

## **Does the Density-Dependent Growth of Sardine Truly Exist?**

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## Abstract

This paper reviews two studies discussing density-dependent growth using Japanese sardine data. However, the results and interpretation of these two papers indicate inconsistencies and conflict with each other. This study shows that the length of sardines in year t can be explained by the values of the three-year moving average of reproductive success in year t - 3. This indicates that the existing density-dependent growth of sardines is questionable and that environmental conditions determine the growth of fish.

#### **Subject Areas**

Marine Biology

## **Keywords**

Density-Dependent Growth, Density-Independent Growth, Reproductive Success, RPS, Japanese Sardine, Zooplankton

## **1. Introduction**

The density-dependent effect is a key factor in the discussion of population fluctuations of fish. The maximum sustainable yield (MSY), the main management theory, was constructed based on the concept of density-dependent effect. Many phenomena related to density-dependent effects have been observed in several instances, such as survival rate, growth rate, and fecundity.

The concept of MSY is generally discussed by assuming constant carrying capacity, where environmental conditions, such as physical and biological, are constant. The increase in fish population directly reduces food per fish, living space per fish, and others, and this directly impacts fish populations, including the survival rate, growth rate, and fecundity. Based on this basic concept, several extended theories have been proposed. They assume two or more levels of carrying capacity, and within the period when the carrying capacity is constant, the usual concept of MSY operates.

In this study, we reviewed two research articles that discussed density dependency in growth. The first study was recently published by Kamimura *et al.* [1]. Hereafter, we call this "Paper 1". This study compared the density dependency in the growth of the Japanese sardine between two periods, 1976-1982, excluding 1979, and 2011-2018; they concluded that density-dependent growth was observed in both periods, and a much stronger density-dependent growth was observed in 2011-2018. In this period, the authors noted that the stronger density dependency in growth occurred owing to lower food availability. However, we disagree with this interpretation as Figure 7(b) in Paper 1 shows that the wet weight of zooplankton from 2011 to 2018 did not drastically differ from that of the 1976 to 1982 period.

The average wet weight of zooplankton at the beginning of the 1970s was approximately twice that of the amount in 2010s; however, the average number of fish in the 2011 to 2018 period was 374 hundred million, which was one-seventh of the 1976-1982 period. Therefore, it is considered that the zooplankton per fish in the 2011 to 2018 was much higher than that in the 1976-1982 period. We doubt the difference in growth due to the difference in zooplankton biomass, as Paper 1 insisted.

The second method was proposed by Wada and Kashiwai. [2] Hereafter, we call this "Paper 2". Kamimura *et al.* [1] used the growth equations proposed by Wada and Kashiwai [2]; they compared the growth from 1976-1979 and from 1980-1986 and concluded that the 1976-1979 period showed a high growth potential and clear density-dependent decline in growth, but 1980-1986 period showed a low potential growth and the growth was density-independent. Here we question why the growth from 1980 to 1986 is density-independent, regardless of the high level of sardine abundance. They noted that sardines increased their feeding area to maintain abundant food resources. However, as noted by them, there was no evidence that the feeding area had largely changed before and after 1980.

Therefore, the results and interpretation of these two studies seemed inconsistent and conflicted with each other. A more acceptable interpretation that can uniformly explain these phenomena should be proposed. The aim of this paper is to discuss the results of these two studies and propose a new interpretation. The hypothesis assumed in this study was that the growth of fish is determined by environmental conditions, mainly during their initial stage (0-year-old or juvenile). We also assumed that reproductive success (RPS) could be used as an index of environmental conditions when growth is determined.

#### 2. Materials and Methods

#### 2.1. Materials

Data on the number of sardines and RPS for the Pacific stock of Japanese sardine

after 1976 were provided by the Fisheries Agency and Fisheries Research Agency of Japan [3]. Data prior to 1975 were obtained from Wada and Jacobson [4]. The asymptotic standard length (Hereafter, we call this "length") of sardine from 1976 to 1982, except 1979, and from 2011 to 2018 were obtained from Table 1 of Paper 1 [1]. The number of sardines in the waters off the southeastern coast of Hokkaido (Doto region) during 1976-1986 was obtained from Table 1 in Paper 2 [2]. The individual growth of sardine from 1976 to 1986 was obtained from Figure 4 of Paper 2 [2].

#### 2.2. Methods

First, we compared the results of the two studies. Next, we compared the trajectories of population abundance (number of fish), length, and three-year moving average of the RPS. Further, we compared the trajectories of length in year t with the three-year moving average of year t - k (k = 0, 1, ..., 4). We then estimate the parameter of the regression line for the length in year t against the three-year moving average in year t - 3. The data on the individual growth of sardines obtained from Paper 2 were also examined in the same manner.

## 3. Results

#### 3.1. Comparison of the Results Obtained by Papers 1 and 2

**Figure 1** shows the data periods used in Papers 1 and 2. In **Figure 1**, *N* denotes the average number of fish per period. The red circle indicates 374 hundred million



**Figure 1**. Period used in the analysis, average number of fish per period, density-dependent or independent growth detected, and the interpretation of the results is presented in Papers 1 and 2, respectively. The bottom shows the case with added results when the abundance in the Doto region was used. One red circle indicates 374 hundred million fish.

fish. In Paper 1, two data periods were used from 1976 to 1982, except for 1979 and 2011 to 2018. The authors of Paper 1 noted that density-dependent growth was observed in both periods, and stronger density-dependent growth was observed in the 2011 to 2018 period. We did not use the length data used in Paper 1. Then, instead of length, we used the asymptotic standard length listed in Table 1 of Paper 1.

**Figure 2** shows the relationship between the asymptotic standard length and the population abundance of sardines. The closed circles indicate data from 1976 to 1982, except for 1979, and the open circles indicate data from 2011 to 2018. Both slopes of the regression lines were significantly negative; that is, the 1976 to 1982 period was -0.512 (p = 0.034), and the 1976 to 1982 period was -0.406 (p = 0.012). The pattern shown in **Figure 2** is similar to that in Figure 6 of Paper 1 [1]. Therefore, we can discuss density-dependent growth using the asymptotic standard length.

Why was the density dependency for the 2011 to 2018 period much stronger than that for the 1976 to 1982 period? The authors of Paper 1 noted that in the 2011 to 2018 period, the zooplankton biomass in July in the summer feeding grounds was lower than that in the 1976 to 1982 period. However, Figure 7b of Paper 1 shows that the wet weight of zooplankton did not drastically differ between the two periods. Further, as shown in **Figure 1**, the average number of fish in the 2011 to 2018 period was one-seventh of that of the 1976 to 1982 period. Therefore, if zooplankton biomass was the cause of the difference in density-dependent growth, a much greater difference in zooplankton biomass should exist between the two periods.

**Figure 3** shows the relationship between the asymptotic standard length and the sardine population abundance in the Doto region. In this case, the slope of



Figure 2. Relationship between the length and the population abundance of sardine.



**Figure 3.** Relationship between the length and the population abundance of sardine in the Doto region.

the regression lines for the former period was -0.0375 and with a significant probability of p = 0.274; that is, the slope was not significantly negative, and density-dependent growth was not detected.

Even in the case of **Figure 2**, the length from 1978 to 1982 appears to be density-independent. The slope of the regression line for the data from 1978 to 1982 and the 95% confidence intervals were -0.0162 (p = 0.505) and (-0.123, 0.0704); that is, the lengths from 1978 to 1982, shown in **Figure 2**, were also considered as density-independent growth.

The middle part of **Figure 1** shows a summary of Paper 2. In Paper 2, data from 1976 to 1986 were used. The data were divided into two periods: 1976-1979 and 1980-1986. They noted that density-dependent growth was observed in the former period; however, density-independent growth was observed in the latter period. Exploring the reasons for these differences, the authors of Paper 2 considered that the feeding ground was enlarged in the latter period to maintain a high abundance of food resources. It is well known that the distribution of sardines changes significantly according to population size. However, as they noted themselves, there is no evidence that the distribution of sardines was quite different before and after 1980.

Both papers used the same 7-year data from 1976 to 1982, and the year of use in Paper 2 was only 4 years longer. However, these results were varied. In Paper 1, density-dependent growth was detected for 1976-1982. However, in Paper 2, density-dependent growth was detected from 1976 to 1979, and density-independent growth was detected from 1980 to 1986.

When we used the abundance data in the Doto region, the length of the 1978 to 1982 period showed density-independent growth. Therefore, there is a possi-

bility that density-independent growth continued for a relatively long period from 1976 to 1986, although the population size had historically been large (**Figure 1**, bottom). Therefore, a new question has arisen. If the sardine population succeeded in avoiding density-dependent effects and maintaining density-independent growth by expanding its feeding grounds, why did it collapse in 1988? Therefore, it is considered that both conclusions; that is, the weaker or stronger density-dependent growth occurred owing to the different abundance of zooplankton (Paper 1), and the density-dependent growth and density-independent growth occurred because of the different sizes of feeding grounds (Paper 2), seemed questionable.

# 3.2. Analyze the Asymptotic Standard Length of Paper 1 (Analysis 1)

We analyze the asymptotic standard length. The top panel of **Figure 4** shows the trajectory of the number of fish from 1976 to 2018. The blue open circles indicate the data corresponding to the closed circles in **Figure 2**, and the red open circles indicate the data corresponding to the open circles in **Figure 2**. Closed red circles indicate the trajectory of the number of fish in the Doto region. The middle part of **Figure 4** shows its length. The bottom of **Figure 4** shows the RPS (black points) and the three-year moving average of the RPS (purple line). In the



**Figure 4.** Trajectory of population abundance (top), length (middle) and RPS (bottom). The purple line indicates the three-year moving average of RPS. The closed red circles indicate the trajectory of the number of fish in the Doto region.

first two years, 1976 and 1977, the length was high; however, in the next four years, 1978, 1980, 1981, and 1982, it was low. The reason why the length in the latter period decreased is generally explained by a density-dependent effect due to the increase in sardine abundance. However, this may not be valid because the abundances in the Doto region in 1977 and 1980 seem almost the same, al-though the lengths are quite different, and the abundance in the Doto region in 1982 is 3.4 times larger than in 1980; however, the lengths in 1982 and 1980 seem almost the same.

The top of **Figure 5** is the same as that in the middle of **Figure 4**; that is, the trajectory of length is shown again to compare the fluctuations easily between the length and RPS. The middle and bottom of **Figure 5** show the trajectory of the RPS and the three-year moving average in year t - 3, which are plotted at year t on the x-axis, in order to compare the fluctuations easily between the length in year t and the RPS three years ago. The scale of the y-axis in the middle of **Figure 5** is almost 10 times larger than that at the bottom of **Figure 5**. The middle and bottom of **Figure 5** show that the up and down of the length and that of the RPS coincide well. For instance, the high lengths in 1976 and 1977, which is plotted on the x-axis in 1976 and 1977. The low length in 1978, 1980,



**Figure 5.** Trajectory of length (top), RPS in three years ago shown in large scale (middle), and RPS three years ago shown on a small scale (bottom). The purple lines indicate the three-year moving average in three years ago. The three-year moving average in year t-3 is plotted at year t of the x-axis.

1981, and 1982 coincided well with the low three-year moving average of the RSP in 1975, 1977, 1978, and 1979, respectively. The high lengths in 2011, 2012, 2013, and 2014 coincided well with the high three-year moving average of RSP in 2008, 2009, 2010, and 2011, respectively. The low lengths in 2015, 2016, 2017, and 2018 coincided with the low three-year moving average of RSP in 2012, 2013, 2014, and 2015, respectively. It is considered that the length becomes high or low depending on the environmental conditions in the years when the fish were born.

**Figure 6** shows the relationship between the length in year *t* and the threeyear moving average in year t - 3. The slope of the regression line was 0.0327, which was not significant (p = 0.131). However, the RPS in 1976 and 1977 was extremely high, so we excluded the data from 1976 and 1977 and recalculated the regression line between the length in year *t* and the three-year moving average in year t - 3 (**Figure 7**). **Figure 7** shows a clear positive relationship between the length in year *t* and the three-year moving average in year t - 3. The slope of the regression line was 0.625, which was statistically positive (p = 0.00834).

#### 3.3. Reanalyze the Data of Paper 2 (Analysis 2)

We adopted the same approach as the individual growth data in Paper 2 [2]. The top part of **Figure 8** is the same as that in **Figure 4**. The top of **Figure 8** shows the trajectories of the population abundance of sardines from 1976 to 2018. The blue open circles indicate the years in which individual growth data were used. Closed red circles indicate the trajectory of the number of fish in the Doto region.



**Figure 6.** Relationship between the length in year *t* and the three-year moving average of RPS in year t - 3.



**Figure 7.** Relationship between the length in year *t* and the three-year moving average of RPS in year t - 3. The data of 1976 and 1977 are excluded.



**Figure 8.** Trajectory of population abundance (top), growth (middle) and RPS (bottom). The purple line indicates the three-year moving average of RPS. The closed red circles indicate the trajectory of the number of fish in the Doto region.

The middle part of **Figure 8** shows the individual growth obtained from Paper 2 [2]. The bottom of **Figure 8** is the same as that in **Figure 4**. Individual growth in

the first four years seems to decrease with an increase in the population. However, when we used the abundances in the Doto region, the interpretation changed. The abundance from 1980 to 1986 largely fluctuated, even though individual growth for those years seemed to be constant. Therefore, it is difficult to explain the difference in individual growth between these two periods by the difference in the feeding area, as the authors of Paper 2 noted, without showing any evidence.

The top of **Figure 9** is the same as that in the middle of **Figure 8**; that is, the trajectory of the individual growth is shown again to compare the fluctuations easily between individual growth and RPS. The middle and bottom parts of **Figure 9** are the same as those in the middle and bottom parts of **Figure 5**. **Figure 9** shows that the pattern of individual growth is similar to that of the three-year moving average of RPS. For instance, the high individual growth in 1976-1977 coincided well with the high three-year moving average of RSP from 1973 to 1974, which was plotted on the *x*-axis from 1976 to 1977. The low individual growth from 1980 to 1986 coincided well with the low three-year moving average of the RSP from 1977 to 1983. It is considered that individual growth becomes high or low is also determined by environmental conditions in the years when the fish were born.



**Figure 9.** Trajectory of growth (top), RPS in three years ago shown in large scale (middle), and RPS three years ago shown on a small scale (bottom). The purple lines indicate the three-year moving average in three years ago. The three-year moving average in year t - 3 is plotted at year t of the x-axis.

**Figure 10** shows the relationship between individual growth in year *t* and the three-year moving average in year t - 3. **Figure 10** shows a clear positive relationship between individual growth in year *t* and the three-year moving average in year t - 3. The slope of the regression line was 0.0125, which was significantly positive (p = 0.00784). When the data for 1976 and 1977 are excluded, as shown in **Figure 7**, a significant positive slope is also obtained; that is, the slope of the line was 0.126, which was statistically positive (p = 0.00688).

#### 3.4. The Mechanism that Produces an Apparent Density-Dependency

Next, we discuss the mechanism that produces an apparent density dependency using the long trajectories of recruitment (top), spawning stock biomass, SSB (middle), and RPS (bottom) of the sardine (Figure 11). All the data were transformed on a natural logarithmic scale. The horizontal line in each figure represents the average value. The fluctuation pattern of recruitment coincided well with that of the RPS. The RPS in the 1960s was below average, and recruitment was also below average. However, the RPS suddenly began to increase in 1969 and continuously increased to an extremely high level in 1970, 1971, and 1973 (red open circles). According to this extremely high RPS, recruitment began to increase considerably from far below the average to above the average (red open circles).

According to the increase in recruitment, SSB also began to increase with a couple of years of delay (red open circles). The extremely large RPS finished in 1974, and the large RPS, which exceeded the average, continued for more than



**Figure 10.** Relationship between the individual growth in year *t* and the three-year moving average of RPS in year t - 3.



Figure 11. Trajectory of population abundance (top), spawning stock biomass (middle) and RPS (bottom) of Japanese sardine.

10 years (red broken circle). According to the continuously high SRP from 1974 to 1985, recruitment increased further from 1980 to 1987. The SSB also continued to increase and reached its maximum value in 1988, with a 2 years delay from the high recruitment in 1986.

However, good environmental conditions never persist, and poorer environmental conditions are necessary. The years from 1988 to 1991 indicate the years when an abrupt change from good to poor environmental conditions occurred. The RPS values from 1988 to 1991 were extremely low (blue open circles). This change in the RPS directory affected recruitment, which dropped abruptly in 1988. The extremely low RPS was completed in 1991; however, poor environmental conditions continued until 2004 (blue broken circle). In other words, the RPSs during this period were below the average. Recruitment continued to decrease until 2004, and SSB reached its lowest level over the years. The environmental condition changed again; that is, the RPS suddenly changed from bad to good in 2008 and 2010 (green open circles). The level was not as extreme as at the beginning of the 1970s; however, the successive huge RPS made the extremely low recruitment jump to the average (green open circles). The high RPS continued after 2010. Therefore, recruitment and SSB increased after 2010. As explained above, the fluctuation of recruitment and SSB was controlled by the RPS, which was considered to be an indicator of environmental conditions.

Figure 12 schematically illustrates the mechanism described above. The upper



**Figure 12.** Mechanism that produces an apparent density-dependency. Trajectory of environmental conditions, *i.e.*, RPS (top), and the environmental conditions produce the different phase in recruitment and SSB (bottom).

figure shows the trajectory of the environmental condition; that is, the trajectory of the RPS. In Phase 1, the environmental conditions were poor for the species, and the strength of recruitment and population abundance was also low, as shown in the lower figure of **Figure 12**. However, Phase 1 suddenly changed to Phase 2 because of the sudden change from poor to extremely good environmental conditions. The strength of recruitment also increased from low to extremely high, corresponding to the period from 1969 to 1973, as shown at the bottom of **Figure 11**. The SSB also increased because of this jump in recruitment. As shown at the bottom of **Figure 11**, after the extremely good condition of the RPS had finished, the good condition continued for more than 10 years. Recruitment then increased continuously (Phase 3). According to the increase in recruitment, SSB also increased with a 2- or 3-year time lag. The SSB further increased and reached an extremely high level (Phase 4).

However, Phase 4 suddenly dropped into Phase 5 due to a sudden change from good to extremely bad environmental conditions. The recruitment strength also dropped to an extremely low level (Phase 5). This implies that an abrupt change from Phase 4 to Phase 5 occurred at a high population size. As shown at the bottom of **Figure 11**, the extremely poor conditions of the RPS had finished, and the bad conditions continued for more than 10 years. Recruitment subsequently decreased continuously. According to the decrease in recruitment, SSB also decreased with a two- or three-year time lag. Finally, the SSB further decreased and reached an extremely low level (Phase 1).

Notable increases in recruitment always occur when the population abundance is extremely low, and a decrease in recruitment always occurs when the population abundance is extremely high. This is the mechanism by which apparent density dependency is commonly detected. In other words, environmental conditions are the true trigger to change the phase and not a density-dependent effect.

This mechanism can also be applied to the density dependence of the growth. In other words, when environmental conditions were poor, growth was also low. However, the environmental conditions suddenly changed from bad to good, and the growth also changed from low to high. Good environmental conditions continued for several years, SSB reached a high level, and growth was maintained at a high level. However, the environmental conditions suddenly changed from good to poor at high population levels. In response to this environmental change, growth also changed from high to low. Therefore, when we focus on the relationship between growth and population size, higher growth occurs when the population size is small, and lower growth occurs when the population size is large. This is the mechanism by which the apparent density dependency in growth is commonly detected. In other words, environmental conditions, and not the density-dependent effect, are the true trigger to change growth.

#### 4. Discussion

This study first highlights the discrepancies between Papers 1 and 2. The results of the two papers were different. Paper 1 detected density-dependent growth; however, Paper 2 detected density-dependent and density-independent growth for almost the same period of Paper 1. Although Paper 1 did not refer to the distribution of the feeding ground, Paper 2 noted that the differences in density-dependent or density-independent growth were caused by the difference in feeding ground size without showing any evidence. In addition to the validity of the discussion noted in Papers 1 and 2, we explored how both phenomena can be uniformly explained without any discrepancy.

In this study, we propose a new interpretation that clearly explains the phenomena observed in Papers 1 and 2. To construct a new interpretation, we propose the following hypotheses: that is, "the growth of the fish is determined by the environmental conditions during their juvenile period (or 0-year-old)". Further, we assumed that the RPS could be used as an index of environmental conditions that control growth. Therefore, there is a time lag between the year when the 0-year fish is affected by environmental conditions and the 0-year fish grows up to, for instance, two to four years old. This corresponds to the reason why using the three-year moving average of the RPS is useful, and the three-year time lag in the three-year moving average of the RPS is chosen to explain the fluctuations of the length.

The results show that the trajectory of the length shown in Analysis 1 and the trajectory of the individual growth in Analysis 2 can be explained by the same mechanism; that is, the length and individual growth are determined by the le-

vels of the three-year moving average of the RPS three years ago. These results show the validity of the hypothesis mentioned above; that is, the length and individual growth are determined by the environmental conditions in which they are born. The density-dependent effect does not directly cause differences in length and individual growth.

Sakuramoto showed that the fluctuations of RPS could be reproduced well using only environmental factors, such as the index of Arctic oscillation and the index of Pacific decadal oscillation, not only for the sardine population but also for many other species [5] [6] [7] [8] [9]. This indicates that, as we explained in **Figure 11** and **Figure 12**, environmental conditions determine the RPS, the RPS directly determines the recruitment, and the recruitment determines the SSB with a certain time lag. Therefore, environmental conditions are the main factors controlling population fluctuations and not the density-dependent effect. We also discussed that this interpretation is applicable to the growth of fish.

The main fisheries management theory, such as the MSY or stock-recruitment relationship, is established by the concept that surplus production or recruitment is determined by the size of population abundance; however, as shown in this paper, it is not valid, and it is the reverse; that is, environmental conditions determine the recruitment and recruitment determines the population abundance. Therefore, environmental conditions are the basic factors that control population fluctuation, survival rate, fecundity, growth, etc.

Before concluding this discussion, let us introduce another typical example of a misunderstanding related to density dependency. Wada and Jacobson [3] noted that the RPS of sardines decreased with the density of sardines. However, if the data of four years when the RPS was extremely low from 1988 to 1991, in which period we often mentioned in this paper, were excluded from the analysis, a density-dependent decrease was not detected [10]. Further, incorporating the data of the last four years from 1992 to 1995, which they neglected from the analysis, a quite different pattern appeared; that is, two loops appeared, both of which had negative slopes. Sakuramoto showed that when observed errors existed in the SSB and a regime shift existed, the two apparent decreasing slopes mentioned above could be reproduced [10] [11] [12].

Many traps exist, and we believe that a density-dependent effect exists [13] [14]. The results of the two papers discussed in this paper are also the case falling into the trap. It is true that the food per fish must be related to the growth of fish; however, the food per fish is determined by environmental conditions and not by the density of fish alone. The conclusion of this study is that the length of sardines is determined by environmental conditions and not by density-dependent effects.

#### **5.** Conclusion

This study shows that the length of sardines in year t can be explained by the values of the three-year moving average of reproductive success in year t - 3. This indicates that the existing density-dependent growth of sardines is questionable

and that environmental conditions determine the growth of fish.

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#### **Conflicts of Interest**

The author declares no conflicts of interest.

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