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## The Niches of the Far Eastern Sardine and Japanese Anchovy

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### Abstract

The mean spawning seasons and locations and food items in stomachs of the Far Eastern sardine *Sardinops melanosticta* (Temminck and Schlegel) and Japanese anchovy *Engraulis japonica* (Houttuyn), which were considered as three dimensions of time, habitat and resource of the niches, were examined and compared with those of the chub mackerel *Scomber japonicus* (Houttuyn). The sardine and anchovy were far from each other in the time and habitat dimensions but close in the resource dimension. Competition coefficients and niche breadths were calculated for sardine and anchovy. A numerical relationship between the sardine and anchovy biomasses was estimated and discussed in light of the possible competition for food between the two species.

## Introduction

Catches of the Japanese anchovy *Engraulis japonica* (Houttuyn), Far Eastern sardine *Sardinops melanosticta* (Temminck and Schlegel) and chub mackerel *Scomber japonicus* (Houttuyn) have fluctuated widely since the 1950s (Fig. 1). As Kawasaki and Omori (1988) noted, the sardine population surged from the early 1970s to the early 1980s, while the anchovy declined, which suggests that competition might have occurred between the two species. This work describes the interactions between the two species by examining their niches and comparing them with the mackerel. A niche generally has three major dimensions: time, habitat and resource (Christiansen and Fenchel 1977). Therefore, the spawning seasons and locations, and foods of the three species were examined.

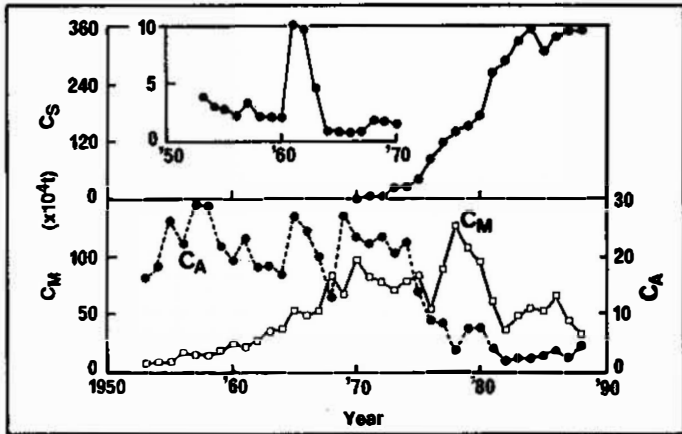


Fig. 1. Fluctuations in catches (in  $10^4$  t) of the Far Eastern sardine ( $C_S$ ), Japanese anchovy ( $C_A$ ) and chub mackerel ( $C_M$ ) landed in the Pacific coast of Japan.

The population dynamics of the anchovy are discussed in light of studies on other anchovy and sardine stocks in eastern boundary current systems and the possible competition for food from the sardine.

## Materials and Methods

### *Food Composition and Competition Coefficients*

Sampling of sardines and anchovies along the Pacific coast of Japan was conducted from April 1988 to December 1989 to examine the characteristics of food in the stomachs. Three areas ( $A_1$ - $A_3$ ) where samples were obtained are indicated in Fig. 2. Stomach contents were filtered with a mesh of  $160 \mu\text{m}$  by which we could effectively divide the contents into two categories, algae and zooplankton. A fraction (10-100%) of the zooplankton was observed under a measuring microscope. All copepods in the fraction were counted and their prosome length measured. The samples were left for about 24 hours before the deposits of algae and zooplankton were put into an electric drier at a temperature of  $90$ - $100^\circ\text{C}$  for 10 hours. The somewhat high temperature was set to shorten drying time; no combustion was observed during drying. The dried weights of the two parts

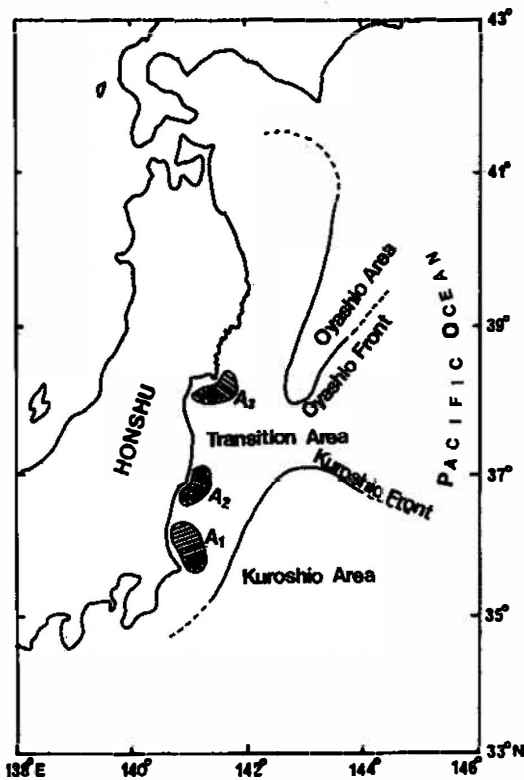


Fig. 2. Locations of sampling of sardine and anchovy ( $A_1$ - $A_3$ ), and the oceanographic structure east of Japan.

were measured. Algal fraction ( $P_a$ ), defined as the proportion of dried algae weight to the total dried weight of stomach contents by sampling area and month for sardine and anchovy, respectively, is given in Tables 1 and 2. The size compositions of copepods for sardine and anchovy are presented by histograms in Fig. 3.

Takeuti (1985) observed food composition in terms of species and size of phytoplankton in stomachs for sardine and anchovy sampled from the Pacific coast of Japan. His data are summarized in Table 3. The same food classification was used in the present study.

Competition coefficients and niche breadths are calculated with the following formulae (Levins 1968):

$$a_{ij} = \sum (P_{ih} P_{jh})^{\sum P_{ih}^2}$$

$$B_i = 1 / \sum P_{ih}^2$$

where  $a_{ij}$  is the competition coefficient of species  $j$  against species  $i$ ,  $B_i$  is the niche breadth of species  $i$ , and  $p_{ih}$  is the proportion of species  $i$  in  $h$ th unit of the resource. The competition coefficient is essentially the ratio of the probability that individuals of two species meet (in the sense of seeking food in the same habitat, or pursuing the same kind of prey) to the probability of encounters between members of one species (Levins 1968). Unless their niche breadths

Table 3. Relative frequency (percentages) of phytoplankton by species and size class in stomachs of the sardine and anchovy (after Takeuti 1985).

Class ( $\mu\text{m}$ )	Species					
	Nt	Cs	Ct	Mn	Lc	Others
<b>Sardine</b>						
0-50	0	25.1	0	14.4	0	2.6
50-100	6.2	5.6	2.4	10.5	0	7.9
100-150	10.5	0.8	0	1.5	8.3	4.3
<b>Anchovy</b>						
0-50	0	20.4	0.8	35.2	0	1.2
50-100	3.8	1.6	1.8	20.1	0	4.9
100-150	5.3	0	0.8	1.8	0.4	2.1

Nt = *Nitzschia* spp., Cs = *Coscinodiscus* spp., Ct = *Chaetoceros* spp., Mn = Minute zooplankton or eggs, Lc = *Licmophora abbreviata*.

The sardine and anchovy foods mainly consist of phyto- and zooplankton, and the total food items were defined to be the 18 phytoplankton items specified each by a particular species and a particular size class (Table 3) together with the 18 copepods items represented each by a particular prosome length class of 0.05 cm (Fig. 3). The incidence of a phytoplankton item in the total food items was calculated as the product of its incidence in the phytoplankton items (Table 3) and the algal fraction ( $P_a$ ), and the incidence of a copepod item as the product of its incidence in the copepod items (Fig. 3) and  $(1-P_a)$ . The algal fraction was obtained by taking an average over all the samples (Tables 1 and 2). These incidences were substituted for  $P_{ih}$  in calculating the competition coefficient and niche breadth.

### Spawning Season and Location

The sardine, anchovy and mackerel spawn throughout the year and the mean spawning season ( $T$ ) of a species is calculated as an egg number-weighted mean:

$$T = \frac{\sum_{i=1}^{12} (i \cdot E_i)}{\sum_{i=1}^{12} E_i}$$

where  $E_i$  is the number of eggs produced in month  $i$ .

The spawning grounds of the three species spread widely and the mean longitude (L) was taken to represent a species' spawning location in a year:

$$L = \frac{\sum_{i=1}^n (i \cdot L_i)}{\sum_{i=1}^n E_i}$$

where n is the number of survey subareas (30'·30'),  $E_i$  is the number of eggs in  $i$ th subarea, and  $L_i$  is the central longitude of the  $i$ th subarea. Egg production data by month and survey subarea were obtained from Mori et al. (1988).

### *Estimation of Biomass*

The biomasses of sardine and anchovy were estimated by dividing catches by exploitation rates, which were assumed to be the same for both species since fishing gears and methods for the two species have been similar (Kondo 1971; Kondo et al. 1976). Exploitation rates were roughly estimated in the following way: Nakai (1960) estimated the sardine's annual survival rates in 1949-54 using catches at successive age groups, the mean of which was 0.51. Wada (1988a) estimated the annual survival rates for 1974-80 year-classes from available stock sizes at successive age groups, the average of which was 0.42. The exploitation rate (E) is calculated from the following two equations (Ricker 1975):

$$S = e^{-F \cdot M}, \text{ or } F = -M \cdot \ln(S)$$

$$E = (1-S)F / (F+M)$$

where S is survival rate, F the instantaneous rate of fishing mortality, and M the instantaneous rate of natural mortality. Assuming M to be 0.37 (Yamanaka 1960), the exploitation rates during the above two periods, around 1952 and 1981, are 22 and 33%, respectively. According to Hiramoto (1981), in the late 1930s, powered fishing vessels enabled fishers to begin offshore operations which reached as far as 20 miles from the coast. Since then, the fishing ground continued to expand with upgrades of both size and power of fishing vessels. In the early 1950s, the echosounder was introduced into fishing, and fishing net material changed from cotton thread to synthetic fiber. Recently, further progress in fishing vessel equipment and in the information interchange system have been attained by

wide application of computer technologies (Wada 1988a). All these suggest that the exploitation rate must have increased, and a linear trend with the slope equal to  $(0.33-0.22)/(81-52)$  during 1952-88 was assumed.

## Results

In nearly all the sardine and anchovy stomach samples, the dominant zooplankton were copepods. In Fig. 3, the mode for sardine occurs at a smaller size than for anchovy. The calculated competition coefficients and niche breadths are as follows:

$$\begin{aligned} a_{SA} &= 0.79, & a_{AS} &= 0.81 \\ B_S &= 15.23, & B_A &= 15.55 \end{aligned}$$

where S and A denote sardine and anchovy, respectively. The niche breadths of the two species are nearly the same.

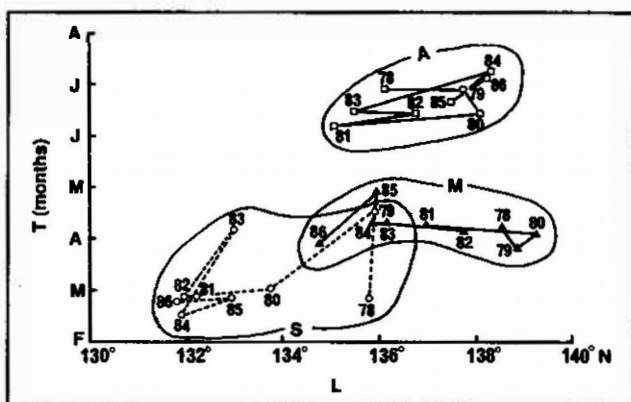


Fig. 4. Mean spawning seasons (T) and longitudes (L) of the Far Eastern sardine (S), Japanese anchovy (A) and chub mackerel (M) during 1978-86.

The relationship among the anchovy, sardine and mackerel in terms of spawning season and location is illustrated by plotting the mean spawning seasons against the mean longitudes (Fig. 4). It can be observed that the three species possess different positions in the niche, with anchovy and mackerel close in habitat but far in the time dimension; sardine and mackerel close in time but far in the habitat dimension; and sardine and anchovy far from each other in both habitat and time dimensions.

A numerical relationship between the estimated biomasses of the anchovy and sardine (A and S) for 1953-88 was obtained using the least-squares method:

$$A = K \cdot r \cdot S^q \quad (n=36, \text{ss}=8,355.5)$$

where  $K=99.7$ ,  $r=6.35$ ,  $q=0.39$ , and  $ss$  denotes the sum of squares of residuals. A and S are in  $10^4$  tonnes. The estimated biomasses of anchovy and the ones calculated from the above relationship are compared in Fig. 5.

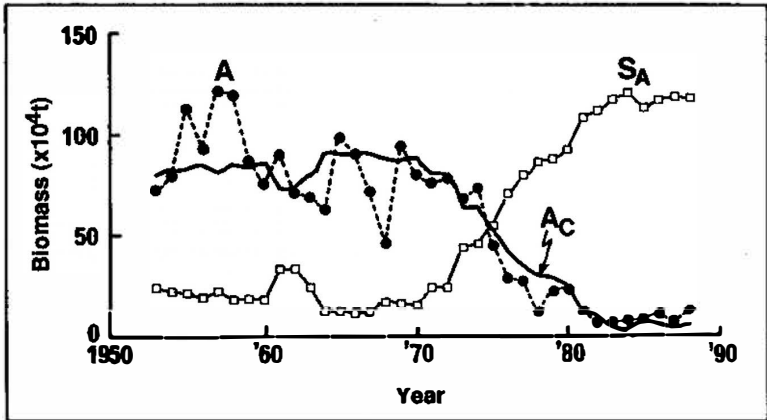


Fig. 5. Estimated biomasses of the Japanese anchovy (A) and the ones ( $A_C$ ) calculated from Equation 1 (see text), and estimated biomasses of the sardine within anchovy's niches ( $S_A$ ).

## Discussion

The antagonistic fluctuation in abundance between an anchovy and sardine pair is also a common phenomenon to four eastern boundary current systems: California, Peru, Canary and Benguela (Lluch-Belda et al. 1989). In a comparative study of climatology of environmental processes in relation to eastern boundary current pelagic fish (pilchard and anchovy) reproduction, Parrish et al. (1983) suggest that temperature, transport and turbulence patterns greatly influence the timing and location of spawning grounds. Bakun and Parrish (1982) compare the California and Peru current systems in terms of three environmental processes: turbulent mixing, offshore transport and upwelling intensity. They noticed that a



consistent pattern of avoidance of centers of maximum upwelling is the reproductive strategy of anchovies. Bakun and Parrish (1990) found that the peak spawning activity of the Brazilian sardine (*Sardinella aurita*) during summer serves to place larvae into a stable and enriched environment, which is a similar strategy utilized by the more temperate *Sardinops* and *Sardina* stocks of eastern boundary current systems. These previous works suggest that while environmental factors can influence the reproductive successes of sardine and anchovy stocks, these fishes seem to have developed a reproductive strategy to minimize adverse environmental influence.

As for the antagonistic fluctuations in abundance of anchovies and sardines, there is little published evidence suggesting that the sardines benefit from changes in some physical environmental factors while the anchovies suffer from them or *vice versa*. As Bakun (1986) notices, attempts to relate variations in reproductive successes of fish populations to variability in the environment have been generally unsuccessful. However, the roles played by physical environmental factors in population dynamics of anchovy and sardine should not be rejected since, as Bakun (1986) suggests, a variety of processes, varying widely over a broad range of time and space scales, is potentially involved.

Biological processes, mainly food competition here, may play an important role in anchovy and sardine dynamics. According to Kondo (1971) and Kondo et al. (1976), both sardine and anchovy feed on copepod eggs and copepods at the nauplius and copepodite stages during the postlarval stage, and they begin to utilize phytoplankton in addition to zooplankton (mainly copepods) at the juvenile stage with sardine dependent on phytoplankton to a greater extent than anchovy. Sato et al. (1968) observed stomachs of mackerel sampled from a wide area along the Pacific coast of Japan during 1963-66 and found that crustaceans (mainly Copepoda, Euphausiacea and Amphipoda) were the main food, followed by anchovy, which was often dominant during summer and autumn. On the basis of examining samples from northern coastal areas east of Japan in 1972, 1975 and 1976, Iizuka (1976) noticed that in May-August, anchovy and crustaceans were major foods for mackerel younger than one year, and crustaceans were the main food for mackerel of one and two years old; during September-December, anchovy was dominant as food for mackerel up to two years old. From these works, it is obvious that sardine and anchovy are much

closer than sardine (or anchovy) and mackerel with regard to food items.

The far distance between sardine and anchovy in the time-habitat niche may be a result of trying to ease severe competition for food which is another dimension of the niche. The food shortage could become crucial if the two species spawn at the same time and area. The far distance thus may not suggest a weak interaction, but a severe interaction in another determinant dimension of the niche. The positions of mackerel and anchovy in the time-habitat niche may be the result of a trade-off between predatory effort by predator and the prey trying to escape predation.

The numerical relationship between estimated biomasses of anchovy and sardine ( $A+r \cdot S^q=K$ ) can be interpreted as follows: the niche suitable for the anchovy determines the upper limit of its biomass ( $K$ ) and is shared with its competitor, sardine;  $r \cdot S^q$  can be regarded as the sardine's biomass that is equivalent to the anchovy's in occupying anchovy's niche, which could be roughly the product of sardine's biomass within anchovy's niche ( $S_A$ ) and its competition coefficient against the anchovy. Although the niche generally has three dimensions, it is known from the forgoing part that the anchovy and sardine are far from each other in time and habitat dimensions, and the competition between them may be largely due to food overlap. Therefore, the following relationship may roughly hold:  $r \cdot S^q = S_A \cdot a_{AS}$ , or  $S_A = r \cdot S^q / a_{AS}$ , and a rough estimation of the sardine's biomass within the anchovy's niche (Fig. 5) is possible.

The sardine has exhibited large expansions and contractions of range concomitant with changes in its abundance. At high levels of abundance, the sardine spawning grounds move southwestward and their feeding range extends (Nakai 1962; Watanabe 1975; Kawasaki and Omori 1988; Wada 1988b). However, the anchovy has not exhibited large changes in its range. This may explain why  $S_A$  is not proportional to the sardine's biomass but to a power function of it with the power less than 1.

As noticed above, the food items of sardine and anchovy at both larval and adult stages are very close to each other. Food shortages can occur when either or both of the two species are at high density levels. Therefore the sardine's competition for food could be one of the possible dominant causes of the anchovy's decline during the early 1970s to the early 1980s.

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