21.Response of Plankton and Fish Production Dynamics to Sardine Abundance Regime Shifts in the Oyashio Current Region

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Abstract

First order estimates of annual production, seasonal biomass patterns, and production to biomass ratios were determined for major components of the pelagic food-web observed during the high sardine abundance regime of the 1980s in the Oyashio current region off Hokkaido using a one-dimensional ecosystem model. The model consists of diatoms, copepods, euphausiids, walleye pollock, and Pacific sardine, and it was forced using time dependent functions of sea surface temperature, mixed layer depth, mixing rate, surface light, and sardine migration. The model estimates diatom production during the 1980s to be about 2293 t km^{-2} y^{-1}, zooplankton production between 119 to 271 t km^{-2} y^{-1}, sardines 23 t km^{-2} y^{-1} , and pollock production 7 t km^{-2} y^{-1}. Sensitivity analyses indicated that euphausiid and pollock production were most sensitive to changes in zooplankton feeding parameters. Diatom and sardine production were most sensitive to changes in physical forcing parameters, while copepod production was sensitive to both zooplankton feeding parameters and physical forcing parameters. To address the relative importance of sardine biomass on whole system production dynamics we conducted a model experiment whereby sardine biomass was set to zero. Euphausiid production responded drastically to a reduction in sardine biomass. In addition, pollock production was enhanced with the removal of sardines. These results imply that the presence of high biomass of sardines may act as competitors to other planktivores and to euphausiids for limited diatom and copepod production in feeding grounds.

Introduction

The Japanese sardine (*Sardinops melanostictus*) population has fluctuated between high and low abundance regimes corresponding with ocean-climate changes (Lluch-Belda *et al.*,1992). During the high abundance regime, for instance the 1980s in recent years, abundant of sardines migrate into the Oyashio Current region off Hokkaido to feed in summer and autumn. However, during the low abundance regime, their habitat is restricted in the coastal areas off the mid- to southern part of Japan, and their migration to the Oyashio region is very scarce. On the other hand, this region is also important as a feeding ground

for resident and migrate fishes such as walleye pollock (*Theragra chalcogramma*) and Pacific saury (*Cololabis saira*). Therefore, how the presence of abundant sardine will affect to production of plankton and fish in this region is very important question for better understanding on the dynamics of ecosystem of this region.

In this study, we develop a dynamic food-web simulation model of the dominant pelagic fish (sardine and pollock) and plankton observed during the high sardine abundance regime in the 1980s, as forced by time-dependent patterns in water temperature, mixing rate, and mixed layer depth, and sardine migrations. Then we examine the response of plankton and fish production with the changes in physical forcing and sardine migration.

Pelagic Food Web Structure

We considered the waters on continental shelf and slope shallower than 1,000m along the southeastern coast of Hokkaido as the study area. This area almost corresponds to fishing grounds for sardine purse seine fishery in the 1980s, and it has a surface area of about 12,800 km².

The summer food web observed in the Oyashio region during the 1980s is summarized in Fig. 1. The Japanese sardine and walleye pollock dominated the total fish biomass. These fish feed primarily on plankton, diatoms, copepods, and euphausiids.
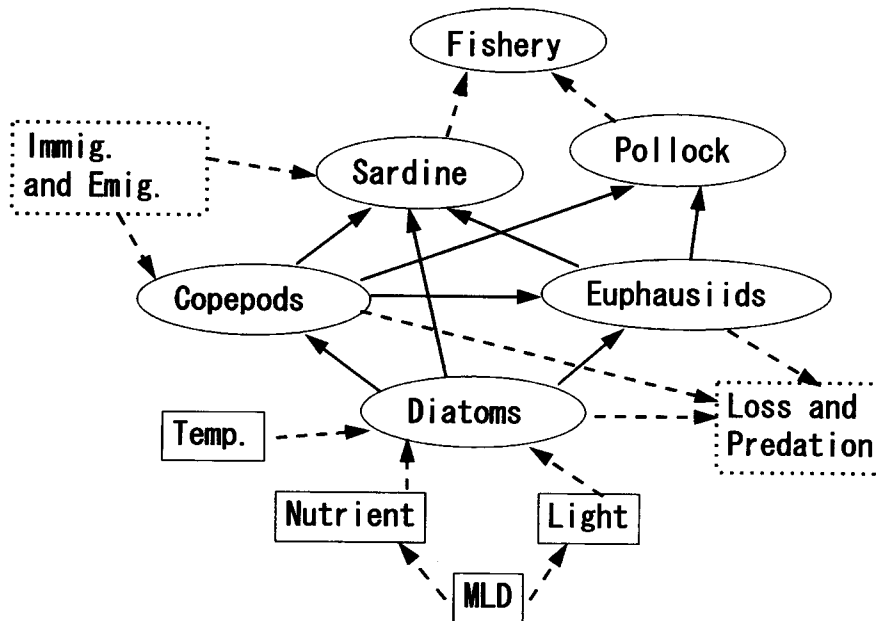

Fig. 1. Overview of the feeding interactions (solid lines and arrows) and other processes included in the Oyashio region model during the 1980s. Water temperature affects diatom growth, all feeding interactions, and sardine biomass.

The dominant phytoplankton in the Oyashio region are diatoms. Based on resent satellite images, the spring bloom normally begins near the end of March, peaks in early May, and ends in late July. Primary production has been estimated to average 160g $Cm^{-2}y^{-1}$ or 2368 t (wet) $km^{-1} y^{-1}$ (Taniguchi, 1972).

Net sampling indicates that the dominant zooplankton in the study area are copepods (Taka *et al.*, 1980; Odate, 1994). Zooplankton standing stock reaches a maximum of 30 - 90 g m^{-2} (or 30 - 90 t km^{-2}) between early-May to mid-June (Odate, 1994). Copepods immigrate into the surface layer during the spring bloom. In the autumn most of the copepod biomass emigrates vertically to deeper waters where they overwinter. Seasonal changes in euphausiid biomass are not well documented. However, net catches and stomach contents of pollock suggest that the biomass is low in spring and high in autumn (Maeda *et al.*, 1980; O. Yamamura, unpubl. data). Maeda et al. (1980) also suggested that euphausiids distribute in surface layer during the young stages but move to deeper waters with their growth.

Sardines immigration into the region is usually started in early-June and finished by late-July. It is estimated that when sardines were abundant in the mid 1980s, about 3 million t of fish passed through the Oyashio region. About 1 million t stayed in the area to feed, while the remaining 2 million t migrated to more northern or offshore feeding grounds (Wada, 1988). This northern component of the stock re-entered the Oyashio region later in the summer on their return migration to the spawning grounds off southern Honshu. This complex immigration - emigration pattern causes the biomass of sardine in the Oyashio region to be bimodal. The diet of sardines has been found to include three principal prey diatoms, copepods, and euphausiids. During the feeding period in summer an average sized sardine (70 g = 18 cm) grows about 0.14 g d^{-1} (or 0.2% of the body weight d^{-1}). The annual catch in the Oyashio region is about 1 million t (78 t km^{-2}).

There are about 310,000 t (24 t km^{-2}) of walleye pollock in the Oyashio region. The average (age-composition weighted) pollock body weight is about 359 g. The age composition weighted diet is 46% euphausiids, 30% copepods, and 24% mesopelagic fish. The observed pollock growth rate averages 188 g $individual^{-1} y^{-1}$ (or about 0.14% of the stock biomass d^{-1}). The annual pollock catch in the Oyashio region is about 67,000 t y^{-1} (5.2 t km^{-2}).

Model Description
The pelagic food-web and physical oceanographic processes of the Oyashio region were modeled dynamically using STELLA-II software (High Performance Inc.) . The model is forced by physical functions input as time dependent processes (after Robinson and Ware, 1994). Biomass and production estimates of food-web components are calculated daily for January 1 to December 31.

Daily diatom biomass is modeled by numerically integrating growth, grazing losses to copepods, euphausiids, and sardines, and a mixing loss. The maximum diatom growth

rate (expressed as doublings/day) is a function of water temperature (after Eppley, 1972) and average day length. We assume that the maximum growth rate is light-limited in winter and nitrogen (N)-limited in summer. In general, N is high in winter and peaks between February and March (Tanaka *et al.*, 1991). The only sources of N included in the model are: 1) the amount of N in the mixed layer in spring, 2) the amount of N excreted by zooplankton and fish in the mixed layer, and 3)diffusion of N across the pycnocline (after Evans and Parslow, 1985). We employed the Parsons and Takahashi (1973) formulation for estimating the average light in the mixed layer using the information about day length, surface light levels, the MLD, and a phytoplankton self-shading factor. We have also included a term to account for diatom biomass losses due to sinking, advection, and grazing from other organisms.

Zooplankton (copepods and euphausiids) biomass is modeled by numerically integrating growth, immigration, emigration, mortality and unspecified losses. The growth rate is equal to a variable ingestion rate multiplied by a constant gross growth efficiency. The ingestion rate is a function of pray biomass (using a Michaelis-Menten feeding function), and water temperature. Mortality is modeled as a function of predation, and varies in proportion to the predator biomass. In the model, copepods and euphausiids migrate into the surface layer during the spring bloom, and emigrate from the surface to deeper layer in the autumn with a decline in diatom production. We have included a copepod loss term to account for unspecified processes such as advection, mortality due to other predators, and losses due to senescence. For euphausiids, we have also included a miscellaneous predation loss term which are inversely related to copepod biomass.

In modeling fish biomass dynamics we considered their growth, seasonal migration patterns, and losses due to the fishery. The growth rate is modeled using a variable ingestion rate multiplied by a constant gross growth efficiency. The daily prey ingestion is equal to a maximum daily ingestion rate multiplied by a Michaelis-Menten function which considers the prey biomass. We have modeled the seasonal migration of sardines as being dependent on water temperatures in the Oyashio region, and on the biomass of sardines in the southern waters. The fishery normally opens on July 1 and closes around the end of October. The catch rate is assumed to be proportional to 1% of the biomass in the Oyashio region on any given day. Natural mortality of pollock is assumed to be constant throughout the year. The annual catch rate of pollock was assumed constant at 5.5 t y^{-1}.

Results and Discussion
Standard model run during the 1980s

The seasonal biomass patterns of simulated biological components and biomass flows among the components were shown in Fig. 2 and 3, respectively. The seasonal biomass patterns were consistent with observations. The annual diatom production was estimated about 2293 t wet weight (WW) km^{-2} y^{-1}, with an average annual biomass of 97 t WW km^{-2}. In contrast, the annual production to biomass ratio (P/B) for diatoms was only

24. The majority of annual diatom production was lost to copepod predation (31%), while only 5% was lost to sardine predation. The simulated annual production of copepods is about 271 t WW km^{-2} y^{-1}, with an average annual biomass of about 26 t WW km^{-2}. This translates into a P/B ratio of about 10.4. The majority of copepod biomass is lost to predation by euphausiids, and to sardines. The majority of euphausiid biomass is lost to miscellaneous predation (67%), pollock predation (19%), and sardine predation (18%). The simulated annual euphausiid production is about 119 y^{-1}.
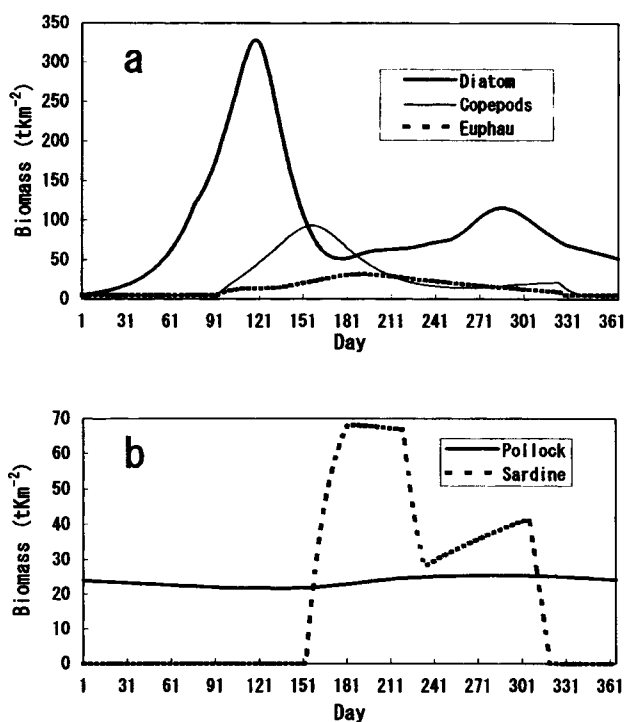

Fig. 2. Seasonal biomass patterns for plankton (a) and fishes (b) of
the standard model run during the 1980s.

Pollock biomass remains relatively constant in the Oyashio region year-round at between 21-25 t WW km^{-2}. The simulated annual pollock production is about 7 t WW km^{-2} y^{-1} with an annual P/B ratio of 0.3. The fishery removes 72% of the annual pollock production . The sardine seasonal biomass pattern is bimodal reflecting the mass movement of fish into and out of the Oyashio region. The annual sardine production is 20t WW km^{-2}y^{-1}. The annual P/B of sardines is about 4 times greater than pollock.
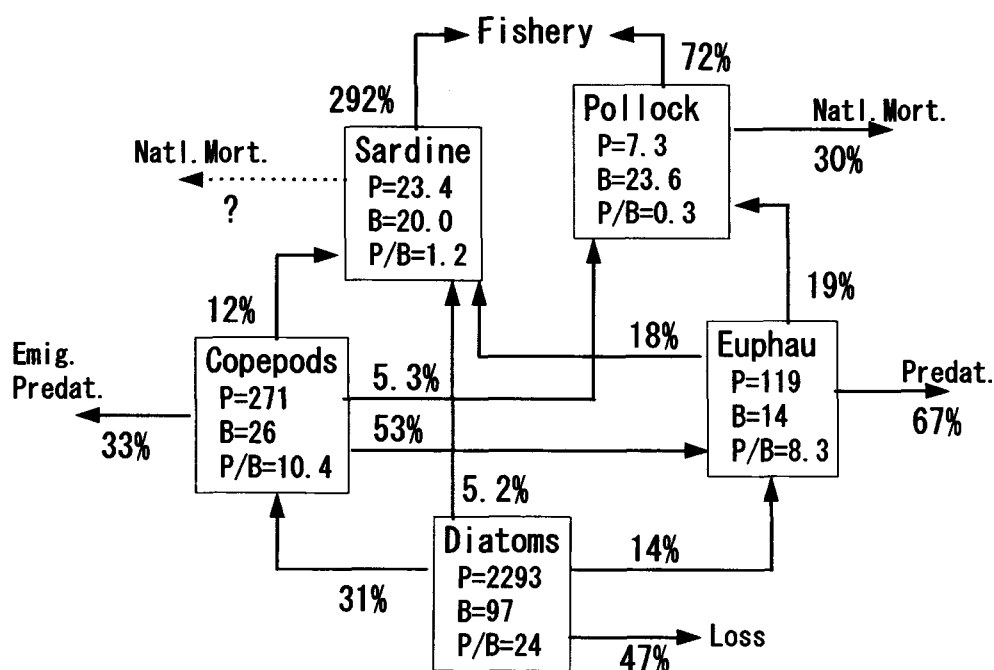
Fig. 3. Flow diagram of the standard model run during the 1980s. Flows are expressed
by percentage of biomass (P: annual production (t km^{-2}y^{-1}); B: mean annual
biomass (t km^{-2})).

Sensitivity analysis of the standard 1980s model run

To examine the implications of parameter uncertainty on model output, total of 33
parameters of the model were increased or decreased by 20% of their nominal values, while
remaining parameters were held constant. Relative changes in annual production of
plankton and fish were used to gauge the sensitivity of the model (After Robinson and Ware
1994).

In general, the model was fairly insensitive to parameter perturbations. However,
some parameters affected significantly to the production. Growth parameters of copepods
and euphausiids, such as gross growth efficiency and maximum food ingestion rate affected
to their own production themselves, and also affected to the predators (especially pollock)
production. Pollock showed greater sensitivity than sardine to perturbations in plankton
feeding parameters. This greater sensitivity in pollock production can be linked to a high
dependence of euphausiids in its diet. In addition, physical forcing functions, such as
mixing rate between the upper mixed layer and nutrient rich deeper water, and mixed layer
depth, affected to diatoms, copepods, and euphausiids production, and also affected to the
production of sardine and pollock as predators of them.

We conclude that the model is relatively insensitive to most parameter perturbations. This is because the majority of parameters are taken from well-founded empirical observations or from literature values. The parameters of greatest uncertainty (physical mixing and some zooplankton feeding parameters) caused the greatest variability in simulated annual production. The research team is presently increasing the complexity and understanding of the physical mixing processes, so as to reduce the uncertainty in these model parameters.

Comparison of system production dynamics

To investigate detailed seasonal changes in system properties and production dynamics between high and low sardine abundance regimes, we conducted a model experiment whereby sardine biomass was reduced to zero. We compare the results of the model experiment with the standard run in the 1980s (Table 1). In addition, we compared the production dynamics with results from a simulation model describing the plankton and fish production dynamics on the summer feeding grounds of sardine in the California Current, during the 1980s (Table 1).

Table 1. Comparison of simulation results of the Oyashio region standard model with production dynamics for sardine low abundance regime of the Oyashio region and the northern California current region.

Area	Property	Diatom	Cope	Euphau	Pollock	Sardine	Fish Total
Oyashio (High abundance regime)	Production (tkm^{-2}y^{-1})	2293	271	119	7.3	23.4	30.7
	Biomass (tkm^{-2}y^{-1})	97	26	14	23.6	20.0	43.6
	P/B ratio	23.7	10.4	8.3	0.3	1.2	0.7
	TE(%)		11.8	5.2	0.3	1.0	1.3
Oyashio (Low abundance regime)	Production	2303	225	153	10.8		10.8
	Biomass	105	22	18	24.8		24.8
	P/B ratio	22.0	10.0	8.5	0.4		0.4
	TE(%)		9.8	6.6	0.5		0.5
Northern California*	Production	4929	368	179			49
	Biomass	40	13	22			33
	P/B ratio	12.3	27	7.9	`		1.5
	TE(%)		7.3	3.6			1.0

*Robinson and Ware (1994)

In the case that sardine migration was zero, primary production did not changed. However, production decreased to 17 % in copepods. In euphausiids and pollock, the production increased to 1.3 and 1.5 times of that in the 1980s, respectively. From this results we supposed that sardine is a competitors to euphausiids and pollock for food in the Oyashio region. We also supposed that the increase of grazing pressure by euphausiids and pollocks reduced the copepods production.

In the comparison between the Oyashio region and the northern California current region, primary production of the northern California current region was 2.1 times higher

than that of the Oyashio region. However, sum of the copepods and euphausiids production was not so deferent between the both regions. The transfer efficiency from primary production to zooplankton production in the Oyashio region was 1.5 times higher than that of the northern California current region. In fish components, total production and P/B ratio in the northern California current region were higher than those in the Oyashio region. However, the transfer efficiency in the Oyashio region was higher than that in the northern California current region.

In the Oyashio region, primary production provided by a spring bloom transfers to zooplankton which has large body size and long life span, such as *Neoclanus,* with high efficiency. This may be a reason of the higher fish production in the region.

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