Abstract.– Most growth models are age-dependent only. Although their modifications can be used to consider, implicitly, the seasonal growth of animals and the effects of tagging, a general framework is unavailable for explicitly incorporating time and time-dependent factors (i.e. ambient temperature and food availability) in age-dependent growth models. In this paper, I derived general age- and time-dependent growth models for animals and gave a comprehensive list of special cases for age- and time-dependent growth models of von Bertalanffy, logistic, and Gompertz types. Such models explicitly incorporate age, time, and their dependent factors and are useful for modeling growth at age and time (e.g. from length-at-age data), incremental growth at age and time increments (e.g. length increments at age and time increments data from tagging studies), the effects of tagging, and the effects of many population characteristics. I also examined their data requirements, their independence of the start of time and adjustment of estimates of parameters essential for ensuing applications, and concluded that age- and time-dependent growth models are useful for subsequent applications, if and only if they are independent of the start of time or time-homogeneous and if estimates of their parameters are properly adjusted. A scheme for such an adjustment is proposed and demonstrated. Finally, I used nine special cases of these general models to analyze tagging data on a centropomid perch (*Lates calcarifer* (Bloch)). Such analyses suggested that tagging is antagonistic to fish growth and leads to a shrinkage of size and that *L. calcarifer* exhibits a strong seasonality in growth, namely its length grows fastest at the start of autumn, grows less until a full stop in the middle of winter, shrinks until the middle of spring, and resumes a positive growth for another cycle.

General age- and time-dependent growth models for animals

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Most growth models relate an animal's size to its age alone, are independent of time, and are meant to be useful at all times. Some factors (e.g. ambient temperature and food availability) that are known to affect the growth of animals vary with time, however. Consequently, time has been incorporated in age-dependent growth models implicitly, to consider seasonal (Pitcher and Macdonald, 1973; Appeldoorn, 1987; Smith and McFarlane, 1990; Pauly et al., 1992; Pauly and Gaschütz[1]) and biphasic (Soriano et al., 1992) growth of animals, and the effects of tagging (Xiao, 1994). Xiao's (1996, equations 3.0–4.2, p. 1676–1677) deterministic extensions of the classical von Bertalanffy (1938), logistic (Verhulst, 1838), and Gompertz (1825) growth models also serve these purposes. Similarly, Wang (1998) derived a set of age- and time-dependent growth models for a special case of the von Bertalanffy (1938) growth equation and even constructed distribution-free and consistent estimating functions for estimating their parameters. Although these implicit age- and time-dependent growth models can describe a set of data better than age-dependent growth models, a general framework is unavailable for an explicit incorporation of time and time-dependent factors.

However, an explicit entry of age, time, and time-dependent factors into growth models is essential for studying the effects of many char-

acteristics of a population (e.g. its age composition, size composition, density, and size- or age-specific mortalities) on the growth of its individuals (Moulton et al., 1992; Walker et al., 1998). Indeed, much insight can be gained by examining density-dependent growth alone. This is because density-dependent growth can be effected by 1) compensatory decreases in natural mortality, which may result from a decrease in predation, cannibalism, competition or diseases; 2) compensatory increases in fecundity when food is more readily available or fetal mortality decreases; and 3) compensatory increases in growth rate when more food induces earlier maturity and greater fecundity for each age class (Holden, 1973). For these studies to be feasible, equations for the sizes of individual animals at age *a* at time *t* in a population must be coupled with those of their numbers at age *a* (or size) at time *t*.

Just as an increase in dimension can reveal new horizons, an explicit incorporation of time and time-dependent factors in age-dependent growth models can be of great use and promise. It also poses interesting philosophical and practical problems. Indeed, in general, time-dependency makes age- and time-

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[1] Pauly, D., and G. Gaschütz. 1979. A simple method for fitting oscillating length growth data, with a program for pocket calculators. ICES Council Meeting 1979/ G:24, 26 p.

dependent growth models depend on the start of time and thereby renders them useless, unless the start of time is known. Of course, the start of time (if it did start at all) is unknown (although some may settle for the Big Bang) and remains a subject of philosophical debate. It is obvious, then, that, for practical purposes, workable age- and time-dependent growth models must be independent of the start of time. But, under what conditions are they so? How should estimates of their parameters be adjusted to make these models useful for subsequent applications at all times? To answer these questions, both age and time must enter a growth equation, explicitly.

In this paper, I derive general age- and time-dependent growth models for animals and give a comprehensive list of special cases for age- and time-dependent von Bertalanffy (1938), logistic (Verhulst, 1838), and Gompertz (1825) growth models. Such models explicitly incorporate age, time, and their dependent factors and are useful for modeling growth at age and time (e.g. from length-at-age data), incremental growth at age and time increments (e.g. from length increments at age and time increments from tagging studies), the effects of tagging, and the effects of population characteristics. I also examine their data requirements, their independence of the start of time, and adjustment of estimates of their parameters for ensuing applications. Finally, I use nine special cases of these general models to analyze data on length increments at age and time increments from a tagging study of a centropomid perch (*Lates calcarifer* (Bloch)) in the Northern Territory, Australia.

General age- and time-dependent growth models

Just as a formal derivation of age-dependent growth models necessitates use of ordinary differential equations, a formal derivation of age- and time-dependent growth models entails use of partial differential equations. This is because both age and time must be taken into explicit account. Readers unfamiliar with first order partial differential equations may wish to skip immediately to Equations 6–6.3, 10–10.3, and 14–14.3, with little loss of comprehension.

Now, let $0 \leq y(a,t) < \infty$, $-\infty < a_0 \leq a < \infty$, $0 \leq t_0 \leq t < \infty$, denote the size of an individual of a species of animal of age a at time t, with an arbitrary reference age a_0 and an arbitrary reference time t_0. Suppose that the change in its size at age a at time t in a small time interval of length Δt is proportional to a function of $y(a,t)$ and Δt, such that

$$y(a + \Delta a, t + \Delta t) - y(a,t) = K(a,t)f(y(a,t))\Delta t,$$

where $K(a,t)$ is its instantaneous rate of growth in size at age a and time t, and can capture the effects of age, time, and their dependent factors. Dividing both sides of this equation by Δt, Taylor series expansion of $y(a+\Delta a,t+\Delta t)$ in the neighbourhood of (a,t) as

$$y(a + \Delta a, t + \Delta t) = y(a, t) +$$
$$\frac{\partial y(a, t)}{\partial a}\Delta a + \frac{\partial y(a, t)}{\partial t}\Delta t + O(\Delta t),$$

passing to the limit $\Delta t \to 0$, assuming that

$$\lim_{\Delta t \to 0} O(\Delta t) \to 0,$$

and assuming further that

$$\frac{da}{dt} = 1,$$

yield a first order partial differential equation

$$\frac{\partial y(a, t)}{\partial a} + \frac{\partial y(a, t)}{\partial t} = K(a, t) f(y(a, t)). \tag{1}$$

To solve this equation, I use the following approach. Suppose that the solution of $y(a,t)$ is known. Let $a=t+c$, or $c=a-t$, then

$$w_c(t) = y(t+c,t) \qquad t \geq t_c = \max(t_0, a_0 - c)$$

for a fixed value of $c \in R$. Because $y(a,t)$ satisfies Equation 1, we obtain

$$\frac{dw_c(t)}{dt} = K(t+c,t)\, f\!\left(w_c(t)\right). \qquad t \geq t_c$$

(2)

Equations 1 and 2 are too general to be solved analytically. Now, I examined three of their special cases for $f(y(a,t))$. For each of these special cases, Table 1 describes where to find equations corresponding to various quantities of interest, and Table 2 describes where to find equations corresponding to various special cases of the solution for $y(a,t)$.

Age- and time-dependent growth models of von Bertalanffy (1938) type I

If $f(y(a,t))=y_{max}(a,t)-y(a,t)$, Equations 1 and 2 become, respectively,

$$\frac{\partial y(a,t)}{\partial a} + \frac{\partial y(a,t)}{\partial t} = K(a,t)\left[y_{\max}(a,t) - y(a,t)\right]$$

(3)

$$\frac{dw_c(t)}{dt} = K(t+c,t)\left[y_{\max}(t+c,t) - w_c(t)\right]. \qquad t \geq t_c$$

(4)

Of its many interpretations, $y_{max}(a,t)$ can represent the asymptotic size of an average individual as age approaches infinity.

Solution of Equation 4 as an initial value problem with $w_c(t)|_{t=t_c} = w_c(t_c)$ yields

$$w_c(t) = w_c(t_c)\, e^{-\int_{t_c}^{t} K(s+c,s)\,ds} \;+\;$$

$$\int_{t_c}^{t} K(s+c,s)\, y_{\max}(s+c,s)\, e^{-\int_{s}^{t} K(\xi+c,\xi)\,d\xi}\, ds. \qquad t \geq t_c$$

(5)

If $a-a_0<t$, then $c<0$, $-c>0$, then $t_c=a_0-c=t-a+a_0$; if $a-a_0 \geq t$, then $c \geq 0$, $-c \leq 0$, then $t_c=t_0$. In other words,

$$y(a,t) = \begin{cases} y(a_0, t-a+a_0)\, e^{-\int_{t-a+a_0}^{t} K(s+a-t,s)\,ds} + \int_{t-a+a_0}^{t} K(s+a-t,s)\, y_{\max}(s+a-t,s)\, e^{-\int_{s}^{t} K(\xi+a-t,\xi)\,d\xi}\, ds & a-a_0 < t \\[2em] y(t_0+a-t, t_0)\, e^{-\int_{t_0}^{t} K(s+a-t,s)\,ds} + \int_{t_0}^{t} K(s+a-t,s)\, y_{\max}(s+a-t,s)\, e^{-\int_{s}^{t} K(\xi+a-t,\xi)\,d\xi}\, ds. & a-a_0 \geq t \end{cases}$$

(6)

If $y_{max}(s+a-t,s)=y_{max}=$constant in Equation 6, then

Table 1

Equations corresponding to various quantities of interest for von Bertalanffy (type I) (VB type I), von Bertalanffy (type II) (VB type II), and Gompertz growth equations.

Quantity	VB type I	VB type II	Gompertz
Partial derivative of $y(a,t)$	Equation 3	Equation 7	Equation 11
Derivative of $w_c(t)$	Equation 4	Equation 8	Equation 12
Solution for $w_c(t)$	Equation 5	Equation 9	Equation 13
Solution for $y(a,t)$	Equation 6	Equation 10	Equation 14

Table 2

Equations corresponding to various special cases of the solution for $y(a,t)$ for von Bertalanffy (type I) (VB type I), von Bertalanffy (type II) (VB type II), and Gompertz growth equations.

Assumption about $y_{max}(a,t)$	Assumption about $K(a,t)$	VB type I	VB type II	Gompertz
none	none	6	10	14
$y_{max}(a,t)$=constant	none	6.0	10.0	14.0
$y_{max}(a,t)$=constant	$K(a,t)$=constant	6.1	10.1	14.1
$y_{max}(a,t)$=constant	$K(a,t) = K_0 + A\cos\dfrac{2\pi}{T}(t-t_\phi)$	6.2	10.2	14.2
$y_{max}(a,t)$=constant	$K(a,t)=K_{max}-(K_{max}-K_{min})e^{-(a-a_0)/a}$ if $a-a_0<t$; $K(a,t)=K_{max}-(K_{max}-K_{min})e^{-(t-t_0)/a}$ if $a-a_0\geq t$	6.3	10.3	14.3

$$y(a,t) = \begin{cases} y_{max} - \left[y_{max} - y(a_0, t-a+a_0)\right]e^{-\int_{t-a+a_0}^{t} K(s+a-t,s)\,ds} & a-a_0 < t \\[2em] y_{max} - \left[y_{max} - y(t_0 + a - t, t_0)\right]e^{-\int_{t_0}^{t} K(s+a-t,s)\,ds}. & a-a_0 \geq t \end{cases} \tag{6.0}$$

If $K(s+a-t,s)=K_0=$constant in equation 6.0, then

$$y(a,t) = \begin{cases} y_{max} - \left[y_{max} - y(a_0, t-a+a_0)\right]e^{-K_0(a-a_0)} & a-a_0 < t \\[0.5em] y_{max} - \left[y_{max} - y(t_0 + a - t, t_0)\right]e^{-K_0(t-t_0)}. & a-a_0 \geq t \end{cases} \tag{6.1}$$

which is the age- and time-dependent von Bertalanffy (1938) growth model, or (if $a–a_0$ or $t–t_0$ is interpreted as time at liberty) Fabens (1965) growth model, with parameters K_0 and y_{max}.

Since many factors (e.g. ambient water temperature and food availability) vary seasonally, the instantaneous rate of growth of many animals $K(a,t)$ fluctuates seasonally. If data are available on $K(a,t)$ as a function of these factors, their relationships can be hypothesized. In reality, however, few such data are available. Nonetheless, one can still hypothesize about a temporal trend in $K(a,t)$ and attribute it to the combined effects of all responsible factors. For example, as a first approximation, $K(a,t)$ is seasonal because of seasonal changes in ambient water temperature and food availability and can be approximated by a sine or cosine curve. Thus, if

$$K(s+a-t,s) = K_0 + A\cos\frac{2\pi}{T}(s-t_\phi)$$

in Equation 6.0, an application of the trigonometric function-difference relation

$$\sin(\alpha) - \sin(\beta) = 2\cos\left(\frac{1}{2}(\alpha+\beta)\right)\sin\left(\frac{1}{2}(\alpha-\beta)\right)$$

gives

$$y(a,t) = \begin{cases} y_{max} - \left[y_{max} - y(a_0, t-a+a_0)\right]e^{-K_0(a-a_0)-\frac{AT}{\pi}\sin\frac{\pi}{T}(a-a_0)\cos\frac{2\pi}{T}\left(t-t_\phi-\frac{1}{2}(a-a_0)\right)} & a-a_0 < t \\[1em] y_{max} - \left[y_{max} - y(t_0 + a - t, t_0)\right]e^{-K_0(t-t_0)-\frac{AT}{\pi}\sin\frac{\pi}{T}(t-t_0)\cos\frac{2\pi}{T}\left(t-t_\phi-\frac{1}{2}(t-t_0)\right)}, & a-a_0 \geq t \end{cases} \tag{6.2}$$

where K_0, y_{max}, A, T, and t_ϕ are model parameters to be estimated or specified.

Many species of animals are tagged for a variety of purposes. Tagging can affect the growth of some animals positively, neutrally, or negatively. Indeed, some animals may slow down their growth, cease their growth, or even shrink in size after tagging. A proper functional form of $K(a,t)$ is needed to infer these consequences of tagging. If $K(s+a–t,s)=K_{max}-(K_{max}-K_{min})e^{-(s-t+a-a_0)/\alpha}$ if $a-a_0<t$ and $K(s+a-t,s)=K_{max}-(K_{max}-K_{min})e^{-(s-t_0)/\alpha}$ if $a-a_0\geq t$ in Equation 6.0, then (note that $t-a+a_0-t_0=0$, or $t-t_0=a-a_0$)

$$y(a,t) = \begin{cases} y_{max} - [y_{max} - y(a_0, t-a+a_0)]e^{-K_{max}(a-a_0)-\alpha(K_{max}-K_{min})[e^{-(a-a_0)/\alpha}-1]} & a-a_0 < t \\ y_{max} - [y_{max} - y(t_0+a-t, t_0)]e^{-K_{max}(t-t_0)-\alpha(K_{max}-K_{min})[e^{-(t-t_0)/\alpha}-1]}, & a-a_0 \geq t \end{cases} \qquad (6.3)$$

where K_{max}, K_{min}, y_{max}, and α are model parameters to be estimated or specified. Clearly, the functional form of $K(a,t)$ serves its purpose well. This is because $K_{max}<K_{min}$, $K_{max}=K_{min}$, and $K_{max}>K_{min}$ indicate, respectively, positive, no, and negative effects of tagging on the growth of animals; and $K_{min}<0$, $K_{min}=0$, and $K_{min}>0$ suggest, respectively, a shrinkage, cessation of growth, and a slower growth of tagged animals immediately after tagging.

Age- and time-dependent growth models of von Bertalanffy (1938) type II

If

$$f(y(a,t)) = \frac{y(a,t)}{p}\left[1-\left(\frac{y(a,t)}{y_{max}(a,t)}\right)^p\right],$$

Equations 1 and 2 become, respectively,

$$\frac{\partial y(a,t)}{\partial a} + \frac{\partial y(a,t)}{\partial t} = K(a,t)\frac{y(a,t)}{p}\left[1-\left(\frac{y(a,t)}{y_{max}(a,t)}\right)^p\right] \qquad (7)$$

$$\frac{dw_c(t)}{dt} = K(t+c,t)\frac{w_c(t)}{p}\left[1-\left(\frac{w_c(t)}{y_{max}(t+c,t)}\right)^p\right]. \qquad t \geq t_c \qquad (8)$$

Solution of Equation 8 (a Bernoulli's equation) as an initial value problem with $w_c(t)|_{t=tc} = w_c(t_c)$ yields

$$w_c(t) = \left[\frac{1}{w_c(t_c)^p}e^{-\int_{t_c}^t K(s+c,s)\,ds} + \int_{t_c}^t \frac{K(s+c,s)}{y_{max}(s+c,s)^p}e^{-\int_s^t K(\xi+c,\xi)\,d\xi}\,ds\right]^{-1/p}. \qquad t \geq t_c \qquad (9)$$

If $a-a_0<t$, then $c<0$, $-c>0$, then $t_c=a_0-c=t-a+a_0$; if $a-a_0\geq t$, then $c\geq0$, $-c\leq0$, then $t_c=t_0$. In other words,

$$y(a,t) = \begin{cases} \left[\frac{1}{y(a_0, t-a+a_0)^p}e^{-\int_{t-a+a_0}^t K(s+a-t,s)\,ds} + \int_{t-a+a_0}^t \frac{K(s+a-t,s)}{y_{max}(s+a-t,s)^p}e^{-\int_s^t K(\xi+a-t,\xi)\,d\xi}\,ds\right]^{-1/p} & a-a_0 < t \\ \left[\frac{1}{y(t_0+a-t, t_0)^p}e^{-\int_{t_0}^t K(s+a-t,s)\,ds} + \int_{t_0}^t \frac{K(s+a-t,s)}{y_{max}(s+a-t,s)^p}e^{-\int_s^t K(\xi+a-t,\xi)\,d\xi}\,ds\right]^{-1/p}. & a-a_0 \geq t \end{cases} \qquad (10)$$

If $p=1$, Equations 7–10 and their special cases are reduced to age- and time-dependent growth models of logistic (Verhulst, 1838) type.

If $y_{max}(s+a-t,s)=y_{max}=$constant in Equation 10, then

$$y(a,t) = \begin{cases} \left[\frac{1}{y_{max}^p}-\left(\frac{1}{y_{max}^p}-\frac{1}{y(a_0, t-a+a_0)^p}\right)e^{-\int_{t-a+a_0}^t K(s+a-t,s)\,ds}\right]^{-1/p} & a-a_0 < t \\ \left[\frac{1}{y_{max}^p}-\left(\frac{1}{y_{max}^p}-\frac{1}{y(t_0+a-t, t_0)^p}\right)e^{-\int_{t_0}^t K(s+a-t,s)\,ds}\right]^{-1/p}. & a-a_0 \geq t \end{cases} \qquad (10.0)$$

If $K(s+a-t,s)=K_0=$constant in Equation 10.0, then

$$y(a,t) = \begin{cases} \left[\dfrac{1}{y_{max}^p} - \left(\dfrac{1}{y_{max}^p} - \dfrac{1}{y(a_0, t-a+a_0)^p}\right)e^{-K_0(a-a_0)}\right]^{-1/p} & a-a_0 < t \\[4mm] \left[\dfrac{1}{y_{max}^p} - \left(\dfrac{1}{y_{max}^p} - \dfrac{1}{y(t_0+a-t, t_0)^p}\right)e^{-K_0(t-t_0)}\right]^{-1/p} & a-a_0 \geq t \end{cases}$$

(10.1)

with parameters K_0 and y_{max}.

If

$$K(s+a-t, s) = K_0 + A\cos\frac{2\pi}{T}(s-t_\phi)$$

in Equation 10.0, then

$$y(a,t) = \begin{cases} \left[\dfrac{1}{y_{max}^p} - \left(\dfrac{1}{y_{max}^p} - \dfrac{1}{y(a_0, t-a+a_0)^p}\right)e^{-K_0(a-a_0)-\frac{AT}{\pi}\sin\frac{\pi}{T}(a-a_0)\cos\frac{2\pi}{T}\left(t-t_\phi-\frac{1}{2}(a-a_0)\right)}\right]^{-1/p} & a-a_0 < t \\[4mm] \left[\dfrac{1}{y_{max}^p} - \left(\dfrac{1}{y_{max}^p} - \dfrac{1}{y(t_0+a-t, t_0)^p}\right)e^{-K_0(t-t_0)-\frac{AT}{\pi}\sin\frac{\pi}{T}(t-t_0)\cos\frac{2\pi}{T}\left(t-t_\phi-\frac{1}{2}(t-t_0)\right)}\right]^{-1/p}, & a-a_0 \geq t \end{cases}$$

(10.2)

where K_0, y_{max}, A, T, and t_ϕ are model parameters to be estimated or specified.

If $K(s+a-t,s)=K_{max}-(K_{max}-K_{min})e^{-(s-t+a-a_0)/\alpha}$, if $a-a_0<t$ and $K(s+a-t,s)=K_{max}-(K_{max}-K_{min})e^{-(s-t_0)/\alpha}$, if $a-a_0\geq t$ in Equation 10.0, then (note that $t-a+a_0-t_0=0$, or $t-t_0=a-a_0$)

$$y(a,t) = \begin{cases} \left[\dfrac{1}{y_{max}^p} - \left(\dfrac{1}{y_{max}^p} - \dfrac{1}{y(a_0, t-a+a_0)^p}\right)e^{-K_{max}(a-a_0)-\alpha(K_{max}-K_{min})[e^{-(a-a_0)/\alpha}-1]}\right]^{-1/p} & a-a_0 < t \\[4mm] \left[\dfrac{1}{y_{max}^p} - \left(\dfrac{1}{y_{max}^p} - \dfrac{1}{y(t_0+a-t, t_0)^p}\right)e^{-K_{max}(t-t_0)-\alpha(K_{max}-K_{min})[e^{-(t-t_0)/\alpha}-1]}\right]^{-1/p}, & a-a_0 \geq t \end{cases}$$

(10.3)

where K_{max}, K_{min}, y_{max}, and α are model parameters to be estimated or specified.

Age- and time-dependent growth models of Gompertz (1825) type

If

$$f(y(a,t)) = \lim_{p\to 0}\frac{y(a,t)}{p}\left[1-\left(\frac{y(a,t)}{y_{max}(a,t)}\right)^p\right] = y(a,t)\left[\log_e(y_{max}(a,t)) - \log_e(y(a,t))\right],$$

Equations 1 and 2 become, respectively,

$$\frac{\partial y(a,t)}{\partial a} + \frac{\partial y(a,t)}{\partial t} = K(a,t)\,y(a,t)\left[\log_e(y_{max}(a,t)) - \log_e(y(a,t))\right]$$

(11)

$$\frac{dw_c(t)}{dt} = K(t+c,t)\,w_c(t)\left[\log_e(y_{max}(t+c,t)) - \log_e(w_c(t))\right]. \qquad t \geq t_c$$

(12)

Notice that Equation 12 can be written as a linear ordinary differential equation for $\log_e(w_c(t))$, i.e. as

$$\frac{d\log_e(w_c(t))}{dt} = -K(t+c,t)\log_e(w_c(t)) + K(t+c,t)\log_e(y_{max}(t+c,t)).$$

Thus, to obtain equations under the assumption corresponding to Equations 7–10.3, one can either take limits of equations 7–10.3 for $p \to 0$ or solve Equation 12 directly. I chose the latter, without resort to applying the L'Hôpital's rule to log-transformed quantities to evaluate these limits. Solution of Equation 12 as an initial value problem with $w_c(t)|_{t=t_c} = w_c(t_c)$ yields

$$w_c(t) = w_c(t_c) e^{-\int_{t_c}^{t} K(s+c,s)\,ds} \; e^{\int_{t_c}^{t} K(s+c,s)\log_e(y_{max}(s+c,s)) e^{-\int_{s}^{t} K(\xi+c,\xi)\,d\xi}\,ds} . \qquad t \geq t_c \tag{13}$$

If $a - a_0 < t$, then $c < 0$, $-c > 0$, then $t_c = a_0 - c = t - a + a_0$; if $a - a_0 \geq t$, then $c \geq 0$, $-c \leq 0$, then $t_c = t_0$. In other words,

$$y(a,t) = \begin{cases} y(a_0, t-a+a_0) e^{-\int_{t-a+a_0}^{t} K(s+a-t,s)\,ds} \; e^{\int_{t-a+a_0}^{t} K(s+a-t,s)\log_e(y_{max}(s+a-t,s)) e^{-\int_{s}^{t} K(\xi+a-t,\xi)\,d\xi}\,ds} & a-a_0 < t \\[2em] y(t_0+a-t, t_0) e^{-\int_{t_0}^{t} K(s+a-t,s)\,ds} \; e^{\int_{t_0}^{t} K(s+a-t,s)\log_e(y_{max}(s+a-t,s)) e^{-\int_{s}^{t} K(\xi+a-t,\xi)\,d\xi}\,ds} . & a-a_0 \geq t \end{cases} \tag{14}$$

If $y_{max}(s+a-t,s) = y_{max} = $ constant in Equation 14, then

$$y(a,t) = \begin{cases} y_{max}\left[\dfrac{y(a_0,t-a+a_0)}{y_{max}}\right]^{e^{-\int_{t-a+a_0}^{t} K(s+a-t,s)\,ds}} & a-a_0 < t \\[2em] y_{max}\left[\dfrac{y(t_0+a-t,t_0)}{y_{max}}\right]^{e^{-\int_{t_0}^{t} K(s+a-t,s)\,ds}} . & a-a_0 \geq t \end{cases} \tag{14.0}$$

If $K(s+a-t,s) = K_0 = $ constant in Equation 14.0, then

$$y(a,t) = \begin{cases} y_{max}\left[\dfrac{y(a_0,t-a+a_0)}{y_{max}}\right]^{e^{-K_0(a-a_0)}} & a-a_0 < t \\[2em] y_{max}\left[\dfrac{y(t_0+a-t,t_0)}{y_{max}}\right]^{e^{-K_0(t-t_0)}} , & a-a_0 \geq t \end{cases} \tag{14.1}$$

which is the age- and time-dependent Gompertz (1825) growth model, with parameters K_0 and y_{max}.
   If

$$K(s+a-t,s) = K_0 + A\cos\frac{2\pi}{T}(s-t_\phi)$$

in Equation 14.0, then

$$y(a,t) = \begin{cases} y_{max}\left[\dfrac{y(a_0,t-a+a_0)}{y_{max}}\right]^{e^{-K_0(a-a_0)-\frac{AT}{\pi}\sin\frac{\pi}{T}(a-a_0)\cos\frac{2\pi}{T}\left(t-t_\phi-\frac{1}{2}(a-a_0)\right)}} & a-a_0 < t \\[2em] y_{max}\left[\dfrac{y(t_0+a-t,t_0)}{y_{max}}\right]^{e^{-K_0(t-t_0)-\frac{AT}{\pi}\sin\frac{\pi}{T}(t-t_0)\cos\frac{2\pi}{T}\left(t-t_\phi-\frac{1}{2}(t-t_0)\right)}} , & a-a_0 \geq t \end{cases} \tag{14.2}$$

where K_0, y_{max}, A, T, and t_ϕ are model parameters to be estimated or specified.

If $K(s+a-t,s)=K_{max}-(K_{max}-K_{min})e^{-(s-t+a-a_0)/\alpha}$ if $a-a_0<t$ and $K(s+a-t,s)=K_{max}-(K_{max}-K_{min})e^{-(s-t_0)/\alpha}$ if $a-a_0 \geq t$ in Equation 14.0, then (note that $t-a+a_0-t_0=0$, or $t-t_0=a-a_0$)

$$y(a,t) = \begin{cases} y_{max}\left[\dfrac{y(a_0,t-a+a_0)}{y_{max}}\right]^{e^{-K_{max}(a-a_0)-\alpha(K_{max}-K_{min})[e^{-(a-a_0)/\alpha}-1]}} & a-a_0 < t \\[2em] y_{max}\left[\dfrac{y(t_0+a-t,t_0)}{y_{max}}\right]^{e^{-K_{max}(t-t_0)-\alpha(K_{max}-K_{min})[e^{-(t-t_0)/\alpha}-1]}} & , \quad a-a_0 \geq t \end{cases} \qquad (14.3)$$

where K_{max}, K_{min}, y_{max}, and α are model parameters to be estimated or specified.

Data requirements for parameter estimation

Equations 6, 10, and 14, and their special cases are segmented functions; they provide flexibility in the analysis of growth data. Thus, by appropriately choosing time t (which is a relative quantity), one can use either segment ($a-a_0<t$ or $a-a_0 \geq t$) for an individual animal or for a group of individuals, or use both segments ($a-a_0<t$ and $a-a_0 \geq t$) for a group of individuals. It is, however, more convenient to use only one segment in a single analysis. Indeed, although growth parameters can be estimated by use of either segment of any of Equations 6.1, 6.2, 6.3; 10.1, 10.2, 10.3; 14.1, 14.2, 14.3, it is easier to use the segment for $a-a_0<t$, by letting time t start before the animals, whose growth is to be modeled, are born, unless time is allowed to take negative values. Use of the other segment, i.e., that for $a-a_0 \geq t$, gives identical results, but it is tortuous and requires first calculating $y(t_0+a-t,t_0)$.

Data requirement for estimation of parameters in a growth model is a function of the generality of that model: the more general it is, the more data it generally requires. Equations 6, 6.0, 10, 10.0, 14, and 14.0 generally require knowledge of two ages a_0 and a, time t, and two sizes $y(a_0,t-a+a_0)$ and $y(a,t)$ if $a-a_0<t$; or knowledge of two times t_0 and t, age a, and two sizes $y(t_0+a-t,t_0)$ and $y(a,t)$ if $a-a_0 \geq t$.

By contrast, use of Equations 6.1, 10.1, and 14.1 only requires knowledge of the difference between two ages $a-a_0$, and two sizes $y(a_0,t-a+a_0)$ and $y(a,t)$; or of the difference between two times $t-t_0$, and two sizes $y(t_0+a-t,t_0)$ and $y(a,t)$. Equation 6.1 has been widely used to model tagging data, where a_0 or t_0 is interpreted as time at release, a or t as time at recapture, $a-a_0$ or $t-t_0$ as time at liberty, $y(a_0,t-a+a_0)$ or $y(t_0+a-t,t_0)$ as size at release, and $y(a,t)$ as size at recapture. It has also been used extensively to model size at age data (obtained, say, by ageing animals by reading marks in their hard parts), where a_0 or t_0 is interpreted as age at birth, a or t as age, $y(a_0,t-a+a_0)$ or $y(t_0+a-t,t_0)$ as size at birth, and $y(a,t)$ as size at

age. However, it is rare to know an animal's two ages and their corresponding sizes; what are commonly measured are one age and its corresponding size. Consequently, it is common practice to fit Equation 6.1 into such size-at-age data to estimate age at birth a_0 or t_0, as well as the growth parameters, thereby implicitly assuming, for all animals concerned, that the size at birth $y(a_0,t-a+a_0)$ or $y(t_0+a-t,t_0)$ is zero and that the age at birth a_0 or t_0 is the same. Exactly the same argument applies to Equations 6.2, 6.3, 10.1, 10.2, 10.3, 14.1, 14.2, and 14.3.

Data analysis

Barramundi *L. calcarifer* is a protandrous fish found in estuaries and other coastal areas of the Indo-West Pacific (Griffin, 1987). Between August 1977 and June 1980, 4933 barramundi with a body total-length range of about 10–100 cm were captured by a combination of lure fishing, tidal trap, seine, and gill net. They were measured to the nearest centimeter, tagged with the then commonly used, but apparently physically and physiologically damaging, Floy FT-2 dart tags for fish >35 cm and FD-67 anchor tags for fish <35 cm, and released in rivers flowing into the Van Diemen Gulf and the Gulf of Carpentaria of northern Australia (Davis and Reid, 1982). Of those tagged, 312 fish of a total length of 23–92 cm (mean=60 cm, SE=13 cm) were recaptured, but only 308 are used in the analysis below owing to incomplete recapture information. The time at liberty ranged from zero to 932 d, with a mean of 219 d (SE=211 d), and the length increment from –21 to 35 cm, with a mean of 6 cm (SE=8 cm). Negative increments in length are often observed in a tagging experiment because tagged animals can shrink in size immediately after tagging.

Let a_0 or t_0 denote time at release, a or t, time at recapture, $a-a_0$ or $t-t_0$, time at liberty, $y(a_0,t-a+a_0)$ or $y(t_0+a-t,t_0)$, the length of a fish at release, $y(a,t)$,

its length at recapture, and y_{max}, its maximum length. The segments of Equations 6.1, 10.1, 14.1; Equations 6.2 (p=1), 10.2 (p=1), 14.2 (p=1); and Equations 6.3, 10.3, 14.3, all for $a-a_0<t$, were fitted into the tagging data, by using the nonlinear least squares method, under the assumptions that T=365.25 d, time started (i.e. time t=0) on 1 January 1960 (see below for its significance), and errors in $y(a,t)$ follow independent normal distributions, with a mean of $\hat{y}(a,t)$ and a constant variance of σ^2 (Table 3). A likelihood ratio test suggests that Equation 6.1 is significantly different from Equation 6.2 ($F_{2,304}$=48.6892, P<0.0001) or from Equation 6.3 ($F_{2,304}$=4.1238, P=0.0171); Equation 10.1 (p=1) is significantly different from Equation 10.2 (p=1) ($F_{2,304}$=45.3460, P<0.0001) or from Equation 10.3 (p=1) ($F_{2,304}$=3.3241, P=0.0373); and Equation 14.1 is significantly different from Equation 14.2 ($F_{2,304}$=46.8516, P<0.0001) or from Equation 14.3 ($F_{2,304}$=3.5345, P=0.0304). Thus, Equations 6.2, 6.3; Equations 10.2 (p=1), 10.3 (p=1); and Equations 14.2, 14.3, and their associated estimates of parameters seem adequate for describing the tagging data. Selection between equations 6.2 and 6.3, between Equations 10.2 and 10.3, and between Equations 14.2 and 14.3 by developing more general models of $K(a,t)$ was not successful because of a lack of data.

Are equations 6.1, 6.2, 6.3; 10.1, 10.2, 10.3; 14.1, 14.2, 14.3 independent of the start of time?

An age- and time-dependent growth model is useful, if and only if it is independent of the start of time or if it is time-homogeneous. The reason for this is that start of time is unknown. For Equations 6.0, 10.0 and 14.0 to be useful,

$$\int_{t-a+a_0}^{t} K(s+a-t,s)\,ds$$

if $a - a_0 < t$ or

$$\int_{t_0}^{t} K(s+a-t,s)\,ds$$

if $a-a_0 \geq t$ must be independent of the start of time t. Obviously, Equations 6.1, 6.2, 6.3; 10.1, 10.2, 10.3; 14.1, 14.2, and 14.3 all are independent of the start of time, where time t appears as time differences $t-t_0$ or $t-t_\phi$.

However, interesting differences exist among them. Equations 6.1, 6.3, 10.1, 10.3, 14.1, and 14.3 apply on any time scales, without any adjustment of estimates of their parameters in subsequent applications because they depend on time difference $t-t_0$ or age difference $a-a_0$ only. By contrast, Equations 6.2, 10.2 and 14.2 and estimates of their parameters must be properly adjusted for this purpose. Specifically, the estimate of parameter t_ϕ in Equations 6.2, 10.2, and 14.2 must be correctly adjusted before their subsequent applications. To make such an adjustment, suppose that all growth parameters are estimated from tagging data by using one segment of Equation 6.2, 10.2, or 14.2 on one time scale (regression time scale, Fig. 1), with time t, parameter t_ϕ (estimated), and a reference time t_r (known). Now, Equation 6.2, 10.2, or 14.2 is to be applied in a future fish stock assessment on another time scale (application time scale, Fig. 1), with time t', parameter t_ϕ' (unknown,
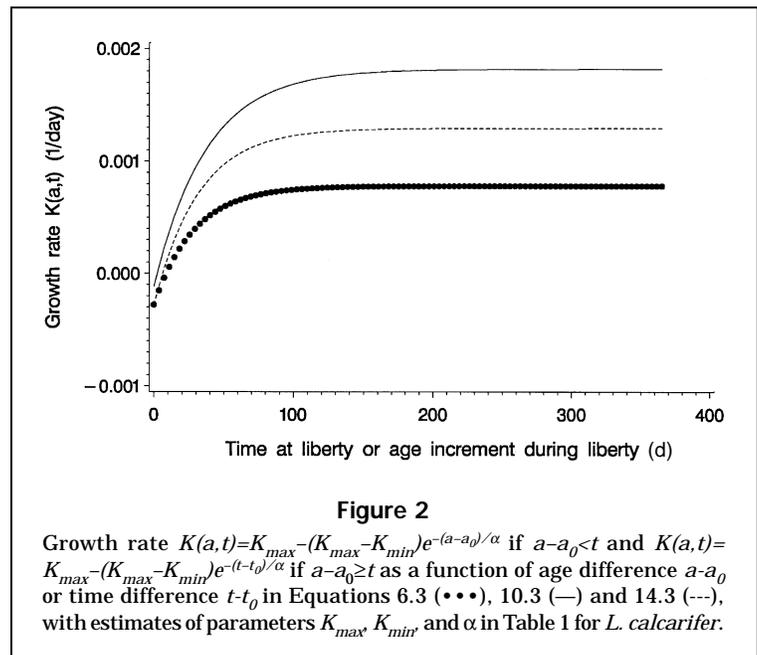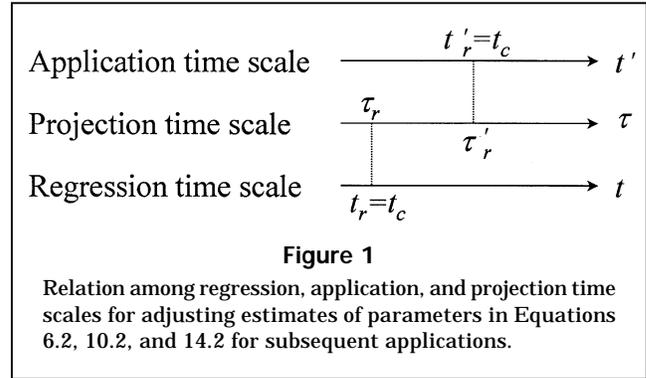

Table 3

Estimates and (in parentheses) standard errors of parameters by fitting Equations 6.1, 6.2, 6.3; 10.1 (p=1), 10.2 (p=1), 10.3 (p=1); and 14.1, 14.2, 14.3 to the barramundi tagging data using the least squares method under the assumptions that T=365.25 d, time started (i.e. time t=0) on 1 January 1960, and errors in $y(a,t)$ follow independent normal distributions, with a mean of $\hat{y}(a,t)$ and a constant variance of σ^2. P<0.0001; n=308; — = not applicable.

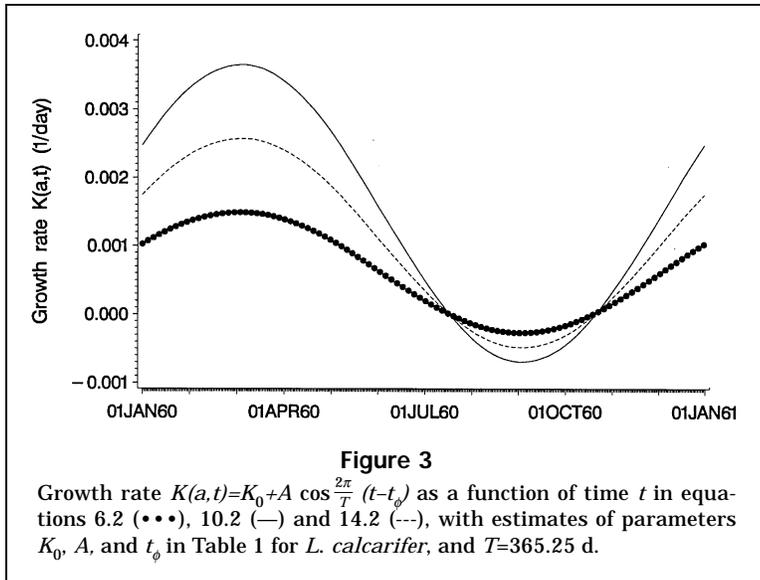| Equation	$\hat{y}_{max}(a,t)$ (cm)	$\hat{K}_0$ or $\hat{K}_{max}$ (·d^{-1})	$\hat{A}$ or $\hat{K}_{min}$ (·d^{-1})	$\hat{t}_\phi$ or $\hat{\alpha}$ (d)	df_1, df_2, F	$\hat{\sigma}^2$ (cm^2)	R^2
6.1	113.4724 (9.6232)	0.00065 (0.00013)	—	—	2,306,30965.9769	22.8923	0.9951
6.2	114.4452 (8.6686)	0.00061 (0.00011)	0.00088 (0.00018)	62.7197 (06.8279)	4,304,20333.2870	17.4525	0.9963
6.3	110.1152 (8.5316)	0.00078 (0.00017)	–0.00028 (0.00121)	28.7594 (41.6473)	4,304,15801.1643	22.4343	0.9952
10.1	94.7255 (3.2775)	0.00161 (0.00014)	—	—	2,306,30895.5263	22.9443	0.9951
10.2	96.2908 (3.0613)	0.00148 (0.00012)	0.00217 (0.00028)	63.5155 (06.7582)	4,304,19947.8597	17.7884	0.9962
10.3	94.4251 (3.1934)	0.00182 (0.00020)	–0.00012 (0.00250)	37.3267 (63.1348)	4,304,15684.0774	22.6010	0.9952
14.1	100.5592 (4.8653)	0.00114 (0.00014)	—	—	2,306,31051.6220	22.8295	0.9951
14.2	102.1717 (4.5198)	0.00104 (0.00011)	0.00153 (0.00022)	63.2525 (06.7674)	4,304,20202.0707	17.5654	0.9963
14.3	99.6456 (4.6446)	0.00129 (0.00018)	–0.00028 (0.00203)	31.6268 (51.7115)	4,304,15784.7666	22.4575	0.9952

to be calculated), and a reference time t_r' (known). Both reference times must be chosen properly, such that $t_r=t_c$ on t_r's scale and $t_r'=t_c$ on t_r''s scale, where t_c is an arbitrarily chosen time. For example, $t_r=0$ on t_r's scale; $t_r'=0$ on t_r''s scale. Projection of both $t_r=t_c$ on t_r's scale and $t_r'=t_c$ on t_r''s scale onto a third time scale (projection time scale, Fig. 1) to find their time difference on the third time scale $\tau_r'-\tau_r$. It is this time difference that is to be used to calculate t_ϕ'. To do so, let $t_r-t_\phi=t_r'-t_\phi'$, or $t_\phi'=t_\phi+t_r'-t_r=t_\phi+\tau_r'-\tau_r$, $t-t_\phi=t'-t_\phi'=t'-t_\phi-t_r'+t_r=t'-t_\phi-\tau_r'+\tau_r$. Therefore, in Equations 6.2, 10.2, and 14.2, replacement of $t-t_\phi$ with $t'-t_\phi-\tau_r'+\tau_r$, of $a-a_0$ with $a'-a_0'$, and of $t-t_0$ with $t'-t_0'$ will give the correct growth models for the future fish stock assessment on the required time scale (application scale). For the barramundi growth described by equation 6.2, $\hat{t}_\phi= 62.7197$ d, $t_r=0$ corresponds to $\tau_r=1$ January 1960 (row 2, Table 3), $t_r'=0$ corresponds to $\tau_r'=1$ January 1999, then $t_\phi'=\hat{t}_\phi+\tau_r'-t_r=62.7197+(1$ January 1999$)-($January 1, 1960$)=62.7197+14245=14307.7197$ d. Therefore, replacement of $t-t_\phi$ with $t'-14307.7197$, of $a-a_0$ with $a'-a_0'$, and of $t-t_0$ with $t'-t_0'$ in the model concerned will give the correct growth models for the future (when time starts on 1 January 1999) barramundi stock assessment on the required time scale (application scale). In this example, the third time scale (projection time scale) is, of course, calendar time.

Discussion

This work presents general age- and time-dependent models for the growth of animals and a comprehensive list of their useful special cases, forming a basis for obtaining quantitative information on the growth of animals experiencing changes in age, time, and age- and time-varying factors. These models have many applications. An obvious one would be to examine both the short- and long-term effects of tagging on the growth of animals by use of Equations 6.3, 10.3, and 14.3; $K_{max}<K_{min}$, $K_{max}=K_{min}$, and $K_{max}>K_{min}$ indicate, respectively, positive, no, and negative effects of tagging on the growth of animals. Similarly, $K_{min}<0$, $K_{min}=0$, and $K_{min}>0$ suggest, respectively, a shrinkage, cessation of growth, and a slower growth of tagged animals immediately after tagging. In the case of the *L. calcarifer* (Fig. 2), tagging seems to have been antagonistic to its growth ($K_{max}>K_{min}$) and led to a shrinkage of its size ($K_{min}<0$). This conclusion is tentative, however, because of the large standard error of $\hat{\alpha}$.

Figure 1

Relation among regression, application, and projection time scales for adjusting estimates of parameters in Equations 6.2, 10.2, and 14.2 for subsequent applications.

Figure 2

Growth rate $K(a,t)=K_{max}-(K_{max}-K_{min})e^{-(a-a_0)/\alpha}$ if $a-a_0<t$ and $K(a,t)= K_{max}-(K_{max}-K_{min})e^{-(t-t_0)/\alpha}$ if $a-a_0\geq t$ as a function of age difference $a-a_0$ or time difference $t-t_0$ in Equations 6.3 (•••), 10.3 (—) and 14.3 (---), with estimates of parameters K_{max}, K_{min}, and α in Table 1 for *L. calcarifer*.

Another application would be to study how age- and time-dependent factors other than age and time affect the growth of animals. For example, one can hypothesize about the functional forms of $K(a,t)$, such as $K(a,t)=\alpha T(t-t_r)^\beta$, where $T(t)$ is ambient temperature, availability of food, or pH value; t_r (a time lag or lead), and α and β are all parameters to be estimated or specified. Such a model is ideal for analyzing data on the length or weight of an individual animal at age and time, which may be available, say, from aquaculture operations. It might also be useful for analyzing data from mark-recapture experiments, where ambient temperature or food availability of a tagged animal is measured continuously from the time of its tagging to the time of its recapture. Indeed, if *L. calcarifer* had been tagged with a "smart" tag that could record ambient temperature or food availability, analysis would have been made of their

Figure 3

Growth rate $K(a,t)=K_0+A \cos\frac{2\pi}{T}(t-t_\phi)$ as a function of time t in equations 6.2 (•••), 10.2 (—) and 14.2 (---), with estimates of parameters K_0, A, and t_ϕ in Table 1 for *L. calcarifer*, and T=365.25 d.

Finally, notice my use of the length at recapture rather than length increment of a tagged individual as the independent variable in relevant models and in the data analysis. This was to avoid error propagation. The variance of the length increment is

$$V(L_2 - L_1) = V(L_2) + V(L_1) -$$
$$2\rho(L_1, L_2)\sqrt{V(L_1)V(L_2)} ,$$

where $\rho(L_1, L_2)$ is the correlation coefficient between lengths L_1 and L_2.

A higher value of noise to signal ratio is expected if length increments are used; the higher value of noise to signal ratio helps mask patterns in the data and makes their analysis difficult.

lengths at release and recapture and at times at liberty in the above application. It should be noted, however, that the information from a tagging experiment is limited. It might not be possible to estimate all the parameters in the model reliably, as in the case of the *L. calcarifer* data. Such a limitation also applies to extracting environmental signals from growth data.

More importantly, all the above models can be used to study the population dynamics of some species of animals, simply by letting *y(a,t)* denote the number of individuals of a species of animals of age *a* at time *t*. Indeed, similar models in studies of population dynamics also lead to partial differential equations (e.g. Nisbet and Gurney, 1982).

It is interesting that *L. calcarifer* is a tropical and subtropical species of fish and yet exhibits a strong seasonal growth. For all three models (Equations 6.2, 10.2, or 14.2), its growth rate *K(a,t)* reaches its maximum on 3 or 4 March (i.e. at the start of autumn), slows down to zero on 17 July (i.e. in the middle of winter), reaches its minimum on 2 or 3 September (i.e. at the start of spring), returns to zero on 19 or 20 October (i.e. in the middle of spring), and comes back to its maximum rate on 3 or 4 March (i.e. at the start of autumn) (Fig. 3). Thus, its length grows fastest on 3 or 4 March (i.e. at the start of autumn), grows less until a full stop on 17 July (i.e. in the middle of winter), shrinks until 19 or 20 October (i.e. in the middle of spring), and resumes a positive growth for another cycle. Thus, *L. calcarifer* does not grow in length for three months in a year, from 17 July (i.e. in the middle of winter) to 19 or 20 October (i.e. in the middle of spring). Such a strong seasonality in growth seems related to the seasonal availability of food and seasonal changes in water temperature.

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