Population reproductive potential: Evaluation of long-term stock productivity

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ABSTRACT: In order to avoid recruitment overfishing, fish stocks must have sufficient reproductive ability. The spawning stock biomass (SSB), which ignores the value of immature fish, is widely used as an index of stock sustainability. From the perspective of sustainability, immediate reproduction, as well as future spawning, must be considered. We developed an index of long-term stock productivity, called the population reproductive potential (PRP). PRP is defined as the expected total reproductive value of the standing stock. We used PRP to assess the western Atlantic bluefin tuna (WBT) stock. The trends in SSB, numbers (N), biomass and PRP of WBT are inconsistent when compared to each other, due to fluctuation in age composition. We evaluated the long-term productivity of WBT by computer simulation and compared the result with trends in the abundance indices. The result of the computer simulation was highly consistent with the trend in the PRP. Short-term trends in SSB and N often do not reflect long-term stock trends, because they are highly sensitive to age-composition dynamics. The PRP is useful for evaluating stock trends, especially when the age composition is unstable.

KEY WORDS: population reproductive potential, reproductive value, stock abundance index, western Atlantic bluefin tuna.

INTRODUCTION

The spawning stock biomass (SSB) is generally used to decide whether a fish stock has sufficient productivity. Although a large number of studies have examined the sustainable level of SSB1-4 it is doubtful whether SSB is an appropriate index of stock sustainability. For example, SSB ignores the value of immature fish, which are indispensable for long-term sustainability. Therefore, decision-making that depends on SSB tends to be shortsighted.

For sustainable use of fish stock, a unit of stock abundance that represents long-term stock productivity is needed. Katsukawa5 developed the unit stock abundance, which is defined as the expected total reproductive value of the standing stock. The unit (which we now call population reproductive potential (PRP)) evaluates stock productivity by considering both immediate and future spawning. However, the effectiveness of PRP for stock assessment and fisheries management has not yet been presented. The aim of the present paper is to investigate effectiveness of PRP by numerical analysis and computer simulation. We compared the future stock level and PRP and examined if PRP can be used for the benchmark of long-term stock productivity. As an example, we present a stock assessment based on PRP, using the western Atlantic bluefin tuna population.

METHODS

Definition of population reproductive potential

In order to evaluate the sustainability of a fish stock, we should consider both immediate and future spawning of the standing stock. In biology, Fisher’s reproductive value6 is widely used as an index of the reproductive contribution of an individual:

$$RV_i = \sum_{x=1}^{\text{MAX}} \left[ e^{-r(x-i)} \cdot m_x \cdot l_x \right]$$

(1)

where $RV_i$ is Fisher’s reproductive value for an age $i$ individual, $r$ is the instantaneous growth rate of the population, $m_x$ is the average number of offspring of an individual at age $x$, $l_x$ is the survival rate of an age $i$ individual until the spawning season at
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Analysis based on a matrix model

We analytically investigated the relationship between the initial PRP level and the stock level after long projection. The dynamics of a density-independent age-structured population can be expressed as:

\[ n(t) = A \cdot n(t-1) = A^t \cdot n(0) \]  

(3)

where \( n(t) \) is a column vector with entries representing the number of (female) individuals of each age at time \( t \), and \( A \) is a time-independent projection matrix (Leslie matrix) with non-negative entries \( a_{ij} \). We compared convergence stock level and initial PRP level.

Example of stock assessment using the western Atlantic bluefin tuna

We used PRP to assess the western Atlantic bluefin tuna (\( Thunnus thynnus \)) stock as an example. The western Atlantic bluefin tuna (WBT) is a long-lived migratory species that reaches a length of 4 m and weights exceeding 500 kg. WBT commands a high price (more than $40 US per kg) on the raw seafood market in Japan. Due to the high market value, this stock was heavily exploited through the 1970s. In 1998, the International Union for Conservation of Nature and Natural Resources (IUCN) listed WBT as critically endangered. Matsuda \textit{et al.} objected to this listing because the absolute population size of WBT is still large and the extinction probability within the next half-century is negligible if the recent rate of population decline does not increase in the future.

The International Commission for the Conservation of Atlantic Tunas (ICCAT) is responsible for managing WBT. In 1982, the ICCAT started a management program for WBT and prohibited the capture of WBT, except for a catch quota. The effectiveness of WBT management has been the subject of controversy. Safina pointed out a decline in breeders and commented that the acronym ICCAT appears to represent the International Commission to Catch All the Tuna. Sissenwine \textit{et al.} concluded that total allowable catch (TAC) management of western Atlantic bluefin tuna since 1982 has had some success, and that some increase in the immediate future is likely. Although Safina and Sissenwine reached different conclusions, both related mainly to the trend of breeders. We consider the stock trend of WBT including the value of immature fish, in light of the PRP.
Table 1 shows the life history parameters of WBT.\textsuperscript{11} We assumed a natural mortality $M=0.14$ for all age classes. To calculate the reproductive value (RV), we used the geometric mean of the fishing mortality coefficient $F$ for the period 1982–95\textsuperscript{11} as shown in Table 1. We approximated fecundity $m_x$ as the product of the maturation rate $f_x$ and body weight at mid-year $w_x$. We assumed that the spawning season is at mid-year. Thus, RV at the beginning of the year is expressed by the fishing mortality coefficient at age $i(F_i)$ and the natural mortality coefficient ($M$).

\begin{equation}
RV_i = \sum_{x=i}^{\text{MAX}} [m_x \cdot f_x] = \sum_{x=i}^{\text{MAX}} \left[ f_x \cdot w_{x+0.5} \cdot \exp \left\{ 0.5F_x + 0.5M + \sum_{y=i}^{x-1}(F_y + M) \right\} \right].
\end{equation}

(4)

The reproductive value-at-age (RV) is shown in Table 1. $RV_{10}$, is affected by the average age of 10+ ($\bar{a}_y$) and is empirically approximated by $82.2 \bar{a}_y + 107$ ($R^2>0.98$ for $10<\bar{a}_y<20$). The value of $\bar{a}_y$ is assumed to be 12.5, 12.4, 12.0, 11.5, 12.0, 12.0, 11.9, 11.6, 11.7, 11.5, 11.4, 11.9, 11.3 and 11.9 for 1982–95\textsuperscript{11}, respectively.

\begin{equation}
PRP = \sum_{i=1}^{9} (N_i \cdot RV_i) + N_{10+} (82.2 \bar{a}_{10+} + 107)
\end{equation}

(5)

RV increases with age, which means that an old individual contributes more to spawning than a young individual. Thus, the productivity of immature fish is overestimated, if we use N as the abundance index. In contrast, RV per body weight decreases with age. This means that biomass underestimates the reproductive contribution of young individuals, and SSB ignores individuals with a high RV per body weight.

Figure 2 shows the trend in WBT abundance expressed by the PRP, spawning stock biomass (SSB), biomass, and the total number of age 1–10 +fish (N) of WBT.\textsuperscript{11} All abundance units are standardized using the 1982 level. Following the introduction of the management program, the trends became inconsistent. SSB decreased monotonously, while N peaked in 1990. This inconsistency is due to the age-composition fluctuation caused by the newly introduced management program. Fishing pressure on young cohorts declined drastically after 1982, and this change in the fishing pattern caused age-composition fluctuation (Table 2). N and SSB showed opposite reactions to the age-composition fluctuation. SSB increased when mature cohorts were abundant (in 1982), while N increased when young cohorts were abundant (in 1990). The trend in PRP is intermediate between the trends in N and SSB. If age composition is unstable, we must be sensitive to the choice of stock abundance index.

Computer simulation can be used to evaluate the trend of a stock with an unstable age composition. We projected the WBT population under...
constant fishing mortality, starting from the numbers-at-age in 1982–1995. It is rational to assume that the stock with the higher level in the future has the higher long-term productivity. The stock level after a long projection, therefore, represents the long-term productivity of the initial stock.

We projected WBT dynamics under constant fishing mortality (geometric mean of F between 1982 and 1995, shown in Table 1). We used the model described by SCRS\textsuperscript{12} for our projection, which is summarized as follows. Let $N_{i,y}$ be the number of age $i$ individuals at the beginning of year $y$. The dynamic can be expressed as:

$$N_{i+1,y+1} = N_{i,y}e^{-Z_i} \quad \text{(for } 1 \leq i \leq 9) \quad (6)$$

where $Z_i = F_i + M$. Individuals older than 9 years are grouped as 10+. The number at age 10+ is expressed as:

$$N_{10+,y+1} = N_{10+,y} + N_{9,y}e^{-Z_9}. \quad (7)$$

The average age of mid-year 10+ fish in year $y$ ($\bar{A}_{10+}$) is expressed as:

$$\bar{A}_{10+} = \frac{(\bar{A}_{10} + 1)N_{10+,y}e^{-Z_{10+}} + 10.5N_{9,y}e^{-Z_9}}{N_{10+,y}e^{-Z_{10+}} + 9N_{9,y}e^{-Z_9}}. \quad (8)$$

The weight at age $i$ ($w_i$) is calculated using the following equation:

$$w_i = 28.61 \cdot 10^{-6} \cdot \{380.1[1 - \exp(-0.0787(i + 0.731))]\}^{2.929}. \quad (9)$$

ICCAT used the following two-line model to calculate recruitment:

$$N_{1,y+1} = \frac{70574 \cdot SSB_y}{8241} \cdot e_y \quad \text{(if } SSB_y < 8241 \text{MT}), \quad (11)$$

$$N_{1,y+1} = 70574 e_y \quad \text{(if } SSB_y = 8241 \text{MT}), \quad (12)$$

where $e_y$ is a log-normally distributed random variable whose mean is 1 and SD is 0.4. This recruitment model (11) is unrealistic for long-term projections, because recruitment saturates at the geometric mean $SSB$ between 1985 and 1991, which is one-fourth the level in the early 1970s. Thus, we used a one-line model (12), and the Beverton-Holt S-R model fitted using the S-R relationship between 1970 and 1995 (13).

$$N_{1,y+1} = \frac{70574 \cdot SSB_y}{8241} e_y. \quad (11)$$

$$N_{1,y+1} = \frac{6.56}{2.61 \cdot 10^{-5} + \frac{1}{SSB_y}} e_y. \quad (12)$$

**RESULTS**

**Analysis based on a matrix model**

Lande and Orzack\textsuperscript{13} showed that this equation can be approximated as:

$$A^t \cdot \mathbf{n}(0) = e^{rt}(\mathbf{v}^t \cdot \mathbf{n}(0))\mathbf{u}, \quad (13)$$

where $\mathbf{v}^t$ and $\mathbf{u}$ are the dominant left and right eigenvectors of matrix $A$, and they are standardized as $\mathbf{v}^t \cdot \mathbf{u} = 1$; $r$ is the eigenvalue of $A$ corresponding to the eigenvector $\mathbf{u}$. It is known that $r$ is equivalent to the instantaneous growth rate, and that $\mathbf{v}$ and $\mathbf{u}$ are proportional to the reproductive value and stable age composition, respectively.\textsuperscript{14} Equation 13 indicates that the age composition of a population will converge at a finite time, and the stock size after age-composition convergence is proportional to $\mathbf{v}^t \cdot \mathbf{n}(0)$ (Note that $e^{rt}$ and $\mathbf{u}$ are independent of initial stock size.) By definition, $\mathbf{v}^t \cdot \mathbf{n}(0)$ is equivalent to the initial PRP. This means that the stock level after a long projection is linearly related to the initial PRP level. This means that we can forecast the future stock level from standing stock size and life-historical parameters. Because PRP is proportional to the future stock level, PRP is thought to be a good indicator of the long-term productivity of the standing stock.

**Stock assessment of the western Atlantic bluefin tuna**

Figure 3 shows projections starting from 1982, 1990, and 1995, using the one-line (11) and Beverton-Holt (12) models. We present the average $SSB$, $N$, and PRP of 100 replications. For each replication, we used a different set of random environmental variables ($e_y$) that affect recruitment. Since we assumed stable fishing mortality, the amplitude of the fluctuation diminished, and the stock trend became stable after 20 years. The projections start-
We evaluated the trend in WBT after 1982, using the long-term projection, and compared this to the initial stock level. Let \( SSB_{Y+20} \), \( N_{Y+20} \) and \( PRP_{Y+20} \) be SSB, N, and PRP after a 20-year projection starting from year \( Y \), respectively. Figure 4 shows the trends in the average \( SSB_{Y+20} \), \( N_{Y+20} \) and \( PRP_{Y+20} \) over 100 replications for \( Y \) between 1982 and 1995. The trends in \( SSB_{Y+20} \), \( N_{Y+20} \) and \( PRP_{Y+20} \) are highly consistent with the trend in the initial PRP \( (PRP_Y) \), and inconsistent with the trends in the other abundance units, such as \( SSB_Y \) and \( N_Y \). Therefore, we concluded that PRP is a good indicator of long-term stock productivity, and that the short-term trends of the SSB and N are often misleading due to the fluctuation in the age composition.

**DISCUSSION**

**Merit and demerit of population reproductive potential**

In order to examine effectiveness of PRP as index of stock sustainability, we compared the initial PRP level and future stock size. Our analysis and simulation revealed that the PRP is proportional to the future stock level, which will be realized after a long projection. Therefore, PRP represents stock sustainability and PRP should be used for decision-making of fisheries management whose objective is stock sustainability.

The idea of PRP and reproductive value can be used to estimate and limit the reproductive damage caused by fisheries. The prevailing TAC limits the total weight of the yield. As we have seen, the body weight of a fish is not proportional to the reproductive contribution of an individual. For example, young WBT have a higher RV per weight than older fish. If damage to a stock is estimated from the weight of the yield, the impact of exploiting young fish is underestimated. The stock reproductive damage should be evaluated using the total RV of yield. If we set an upper limit to the total RV of the fish removed, the reproductive damage to a fish stock can be restricted more strictly.

Our analysis showed that if the population dynamic can be expressed by a matrix model, the future stock level will be proportional to the initial PRP. In many cases, the population dynamics is known to be non-linear. For example, a linear population dynamics model predicts exponential growth, but real population size is limited by a non-linear density-dependent effect. The density-dependent effect is thought to be negligible when stock level is very low. Therefore, PRP seems to be an appropriate unit for conservation purposes.
Population reproductive potential

RV is related to spawning per recruit (SPR) analysis, which is familiar to fisheries scientists. If the stock level is stable ($r = 0$), the reproductive value of the just-recruited individual is equivalent to SPR. Although both SPR and PRP represent the lifetime fecundity of an individual, the uses of SPR and PRP (the extension of RV) are very different. SPR analysis is used to estimate the upper limit of sustainable fishing mortality, or the index of stock condition in terms of whether the stock is overfished. In contrast, PRP represents the long-term productivity of the standing stock, and is used as an index of stock condition in terms of whether the stock is depleted.

Trend of western Atlantic bluefin tuna

Our simulation revealed that the overall stock productivity of WBT was constant during the 1980s. We do not need to be pessimistic about the SSB decline in the 1980s, because the decline in mature fish was compensated for by an increase in immature fish. If the age composition is unstable, we must pay attention to the choice of the abundance unit. As N and SSB overemphasize certain age-classes, the short-term trends in N and SSB are often inconsistent with the long-term stock trend. PRP is robust to age-composition dynamics, because the long-term reproductive contribution of each age-class is evaluated explicitly from the life history. PRP is especially useful for monitoring the effect of a newly introduced management program, because age composition usually fluctuates after the introduction of a new program.

The PRP of WBT has been decreasing slightly since 1990. Since fishing mortality has been stable or declining since 1990, the decrease in PRP is thought to have been caused by recruitment failure. It is doubtful that recruitment failure.

The PRP is an information-demanding unit. Natural mortality, fecundity-at-age and number of individual-at-age are needed for calculation of PRP. Such information is not available for many stocks. Therefore, the use of PRP may be limited to stocks with this information. The assessment based on PRP is vulnerable to errors in the variety of parameters. In the present study, we assumed no bias in the estimation of natural mortality. If the estimation of $M$ is highly uncertain, we have to consider the effect of the uncertainty. In this case, PRP should be expressed by the function of $M$, such as $PRP_M = 0.14$. If $M$ is biased 50–150% from 0.14 ($0.07 \leq M \leq 0.21$), PRP ranges from $PRP_{F = 0, M = 0.21}$ to $PRP_{F = 0, M = 0.07}$. The PRP in 1982 is biased from 75% to 145% of the $PRP = 0, M = 0.14$. The value of PRP tends to be highly vulnerable to the estimation of $M$. But the trend of PRP is usually robust, because $M$ usually affects all RV equally.

The choice of abundance unit for the reference point of fisheries management is fundamentally related to the information availability and the goals of management. If the goal is to maximize yield, we need to keep the parental stock at the most productive level (i.e. the MSY level). In this case, the target stock level should be set using SSB, which represents instantaneous stock productivity. For sustainable use of a stock, we must consider both immediate and future spawning. A lower SSB threshold is commonly used to ensure stock sustainability; however, lower threshold stock size should be set using PRP, rather than SSB, because long-term productivity is necessary for stock sustainability. To set the PRP threshold, we can use the same procedure as used to set the SSB threshold. If we assume equilibrium, the PRP level corresponding to a certain $F$ can be calculated. Therefore, we can set the PRP threshold level using an $F$-based reference point, such as $F_{MSY}$ or $F_{MED}$. Otherwise, we can set the PRP threshold using a pristine PRP level.

**Fig. 4** Stock abundance after a 20-year projection, starting from 1982 to 1995. $SSBY_{Y+20}$, $NY_{Y+20}$ and $PRPY_{Y+20}$ indicate SSB, N and PRP after a 20-year projection starting from year $Y$, respectively. All measures are standardized using the 1982 stock level.
occurred in recent years. SRCS\textsuperscript{13,14} estimates recruitment in recent years using the stock-recruitment relationship (equation 10) and estimation of parental abundance (SSB). A recruitment failure is not observed in survey or fishery data. Therefore, the recent decline in PRP is probably an artifact of a pessimistic stock-recruitment model. The management program of ICCAT has had some success, because it has stopped the stock decline trend. Although the WBT stock seems to have been stable over the last 20 years, it remains low, and to achieve successful management stricter measures are required from ICCAT.

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