

Relationships between environmental conditions and fluctuations in the recruitment of Japanese sardine, *Sardinops melanostictus*, in the northwestern Pacific

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We investigated the relationships between environmental conditions and fluctuations in the recruitment of Japanese sardine, *Sardinops melanostictus*, in the northwestern Pacific. Stock-recruitment relationships were estimated based on Ricker, Beverton–Holt, power, linear, and proportional models. The error terms of the stock-recruitment relationship were assumed to follow normal or log-normal distributions. Furthermore, we calculated the correlation coefficients between environmental factors and residuals by subtracting estimated values from observed values. The correlation coefficients were calculated using two different datasets: the entire dataset (1976–2004), and the entire dataset minus data from 1988 to 1991, as crucial failures in recruitment occurred during this period. Analysis of the full dataset yielded a greater number of environmental factors with significant correlation coefficients than did analysis of the partial dataset. This finding suggests that the crucial failures in recruitment can be explained by environmental factors (e.g., Arctic Oscillation, Pacific Decadal Oscillation, sea surface temperature of southern area of the Kuroshio Extension), especially those factors that occurred during the spawning season, which are critical in terms of population fluctuations. These environmental factors should be taken into account in recruitment forecasting models.

Key words: Kuroshio Extension, Arctic Oscillation, sardine, stock-recruitment relationship, Ricker, Beverton–Holt

Introduction

In the Japanese fishery, the Japanese sardine, *Sardinops melanostictus*, is one of the most important species in the northwestern Pacific. In 1997, the Japanese Government introduced a total allowable catch (TAC) system for seven species including sardine.

Previous studies have documented considerable temporal fluctuations in sardine abundance (Kuroda, 1991; Sugisaki et al., 1994; Zenitani et al., 1995; Kubota et al., 1999). Sardine numbers were very high in the 1980s, but decreased markedly in the early 1990s, and have remained low since then. Figure 1 shows temporal trends in recruitment, as determined by the number of 0-year-old fish and spawning stock biomass (SSB). Figure 2 shows the trajectory in recruitment per SSB (RPS), defined as recruitment divided by SSB (number of recruitments per 1 kg SSB). From 1988 to 1991, RPS was remarkably low—SSB was very high and recruitment was extremely low. Therefore, both SSB and environmental factors should be taken into account in seeking to understand the sardine stock-recruitment relationship.

Tomosada (1988) analyzed long-term fluctuations in catch and water temperature, and showed that the catch is larger when water temperatures are favorable—the catch is large when water temperatures are high in the spawning areas and nursery grounds, and when water temperatures are low in the fishing ground located south of Hokkaido. Noto and Yasuda (1999) showed that variations in sea surface temperature in the southern area of the Kuroshio Extension during February coincide with variations in the sardine catch. Noto (2003) raised the possibility that environmental conditions, as represented by the sea surface tem-

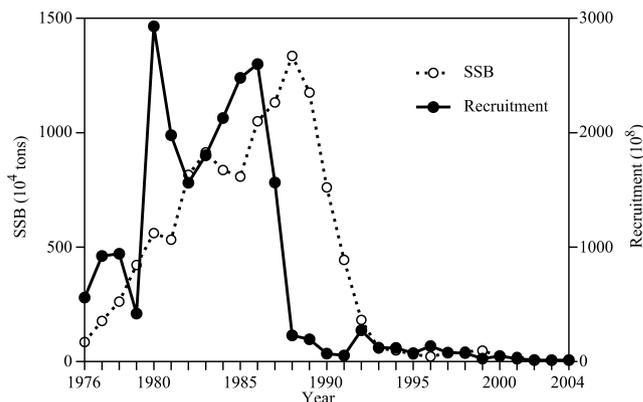


Figure 1. Temporal trends in the recruitment and spawning stock biomass (SSB) of Japanese sardine. Data from Nishida et al. (2005).

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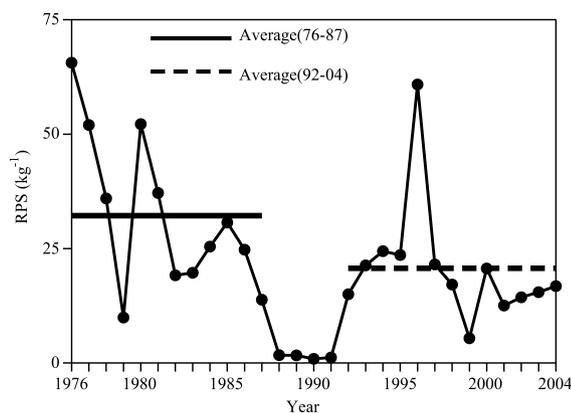


Figure 2. Trends in recruitment per spawning stock biomass (RPS) of Japanese sardine. Horizontal lines show the average for two periods. Data from Nishida et al. (2005).

perature in the southern area of the Kuroshio Extension during winter, determine annual changes in the survival of sardine, and also influence long-term fluctuations in the population, as well as their distribution and migration pattern. Sunami (1993) noted that water temperatures and variations in the abundance of zooplankton (a sardine food source) influence the early growth stage in sardine (from 0- to 1-year-old). Such growth, particularly at early stages, determines the sardines' survival rate.

To date, stock-recruitment relationships (SRRs) have been discussed mainly in the context of density effects (Ricker, 1954; Beverton and Holt, 1957). It is recognized that environmental conditions are important in terms of recruitment but it is difficult to identify exactly which environmental conditions are significant in this regard. Thus, in previous studies, environmental conditions have been treated as a random variable and have not been included in SRR models. SRRs are generally described by the Ricker model (Ricker, 1954) or the Beverton–Holt model (Beverton and Holt, 1957); however, there exists a poor fit between the values calculated using these models and measured SRR data, probably because environmental conditions are not taken into account (Sakuramoto, 2005).

Chen and Irvine (2001) developed a new SRR model that incorporates environmental effects—this model shows better performance than the traditional Ricker model. Yatsu et al. (2003) investigated the reproduction success of sardine with respect to water temperature, zooplankton density, intra-species competition, and density-dependent processes. Furthermore, Yatsu et al. (2005) analyzed the fluctuations in recruitment and stock production for the Japanese sardine and chub mackerel *Scomber japonicus* using a wide range of environmental data. The authors then developed models of the stock-recruitment relationship taking into account environmental variables. They concluded

that environmental effects are important in terms of recruitment and surplus production, but that fishing also plays a role.

The studies above did not explain the circular or spiral shapes observed in plots of SRR data that resulted from connecting the plots from year to year (Walters, 1987; Zheng and Kruse, 2003; Sakuramoto, 2005). Sakuramoto (2005) analyzed the SRR data available for several species and sought to explain the mechanisms underlying the obtained patterns, concluding that spiral shapes can occur when recruitment is proportional to SSB, and that cyclic fluctuations in SSB (e.g., fluctuations associated with environmental conditions) are independent of stock density. Shimoyama et al. (2007) reported a proportional relationship between the recruitment of Japanese sardine and SSB (i.e., SRR is expressed by a straight line through the origin). The authors found no evidence of a density-dependent effect, suggesting that the commonly held assumption of a density-dependent relationship in SRR might in fact be incorrect. Their results indicate that environmental conditions (e.g., sea surface temperatures in the southern area of the Kuroshio Extension during February) are a key factor in determining recruitment success. However, the authors did not perform a detailed analysis of the relationship between environmental factors and recruitment. In the present study, we discuss SRR and its relationships with environmental factors.

Materials and Methods

We used biological data on sardine stock abundance for the northwestern Pacific stock from 1976 to 2004, as obtained from Stock Assessment and Evaluation for the Pacific Stock of Japanese Sardine (fiscal year 2005) (Nishida et al., 2005). Oceanographic data were obtained from the following sources:

- (1) ALPI (Aleutian Low Pressure Index, Fisheries and Oceans Canada, Pacific Region. Web: <http://www.pac.dfo-mpo.gc.ca/sci/sa-mfpd/downloads/alpi.txt>);
- (2) AO (Arctic Oscillation, NOAA Climate Prediction Center. Web: http://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/monthly.ao.index.b50.current.ascii.table);
- (3) NPI (North Pacific Index, NCAR. Web: <http://www.cgd.ucar.edu/cas/jhurrell/indices.data.html#NPImon2006/02/21>);
- (4) PNA (Pacific North/American pattern, NOAA Climate Prediction Center. Web: <http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/norm.pna.monthly.b5001.current.ascii.table>);
- (5) POL (Polar/Eurasia Pattern, NOAA Climate Prediction Center. Web: ftp://ftp.cpc.ncep.noaa.gov/pub/cpc/wd52dg/data/indices/tele_index.nh2006/02/21);

- (6) Sea surface temperature at Enoshima in Miyagi Prefecture (ESST). (Miyagi Prefecture Fisheries Technology Institute, pers. com., 2005);
- (7) Sea surface temperature over the southern area of the Kuroshio Extension from 30°N to 35°N and 145°E to 180° (KEST) (Japan Meteorological Agency, Japan. Web: <http://www.jmbsc.or.jp/hp/other/link.html>);
- (8) PDO (Pacific Decadal Oscillation Index, JISAO. Web: <http://jisao.washington.edu/pdo/PDO.latest>);
- (9) Abundance of zooplankton (ZPKD) in the Kuroshio-current areas of the North-Pacific region (Odate, 1994);
- (10) OEST (SST off Enoshima); we calculated the mean water temperature of the SST off Enoshima from 38°N to 40°N and 145°E to 160°E (Japan Meteorological Agency, Japan. Web: <http://www.jmbsc.or.jp/hp/other/link.html>); and
- (11) SGST (average SST over the spawning ground); we calculated the mean water temperature in the waters from 30°N to 35°N and 130°E to 140°E (Meteorological Agency, Web: <http://www.jmbsc.or.jp/hp/other/link.html>), which we assumed to be the main sardine spawning ground, as inferred from Figs 2 to 6a–c in Zenitani (2001).

Zooplankton data cover the period from 1976 to 1999; other biological data cover the period from 1976 to 2004. ALPI data cover the period from January to March, and other environmental data cover the period from January to December.

Reproduction of sardine and environmental factors

Following Shimoyama et al. (2007), we adopted five reproduction models: the Ricker, Beverton–Holt (B–H), power, linear, and proportional models. To demonstrate the compatibility of the five reproductive models with the data, we referred to the results presented by Shimoyama et al. (2007) when the five reproduction models were adopted for the data set excluding the data from 1988 to 1991 (Fig. 3). This data set is termed Group A (see below).

We calculated the correlation coefficients between the environmental factors and the residuals ε_i determined as follows:

$$\varepsilon_i = R_i - \hat{R}_i \quad (1)$$

$$\varepsilon_i = \ln R_i - \ln \hat{R}_i \quad (2)$$

where R_i and \hat{R}_i denote the recruitments observed and estimated using the models, respectively. We calculated the correlation coefficient between ε_i and monthly environmental factors. Following Shimoyama et al. (2007), the correlation was calculated using two datasets: the entire dataset (1976–2004) and Group A (the entire dataset minus data

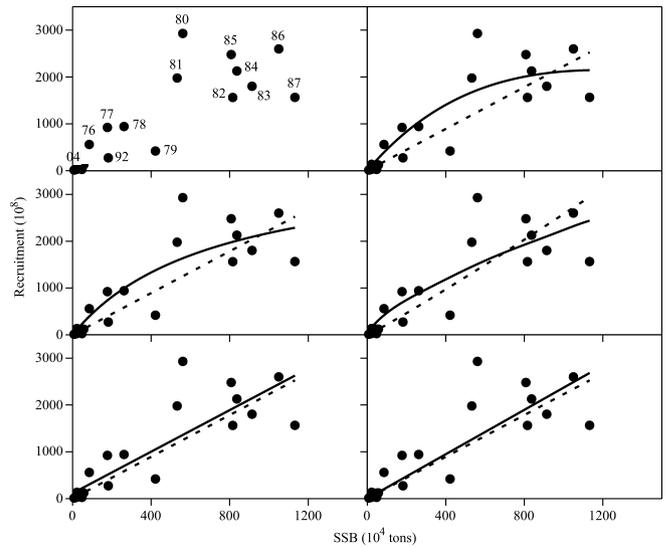


Figure 3. Stock-recruitment relationship for Japanese sardine in the northwestern Pacific from 1976 to 2004, excluding 1988–1991. Solid and dashed lines indicate the models in which error terms follow normal and log-normal distributions, respectively. Number at top-left indicate the year (Shimoyama et al., 2007).

Table 1. Four different data treatments (entire or partial dataset, and normally or logarithmically distributed errors).

Case No.	Data	Error term
I	All data	Normal distribution
II	All data	Log-normal distribution
III	Group A	Normal distribution
IV	Group A	Log-normal distribution

for the period 1988–1991, when crucial failures in recruitment occurred). We then tested 20 scenarios: the five models with each of the four different data treatments (entire or partial data set, and normally or logarithmically distributed errors) (Table 1). Based on the results of the correlation analysis, we selected three significant environmental factors, and investigated the relationship between these factors and recruitment number or the residuals. The residuals were calculated by equation (2), as model performance is better when logarithmic error terms are employed than when errors with a normal distribution are considered (Shimoyama et al., 2007). Furthermore, we analyzed the relationships among these environmental factors. Finally, to investigate the relationships among plankton biomass and environmental factors, we calculated the correlation coefficients between zooplankton biomass within the Kuroshio district (Odate, 1994) and environmental indices for each

month.

Results

The results of correlation analyses are listed in Tables 2 and 3. Table 2 shows the months in which correlation coefficients were significant when all the data were analyzed, and Table 3 shows those months with significant correlation coefficients when Group A data were analyzed. We observed no significant difference between Cases I (normally distributed error) and II (logarithmically distributed error) (Table 2). There exists a significant relationship between the residuals in recruitment ε_i and the following environmental indices: AO, POL, ESST, KEST, and PDO. However, we obtained significantly different results when analyzing Group A data (Table 3) compared with analyzing all the data

(Table 2). Many months that showed a significant correlation coefficient when the entire dataset was analyzed (Table 2) were not significant when the partial dataset was analyzed (Table 3). This finding indicates that the failures in recruitment that occurred from 1988 to 1991 were critically related to environmental factors.

In Cases I and II, the results that the number of the month showed a significant correlation coefficient are similar regardless of the employed SRR model—there exists a significant correlation coefficient between the residuals and PDO during the spawning season. The main spawning season of Japanese sardine is February–March (Watanabe et al., 1996; Zenitani, 2001). Significant correlation coefficients were also obtained between the residuals and AO in winter, POL in October and December, and KEST in Feb-

Table 2. Months in which error terms were significantly correlated with environmental factors when all data were analyzed. Bold and plain fonts indicate 1 and 5% levels of significance, respectively. X in ALPI denotes the 5% significant level.

Model	Distribution of error terms	Environmental factors							
		ALPI	AO	NPI	PNA	POL	ESST	KEST	PDO
Ricker	Normal	X	1, 2, 12	—	8	10, 12	2, 3, 4, 5, 6, 11, 12	2, 3	1, 2, 3, 4, 12
B–H	Normal	—	1, 2, 12	—	8	10, 12	3, 4, 6, 12	2, 3	1, 2, 3, 4, 12
Power	Normal	—	1, 2	1	8	10, 12	3, 4, 5, 6, 12	2, 3	2, 3, 4, 12
Linear	Normal	—	1, 2	1	8	10	3, 4, 6, 12	1, 2, 3	2, 3
Proportion	Normal	—	1, 2	1	—	10	—	2, 3	2
Ricker	Log-normal	—	1, 2, 12	—	—	4, 10, 12	1, 2, 4, 5, 6, 11, 12	1, 2, 3	1, 2, 3, 4, 11, 12
B–H	Log-normal	—	1, 2, 12	1	—	4, 10, 12	1, 2, 4, 5, 6, 11, 12	1, 2, 3	1, 2, 3, 4, 12
Power	Log-normal	—	1, 2, 12	1	—	4, 10	4, 11, 12	1, 2, 3	1, 2, 3, 4, 12
Linear	Log-normal	—	1, 2, 12	—	—	4, 10	—	1, 2, 3	2, 3, 4
Proportion	Log-normal	—	1, 2, 12	—	—	4, 10	—	2, 3	2, 3, 4, 12

Table 3. Months in which error terms were significantly correlated with environmental factors when Group A data were analyzed. Bold and plain fonts indicate 1 and 5% levels of significance, respectively.

Model	Distribution of error terms	Environmental factors							
		ALPI	AO	NPI	PNA	POL	ESST	KEST	PDO
Ricker	Normal	—	—	—	8	—	6	—	—
B–H	Normal	—	—	—	8	—	6	—	—
Power	Normal	—	—	—	8	—	6	2	—
Linear	Normal	—	—	—	8	—	—	2	—
Proportion	Normal	—	—	—	8	—	—	—	—
Ricker	Log-normal	—	12	—	—	—	1, 5, 11, 12	1, 2, 3	—
B–H	Log-normal	—	12	—	—	—	1, 11, 12	1, 2, 3	—
Power	Log-normal	—	12	—	—	—	1, 11	1, 2, 3	—
Linear	Log-normal	—	12	—	—	—	1, 11, 12	1, 2, 3	—
Proportion	Log-normal	—	12	—	—	—	1, 11, 12	1, 2, 3	—

ruary and March.

In Case IV (Group A, logarithmically distributed error), the results are similar regardless of the employed SRR model—significant correlation coefficients were found between the residuals and AO in December, ESST in November–January, and KEST in January–March. When Group A data were analyzed, Cases III (normally distributed error) and IV (logarithmically distributed error) yielded different environmental factors with significant correlation coefficients. In Case III, only PNA in August, ESST in June, and KEST in February showed significant correlation coefficients. This result differs markedly from the results obtained in Cases I and II.

In Cases I and II, KEST in February, AO in February, and PDO in February showed significant correlations with residuals, regardless of the model and error term. Figure 4 shows the temporal trends of these key environmental indices, and Figure 5 shows the relationship between recruitment or ε_i and three key environmental factors, where ε_i was calculated by equation (2) and, as an example, the Ricker model was applied. Table 4 shows the results of the regression analysis. When recruitment number is used as the dependent variables, regardless of dataset (all data or Group A), the slopes are significant and extremely small P-values were obtained. This indicates the possibility that those three environmental factors had much influence on the sardine reproductions. When the error terms, ε_i is used as the dependent variables, the results were different. The slopes were significant against AO, PDO and KEST when all data are used; however, the slopes were not significant

against AO and PDO when Group A data is used.

When residual, ε_i is used as the dependent variables and KEST is used as the independent variable, regardless of dataset (all data or Group A), the slopes are significant and extremely small P-values were obtained. Further, in the case when all data are used, the slope is steeper than the case when the Group A data is used. That is, the residuals,

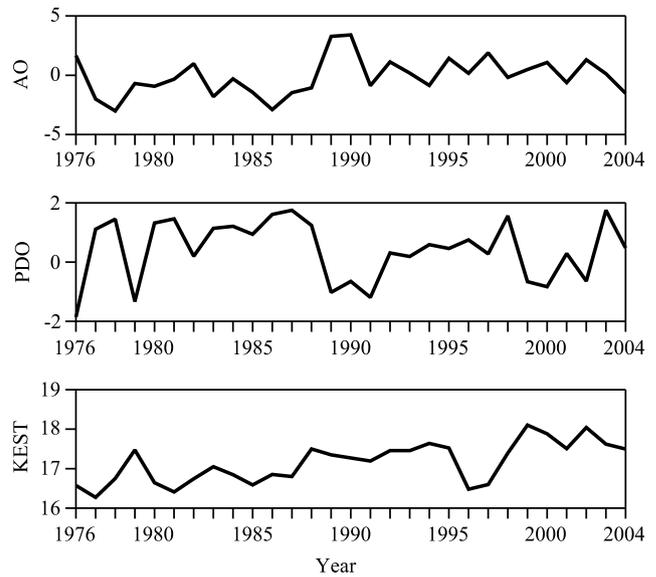


Figure 4. Yearly changes in Arctic Oscillation (AO) in February, Pacific Decadal Oscillation (PDO) in February, and sea surface temperature of the southern area of the Kuroshio Extension (KEST) in February.

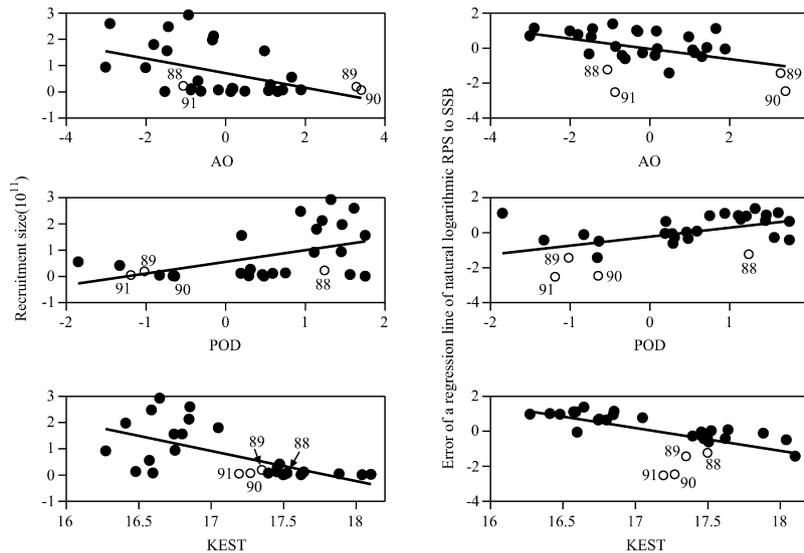


Figure 5. Regression analysis between three environmental indices and recruitment number (left) or residuals (right). AO: yearly change in Arctic Oscillation in February; PDO: Pacific Decadal Oscillation in February; KEST: sea surface temperature of the southern area of the Kuroshio Extension in February; ε_i : residuals calculated by equation (2), adopting the Ricker model. Open circles with number indicate the years 1988, 1989, 1990 and 1991, respectively.

Table 4. Regression analysis between three environmental factors and recruitment or error terms. R, er, a, b and Cor. Coef. denote the recruitment number, residuals, intercept and slope of the regression line, and the correlation coefficient, respectively.

x	y	a	b	P-value	Cor. Coef.
All data (1976-2004)					
AO	R	711 (10 ²)***	-278 (10 ²)***	9.40 (10 ⁻³)	-0.474
PDO	R	556 (10 ²)**	445 (10 ²)**	6.90 (10 ⁻³)	0.491
KEST	R	204 (10 ⁴)***	-115 (10 ³)***	3.18 (10 ⁻⁴)	-0.622
AO	er	-0.0296	-0.290*	1.60 (10 ⁻³)	-0.443
PDO	er	-0.209	0.508**	5.41 (10 ⁻³)	0.503
KEST	er	21.2***	-1.29***	2.64 (10 ⁻⁴)	-0.628
Excluding the years, 1988, 1989, 1990, and 1991, from all data					
AO	R	726 (10 ²)***	-358 (10 ²)*	1.02 (10 ⁻²)	-0.504
PDO	R	581 (10 ²)**	470 (10 ²)**	1.74 (10 ⁻²)	0.471
KEST	R	199 (10 ⁴)***	-112 (10 ³)**	1.00 (10 ⁻³)	-0.678
AO	er	-0.0143	-0.0464	0.602	-0.110
PDO	er	-0.0573	0.106	0.394	0.178
KEST	er	13.3***	-0.779***	4.13 (10 ⁻⁵)	-0.725

*, ** and *** indicate 5, 1 and 0.1% levels of significance, respectively.

Table 5. Months in which sea surface temperatures showed significant correlation coefficients. Bold and plain fonts indicate 1 and 5% levels of significance, respectively.

Environmental factors	Month	Environmental factors			
		ESST	KEST	OEST	SGST
ESST	Jan.	2, 3, 4, 5, 6, 7, 8, 10, 11, 12	2	1, 2, 3	2
	Feb.	3, 4, 5, 6, 7, 10	2	1, 2, 3, 4	—
	Mar.	4, 5, 6	—	1, 2, 3	3
	Apr.	5, 6	2, 3	1, 2, 3, 4	—
	May	6, 7, 9, 10	2, 3	1, 2, 3, 4	2
	June	7, 11, 12	2, 3	1, 2, 3, 4	—
	July	8, 9, 10, 11, 12	—	1, 2, 3	—
	Aug.	9, 10, 11, 12	—	—	—
	Sep.	10, 11, 12	—	—	—
	Oct.	11, 12	2	3	2
	Nov.	12	2	—	—
	Dec.	—	2, 3	3	2
KEST	Jan.	—	2, 3	—	1, 2
	Feb.	—	3	1, 2	1, 2
	Mar.	—	—	—	1, 2
OEST	Jan.	—	—	2, 3, 4	2
	Feb.	—	—	3, 4	—
	Mar.	—	—	4	—
	Apr.	—	—	—	—
SGST	Jan.	—	—	—	2
	Feb.	—	—	—	—
	Mar.	—	—	—	—

Table 6. Months in which environmental factors showed significant correlation coefficients. Bold and plain fonts indicate 1 and 5% levels of significance, respectively.

Environmental factors	Month	Environmental factors						
		AO	NPI	PNA	POL	ESST	KEST	PDO
ALPI	—	2	1, 2, 3	1, 2, 3	—	—	—	1, 2, 3, 4
AO	Jan.	2	1	—	—	—	1, 2, 3	1
	Feb.	—	1, 2	1, 2	—	3, 4	—	1, 2, 3, 4
	Mar.	—	—	3, 4	—	—	—	—
	Apr.	—	3, 4	4	1, 2, 4	—	—	3, 4
NPI	Jan.	—	—	1	—	2	2, 3	1, 2, 3
	Feb.	—	—	1, 2, 3	—	—	—	2, 3, 4
	Mar.	—	—	3, 4	—	—	—	3, 4
	Apr.	—	—	4	4	—	—	4
PNA	Jan.	—	—	2	—	1, 2, 3, 4	3	1, 2, 3
	Feb.	—	—	4	—	—	—	2, 3, 4
	Mar.	—	—	4	—	—	—	2, 3, 4
	Apr.	—	—	—	—	—	—	3, 4
POL	Jan.	—	—	—	—	—	—	—
	Feb.	—	—	—	—	—	—	—
	Mar.	—	—	—	—	1, 2, 4	—	1, 2
	Apr.	—	—	—	—	—	—	4
PDO	Jan.	—	—	—	—	—	—	2, 3, 4
	Feb.	—	—	—	—	—	—	3, 4
	Mar.	—	—	—	—	—	—	4
	Apr.	—	—	—	—	—	—	—

Table 7. Correlation coefficients between environmental factors in each month and zooplankton biomass within the Kuroshio district (ZPKD).

Environmental factors	Month											
	Jan.	Feb.	Mar.	Apr.	May.	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
ALPI	0.43											
AO	-0.57*	-0.65**	-0.58*	-0.21	-0.60*	-0.16	-0.36	-0.32	0.20	-0.06	-0.48	-0.30
NPI	-0.48	-0.55*	0.03	-0.43	-0.04	0.03	0.00	0.44	0.59*	-0.18	-0.42	-0.25
PNA	0.48	0.63*	0.21	0.33	-0.31	0.33	0.01	-0.28	-0.50	0.35	0.31	0.30
POL	0.03	-0.17	-0.02	-0.62*	-0.35	0.31	0.00	-0.01	-0.04	-0.14	-0.34	-0.50
ESST	-0.15	-0.21	-0.43	-0.24	-0.18	-0.09	-0.18	-0.38	-0.26	-0.47	-0.32	-0.44
KEST	-0.32	-0.42	-0.38	—	—	—	—	—	—	—	—	—
PDO	0.55*	0.65**	0.57*	0.52*	0.42	0.23	0.27	0.45	0.14	0.41	0.30	0.35

** and * denote 1 and 5% significance levels, respectively.

which are the variation in recruitment that could not be explained by Ricker model, can be explained with the variation in KEST regardless of the dataset (all data or Group A). In other words, AO and PDO would be related typically with the crucial failure in recruitment; however, the KEST would be strongly related to the recruitment in whole pe-

riod including the years when the crucial failure in recruitment occurred.

Table 5 shows the result of correlation analyses among ESST, KEST, OEST, and SGST. ESST showed a correlation with the month of the year (i.e., with the season) and ESST showed a correlation with KEST. Therefore, KEST could

be used as an index of environmental factors that affect fluctuations in sardine populations.

Table 6 lists correlation coefficients for each environmental factor over the period January–April. PDO was significantly correlated with several environmental indices, including ALPI, AO, NPI, PNA, and PDO (Table 6). PNA was significantly correlated with ALPI, AO, NPI, and PNA.

Table 7 lists the correlation coefficients between environmental indices and zooplankton biomass (ZPKD) in areas influenced by the Kuroshio Current. AO from January to March and PDO from January to April showed a strong correlation with ZPKD. Thus, environmental factors may influence zooplankton abundance, and this food supply may in turn influence recruitment.

Discussion

In the present study, we considered 20 scenarios in analyzing environmental indices that might affect SRR. We also tested the case in which reproductive success was used as a dependent variable instead of recruitment number. The results indicate that the two cases (i.e., using recruitment number or RPS) yield qualitatively similar results, regardless of whether the entire or partial (Group A) dataset is used. In Cases I and II (entire dataset), we obtained similar results for different models.

Many of the environmental indices have the potential to affect sardine reproduction in winter and spring. The prime spawning season for sardine is February–March (Watanabe et al., 1996; Zenitani, 2001). Shimoyama et al. (2007) reported that KEST in February influences the recruitment number and RPS, consistent with the results presented by Noto and Yasuda (1999) and Yatsu et al. (2005). Noto and Yasuda (1999) found that warmer SST in the southern area of the Kuroshio Extension in winter–spring corresponds to a higher natural mortality coefficient (the mortality coefficient indicates survival from juvenile to 1-year-old fish). Yatsu et al. (2005) noted that SST in the Kuroshio during winter (with no lag) plays an important role in terms of reproductive success. The results of the present study, when analyzing the full and partial datasets, further emphasize the importance of environmental conditions during winter and spring in terms of sardine reproduction. When all the data were analyzed, many environmental indices showed a significant correlation with sardine reproduction. However, many of these indices did not show a significant correlation with reproduction when the partial dataset was analyzed. This finding indicates that the reproductive failure that occurred from 1988 to 1991 would be caused by environmental factors.

In the present study, AO in February shows a correlation with PDO in January–April and with PNA in January–February (Table 6). Yatsu et al. (2005) obtained similar

results, reporting that broad-scale environmental indices (PDO and AO) are potentially useful in understanding and predicting environmental effects on the productivity and recruitment of sardine and chub mackerel.

SST in Enoshima (ESST) was also related to recruitment. Although the sardine spawning areas show temporal change in terms of their distribution and extent (Zenitani, 2001; Takasuka et al., 2008), Enoshima is not a sardine spawning area. However, juveniles grow and move to northern areas with the Kuroshio Current, then migrate to the Oyashio cold water current areas in summer for feeding (Kuroda, 1991; Kikuchi et al., 1992; Ebisawa and Kinoshita, 1998; Kinoshita et al., 1999).

Several studies have examined the relationships between environmental conditions and the size and body length of sardine larvae (Watanabe et al., 1996; Zenitani, 1995). Furthermore, water temperature is closely related to the depth of the mixed layer, which in turn is related to nutrient supply (Watanabe, 2003). The survival rate of sardine is affected by the abundance of other organisms such as the plankton and fish that make up their food source. Changes in survival rate result in a change in population size. The distribution of sardine changes according to population size (Watanabe, 1987; Kikuchi et al., 1992; Sugisaki et al., 1994; Zenitani et al., 1995; Yasunaka and Hanawa, 2003), and a change in distribution results in turn in a change in population size, and so on.

The characteristics of the Kuroshio Current may also affect sardine abundance (Watanabe, 1987; Kikuchi et al., 1992). The mechanism behind fluctuations in the sardine population is complicated; however, given that density-dependent mechanisms are not the direct cause of fluctuations in sardine population (Sakuramoto, 2005) and that SRR in Japanese sardine can be expressed by a simple line through the origin for a wide range of SSB (from 0 to 15 million t) (Shimoyama et al., 2007), we conclude that the fundamental causes of fluctuations in sardine population would have strong relation to the environmental conditions rather than the density effect. Therefore, it would not be useful to develop management policy based on the density-dependent effect. Instead, it would be best to develop a revised management policy based on a new concept that does not consider the density-dependent effect and that focuses on environmental conditions.

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北西太平洋におけるマイワシの加入量変動と環境変動の関係

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マイワシ太平洋系群の加入量変動と環境変動との関係を調べた。再生産関係を表すモデルとして、Ricker型、Beverton-Holt型、指数型、線形型、比例型のモデルを用い、それぞれ正規型、対数正規型の誤差分布を仮定した。モデルからの残差と月別環境指標との相関分析を行った。相関分析は期間の異なる2つのデータセット（①全期間1976-2004と②全期間から加入量の激減した1988-1991を除いた期間）に対して行った。その結果、有意な相関を示す月、

および環境指標は②よりも①のデータセットの場合に極めて多く検出された。このことは、1988-1991の加入の失敗が北極振動、太平洋10年振動、黒潮統流域などの海洋環境の変動により説明可能であることを示唆した。特に、産卵期間と考えられる期間（月）の環境指標との相関が高かった。今後、加入量の予測モデルの作成を試みる場合にこれらの環境要因が重要な指標になると考えられた。

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