年齢の関数としての自然死亡係数

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Age Dependence of Natural Mortality Coefficient in Fish Population Dynamics

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From a viewpoint of life history of fish, the natural mortality can be divided into three phases: initial, stable death, and death by senescence, and the respective phases correspond to the three growth phases: early, stable growth, and sencescence. According to the relation between natural motality and the growth, a functional formula of the natural mortality coefficient is given in this study. When the von Bertalanffy's growth parameters are known, the natural mortality coefficient can be calculated for each age. As a function of age, the natural mortality coefficient has some general characters throughout the life.

Natural mortality is one of the key factors in fish population dynamics.[1] After the mortality at initial phase is over, natural mortality coefficient is often assumed to be constant irrespective of age in the fishery dynamics. However, the qualitative concept about natural mortality is given by a mortality pattern (so called bathtub curve).[2] This indicates the natural mortality cannot be assumed to be constant throughout the life. According to the bathtub curve,[2] the natural mortality can be divided into three phases: initial, stable death, and death by senescence, and the respective phases correspond to the three growth phases:[3] early, stable growth, and senescence in a fish population.

On the basis of the relation between natural mortality and the growth, we conducted the function of the natural mortality coefficient in this study.

Models and their Analyses

According to the correspondence of the mortality phases and the growth phases,[3] the natural mortality coefficient $M(t)$ is assumed to be inversely proportional to the growth measure $G(t)$. Thus

$$M(t)=\frac{C}{G(t)}\,. \qquad (1)$$

Here, $G(t)$ is represented as follows:[3]

$$G(t)=\begin{cases}1-e^{-k(t-t_0)}\,, & t\leqq t_M\\ a_0+a_1(t-t_M)+a_2(t-t_M)^2\,, & t\geqq t_M\end{cases} \qquad (2)$$

$$\begin{cases}a_0=1-e^{-k(t_M-t_0)}\\ a_1=ke^{-k(t_M-t_0)}\\ a_2=-\dfrac{1}{2}k^2e^{-k(t_M-t_0)}\end{cases} \qquad (3)$$

and

$$t_M=-\frac{1}{k}\ln|1-e^{kt_0}|+t_0\,. \qquad (4)$$

In equation (2), $G(t)$ is dimensionless and $0<G(t)<1$; k, growth coefficient, and t_0 is an adjustment parameter in von Bertalanffy's growth equation, and t_M is age at end of reproductive span, *i.e.* age at the intersection of the stable and senescent growth phases. In equation (1), C is a proportional constant. Theoretically, it can be assumed to be $C=k$, for a reason described later (see section of Discussion). Therefore, equation (1) is reduced to the following equation:

$$M(t)=\frac{k}{G(t)}\,, \qquad (5)$$

or

$$M(t)=\begin{cases}\dfrac{k}{1-e^{-k(t-t_0)}}\,, & t\leqq t_M\\ \dfrac{k}{a_0+a_1(t-t_M)+a_2(t-t_M)^2}\,, & t\geqq t_M\,.\end{cases} \qquad (6)$$

This is a fundamental formula of the natural mortality coefficient $M(t)$, and the value of $M(t)$ is not constant but dependent on age.

When the growth parameters k and t_0 of von Bertalanffy's equation are known, constants a_0, a_1

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and a_2 of senescence and the age t_M at end of reproductive span may be calculated by equations (3) and (4) based on the growth continuity at t_M. Thus, natural mortality coefficient $M(t)$ can be calculated at age t by equation (6).

Survival Process in a Natural State

Survival process of a year class in a natural state is formulated as follows:

$$\frac{dN(t)}{N(t)dt}=-M(t)\ , \qquad (7)$$

or

$$N(t)=N(0)e^{-\int_0^t M(t)dt}\ , \qquad (8)$$

where $N(t)$ is a population size at age t, and $N(0)=N(t)|_{t=0}$. If $M(t)$ is taken as constant irrespective of age, the solution of equation (7) or (8) is an exponential curve in $t-N(t)$ plane.[4] The $M(t)$ as shown in the above equation (5) or (6) is represented by a function of age. Solving the equation (7) or (8),

$$N(t)=\begin{cases} N(0)\dfrac{1-e^{kt_0}}{1-e^{-k(t-t_0)}}e^{-kt}\ , & t\leqq t_M \\ N(t_M)\left[\dfrac{2a_2(t-t_M)(a_1-\sqrt{a_1^2-4a_0a_2})+4a_0a_2}{2a_1(t-t_M)(a_1+\sqrt{a_1^2-4a_0a_2})+4a_0a_1}\right]^{\frac{k}{\sqrt{a_1^2-4a_0a_1}}}\ , & t\geqq t_M \end{cases} \qquad (9)$$

and

$$N(t_M)=N(t)|_{t=t_M}=N(0)\frac{1-e^{kt_0}}{1-e^{-k(t_M-t_0)}}e^{-kt_M}\ . \qquad (10)$$

Estimation of S_0 and $\overline{M}$

The natural survival rate per unit time (*e.g.* one year) in $[t, t+\varDelta]$ is presented by $S_0(t, t+\varDelta)$ as:

$$N(t+\varDelta)=N(t)S_0(t, t+\varDelta)^{\varDelta}\ ,$$

or

$$S_0(t, t+\varDelta)=\left(\frac{N(t+\varDelta)}{N(t)}\right)^{1/\varDelta}\ . \qquad (11)$$

From equation (8),

$$\frac{N(t+\varDelta)}{N(t)}=e^{-\int_t^{t+\varDelta}M(t)dt}\ .$$

Substituting this into equation (11),

$$S_0(t, t+\varDelta)=(e^{-\int_t^{t+\varDelta}M(t)dt})^{1/\varDelta}$$
$$=e^{-\frac{1}{\varDelta}\int_t^{t+\varDelta}M(t)dt}\ , \qquad (12)$$

and average natural mortality coefficient during $[t, t+\varDelta]$, $\overline{M}(t, t+\varDelta)$, is presented as:

$$\overline{M}(t, t+\varDelta)=-\ln S_0(t, t+\varDelta)$$
$$=\frac{1}{\varDelta}\int_t^{t+\varDelta}M(t)dt\ . \qquad (13)$$

From this formula, $\overline{M}(t, t+\varDelta)$ can be represented by a mathematical average of $M(t)$ in $[t, t+\varDelta]$.

If t and $t+\varDelta$ are given, $S_0(t, t+\varDelta)$ and $\overline{M}(t, t+\varDelta)$ may be calculated by equations (12) and (13).

In the case of $t+\varDelta\leqq t_M$ $(\varDelta>0)$, equation (13) is reduced to

$$\overline{M}(t, t+\varDelta)=\frac{1}{\varDelta}\ln\frac{e^{k(t+\varDelta)}-e^{kt_0}}{e^{kt}-e^{kt_0}}\ . \qquad (14)$$

Numerical Examples

The above models are applied to two important fish populations in the East China Sea: largehead hairtail *Trichiurus lepturus* and small yellow croaker *Pseudosciaena polyactis*. The calculated results are shown in Fig. 1. The basic parameters k and t_0 in these populations are given as follows:*

T. lepturus: $k=0.3103$ year^{-1}, $t_0=-0.40$ year;

P. polyactis: $k=0.3857$ year^{-1}, $t_0=-0.51$ year.

In the senescence of these populations, *T. lepturus* is subjected to the senescent growth type I (senescence finishes at t_λ), and *P. polyactis* is subjected to the senescent growth type II (it finishes at T_λ).[3] Here, t_λ and T_λ are ecological life span and physiological life span, respectively. Thus the natural mortality coefficient curve of *P. polyactis* shows a bathtub curve on $t-M(t)$ plane, however, that of *T. lepturus* does not show a bathtub curve. In the case of the bathtub curve, the part of $t>t_\lambda$ is not smooth as Fig. 1, because the growth is instabilized at $t>t_\lambda$. Generally speaking, the population size at $t>t_\lambda$ is very small, thus the part of $t>t_\lambda$ in the bathtub curve is of no significance in fishery dynamics.

In order to test the above theory, the estimated

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Table 1. Estimated results about the average natural mortality coefficient $\bar{M}(t, t+\Delta)$ in the past and by equation (14) in various species of fish

No.	Species	$[t, t+\Delta]$	k	t_0	X	Y
1	*Trichiurus lepturus*[5]	[0, 2]	0.3013	−0.40	1.05	1.06
2	*Trichiurus lepturus*[6]	[2, 5]	0.3013	−0.40	0.44	0.45
3	*Navodon septentrionalis*[7]	[1, 10]	0.1233	−1.546	0.26	0.24
4	*Etrumeus teres*[8]	[0, 2]	0.2594	−0.9372	0.69	0.71
5	*Pleurogrammus azous*[9]	[2, 7]	0.213	−1.858	0.31	0.30
6	*Seriola quinqueradiata*[10]	[1, 6]	0.449	−0.113	0.58	0.62
7	*Thunnus albacares*[11]	[3, 8]	0.292	−0.04	0.40	0.38

X, $\bar{M}(t, t+\Delta)$ in the past; Y, $\bar{M}(t, t+\Delta)$ by equation (14).

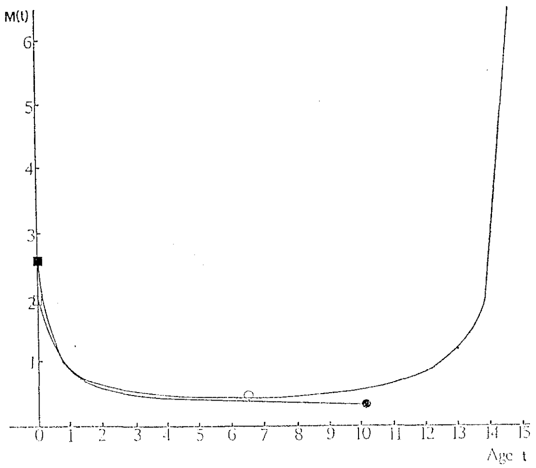

Fig. 1. Transitional trends of natural mortality coefficient $M(t)$ (year^{-1}) by age t (year). Closed marks: largehead hairtail *Trichiurus lepturus*; Open marks: small yellow croaker *Pseudosciaena polyactis*. Marks indicate coordinates: quadrangle, $(0, M(0))$; circle, $(t_\lambda, M(t_\lambda))$.

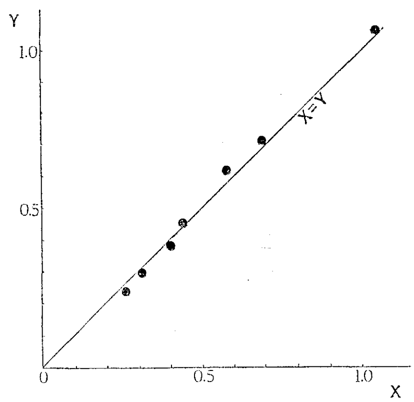

Fig. 2. A comparison between the two estimated results about average natural mortality coefficient $\bar{M}(t, t+\Delta)$ in the past and by equation (14). X-coordinate, $\bar{M}(t, t+\Delta)$ in the past; Y-coordinate, $\bar{M}(t, t+\Delta)$ by equation (14). The data points are from Table 1.

results about the average natural mortality coefficient of some fish populations in the past and by equation (14) are given in Table 1 and plotted in Fig. 2. From this, it was found that the functional form of $M(t)$ shown in this study is suitable for fish population dynamics.

Discussion

General Characters of $M(t)$

In order to know the general characters of the natural mortality coefficient $M(t)$, two parameters about age are introduced:[3] ecological life span t_λ,

$$t_\lambda = t_M + \frac{1}{k}, \tag{15}$$

and physiological life span T_λ,

$$T_\lambda = t_M + \frac{1}{k}[1 + \sqrt{2e^{k(t_M - t_0)} - 1}]. \tag{16}$$

The t_M in these equations are given by equation (4). Growth of senescence in a fish population can be analysed by a quadratic parabola equation (part of $t \geqq t_M$ in equation (2))[3]. When $dG(t)/dt = 0$, $t = t_\lambda$; and when $G(t) = 0$, $t = T_\lambda$, here, $T_\lambda > t_\lambda > t_M$.

In equation (6), if $t < t_\lambda$, $M(t)$ decreases as age t increases, and it becomes minimum at t_λ. If $t > t_\lambda$, $M(t)$ increases as age t increases. Specially, when $t = T_\lambda$,

$$M(T_\lambda) = \lim_{t \to T_\lambda} M(t) = \infty. \tag{17}$$

The equation (17) means that the part of a population living to T_λ must die at T_λ.

In addition, when $t = t_0$,

$$M(t_0) = \lim_{t \to t_0} M(t) = \infty. \tag{18}$$

However, in the case of fish, $G(t) > 0$, thus $t > t_0$. From this the value of $M(t)$ at initial phase

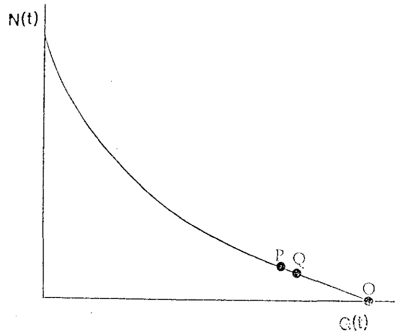

Fig. 3. $G(t)-N(t)$ plane. $G(t)$, growth measure at age t; $N(t)$, population size in a natural year class at age t; see text.

doesn't become infinitely great, but it is very large, and the value remarkably changes with age. When initial phase is over, $M(t)$ becomes small, and it has a stable phase (see Fig. 1). However, strictly speaking, even if it is in the stable phase, $M(t)$ is not constant irrespective of age but the change with age is very small. Thus, we can look upon the natural mortality coefficient in the stable death phase as a constant, for an approximate estimation. In this case, it may be calculated by equation (14), here, t and $t+\Delta$ are the beginning point and the end of the stable death phase, respectively.

Appositeness of the Assumption: $C=k$

On $G(t)-N(t)$ plane (Fig. 3), $P(G(T), N(T))$ and $Q(G(T+\tau), N(T+\tau))$ are two points in the stable phase, and point $O(1, 0)$ is at end of the phase as T becomes infinity, theoretically. When T is very large and $\tau>0$, the part of $G(t)>G(T)$ in $G-N$ curve is approximated by a straight line, thus

$$\frac{N(T)-0}{G(T)-1}=\frac{N(T+\tau)-0}{G(T+\tau)-1}, \qquad (19)$$

and when $T\gg\tau$, we can write

$$\overline{M}(0, T)=\overline{M}(0, T+\tau). \qquad (20)$$

From equations (2), (8) and (13), $G(t)$ and $N(t)$ are represented as follows:

$$G(t)=1-e^{-k(t-t_0)}$$
$$N(t)=N(0)e^{-\overline{M}(0,t)t}$$

so we get

$$\overline{M}(0, T)=k. \qquad (21)$$

If $T\to\infty$, then clearly the equation (21) is true in the strict sense. Thus it is reduced to

$$\overline{M}(0, \infty)=k. \qquad (22)$$

In addition, when $M(t)$ is given by equation (1),

$$\overline{M}(0, T)=\frac{1}{T}\int_0^T M(t)dt=C+\frac{C}{kT}\ln\frac{1-e^{-k(T-t_0)}}{1-e^{kt_0}}, \qquad (23)$$

where, T is a point in the stable phase. If $T\to\infty$, then

$$\overline{M}(0, \infty)=\lim_{T\to\infty}\overline{M}(0, T)=C. \qquad (24)$$

Comparing the two equations (22) and (24), we get

$$C=k.$$

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