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Stock assessment of the shortfin mako shark (*Isurus oxyrinchus*) in the Northwest Pacific Ocean using per recruit and virtual population analyses

Jui-Han Chang [1], Kwang-Ming Liu *

Institute of Marine Affairs and Resource Management, National Taiwan Ocean University, 2 Pei-Ning Road, Keelung 20224, Taiwan

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ABSTRACT

The shortfin mako shark (*Isurus oxyrinchus*) is a cosmopolitan species abundant in the Northwest Pacific. Some aspects of its biological information have been well documented yet its population dynamics is poorly known. The objective of this study is to assess the population status of the shortfin mako in the Northwest Pacific. The whole weights of 68,943 female and 64,338 male shortfin mako landed at Nanfangao and Chengkung fish markets, eastern Taiwan from 1990 to 2004 were converted to total length and the age for each individual was estimated based on the sex-specific von Bertalanffy growth equation. Total mortality obtained with length-converted catch curves ranged from 0.175 yr^{-1} to 0.272 yr^{-1} for females and from 0.196 yr^{-1} to 0.286 yr^{-1} for males. Natural mortality estimated from Peterson and Wroblewski's equation were 0.077–0.244 yr^{-1} for females and 0.091–0.203 yr^{-1} for males. Based on virtual population analysis, the highest fishing mortality occurred in ages 6–10 years for females and 7–12 years for males. Increases of fishing mortality in ages 3–5 years for females and 3–6 years for males since 1996 indicated that the young shortfin mako experienced higher fishing pressure in recent years. Both deterministic and stochastic simulations showed that annual spawning potential ratio (SPR) of shortfin mako was lower than the biological reference point (BRP) of SPR 35% and had a decreasing trend since 2000. Current fishing mortality (0.066 yr^{-1}) was greater than the BRP of $F_{30\%}$ (0.052 yr^{-1}), $F_{35\%}$ (0.045 yr^{-1}), $F_{40\%}$ (0.04 yr^{-1}) and $F_{0.1}$ (0.063 yr^{-1}) suggesting that this stock might have been overexploited. Therefore, to ensure sustainable utilization, a management measure of 32% reduction of current fishing effort was suggested for the shortfin mako stock in the Northwest Pacific.

1. Introduction

In general, large sharks are extremely susceptible to overfishing because of their low reproductive rate and direct relationship between stock and recruitment (Holden, 1974, 1977). An increase in shark catches may necessitate the implementation of a management plan for the sustainable use of the resource. However, development of fishery management plans can be difficult, when there is a lack of adequate fisheries and biological data of sharks.

The shortfin mako shark, *Isurus oxyrinchus*, is widely distributed in tropical and subtropical waters (Compagno, 2001). It is not only caught by offshore fisheries but also is one of the major by-catch shark species for the tuna longline fishery in the open seas. The shortfin mako comprised 2.7% (ranked fourth) of the shark-fin trade in Hong Kong (Clarke et al., 2006), which suggested an average of 500,000 individuals were killed annually in the world. This species is commonly found over the continental slope in the Northwest Pacific with highest abundances in eastern Taiwan waters (Fig. 1) (Joung and Hsu, 2005). It is common and commercially important to Taiwan fisheries since the 1930's (Liu et al., 2001). Nanfangao and Chengkung are the two major offshore longline fishery landing ports in Taiwan (Fig. 1). Annual landings (whole weight) of the shortfin mako at Nanfangao and Chengkung fish markets in eastern Taiwan increased from 362 t in 1990 to 912 t in 2004 with a mean of 525 t, 8886 individuals, which was 23.6% (ranked 1st) of the total annual shark landings (except blue shark, *Prionace glauca*, which was not included in sale records) in the markets between 1990 and 2004 (Fig. 2).

The shortfin mako is a large species (L_{max} = 375 cm *TL* for females, L_{max} = 289 cm *TL* for males) that grows slowly (k = 0.05 yr^{-1} for females, k = 0.056 yr^{-1} for males), matures late (271 cm *TL*, 18 years for females and 210 cm *TL*, 12 years for males), and generates few offspring (4–15 embryos/litter) (Joung and Hsu, 2005; Chang unpublished data). Some aspects of fishery biology including age and growth (Pratt and Casey, 1983; Cailliet et al., 1983; Natanson, 2001; Chan, 2001; Campana et al., 2002a; Ribot-Carballal et al., 2005; Ardizzone et al., 2006; Bishop et al., 2006; Natanson et al.,

* Corresponding author. Tel.: +886 2 2462 2192x5018; fax: +886 2 2462 0291.
E-mail address: kmliu@mail.ntou.edu.tw (K.-M. Liu).
[1] Present address: School of Marine Sciences, University of Maine, Orono, ME 04469, USA.

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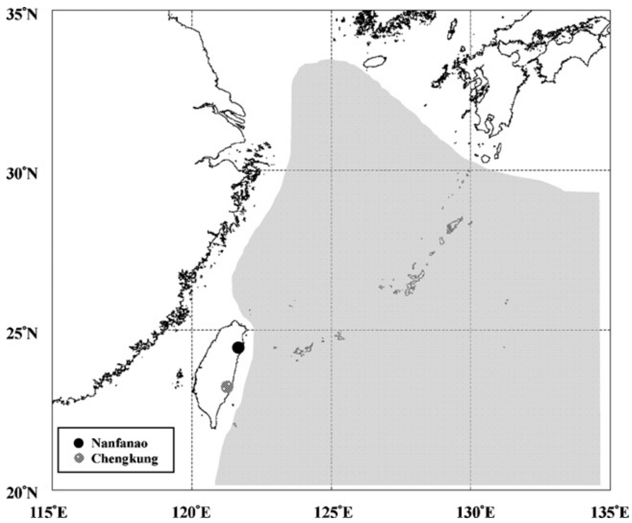

Fig. 1. Fishing ground (gray area) of shortfin mako for Taiwan longline fishery in the Northwest Pacific and the two major offshore longline fishery landing ports in Taiwan.

2006) and reproductive biology (Branstetter, 1981; Stevens, 1983; Gilmore, 1993; Mollet et al., 2000; Duffy and Francis, 2001; Joung and Hsu, 2005) of shortfin mako have been well documented. In the Atlantic Ocean, Nakano and Kiyota (2000) mentioned that the population density of shortfin mako stock has declined based on unstandardized CPUE trend. Campana et al. (2005) found the stock in Atlantic Canadian waters might be subject to growth overfishing. Moreover, the 2004 shark stock assessment meeting of ICCAT concluded the depletion rate of this species in the North Atlantic Ocean was over 40% from 1986 to 2000 and the population might collapse under current fishing level (Anon., 2005). Although the shortfin mako has heightened from the near threatened (NT) to the vulnerable (VU) category on the IUCN's red list (www.IUCN.org, 2007), yet its exploitation level in the Northwest Pacific is still unknown.

The objective of this study is to provide the first information on evaluation of the population status of the shortfin mako in the Northwest Pacific by using virtual population analyses (VPA), spawning per recruit analysis, and yield per recruit analysis (YPR). A fishery management strategy for this stock is proposed based on various biological reference points (BRP).

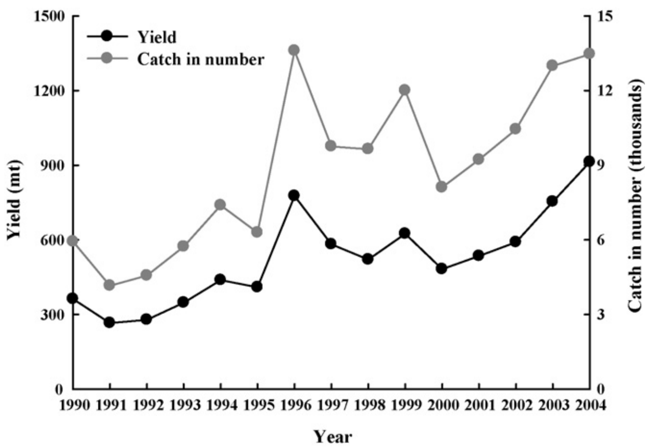

Fig. 2. Annual yield (mt) and catch in number of shortfin mako at Nanfangao and Chengkung fish markets from 1990 to 2004.

2. Materials and methods

2.1. Source of data

The shortfin mako caught in the Northwest Pacific by Taiwanese longliners were mainly landed at Nanfangao and Chengkung fish markets, eastern Taiwan (Fig. 1). All fish were weighed before being auctioned and gutted, so we were able to obtain catches (numbers) and individual whole weights from sale records. However, individual sex and length information was lacking in sale records. The sex of each individual shark landed was randomly assigned based on the weight-specific sex ratio, which was estimated from a total of 1944 samples (1137 of females and 807 of males) collected from 1995 to 2005 at Nanfangao fish market (Chang unpublished data). The χ^2 test showed that the sex ratio of shortfin mako less than 130 kg was not significantly different from 1:1 ($P > 0.05$). Therefore, the sex ratio of this group was set as 1:1. The sex ratio of the sharks greater than 230 kg was set as 1:0 because only female specimens were observed for this size range. As for the fish 130–230 kg, the sex ratio was estimated to be 1:0.39 and 1:0.07 for 130–200 kg and 200–230 kg, respectively. Based on this weight-specific sex ratio, a total of 133, 281 shortfin mako landed at Nanfangao and Chengkung fish market from 1990 to 2004 was separated into 68,943 females and 64,338 males. The whole weights (W) of shortfin mako were then converted to total length (TL) based on the sex-specific W–TL relationship with log-normal error structure (Chang unpublished data). An error term, which was randomly selected from the residuals obtained while deriving the empirical W–TL relationship, was added to the converted TL of each individual in order to account for the uncertainties of the TL estimation:

$$TL = \left(\frac{W}{1.6 \times 10^{-5}}\right)^{1/2.8767} e^{\varepsilon} \text{ for females}(n = 1, 137) \text{ and}$$

$$TL = \left(\frac{W}{1.9 \times 10^{-5}}\right)^{1/2.8433} e^{\varepsilon} \quad \text{for males}(n = 807),$$

where ε is a normally distributed random variable with mean of zero and a standard deviation of σ^2.

Age for each individual was converted from the estimated TL using the sex-specific von Bertalanffy growth equation (VBGE) with log-normal error structure, which was derived from the vertebral band counting data with an assumption of annual band pair deposition (Chang unpublished data). Based on the same procedure described above in the TL estimation paragraph, an error term was added for the converted age of each individual:

$$t = \frac{\ln(L_t\_413.8/-339.8)}{-0.05} e^{\varepsilon} \quad \text{for females}(n = 202) \text{ and}$$

$$t = \left(\frac{\ln(1-(L_t/332.1))}{-0.056} - 6.08\right) e^{\varepsilon} \quad \text{for males}(n = 130),$$

where ε is a normally distributed random variable with mean of zero and a standard deviation of σ^2. Here we assumed that the sex ratio and the percentage females that were pregnant in the landings were the same as our samples and no significant difference on sex ratio, W–TL relationship and age-TL relationship between the shortfin mako landed at Nanfangao and Chengkung fish markets.

2.2. Mortality estimation

The total mortality (Z) was estimated with Pauly's (1983) length-converted catch curve analysis under the assumption that recruitment was constant over years:

$$\ln[n(L_1–L_2)/dt] = a - Zt_{(L1+L2)/2},$$

where $n(L_1–L_2)$ is catch in number between the length interval L_1 and L_2, dt is age difference between L_1 and L_2, a is a constant, and t is the age at the midpoint of L_1 and L_2.

Four methods were used to estimate the natural mortality (M) as followings:

(1) $\ln(M) = \ln(Z) = 0.941–0.873 \ln(t_{max})$ (Hoenig, 1983)
(2) $M = 1.65/t_{mat}$ (Jensen, 1996)
(3) $M = 1.6\,k$ (Jensen, 1996)
(4) $M = (1.92\,\text{yr}^{-1})\,W^{-0.25}$ (Peterson and Wroblewski, 1984),

where t_{max} is longevity in years, t_{mat} is age at maturity, k is the growth coefficient of VBGE, W is body weight in g. The maximum observed fish correspond to age 30.8 and 23.6 (O_{max}) for females and males, respectively (Chang unpublished data). Therefore, t_{max} was estimated at 41 and 31 years for females and males, respectively based on $t_{max} = O_{max} \times 1.3$ (Cortés, 2002). The t_{mat} was age 19 (277 cm TL) and 13 (210 cm TL) for females and males, respectively (Joung and Hsu, 2005; Chang unpublished data).

2.3. Virtual population analysis

Age-specific fishing mortalities (F) for 1990–2003 were estimated based on VPA (Gulland, 1965) with Pope's (1972) approximation approach. As sex-specific growth and t_{max} were found for this species (Chang unpublished data), VPA was conducted by sex and those greater then t_{max} were assigned to be 42^+ and 32^+ age class for females and males, respectively. The converted TL less than the size at birth (74 cm) (Joung and Hsu, 2005) was assigned to be 0^+ age class. The initial values of F for the oldest age class for each year i were derived from $F_i = Z_i - M$, where M is estimated from Hoenig's (1983) equation. The initial values of age-specific F of year 2004 were estimated by $F_{2004,j} = F_{2004} \times S_j/S_{50\%}$, where F_{2004} is the F of year 2004, S_j is the cumulative probability of being captured at age j in year 2004 and was estimated by $S_j = 1/1 + e^{(-0.03\times(l_j-177.43)}$ for females and $S_j = 1/1 + e^{(-0.03\times(l_j-179.57)}$ for males, where l_j is TL at age j, $S_{50\%}$ is the cumulative probability of being capture equals 50%. Selectivity curve of F was chosen to have flat top property, and the ratio of $S_j/S_{50\%}$ was scaled to have the maximum as 1.

2.4. Spawning per recruit analysis

Spawning potential ratio (SPR) was estimated from the following equation (Goodyear, 1993):

$$SPR = \frac{\sum_{t=1}^{t_{max}} m_t W_t \prod_{j=0}^{t-1} l_j}{\sum_{t=1}^{t_{max}} m_t W_t \prod_{j=0}^{t-1} l'_j} \times 100\%,$$

where m_t is the proportion of females mature at age t, W_t is the mean weight of females at age t, $l_j\ (= e^{-(M_j+F_j)})$ is the survival rate of females at age j, $l'_j (= e^{-M_j})$ is the survival rate of females at age j when $F = 0$, and t_{max} is the longevity, 41 years. Age-specific F of females was obtained from VPA in this study and M was estimated from Peterson and Wroblewski's (1984) equation. The m_t was estimated by using following equation (Joung and Hsu, 2005): $Y = 1/1 + e^{(-0.34\times(l_j-277.13)}$, where l_j is TL at age j. All the parameters used in the deterministic simulations were estimated as mentioned above.

In addition to the deterministic simulation, the Monte Carlo method was used to estimate the 95% confidence interval of SPR for each year the based on 1000 simulations. The stochastic simulations were conducted to account for the uncertainties of the life history parameters of shortfin mako including M, age at maturity, and longevity. M was randomly selected from the four methods mentioned above with a weighting of 1:1:1:2. Age at maturity was randomly selected from ages 17–21 years with a weighting of 0.04, 0.26, 0.5, 0.17, and 0.03 based on the probability of maturity for females corresponding to each age (Joung and Hsu, 2005). Longevity was randomly selected from 31–41 years (maximum observed age to estimated longevity) with a uniform distribution.

2.5. Yield per recruit analysis

Yield per recruit (YPR) analysis was used for the purpose of calculating the $F_{0.1}$, where it is the F corresponding to 1/10 of the initial slope of the YPR curve (Gulland and Boerema, 1973), for the shortfin mako in the Northwest Pacific. YPR were estimated from the following equation (Beverton and Holt, 1957; Murawski, 1984; Pikitch, 1987; Gribble and Dredge, 1994):

$$Y = \sum_{t_c}^{t_{max}} C_t W_t,$$

where Y is yield, t_c is age at first capture (set as age 3), t_{max} is the longevity and W_t is the weight at age t which can be estimated from the $W–TL$ relationship and VBGE (Chang unpublished data). The above equation can be recast by using the catch equation and Ricker's (1975) exponential survival function:

$$\frac{Y}{R} = \sum_{t_c}^{t_{max}} \left[\frac{W_t F(S_t/S_{50\%})}{S_t F + M_t} (1 - e^{-S_t F - M_t})\, e^{-\sum_{j=t_c}^{t-1}((S_t/S_{50\%})F + M_j)} \right],$$

where M_j is the cumulative age-specific natural mortality estimated from Peterson and Wroblewski's (1984) equation and S_j is the cumulative probability of being captured at age j and was estimated by $S_j = 1/1 + e^{(-0.04\times(l_j-168.91)}$, where l_j is TL at age j, $S_{50\%}$ is the cumulative probability of being capture equals 50%. Selectivity curve of F was chosen to have flat top property, and the ratio of $S_j/S_{50\%}$ was scaled to have the maximum as 1.

2.6. Biological reference point

The $F_{30\%}$, $F_{35\%}$, $F_{40\%}$, and $F_{0.1}$ were calculated and chosen as the BRP in this study. The $F_{30\%}$, $F_{35\%}$, and $F_{40\%}$, are F that corresponded to SPR = 30%, 35%, and 40%, respectively and were calculated based on the same M and selectivity curve of F used to derive $F_{0.1}$.

3. Results

3.1. Size and age composition of the catch

The TL compositions of shortfin mako showed that the major proportion of catch fell in the range of 170–205 cm for both sexes in 1990–2002, which account for an average of 51% and 53% of the annual catch for females and males, respectively. However, during this period, the proportion of catch within this size range decreased from 65% to 30% for females and 68% to 34% for males and the proportion of catch within the range of 130–165 cm largely increased from 12% to 30% for females and 12% to 31% for males. The major proportion of catch shifted to both 130–165 cm (with an average of

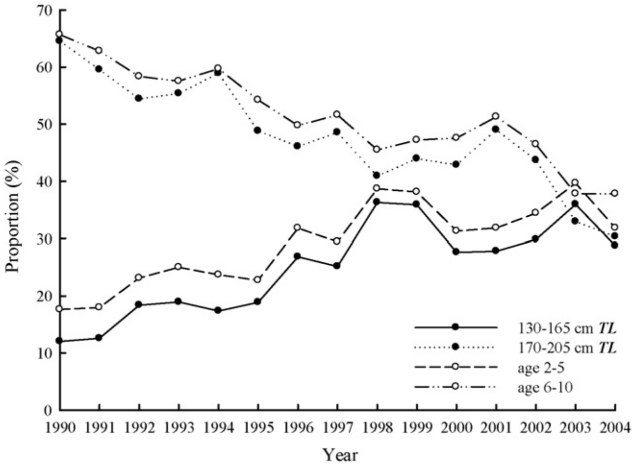

Fig. 3. The proportion of catch of the female shortfin mako within two size (130–165; 170–205 cm *TL*) and age (2–5; 6–10 years) ranges at Nanfangao and Chengkung fish markets from 1990 to 2004.

32% for females and 36% for males) and 175–205 cm (with an average of 32% for females and 34% for males) size ranges for both sexes in 2003–2004 (Figs. 3 and 4). A similar pattern was found in the age composition of catches. The major proportion of the catch fell in ages 6–10 years for females (with an average of 54%) and 6–11 years for males (with an average of 52%) in 1990–2002 and shifted to ages 2–5 years for both sexes (with an average of 36% for females and 35% for males), 6–10 years for females (with an average of 38%) and 6–11 years for males (with an average of 36%) in 2003–2004 (Figs. 3 and 4).

3.2. Mortality

The total mortality estimated with Pauly's (1983) length-converted catch curve ranged from 0.175 yr^{-1} in 2001 to 0.272 yr^{-1} in 1991 with a mean of 0.210 yr^{-1} for females, and from 0.196 yr^{-1} in 2004 to 0.286 yr^{-1} in 1990 with a mean of 0.244 yr^{-1} for males (Fig. 5).

The natural mortality estimated with four methods was as followings: (1) Hoenig's (1983) equation: M was 0.100 yr^{-1} for females and 0.128 yr^{-1} for males, (2) Jensen's (1996) equation 1: M was 0.087 yr^{-1} for females and 0.127 yr^{-1} for males, (3) Jensen's (1996) equation 2: M was 0.078 yr^{-1} for females and 0.089 yr^{-1} for males, (4) Peterson and Wroblewski's (1984) equation: M was 0.077–0.244 yr^{-1} for females and 0.091–0.203 yr^{-1} for males (Table 1).

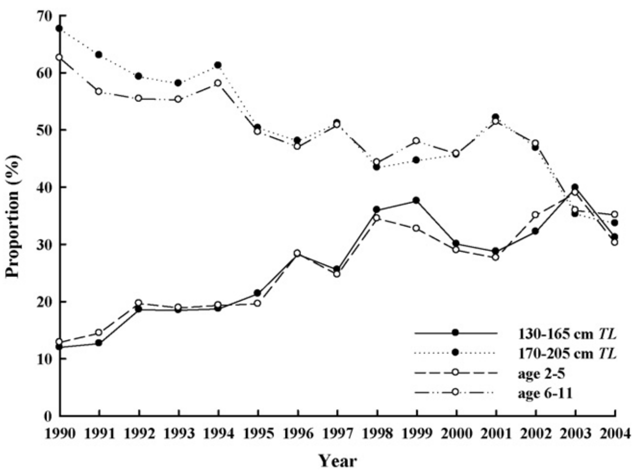

Fig. 4. The proportion of catch of the male shortfin mako within two size (130–165; 170–205 cm *TL*) and age (2–5; 6–11 years) ranges at Nanfangao and Chengkung fish markets from 1990 to 2004.

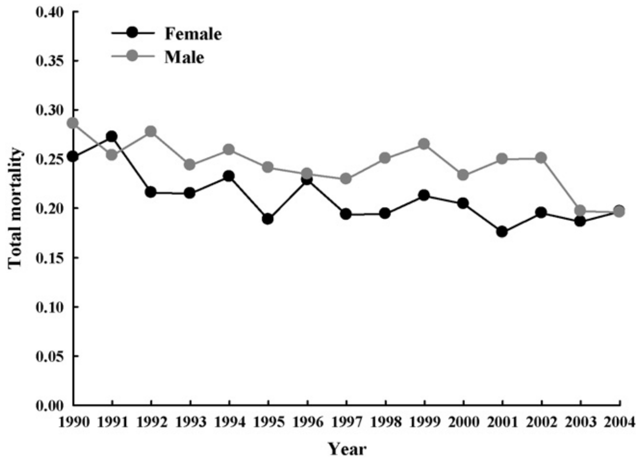

Fig. 5. Estimated total mortality (Z) of shortfin mako from 1990 to 2004.

3.3. Virtual population analysis

Estimated age-specific fishing mortality indicated that females of ages 6–10 years (0.036–0.145 yr^{-1}; mean = 0.08 yr^{-1}) and males of ages 7–12 years (0.017–0.072 yr^{-1}; mean = 0.043 yr^{-1}) experienced the highest fishing pressure during 1990–2003. Meanwhile, the average F increased from 0.020 yr^{-1} (0.006–0.038 yr^{-1}) in 1990–1995 to 0.046 yr^{-1} (0.022–0.074 yr^{-1}) after 1996 for females at ages 3–5 years, and from 0.01 yr^{-1} (0.003–0.020 yr^{-1}) in 1990–1995 to 0.034 yr^{-1} (0.02–0.053 yr^{-1}) after 1996 for males at ages 3–6 years (Figs. 6 and 7). The results showed that the young shortfin mako experienced higher fishing pressure in recent years.

3.4. Spawning per recruit analysis

In the deterministic simulations, SPR ranged from 14% in 1996 to 43% in 1991 with a mean of 28%. The SPR were high in 1990–1994, with a value of 43%, 41% and 35% in 1991, 1992, and 1993, respectively, which were higher than BRP of SPR 35% (Fig. 8). A similar trend was found in stochastic simulations that the SPR were estimated to be 46% (43–50%), 44% (41–49%), and 35% (32–38%) in 1991, 1992, and 1993, respectively (Fig. 9). However, SPR were lower than BRP of SPR 35% and had a decreasing trend since 2000 in both simulations. There was a negative correlation between SPR and annual catch in number ($r = -0.96$) (Fig. 8). The SPR was high in those years when catches were at low level (e.g., 1991, 1992, 1993), but was low in those years when catches were at high level (e.g., 1996, 1999, 2003).

3.5. Biological reference points

The F corresponding to the BRP of $F_{30\%}$, $F_{35\%}$, $F_{40\%}$, and $F_{0.1}$ were estimated to be 0.052 yr^{-1}, 0.045 yr^{-1}, 0.04 yr^{-1}, and 0.063 yr^{-1}, respectively. The four BRP are comparable because the parameters that were used in the analyses such as M and longevity were estimated under same conditions. Current fishing mortality ($F_{2003} = 0.066$ yr^{-1}) was greater than $F_{30\%}$, $F_{35\%}$, $F_{40\%}$, and $F_{0.1}$ suggesting that this stock might have been overexploited (Fig. 10).

Table 1
Natural mortality (M) estimated from four methods: (1)) method using longevity in years (2)) method using age at maturity (3) 6 method using growth coefficient of VBGE (4)) method using age-specific body weight (g); for shortfin mako in the Northwest Pacific.

Age	Female				Male			
	Hoenig	Jensen 1	Jensen 2	P&W	Hoenig	Jensen 1	Jensen 2	P&W
0	0.1002	0.0868	0.0784	0.2443	0.1279	0.1269	0.0890	0.2027
1	0.1002	0.0868	0.0784	0.2115	0.1279	0.1269	0.0890	0.1853
2	0.1002	0.0868	0.0784	0.1886	0.1279	0.1269	0.0890	0.1719
3	0.1002	0.0868	0.0784	0.1716	0.1279	0.1269	0.0890	0.1611
4	0.1002	0.0868	0.0784	0.1584	0.1279	0.1269	0.0890	0.1523
5	0.1002	0.0868	0.0784	0.1480	0.1279	0.1269	0.0890	0.1449
6	0.1002	0.0868	0.0784	0.1394	0.1279	0.1269	0.0890	0.1387
7	0.1002	0.0868	0.0784	0.1323	0.1279	0.1269	0.0890	0.1334
8	0.1002	0.0868	0.0784	0.1263	0.1279	0.1269	0.0890	0.1288
9	0.1002	0.0868	0.0784	0.1211	0.1279	0.1269	0.0890	0.1248
10	0.1002	0.0868	0.0784	0.1166	0.1279	0.1269	0.0890	0.1213
11	0.1002	0.0868	0.0784	0.1127	0.1279	0.1269	0.0890	0.1182
12	0.1002	0.0868	0.0784	0.1093	0.1279	0.1269	0.0890	0.1154
13	0.1002	0.0868	0.0784	0.1063	0.1279	0.1269	0.0890	0.1129
14	0.1002	0.0868	0.0784	0.1036	0.1279	0.1269	0.0890	0.1106
15	0.1002	0.0868	0.0784	0.1011	0.1279	0.1269	0.0890	0.1086
16	0.1002	0.0868	0.0784	0.0989	0.1279	0.1269	0.0890	0.1068
17	0.1002	0.0868	0.0784	0.0969	0.1279	0.1269	0.0890	0.1051
18	0.1002	0.0868	0.0784	0.0951	0.1279	0.1269	0.0890	0.1036
19	0.1002	0.0868	0.0784	0.0935	0.1279	0.1269	0.0890	0.1022
20	0.1002	0.0868	0.0784	0.0920	0.1279	0.1269	0.0890	0.1009
21	0.1002	0.0868	0.0784	0.0906	0.1279	0.1269	0.0890	0.0997
22	0.1002	0.0868	0.0784	0.0894	0.1279	0.1269	0.0890	0.0987
23	0.1002	0.0868	0.0784	0.0882	0.1279	0.1269	0.0890	0.0977
24	0.1002	0.0868	0.0784	0.0871	0.1279	0.1269	0.0890	0.0967
25	0.1002	0.0868	0.0784	0.0861	0.1279	0.1269	0.0890	0.0959
26	0.1002	0.0868	0.0784	0.0852	0.1279	0.1269	0.0890	0.0951
27	0.1002	0.0868	0.0784	0.0843	0.1279	0.1269	0.0890	0.0944
28	0.1002	0.0868	0.0784	0.0835	0.1279	0.1269	0.0890	0.0937
29	0.1002	0.0868	0.0784	0.0828	0.1279	0.1269	0.0890	0.0931
30	0.1002	0.0868	0.0784	0.0821	0.1279	0.1269	0.0890	0.0925
31	0.1002	0.0868	0.0784	0.0815	0.1279	0.1269	0.0890	0.0919
32	0.1002	0.0868	0.0784	0.0809	–	–	–	–
33	0.1002	0.0868	0.0784	0.0803	–	–	–	–
34	0.1002	0.0868	0.0784	0.0798	–	–	–	–
35	0.1002	0.0868	0.0784	0.0793	–	–	–	–
36	0.1002	0.0868	0.0784	0.0788	–	–	–	–
37	0.1002	0.0868	0.0784	0.0784	–	–	–	–
38	0.1002	0.0868	0.0784	0.0780	–	–	–	–
39	0.1002	0.0868	0.0784	0.0776	–	–	–	–
40	0.1002	0.0868	0.0784	0.0772	–	–	–	–
41	0.1002	0.0868	0.0784	0.0769	–	–	–	–

4. Discussions

The estimations of VPA, SPR and YPR in this study were based on the hypothesis that the shortfin mako in the Northwest Pacific is a unit stock. The recent stock assessment of shortfin mako in the Atlantic Ocean was conducted using two stocks (North and South) hypothesis based on mark-recapture results (Anon., 2005). Similar findings may occur in the Pacific and our assumption of a unit stock in the North Pacific might be reasonable. Heist et al. (1996) and Schrey and Heist (2003) proposed a unit stock for the shortfin mako in the east Pacific across the equator based on DNA analysis. However, the stock structure in the west Pacific is still unknown. To clarify this problem, a suitable stock identification study with method such as mark-recapture or molecular technology is needed in the future.

Bigelow and Schroeder (1948) and Pratt and Casey (1983) documented the existence of sexual dimorphism for the shortfin mako, with females reaching up to 362 cm *FL* and males up to 250 cm *FL*. The sex ratio of shortfin mako less than 240 cm *FL* (corresponding to 150 kg) was 1:1 but females dominated for fish larger than this size in the Gulf of Mexico (Casey and Kohler, 1992). We believe our similar assumption of sex ratio being 1:1 for fish less than 130 kg and 1:0 for fish larger than 230 kg was reasonable. As for the fish between 130 kg and 230 kg, the sex ratio was estimated based on our observations (159 females, 48 males). However, more specimens were needed to improve the estimation.

The *W*–*TL* relationship between sexes was significantly different for shortfin mako (Chang unpublished data), so we carried out the weight to total length conversion by sex accordingly. However, no significant difference between sexes in *W*–*TL* relationship was documented by other authors (Stevens, 1983; Cliff et al., 1990; Kohler et al., 1995). Sample size and size range of specimens were the two most likely factors resulted in the discrepancy. Chang's (unpublished data) estimation was based on a data set of large sample size and wide size range (n = 1944, 80–375 cm *TL*). However, Stevens (1983) and Cliff et al. (1990) carried out the estimation based on much smaller sample size and narrower size range (n = 80, 58–343 cm *TL* and n = 143, 80–260 cm *PCL*, respectively). Given a larger sample size and wider size range of specimens, Chang's (unpublished data) equations should be the best describing the sex-specific *W*–*TL* relationship for shortfin mako.

The accuracy of age determinations may have great impact on the results of stock assessment studies (Lai and Gunderson, 1987; Richards et al., 1992; Morison et al., 1998). The debate on the periodicity of band pair formation of shortfin mako has been continued over the past two decades. Pratt and Casey (1983) proposed a biannual band pairs deposition based on consistency with length-frequency and tag/recapture data. However, Cailliet et al. (1983)

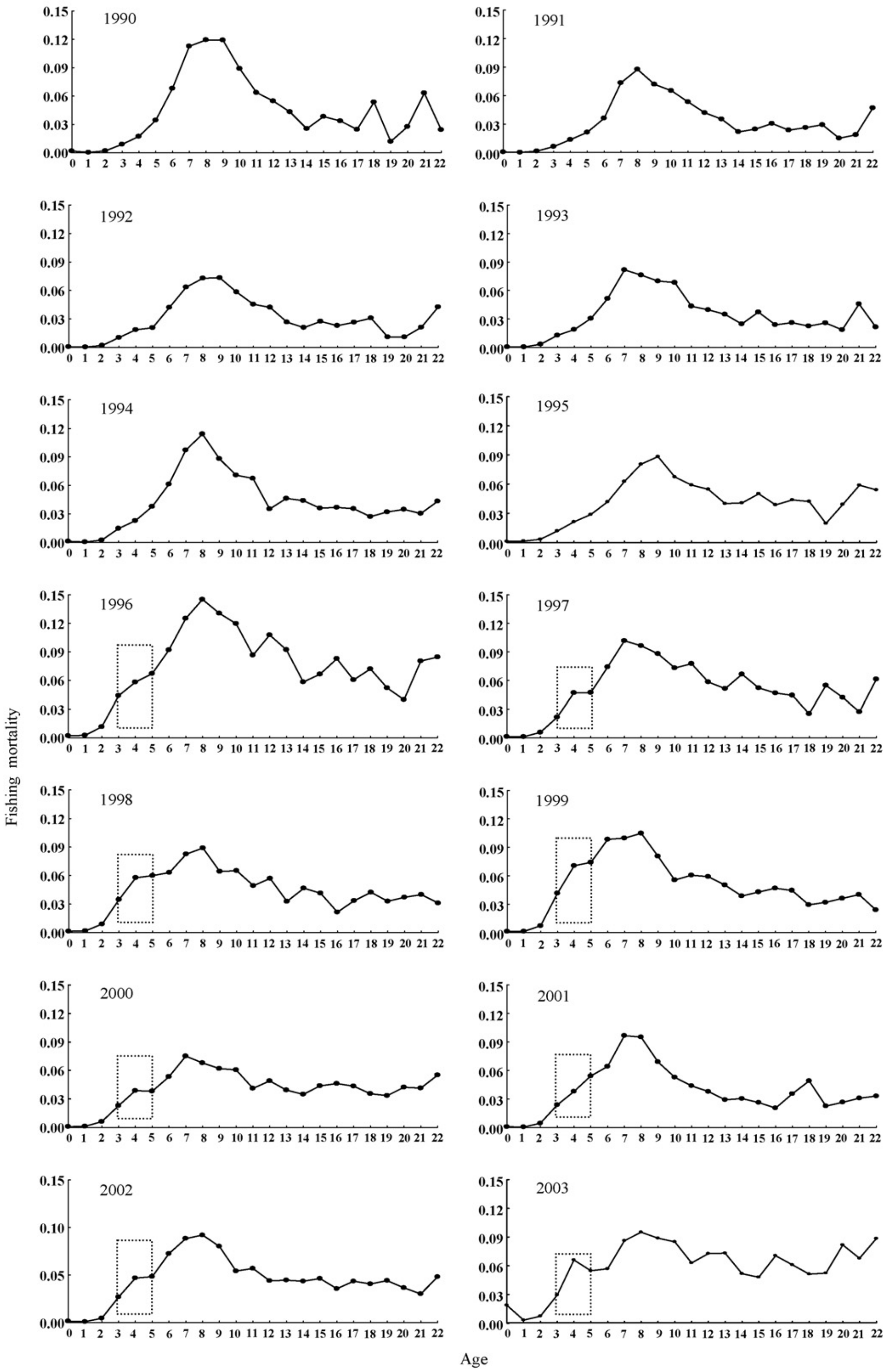

Fig. 6. Estimated age-specific fishing mortality (*F*) (0–22 years) from VPA of female shortfin mako (1990–2003) in the Northwest Pacific. The ages 3–5 years where young females experienced higher fishing pressure since 1996 have been circled in the boxes.

suggested an annual band pair deposition using vertebral band counting. In recent years, Natanson (2001), Ribot-Carballal et al. (2005), Bishop et al. (2006) and Chang (unpublished data) all supported the annual band pair deposition hypothesis. Furthermore, Ardizzone et al. (2006) and Natanson et al. (2006) both confirmed the annual deposition of band pair by using bomb radiocarbon and tagging experiments. Hence, the assumption of annual band pair deposition of vertebral centrum in this study is believed to be reasonable.

Chang (unpublished data) found that females mature older (18 vs. 12 years) and reach a larger maximum size than males. In addition, as significant difference on VBGE between sexes was found

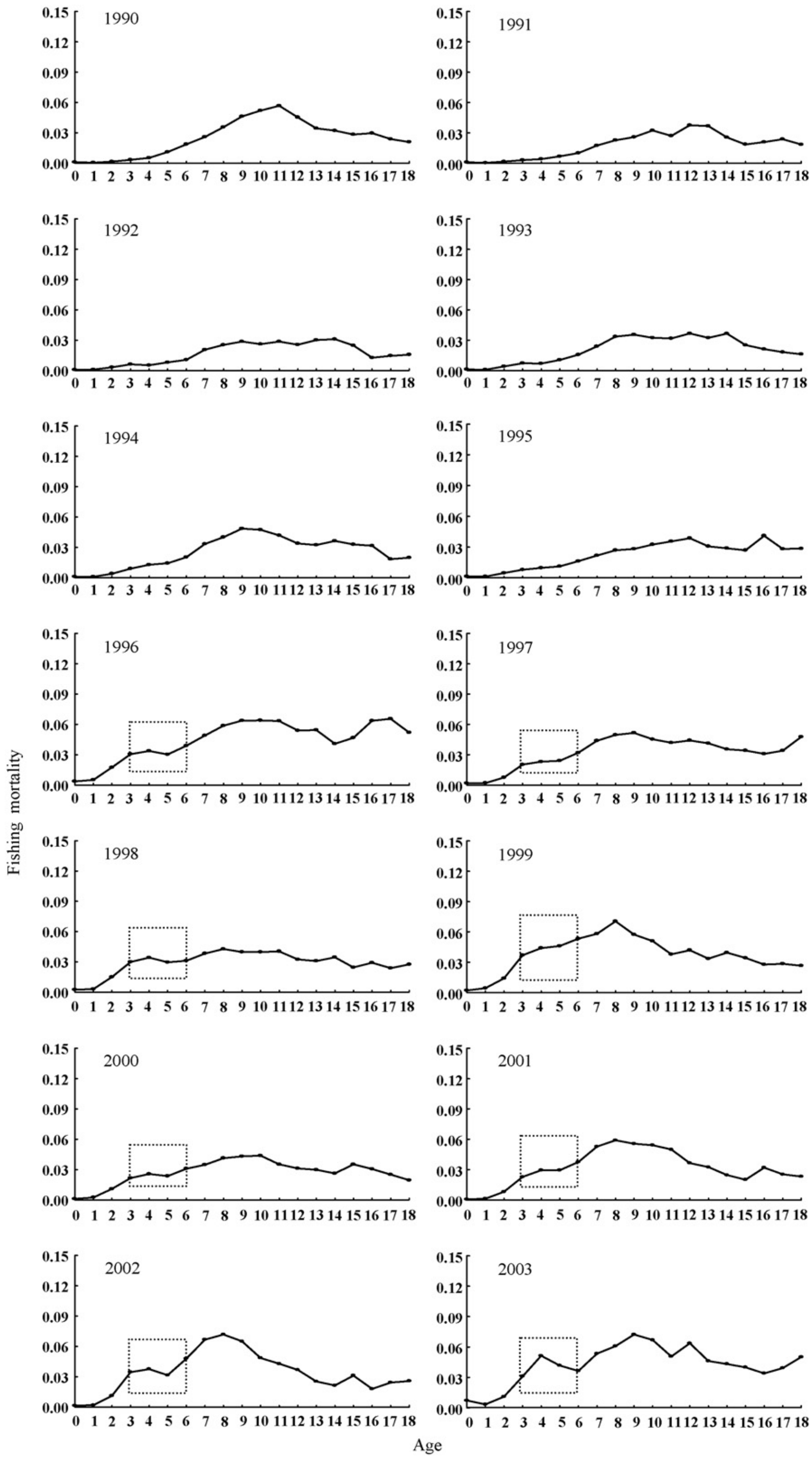

Fig. 7. Estimated age-specific fishing mortality (*F*) (0–18 years) from VPA of male shortfin mako (1990–2003) in the Northwest Pacific. The ages 3–6 years where young males experienced higher fishing pressure since 1996 have been circled in the boxes.

from the maximum likelihood ratio test (Chang unpublished data), using the sex-specific parameters to estimate age is believed to be reasonable.

Joung and Hsu (2005) documented that the size at birth is 74 cm *TL* for shortfin mako based on the smallest free swimming individual captured and the largest embryos to be delivered. Therefore, it is likely that the free swimming individual is greater than 74 cm *TL*. As the full term embryos per litter can weigh up to 40 kg (Joung and Hsu, 2005), some converted *TL* of pregnant female individuals might be overestimated and greater than the maximum observed length (375 cm). Our assignment of 0^+ and 42^+ for individuals smaller than 74 cm or greater than 375 cm *TL* is believed to be reasonable.

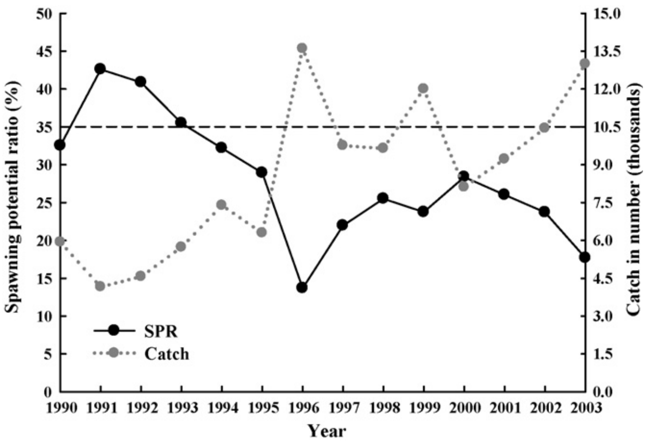

Fig. 8. Estimated SPR and annual catch in number of shortfin mako at Nanfangao and Cheng Kung fish markets from 1990 to 2003.

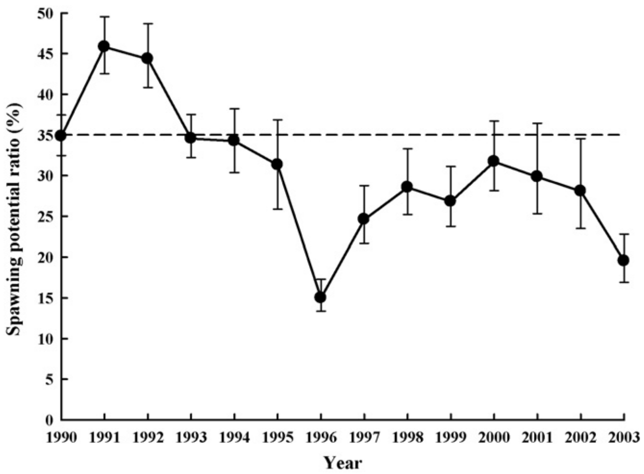

Fig. 9. Estimated SPR with 95% confidence intervals of shortfin mako from 1990 to 2003.

In this study, Pauly's (1983) length-converted catch curve was used to estimate *Z*. However, this approach cannot account for the increase of fishing pressure on young fish if the proportions of major targeting age classes are unchanged. The proportion of catch in females within the size range of 130–165 cm *TL* averaged 16% in

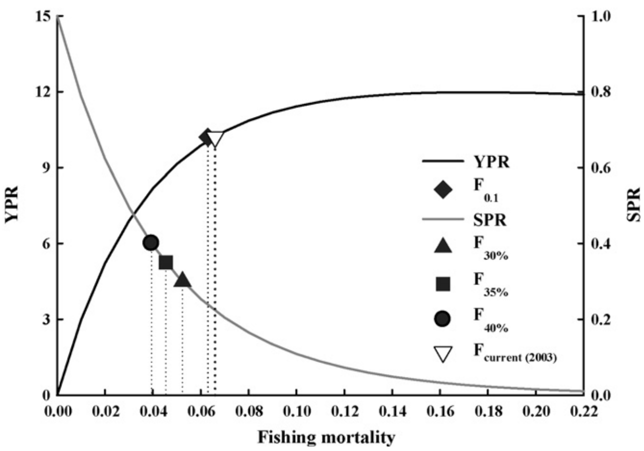

Fig. 10. YPR and SPR curves with current fishing mortality (2003) and biological reference points $F_{30\%} = 0.052\ yr^{-1}$, $F_{35\%} = 0.045\ yr^{-1}$, $F_{40\%} = 0.04\ yr^{-1}$, and $F_{0.1} = 0.063\ yr^{-1}$ of shortfin mako.

the period of 1990–1995, increased to 30% in 1996–2004, and it increased from 17% to 32% for males. Two peaks (the minor one for young fish and the major one for old fish) were observed from the length-frequency distributions since 1996. However, the minor peak cannot be taken into account on estimating of *Z* based on Pauly's method. Alternate approaches such as Paloheimo's (1980) single cohort method can be used to estimate *Z* (Ricker, 1975) and have been applied to gummy shark (*Mustelus antarcticus*) (Walker, 1992) and porbeagle shark (*Lamna nasus*) (Campana et al., 2002b). However, this approach was not used in this study due to the lack of fishing effort data. Since *Z* cannot reflect the shifting catch composition, we estimated age-specific *F* from VPA.

Virtual population analysis is a standard method to estimate fishing mortality of fish stock. The representative of VPA results relies upon the initial estimation of terminal *F*, however, it is less sensitive if back calculation is chosen as the estimation procedure (Pope, 1972; Quinn and Deriso, 1999). Therefore, although the estimations are also sensitive to *M*, catch at age estimations and migration, VPA is still fairly robust for analyzing the historical change of the *F* (Quinn and Deriso, 1999) based on the assumptions that these effects are constant through years. Usually, VPA was applied to estimate sexes-combined *F*. As the sexual dimorphism was found for shortfin mako and the sex ratios were available to be estimated, the sex-specific approach used in this study was believed to be a better and more reasonable process. Similar approaches were used in school shark (*Galeorhinus galeus*) (Punt and Walker, 1998) and swordfish (*Xiphias gladius*) (Wang et al., 2007).

Natural mortality of marine animals is often difficult to estimate. Because little is known of the life history parameters of sharks, Hoenig's (1983) relationship between longevity and *Z* has been adopted to estimate *M* by many authors (Hoenig and Gruber, 1990; Hoff, 1990; Cailliet, 1992; Cailliet et al., 1992; Cortés, 1995; Sminkey and Musick, 1995; Au and Smith, 1997; Cortés, 1998). The accuracy of *M* depends on the estimated longevity. Cailliet et al. (1992) mentioned that the longevity of sharks can be estimated as the age at which 95% of L_∞ is reached. However, due to the uncertainty of L_∞ estimation, large discrepancy was found on the estimated longevities for female shortfin mako in different studies based on Cailliet et al. (1992)'s method (219 years in New Zealand waters, 38 years in North Western Atlantic waters, and 56 years in present study). On the contrary, those estimated from the equation of Cortés (2002) were comparable in different waters (36 years in New Zealand waters, 42 years in North Western Atlantic waters, and 41 years in present study). Hence, Cortés's (2002) equation was suggested to be used to estimate the longevity of shortfin mako. Hoenig's (1983) method does not account for variations in *M* at different ages, but *M* may decrease with increasing age and can be affected by many biological and environmental factors. Cortés (2000) documented that *M* estimated from Peterson and Wroblewski's (1984) method can be applied to sharks. This method accounts for size-specific mortality but still ignores other biological and environmental effects. Walker (1998) proposed that *M* of sharks decreases with age during the first few years of life and then increases with age during the last year of life. In this study, age-specific selectivity has been applied in our analyses but the U shape mortality has not been observed, thus it has not been used in this study. The *M* estimated from four methods was randomly chosen based on a weighting of 1:1:1:2 in stochastic simulations. Since estimation of *M* is essential in stock assessment, more effort is needed to get a more robust estimator of *M* in the future.

Beside natural mortality and longevity, age at maturity is also one of the uncertainties that may affect the results of spawning per recruit analysis. Excepting the age 7 years reported by Pratt and Casey (1983) with an assumption of biannual band pair deposition, most studies suggested similar age at maturity of females (15–21 years) in different waters (Ribot-Carballal et al., 2005;

Bishop et al., 2006; Chang unpublished data; Natanson et al., 2006) based on the annual band pair deposition assumption. In present study, we applied stochastic approaches in estimating annul SPRs, which account for the biological features that the age at maturity and longevity varies among years and M varies among ages, This approach did account for the annual and among age variations of the life history parameters and improved the quality of the results.

The biological reference points $F_{30\%}$, $F_{35\%}$, $F_{40\%}$, and $F_{0.1}$ were derived using per recruit analyses in present study. The disadvantages of the analyses go toward the assumption of constant F over many age classes since we assumed knife-edge selectivity. This assumption implied that the BRPs derived from the analyses are applicable to all the fully recruited year classes. It is often not realistic in most situations due to the variation of the stock abundance, and the effect of gear efficiency and fishing effort among ages (Haddon, 2001; Quinn and Deriso, 1999). However, the assumption still possess two characteristics of fishing activity, that are the competition between number of fish and the unit effort it suffered and the competition between M and F for fish (Quinn and Deriso, 1999).

The $F_{0.1}$, derived from yield per recruit model, has been used in fishery management of teleosts for many years to reduce the opportunity of overfishing (Mace, 1994). However, most fish stocks are likely overexploited based on this management criterion (Punt, 2000). Compared to teleosts, sharks have a higher chance of overfishing under this criterion because of their low reproductive rate (Musick, 1999). Campana et al. (2002b) concluded that $F_{0.1}$ was not suitable as the management benchmark for porbeagle shark as its stock could collapse using this BRP. As $F_{0.1}$ was higher than any other BRP, it was not chosen as the BRP for the shortfin mako.

The spawning potential ratio, which accounts for the effect of fishing on the spawning stock, is a preferred management criterion that 20–30% has been commonly used as the reference point and 30–40% been used as a level of F_{MSY} (Clark, 1991; Goodyear, 1993; Mace and Sissenwine, 1993). Mace and Sissenwine (1993) concluded that SPR must be greater than 30% to avoid overfishing for chondrichthyans. Recently, Punt (2000) proposed the management reference points of SPR = 30% and 40% for gummy shark, and school shark, respectively; the United States also set a reference point of SPR = 35% for pelagic sharks (Anon., 1997). These two criteria are compatible with Mace and Sissenwine's (1993) point of view. Considering the low productivity and the close relationship between spawner and recruitment of shortfin mako, a reference point of SPR = 35% seems to be appropriate.

5. Conclusions

The results of VPA showed that the young shortfin mako experienced higher fishing pressure in recent years. Moreover, the SPR were lower than the BRP SPR = 35% and showed a downward trend in recent years and the current fishing mortality $F_{2003} = 0.066\,\mathrm{yr}^{-1}$ was greater than the BPR $F_{35\%} = 0.045\,\mathrm{yr}^{-1}$ suggesting that the stock might have been overexploited. To ensure sustainable utilization, a reduction of 32% of current fishing effort was suggested for the shortfin mako stock in the Northwest Pacific.

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