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## Assessing environmental effects on recruitment of Japanese common squid (*Todarodes pacificus*) in the Japan Sea using a biomass dynamics model

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### Abstract

Effects of variation in sea surface temperature (SST) on recruitment of the Japanese common squid (*Todarodes pacificus*) in the Japan Sea were investigated using a biomass dynamics model. Two extreme cases where the spawner–recruit relationship approaches a linear form were examined: 1) when the stock size is far below the carrying capacity, and 2) when the stock size is near the carrying capacity. For each case, we developed a recruit index estimated from the fishing mortality rate and catch data, and proposed that annual changes in the indexes were due to environmental variation. Assuming that the true reproductive potential occurs somewhere between the two cases, years of good and poor recruitment were identified based on the indexes. Seasonal changes in SST around Japan during 1971–1995 were compared with changes that occurred in the indexes, and years of poor recruitment were found to correspond closely to years of lower than normal SST in winter and spring. Cold winters influenced by strong northwesterly winds were also associated with lower levels of recruitment.

**Key words:** squid, recruitment, biomass dynamics model

### Introduction

Squids generally live about one year (Jackson, 1994), so recruitment can be highly variable and difficult to predict (Pauly, 1985; Boyle and Boletzky, 1996; Rodhouse, 2001). Without some understanding of the processes that drive this variability, management of squid stocks is difficult. Recent studies have suggested that recruitment variability in some squids is driven by the environment (e.g., Waluda et al., 1999; Agnew et al., 2000; Dawe et al., 2000). A better understanding of how squid recruitment responds to environmental variability would greatly benefit both fishers and fishery managers.

The Japanese common squid (*Todarodes pacificus*) is distributed around Japan (Murata, 1990) and the target of the country's largest squid fishery (FAO, 1998). Three spawning groups (subpopulations) have been identified based on when they spawn: autumn, winter and summer (Hamabe and Shimizu, 1966; Murata, 1989). In the Japan Sea, the autumn–spawning group is dominant (Kasahara, 1991; Murayama et al., 1993)

and spawns mainly from the East China Sea off Kyushu Island to the shelf area off Honshu Island in September and October (Fig. 1b; Okutani and Watanabe, 1983). Paralarvae and juveniles are transported northward into the Japan Sea by the Tsushima Current, reaching as far north as 45–46°N in summer (Okutani, 1983). As they near maturity, the squid then return south, spawn and die. Annual catches of *T. pacificus* in the Japan Sea have varied widely over the past three decades (Fig. 2). The causes of this long-term variability are unclear, but two possible mechanisms have been proposed; Murata (1990) and Adachi (1994) argued that temporal patterns in catches and catch per unit effort (CPUE) suggest that the drop in catches during the late 1970s and early 1980s was caused by overfishing, whereas Sakurai et al. (2000) suggested that catch variability was related to changing environmental conditions.

To understand recruitment, information on annual changes in stock size is needed. However, the lifespan of squids is too short to calculate stock size from conventional age-based cohort analysis, as is standard in longer-lived fished species. For short-lived species, simple

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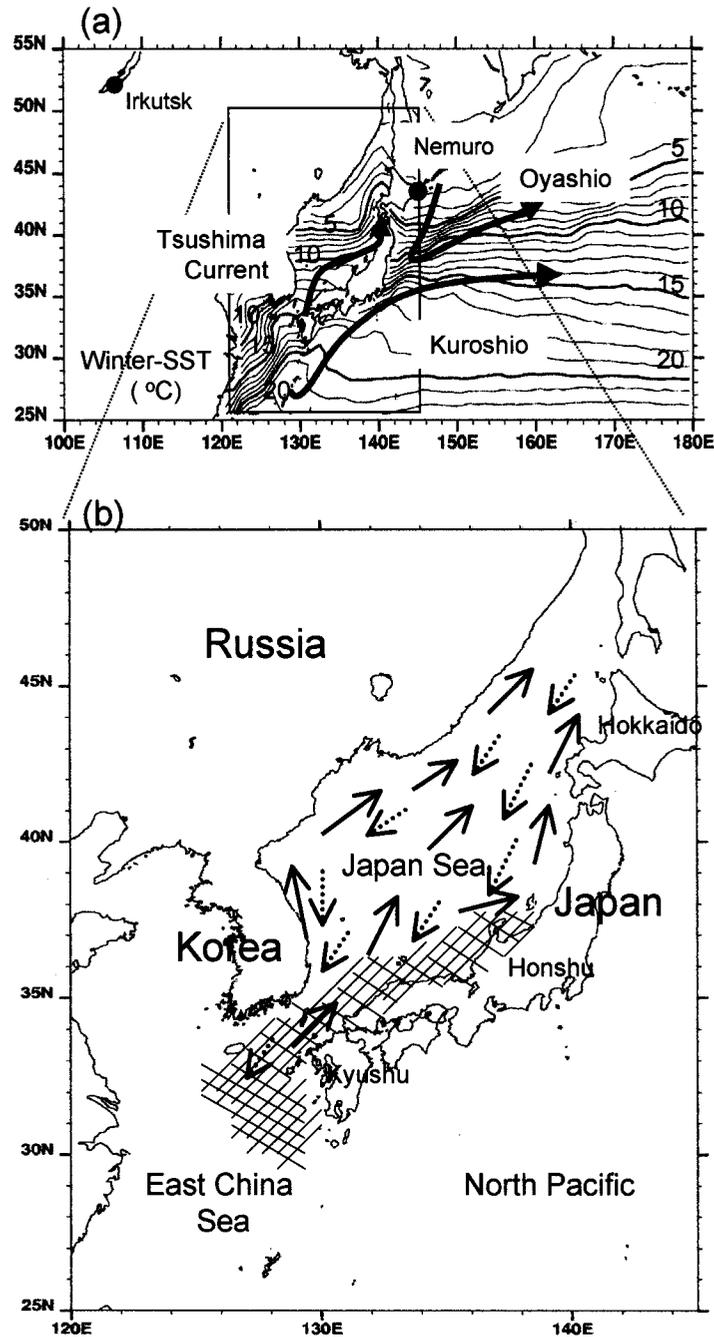


Fig. 1. (a) Isotherms show mean sea surface temperatures (SSTs) in winter (January–March) during 1972–1996. Also shown are current systems around Japan, and the meteorological stations of Irkutsk, Russia and Nemuro, Japan. (b) Main spawning ground (meshed region) and migration direction (arrows) of the autumn-spawning group of *Todarodes pacificus* around Japan (after Kasahara, 1991).

population models that ignore age structure and consider biomass (generally called biomass dynamics models) are useful for examining recruitment (e.g., Hilborn and Walters, 1992; Roel and Butterworth, 2000). Use of these models requires times-series data on catches and abundance, the latter generally expressed as an index (e.g., catch per unit of fishing effort (CPUE)). Recently, it has been suggested that CPUE

data from fished populations can be a poor index of stock abundance because the catchability–abundance relationship is often complex and non-linear, and the spatial distribution of fished populations is often heterogeneous (Hilborn and Walters, 1992). However, CPUE data are commonly used as a stock–abundance index for *T. pacificus* in the Japan Sea because its catches comprise a single year class, so catch data in year

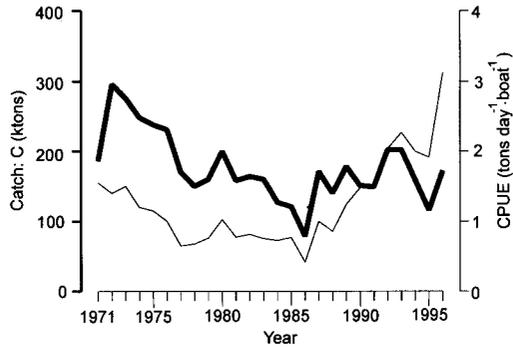


Fig. 2. Annual Japanese commercial catch  $C$  (ktons, thick line) and catch per unit of fishing effort CPUE (tons·boat<sup>-1</sup>·day<sup>-1</sup>, thin line) of *Todarodes pacificus* in the Japan Sea during 1971-1996.

$n$  can directly represent the stock conditions. Annual catch and CPUE data may include some uncertainty, and if the abundance inferred from the CPUE data is inaccurate, the estimated recruit index will show meaningless variations unrelated to environmental conditions. However, when a clear relationship occurs between the values of recruitment estimated assuming recruit biomass is proportional to CPUE and environmental variables, these CPUE data can provide useful information as a stock-abundance index.

Annual CPUE cannot simply be used as an index of "recruitment" when comparing recruitment to annual changes in environmental conditions. In biomass dynamics models, the stock-recruit relationship shows non-linear behavior when stock size is near the carrying capacity. Furthermore, periods of high stock abundance do not always correspond to periods of good recruitment, because a time lag can occur between variations of stock size and of recruitment. For example, when the stock size is far below the carrying capacity, the period of good recruitment corresponds to the period of increasing stock size, not to the period of high stock abundance (Isoda and Azumaya, 1998). When stock size is near the carrying capacity, the phase lag between periodical variation of the stock and that of recruitment becomes more complex due to the nonlinear stock-recruit relationship (Isoda, 2000). Such a time/phase lag is frequently several years long in annual species like squids.

In this paper, we consider two extreme cases (when stock size is far below the carrying capacity and when it is near the carrying capacity) and assume that the actual stock size will occur between these extremes. We then propose a method for estimating annual changes in recruitment of *T. pacificus* in the Japan Sea due to environmental factors, based on catch and CPUE data using a biomass dynamics model. Finally, we examine the relative changes that occurred in recruitment during

1971-1995 and compare these changes to changes in seasonal environmental conditions (sea surface temperature (SST) and wind strength).

## Materials and methods

### Data

Our model is based on a simple biomass dynamics model that estimates relative changes in recruitment based on variation in stock size using catch and CPUE data. These data were collected from the Japanese fishery in the Japan Sea during 1972-1996 (Fig. 2); data from 1978-1996 are based on an integrated analysis by the Japan Sea National Fisheries Research Institute (JSNFRI), and those from 1972-1977 were published in JSNFRI (1983).

### The model

We begin by giving a brief summary of the model used. (1) Since fishing affects the abundance, the fishing mortality rate was examined by assuming that the recruit biomass is approximately proportional to CPUE. (2) Spawning stock size remains after the fishing, and can contribute to spawning in year  $n$ . (3) A simple spawner-recruit relationship between recruit biomass in year  $n+1$  and spawning stock in year  $n$  was assumed using the logistic equation in our model. (4) Our model is externally induced by annual changes in mortalities due to environmental factors and fishing. So, we consider that the population fecundity for environmental factors can vary due to annual changes in spawner-recruit parameters such as the intrinsic growth rate or carrying capacity, but this relationship is non-linear. (5) Therefore, two extreme situations were examined: when the stock size is far below the carrying capacity, and when the stock size is near the carrying capacity. Then, the non-linear relation was transformed into a linear form for each case. (6) Next, substituting both the observed catch and estimated fishing mortality data into these linear equations, we can estimate relative annual changes in recruitment as for the intrinsic growth rate or carrying capacity. We call these estimated changes in recruitment "recruit indexes" in our model.

### Fishing mortality rate

One-way to estimate stock abundance is by fishing, but fishing will affect this abundance, so in our model, we first examined the annual fishing mortality rate ( $F$ ). This term will range between 0.0 for an unexploited stock and 1.0 for a fully exploited one. Catch ( $C_n$ ; tons) is expressed as:

$$C_n = F_n B_n \quad (1)$$

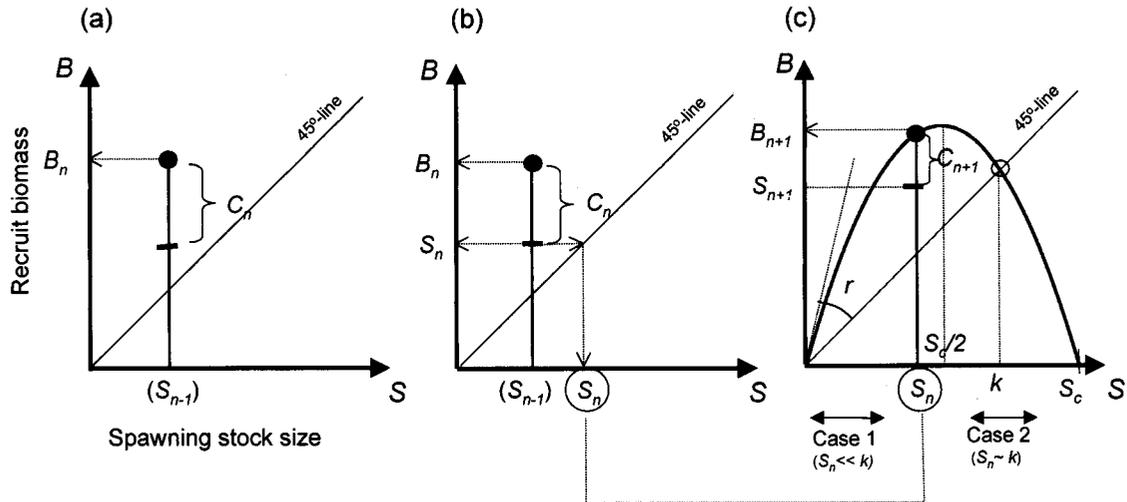


Fig. 3. The graphical iteration method used to determine discrete population growth between recruit biomass ( $B$ ) and spawning stock size ( $S$ ). Subscript  $n$  is the year and the initial spawning stock size is  $S_{n-1}$ . The straight solid line that forms a  $45^\circ$  angle indicates that  $S$  in year  $n$  equals  $B$  in year  $n+1$ . (a) When  $B_n$  is recruit biomass and  $F_n$  is fishing mortality rate in year  $n$ , the catch ( $C_n$ ) is expressed as equation (1). Assuming  $B_n$  is directly proportional to  $CPUE_n$  as equation (2),  $F_n$  can be estimated from equation (3). (b)  $S_n$  that remains after fishing can contribute to spawning in year  $n$  and is given by equation (4). (c) The spawner-recruit relationship between  $B_{n+1}$  and  $S_n$  is written as equation (5). Our model simply assumes the discrete logistic growth rate of equation (6), which is plotted as a parabolic curve. It gives the difference equation of (7) using the intrinsic growth rate  $r$  and the carrying capacity  $k$ . Where the parabolic curve and a solid line with  $45^\circ$  angle intersect (open circle in (c)), the population is at equilibrium of  $k$  since  $S_n = B_{n+1}$ . In the preset study, the spawner-recruit relationship was mathematically linearized at  $S_n \ll k$  (Case 1) and  $S_n \approx k$  (Case 2) to estimate the annual changes in the recruit index for each case.

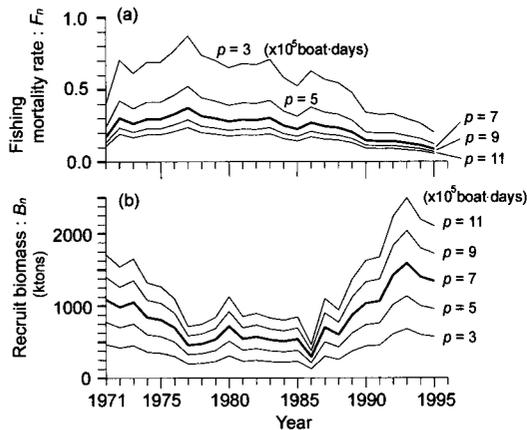


Fig. 4. Estimated fishing mortality rate  $F_n = C_n / (p CPUE_n)$  (a) and recruit biomass  $B_n = p CPUE_n$  (b) for selected proportional parameter  $p$  values between  $3 \times 10^5$  and  $11 \times 10^5$  boat-days.

where  $F_n$  is the fishing mortality rate in year  $n$ , and  $B_n$  is the recruit biomass (i.e., the adult biomass before fishing) in year  $n$ . Through the egg production from spawning stock size  $S_{n-1}$  in year  $n-1$ , the recruit biomass increases to  $B_n$  in year  $n$  (Fig. 3a). The fishery targets this pre-spawning biomass  $B_n$ , and catch  $C_n$  is estimated by multiplying  $F_n$  and  $B_n$ .

We assume that recruit biomass in year  $n$  is proportional to  $CPUE_n$  (tons $\cdot$ boat $^{-1}\cdot$ day $^{-1}$ ). When its proportional parameter is  $p$  (this term is the inverse of the catchability coefficient and is expressed in “boat-days”), the recruit biomass in year  $n$  is written as:

$$B_n = p CPUE_n \quad (2)$$

We can combine equations (1) and (2) to get

$$F_n = C_n / (p CPUE_n) \quad (3)$$

The value of  $p$  is not known, but since  $F_n < 1$ , then  $p > C_n / CPUE_n$ . In the *T. pacificus* fishery,  $C_n$  and  $CPUE_n$  have values on the order of  $10^5$  tons and  $10^0$  tons $\cdot$ boat $^{-1}\cdot$ day $^{-1}$ , respectively (Fig. 2), so  $p$  will be greater than about  $10^5$  boat-days. Based on equations (2) and (3), we show that as  $p$  increases from  $3 \times 10^5$  to  $11 \times 10^5$  boat-days, the recruit biomass increases and fishing mortality rate decreases (Fig. 4). Also, as  $p$  increases above  $7 \times 10^5$  boat-days, variation in  $F_n$  becomes stable within a range of 0.1–0.35 (Fig. 4a).

#### Spawner-recruit relationship

Since *T. pacificus* has a one-year lifespan, the spawning stock size  $S_n$  that remains after fishing, and which can contribute to spawning in year  $n$ , is given by

$$S_n = B_n - C_n$$

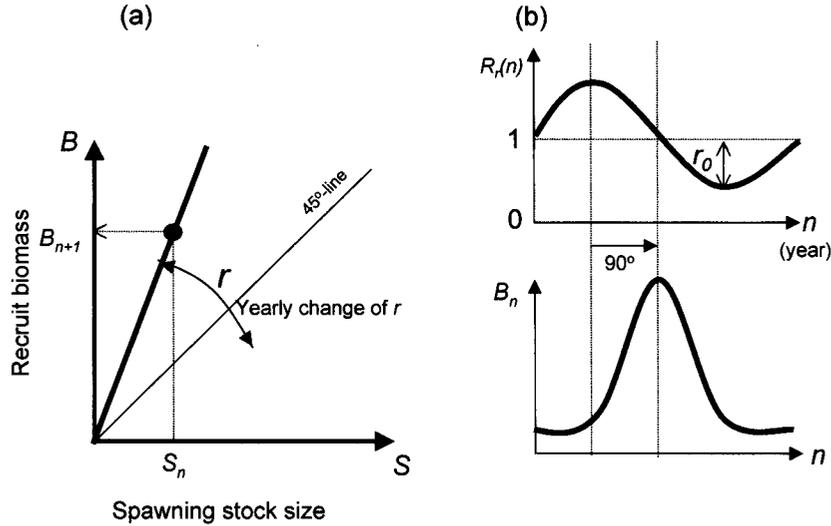


Fig. 5. Case 1: (a) The linearized discrete logistic equation at  $S_n \ll k$  is plotted as the thick solid line is expressed by equation (8) or equation (9). (b) An example of  $B_n$  response to a time-varying  $r$ . In this case, the recruit index is expressed by  $R_r(n) = r + 1$ . The upper panel is the variation of  $R_r(n)$  with a period of  $2\pi/\omega$  ( $\omega$  is the frequency of periodical variation of  $R_r(n)$ ). The lower panel is the theoretical temporal variation of  $B_n$  in response to the  $R_r(n)$ -variation. Isoda and Azumaya (1988) found an analytical solution of  $B_n \approx \exp\{(r_0/\omega)\cos(\omega/2)\} \exp\{(-r_0/\omega)\cos(\omega n)\}$  for the periodical variation of  $R_r(n) = r_0 \sin(\omega n) + 1$ . The phase of  $B_n$  abundance lags  $90^\circ$  from the maximum- $R_r(n)$ , and its biomass increases and decreases exponentially (Isoda and Azumaya, 1998).

$$= (1 - F_n)B_n \quad (4)$$

This equation is shown graphically in Fig. 3b. The  $y$ -value of  $B_n - C_n$  on the  $45^\circ$  solid line gives the spawning stock size  $S_n$  in year  $n$ . Using a simple production model, the spawner-recruit relationship between  $B_{n+1}$  (recruit biomass in year  $n+1$ ) and  $S_n$  (spawning stock size in year  $n$ ) can be written as

$$B_{n+1} = \alpha_n S_n \quad (5)$$

where  $\alpha_n$  is the biomass growth rate from year  $n$  to year  $n+1$ . The logistic equation can simply express a stable equilibrium stock size, so the following discrete logistic growth rate was used:

$$\alpha_n = b(S_c - S_n)/S_c \quad (6)$$

where  $b$  is the maximum growth rate, and  $S_c$  is the maximum spawning stock size. This relation shows that  $\alpha_n$  linearly decreases from a maximum of  $b$  at  $S_n = 0$  to a minimum of 0 at  $S_n = S_c$ . We can substitute equation (6) into equation (5) to get the following difference equation of the logistic growth model:

$$B_{n+1} - S_n = r(1 - S_n/k) S_n \quad (7)$$

where  $r (= b - 1)$  is the intrinsic growth rate ( $\text{year}^{-1}$ ), and  $k (= (b - 1) S_c / b)$  is the carrying capacity (i.e., the equilibrium stock size in tons). A plot of  $B_{n+1}$  against  $S_n$  (i.e., the spawner-recruit curve) shows that surplus production is 0 at  $S_n = 0$ , and that the recruit biomass ( $B_{n+1}$ ) reaches a maximum at  $S_n = S_c/2$  (Fig. 3c).

Using such a logistic diagram is a convenient way to graphically follow the growth of a population in discrete time steps. We then can begin the next iteration from  $S_n$  in year  $n$ , which results in the recruit biomass of  $B_{n+1}$  in year  $n+1$ . Again, spawning stock size  $S_{n+1}$  in year  $n+1$  can be estimated by  $B_{n+1} - C_{n+1}$ .

If the parameters  $r$  and  $k$  do not change over time when  $F_n \sim 0$ , the modeled stock size will grow or decline toward the carrying capacity ( $k$ ). Stock size changes annually, and in fishery assessment, such variation is considered mainly in relation to fishing effort under a constant reproductive relationship. Our model is externally induced by annual changes in both the spawner-recruit relationship and fishing mortality. That is, the population fecundity does not remain constant over time; it can vary due to annual changes in spawner-recruit parameters such as the intrinsic growth rate ( $r$ ) and carrying capacity ( $k$ ). For example, it may be considered that the change in  $r$  is caused by annual differences in the egg production rate for a given stock biomass or the mortality rate during the early life stages, and the change in  $k$  is caused by annual differences in zooplanktonic food resources in the habitat area. We can regard the change in these parameters as the environmental factors in the present model.

#### Recruit indexes for annual recruitment

The current stock size of *T. pacificus* is unknown, so we considered the two extreme situations shown in Fig.

3c : when the stock size is far below the carrying capacity (Case 1), and when the stock size is near the carrying capacity (Case 2). These cases were chosen because, although the spawner-recruit relationship represented by equation (7) is non-linear, it approaches a linear form for both cases. The actual stock size was presumed to lie between these extremes.

First, equation (7) was transformed into a linear form for each case. Substituting both the observed catch ( $C_n$ ) and estimated fishing mortality ( $F_n$ ) data into these linear models, we can estimate relative annual changes in recruitment for different values of  $r$  (Case 1) and  $k$  (Case 2).

For Case 1, changes in recruitment were examined based on the recruit index  $R_r(n)$ . Since  $S_n \ll k$ ,  $S_n/k$  in equation (7) becomes zero, hence :

$$B_{n+1} - S_n = r S_n \quad (8)$$

We can substitute equation (4) into equation (8) to get :

$$B_{n+1} = (r+1) (1-F_n) B_n \quad (9)$$

This equation is shown graphically in Fig. 5a. Replac-

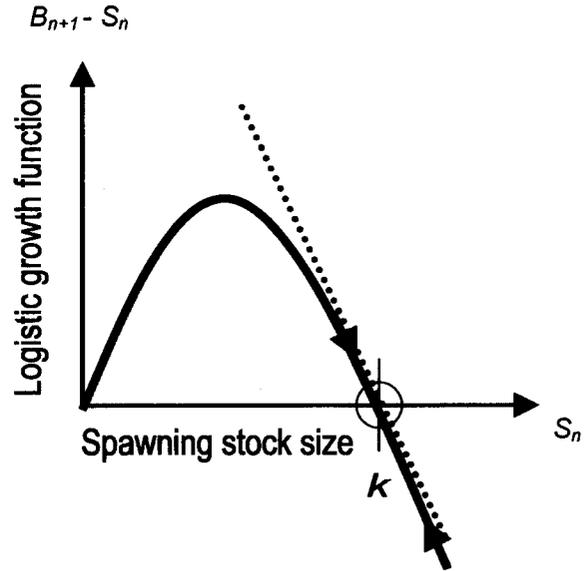


Fig. 6. Illustration of relation between logistic growth function of  $B_{n+1} - S_n$  and spawning stock size of  $S_n$ . The equilibrium point  $S_n = k$  is stable due to the local stability analysis. In Case 2, the population dynamics near the carrying capacity was approximated by the liner relationship (see dotted line).

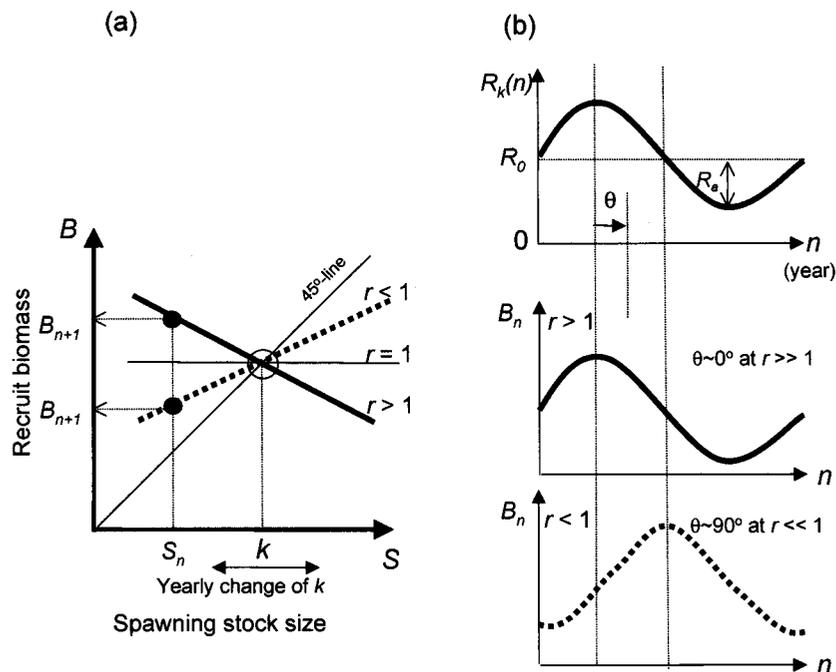


Fig. 7. Case 2: (a) The linearized discrete logistic equations at  $S_n \approx k$  are plotted as three straight lines at  $r < 1$  (thick solid),  $r = 1$  (thin solid), and  $r > 1$  (thick dotted). They are expressed by equation (11) or equation (12). (b) An example of  $B_n$  response to a time-varying  $k$ . In this case, the recruit index is expressed as  $R_k(n) = rk$ . The upper panel is the variation of  $R_k(n)$  with a period of  $2\pi/\omega$  ( $\omega$  is the frequency of periodical variation of  $R_k(n)$ ). The lower two panels are the theoretical temporal variations of  $B_n$  in response to  $R_k(n)$ -variation at  $r > 1$  and  $r < 1$ , respectively. Isoda (2000) found an analytical solution of  $B_n \approx \{R_0 + [rR_a / (r^2 + \omega^2)^{1/2}] \sin(\omega n - \theta)\} / r$  for the periodical variation of  $R_k(n) = R_0 + R_a \sin(\omega n)$ . The phase of  $B_n$  abundance lags  $\theta = \tan^{-1}(\omega/r)$  from the maximum- $R_k(n)$ . When  $r > 1$  or  $R_k(n)$  has long-term variation,  $B_n$  is nearly in phase with  $R_k(n)$ -variation. When  $r < 1$  or  $R_k(n)$  has short-term variation,  $B_n$  lags about  $90^\circ$  from the  $R_k(n)$ -variation.

ing the parameter  $r+1$  with  $R_r(n)$  (expressed in year<sup>-1</sup> units) and substituting equation (1) into equation (9), we get the following equation for  $R_r(n)$  as a function of  $C_n$  and  $F_n$ :

$$\begin{aligned} R_r(n) &= B_{n+1}/((1-F_n) B_n) \\ &= (C_{n+1}/F_{n+1})/((1-F_n)F_{n+1} C_n) \quad (10) \end{aligned}$$

For Case 2, changes in recruitment were examined based on the recruit index  $R_k(n)$ . From the discrete logistic equation in (7), we illustrate the relation between the growth function  $B_{n+1}-S_n$  and the spawning stock size  $S_n$  (Fig. 6). The equilibrium point  $S_n=k$  is stable as long as  $r$  is positive, but this method for evaluating stability is strictly valid only for relatively small perturbations. Here, by assuming linear dynamics near the carrying capacity, the population dynamics can be approximated by the following linear relationship with slope  $-r$  (e.g., Isoda, 2000):

$$B_{n+1} - S_n = -r (S_n - k) \quad (11)$$

We can substitute equation (4) into equation (11) to get

$$B_{n+1} = (1-r)(1-F_n)B_n + rk \quad (12)$$

Replacing the parameter  $rk$  with  $R_k(n)$  (expressed in ton·year<sup>-1</sup> units) and using equation (1), reproduction can then be represented by a change in  $R_k(n)$  of the carrying capacity in year  $n$ :

$$\begin{aligned} R_k(n) &= B_{n+1} + (r-1)(1-F_n) B_n \\ &= C_{n+1}/F_{n+1} + (r-1)(1-F_n)C_n/F_n \quad (13) \end{aligned}$$

The value of  $R_k(n)$  will depend on the intrinsic growth rate ( $r$ ). If  $r=1$ ,

$$\begin{aligned} R_k(n) &= C_{n+1}/F_{n+1} = B_{n+1} \\ &= I k(n). \quad (14) \end{aligned}$$

where  $k(n)$  is the carrying capacity in year  $n$ . Thus, the recruit biomass  $B_{n+1}$  in year  $n+1$  will be determined completely by this carrying capacity. For  $r>1$  and  $r<1$ , the term  $(r-1)(1-F_n) B_n$  will be positive and negative, respectively. Thus, for  $r>1$ ,

$$R_k(n) = B_{n+1} + (r-1)(1-F_n) B_n \quad (15)$$

and for  $r<1$ ,

$$R_k(n) = B_{n+1} - (1-r)(1-F_n) B_n \quad (16)$$

We show stock-recruitment curves for different  $r$  values (Fig. 7a). To estimate  $R_k(n)$  for  $r<1$  and  $r>1$ ,  $r=0.5$  and  $r=1.5$  were selected as representative examples of each case. When we chose other values for  $r$ , the typical patterns of  $R_k(n)$ , especially the years with maximum and minimum values, were almost identical to those for  $r=0.5$  and  $1.5$ , respectively (not shown). However, population growth behaves as a period-doubling scheme at  $r>2$  and becomes chaotic at  $r>2.57$  in

the discrete logistic model, hence the selected values of  $r<2$  will be appropriate for estimating  $R_k(n)$ .

Here, the theoretical response of a model stock due to an idealized time-varying  $R_r(n)$  and  $R_k(n)$  will be introduced using a simple sine curve with a period of  $T$  years and assuming  $F_n=0$  in equations (9) and (12), based on the studies of Isoda and Azumaya (1998) and Isoda (2000). Figure 5a shows a schematic example of  $B_n$  response to a time-varying  $r$  on a diagram of relation between  $B_{n+1}$  and  $S_n$ . In this case, the recruit index is expressed by  $R_r(n)=r+1$ . When the periodical variation of  $R_r(n)$  is  $r_0 \sin(\omega n)+1$  ( $r_0$  is the amplitude of  $R_r(n)$ ,  $\omega=2\pi/T$  is the frequency), the temporal response of  $B_n$  is a function of  $\exp\{-r_0/\omega\}\cos(\omega n)$  (Isoda and Azumaya, 1998). Such a phase lag between  $R_r(n)$  and  $B_n$  may be shown graphically in Fig. 5b. For the time-varying  $R_r(n)$ , the model stock  $B_n$  increases exponentially when  $R_r(n)>1$  and decreases exponentially when  $R_r(n)<1$  at any periodical variation, i.e., the phase in  $B_n$  always lags 90° (or  $T/4$  years) from the time of maximum- $R_r(n)$ . It is important to note that good recruitment for  $R_r(n)$  does not correspond to high stock abundance, but rather to an increase in stock size.

Figure 7a shows a schematic example of  $B_n$  response to a time-varying  $k$  on the diagram of relation between  $B_{n+1}$  and  $S_n$ . In this case, the recruit index is expressed as  $R_k(n)=rk$ . The linearized discrete logistic equations at  $S_n \approx k$  are plotted as three straight lines at  $r<1$  (thick solid),  $r=1$  (thin solid), and  $r>1$  (thick dotted). When the periodical variation of  $R_k(n)$  is  $R_0 + R_0 \sin(\omega n)$  (upper panel in Fig. 7b), the temporal response of  $B_n$  is a function of  $\sin(\omega n - \theta)$  (Isoda, 2000). This solution shows that the model stock  $B_n$  maximum lags from the maximum- $R_k(n)$  with the phase-lag  $\theta$ :

$$\theta = \tan^{-1}(\omega/r) \quad (17)$$

where  $r$  is the intrinsic growth rate. This shows that  $B_n$  is in phase with the carrying-capacity index  $R_k(n)$  variation (i.e.,  $\theta=0^\circ$ ) when  $\omega$  approaches zero, i.e., for long-term periodicity, or when  $r$  is much greater than 1 (middle panel in Fig. 7b). On the other hand, the phase in  $B_n$  lags 90° from the time of the maximum carrying capacity  $R_k(n)$  when  $\omega$  approaches infinity, i.e., for short-term periodicity, or when  $r$  is much smaller than 1 (lower panel in Fig. 7b).

Thus, recruit-biomass ( $B_n$ ) maxima lag behind the maxima in  $R_r(n)$  or  $R_k(n)$  within a phase range of 0° to 90°. As a result, years of recruit biomass maxima do not necessarily correspond to years of good recruitment. Therefore, our proposed recruit indexes of  $R_r(n)$  and  $R_k(n)$  are essentially estimated from a temporal gradient of recruit biomass between year  $n$  and year  $n+1$  as

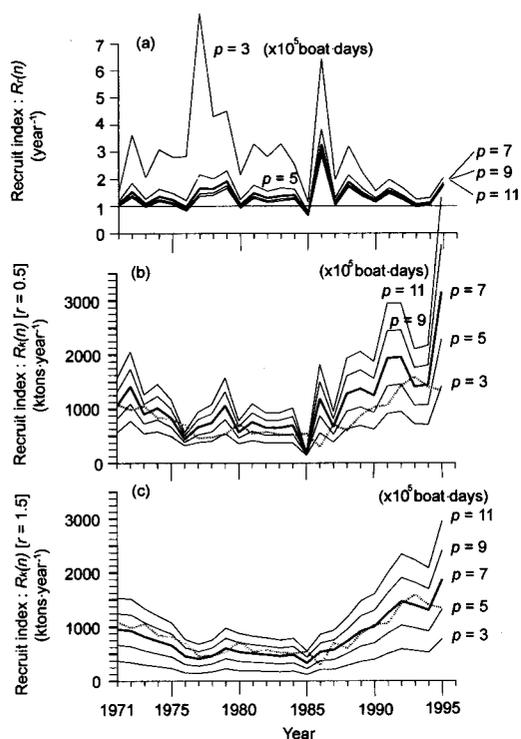


Fig. 8. Annual variations in estimated recruit indexes of (a)  $R_r(n)$ , (b)  $R_k(n)$  [ $r=0.5$ ], and (c)  $R_k(n)$  [ $r=1.5$ ] for selected  $p$  values from  $3 \times 10^5$  to  $11 \times 10^5$  boat-days. Dashed lines in Fig. 7b and 7c show recruit biomass  $B_n$  (ktons) at  $p=7 \times 10^5$  boat-days.

shown in equations (10) and (13). Based on these new criteria, years of concurrent maxima in  $R_r(n)$  and  $R_k(n)$  were identified as “good” recruitment years, and years of concurrent minima were identified as “poor” recruitment years.

### Environment

Changes in recruitment were compared to changes in sea surface temperature (SST) and wind stress. In the Japan Sea, SST variation in winter accurately reflects the ocean conditions due to the development of the surface mixed layer, whose maximum depth of about 100–140 m corresponds to the maximum depth of the Tsushima Current water (Kim and Isoda, 1998). Warm water of the Tsushima Current branching from the Kuroshio enters the Japan Sea, and flows northeastward mainly in the southern part of the sea (Fig. 1a).

*T. pacificus* that hatch in autumn of year  $n$  generally recruit into the fishery late spring/early summer of the year  $n+1$  (H. Kidokoro, Japan Sea National Fisheries Research Institute, Niigata, Japan, personal communication). Thus, before recruiting into the fishery, the squid can go through four seasons: autumn of  $n$ , winter of  $n+1$ , spring of  $n+1$  and summer of  $n+1$ . To compare differences in temperature for good and poor

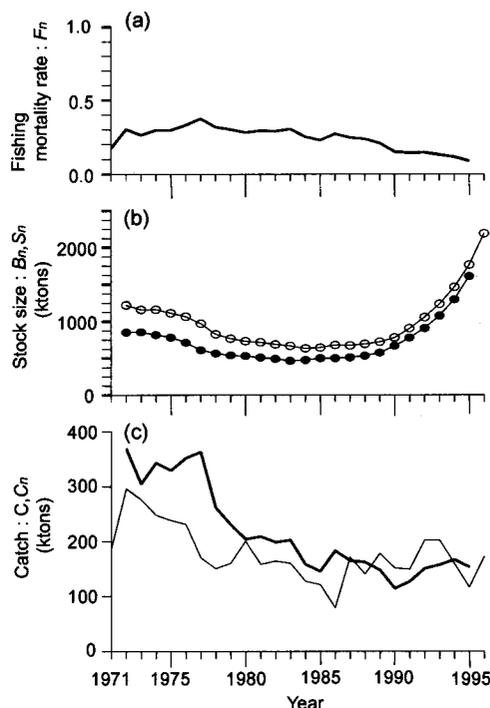


Fig. 9. (a) Estimated  $F_n$  at  $p=7 \times 10^5$  boat-days; (b) calculated spawning stock size ( $S_n$ , closed circle) and recruit biomass ( $B_n$ , open circle); (c) comparison of observed catch ( $C$ , thin line) and calculated catch ( $C_n$ , thick line). In all calculations,  $R_0$  was set at 1.33, which is the mean value of  $R_r(n)$  during 1971–1995.

recruitment years for these four seasons (autumn: October–December, winter: January–March, spring: April–June, summer: July–September), season-specific SST values between good and poor recruitment years were compared. SST patterns were determined for  $1^\circ \times 1^\circ$  grid points between  $25^\circ\text{N}$  and  $50^\circ\text{N}$ , and between  $120^\circ\text{E}$  and  $145^\circ\text{E}$  using data collected by the Japan Meteorological Agency during 1971–1996 from both research ships and satellites.

Wind strength was assessed using the Monsoon Index (MOI), which indicates wintertime wind stress over the Eurasian Continent to the North Pacific and is defined as the difference in sea-level atmospheric pressure between Nemuro, Japan ( $43.02^\circ\text{N}$ ,  $145.45^\circ\text{E}$ ), and Irkutsk, Russia ( $52.16^\circ\text{N}$ ,  $104.21^\circ\text{E}$ ) (Fig. 1a). Positive anomalies in this index are associated with strong northwesterly winds.

## Results

### Recruitment

Both indices of recruitment  $R_r(n)$  and  $R_k(n)$  vary over time (Fig. 8);  $R_r(n)$  and  $R_k(n)$  [ $r=0.5$ ] show high short-term ( $<5$ -year) variation, with similar temporal patterns in maxima and minima, and  $R_k(n)$  [ $r=$

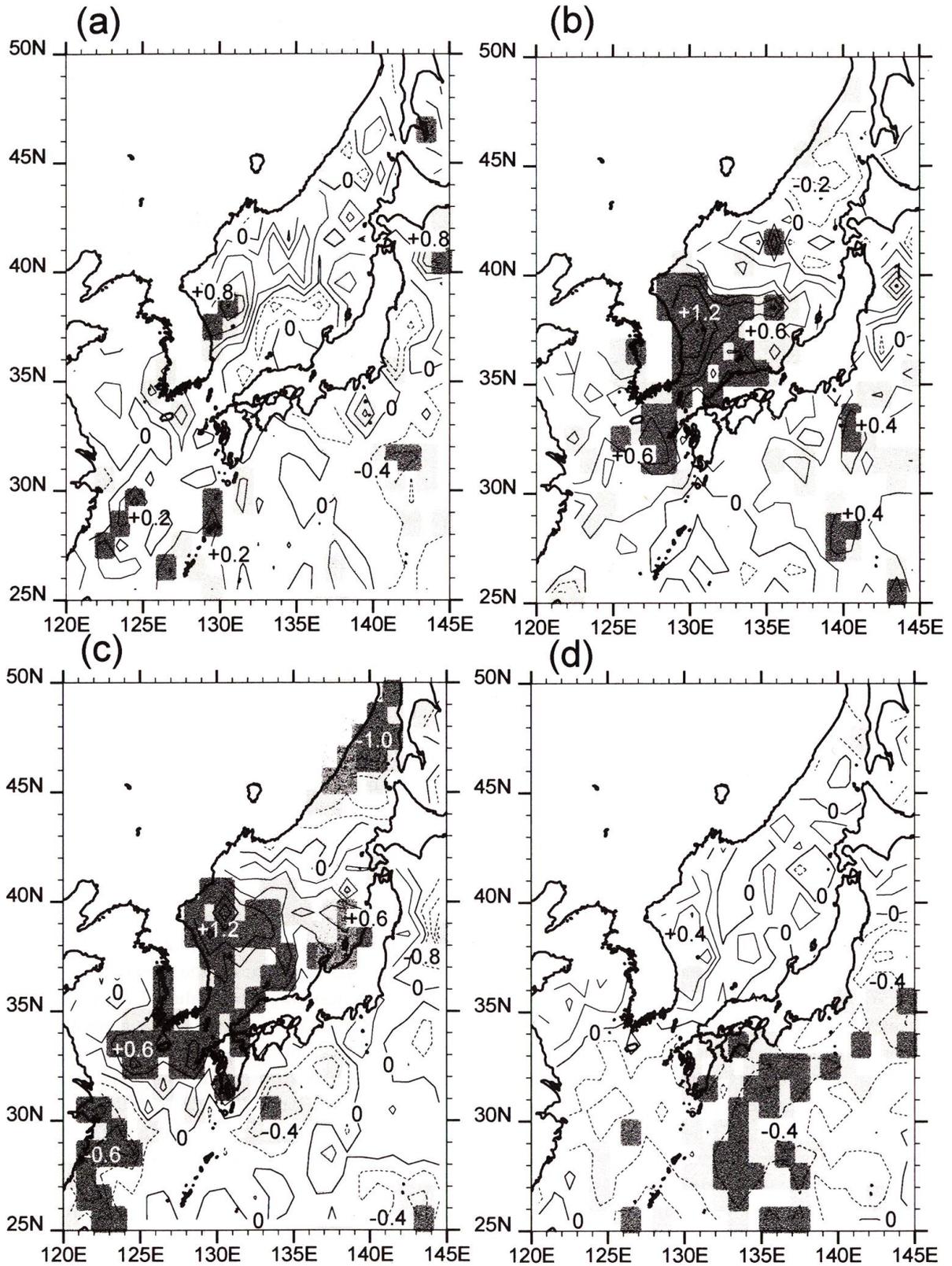


Fig. 10. Horizontal distributions of seasonal differences in sea surface temperatures SSTs ( $^{\circ}\text{C}$ ) between good-recruitment years and poor-recruitment years; autumn (a), winter (b), spring (c), and summer (d). Dark and light gray grids indicate significant difference in SSTs with confidence greater than 95% and 90% according to Student's  $t$ -test.

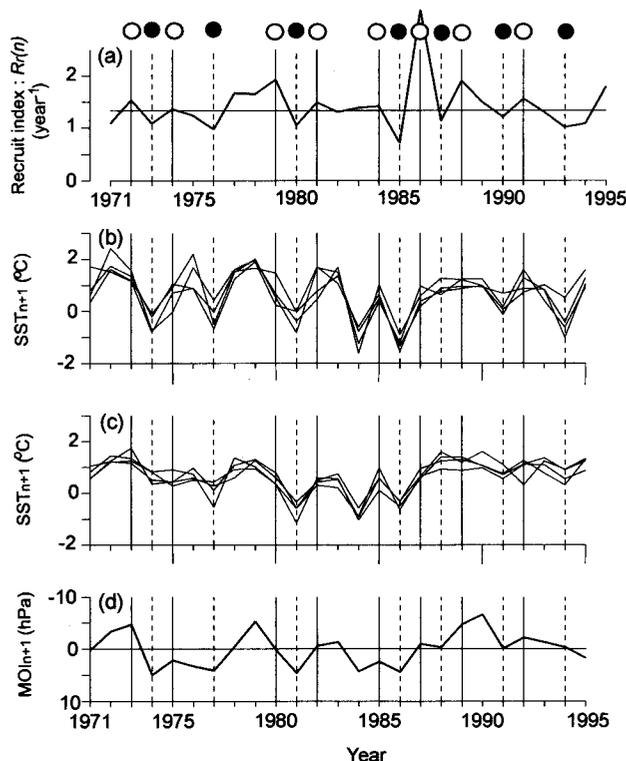


Fig. 11. Annual variations in (a) recruit index of  $R_r(n)$  at  $p=7 \times 10^5$  boat·days, (b) winter- $SST_{n+1}$  anomalies east of Korea ( $36^\circ-38^\circ\text{N}$ ,  $129^\circ-131^\circ\text{E}$ ), (c) winter- $SST_{n+1}$  anomalies west of Kyushu ( $32^\circ-34^\circ\text{N}$ ,  $127^\circ-129^\circ\text{E}$ ), and (d) Asian winter monsoon index ( $MOI_{n+1}$ ). Vertical solid and broken lines with symbol “○” and “●” indicate years of relatively good and poor levels of recruitment, respectively, determined from  $R_r(n)$  or  $R_k(n)$  [ $r=0.5$ ]. Note that the x-axis is offset one year in Fig. 11a.

0.5] and  $R_k(n)$  [ $r=1.5$ ] show a long-term increase beginning in the mid-1980s.

The phase lag  $\theta$  between the recruit-biomass maximum and the maximum- $R_k(n)$  estimated using equation (17) for a 2-5 year period and  $r=0.5$  year<sup>-1</sup> (Fig. 8b) ranged from  $68^\circ$  to  $81^\circ$ , which is close to  $90^\circ$  in the case of  $R_r(n)$  variation. Thus, the coincidence in the temporal patterns of good and poor recruitment between  $R_r(n)$  and  $R_k(n)$  [ $r=0.5$ ] can be understood by the  $\sim 90^\circ$  phase lag that occurs between the maxima of recruit-biomass and both recruit indexes. For a 25-year period at  $r=0.5$  year<sup>-1</sup> (Fig. 8b) and  $r=1.5$  year<sup>-1</sup> (Fig. 8c), the phase lag between recruit biomass ( $B_n$ ) and  $R_k(n)$  is 1.9 years ( $\theta=27^\circ$ ) and 0.6 years ( $\theta=10^\circ$ ), respectively. If the carrying capacity varies over a long-term ( $>10$  year) scale, the recruit biomass can show variation that is nearly in phase with that of the carrying capacity.

However, we found no long-term periodicity in the  $R_r(n)$  time series. For  $R_r(n)$ , the long-term variation in recruit biomass ( $B_n$ ) can be explained by variations in fishing mortality as discussed below. For a constant recruit index  $R_0$  of  $R_r(n)$  (i.e., where there is no change in the environment), the predicted model affected by the

fishing rate  $F_n$  can be simply rearranged from equation (9) as:

$$B_{n+1} = R_0(1 - F_n)B_n \quad (18)$$

Minimum and maximum values of  $R_r(n)$  were similar for all  $p$  values greater than  $p=5 \times 10^5$  boat·days (Fig. 8a), so we chose  $p=7 \times 10^5$  boat·days as an example to examine relative changes in the spawner-recruit relationship. The resulting mean value of  $R_r(n)$  from 1971 to 1995 is  $R_0=1.33$ . Next, we set the temporal change of  $F_n$  at  $p=7 \times 10^5$  boat·days and the initial biomass at  $B_1$  (starting year  $n=1$  is 1971), and then calculated the stock sizes ( $S_n$  and  $B_n$ ) and estimated catches ( $C_n$ ) from 1972 to 1996 (Fig. 9). During 1972-1977, catches were high and the stock sizes declined slightly. After 1977, catches and fishing mortality rate ( $F_n$ ) both declined. After about 1983, catches were stable, while the stock size gradually increased.

Changes in long-term catches of *T. pacificus* have been attributed to both fishing variability (Murata, 1990; Adachi, 1994) and environmental change (Sakurai et al., 2000). Our results show that long-term variation in stock size can be interpreted by both long-term variation of fishing effort and long-term change in the

carrying capacity. It is not clear which is more important, but the short-term (<5-year) variability of  $R_r(n)$  and  $R_k(n)$  [ $r=0.5$ ] cannot be attributed to variation in fishing effort (Fig. 9), suggesting that this short-term variability is possibly related to environmental effects independent of fishing effort.

Even though stock size was not known, concurrent good and poor years of  $R_r(n)$  and  $R_k(n)$  [ $r=0.5$ ] could be used to examine changes in recruitment driven by the environment. Based on this criterion, during 1971–1995, we identified eight years of good recruitment (1972, 1974, 1979, 1981, 1984, 1986, 1988 and 1991) and seven years of poor recruitment (1973, 1976, 1980, 1985, 1987, 1990, and 1993) (Figs. 8a and 8b). To determine the value of these results, short-term change in these recruit indexes were compared with environmental variations that occurred in the Japan Sea.

### Recruitment and the environment

Significant differences in SSTs occurred between good- and poor-recruitment years in the southern part of the Japan Sea, i.e., the Tsushima Current area, in winter and spring (Fig. 10). Large (> 0.5°C) differences in SSTs occurred in offshore areas east of Korea and west of Kyushu near the main spawning area. SSTs did not differ between good and poor years during autumn of year  $n$  or during summer of year  $n+1$ . This suggests that SSTs were significantly lower during winter and spring of year  $n+1$  than during the same seasons in years of good recruitment.

Next, we chose winter-SST anomaly taken from two areas east of Korea (36°–38°N, 129°–131°E) and west of Kyushu (32°–34°N, 127°–129°E), compared the recruit index  $R_r(n)$  with environmental conditions (SSTs and MOI), and found a surprisingly clear relationship between recruitment and the environment; namely that low SST in winter corresponded well with low recruitment (Figs. 11a–c). This relationship suggests the usefulness of using short-term recruit indexes. Winters of low SST were also years of strong northwesterly winds (Fig. 11d), suggesting that strong outbreaks of cold air in winter were probably responsible for the lower SST in winter.

### Discussion

This study proposes a new method for estimating annual variation of relative recruitment using a simple biomass dynamics model. Roel and Butterworth (2000) used a similar, though more complex, model to estimate recruitment in the South African chokka squid *Loligo vulgaris reynaudii*. ICES (1988) strongly favored the use of such models for cephalopod stocks, yet they

remain seldom used for these stocks.

Years of poor recruitment corresponded closely to years of lower than normal sea surface temperatures. Similar patterns of reduced recruitment following periods of reduced temperatures have been reported for the squids *Illex illecebrosus* (Dawe and Warren, 1993) and *Ommastrephes bartramii* (Yatsu et al., 2000), however some species show a negative correlation between temperature and recruitment (e.g., *Loligo gahi*, Agnew et al., 2000; *Illex argentinus*, Waluda et al., 1999).

Reduced recruitment into the fishery corresponded with lower than normal temperatures in the winter and spring preceding the fishery. Squid of the autumn-spawning group hatch mainly during September through November, so reduced temperatures in winter and spring would have affected squid that were 2–8 months old. Sakurai et al. (2000) suggested that long-term variation in recruitment is related to the effect of temperature on larval production, however our results suggest that short-term variation in recruitment is related to temperature and weather conditions that prevail later in the life cycle.

The processes underlying the relationship between winter/spring SSTs and recruitment in *Todarodes pacificus* are unknown. However, Bakun and Csirke (1998) have described several possible mechanisms by which reduced temperatures during this period could adversely affect recruit success by delaying the development of prey for the young squid (i.e., the match/mismatch hypothesis of Cushing, 1975) and slowing the growth of squid, thus increasing the period during which they are highly vulnerable to predation. Zooplankton biomass also tends to decrease in the southern Japan Sea during years of decreased temperature (Hirota and Hasegawa, 1999; Minami et al., 1999; Kang et al., 2002), which could also adversely affect the year class.

When climatic effects on fished populations are examined, SST is generally the first factor considered, mainly because it is the easiest oceanic physical variable to observe in upper layer waters. However, correlation between a response in a population and temperature variation does prove temperature itself is actually the causative agent causing the biological change (Bakun, 1996). Rather, temperature might act as a surrogate variable for some other process affecting the population. In the present study, winters of low SST were also years of strong northwesterly winds, which could also adversely affect recruitment. Strong northwesterly winds will cause a southwestward flow in the surface Ekman layer (0–50 m depth), which is where most of the early stages of *T. pacificus* occur (Watanabe, 1965). In such a flow, young stages in and near the Tsushima/Korea Strait (between Korea and Kyushu) would be pushed

inshore of Korea (Nakata et al., 2000), interrupting their northeastward transport to the northern feeding grounds. Wind-generated turbulence has been shown to lead to recruitment failure in fish larvae (Lasker, 1975, 1978). Sakurai et al. (2003) have also suggested that strong winds might cause damage to egg masses, resulting in reduced hatching success.

Our results suggest fishery managers might be able to better predict years of poor recruitment based on SST and wind data collected in winter and spring. Japanese fisheries scientists now determine the acceptable biological catch (ABC) of the *T. pacificus* fishery in the Japan Sea using several data sources, including plankton surveys for paralarvae and jig-fishing surveys in June and July for pre-recruits (H. Kidokoro, Japan Sea National Fisheries Research Institute, Niigata, Japan, personal communication). Such surveys offer one way of predicting recruitment, however understanding the effects of environmental variables such as wind stress and winter-SST in year  $n-1$  on recruitment will help managers better predict future stock size.

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