estimation plutôt imprécise, particulièrement pour les espèces se reproduisant plusieurs fois au cours de l'année. La méthode proposée, bien qu'elle assume également une seule cohorte de 0+, reste adéquate pour toutes les classes d'âge supérieures à 0+, même pour les espèces ayant une longue période de reproduction.

En conclusion les modèles polynomiaux (variantes quadratique et linéaire) étaient les meilleurs modèles pour décrire la croissance saisonnière chez les 16 espèces de poissons étudiées. L'utilisation de la croissance saisonnière pour déterminer le début de la saison de croissance semble être une méthode fiable quand un échantillon suffisamment grand et réparti en différentes classes d'âge est disponible. Cette méthode devrait être priorisée puisqu'elle consiste en une méthode objective produisant une estimation ponctuelle du début de la saison de croissance. Cette méthode permet également de déterminer simultanément le début de la saison de croissance selon les années et les classes d'âge (s'il y a lieu). Une prochaine étape serait d'identifier les facteurs initiant la croissance saisonnière afin de mieux déterminer la durée de la saison de croissance et d'intégrer ces informations dans l'étude de la dynamique des populations.

**CHAPITRE 2. MODELLING SEASONAL INCREMENTS IN SIZE TO
DETERMINÉ THE ONSET OF ANNUAL GROWTH IN FISH**

STÉPHANIE GAGNÉ AND MARCO A. RODRÍGUEZ[†]

Département de chimie-biologie, Université du Québec à Trois-Rivières

3351 boul. des Forges, Trois-Rivières, Québec, G9A 5H7, Canada

[†]Author to whom correspondence should be addressed. Tel.: 1-819-376-5011 #3363; fax:
1-819-376-5084; email: marco.rodriquez@uqtr.ca

Abstract

A new method based on modelling of seasonal growth increments (SGI) in body length was found adequate for determining the date of onset of fish growth for 16 fish species in a fluvial lake. Model comparisons indicated that polynomial (linear or quadratic) functions provided overall the best fits to seasonal growth and were more likely to avoid convergence problems than alternative models. There was little evidence for differences in the date of onset of growth between two study years, nor among age classes within individual species. The onset of growth also was to some extent synchronised among species and was concentrated within a narrow window of approximately two weeks, between 18 May and 2 June, which corresponded to mean water temperatures between 16.1 and 17.3 °C. There was no apparent relationship between date of onset and species' thermal preferenda or preference. The SGI method can contribute to a better understanding of environmental influences on the onset of growth and the length of the growth season, and of thermal thresholds for growth, including their relevance for calculation of degree-day metrics.

Key words: AIC information criterion; age classes; back-calculation; hard structures; model comparisons; Lake St. Pierre

Introduction

Growth is a fundamental aspect of fish ecology and a crucial element in fisheries research and management (Summerfelt & Hall, 1987). Growth patterns can be compared among sexes, cohorts or populations, and related to environmental variables to help understand biotic and abiotic factors affecting growth rate (Francis, 1990). Water temperature and the duration of the growing season are reliable predictors of fish growth and size (Conover, 1990; Power & van den Heuvel, 1999; Neuheimer & Taggart, 2007). Growth and fish size in turn influence several ecological characteristics of populations, such as predator-prey interactions, reproduction, and vulnerability to fishing (Neuheimer & Taggart, 2007). The timing and duration of seasonal growth are particularly important for juvenile fish because their susceptibility to predation and overwinter mortality are often size-dependent. For example, the capacity to achieve a given size at the end of the first growing season can determine over-winter mortality in bluegill (Cargnelli & Gross, 1996). Risk of predation can also be size-dependent, e.g., when predator gape size set limits on prey size and larger prey attain thus a size refuge (Rice *et al.*, 1993; Olson, 1996). Greater swimming ability in larger prey may also contribute to predator avoidance (Brooking *et al.*, 1998). Methods for obtaining precise estimates of the date of onset of seasonal growth can help assess the length of the growth season and its implications for fish growth and population dynamics.

Analyses of the marginal increment ratio (MIR), a measure of the relative growth since the formation of the most recent annulus (Silva & Stewart, 2006), are commonly used to corroborate constant periodicity in the formation of hard structures. The MIR is calculated as:

$$MIR = \frac{S_c - S_a}{S_a - S_{a-1}},$$

where S_c is the radial structure length at the time of capture, S_a and S_{a-1} are lengths of the ultimate and penultimate annuli from the focus respectively (Chung & Woo, 1999). The MIR can also be used to estimate the timing of annuli formation and, consequently, the onset of growth. When the MIR is plotted as a function of time, the period of formation of true annuli should correspond to the trough in an approximately sinusoidal yearly cycle. However, the onset of the growing season can only be broadly determined, with monthly or seasonal precision (Chung & Woo, 1999; Harada & Ozawa, 2002); instead, it would be desirable to obtain a point estimate accompanied by a measure of its precision. Furthermore, the MIR can be obtained only for fish of age 1+ and older, because 0+ fish have not yet formed a complete annulus (Cailliet *et al.*, 2006). For the latter, direct counts of daily increments in otoliths may allow for estimation of the onset of growth, because the hatching date can often be estimated precisely by otolith analysis in larval and young juvenile fish (Cargnelli & Gross, 1996).

This study presents a method for estimating the date of onset of fish growth and measuring the variability about this estimate. The method is based on modelling seasonal growth increments (SGI), measured as the difference between body length at capture and back-calculated length-at-age from the outermost annuli, for several age classes simultaneously. To illustrate the SGI method, the date of onset of growth was determined for 16 fish species from a temperate fluvial lake. Several models were used to describe growth patterns and their performance was compared by means of an information criterion (Burnham & Anderson, 2002). Because temperature directly influences physiological processes determining fish growth (Brett, 1979) and may contribute to initiating seasonal fish growth, model results were used to obtain the water

temperature at the onset of growth for each species. An attempt was then made to relate the water temperature at the onset of growth to the thermal preferenda of the 16 species.

Methods

Study system and field sampling

Lake St. Pierre (46°12'N; 72°49'W) is the largest fluvial lake in the St. Lawrence River system and the largest freshwater floodplain in Quebec, Canada. The lake is shallow (mean depth = 3.1 m at mean discharge), with the exception of a central navigation channel that reaches depths >13 m, and has a variable surface area that fluctuates between 387 and 501 km² depending on water level (Hudon, 1997). Approximately 50 freshwater fish species are resident in the lake.

Fish were collected from the shallow littoral zone (<2.5 m depth) by electrofishing (Smith-Root CataRaft boat) along 80 transects parallel to the north and south shorelines in the summer of 2003 (29 July - 14 September) and 2004 (9 June - 24 August). Individual transects were defined by the trajectories covered during 20 minutes of fishing (approx. 650 m in length at 2 km·h⁻¹). Fish were measured (total length, T_L ; nearest mm), weighed (nearest 0.1 gm). A subsample of fish (4-30 cm T_L) from each transect were kept on dry ice and later transferred to the laboratory for extraction of hard structures.

Water temperature (daily mean) was derived from air temperature by means of a time-series regression model, calibrated as follows. Daily mean water temperatures were obtained from four recorders (Minilog, VEMCO, Shad Bay, Nova Scotia; ± 0.1 °C) placed in the shallow littoral of the lake at depths < 2 m and 0.2 m from the bottom of the water column. The calibrated model was obtained by regressing water temperature for day X , WaterT_X , against three predictors: the air temperatures (daily mean for the Lake St. Pierre Station, Environment Canada) for that day, AirT_X , and the two preceding days, AirT_{X-1} , and AirT_{X-2} . The coefficient of determination of the multiple regression model (adjusted $R^2 = 0.94$) indicated that air temperatures were suitable predictors of water temperature in the lake. The overall pattern of seasonal variation in water temperature, rapid rise in spring and slower change over the summer, was similar in the two study years (Figure 2.1).

Age determination and back-calculation

A total of 1066 fish for 16 species (ages 0+ to 5+) were available for analysis (Table 2.1). Hard structures for age determination were prepared following DeVries & Frie (1996). Scales were used for all species except for brown bullhead *Ameiurus nebulosus* (Lesueur) (spines), white sucker *Catostomus commersonii* (Lacepède) (pectoral fin rays), and yellow perch *Perca flavescens* (Mitchill), walleye *Sander vitreus* (Mitchill) and sauger *Sander canadensis* (Griffith & Smith) (opercula) (Table 2.1). Scales were cleaned in water and mounted between microscope slides. Pectoral fin rays and spines were embedded in epoxy resin, cut transversally, near the articulation, into thin sections with a gem saw, and mounted on a microscope slide with Cytoseal. Opercula were cleaned, dried in paper envelope, and clarified with Cytoseal.

Age determination and measurement of growth increments were done using a binocular stereoscope (Leica MS5) connected to an image analysis system (high-performance color CCD camera, Cohu model 8285; Matrox Meteor-II frame grabber; SigmaScan Pro software version 5.0). The total length of the structure was measured from the focus to the outer edge of the structure. The first increment length, the distance from the focus of the structure to the first annulus, and the yearly increments between subsequent annuli, were measured along a single linear path.

Age determinations were validated by length-frequency analysis (Petersen method; DeVries & Frie, 1996). The Fraser-Lee method (Francis, 1990) was used to back-calculate fish length-at-age, following Smedstad & Holm (1996) and Johal *et al.* (2001). The seasonal growth increment (SGI), a measure of increase in body length (mm) since the onset of the growth season, was calculated as the difference between length at capture (L_c) and back-calculated length obtained from the outermost annuli (L_a).

Growth models

A broad variety of models has been used to assess annual or daily fish growth (Campana & Jones, 1992; Katsanevakis, 2006), probably reflecting the dependence of the functional form of fish growth on diverse factors such as species, location, age classes, and weight classes of the fish (Schaalje *et al.*, 2002). Because there is no clear consensus on which function of age is most

appropriate for modelling fish growth (Chen *et al.*, 1992), six candidate functions were examined:

Polynomial, linear:
$$SGI = \alpha (d - d_0)$$

Polynomial, quadratic:
$$SGI = \alpha (d - d_0)(\beta - d)$$

von Bertalanffy:
$$SGI = \alpha (1 - e^{-\beta(d-d_0)})$$

Modified Farazdaghi and Harris:
$$SGI = \frac{\alpha}{\left(1 + \frac{\beta}{d - d_0}\right)}$$

Modified Freundlich:
$$SGI = \alpha d^{\frac{\beta}{d-d_0}}$$

Modified Chapman-Richards:
$$SGI = \alpha (1 - \beta^{-(d-d_0)})$$

where SGI is the seasonal growth increment in total length, d is a variable coding for the number of days elapsed from 1 March until the day of capture, and d_0 is the day marking the seasonal onset of growth. The first two functions are linear or quadratic polynomials. They are not cast in their conventional general form, but are instead reparametrized to the factored form to directly obtain d_0 , which corresponds to the x-intercept of the curve, and its associated standard error from the nonlinear estimation procedure. In the factored form of the quadratic function, α is a scaling factor and d_0 and β are the real roots (Figure 2.2). The four remaining functions are well-known growth models (Ratkowsky, 1990; Schaalje *et al.*, 2002), modified by setting the exponent γ to 1. In these models, α reflects scale and β , curvature.

The *nls* function (R version 2.3.1; R Development Core Team, 2006) was used to obtain least-squares parameter estimates for all models. Model comparisons were based on the Akaike's information criterion (AIC), which penalizes the maximized likelihood by the number of parameters in the model (Burnham & Anderson, 2002). The difference in AIC between a reference and an alternative model, ΔAIC , was obtained as $\text{AIC}_{\text{alternative}} - \text{AIC}_{\text{reference}}$.

In all models, parameters α and β were allowed to vary among age classes, by using the following representation:

$$\alpha \text{ (or } \beta) = \delta_{\phi} + \sum_{i=\phi+1}^n k_i D_i$$

where δ_{ϕ} is a baseline value for the youngest age class, ϕ , k_i is an age-specific effect for age class i quantifying the difference in α (or β) between that age class and the youngest age class, the D_i are a set of binary (0, 1) dummy variables coding for age class, and n is the oldest age class. Age classes represented by fewer than four individuals were excluded from the analyses to meet sample size requirements for parameter estimation. Base models assuming constancy in d_0 among years and age classes were built for the six candidate growth functions and compared by means of the AIC.

For each species, the selected base model was then compared to a year-effect model, to assess whether d_0 differed between years. The age-effect model was built by allowing d_0 in the base model to vary between years:

$$d_0 = \delta_{03} + k_{04} D_{04}$$

where k_{04} is a year-specific effect quantifying the difference in d_0 between 2003 and 2004, and D_{04} is a binary (0, 1) dummy variable identifying year of growth. Similarly, the selected base model was compared to an age-effect model, to assess whether d_0 differed between age classes. In this case, d_0 in the base model was replaced by age-specific values as explained previously for the α and β parameters in the base model.

Thermal preferenda and thermal preference

Thermal preferenda for all species were obtained from studies reviewed in Coutant (1977), Jobling (1981), and Wismer & Christie (1987). When specified, the setting (field or laboratory), season, and habitat (river or lake) were noted for each study. Identical preferendum values obtained from different studies were tallied as independent results. Different subsets of studies were selected for analysis to match the conditions of the present study to varying degrees, e.g., field studies conducted in summer, or all but winter studies. For each species and subset of studies, the water temperature associated to the estimated date of onset for seasonal growth was related to the final temperature preferenda by model II linear regression (Systat version 10.2; SPSS Inc., 2002), and a relationship was deemed significant if the confidence interval for its slope excluded zero. The species were also assigned a thermal preference class (cold; cold/cool; cool; cool/warm; or warm) following Coker *et al.* (2001).

Results

Polynomial (linear or quadratic) models provided the best fit for 13 of the 16 species (Table 2.2), and the quadratic model was essentially equivalent to the best-fitting model for the three remaining species ($|\Delta\text{AIC}| < 2$ units; Burnham & Anderson, 2002). Parameter estimation always converged for the linear model, but failed to converge in some cases for the quadratic model (5 species) and the four alternative models (7-9 species). Examples of linear and quadratic fits are presented in Figure 2.3.

Comparisons of the best-fitting polynomial (base model) to the year-effect model failed to detect inter-year differences in d_0 for 10 of the 11 species for which sufficient data were available (Table 2.3). Comparisons of the best-fitting polynomial (base model) to the age-effect model failed to detect differences in d_0 among age classes for 11 of the 12 species for which sufficient data were available (Table 2.3). The only exception, *Notemigonus crysoleucas* (Mitchill), had a small ΔAIC (-2.3).

The best-fitting polynomial models were used to determine the date of onset date of fish growth for all species (Table 2.4). With the exception of *Notropis heterolepis* Eigenmann & Eigenmann, for which the standard error exceeded the point estimate and the R^2 value was very low, the point estimates for the date of onset were concentrated between 2 May and 11 June. Estimation of the date of onset also was imprecise for *Fundulus diaphanus* (Lesueur) and *Pimephales notatus* (Rafinesque), both of which had large standard errors. For the 13 remaining species, R^2 ranged from 0.48 to 0.99.

A narrow temporal window of approximately two weeks, between 18 May and 2 June, contained the point estimates of d_0 for 8 of the 16 species and was intersected by the 95% confidence intervals of all species (Figure 2.4a). Because estimates of d_0 did not vary between years for most species, a smoothed curve for the two study years combined (Figure 2.1) was used to obtain the water temperatures corresponding to the point estimates and 95% confidence intervals of d_0 (this procedure renders the intervals for temperature asymmetric) (Figure 2.4b). Similar to d_0 , a narrow window of approximately 1.2 °C, between 16.1 and 17.3 °C, contained the point estimates of water temperature at the onset of growth for 8 of the 16 species and was intersected by the intervals of all species. There was no apparent relationship between the water temperature corresponding to the onset date and the species' thermal preference according to the classification of Coker *et al.* (2001). No clear relationship could be established either between the water temperature corresponding to the onset date and the thermal preference for any of the subsets of studies examined.

Much of the uncertainty in the estimates of d_0 (as measured by the width of the 95% confidence interval) was accounted for by two factors: the number of fish in the age class with fewest individuals and the number of age classes used for estimation (Figure 2.5). All species having at least two age classes represented and >6 individuals in all age classes (9 species) had 95% confidence intervals < 15 days.

Discussion

The model comparisons indicated that polynomial (linear or quadratic) functions provided overall the best fits to seasonal growth for 16 fish species in Lake St. Pierre, and were more likely to avoid convergence problems than the four alternative models. Application of a growth model should generally be preceded by comparison to multiple alternative models, because not all species or life periods need follow the same growth function (Cailliet *et al.*, 2006). For example, growth of European hake larvae (*Merluccius merluccius* L.) can be fitted by a linear model for the first 20 days of life, and by an exponential model for the first 40 days of life (Álvarez & Cotano, 2005). The daily growth of larval and juvenile fish is generally modelled linearly (Morley *et al.*, 2005; Hwang *et al.*, 2006), but Gompertz (Admassu & Ahlgren, 2000) or exponential models (Fives *et al.*, 1986) may also be used.

There was little evidence for differences in the date of onset of growth between years. The seasonal pattern of temperature variation was very similar in the two study years and perhaps the onset of growth was timed similarly in the two years because the growth response to temperature is integrated over time, thus smoothing the effect of short-term (~ 1 week) fluctuations in temperature.

The date of onset of growth was similar among age classes within individual species. The convergence of different age classes to a common date of onset provides indirect corroboration of the method and points to temperature as a likely environmental determinant of the onset of growth. Although other factors such as food availability or photoperiod may determine the onset

of growth (Brett, 1979), it seems unlikely that these factors would act synchronously on all age classes or show a threshold effect on growth as does temperature (Keast, 1985; McNerny & Held, 1995).

The onset of growth also was to some extent synchronised among species. This restricted variation in date of onset probably partly explains why there was no apparent relationship between date of onset and thermal preferenda or preference. As well, it suggests that the physiological mechanisms underlying the seasonal growth response in the field may be decoupled from those determining thermal preferenda and preference. For Canadian freshwater fishes, seasonal spawning is concentrated in two periods, early summer or autumn (Potts and Wootton, 1984). However, hatching occurs predominantly over a period of about 100 days in the spring. This synchrony may result from the availability of suitable food for young-of-the-year at this period, or, alternatively, may represent a strategy for maximising the length of the growing season.

The SGI method represents an improvement over the MIR as a tool for determining the onset of seasonal growth in fish. First, the MIR may be best suited for analysing only a few age classes at a time, ideally only one (Beckman & Wilson, 1995). Moreover, the 0+ age class can not be included in MIR analyses because the calculation requires data on growth for the preceding year. The SGI method uses simultaneously and integrates the growth data from all age classes, and can detect departures from a common growth pattern by comparing the base and age-effect models. Second, MIR analysis estimates the onset of the growing season only with monthly or seasonal precision, in contrast with the point estimate and associated range provided

by the SGI method. The inadequacy of MIR analyses for determining the timing of growth events has been noted previously (Beckman & Wilson, 1995). The improved performance of the SGI method relative to selection of minima in a time series of MIR stems in part from simple geometry: it is easier to determine precisely the point of intersection of several growth curves with the X-axis (Figures 2.2, 2.3) than the trough in a curve traced approximately through discrete time points.

The onset of growth may also be established from the spawning period (Braaten & Guy, 2002). However, this method is imprecise for species having a protracted spawning period. The SGI method also assumes that reproduction is relatively discrete in time, and this could introduce considerable uncertainty in the estimates of the date of onset for the 0+ age class. Another alternative method for determining the onset of growth, counts of otolith daily increments, can be very precise but is labour-intensive and restricted to younger individuals.

The SGI method is potentially subject to the pitfalls inherent to all methods relying on age determination and back-calculation, including ambiguity introduced by spurious growth marks and difficulty in ageing older fish accurately. Estimates of the date of onset of growth can be rendered more precise by increasing the number of age classes and the sample size for all age classes included in the analysis. Additionally, ensuring that the temporal distribution of samples spans a broad enough portion of the growth period will enhance the precision of parameter estimates and thus the power of the method to resolve the date of onset. The importance of these sampling requirements will likely vary from system to system; therefore, further tests of the SGI method should allow for a more thorough evaluation of the method's usefulness and limitations.

In conclusion, the SGI method can contribute to a better understanding of environmental influences on the onset of growth and the length of the growth season, and of thermal thresholds for growth, including their relevance for calculation of degree-day metrics. These aspects in turn have potential applications in studies of thermal physiology, population dynamics, and fisheries research and management.

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TABLE 2.1. Number of fish, by species and age class, and hard structure used for back-calculation.

Species	Common name	Number of fish, by age class						Hard structure
		0+	1+	2+	3+	4+	5+	
<i>Ameiurus nebulosus</i> (Lesueur)	Brown bullhead			63	40	10	6	Pectoral spine ¹
<i>Catostomus commersonii</i> (Lacepède)	White sucker	23	17	7				Pectoral fin ray ¹
<i>Etheostoma olmstedi</i> Storer	Tessellated darter	14	28	8				Scale ²
<i>Fundulus diaphanus</i> (Lesueur)	Banded killifish	4	56					Scale ¹
<i>Hybognathus regius</i> Girard	Eastern silvery minnow		7	24	10			Scale ¹⁻³
<i>Lepomis gibbosus</i> (Linnaeus)	Pumpkinseed	16	13	12				Scale ¹
<i>Notemigonus crysoleucas</i> (Mitchill)	Golden shiner		49	16				Scale ¹⁻³
<i>Notropis atherinoides</i> Rafinesque	Emerald shiner	12	37					Scale ¹⁻³
<i>Notropis heterolepis</i> Eigenmann & Eigenmann	Blacknose shiner		17					Scale ¹⁻³
<i>Notropis hudsonius</i> (Clinton)	Spottail shiner	4	29					Scale ¹⁻³
<i>Perca flavescens</i> (Mitchill)	Yellow perch	62	146	48	33	12		Operculum ³
<i>Percina caprodes</i> (Rafinesque)	Logperch	22	38					Scale
<i>Percopsis omiscomaycus</i> (Walbaum)	Trout-perch	30	26	4				Scale ³

TABLE 2.1. Continued

<i>Pimephales notatus</i> (Rafinesque)	Bluntnose minnow	24	4	Scale ¹⁻³
<i>Sander canadensis</i> (Griffith & Smith)	Sauger	31	6	Operculum ³
<i>Sander vitreus</i> (Mitchill)	Walleye	46	12	Operculum ³

¹Jearld (1983); ²Knight & Ross (1992); ³Mackay *et al.* (1990)

TABLE 2.2. Differences in Akaike's information criterion (AIC) for the six models examined in this study. For each species, the best model has a value of zero for the Δ AIC. The number of model parameters is given by the number of age classes n ($n + 1$ for the linear model, and $2n + 1$ for all other models). Missing values indicate that the estimation procedure did not converge.

Species	Number of fish	Age classes included (number of age classes)	Model					
			Polynomial, linear	Polynomial, quadratic	von Bertalanffy	Farazdaghi and Harris	Freundlich	Chapman-Richards
<i>A. nebulosus</i>	119	2+, 3+, 4+, 5+ (4)	19.70	0	9.83	11.65	10.77	9.83
<i>C. commersonii</i>	47	0+, 1+, 2+ (3)	0					
<i>E. olmstedii</i>	50	0+, 1+, 2+ (3)	4.06	0	0.64	1.87		0.64
<i>F. diaphanus</i>	60	0+, 1+ (2)	15.06	0				
<i>H. regius</i>	41	1+, 2+, 3+ (3)	1.24	0	1.36	2.21		1.36
<i>L. gibbosus</i>	41	0+, 1+, 2+ (3)	0	2.97				
<i>N. crysoleucas</i>	65	1+, 2+ (2)	0					
<i>N. atherinoides</i>	49	0+, 1+ (2)	6.69	0.55		0.06	0	
<i>N. heterolepis</i>	17	1+ (1)	0	1.90	1.94	1.95	1.95	1.94
<i>N. hudsonius</i>	33	0+, 1+ (2)	1.88	0.13	0.04	0	0.05	0.04

TABLE 2.2. Continued

<i>P. flavescens</i>	301	0+, 1+, 2+, 3+, 4+ (5)	26.99	0	0.69	1.20	1.33	0.69
<i>P. caprodes</i>	60	0+, 1+ (2)	26.43	1.46	2.07	3.16	0	2.07
<i>P. omiscomaycus</i>	60	0+, 1+, 2+ (3)	0					
<i>P. notatus</i>	28	1+, 2+ (2)	0					
<i>S. canadensis</i>	37	0+, 1+ (2)	0					
<i>S. vitreus</i>	58	0+, 1+ (2)	0	2.47	2.17	2.05	1.44	2.17

TABLE 2.3. Comparison of the selected base model (linear or quadratic polynomial) with two alternative extended models incorporating the effects of year or age class on the day of onset of growth, d_0 . Akaike's information criterion (AIC) (for the base model) and Δ AIC (for the alternative models) are reported for each species. Positive Δ AIC values favour the base model over the extended model.

Species	Number of fish,		Base model Model	Base model		Year effect model		Age effect model	
	by year			Number of		Number of		Number of	
	2003	2004		parameters	AIC	parameters	Δ AIC	parameters	Δ AIC
<i>A. nebulosus</i>	6	113	Quadratic	9	258.8	10	0.6	12	4.4
<i>C. commersonii</i>	14	33	Linear	4	148.2	5	-9.8	6	1.6
<i>E. olmstedii</i>	14	36	Quadratic	7	92.5	8	1.9	9	3.8
<i>F. diaphanus</i>		60	Quadratic	5	34.2	One year only		No convergence	
<i>H. regius</i>	16	25	Quadratic	7	35.6	8	1.5	9	3.8
<i>L. gibbosus</i>	1	40	Linear	4	59.3	5	1.1	6	0.9
<i>N. crysoleucas</i>	9	56	Linear	3	135.3	4	1.3	4	-2.3
<i>N. atherinoides</i>	17	32	Quadratic	5	83.0	6	0.4	No convergence	

TABLE 2.3. Continued

<i>N. heterolepis</i>		17	Linear	2	-35.1	One year only		One age class only	
<i>N. hudsonius</i>	6	27	Quadratic	5	-10.4	No convergence		No convergence	
<i>P. flavescens</i>	126	175	Quadratic	11	581.8	12	2.0	15	7.7
<i>P. caprodes</i>	23	37	Quadratic	5	94.2	6	2.0	6	1.7
<i>P. omiscomaycus</i>	10	50	Linear	4	100.2	5	1.6	6	1.9
<i>P. notatus</i>		28	Linear	3	11.4	One year only		4	1.9
<i>S. canadensis</i>		37	Linear	3	140.7	One year only		4	2.0
<i>S. vitreus</i>	9	49	Linear	3	216.4	4	1.8	4	0.7

TABLE 2.4. Estimate and standard error for the day of growth onset, d_0 , for the selected model (linear or quadratic polynomial), and associated date, by species. R^2 values are reported also.

Species	Selected	d_0 (std. error)	Date of onset of	R^2
	model		growth	
<i>A. nebulosus</i>	Quadratic	98.7 (2.0)	6 June	0.62
<i>C. commersonii</i>	Linear	92.3 (3.4)	31 May	0.91
<i>E. olmstedii</i>	Quadratic	89.6 (7.1)	28 May	0.89
<i>F. diaphanus</i>	Quadratic	68.5 (54.9)	7 May	0.92
<i>H. regius</i>	Quadratic	94.0 (6.1)	2 June	0.48
<i>L. gibbosus</i>	Linear	85.7 (6.5)	24 May	0.89
<i>N. crysoleucas</i>	Linear	66.1 (6.6)	5 May	0.65
<i>N. atherinoides</i>	Quadratic	96.5 (6.8)	4 June	0.92
<i>N. heterolepis</i>	Linear	42.2 (61.2)	11 April	0.18
<i>N. hudsonius</i>	Quadratic	103.2 (6.2)	11 June	0.99
<i>P. flavescens</i>	Quadratic	84.3 (3.3)	23 May	0.92
<i>P. caprodes</i>	Quadratic	94.1 (4.6)	2 June	0.96
<i>P. omiscomaycus</i>	Linear	63.2 (11.9)	2 May	0.94
<i>P. notatus</i>	Linear	69.5 (24.6)	8 May	0.35
<i>S. canadensis</i>	Linear	82.1 (12.0)	21 May	0.70
<i>S. vitreus</i>	Linear	80.0 (6.4)	19 May	0.88

Figure captions

Figure 2.1. Water temperature (daily mean) for Lake St. Pierre for the period 1 April – 1 October in the two study years (— 2003; ---- 2004). A smoothed curve (cubic spline function; smoothing window = 0.2) for both years combined is presented also (—).

Figure 2.2. Graphical representation of the quadratic model of seasonal growth increments for fish in three different age classes. The parabolas for each age class are characterized by three parameters: their roots (d_0 and β) and a scaling factor, α , which jointly define the maximum height of the parabola. The three age classes are represented as having the same value for parameter d_0 , the day of the onset of seasonal growth, but different values for α and β . Formulas for the maximum height and corresponding date are given also.

Figure 2.3. Model fits to seasonal growth for a) *Sander vitreus* and b) *Percopsis omiscomaycus* (linear model), and c) *Notropis atherinoides* and d) *Percina caprodes* (quadratic model). Symbols represent individuals in the 0+ (O), 1+ (Δ), and 2+ (\square) age classes.

Figure 2.4. Estimates and associated 95% confidence intervals for the date of onset of seasonal growth (a) and water temperature corresponding to the date of onset (b), for 16 fish species in Lake St. Pierre. The vertical dashed lines enclose the narrowest interval of dates (a) or temperatures (b) that intersects all of the 95% confidence intervals. Estimates were obtained from fits of the linear or quadratic growth models to seasonal growth increments for 2003 and

2004. Numerical codes for thermal preference (from Coker *et al.*, 2001) are given in parentheses next to species names: 1=cold; 2=cold/cool; 3=cool; 4=cool/warm; 5=warm.

Figure 2.5. Uncertainty in the estimated date of onset of growth (width of the 95% confidence interval) as a function of the number of fish in the smallest age class and the number of age classes used for estimation. Each symbol corresponds to one fish species. The dotted line separates estimates for which uncertainty is <15 days from more variable estimates. The number of age classes is coded by symbols: 1 (○), 2 (Δ), 3 (□), 4 (●), and 5 (▲).

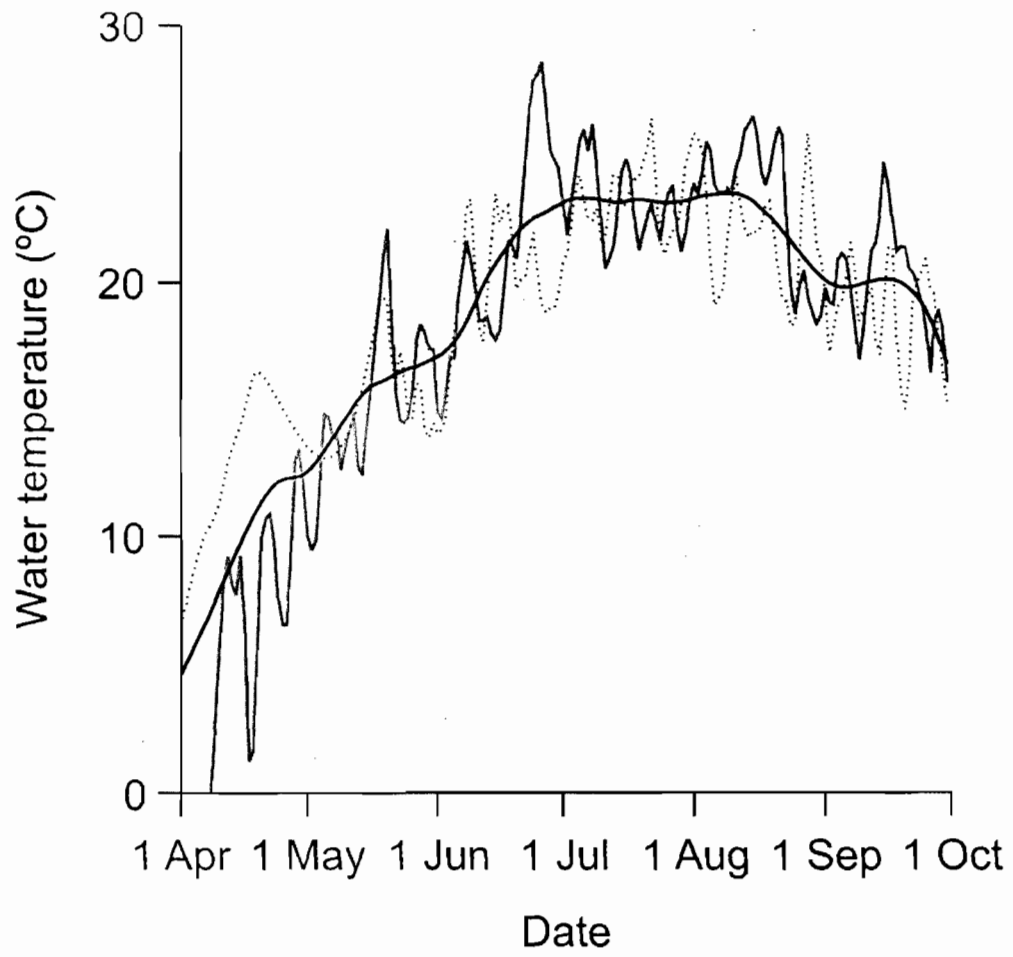


Figure 2.1. Gagné and Rodríguez

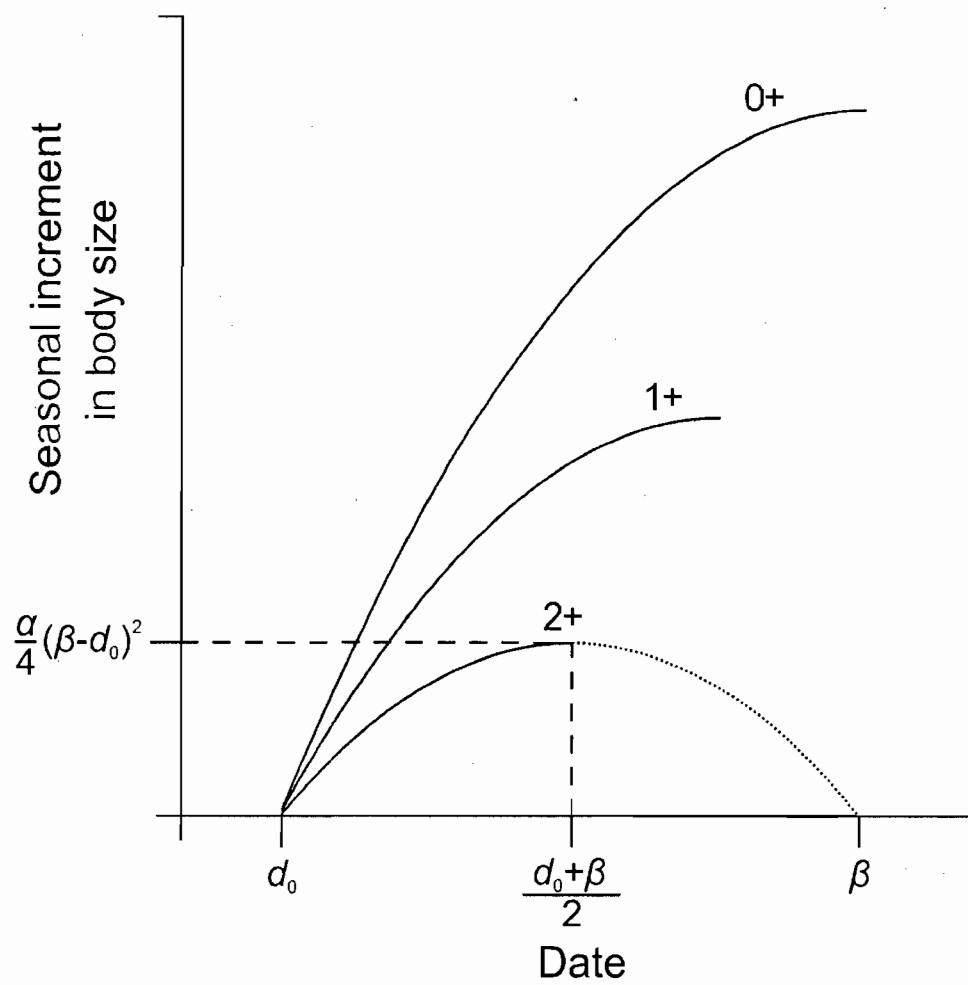


Figure 2.2. Gagné and Rodríguez

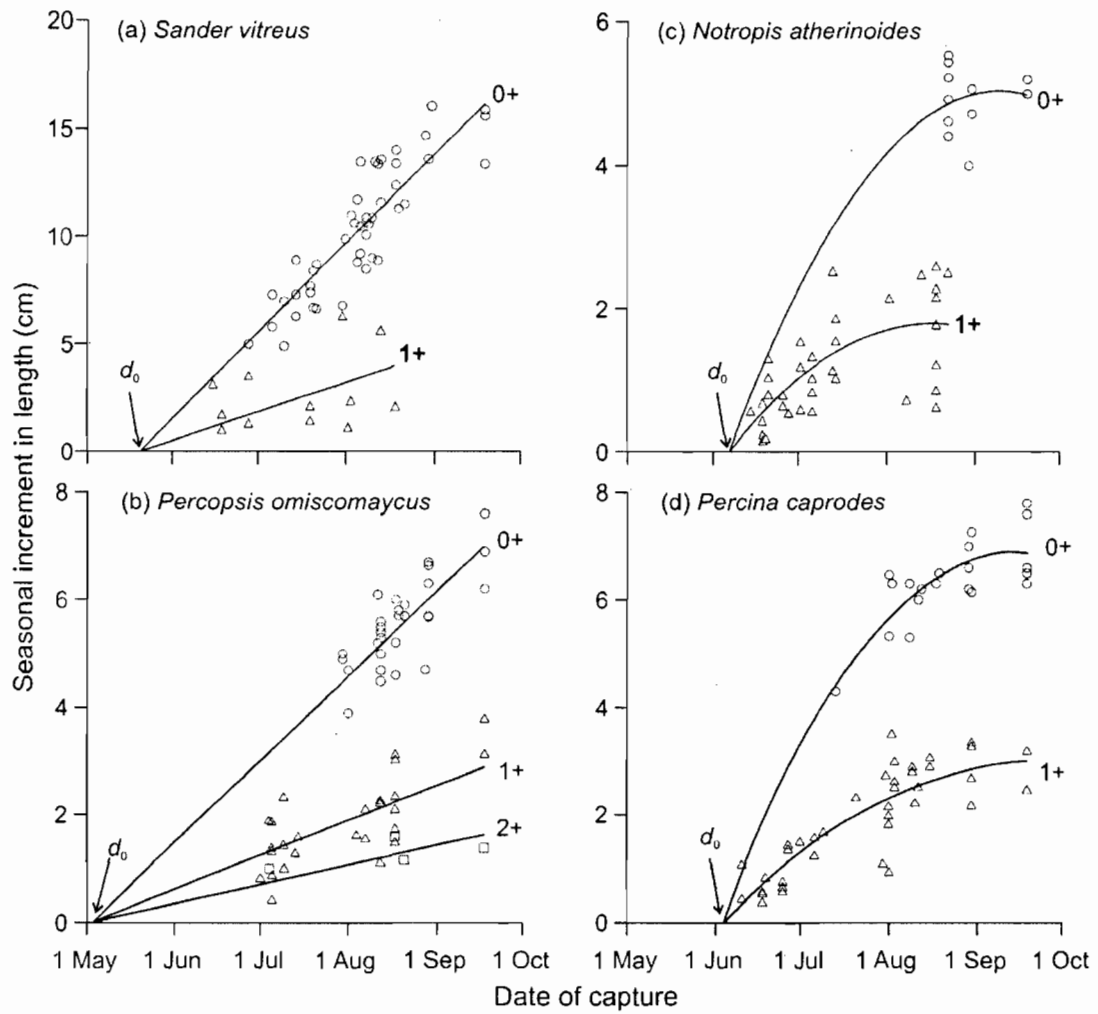


Figure 2.3. Gagné and Rodríguez

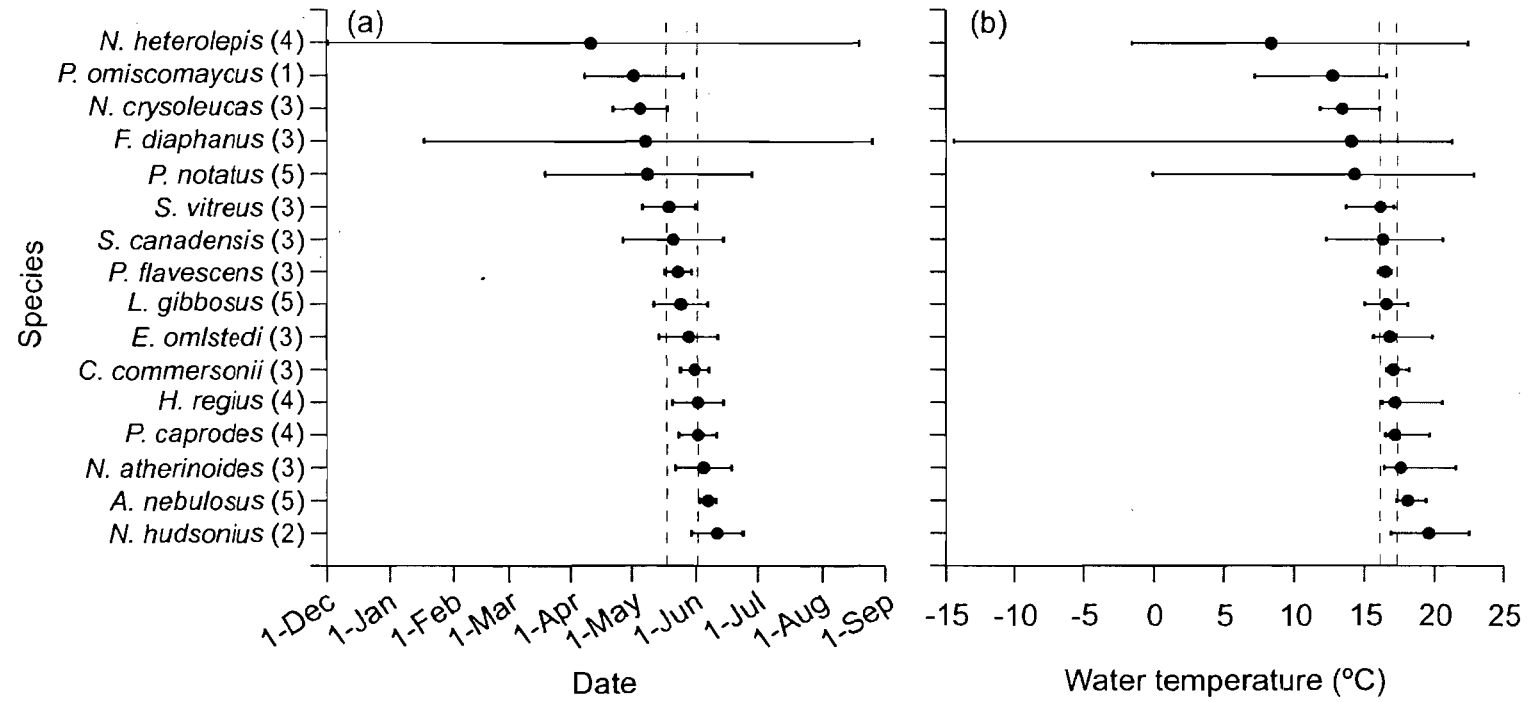


Figure 2.4. Gagné and Rodríguez

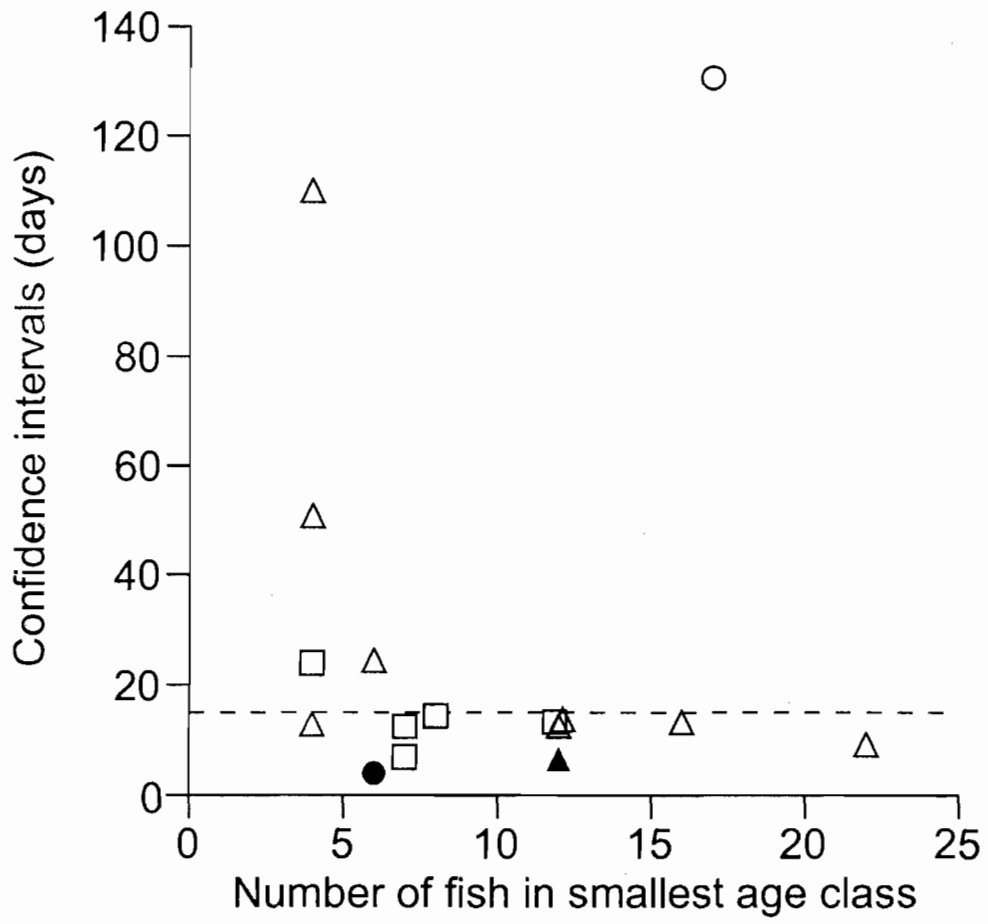


Figure 2.5. Gagné and Rodríguez