Long-term Variation in Mesozooplankton Biomass Caused by Top-down Effects: A Case Study in the Coastal Sea of Japan

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November 24, 2022

Abstract

Mesozooplankton biomass plays a key parameter in the recruitment processes of fish and biogeochemical processes. Four decadal observations in the coastal Sea of Japan, the marginal sea of the North Pacific, indicate that wet weight-based mesozooplankton biomass is controlled by both environment-induced bottom-up and predatory-induced top-down processes. Interannual variations in mesozooplankton biomass using a generalized linear model approach showed a decrease in biomass during the 1980s, followed by a rapid increase in the early 1990s, and a gradual decrease in the 2010s. These interannual variations were the mirror image of the small pelagic planktivorous fish biomass. The difference in zooplankton biomass from the previous year was negatively correlated with the difference in small pelagic planktivorous fish biomass, which was supported by a Granger causality analysis. Therefore, the results of this study indicate that top-down control is one of the main causes of long-term variations of zooplankton biomass in the ocean.

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Key Points:

1. Over four decadal observations on mesozooplankton biomass were conducted in the Sea of Japan.

2. These interannual variations of mesozooplankton were the mirror image of the small pelagic planktivorous fish biomass.

3. The first report on top-down control of zooplankton biomass in their long-term variations in the ocean.

Abstract

Mesozooplankton biomass plays a key parameter in the recruitment processes of fish and biogeochemical processes. Four decadal observations in the coastal Sea of Japan, the marginal sea of the North Pacific, indicate that wet weight-based mesozooplankton biomass is controlled by both environment-induced bottom-up and predatory-induced top-down processes. Interannual variations in mesozooplankton biomass using a generalized linear model approach showed a decrease in biomass during the 1980s, followed by a rapid increase in the early 1990s, and a gradual decrease in the 2010s. These interannual variations were the mirror image of the small pelagic planktivorous fish biomass. The difference in zooplankton biomass from the previous year was negatively correlated with the difference in small pelagic planktivorous fish biomass, which was supported by a Granger causality analysis. Therefore, the results of this study indicate that top-down control is one of the main causes of long-term variations of zooplankton biomass in the ocean.

Plain Language Summary

Mesozooplankton is the prey of many types of fish and export carbon and nitrogen from the surface ocean to the deep ocean. To identify changes in the zooplankton abundance and their reasons, wet weights of plankton net samples were measured over four decades from 1967 to 2019 in the Sea of Japan, surrounding Japan, Korea, and Russia. Yearly variations of wet weights were the mirror image of the small pelagic planktivorous fish biomass, that is, sardine, anchovy, and round herring. In addition, the increase (decrease) of wet weights was also related to the decrease (increase) of small pelagic planktivorous fish

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biomass. These results suggested yearly variation of zooplankton biomass in this sea is controlled by the feeding activity of fish.

1 Introduction

Mesozooplankton, mainly copepods but also including cladocerans and tunicates, link primary production and higher trophic production in marine ecosystems and regulate the biogeochemical cycles of the ocean [*Sommer and Stibor*, 2002; *Verity and Smetacek*, 1996]. Many species of fish and their larvae prefer to feed on mesozooplankton and their larvae [*Robert et al.*, 2014], and the abundance of mesozooplankton is a key parameter in the recruitment processes of fish [*Beaugrand et al.*, 2003]. The metabolism and migration processes of mesozooplankton activate the elemental (carbon and nitrogen) cycles of the ocean known as "active flux" [*Hernández-León et al.*, 2019; *Longhurst et al.*, 1990; *Steinberg et al.*, 2000]. This suggests that mesozooplankton abundance plays a significant role in the food supply for humans and in regulating carbon dioxide concentration in the atmosphere.

The mesozooplankton biomass in the ocean is controlled by both bottom-up and top-down processes [*Kiørboe*, 1997]. Relationships between temperature and mesozooplankton abundance have been reported in many marine ecosystems [*Richardson*, 2008] and are changing with global climate change [*Beaugrand*, 2005; *Roemmich and McGowan*, 1995]. Hence, zooplankton communities are considered to represent the effects of climate forcing in the marine pelagic food web [*Beaugrand*, 2005; *Mackas et al.*, 2006]. In addition to temperature, primary production also controls mesozooplankton abundance [*Messié and Chavez*, 2017]. Compared to studies on "bottom-up" processes, studies on "top-down" controls of mesozooplankton abundances are poor [*Kiørboe*, 1997].

The Sea of Japan, a semi-closed marginal sea of the western North Pacific, is one of the hotspots of anthropogenic change in the world [*Chen et al.*, 2017; *Wu et al.*, 2012]. The sea surface temperature increased more than 12 times the global rate from 1986 to 1998 [*Belkin*, 2009], the pH decreased even in deep waters [*Chen et al.*, 2017], and there is a decline in phosphates in the surface water [*Kodama et al.*, 2016]. This sea is also important for local and global fisheries because many commercially valuable fish species such as Japanese sardine (*Sardinops melanostictus*), Japanese anchovy (*Engraulis japonicus*), common squid (*Todarodes pacificus*), and Pacific bluefin tuna (*Thunnus orientalis*), use the Sea of Japan as spawning, nursery, and feeding grounds [*Furuichi et al.*, 2020; *Goto*, 2002; *Hiroshige Tanaka et al.*, 2020]. The Japanese sardine is the dominant fish [*Tian et al.*, 2014]. According to data from the 1980s, it had a large biomass (~10^7 t based on wet weight) [*Ohshimo et al.*, 2009], which was the same as the daytime mesozooplankton biomass (~10^7 tonnes) during that period [*Hirota and Hasegawa*, 1999]. In contrast, Japanese sardine biomass decreased to <10^4 t in the 2000s [*Ohshimo et al.*, 2009], and no other fish compensated for the loss of sardine biomass [*Tian et al.*, 2014].

We hypothesised that the "top-down" effect on mesozooplankton caused by pre-

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dation from small planktivorous fish varies in the coastal Sea of Japan along with "bottom-up" effects, including global warming. Top-down control of mesozooplankton biomass by sardines was also reported in the Oyashio area, the western North Pacific Subarctic region [*Tadokoro et al.*, 2005]. On the Pacific side, however, horizontal advection is another key process for controlling zooplankton biomass [*Chiba et al.*, 2013], suggesting that physical processes containing teleconnections makes the top-down processes ambiguous. The Sea of Japan can be treated as an oceanic microcosm [*Chen et al.*, 2017; *Wu et al.*, 2012]; thus, we expected to detect "top-down" processes in this sea. Here, we investigated the long-term variation of mesozooplankton biomass in the coastal Sea of Japan over four decades from the 1970s to 2010s and statistically confirmed that the "top-down" control of mesozooplankton biomass by small pelagic fish is the major cause of long-term variations in mesozooplankton biomass.

2 Materials and Methods

The wet weight data of plankton samples from the coastal Sea of Japan were used as the mesozooplankton biomass. This sampling area is bounded by 33° N to 48° N and 128° E to 142° E, similar to *Hirota and Hasegawa* [1999] which includes the north-eastern East China Sea **(Figure 1)**. The wet weight dataset in *Hirota and Hasegawa* [1999] from 1966 to 1990 was added to monthly egg survey samples conducted in the coastal Sea of Japan from 1978 to 2019. Duplicates of these two datasets were removed based on the geophysical position, sampling date and time, and wet weight values. As a result, 113,029 wet weight samples were collected from 1965 to 2019. The mesozooplankton samples were the remnants of monthly egg survey samples [*Furuichi et al.*, 2020; *Suzuki et al.*, 2018] collected using plankton nets that caught fish eggs and larvae, and squid. Jellyfish and garbage were identified and removed from the nets, and then the wet weight was measured [*Hirota and Hasegawa*, 1999]. Monthly egg surveys had been conducted by 17 prefectural institutes and two national fisheries research institutes along the Japanese coast in the Sea of Japan and East China Sea since 1978 [*Goto*, 1998]. The sampling methods and strategies were same as those in the western North Pacific reported in *Takasuka et al.* [2017] where the mesh size of the nets was 0.335 mm or 0.33 mm, Long North Pacific (LNP), North Pacific (NP), Maru-toku (MT), and Maru-naka (MN) nets were used for sampling, and the net towed vertically to 150 m depth or 10 m above the bottom (when the bathymetry was <160 m). Sea surface temperatures (SST) were included in the database.
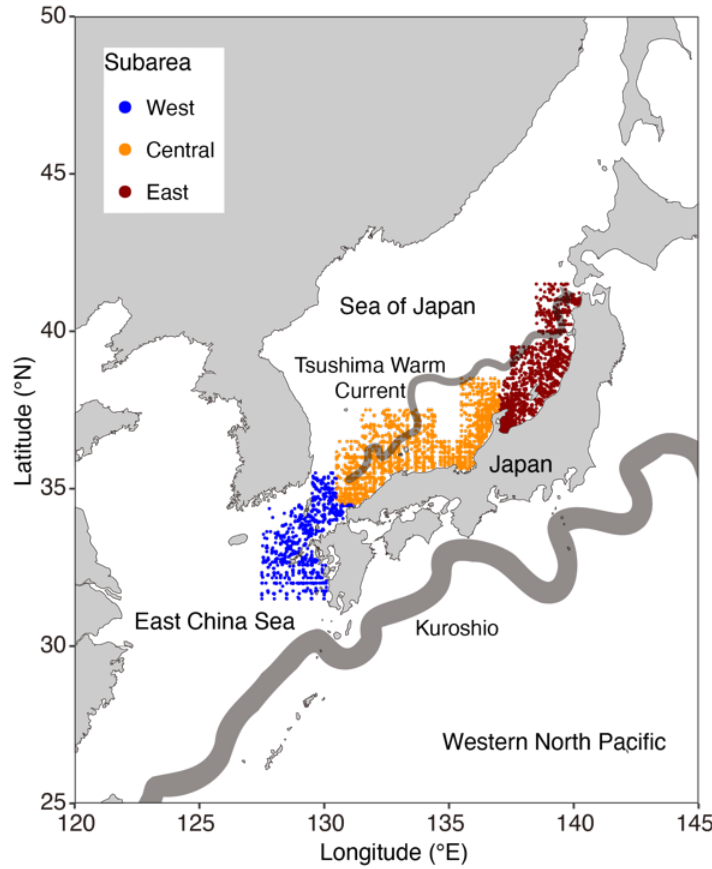
Figure 1 Distributions of sampling stations in this study. The colored dots indicate the stations with observed wet weight values and are used in the statistical analyses. The colors are corresponding to the subareas. The symbols indicate that stations observed the plankton assemblages. The line in the Sea of Japan and in the western North Pacific represents the Tsushima Warm Current, and Kuroshio, respectively.

Quality control of the datasets was conducted before further analyses. Some unreasonable and incomplete data were removed; for example, data that did not record the sampling date and time or recorded a non-existent date and time. Second, the filtration volume was recorded in many cases, but some were missing. To account for the missing data, linear regression models between the filtration volume and wire length were calculated for every sampling gear, and then the filtration volume was calculated based on the wire length and this model. Based on these relationships, filtration volumes outside the ranges of the 95% confidence interval were considered outliers, and subsequently removed. Third, zooplankton biomass is not vertically homogeneous [*Hirakawa et al.*, 1990]. Therefore, data from the samples towed from >400 m depth were removed. Fourth, we removed data for which the SST was not recorded. In addition, the monthly

mean SST and standard deviations (SDs) were calculated, and data with SST without the mean ± 3SD values were also removed. Fifth, the distribution of the sampling sites varied temporally. To remove geographical sampling bias, the data for the calculation of long-term variations were geographically limited to the area where sampling was continuously conducted. We set a 1° × 1° grid and removed the areas where sampling was not conducted over a decade after the 1970s. As a result, the observation areas were only limited to the Japanese coastal area **(Figure 1)**, and the number of datasets remaining after these quality control processes was 71,889. We did not apply any quality control processes to the wet weight data.

We divided the coastal Sea of Japan into three subareas: west (<130°30'E, $n = 12,827$), centre (130° 30'E –137°E, $n = 33,940$), and east (137°E, $n = 25,122$) **(Figure 1)**. The Tsushima Warm Current flows from west to east along the coastal area of the Sea of Japan [*Kawabe*, 1982]. The division of subareas was historically used in ministerial documents, but was based on biological evidence, such as fish assemblages [*Yoshida and Ito*, 1957].

The wet weight per cubic meter, calculated by dividing the wet weight of the plankton sample by the filtration volume, did not show a normal distribution (*Kolmogorov–Smirnov* test, $p < 0.001$); thus, the median of wet weights was treated as a representative value, and statistical dispersion was shown by the first and third quartiles (Q1 and Q3, respectively).

To identify the interannual, monthly, and daily variations, a generalized linear model approach was applied using R software [*R Core Team*, 2022] because the simple arithmetic medians of the measurements contained sampling bias. The results of the simple arithmetic medians of the measurements were shown in **Supporting Text**. The error distribution of the wet weight per cubic meter was assumed to show a gamma distribution, and the "log" link function was set to model the wet weight. The model was applied to the dataset divided into subareas (west, central, and east). All the explanatory parameters were transformed into categorical variables. The full model is as follows:

WWsubarea ~ glm(year + bimonth + bihour + sst + bathy) (1)

where WWsubarea, sst, and bathy represent the wet weight per cubic meter of subarea, sea surface temperature, and bathymetry at the station, respectively. Year, hour, and sst were binned every 1 year, 2 hours (bihour) and 1° C, respectively, to treat them as categorical values. The days from 1st January were binned every 61 days and treated as a bimonth. The bathymetry of the sampling stations was based on ETOPO1 [*Pante and Simon-Bouhet*, 2013], and was divided into three categories: shelf (<200 m depth), slope (200–500 m depth), and deep (500 m depth) waters. The collinearity of the three full models was checked, and the variance inflation factor adjacent to the degrees of freedom was always <2. The final model was selected using the Akaike information criterion (AIC). We removed data from the GLM analyses when the data were 10 in each category, for example, when there were only four samples with an SST of 4° C.

We also conducted the GLM approach, including sea surface height and sea surface chlorophyll *a* concentration, using datasets collected after 1998 to identify the effects of ocean current and primary productivity (**Supporting Text**).

The effects on the environmental parameters, including interannual variations in wet weight per cubic meter, were calculated using least squares mean (lsmean) values. The log-link function was used in the GLMs, and thus, the standard error (SE) values were shown as the power of Napier's constant (e). Instead of SE, the 95% confidence intervals (CI) were set as lsmean $\pm$ 1.96 $\times$ SE and shown as the error ranges. The interannual variations in mean mesozooplankton biomass in the Sea of Japan were estimated using the yearly lsmean values and the area of the subareas, which corresponds to a 0.1° $\times$ 0.1° grid (384, 767, and 522 in the western, central, and eastern subareas, respectively).

To identify the top-down effects of small pelagic fish on mesozooplankton biomass, interannual variations in mesozooplankton wet weight were compared with the biomass of small pelagic fish in the coastal Sea of Japan. The dominant small pelagic fish species in the coastal Sea of Japan are Japanese sardine, Japanese anchovy, and Pacific round herring [*Tian et al.*, 2014], and they mainly prey on zooplankton [*Baba et al.*, 2018; *H. Tanaka et al.*, 2006]. The interannual variations in these biomasses within the study area were obtained from stock assessment reports after 1977 [*Kurota et al.*, 2020; *Muko et al.*, 2020; *Yoda et al.*, 2020]. These datasets are time-series, and thus, testing for a unit root is required [*Phillips and Perron*, 1988]. Here, we applied the *Dickey-Fuller* test to every time-series dataset for a unit root test. We also tested the autocorrelation of disturbances using the *Durbin-Watson* test. When the *Dickey-Fuller* test was not significant (*i.e.,* the data had unit roots), the *Durbin-Watson* test was significant (*i.e.,* residuals of the regression analysis did not have autocorrelation at lag 1), and iterated differences of these two time-series data were calculated and compared. Granger causality was computed between the two relationships using the *vars* package in R [*Pfaff*, 2008]. A bootstrap test was conducted 1000 times.

To confirm the assemblages of plankton samples, wet weights were measured for each taxonomic group ($n = 740$). Possibly the samples contained diatoms, but the wet weights of the taxonomical groups in these data indicated that diatoms (classified as others) were <10% based on the IQR (median: 0.6%, Q1–Q3: 0–10.3%). Therefore, wet weight may be treated as a representative value of mesozooplankton biomass. We also counted the number of individuals at the genus level by microscopic observation in some samples ($n = 269$) from the 1970s (April 1972 and 1973), 1980s (March–May 1985 and 1990), 2000s, and the 2010s (**Supporting Text**).

3 Results

The wet weight per cubic meter was 0.025–11.8 g m^{-3}(median: 0.070 g m^{-3}, Q1–Q3: 0.036–0.14 g m^{-3}). The differences in subareas were significant (ANOVA, $p < 0.001$, degree of freedom = 2, $n = 71,889$), and the median (Q1–Q3) wet

weight was 0.099 g m^{-3} (0.053–0.187 g m^{-3}), 0.073 g m^{-3} (0.038–0.149 g m^{-3}), and 0.055 g m^{-3} (0.029–0.108 g m^{-3}) in the western, central, and eastern subareas, respectively.

In the GLM approach, full models were always selected as those with the lowest AIC values. The deviance explained [$100 \times (1 - \text{residual deviance/null deviance})$] was 35.3%, 33.4%, and 23.2% in the GLMs of the western, central, and eastern subareas, respectively. All explanatory variables in the three models were significant (ANOVA, $p < 0.001$). The effects of SST, month, sampling time and bathymetry were described and visualized in the Supporting Text.

The interannual variations in lsmean values showed that wet weight was low in the 1980s, elevated in the 1990s, and then decreased gradually in the 2010s **(Fig-**
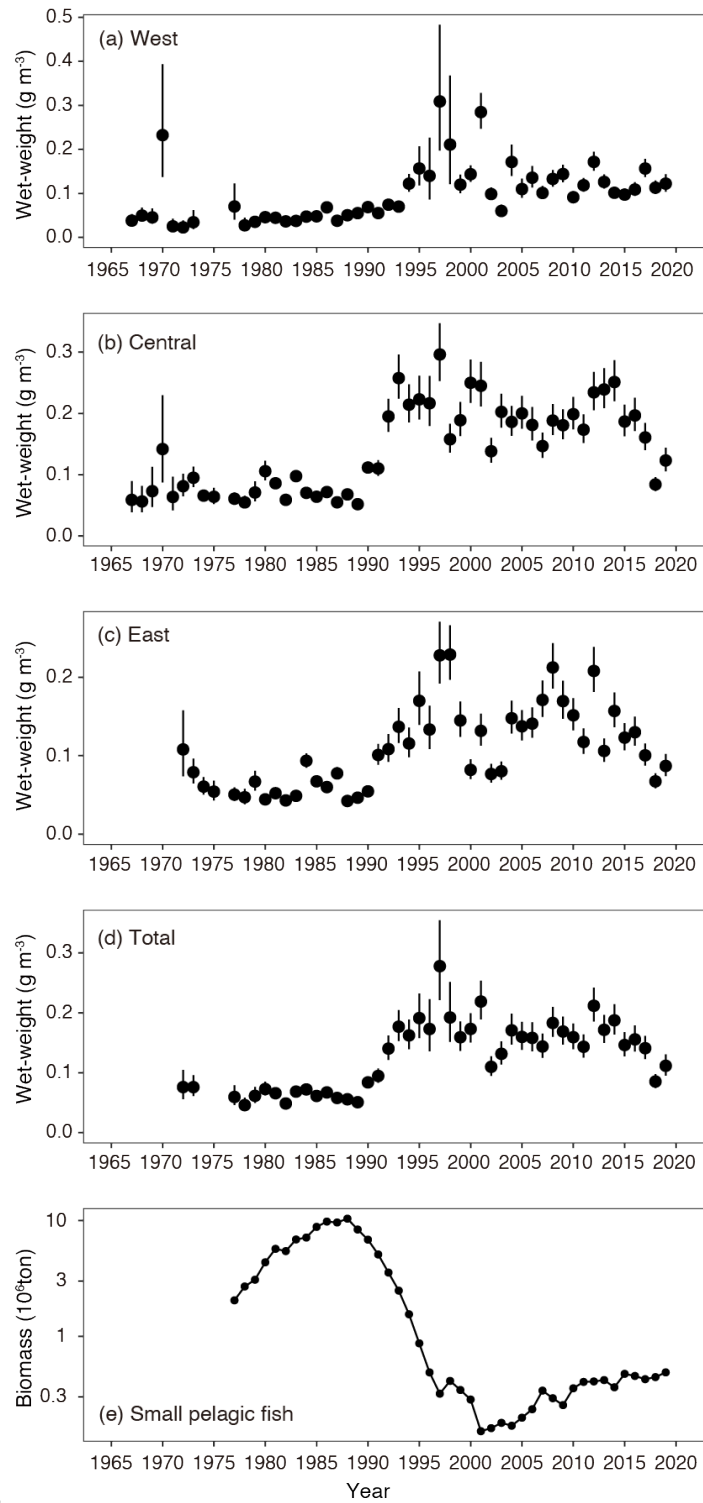
mean values for the western, central, and eastern subareas were observed in 1997 (mean: 0.309 g m^{-3}, CI: 0.198–0.483 g m^{-3}), 1997 (mean: 0.296 g m^{-3}, CI: 0.253–0.347 g m^{-3}), and 1998 (0.229 g m^{-3}, CI: 0.197–0.266 g m^{-3}), respectively **(Figure 2a–c)**. The lowest mean values were observed in 1972 (0.0227 g m^{-3}, CI: 0.0134–0.0384 g m^{-3}), 1989 (0.0517 g m^{-3}, CI: 0.0474–0.00563 g m^{-3}), and 1988 (0.0425 g m^{-3}, CI: 0.0386–0.0467 g m^{-3}) in the western, central, and eastern subareas, respectively **(Figure 2a–c)**. The variations showed jumps in the late 1980s and the early 1990s in all three subareas **(Figure 2a–c)**. In the western subarea, wet weights almost doubled from 1993 (mean: 0.0699 g m^{-3}) to 1994 (0.122 g m^{-3}). In the central subarea, lsmeans almost doubled from 1989 (0.0517 g m^{-3}) to 1990 (0.111 g m^{-3}), and then from 1991 (0.110 g m^{-3}) to 1992 (0.194 g m^{-3}). In the eastern subarea, a jump was observed from 1990 (0.0547 g m^{-3}) to 1991 (0.101 g m^{-3}). Based on the results of the three subareas, the lsmean-based biomass in the coastal Sea of Japan was lowest in 1989 (mean: 0.0509 g m^{-3}, CI: 0.0462–0.0564 g m^{-3}) and highest in 1997 (mean: 0.278 g m^{-3}, CI: 0.221–0.354 g m^{-3}, **Figure 2d)**.

The interannual variation of small pelagic fish biomass peaked in 1988 (10.3 $\times$ 10^6 t) but decreased to 0.869 $\times$ 10^6 t in 1995 **(Figure 2e)**. The biomass was lowest in 2001 (0.151 $\times$ 10^6 t, **Figure 2e)** and at that time, anchovies were the dominant species (0.130 $\times$ 10^6 t).

Figure 2 Interannual variations in least squares mean (lsmean) wet weight values in the (a) west, (b) central and (c) east subareas, and (d) mean wet weight values in the observation areas calculated from the values of three subareas. The dots and vertical bars are the lsmean with 95% confident intervals. (e) Interannual variations of small pelagic fish biomass (sum of Japanese sardine, anchovy and Pacific round herring) in the Tsushima Warm Current area.

The lsmean-based mesozooplankton biomass and small planktivorous fish biomass could not ignore the presence of unit roots (*Dickey-Fuller* test, $p > 0.4$), but their relationship did not have autocorrelation of disturbances (*Durbin-Watson* test, $p < 0.001$). Therefore, the iterated differences between these two time-series data were calculated. A significant negative correlation was observed between the differences in the lsmean-based mesozooplankton biomass in the coastal Sea of Japan and logarithm-transformed small planktivorous fish biomass ($p = 0.0071$, F-statistic = 8.043, degree of freedom [DF] = 40, **Figure 3a**). This relationship was still significant when the data for 1997, 1998, and 2002 were removed ($p = 0.0305$, F-statistic = 5.06, DF = 37) and when the lsmean-based mesozooplankton biomass was transformed into logarithmic values ($p = 0.028$, **Figure 3b**). The Granger causality test indicated that planktivorous fish biomass affected mesozooplankton biomass ($p = 0.018$, F-test = 4.555), but mesozooplankton biomass did not affect planktivorous fish biomass ($p = 0.383$, F-test = 0.7012). Conversely, when log-transformed zooplankton values were used, the log-transformed mesozooplankton biomass caused planktivorous fish biomass ($p = 0.023$, F-test = 6.40), but the planktivorous fish biomass did not cause log-transformed mesozooplankton biomass (p
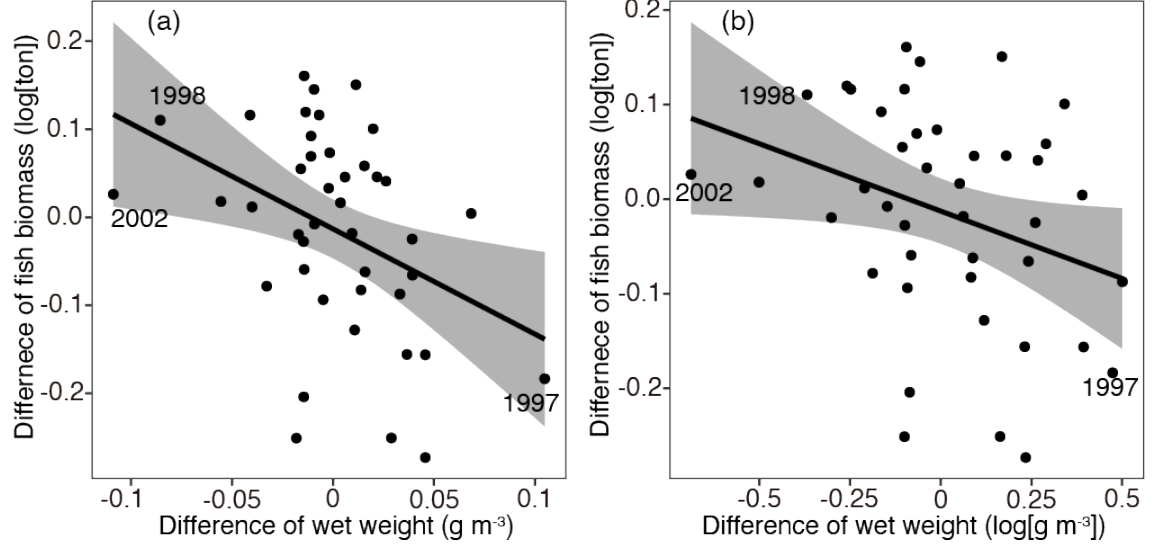
$= 0.119$, F-test $= 3.983$).

Figure 3 Relationship between the difference in small pelagic fish biomass from the previous year and that of mean wet weight. In (a), the mean wet weight value is not transformed into logarithm values, and in (b) it is transformed. The lines with shadows are the regression lines with 95% confidential intervals. The numbers in the panels are the reference years.

4 Discussion

In our study, long-term variation in mesozooplankton biomass was evaluated, and the biomass varied on two decadal scales **(Figure 2)**. Long-term variations in zooplankton biomass are known to occur with warming temperature [*Roemmich and McGowan*, 1995]. For example, in the California Current, the zooplankton biomass decreased with an increase in temperature [*Roemmich and McGowan*, 1995]; however, in the present study, the effect of temperature on zooplankton biomass was spatially different, was not linear, and the lsmean values indicated that warming did not reduce the zooplankton abundance by half **(Supporting Text)**. Primary production is important for mesozooplankton variations, and the impact of bimonthly variations indicated that mesozooplankton biomass showed phenological variations **(Supporting Text)**. In addition, a spring phytoplankton bloom occurred during March/April, elevating the meso-zooplankton biomass. The interannual variation in primary production was rarely observed, but sea surface chlorophyll *a* concentration did not significantly affect interannual variations **(Supporting Text)**. *Chiba et al.* [2005] also indicated that the relationship between primary productivity and mesozooplankton abundance is poor in the southern Sea of Japan. These results suggest that variations in mesozooplankton biomass are significantly affected by bottom-up processes, but they are not the main causes of interannual variation.

In the western North Pacific, horizontal advection is a key process controlling zooplankton biomass [*Chiba et al.*, 2013]. In the southern Sea of Japan, the Tsushima Warm Current flows through the Kuroshio-origin, Changjiang-origin, and Taiwan Warm Current-origin waters [*Isobe*, 1999; *Lie and Cho*, 1994]. Therefore, when the zooplankton biomass varied in the original waters, the effects were possibly observed in the Sea of Japan. In the southern Sea of Japan, surface water exchanges occur almost exclusively over summer [*Kodama et al.*, 2016]. Therefore, if horizontal advection controlled mesozooplankton biomass in the Sea of Japan, the interannual variations must be synchronised in the three subareas or changed from upstream (west) to downstream (east) subareas. However, the variations were neither synchronised nor changed. These results suggest that horizontal advection is not a key process controlling mesozooplankton biomass in the coastal Sea of Japan.

The sardines and anchovies in the Sea of Japan are mostly distributed in the southern part [*Funamoto et al.*, 2004; *Muko et al.*, 2018], and only at depths < 100 m [*Ohshimo*, 1996; *Ohshimo et al.*, 1998]. Zooplankton biomass in the upper 100 m in the Sea of Japan (~500,000 km^2, approximately half of the Sea of Japan) ranged from 1.2–6.9 × 10^6 t. The daily zooplankton ingestion rates of sardines and anchovies are 1–8% (wet weight per wet weight) [*Nikolioudakis et al.*, 2014; *Nikolioudakis et al.*, 2011; *Noguchi et al.*, 1990; *van der Lingen*, 1998a; b]. In the case of Japanese sardines and anchovies, 2–3% of the daily rations are required for growth [*Noguchi et al.*, 1990]. Here, daily rations are assumed to be 2%, which amounts to 1.1–76 × 10^6 t of zooplankton preyed on by fish in a year, which was 20–5400% of zooplankton biomass in the same year. However, this assumption does not consider zooplankton growth. The zooplankton growth rate is dependent on temperature and food conditions [*Huntley and Boyd*, 1984]. Maximum weight specific growth rate of zooplankton is 0.28 d^{-1} at 15° C, and 0.16 d^{-1} at 10° C [*Huntley and Boyd*, 1984]. Assuming a specific growth rate of 0.16 d^{-1}, the small pelagic fish consumed only 93% of the mesozooplankton in 1988. However, the *in situ* secondary production rate is <10% of the zooplankton biomass [*Davis*, 1987; *Kobari et al.*, 2018]. Assuming *in situ* secondary production is 5% of biomass, the small pelagic fish consumed 290% of secondary production in 1988 (the peak of small pelagic fish biomass), >100% from 1980 to 1990, and ~1.5% of secondary production in 2001. These results suggest that small pelagic fish are sufficient in decreasing the zooplankton abundance during the fish-rich periods in the Sea of Japan but have small impacts during fish-deprived periods.

Top-down control of mesozooplankton biomass was also reported in the Oyashio area, the western North Pacific Subarctic region [*Tadokoro et al.*, 2005], and the biomass of the dominant mesozooplankton copepod *Neocalanus* spp. decreased in the late 1970s, when the Japanese sardine biomass started to increase [*Tadokoro et al.*, 2005]. However, in the 2005 publication by *Tadokoro et al.* [2005], statistical approaches to the relationship between sardine biomass and *Neocalanus* biomass were not shown; therefore, our study is the first to statistically show a basin-scale top-down control of mesozooplankton biomass.

Conversely, in the eastern and central North Pacific Subarctic regions, long-term variation in zooplankton biomass is largely controlled by bottom-up processes, and a positive relationship between zooplankton biomass and planktivorous fish was observed [*Brodeur and Ware*, 1992]. These results suggest that top-down processes are not always the dominant factor controlling zooplankton biomass in the ocean. There is no evidence, however, considering the result on the Oyashio [*Tadokoro et al.*, 2005], and large variations in small pelagic fish biomass may be the key factor to actualise top-down control as it occurs in the boundary systems of the world's oceans [*Lluch-Belda et al.*, 1992].

Our Granger causality analyses showed that log-transformed mesozooplankton biomass affected the small pelagic fish biomass. Recent studies [*Takasuka et al.*, 2019a; b] showed that recruitment processes of small pelagic fish are negatively impacted by their densities and food availability is one of the key factors in the recruitment of small pelagic fish and their biomass [*Takasuka et al.*, 2019a; b]. When the mesozooplankton biomass decreased, the food availability of small pelagic fish decreased and negatively affected their recruitment. The small pelagic fish biomass is not only controlled by recruitment but also by natural mortality and fisheries impacts. However, the feedback processes from zooplankton biomass to small pelagic fish biomass were shown in the Granger causality analyses. This feedback process between small pelagic fish and zooplankton biomass likely causes the "regime shift" in small pelagic fish, which repeatedly occurs over several hundred periods in Japanese waters [*Ito*, 1961].

5 Conclusion

In our study, we showed that long-term variation of mesozooplankton biomass based on wet weight in the southern coastal Sea of Japan is under top-down control by small pelagic fish. The effects of climate change on interannual variations were not obvious, although the sea surface temperature in the Sea of Japan is rapidly warming. In addition, the decreased zooplankton biomass negatively affected small pelagic fish biomass. Moreover, top-down controlled zooplankton biomass may affect biogeochemical cycles in the Sea of Japan. Japanese sardines and anchovies are absent at depths greater than 100 m [*Ohshimo*, 1996; *Ohshimo et al.*, 1998], while diel vertical migration of mesozooplankton occurs from 300 m to the surface [*Hirakawa et al.*, 1990]. This suggests that active flux by mesozooplankton is not substituted by small pelagic fish, and biological pumps are expected to be weak during fish-rich periods. In the middle layer of the Sea of Japan, only linear trends have been tested [*Chen et al.*, 2017; *Kodama et al.*, 2016]; thus, future studies are necessary to clarify the relationship between biogeochemical cycles and variation in zooplankton biomass to understand the impact of small pelagic fish on biogeochemical processes.

Acknowledgments

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