**Open Access Library Journal**
2016, Volume 3, e3112
ISSN Online: 2333-9721
ISSN Print: 2333-9705

# Density-Dependent Effect Occurs Regardless of Density

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**How to cite this paper:** Sakuramoto, K. (2016) Density-Dependent Effect Occurs Regardless of Density. *Open Access Library Journal*, **3**: e3112.
http://dx.doi.org/10.4236/oalib.1103112

**Received:** October 2, 2016
**Accepted:** November 1, 2016
**Published:** November 4, 2016



## Abstract

Maximum sustainable yield (MSY) is the most important concept in fisheries resource management. MSY can be established based on the concept of the density-dependent effect. However, the concept that a density-dependent effect controls the fluctuation of the population living in the ocean is controversial. This paper discusses the validity of the density-dependent effect focusing on the stock-recruitment relationship (SRR). In many cases, the SRR shows a clockwise or ant-clockwise loop. If we try to explain the population fluctuations using the density-dependent effect, the clockwise or anti-clockwise loop observed in SRR cannot be explained. However, the mechanism proposed here can well reproduce the phenomena observed in many SRR including the clockwise or anti-clockwise loop. In other words, the most important relationship between stock and recruitment is likely to be the interspecific relationship and/or environmental conditions, not the density-dependent effect. If the density-dependent effect observed in SRR is not real, then the MSY theory is not valid, and all the management procedures based on MSY would also not be valid.

## Subject Areas

Aquaculture, Fisheries & Fish Science

## Keywords

Stock-Recruitment Relationship, Density-Dependent Effect, MSY, Pink Salmon

## 1. Introduction

Maximum sustainable yield (MSY) is the most important concept in fisheries resource management. For instance, fisheries resource management organizations (RFMOs) proposed the so-called "Kobe plot" to manage tuna and tuna-like fishes, which is the plot of $F/F_{\mathrm{MSY}}$ against $B/B_{\mathrm{MSY}}$. Here, $F_{\mathrm{MSY}}$ and $B_{\mathrm{MSY}}$ denote the fishing mortality coefficient $F$ that gives MSY and the biomass $B$ that gives MSY, respectively [1]. When the current $F$ and $B$ are less than $F_{MSY}$ and $B_{MSY}$, it is judged that the current fisheries are undergoing overfishing. MSY is the concept of the density-dependent effect. However, the concept that a density-dependent effect controls the population fluctuations living in the ocean is controversial. Under the concept of MSY, in almost all cases, environmental factors are treated as only a random error term. Sakuramoto, however, insisted that environmental factors are really an important main component in controlling population fluctuations, and a density-dependent effect is derived from environmental factors not from the density. That is, a density-dependent effect is illusory phenomenon [2]-[8]. In other words, the MSY theory is not valid to explain the population fluctuations in marine resources. If this claim is correct, the management procedure should be changed from one that assumes MSY to others that do not assume a density-de- pendent effect. The aim of this study is to discuss the validity of the density-dependent effect that forms the basis of MSY.

## 2. What Is the Density-Dependent Effect?

The density-dependent effect is the phenomenon that the birth rate and/or growth rate, etc., change dependent on the increase of the density. When the death rate decreases and/or the growth rate increases in response to an increase of the density (number of individuals), it is called a positive density-dependent effect. In contrast, when the death rate increases and/or the growth rate decreases according to an increase of the density, it is called a negative density-dependent effect.

When we discuss fluctuations in fisheries resources, we usually focus on the negative density-dependent effect. If we focus on the negative density-dependent effect and environmental factors are regarded as only a random perturbation factor, on average, a density-dependent production model, such as the logistic model, can be acceptable (**Figure 1**). The opposite idea is that environmental factors are the main factors controlling the fluctuation of the populations, and the density-dependent effect does not play an important role.

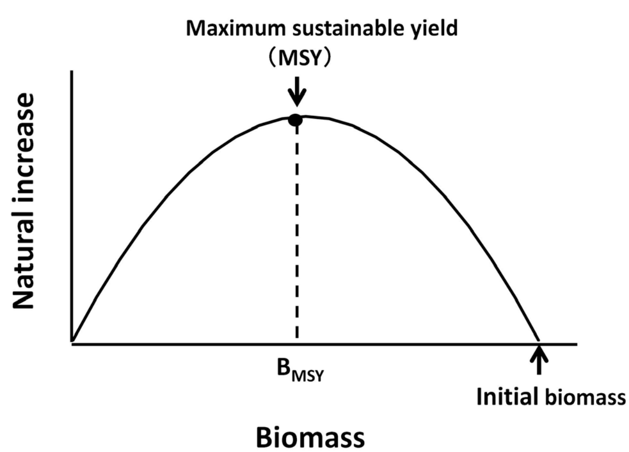


**Figure 1.** Logistic model and MSY.

In the 1950s, almost the same discussion was held regarding the population fluctuations of insects [9]-[17]. Nicolson and his group believed that a density-dependent effect was important to explain the fluctuations of insect populations. In contrast, Andrewartha and his group insisted that a density-dependent effect never played an important role in explaining the fluctuations. These two positions were fiercely debated. One paper published by Smith [13], however, led to a definitive end to the controversy by confirming the position of Nicolson's group. Smith reanalyzed the data of the trips populations (insect pests living on roses, apple trees, and so on), which Andrewartha and his colleagues had collected over 14 years [9] [10], and concluded that a density-dependent effect had clearly been detected. Then the debate was ended with the conclusion that the position of Nicolson's group was valid. However, Sakuramoto [5] pointed out that the analysis performed by Smith [13] was invalid, and the density-dependent effect detected by Smith was only an illusory phenomenon.

## 3. The Relationship between the Reproductive Curve and MSY

In the fisheries sciences, the management of populations in order to achieve the MSY has been discussed. This discussion derived from the assumption that a density-dependent effect exists in the stock-recruitment relationship (SRR, or reproductive curve). However, Sakuramoto insisted that the density-dependent effect detected actually emerged from environmental factors and was only an illusory phenomenon. Therefore, the MSY theory derived from a density-dependent effect was considered to be invalid [2]-[8].

SRR implies a quantitative relationship between the spawning stock biomass (SSB) and their offspring (recruitment, R) (**Figure 2**). R increases as the SSB increases. However, further the SSB increases, the more increment in R is reduced in response to the density-dependent effect, and the further the SSB increases, the more R begins to decrease. This pattern that is usually observed in the SRR is believed to emerge from the density-dependent effect. If this concept is correct, the natural increase is determined by the level of SSB (density), and the natural increase then achieves its maximum value at a certain level of SSB as shown in **Figure 2**. This maximum natural increase is called the MSY.

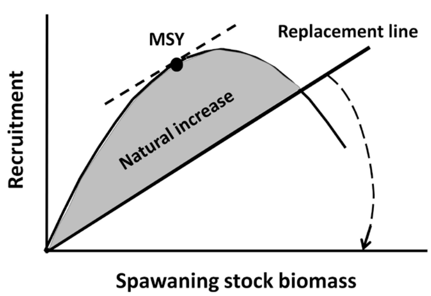


**Figure 2.** Relationship between stock-recruitment relationship and MSY. When the stock-recruitment relationship is on the replacement line, the spawning stock biomass neither increases nor decreases. The difference between recruitment and recruitment on the replacement line is the natural increase (sustainable yield).

As I noted above, I have found that the density-dependent effect that is believed to exist in SRR is not real and that the MSY theory is invalid. However, extremely strong opposing opinions have been expressed by many scientists. Many of those opinions can be summarized as follows: A huge number of phenomena that indicate the density-dependent effect have been observed; that is, when the population level (density) is high, the death rate becomes high and/or the body size becomes small, and vice versa [18]-[21]. These phenomena represent clear evidence that the density-dependent effect really exists, in their view.

## 4. Density-Dependent Effect Occurs Regardless of the Density

I do not deny that a phenomenon that seems to be a density-dependent effect has been observed. My point is that we should separate two seemingly linked phenomena: the increase in the death rate of fish and the high density of fish. Those two phenomena are both derived from changes in environmental conditions. We cannot conclude that the high density of fish increases the death rate of fish due to a density-dependent effect. The true mechanism that links those phenomena is environmental factors, not a density-dependent effect.

In other words, when we try to explain the population fluctuations in response to the density-dependent effect, we do so under the assumption that the environmental condition is constant. In this case, we cannot choose any other interpretation except that the density-dependent effect occurs. However, if we assume that the environmental conditions are not constant, other mechanisms can explain the phenomenon. That is, other factors, such as species interactions and/or environmental factors, seem to be much more reasonable mechanisms for controlling the fluctuation of the fish. Next, I will explain the mechanism by which a density-dependent effect seems to operate to change the population size.

## 5. Simple Fables

Here we explain how a density-dependent effect can occur regardless of the density. Let us focus on the number of fish of fish species A, the abundance of plankton B, which is a prey organism for fish A, fish species C, which is a predator of fish A, and environmental factor D.

1) We consider the case in which the environmental conditions are excellent and the abundance of prey plankton is 10 times larger than the usual level. The number of prey plankton per fish of species A is then 10 times larger than the usual level, and the number of fish of species A increases. However, when the number of fish of species A has increased, the environmental conditions suddenly become worse, and the number of prey plankton decreases to one-tenth. Then the number of prey plankton per each fish of species A decreases to one-tenth, and a severe density-dependent effect occurs, which causes the number of fish of species A decrease. The survival rate of fish of species A and/or the growth rate of fish of species A, etc., also decrease.

2) We consider the case in which the environmental conditions are excellent, and the abundance of prey plankton B is 10 times larger than the usual level. Then the number of prey plankton per fish of species A becomes 10 times larger than the usual level, and the number of fish of species A increases. The excellent environmental conditions continue after the number of fish has increased, and the number of prey plankton further increases to become 10 times larger again. Then the number of prey plankton per fish further increases by 10 times, and the number of fish further increases. That is, whether the number of fish increases or decreases (or whether the death rate increases or decreases) is determined not by their density but by the abundance of prey plankton B; *i.e.*, environmental factors determine whether the number of fish increases or decreases.
3) We consider the opposite case, *i.e.*, the case when the environmental conditions are much worse and the abundance of prey plankton B is one-tenth of the usual level. Then the number of prey plankton per fish becomes one-tenth of the usual level, and the number of fish does not increase but greatly decreases. As a result of the reduction of the number of fish, the number of prey plankton B per fish of species A increases, and then the number of fish begins to increase again. However, in time, if predator C of fish A increases to 10 times the usual level, the number of fish of species A does not increase; rather, it decreases.

It is not necessary to continue this explanation. Whether the number of fish of species A increases or decreases is not determined by the density of fish of species A, but whether the prey plankton B is abundant or not, and/or whether the predator C is abundant or not. That is, environmental factors determine whether the number of fish of species A increases or decreases. This concept is illustrated in Figure 3. That is, the proposal that the growth rate and/or death rate of fish of species A changes in response to a density-dependent effect is not valid. Those changes are all derived from the results of environmental changes.

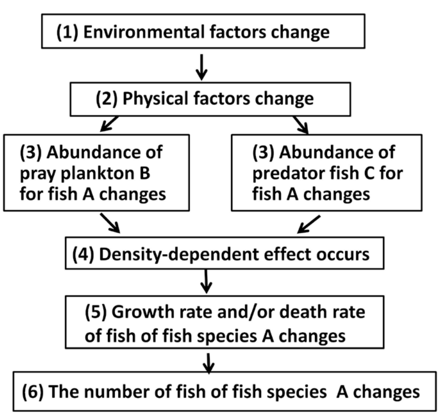


Figure 3. Density-dependent effect occurs regardless of the density. Environmental factors change the physical conditions and the physical conditions determine the abundance of preyplankton B and predator C. Depending on the abundance of preyplankton B and/or predator C, a density-dependent effect occurs. That is, a density-dependent effect occurs in response to the environmental factors, not as a direct result of the density of fish of species A.

Scientists who support a density-dependent effect may insist that they agree with the importance of the effects of the environmental factors; however, if the abundance of the prey plankton drops to one-tenth its normal level, the effect of this reduction must be accelerated by the density of fish that is prevalent at the time. That is, when the number of fish is extremely large, the effect of the reduction of the prey plankton must also be very large. These phenomena imply that the density-dependent effect truly exists.

However, if this is correct, when the SRR is plotted, the plotted points show us, on average, that the recruitment decreases when the density is high and increases when the density is low. However, this does not always occur. Under some conditions, the opposite phenomena commonly occur. Sakuramoto [2] [7] proposed a mechanism by which the recruitment could decrease at a high density and increase at a low density.

## 6. Two Opposite Loops Appear in the SRR

**Figure 4** shows the SRR for North Sea haddock, for which the age-at maturity is 4years old. The data refer to Cushing [22]. Usually the Ricker model is applied [22]; however, when we connected the points in chronological order, the SRR shows the anti-clockwise loop shown in the bottom in **Figure 4** [2]. That is although the SSB in 1963 was extremely low at the same level in 1962, the recruitment in 1963 was greatly lower than in 1962, and although the SSB in 1965 was two times larger than that in 1964, the recruitment in 1965 was much greater than that in 1964. In contrast, although the SSB in 1968 was much lower than that in 1967, the recruitment in 1968 was much lower than that in 1967. These phenomena indicate that although the SSB was large in some years, the recruitment in the next year was increased, and although the SSB was low in some years, the recruitment in the next year was decreased. A similar pattern was observed in the case of Pacific bluefin tuna, for which the age-at-maturity is 5 years old [7].

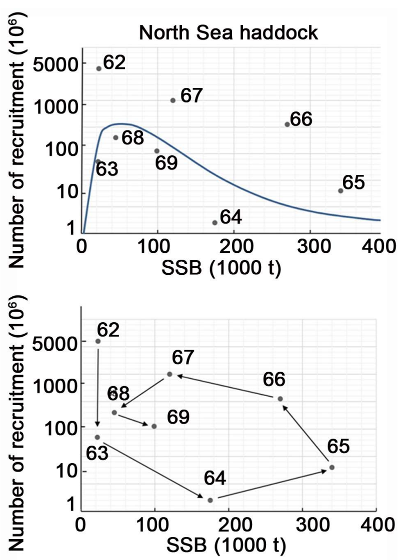


**Figure 4.** Stock-recruitment relationship. Top: The plot under the traditional concept. Bottom: The plot under the new concept proposed by Sakuramoto [2]-[8]. The case of North Sea haddock (Cushing, 1981).

In contrast, opposite cases are commonly observed [2]. **Figure 5** shows the SRR plots for pink salmon. The age-at-maturity of this fish is 2 years old. Usually the Ricker model is applied [23]; however, when we connected the points in chronological order, the SRR shows the clockwise loop shown at the bottom of **Figure 5** [2]. In this case, although the SSB in 1936 was extremely lower than that in 1934, the recruitment in 1936 was much lower than that in 1934. The mechanism by which a clockwise loop or anti-clockwise loop appeared could not be explained by the density-dependent effect. I explain the mechanism by which those loops appear in the next section.

## 7. Mechanism That Derives a Clockwise or Anti-Clockwise Loop

**Figure 6** is a diagram that shows the mechanism by which a clockwise or anti-clockwise loop is derived. Here the trajectory of recruitment R (open circle) is shown by a sine curve with a cycle of 6 years, which is the resultant trajectory determined by environmental factors. The SSB is also shown by the same sine curves with a time lag $k$ that is determined in correspondence with the age-at-maturity. The top and bottom of **Figure 6** shows the cases when the age-at-maturity is 2 years old or 4 years old, respectively. The former corresponds to pink salmon, and latter corresponds to North Sea haddock. The trajectories of R and SSB can be separated into four periods: P1, P2, P3 and P4.

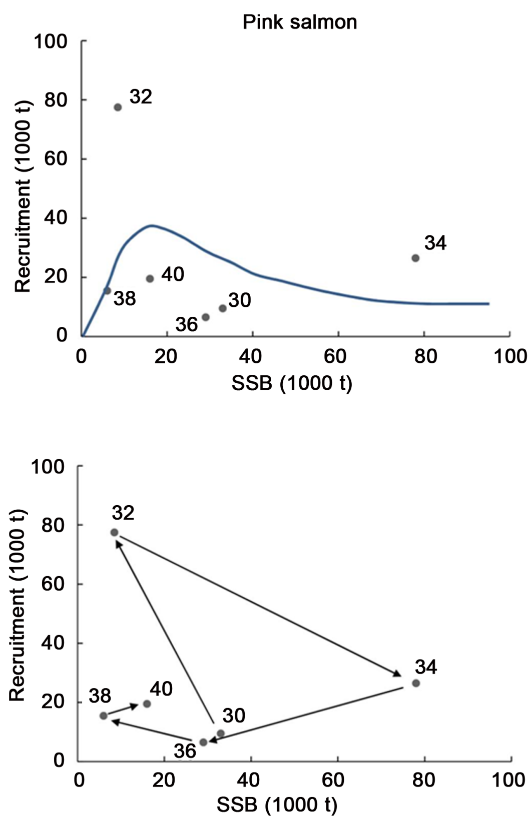


**Figure 5.** Stock-recruitment relationship. Top: The plot under the traditional concept. Bottom: The plot under the new concept proposed by Sakuramoto [2]-[8]. The case of pink salmon (Ricker, 1954).

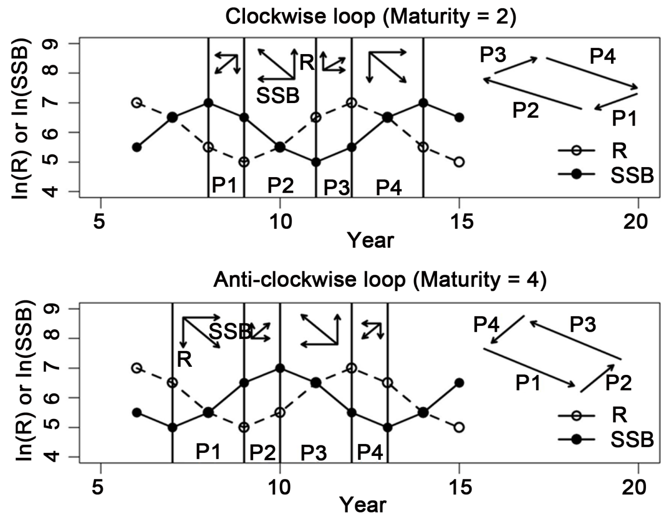


**Figure 6.** Simple simulation analyses. It is assumed that the environmental factor fluctuates according a sine curve with a six-year cycle. Top: The age-at-maturity is 2 years old, which corresponds to pink salmon; Bottom: The age-at-maturity is 4 years old, which corresponds to North Sea haddock.

In period P1 at the top of Figure 6, both R and the SSB decrease. Therefore, in the SRR plane, R moves in the downward direction and the SSB moves in the leftward direction. The direction in which the point on the SRR plane moves is then determined by these two vectors. That is, the point on the SRR plane moves to the southwest. In period P2, R increases and the SSB decreases. Then, on the SRR plane, R moves upward and the SSB moves to the left. Therefore, the point on the SRR plane moves to the northwest. In period P3, both R and the SSB increase. Then, R moves upward and the SSB moves to the right. Therefore, the point on the SRR plane moves to the northeast. In period P4, R decreases and the SSB increases. Then, R moves downward and the SSB moves to the right. Therefore, the point on the SRR plane moves to the southeast. As time passes through P1, P2, P3 and P4, the point on the SRR plane moves following a clockwise loop. Further, the number of years in each period is as follows: one year for P1, two years for P2, one year for P3, and two years for P4. The lengths of the arrows for the periods correspond to these numbers of years. The resultant clockwise loop shown in the upper right in Figure 6 is similar to that shown in pink salmon.

The bottom of Figure 6 shows the case when the age-at-maturity is 4 years old. The trajectories of R and SSB can also be separated into four periods: P1, P2, P3 and P4.In period P1, R decreases and the SSB increases. Then, R moves downward and the SSB moves to the right. Therefore, the point on the SRR plane moves to the southeast. In period P2, both R and the SSB increase. Then, R moves upward and the SSB moves to the right. Therefore, the point on the SRR plane moves to the northeast. In period P3, R increases and the SSB decreases. Then, on the SRR plane, R moves upward and the SSB moves to the left. Therefore, the point on the SRR plane moves to the northwest. In period P4, both R and the SSB decrease. Therefore, in the SRR plane, R moves downward and the SSB moves to the left. The point on the SRR plane moves to the southwest. As time passes through P1, P2, P3 and P4, the point on the SRR plane moves in an anti-clockwise loop. Further, the number of years in each period is as follows: two years for P1, one year for P2, two years for P3, and one year for P4. The lengths of the arrows for the periods correspond to these numbers of years. The resultant anti-clockwise loop is similar to that shown for North Sea haddock.

In general, when the age-at-maturity ($m$) is smaller than the half of the cycle that is determined by environmental factors ($m < k/2$), the SRR shows a clockwise loop, and when the age-at–maturity ($m$) is larger than the half of the cycle that is determined by environmental factors ($m > k/2$), the SRR shows an anti-clockwise loop [2] [7]. Sakuramoto [2] presented other examples, such as the Pacific stock mackerel, Pacific stock herring and North Sea plaice, etc. In this paper, I present the traditional data as examples of SRR that show a clockwise or an anticlockwise loop. However, according to the mechanism that produces the loops shown above, the loops would be observed for almost all of the SRR data. For more than 24 stocks collected from the ocean around Japan, it is currently being investigated which direction of loop would appear in their SRRs. The results strongly supported the above mechanism.

However, the clockwise or anti-clockwise loop observed in SRR cannot be explained using the density-dependent effect. This fact indicates that the most important relationship between stock and recruitment is likely to be the interspecific relationship and/or environmental conditions, not the density-dependent effect, and the density-dependent effect observed in SRR is not real. This is hard to accept for many biologists, however, the following analogy may help for understanding this fact. When we touch a piece of ice, it feels cold, but when we touch boiling water, it feels hot. Nobody doubts that temperature really exists. However, temperature itself is only an illusion, and temperature never be defined with any physical concept. Temperature has no actual substance, and it is only a consequence of molecular motion. This relationship is comparable to the density-dependent effect in biology. A density-dependent effect is only a consequence of the changes in environmental factors, and it is only an illusion, as Sakuramoto noted [6].

## 8. Conclusion

If the density-dependent effect played an important role in controlling population fluctuations, the SRR would never show a clockwise or anti-clockwise loop. The mechanism proposed here coincides well with the phenomena observed in many SRRs. In other words, the most important relationship between stock and recruitment is the interspecific relationship and/or environmental conditions. If the density-dependent effect observed in the SRR is not real, then the MSY theory is not valid, and all of the management procedures based on MSY are also not valid.

## Acknowledgements

I thank Drs. Rikio Satoand Naoki Suzuki for their useful comments, which improved this manuscript.

## Conflict of Interests

The author declares no conflict of interests.

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