

Abstract—When stocks are depleted, direct assessments of population levels are not only difficult but may be highly inaccurate. The work reported here was motivated by the need to manage the collapse of the far eastern sardine (*Sardinops melanostictus*) population. Spawning area was chosen as the first indicator of population size because the spatial spread of the stock increases when the spawning population increases. Our objective was to clarify the relation between spawning area and the spawning biomass of this species off the Pacific coast of Japan in order to estimate biomass with the spawning area data.

The pilchard spawning area (A_1) in a given year was calculated by summing the areas of 1° longitude \times 1° latitude squares where early developmental stage eggs were present. The optimal relationship between A_1 and the spawning biomass (B) was $A_1 = 2.518 B^{0.4610}$, not a simple linear relationship. One cause of the nonlinear relationship seemed to be that pilchard egg aggregations were distributed over space in a patchy manner.

Finally, we introduced an approximate method for estimating the pilchard spawning biomass by using the inverted equation of the optimal relationship between A_1 and B ; ($B = 0.135A_1^{2.1691}$).

The relation between spawning area and biomass of Japanese pilchard, *Sardinops melanostictus*, along the Pacific coast of Japan

Hiromu Zenitani

National Research Institute of Fisheries and Environment of Inland Sea
2-17-5, Maruishi, Ohno-cho Saeki-gun,
Hiroshima, 739-0452 Japan
E-mail address: zenitani@nnf.affrc.go.jp

Sakutaro Yamada

Tokyo University of Fisheries
4-5-7, Konan, Minato-ku,
Tokyo, 108-0075 Japan

Japanese pilchard, *Sardinops melanostictus* (known as “Japanese pilchard” in Japan) is found off the Pacific coast of Japan and is an important commercial species. The pilchard stock has fluctuated widely over a period of several decades (Kondo et al., 1976). The annual catch in Japan peaked at 1.5×10^6 metric tons (t) in the 1930s, but decreased to only 3.0×10^4 t in the 1960s. It recovered to 4.6×10^6 t in the 1970s and reached the second highest peak for this century in 1988. However, the catch in 1995 fell to one-tenth of that in 1988 (Fig. 1).

When stocks are depleted, direct assessments of population levels are not only difficult but may be highly inaccurate (Hewitt et al.¹). In such situations, an alternative method of population assessment is to survey egg or larval populations as a means of estimating biomass (e.g. the egg production method; Lasker, 1981). However, the egg production method (EPM) is expensive and time consuming (Mangel and Smith, 1990).

A biological characteristic of the Japanese pilchard is that its distribution range changes in accordance with stock size. During pilchard stock size increases, the distributional range expands widely (Wada and Kashiwai, 1991). In contrast, when stock size is declining, the distributional range may become quite limited (Hiramoto, 1981). The spawning grounds of Japanese pilchard are known to expand with egg abundance increases and contract with

abundance declines (Watanabe et al., 1996; Zenitani et al., 1998). In general, as the spawning population increases, the spatial spread of the stock also increases (Rosenzweig, 1981; MacCall, 1988). Therefore, the area of spawning grounds (spawning area) was chosen as the first indicator of pilchard population recovery (Smith, 1973; Smith and Hewitt, 1985).

Our objective was to clarify the relationship between pilchard spawning area and spawning biomass off the Pacific coast of Japan, to estimate biomass with spawning area data. Moreover, to explain why the relationship between pilchard spawning area and spawning biomass formed, we used a model in which a patchy egg distribution was assumed.

Materials and methods

Spawning area and spawning biomass

Intensive egg surveys of coastal pelagic fish have been conducted every year since 1978 by the Fisheries Agency of Japan (Mori et al., 1988; Kikuchi and Konishi, 1990; Ishida and Kikuchi, 1992;

¹ Hewitt, R., A. Bindmann, and N. C. Lo. 1984. Procedures for calculating the egg production estimate of spawning biomass. Administrative Report LJ-84-19, Southwest Fisheries Center, La Jolla, CA 92038-0271.

Zenitani et al., 1995). Among these surveys, two governmental institutions, the National Research Institute of Fisheries Science and the Nansei National Fisheries Research Institute, have collaborated on surveys covering the inshore and offshore waters between 128–143°E and 28–36°N since 1978 (Fig. 2). We used data from these surveys covering the waters along the Pacific coast of Japan between 130–142°E and 28–36°N (Fig. 3). In the census, from 149 to 344 ichthyoplankton samples were collected each year by towing two types of conical or cylindrical-conical nets (inside mouth diameter: 45 or 60 cm; mesh aperture: 0.335 mm). Each net was retrieved vertically at 1 m/s from 150 m depth or from the bottom at stations shallower than 150 m.

We calculated two kinds of pilchard spawning area (A_1 and A_2). Pilchard spawning is concentrated into two months, February and March (Watanabe et al., 1996). Therefore, A_1 in any given year was calculated by summing the areas of 1° longitude 1° latitude squares where early developmental A-stage eggs, as categorized by Nakai (1962), were collected during February and March. A_2 was calculated by summing the areas of 1° longitude 1° latitude squares where eggs of any stage were collected during February and March. The length of time elapsing from fertilization to the end of the A stage at the different temperatures, 15.2°, 17.5°, and 20.3°C, are 25, 16, and 10 hours, respectively. The length of time elapsing from fertilization to hatching at the different temperatures, 15.2°, 17.5°, and 20.3°C, are 85, 56, and 34 hours, respectively (Nakai, 1962).

We used the pilchard biomass estimated along the Pacific coast of Japan from 1977 to 1995 by Wada and Jacobson (1998). Biomass estimation was conducted by virtual population analysis (VPA) with the catch-at-age data of the purse-seine fishery. The biomass estimate was for the middle of June, the end of the major spawning season for Japanese pilchard. During the main spawning season, most spawning is done by age-1+ pilchards and a small amount is done by age-1 pilchards (Hiramoto, 1981). The biomass of age-1+ pilchards in year $y - 1$ was assumed to be the spawning biomass (B) in year y .

Model

To test whether spawning area could be correlated with spawning biomass, statistical analyses were performed. We used five relationships between A ($=A_1$ or A_2) and B : $A=f(B)$

- I $f(B)=u_1B$,
- II $f(B)=u_1B+u_2$,
- III $f(B)=u_1B^{u_2}$,

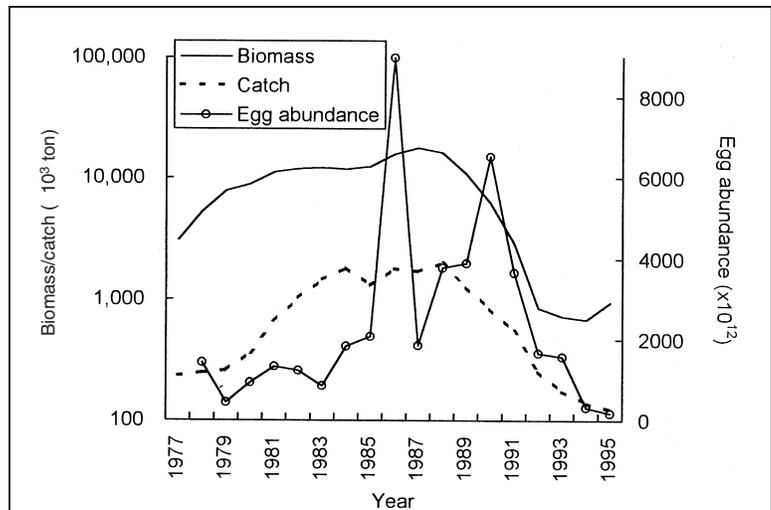


Figure 1

Catch, spawning biomass, and egg abundance of Japanese pilchard along the Pacific coast of Japan from 1978 to 1995 (after Wada and Jacobson, 1998).

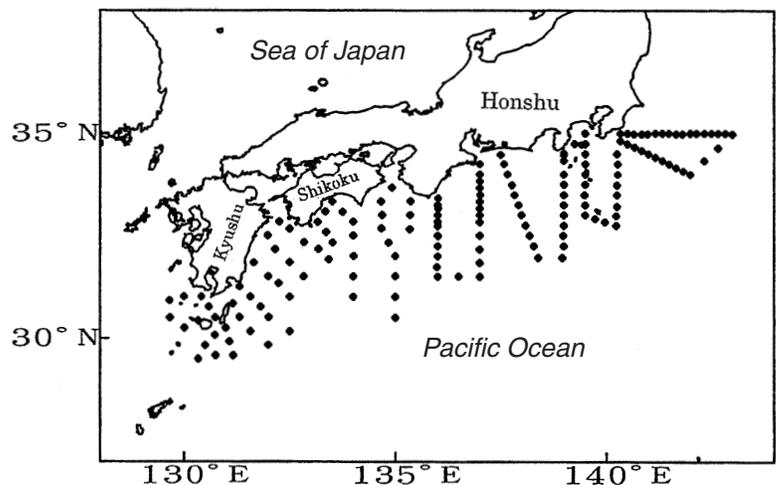


Figure 2

An example of station allocation for the spawning survey of Japanese pilchard in February and March 1994.

- IV $f(B)=u_1 \exp(u_2B)$, and
- V $f(B)=A_s[1 - \{u_1/(u_1 + u_2B)\}^{u_1}]$,

where u_1 , u_2 and A_s were parameters.

Relationship V was obtained by a modification of Mangel and Smith's (1990) model. They used the negative binomial model to describe the contagion of pilchard eggs. It is commonly used in ecological modeling (Pielou, 1977; Zweifel and Smith, 1981; Mangel and Smith, 1990; Zenitani et al., 1998). Mangel and Smith (1990) extended the negative binomial model to include the possibility of failure to detect eggs which are present at a station. According to Mangel and Smith (1990),

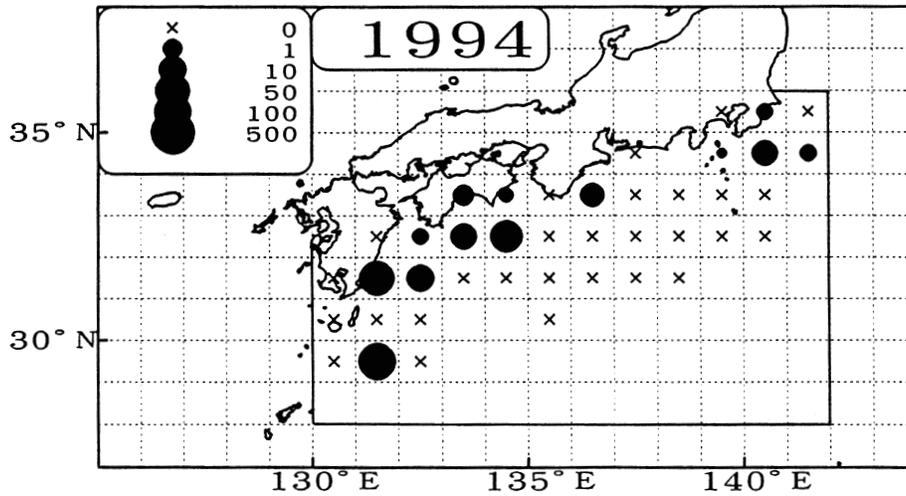


Figure 3

Distribution of pilchard eggs along the Pacific coast of Japan in February and March 1994. Solid circles and crosses show the mean egg density (number of eggs per 0.159 m²) in 1° × 1° squares. Data in the area surrounded by the bold lines was used for the analysis (after Zenitani et al., 1998)

$$E\{N_p\} = N\alpha p \left[1 - \left\{ \frac{k}{k + m\omega} \right\}^k \right], \quad (1)$$

where N_p and N = number of samples with a positive number of eggs and total number of samples in survey area (A_s), respectively;

- α and ω = sampling efficiency parameters;
- p = probability that a observation station is a habitat for spawning stock;
- k = the over-dispersion parameter of negative binomial distribution; and
- m = mean number of eggs at a habitat area for spawning stock.

To simplify, we assumed that $\alpha = 1$, $p = 1$, and $\omega = 1$. Moreover, we assumed that the spawning biomass (B) and total egg abundance (mN) is linearly related, that is $B = \delta mN$, where δ is a constant. Actually, a linear relationship exists between the spawning biomass and egg abundance of the Japanese pilchard (Fig. 4). We assumed that a survey area (A_s) is equally divided by N stations. Because N_p is a random variable, the observed spawning area $A = A(N_p) = \gamma N_p$ is also a random variable, where γ is a proportional constant ($= A_s/N$).

From Equation 1, we thus obtain

$$\begin{aligned} E\{A\} &= \gamma E\{N_p\} \\ &= A_s \left[1 - \left\{ \frac{k}{k + \varepsilon B} \right\}^k \right], \end{aligned}$$

where $\varepsilon = 1/(N\delta)$

If $u_1 = k$, $u_2 = \varepsilon$, $A_s = 640$ (10³ km²), and $A = E\{A\}$, we have relationship V between A and B .

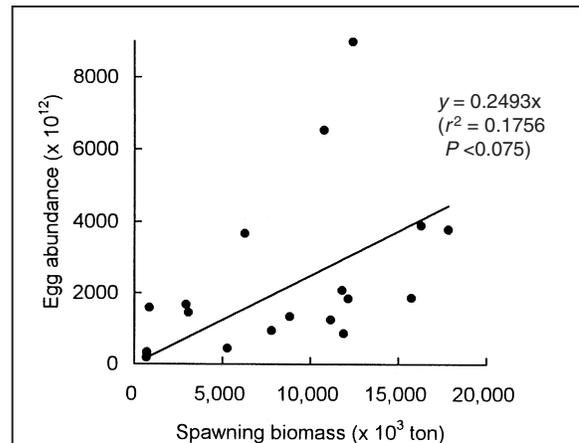


Figure 4

Relationship between the egg abundance and spawning biomass of Japanese pilchard (after Wada and Jacobson, 1998).

Parameters estimation, confidence interval analysis, and selection of the optimal relationship

We assumed that each relationship (I-V) had an error term z ; $\ln(A) = \ln(f(B)) + \ln(z)$; that z had a log-normal distribution; $\ln(z) \sim N(0, \sigma^2)$; and that $N(0, \sigma^2)$ has a normal distribution of mean zero and variance σ^2 . z will take only positive values, so we expected the mean of z , $E\{z\} = \exp(\sigma^2/2)$, to be larger than 0. In addition, the log-normal distribution has a long tail, which is common with ecological data (Hilborn and Mangel, 1997).

Table 1

Estimated parameter values and 95 % confidence intervals (in parentheses) for each relationship between the spawning area (A_1 ; 10^3 km^2) and the spawning biomass (B ; 10^3 metric ton) of Japanese Pilchard along the Pacific Coast of Japan from 1978 to 1995.

Relationship	u_1	u_2	A_s ($10^3/\text{km}^2$)	AIC
I $A_1 = u_1 B$	0.02318 (0.023109–0.023240)			41.2
II $A_1 = u_1 B + u_2$	0.01204 (0.012012–0.012059)	50.048 (49.9144–50.1824)		11.2
III $A_1 = u_1 B^{u_2}$	2.518 (2.5157–2.5208)	0.4610 (0.46087–0.46110)		4.2*
IV $A_1 = u_1 \exp(u_2 B)$	69.604 (69.5169–69.7246)	0.00007941 (0.00079270–0.000079560)		18.0
V $A_1 = A_s \left[1 - \left\{ u_1 / (u_1 + u_2 B) \right\}^{u_1} \right]$	0.1283 (0.12801–0.128509)	0.0001516 (0.00015124–0.00015194)	640	4.3

Asterisk (*) indicates that the relationship is optimal.

Parameter estimation and confidence interval analysis were performed by the following procedure. u_1 and u_2 were estimated by minimizing the sum of squares:

$$\Theta = \sum_y \left(\ln(A_y / \hat{A}_y) \right)^2,$$

where A_y and \hat{A}_y = the observed spawning area in year y and predicted values from relationships I–V, respectively.

The least-squares minimization was performed by the quasi-Newton method in Solver, which is “add in” software for MS-Excel (Microsoft Corp., 1996). The least-squares minimization procedure was stopped if either of the two following conditions were satisfied:

more than 100 iterations were attempted; or

the sum of squared residuals changed by less than 0.01% between iterations.

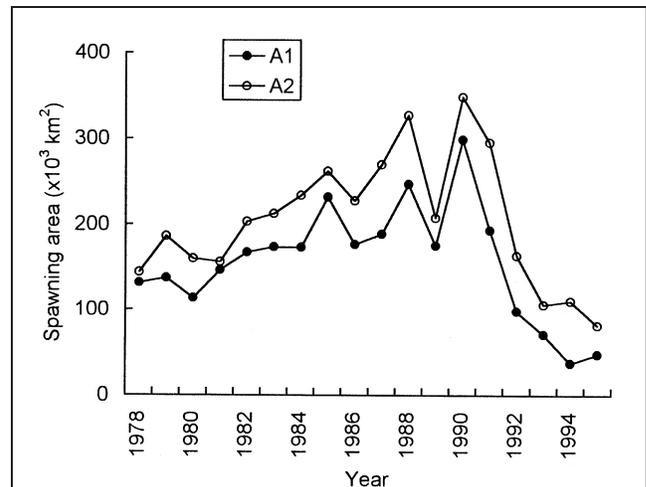
Confidence intervals of the estimators were calculated through a likelihood ratio test. If $\ln(A_y / \hat{A}_y) \sim N(0, \sigma^2)$, then

$U = (u_1, u_2)$ is a parameter vector,

$\hat{U} = (\hat{u}_1, \hat{u}_2)$ is the estimated parameter vector which minimizes the Θ , and

$\hat{U}_I = (u_i, \hat{u}_2)$ is the parameter vector which minimizes the Θ with respect to a certain value of u .

The confidence interval for a certain parameter u_i was given as the region which satisfied the inequality $2 \ln\{L(\hat{U}) / L(U)\} \leq \chi^2(0.95, 1)$, where L and $\chi^2(0.95, 1)$ were the likelihood and 95% value of the χ^2 distribution with one degree of freedom, respectively. The Akaike information criterion (AIC) was used for selecting an optimal relationship within the set of proposed relationships I–V. The AIC is calculated for candidate models, and the most parsimonious one has the lowest AIC (Akaike, 1973).

**Figure 5**

Change in the spawning area of the Japanese pilchard along the Pacific coast of Japan over time. A_1 and A_2 were calculated by summing the areas of 1° longitude \times 1° latitude squares where early developmental stage eggs and eggs of any stage occurred, respectively.

Results

The spawning biomass (B) of the Japanese pilchard experienced a remarkable increase in the 1970s, peaked in 1988, and has been declining since the end of the 1980s (Fig. 1; Wada and Jacobson, 1998). A_1 expanded from 114,000 km^2 in 1980 to 299,000 km^2 in 1990, before shrinking to 38,000 km^2 in 1994 (Fig. 5). Estimated parameters, their confidence intervals for each relationship, and AIC are summarized in Table 1. The value of AIC was at a minimum in relationship III and varied considerably compared to the

Table 2

Estimated parameter values and 95% confidence intervals (in parentheses) for each relationship between the spawning area (A_2 : 10^3 km^2) and the spawning biomass (B : 10^3 metric ton) of Japanese pilchard along the Pacific Coast of Japan from 1978 to 1995.

Relationship	u_1	u_2	A_s ($10^3/\text{km}^2$)	AIC
I $A_2 = u_1 B$	0.03196 (0.031853–0.032075)			48.7
II $A_2 = u_1 B + u_2$	0.01141 (0.011389–0.011438)	102.382 (102.2073–102.5608)		4.7
III $A_2 = u_1 B^{u_2}$	12.304 (12.2926–12.3154)	0.3156 (0.31546–0.31567)		0.9*
IV $A_2 = u_1 \exp(u_2 B)$	116.780 (116.5000–116.9103)	0.00005689 (0.00056782–0.000057001)		7.5
V $A_2 = A_s \left[1 - \left\{ u_1 / (u_1 + u_2 B) \right\}^{u_1} \right]$	0.1176 (0.11737–0.117766)	0.0004710 (0.00046983–0.00047289)	640	3.3

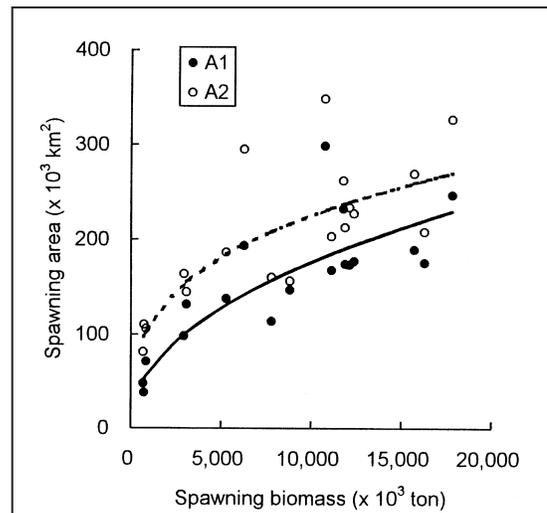
other relationships, except for V. The optimal relationship between A_1 and B was $A_1 = 2.518 B^{0.4610}$ (Table 1, Fig. 6), although the difference in AIC between relationship III and V was small. Relationship III was statistically significant ($r^2 = 0.833$, $n = 18$, $P < 0.001$). A_2 expanded steadily from 144,000 km^2 in 1978 to 327,000 km^2 in 1988 (Fig. 5). The area decreased to 208,000 km^2 in 1989, peaked at 349,000 km^2 in 1990, and then shrank to 82,000 km^2 in 1995. The optimal relationship between A_2 and B was $A_2 = 12.304 B^{0.3156}$ (Table 2, Fig. 6) and was statistically significant ($r^2 = 0.737$, $n = 18$, $P < 0.001$).

Discussion

The spatial distribution of pilchard eggs may increase over time through transportation by wind-driven currents or the Kuroshio frontal eddy current (Kasai et al., 1992). Because the data for calculating A_2 included the presence of eggs at stages long after spawning had occurred, A_2 was an overestimate of the spawning area. Therefore, A_1 may be a better indicator of the spawning area than A_2 . The relationship between A_1 and A_2 was $A_1 = 0.8501 A_2 - 18.468$, and was statistically significant ($r^2 = 0.900$, $n = 18$, $P < 0.001$). However, the calculation of A_1 was more expensive and time consuming because egg developmental stages need to be distinguished. Selection of the indicator will depend on our demand for the precision of biomass estimate.

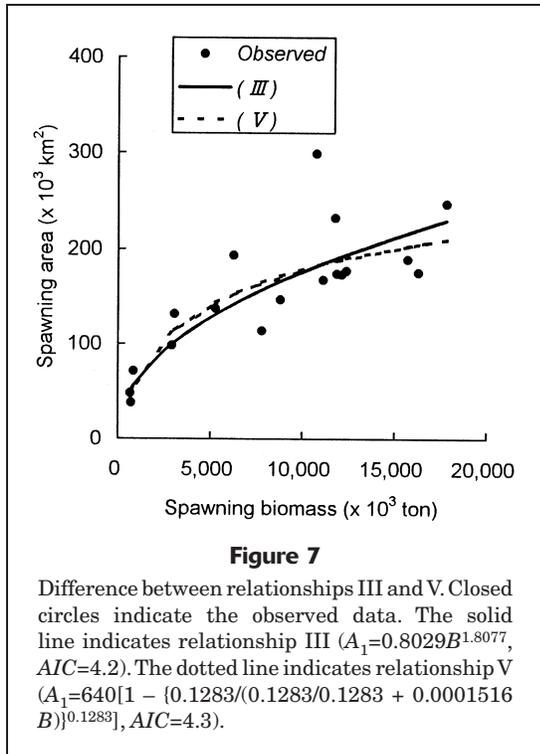
One cause of the nonlinear relationship between the spawning area and spawning biomass seemed to be that pilchard egg aggregations are distributed over space in a patchy manner, in relation of course to the schooling behavior of the adults. Judging from the small difference in AIC between relationship III and V (Table 1) and the similar shapes of III and V (Fig. 7), we believed that the model which assumes a patchy egg distribution seemed reasonable.

An estimate of pilchard spawning biomass can be obtained by using the inverted relationship of III ($B =$

**Figure 6**

Relationship between the spawning area (A_1 or A_2) and spawning biomass of Japanese pilchard. Closed circles = the spawning area (A_1), open circles = the spawning area (A_2). The solid line indicates the optimal relationship between A_1 and the spawning biomass (B) ($A_1 = 0.2518 B^{0.4610}$). The dotted line indicates the optimal relationship between A_2 and the spawning biomass ($A_2 = 12.304 B^{0.3156}$).

$0.135 A_1^{2.1691}$). This estimate of spawning biomass might be useful as an abundance index for tuning VPA, such as the adaptive framework described by Gavaris (1988). Frequently, fisheries managers must estimate the biomass of pelagic stocks. Several techniques of abundance estimation may be successfully applied to the pilchard, including the egg production method, acoustic surveys, systematic aerial surveys, or combinations of these (Watanabe, 1983; Hara, 1983; Hara, 1986). Selection or devel-



opment of methods will depend on management goals, performance of the resource in recovery, and fishery development. We believe that the method in our study provides a new tool for the estimation of Japanese pilchard biomass when information concerning the fishery is limited.

Acknowledgments

The authors would like to thank T. Wada and M. Ishida, National Research Institute of Fisheries Science, for their assistance with data processing. This work was supported in part by the Bio Cosmos Program of the Ministry of Agriculture, Forestry, and Fisheries.

Literature cited

- Akaike, H.
1973. Information theory and an extension of the maximum likelihood principle. *In* International symposium on Information theory (B. N. Petran and F. Csaaki, eds.), p. 267–281. Akademiai Kiado, Budapest.
- Gavaris, S.
1988. An adaptive framework for the estimation of population size. *Canadian Atl. Fish. Sci. Adv. Comm. (CAFSAC) Res. Doc.*, 88/29, 12 p.
- Hara, I.
1983. Estimation of fish density method. *Nippon Suisan Gakkaishi*. 49:1619–1625.
1986. Stock assessment of Japanese pilchard in the waters off southeast coast of Hokkaido using line transect method. *Nippon Suisan Gakkaishi*. 52:69–73.
- Hilborn, R., and M. Mangel.
1997. *The ecological detective. Confronting models with data.* Princeton Univ. Press, Princeton, NJ, 315 p.
- Hiramoto, K.
1981. Studies on the growth and life-cycle of the Japanese sardine *Sardinops melanosticta* (Temminck et Schlegel) in its Pacific sub-population found in Joban and Boso regions. *Bull. Chiba Pref. Fish. Expl. Stn.* 39:1–127.
- Ishida, M., and H. Kikuchi.
1992. Monthly egg productions of the Japanese sardine, anchovy, and mackerels off the southern coast of Japan by egg censuses: January, 1989 through December, 1990. *Nansei National Research Institute and National Research Institute of Fisheries Science, Kochi, Tokyo*, p. 1–72. [In Japanese.]
- Kasai, A., J. K. Kishi, and T. Sugimoto.
1992. Modeling the transport and survival of Japanese sardine larvae in and around the Kuroshio Current. *Fish. Oceanogr.* 1:1–10.
- Kikuchi, H., and Y. Konishi.
1990. Monthly egg productions of the Japanese sardine, anchovy, and mackerels off the southern coast of Japan by egg censuses: January, 1987 through December, 1988. *National Research Institute of Fisheries Science, and Nansei National Research Institute, Tokyo, Kochi*, p. 1–72. [In Japanese.]
- Kondo, K., Y. Hori, and K. Hiramoto.
1976. Life pattern of the Japanese sardine, *Sardinops melanosticta*, and its practical procedure of marine resources researches of the stock (2nd ed.). *In* *Fish. Res. Ser.* 30, *Jap. Resour. Conserv. Assoc.*, Tokyo, 68 p. [In Japanese.]
- Lasker, R.
1981. *Marine fish larvae.* Univ. Washington Press, Seattle, WA, 131 p.
- MacCall, D.
1988. *Dynamic geography of marine fish populations.* Univ. Washington Press, Seattle, WA, 153 p.
- Mangel, M., and P. E. Smith.
1990. Presence-absence sampling for fisheries management. *Can. J. Fish. Aquat. Sci.* 47:1875–1887.
- Microsoft Corporation.
1996. *Microsoft Excel for Windows 95.* Microsoft Corp., Singapore, 228 p.
- Mori, K., K. Kuroda, and Y. Konishi.
1988. Monthly egg productions of the Japanese sardine, anchovy, and mackerels off the southern coast of Japan by egg censuses: January, 1978 through December, 1986. *Tokai Regional Fisheries Research Laboratory, D-12:1–321.* [In Japanese.]
- Nakai, Z.
1962. Studies relevant to mechanisms underlying the fluctuation in the catch of the Japanese sardine, *Sardinops melanosticta* (T. & S.). *Japan. J. Ichthyol.* 9:1–115.
- Pielou, E. C.
1977. *Mathematical ecology.* John Wiley and Sons, New York, NY, 385 p.
- Rosenzweig, M.
1981. A theory of habitat selection. *Ecology*. 62:327–335.
- Smith, P. E.
1973. The mortality and dispersal of sardine eggs and larvae. *Rapp. P.-V. Reun. Cons. Int. Explor. Mer* 164:282–292.
1985. Sea survey design and analysis for an egg production method of anchovy biomass assessment. *U.S. Dep. Commer., NOAA Tech. Rep. NMFS*. 36:17–26.

- Wada, T., and L. D. Jacobson.
1998. Regimes and stock-recruitment relationships in Japanese sardine (*Sardinops melanostictus*), 1951–1995. *Can. J. Fish. Aquat. Sci.* 55:2455–2463.
- Wada, T., and K. Kashiwai.
1991. Changes in growth and feeding ground with fluctuation in stock abundance. *In* Long-term variability of pelagic fish populations and their environments (T. Kawasaki, S. Tanaka, and Y. Toba (eds.), p. 181–190. Pergamon Press, London.
- Watanabe, T.
1983. Spawning survey method. *In* Population dynamics of fishery resources (T. Ishii, ed.), p. 2–29. Koseisha-Koseikaku, Tokyo. [In Japanese.]
- Watanabe, Y., H. Zenitani, and R. Kimura.
1996. Offshore expansion of spawning of the Japanese sardine, *Sardinops melanostictus*, and its implication for egg and larval survival. *Can. J. Fish. Aquat. Sci.* 53:55–61.
- Zenitani, H., M. Ishida, Y. Konishi, T. Goto, Y. Watanabe, and R. Kimura.
1995. Distribution of eggs and larvae of pelagic fish species around Japan. National Research Institute Fishery Agency Resource Management Research Report A-1:1–368. [In Japanese.]
- Zenitani, H., M. Ishida, and S. Yamada.
1998. A relationship between egg abundance and spawning area for fishes under patchy egg distribution. *Bull. Jpn. Soc. Fish. Oceanogr.* 62:97–103. [In Japanese with English abstract.]
- Zweifel, J. R., and P. E. Smith.
1981. Estimates of abundance and mortality of larval anchovies (1951–75): application of a new method. *Rapp. P.-V. Reun. Cons. Int. Explor. Mer* 178:248–259.