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A revisit to Pope's cohort analysis

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Abstract

Gulland's [Gulland, J.A., 1965. Estimation of mortality rates. Annex to Arctic Fisheries Working Group Report (meeting in Hamburg, January 1965). ICES, C.M. 1965, Doc. No. 3 (mimeographed)] virtual population analysis (VPA) is commonly used for studying the dynamics of harvested fish populations. However, it necessitates the solving of a nonlinear equation for the instantaneous rate of fishing mortality of the fish in a population. Pope [Pope, J.G., 1972. An investigation of the accuracy of Virtual Population Analysis using cohort analysis. ICNAF Res. Bull. 9, 65–74. Also available in D.H. Cushing (ed.) (1983), Key Papers on Fish Populations, p. 291–301, IRL Press, Oxford, 405 p.] eliminated this necessity in his cohort analysis by approximating its underlying age- and time-dependent population model. His approximation has since become one of the most commonly used age- and time-dependent fish population models in fisheries science. However, some of its properties are not well understood. For example, many assert that it describes the dynamics of a fish population, from which the catch of fish is taken instantaneously in the middle of the year. Such an assertion has never been proven, nor has its implied instantaneous rate of fishing mortality of the fish of a particular age at a particular time been examined, nor has its implied catch equation been derived from a general catch equation. In this paper, we prove this assertion, examine its implied instantaneous rate of fishing mortality of the fish of a particular age at a particular time, derive its implied catch equation from a general catch equation, and comment on how to structure an age- and time-dependent population model to ensure its internal consistency. This work shows that Gulland's (1965) virtual population analysis and Pope's (1972) cohort analysis lie at the opposite end of a continuous spectrum as a general model for a seasonally occurring fishery; Pope's (1972) approximation implies an infinitely large instantaneous rate of fishing mortality of the fish of a particular age at a particular time in a fishing season of zero length; and its implied catch equation has an undefined instantaneous rate of fishing mortality of the fish in a population, but a well-defined cumulative instantaneous rate of fishing mortality of the fish in the population. This work also highlights a need for a more careful treatment of the times of start and end of a fishing season in fish population models.

Keywords: Age- and time-dependent models; VPA; Cohort analysis; Fishing season; Fish; Aquatic animals

1. Introduction

Gulland's (1965) virtual population analysis (VPA) is commonly used for studying the dynamics of harvested fish populations. However, it necessitates the solving of a nonlinear equation for the instantaneous rate of fishing mortality of the fish in a population. Although this equation can be solved quite easily today, it was computationally very challenging about 3.5 decades ago, when Pope (1972) eliminated this necessity in his cohort analysis by approximating the age- and time-dependent population model that underlies VPA. Pope's (1972) approximation, as it might be called, has become one of the most commonly used age- and time-dependent fish population models in fisheries science, and has spawned a large body of literature (e.g. Gilbert, 1986; Myers et al., 1997; Millar and Meyer, 2000; Toresen and Østvedt, 2000; Jiao and Chen, 2004).

Surprisingly, despite some very interesting work on Gulland's (1965) virtual population analysis and Pope's (1972) cohort analysis (Sims, 1982; MacCall, 1986; Mertz and Myers, 1995), some of its properties are not well understood, for otherwise some age- and time-dependent fish population models, as published in fisheries research journals, might have been formulated somewhat differently, to ensure their internal consistency (see below for details). For example, many assert that Pope's (1972) approximation describes the dynamics of a fish population, from which the catch of fish is taken instantaneously in the middle of the year (Gilbert, 1986, p. 642). However, such an assertion has never been proven, nor has its implied instanta-

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neous rate of fishing mortality of the fish of a particular age been examined, nor has its implied catch equation been derived from a general catch equation. The resolution of these issues happens to have major implications for how an internally consistent, age- and time-dependent population model should be structured.

In this paper, we prove that Pope's (1972) approximation can indeed be derived from an age- and time-dependent population model under the assumption that the catch of fish from the population is taken instantaneously in the middle of the year, examine its implied instantaneous rate of fishing mortality of the fish of a particular age at a particular time, derive its implied catch equation from a general catch equation, and comment on how to structure an age- and time-dependent population model, to ensure its internal consistency. Much of this explanation can be read and understood by anybody with some elementary knowledge of calculus.

2. Gulland's (1965) virtual population analysis

Gulland's (1965) virtual population analysis is based on two equations, of the form

$$N_{i+1} = N_i \exp(-Z_i) \tag{1}$$

$$C_i = \frac{F_i}{Z_i} N_i[1 - \exp(-Z_i)] \tag{2}$$

where N_i is the number of the fish of age i in the year-class, $Z_i = F_i + M_i$ the (constant within a year) instantaneous rate of total mortality of the fish of age i in the year-class, C_i the age-specific catch in the number of the fish of age i in the year-class, F_i the (constant within a year) instantaneous rate of fishing mortality of the fish of age i in the year-class, and M_i is the (constant within a year) instantaneous rate of natural mortality of the fish of age i in the year-class.

Notice here that both equations apply for $F_i, C_i \geq 0$. In particular, Eq. (2) says that if $F_i = 0$, then $C_i = 0$. Also, both equations apply for a unit interval of time (e.g. a year), so that the Z_i in each exponential is actually $Z_i \times 1$, which is a dimensionless quantity. Finally, because F_i is a constant within a year, Eqs. (1) and (2) imply that fishing takes place continuously throughout the year.

Dividing both sides of Eq. (1) by those of Eq. (2) yields

$$\frac{N_{i+1}}{C_i} = \frac{Z_i \exp(-Z_i)}{F_i[1 - \exp(-Z_i)]}, \quad F_i, C_i > 0 \tag{3}$$

Hence, if N_{i+1}, C_i and M_i are known, then it is possible to solve Eq. (3) for F_i, and then use Eq. (1) to obtain N_i. Then Eq. (3) may be used to obtain F_{i-1}, and so on.

3. Pope's (1972) cohort analysis

Eq. (3) is a nonlinear equation of F_i. Although it can be solved quite easily today, it did pose a severe computational problem about 3.5 decades ago, when Pope (1972) simplified Gulland's (1965) virtual population analysis. To do this, he rewrote Eq. (1) as

$$\begin{aligned} N_{i+1} \exp(M_i) &= N_i \exp(-F_i) = N_i - N_i + N_i \exp(-F_i) \\ &= N_i - N_i(1 - \exp(-F_i)) \end{aligned} \tag{4}$$

substituted Eq. (2) in the form of $N_i = C_i(1/F_i)(Z_i/(1 - \exp(-Z_i)))$ into the term $N_i(1 - \exp(-F_i))$ in Eq. (4), and arrived at

$$N_{i+1} \exp(M_i) = N_i - C_i \left(\frac{Z_i}{1 - \exp(-Z_i)} \frac{1 - \exp(-F_i)}{F_i} \right) \tag{5}$$

Observing that, for $0 \leq M_i < 0.3$ year^{-1} and $0 \leq F_i < 1.2$ year^{-1}, the factor

$$\frac{Z_i}{1 - \exp(-Z_i)} \frac{1 - \exp(-F_i)}{F_i} \approx \exp\left(\frac{M_i}{2}\right)$$

with a positive error always smaller than 4% (Fig. 1), Pope (1972) wrote Eq. (5) as

$$N_{i+1} \exp(M_i) \approx N_i - C_i \exp\left(\frac{M_i}{2}\right), \text{ or equivalently,}$$

$$N_{i+1} \approx N_i \exp(-M_i) - C_i \exp\left(\frac{-M_i}{2}\right) \tag{6}$$

In the current literature, Pope's (1972) approximation, as Eq. (6) might be called, takes the slightly different (in notation) form of

$$\begin{aligned} N(a+1, t+1) &= N(a, t) \exp(-M(a, t)) \\ &\quad - C(a, t) \exp\left(\frac{-M(a, t)}{2}\right) \end{aligned} \tag{7}$$

where $N(a,t)$ is the number of fish of age a in the population at time t, $M(a,t)$ the instantaneous rate of natural mortality of the fish of age a at time t, and $C(a,t)$ is the total catch in the

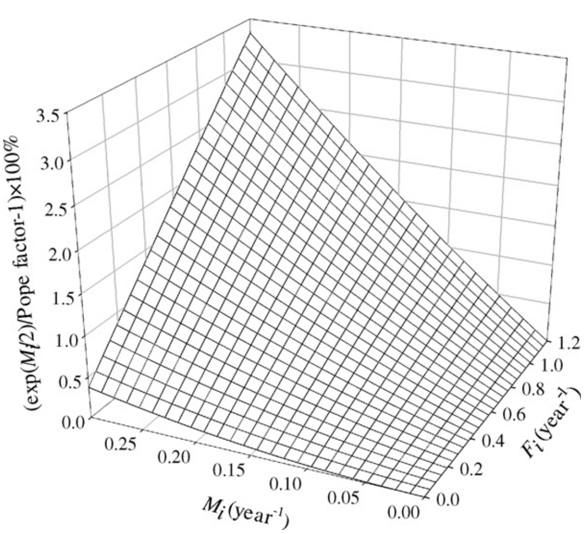

Fig. 1. The relative difference $\left[\exp(M_i/2)/\left(\frac{Z_i}{1-\exp(-Z_i)} \frac{1-\exp(-F_i)}{F_i}\right) - 1\right] \times 100\%$ between $\exp(M_i/2)$ and Pope factor $(Z_i/(1 - \exp(-Z_i)))(1 - \exp(-F_i))/F_i$, as a function of the instantaneous rate F_i of fishing mortality and the instantaneous rate M_i of natural mortality for $0 \leq F_i < 1.2$ year^{-1} and $0 \leq M_i < 0.3$ year^{-1}.