



Clockwise Loops and Anticlockwise Loops Observed in a Stock-Recruitment Relationship

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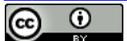
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Abstract

Loop-shaped trajectories are commonly observed in the stock recruitment relationship (SRR). A mechanism has been proposed that explains why the loops emerge in SRR. The aim of this study is to validate the mechanism using data for the stocks of 24 fish species that live in the waters around Japan. The following three questions are examined: 1) whether or not loop shapes are detected in SRRs for all 24 stocks; 2) whether or not the direction of the loops, *i.e.*, clockwise or anticlockwise, changes depending on the age at maturity; and 3) whether or not the slope of the regression line adapted for SRR changes depending on the age at maturity. The results were as follows: 1) loop shapes in SRR were recognized for all 24 stocks analyzed in this study; 2) clockwise loops were dominant when the age at maturity was low, and anticlockwise loops were dominant when the age at maturity was high; 3) the slope of the regression line adapted for SRR has a negative relationship to the age at maturity. When the age at maturity was low, the slope was positive but less than unity. When the age at maturity was high, the slope had no trend and was recognized as statistically zero. These findings will drastically change the concept of SRR. All previous findings obtained by analyzing the SRR may be better to revise essentially.

Subject Areas

Marine Biology

Keywords

Stock Recruitment Relationship, Clockwise Loop, Anticlockwise Loop, Age at Maturity, Japanese Sardine, Japanese Anchovy, Chub Mackerel

1. Introduction

One of the most important tasks in fisheries resource management is to eluci-

date the fluctuation mechanisms in fish populations. One of the key factors in those mechanisms is the stock-recruitment relationship (SRR). Scientists in the field widely believe that a density-dependent effect is also an important factor in controlling population fluctuations [1] [2]. Typical, traditional SRR models include the well-known Ricker [3] and Beverton and Holt [4] models, which are based on a density-dependent mechanism in SRR. Recently, however, the importance of environmental factors has been reported in many studies. For instance, Su *et al.* [5] noted a significant positive effect of sea-surface temperature (SST) on the survival rate of northern pink salmon stocks; conversely, they observed a weak negative effect of SST on the survival rate of southern pink salmon stocks. Sundby [6] noted that the recruitment of Atlantic cod stocks showed the different responses to the temperature changes. The temperature influences the recruitment processes in a large number of ways; partly directly on vital rates in cod, and partly indirectly through trophic transfer. Chen and Irvine [7] proposed a new model in which environmental factors were incorporated and discussed the stock-recruitment relationship using fisheries data of southeast Alaska pink salmon (*Oncorhynchus gorbuscha*) and West Coast Vancouver herring (*Clupea harengus*). They concluded that the model proposed by Chen and Irvine [7] performed better than the traditional Ricker model and a Ricker model that was extended to include environmental effects.

Recently, Sakuramoto proposed a new concept of SRR mechanisms [8]-[13] and showed the mechanisms that explained clockwise or anticlockwise loops emerged in the SRR, using a simulation study. That is, when recruitment, R , fluctuates cyclically in response to environmental factors, and the spawning stock biomass (SSB) also fluctuates cyclically with a time lag (mainly determined by age at maturity), the SRR shows a clockwise loop or an anticlockwise loop for each period of environmental change. The former occurs when age at maturity is less than half of the environmental cycle, and the latter occurs when age at maturity is more than half of the environmental cycle.

Sakuramoto [12] also discussed the slope of the regression line for the plot of $\ln(R)$ against $\ln(SSB)$. When the age at maturity is low enough relative to the length of the cycle of environmental factors, the slope of the regression line is high and close to unity. However, the higher the age at maturity becomes, the more the slope of the regression line decreases. When the age at maturity becomes greater than approximately half the length of the cycle of environmental factors, the slope decreases to almost zero. As a result, the relationship between R and SSB is masked and cannot be detected. Furthermore, when the age at maturity becomes greater than half the length of the cycle of environmental factors, the slope of the regression line becomes negative.

Sakuramoto [12] analyzed the Pacific stock of Japanese sardines and Pacific bluefin tuna and showed that, for the former, the slope of the regression line was close to unity, and three clockwise loops appeared. In contrast, for the latter stock, the slope of the regression line had no significant slope and showed anticlockwise loops. Sakuramoto concluded that no relationship between R and SSB

for Pacific bluefin tuna could be detected could be explained by the mechanism mentioned above.

The aim of this study is to elucidate whether or not this concept can be applied to the stocks of 24 fish species that live in the waters around Japan. That is, we examine: 1) whether or not loops are detected in SRRs for all 24 stocks; and 2) whether or not the direction of the loops, *i.e.*, clockwise or anticlockwise, changes depending on the age at maturity; and 3) whether or not the slope of the regression line adapted for SRR changes depending on the age at maturity.

2. Materials and Methods

2.1. Data

The data used in this study were provided by the Fisheries Agency and Fisheries Research Agency Japan [14], and included: number of recruitments; spawning stock biomass; and age at maturity of fish. The R and SSB for snow crab was estimated by area density method. The R and SSB for other 23 stocks are all estimated by VPA of which method does not assume any stock-recruitment relationship. The species names and stocks names are listed in **Table 1**.

2.2. A Mechanism Produces the Loops

Sakuramoto [12] used four simulation models to reproduce the SRR observed in the Pacific stock of Japanese sardine and Pacific bluefin tuna. Using the same models proposed by Sakuramoto [12], we explain the mechanism that loops are necessary detected in SRR. The basic model of SRR is expressed by Equation (1).

$$R_t = \alpha S_{t-1} \cdot f(\mathbf{x}_t) \quad (1)$$

where R_t , S_{t-1} and $f(\cdot)$ denote the recruitment in year t , spawning stock biomass in year $t - 1$, and a function that evaluates the effects of environmental factors in year t . The vector $\mathbf{x}_t = [x_{t,1}, \dots, x_{t,k}]$ is a list of environmental factors that affect the strength in R, which comprised not only of physical factors such as water temperature, but also biological interactions such as prey-predator relationships. Parameters α and k denote a proportional constant and the number of environmental factors, respectively. That is, equation (1) implies that R_t is proportionally determined by S_{t-1} , and simultaneously, R_t is affected by environmental factors in year t .

Model 1 is the case when environmental effects can be neglected. That is, $f(\mathbf{x}_t)$ in Equation (1) can be assumed to be unity. That is,

$$R_t = \alpha S_{t-1} \cdot \quad (2)$$

where α denotes the recruitment per spawning stock biomass (RPS). The survival process is expressed by

$$S_{t+m} = \gamma R_t \quad (3)$$

For simplicity, m denotes the age at maturity and longevity of the fish. That is, fish reach maturity age at m -year old, then, they spawn their eggs and die. In Equation (3), γ denotes the survival rate during m years or the spawning stock

Table 1. Lines which were judged to be parts of clockwise loops or parts of anticlockwise loops.

Notation	Species	Stock	Clockwise	Anti-clockwise	Age at maturity
a	Round herring <i>Etrumeus teres</i>	the Tsushima Warm Current stock	11	6	1
b	Japanese anchovy <i>Engraulis japonicus</i>	the Pacific stock	32	2	1
c	Japanese anchovy <i>Engraulis japonicus</i>	the Tsushima Warm Current stock	30	5	1
d	Japanese Spanish mackerel <i>Scomberomorus niphonius</i>	Seto Inland Sea stock	10	15	1.5
e	Japanese sardine <i>Sardinops melanostictus</i>	the Pacific stock	23	14	2
f	Japanese sardine <i>Sardinops melanostictus</i>	the Tsushima Warm Current stock	31	18	2
g	Blue mackerel <i>Scomber australasicus</i>	the Pacific stock	7	11	2
h	Japanese horse mackerel <i>Trachurus japonicus</i>	the Pacific stock	17	13	2
i	Japanese horse mackerel <i>Trachurus japonicus</i>	the Tsushima Warm Current stock	25	14	2
j	Yellowback seabream <i>Dentex tumifrons</i>	the Japan Sea and the East China Sea stock	20	12	2
k	Blue mackerel <i>Scomber australasicus</i>	the East China Sea stock	14	6	3
l	Alaska pollock <i>Theragra chalcogramma</i>	Northern Japan Sea stock	19	11	3
m	Chub mackerel <i>Scomber japonicus</i>	the Pacific stock	24	19	3
n	Chub mackerel <i>Scomber japonicus</i>	the East China Sea stock	37	2	3
o	Round-nose flounder <i>Eopsetta grigorjewi</i>	Japan sea stock	8	10	3
p	Pointhead flounder <i>Cleisthenes pinetorum</i>	Japan sea stock	3	12	3
q	Japanese amberjack <i>Seriola quinqueradiata</i>		12	6	3
r	Red sea bream <i>Pagrus major</i>	Western Japan sea and East China Sea stock	15	10	3.5
s	Red sea bream <i>Pagrus major</i>	Eastern Seto Inland Sea stock	14	22	3.5
t	Red sea bream <i>Pagrus major</i>	Central and western Seto Inland Sea stock	23	10	4
u	<i>Bastard halibut</i> <i>Paralichthys olivaceus</i>	Seto Inland Sea stock	11	6	4
v	Japanese pufferfish <i>Takifugu rubripes</i>	Ise and Mikawa Bays stock	3	19	4
w	Alaska pollock <i>Theragra chalcogramma</i>	the Pacific stock	6	35	6
x	Snow crab <i>Chionoecetes opilio</i>	Northern Pacific stock	4	15	≥6

biomass per recruitment (SPR), *i.e.*, $\gamma = 1/\alpha$. Therefore, when the population reproduces according to Model 1, R_t and S_{t+m} are constant regardless of year.

Model 2 is the case in which when $f(\mathbf{x}_t)$ in Equation (1) can be expressed by $1 + r$. That is,

$$R_t = \alpha(1+r)S_{t-1} \quad (4)$$

The increasing or decreasing rate, r , is determined by environmental factors. When environmental factors are good for the stock, r takes positive values ($r > 0$) and R increases. On the contrary, when environmental factors are bad for the stock, r takes negative values ($-1 < r < 0$) and R decreases. In this model, the survival process is the same of that shown in Equation (3).

Model 3 is the case when r in Equation (4) changes cyclically. It can be expressed by a sine curve as defined below:

$$f(\mathbf{x}_t) = 1 + \beta \sin(\omega t) \quad (5)$$

Thus,

$$R_t = \alpha(1 + \beta \sin(\omega t))S_{t-1} \quad (6)$$

Here, β and ω denote the amplitude of the sine curve and angular velocity, respectively. In this model, the survival process is the same of that shown in Equation (3).

Generally, the spawning stock biomass in year $t - 1$ (S_{t-1}) produces the recruitment in year t (R_t), and the recruitment in year t (R_t) becomes the spawning stock biomass in year $t + m$ (S_{t+m}). Then the spawning stock biomass in year $t + m$ (S_{t+m}) produces the recruitment in year $t + m + 1$ (R_{t+m+1}). This cycle repeats infinitely as shown in **Figure 1**. When the year is $t + m + 1$, the SRR can be expressed by Equation (7),

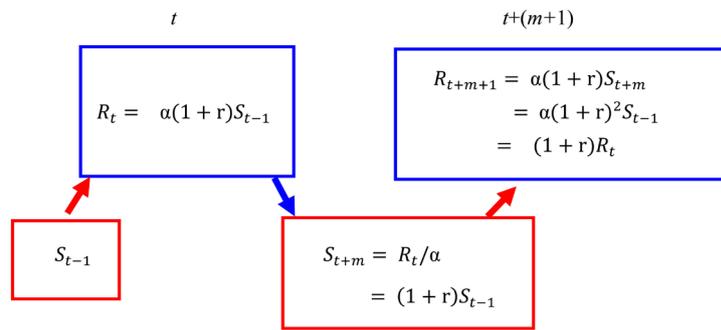
$$R_{t+m+1} = \alpha(1+r)S_{t+m}. \quad (7)$$

As shown in **Figure 1**, Equation (7) can be modified by,

$$R_{t+m+1} = (1+r)R_t. \quad (8)$$

That is, the relationship from S_{t+m} to R_{t+m+1} is replaced by the relationship from R_t to R_{t+m+1} . Equations (7) and (8) reveal an important fact that is hidden behind a SRR. That is, the relationship from S_{t+m} to R_{t+m+1} , which is the SRR itself, is the relationship from R_t to R_{t+m+1} , which is so to speak ‘‘R to R relationship’’. This relationship is the same in Model 3 as shown in **Figure 1**. Therefore, when the environmental factors cyclically fluctuate, such as a sine curve, the stock-recruitment relationship simply means the relationship between R_{t+m+1} and R_t . In other words, a stock-recruitment relationship shows only a relationship between two different points at t and $t + m + 1$ on the same sine curve (**Figure 2**). Therefore, when the recruitment fluctuates cyclically in response to environmental factors, the stock-recruitment relationship necessary shows loop shapes. Further the time lag is small, the SRR shows clockwise loops, and the time lag is large, the SRR shows anticlockwise loops.

Model 2



Model 3

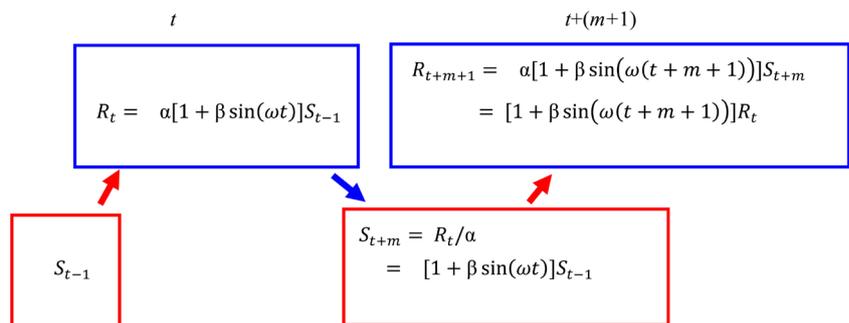


Figure 1. The stock-recruitment relationship in Model 2 and Model 3. The relationship from S_{t+m} to R_{t+m+1} is replaced by the relationship from R_t to R_{t+m+1} .

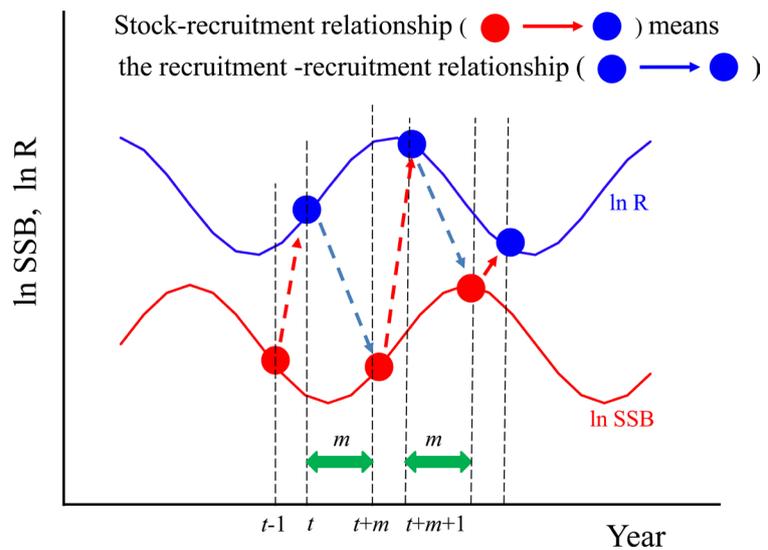


Figure 2. Stock-recruitment relationship. The relationship from S_{t+m} to R_{t+m+1} merely implies the relationship from R_t to R_{t+m+1} .

2.3. Rule for Judging the Clockwise or Anticlockwise Direction of Loops in the SRR

Using actual data for 24 fish stocks, we investigated whether or not loop shapes emerge in SRRs by plotting $\ln(R_{t+m})$ against $\ln(SSB_t)$. Further, we investigated the directions of the loops depending on the age at maturity.

We constructed a rule that determined the direction of the loops, either clockwise or anticlockwise. The direction of the line from year t to year $t + 1$ is judged based on the direction of the line from year $t + 1$ to year $t + 2$ (Figure 3). When the direction of the line from year $t + 1$ to year $t + 2$ is “A” shown in Fig. 3, the line from year t to year $t + 1$ is judged to be part of a clockwise loop. When the direction of the line from year $t + 1$ to year $t + 2$ is “B”, the line from year t to year $t + 1$ is judged to be part of an anticlockwise loop. After all directions of the lines from year t to year $t + 1$ were determined, we modified the judgement regarding the direction. When three successive lines were judged to have clockwise, anticlockwise, and clockwise directions, respectively, we replaced the middle anticlockwise direction with a clockwise direction, and we replaced the judgement with clockwise, clockwise, and clockwise because this seemed to be the more reasonable conclusion. If the series of directions was anticlockwise, clockwise, and anticlockwise, the middle clockwise” was replaced with anticlockwise, and we concluded the directions to be anticlockwise, anticlockwise and anticlockwise.

2.4. Three Regression Methods

In this study, we used three regression methods to plot $\ln(R_{t+m})$ against $\ln(SSB_t)$: the simple, Deming [15], and Passing and Bablok [16]. A simple regression analysis is problematic, because it assumes that the independent variable contains no observation and process errors. Therefore, parameters estimated using a simple regression analysis usually have serious biases [17] [18] [19] [20]. When both independent and dependent variables contain observation and/or process errors, both the Deming and Passing and Bablok regression analyses can effectively re-

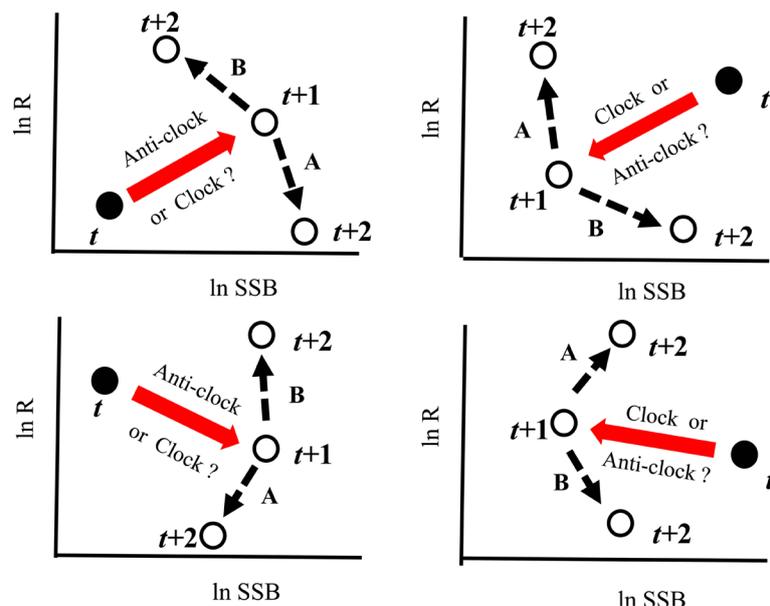


Figure 3. Rule used to judge the direction of the line from t to $t + 1$. When the line from $t + 1$ to $t + 2$ is A, the line from t to $t + 1$ is judged to be part of a clockwise loop. When the line from $t + 1$ to $t + 2$ is B, the line from t to $t + 1$ is judged to be part of an anticlockwise loop.

move the biases inherent in the results of a simple regression analysis. The programs developed by Aoki [21] [22] were used when these two regression analyses were applied to the data.

3. Results

Clockwise or Anticlockwise Loops in the SRR

Figure 4 shows the SRRs for 24 stocks. For almost all 24 stocks, loops were recognized. **Table 1** shows the number of lines that shows a clockwise loop or an anticlockwise loop. We also show the age at maturity. **Table 1** shows that when the age at maturity was equal to one year old, for all three stocks the number of lines that showed a clockwise loop was greater than the number that showed an anticlockwise loop. When the age at maturity was one-half or 2 years old, the number of lines that showed a clockwise loop was dominant except in two stocks. That is, the Seto Island Sea stock of Japanese Spanish mackerel and the Pacific stock of blue mackerel showed the opposite results, *i.e.*, the number of lines that showed an anticlockwise loop was greater than the number that showed a clockwise loop. When the age at maturity was between 3 and 4 years old, loops in both directions appeared. For 8 out of 12 stocks, clockwise loops were dominant, and in the other 4 stocks anticlockwise loops were dominant. When the age at maturity was more than or equal to 6 years old, anticlockwise loops were dominant for both stocks.

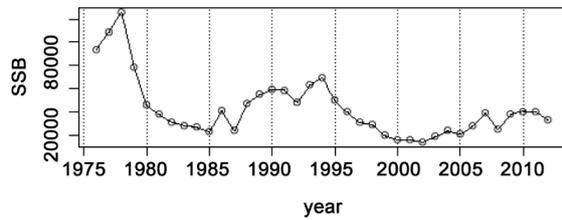
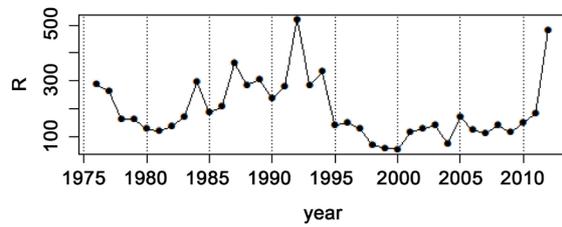
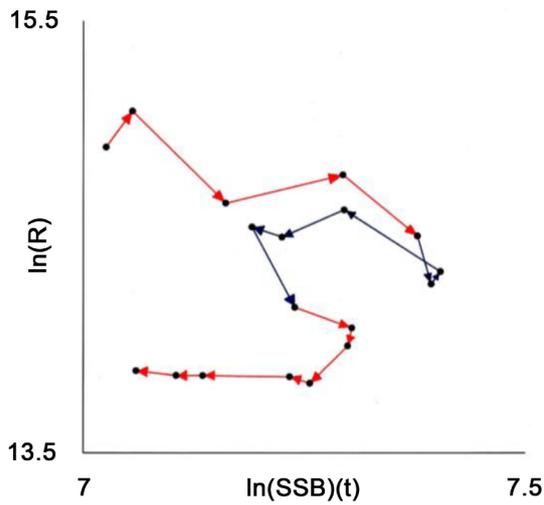
Table 2 shows the results of three regression analyses. **Figure 5** shows the plots of the slope estimated by a simple regression analysis against the age at maturity. The regression line in **Figure 5** is shown below:

$$b = 0.992 - 1.89m \quad (9)$$

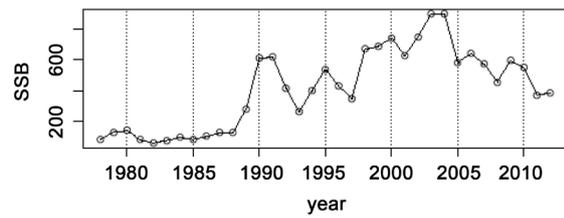
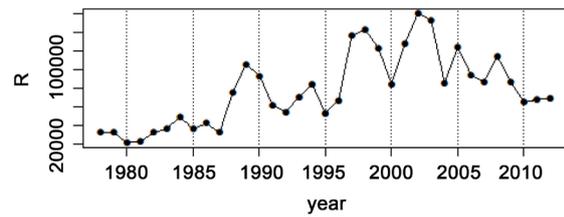
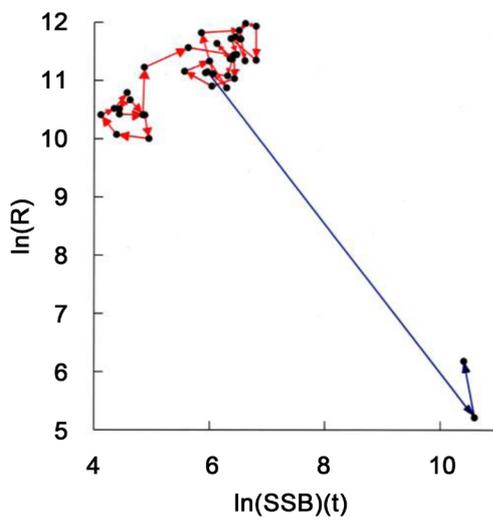
where b and m denote the slope of the regression line and the age at maturity. The p -value of slope b is 0.0125 and the 95% confidence interval of b is $(-0.333, -0.00449)$. That is, a significant negative relationship was detected between the slope of the regression line (b) and the age at maturity (m). This result coincided well with the results of the simulation by Sakuramoto [12].

It is generally believed that simple regression analyses commonly underestimate the slope of the regression line in response to the observed and/or process errors that exist in the independent variable (**Table 2**). Even in cases when the slope was estimated to be less than unity by a simple regression analysis, the slope estimated using Deming and/or Passing-Bablok regression analyses sometimes changed to unity or more than unity. Such changes occurred in 6 stocks, which are shaded blue in **Table 2**. Only 3 out of 24 stocks showed negative slopes for all three regression analyses, and these are shaded red in **Table 2**. The slopes for 8 out of 24 stocks were estimated to be unity or more than unity, and these are shaded green in **Table 2**. For the other 7 stocks, the slopes could not be estimated at least by one method. Therefore, only 3 out of 17 stocks showed negative density-dependent effects, and 14 out of 17 stocks showed no density-dependent effect or positive density-dependent effects.

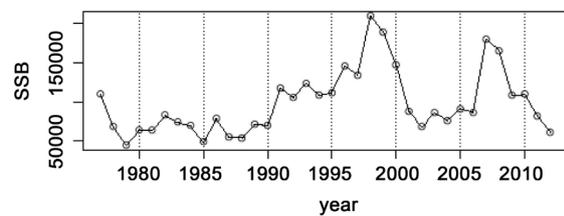
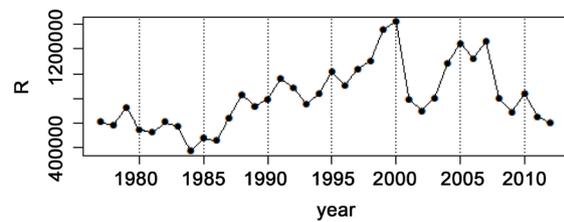
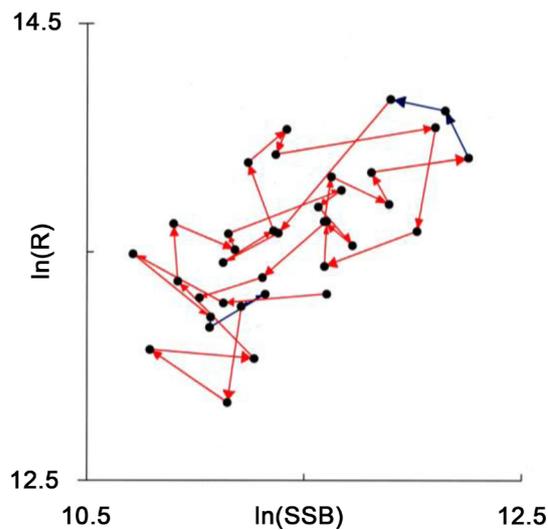
(a) Tshima Warm Current stock of Round herring



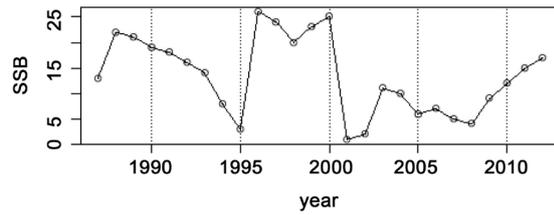
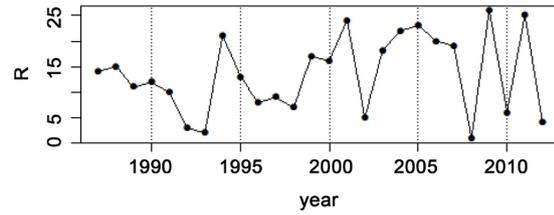
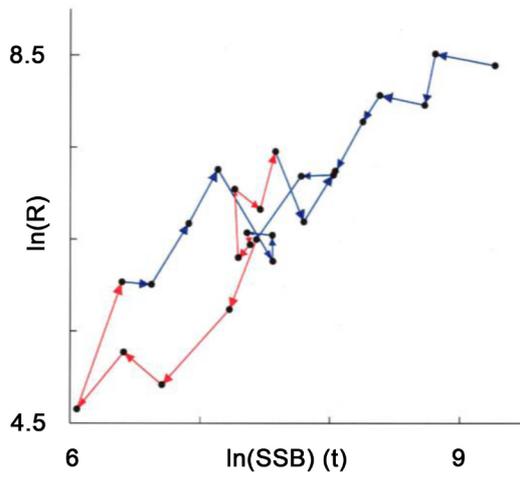
(b) Pacific stock of Japanese Anchovy



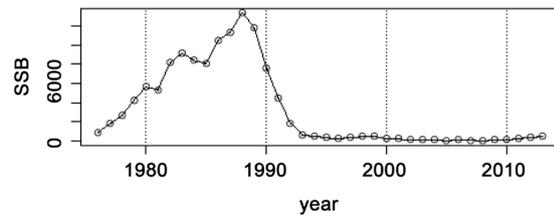
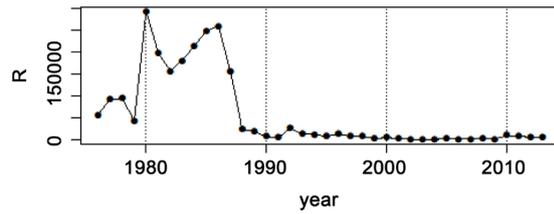
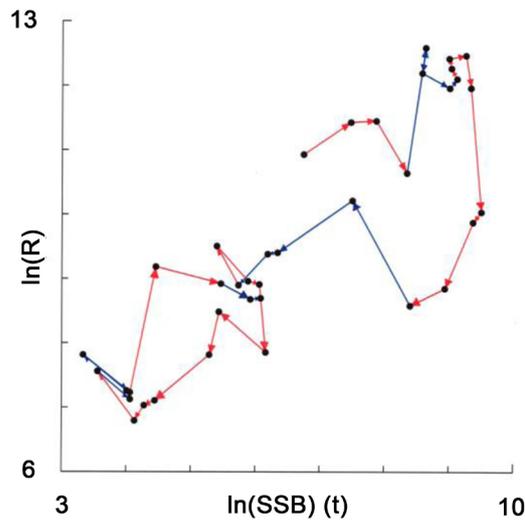
(c) Tsushima Warm current stock of Japanese Anchovy



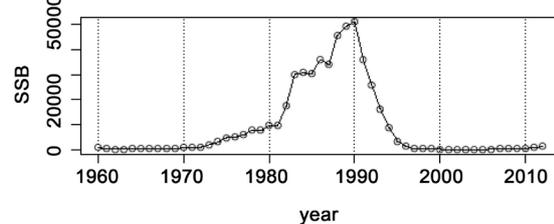
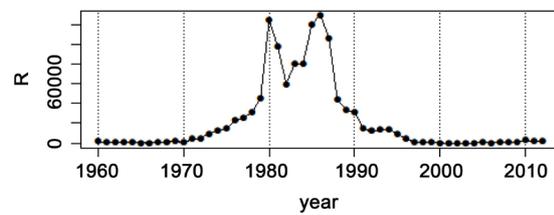
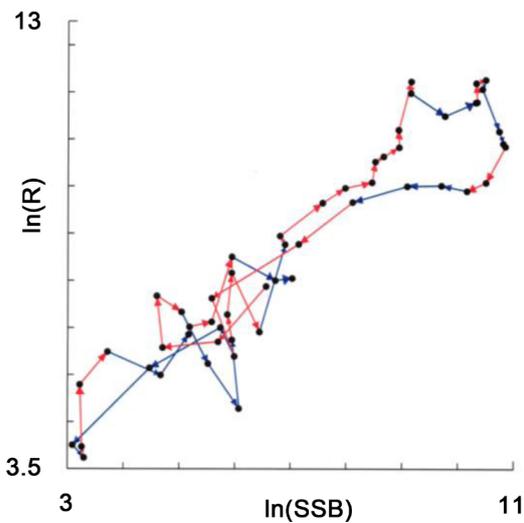
(d) Seto Inland Sea stock of Japanese Spanish mackerel



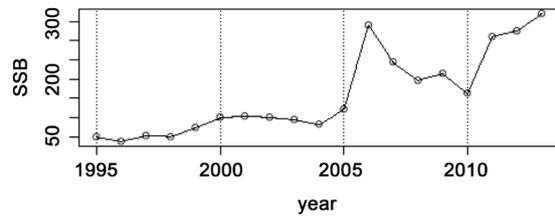
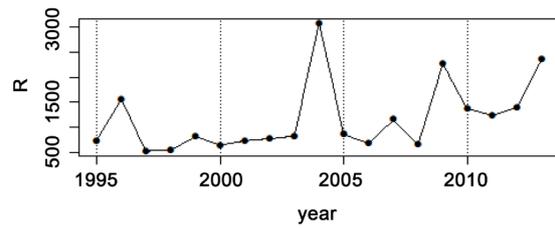
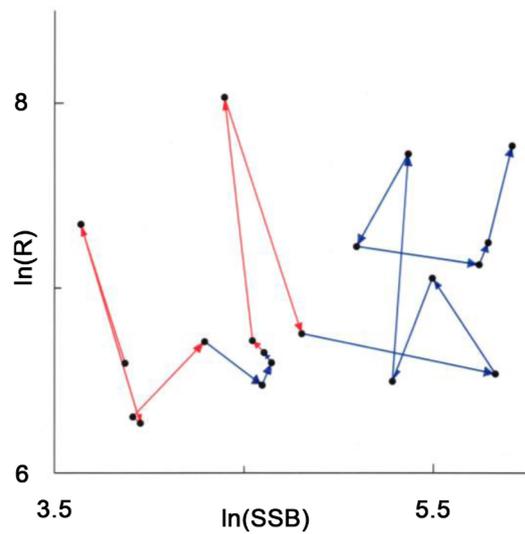
(e) Pacific stock of Japanese sardine



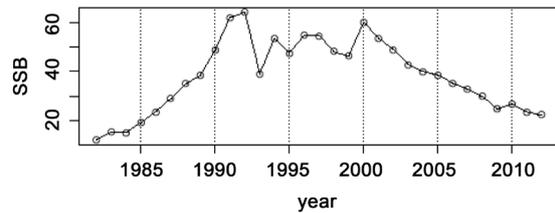
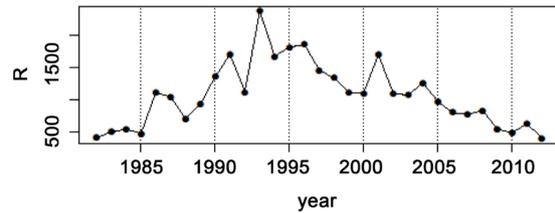
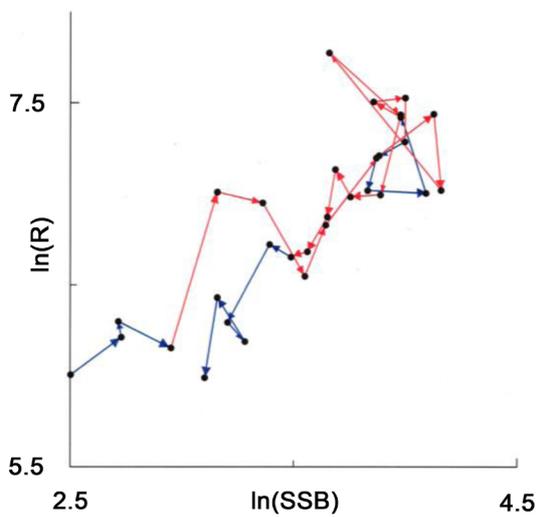
(f) Tsushima Warm Current stock of Japanese sardine



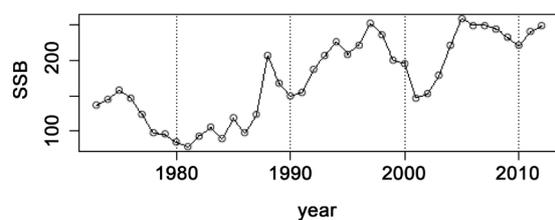
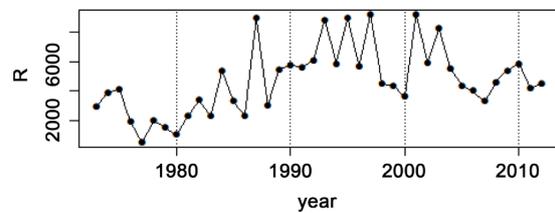
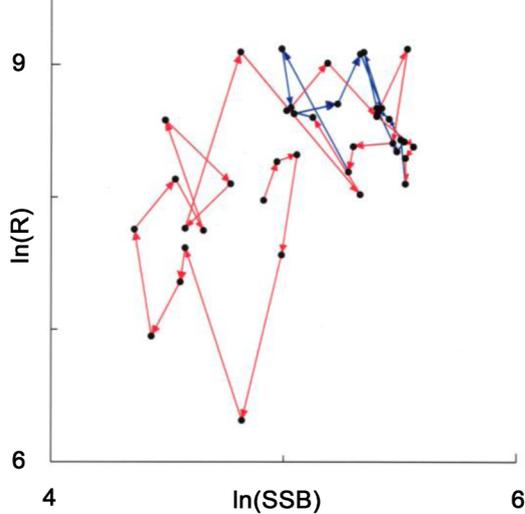
(g) Pacific stock of Blue mackerel



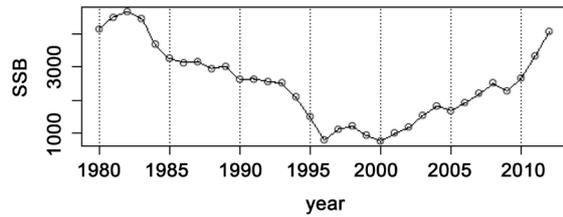
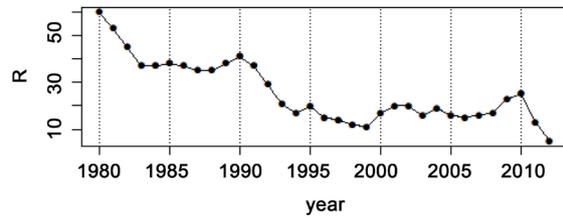
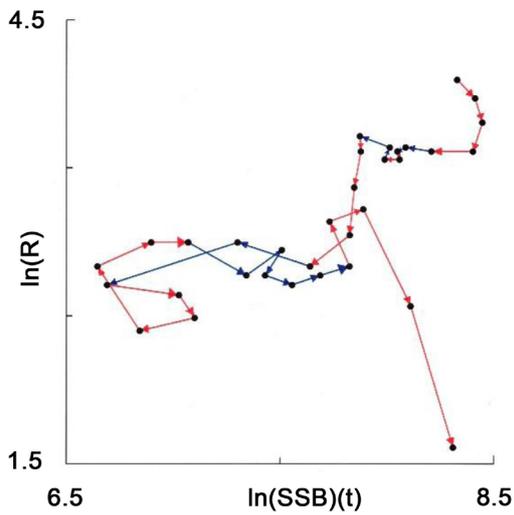
(h) Pacific stock of Japanese horse mackerel



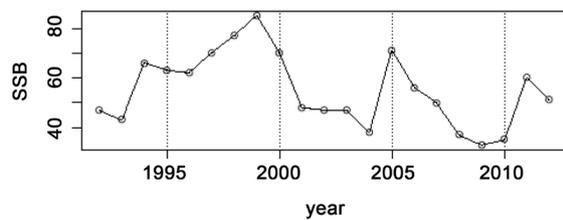
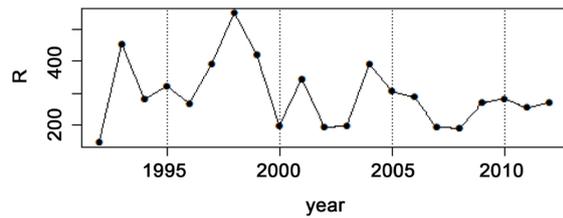
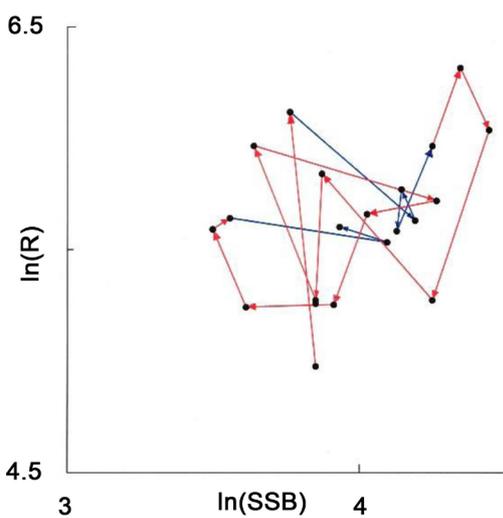
(i) The Tsushima warm current stock of Japanese horse mackerel



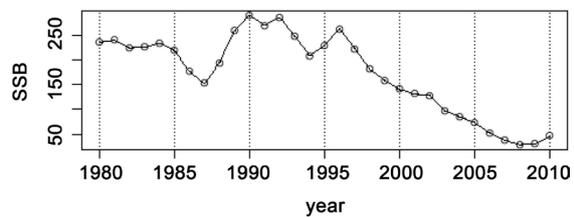
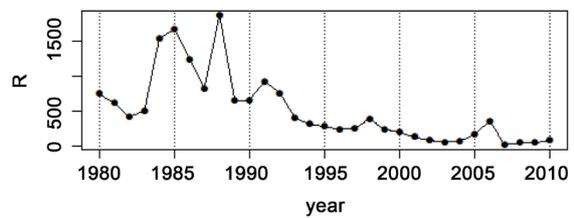
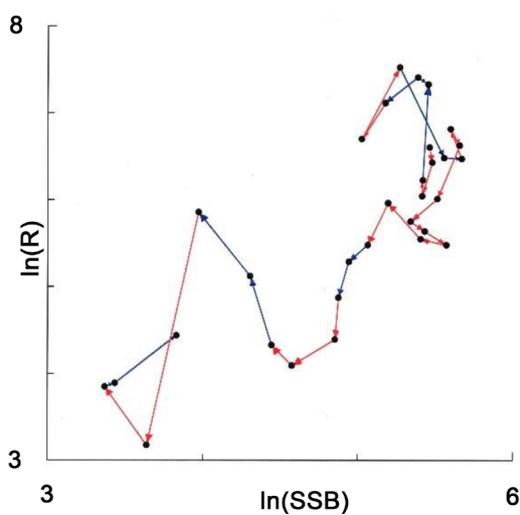
(j) Japan Sea and East China Sea stock of Yellow seabream



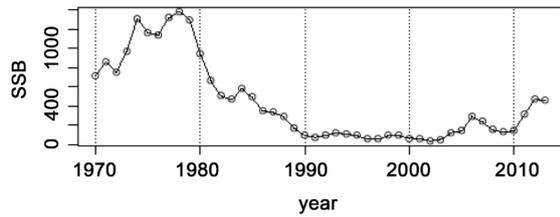
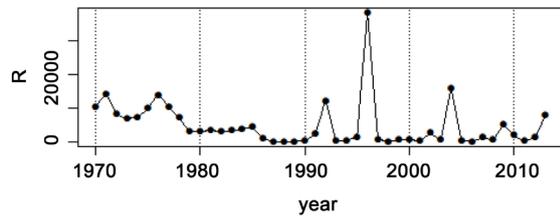
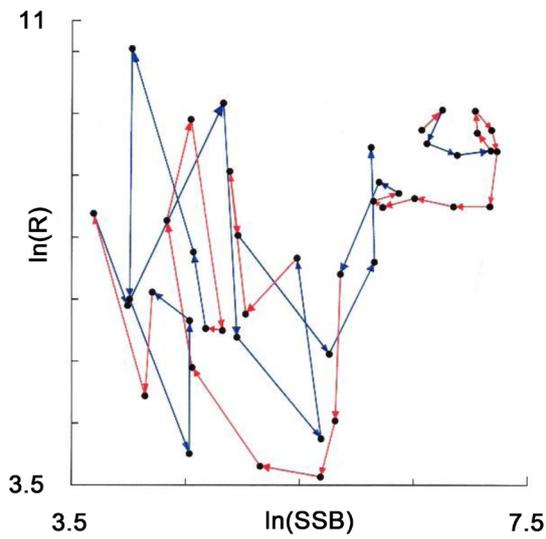
(k) East China Sea stock of Blue mackerel



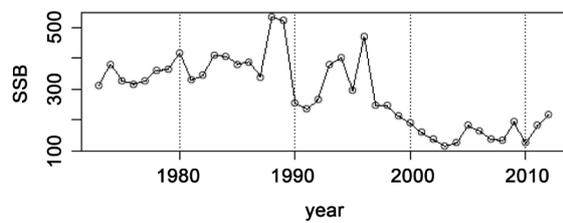
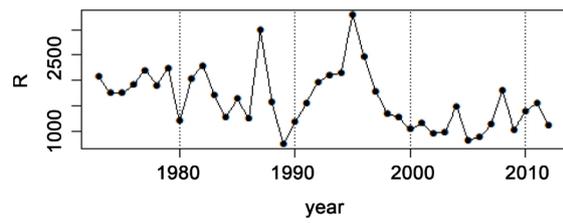
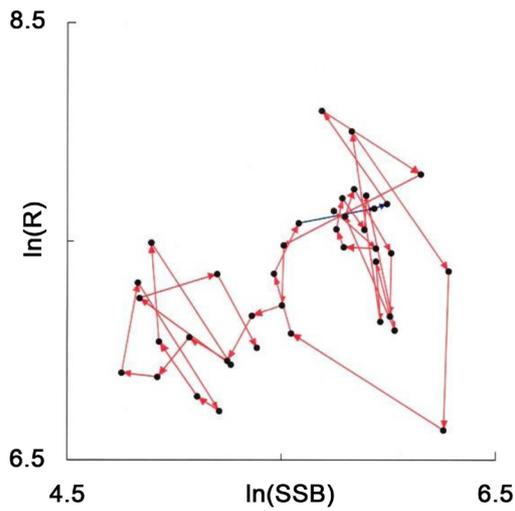
(l) Northern Japan Sea stock of Alaska pollock



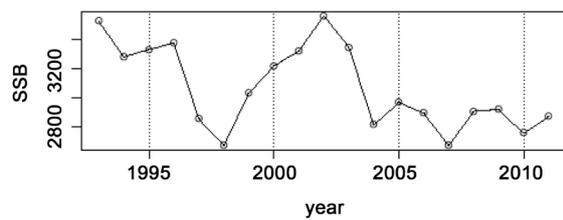
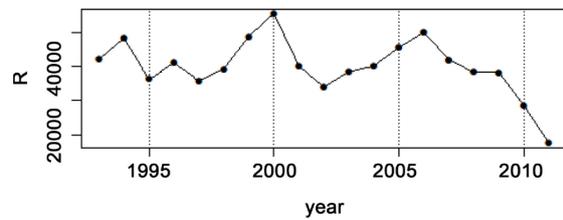
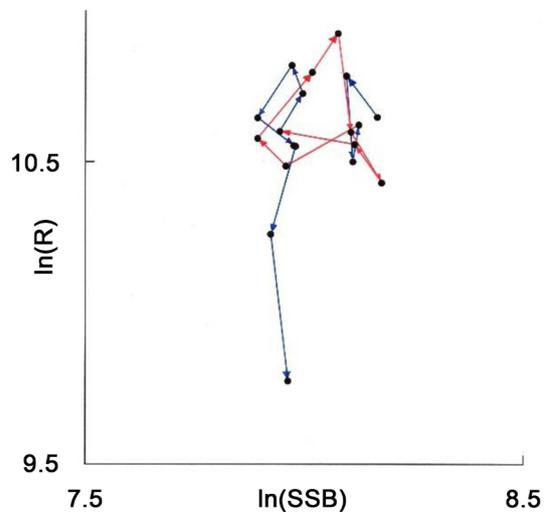
(m) Pacific stock of Chub mackerel



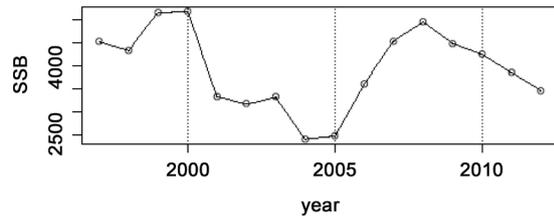
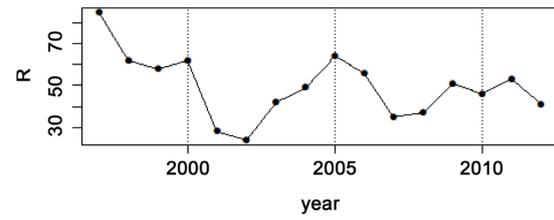
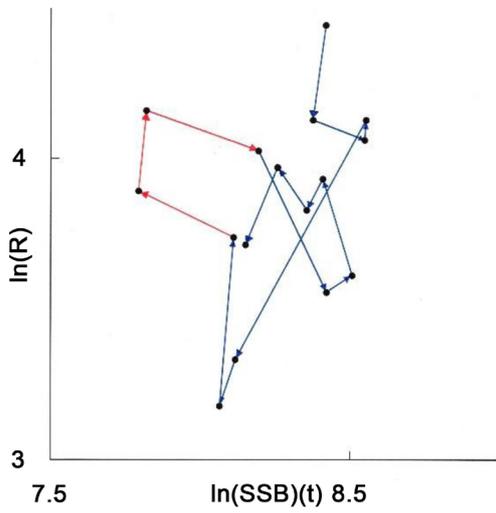
(n) East China Sea stock of Chub mackerel



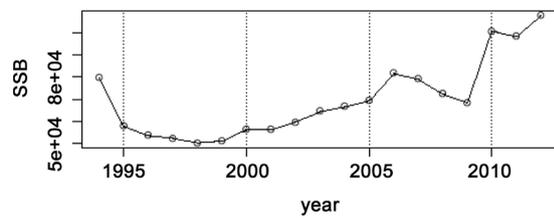
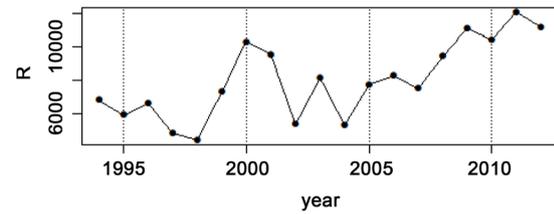
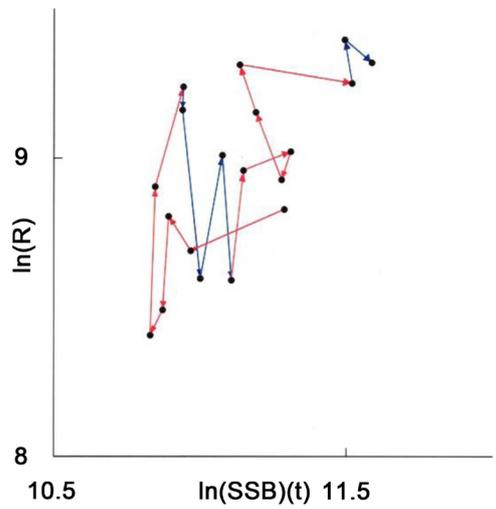
(o) Japan sea stock of Round-nose flounder



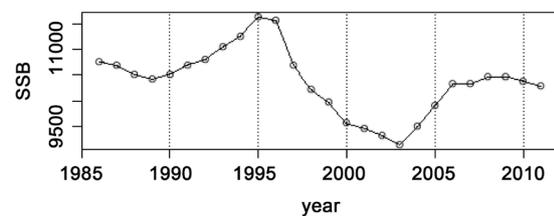
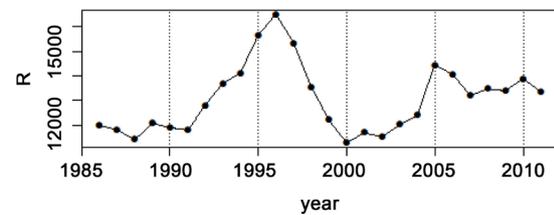
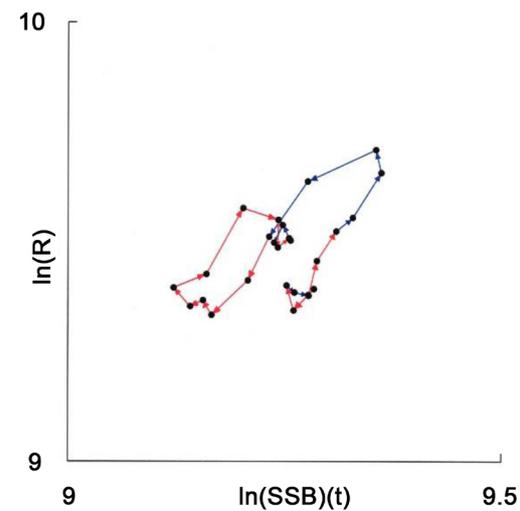
(p) Japan sea stock of Pointhead flounder



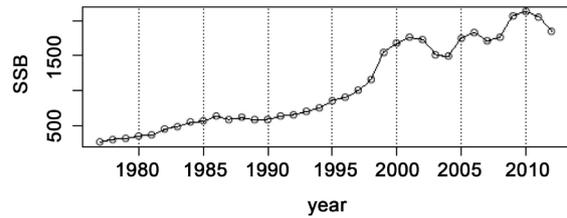
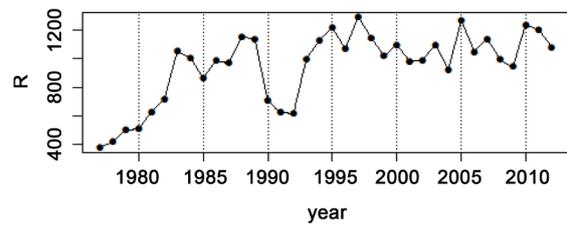
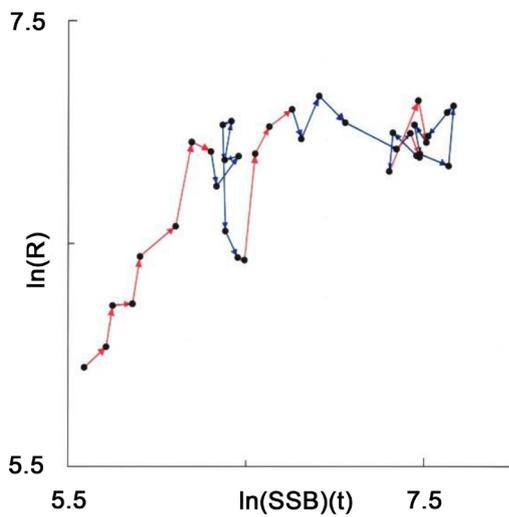
(q) Japanese amberjack



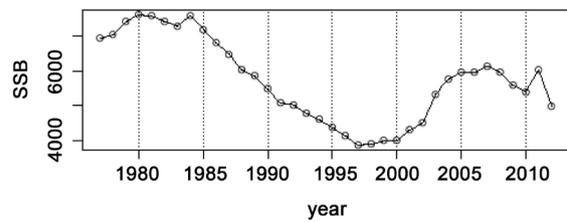
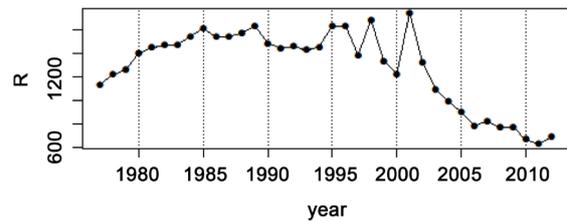
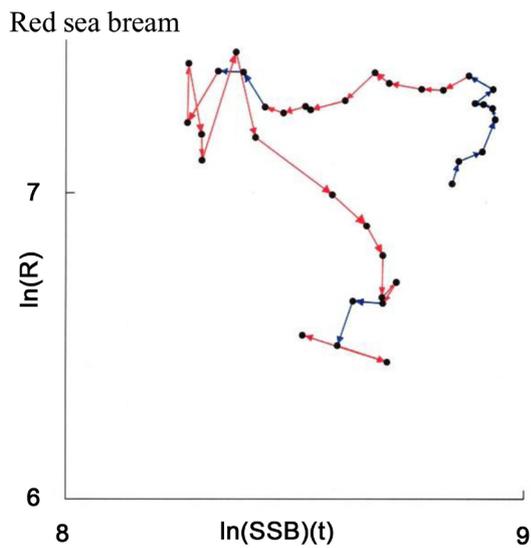
(r) Western Japan Sea and East China Sea stock of Red sea bream



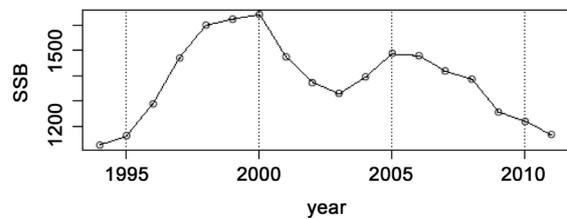
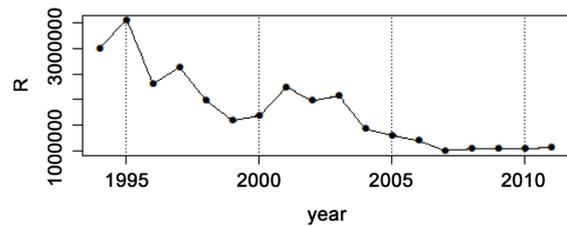
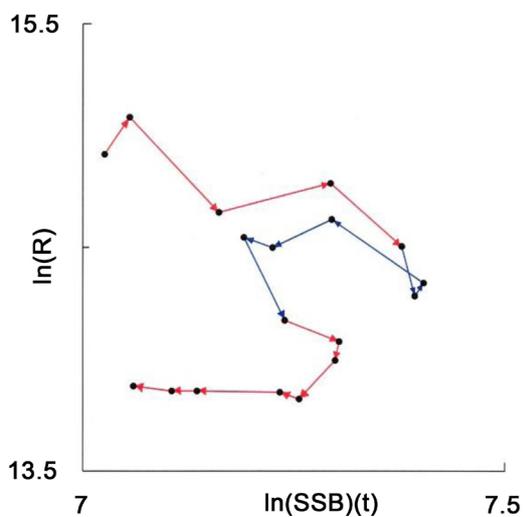
(s) Eastern Seto Inland Sea stock of Red sea bream



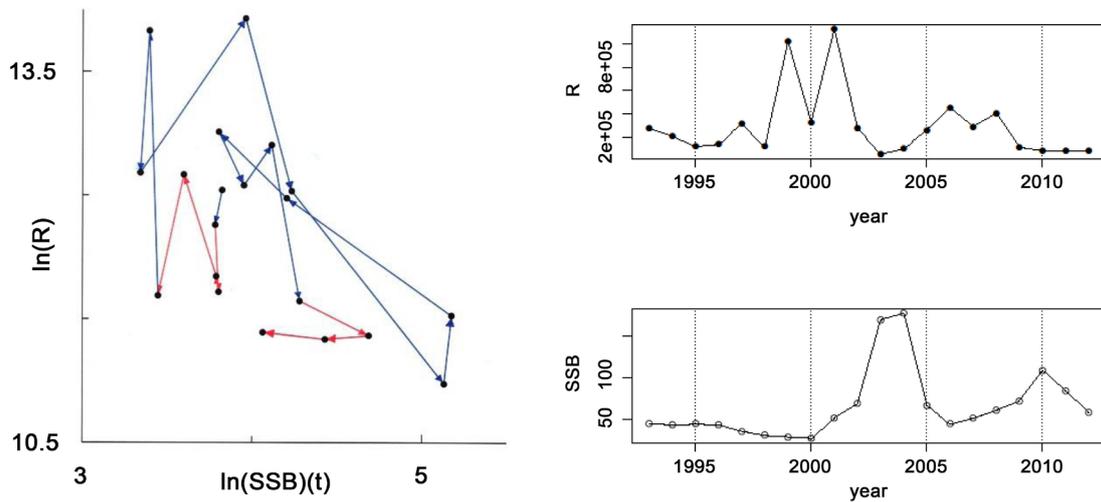
(t) Central and western Seto Inland Sea stock of Red sea bream



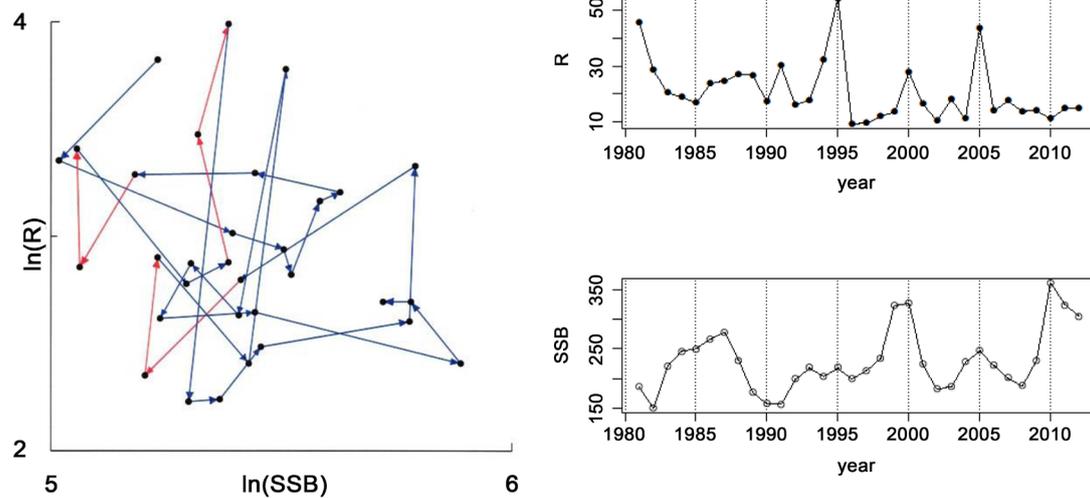
(u) Seto Inland Sea stock of Bastard halibut



(v) Ise and Mikawa Bays stock of Japanese pufferfish



(w) Pacific stock of Alaska Pollock



(x) Northern Pacific stock of Snow crab

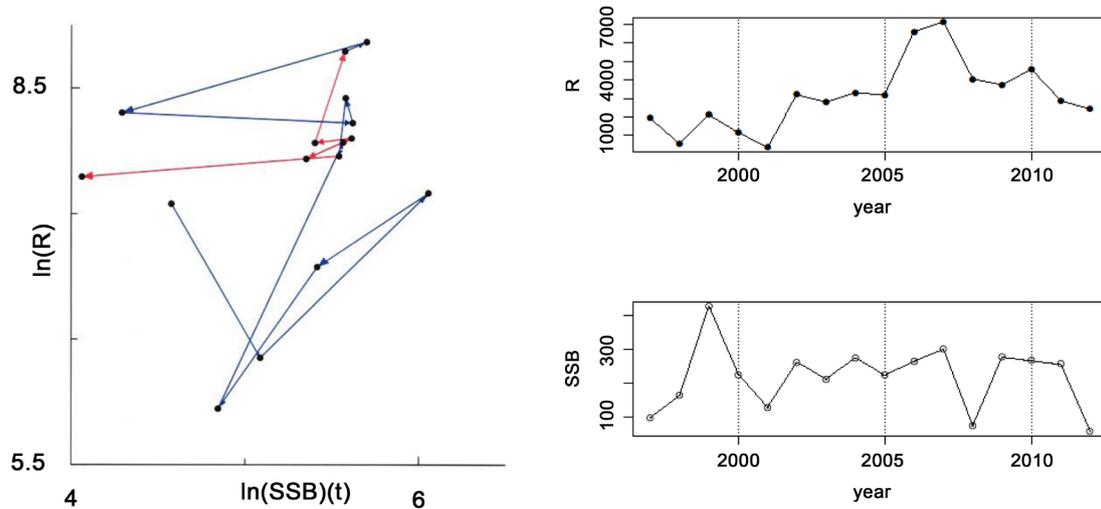


Figure 4. Stock-recruitment relationships for all 24 stocks that live in the waters around Japan. Clockwise loops or anticlockwise loops emerged.

Table 2. Slopes and 95% confidence limits of the regression lines estimated by the simple (OLS), Deming, and Passing-Bablok (P-B) regression methods. Red shows the cases when the estimated slopes were negative for all three methods. Blue shows the cases when the estimated slopes estimated by the simple regression method were less than unity, but, the slopes estimated by the Deming and/or Passing-Bablok (P-B) regression methods were unity or greater than unity. Green shows the cases when the slopes estimated by all three regression methods were equal to unity or greater than unity.

	Species	Stock	Method	Year	Data	m	b	95% confidence limit		p-value	Range of b	
								Lower	Upper			
a	Round herring	the Tsushima Warm	OLS	1976	2012	37	1	0.477	0.173	3.326	3.04 (10 ⁻³)	0 < b < 4
	<i>Etrumeus teres</i>	Current stock	Deming	1976	2012	37		1.013	0.556	1.872		b = 1
			P-B	1976	2012	37		0.973	0.596	1.480		b = 1
b	Japanese anchovy	the Pacific stock	OLS	1978	2012	35	1	0.516	0.383	0.649	4.01 (10 ⁻⁹)	0 < b < 1
	<i>Engraulis japonicus</i>		Deming	1978	2012	35		0.579	0.478	0.661		0 < b < 1
			P-B	1978	2012	35		0.638	0.500	0.844		0 < b < 1
c	Japanese anchovy	the Tsushima Warm	OLS	1977	2012	36	1	0.525	0.309	0.742	2.13 (10 ⁻⁵)	0 < b < 1
	<i>Engraulis japonicus</i>	Current stock	Deming	1977	2012	36		0.729	0.496	1.214		b = 1
			P-B	1977	2012	36		0.779	0.570	1.069		b = 1
d	Japanese Spanish mackerel	Seto Inland	OLS	1987	2012	26	1.5	1.132	0.890	1.373	9.67 (10 ⁻¹⁰)	b = 1
	<i>Scomberomorus niphonius</i>	Sea stock	Deming	1987	2012	26		1.305	1.267	1.635		1 < b < 2
			P-B	1987	2012	26		1.337	1.071	1.632		1 < b < 2
e	Japanese sardine	the Pacific stock	OLS	1976	2013	38	2	0.773	0.603	0.943	5.37 (10 ⁻¹¹)	0 < b < 1
	<i>Sardinops melanostictus</i>		Deming	1976	2013	38		0.908	0.803	0.990		0 < b < 1
			P-B	1976	2013	38		0.977	0.826	1.114		b = 1
f	Japanese sardine	the Tsushima Warm	OLS	1960	2012	53	2	0.912	0.812	1.013	2.20 (10 ⁻¹⁶)	b = 1
	<i>Sardinops melanostictus</i>	Current stock	Deming	1960	2012	53		0.978	0.896	1.086		b = 1
			P-B	1960	2012	53		1.000	0.900	1.100		b = 1
g	Blue mackerel	the Pacific stock	OLS	1995	2013	38	2	0.241	-0.099	0.581	1.55 (10 ⁻¹)	b = 0 (< 1)
	<i>Scomber australasicus</i>		Deming	1995	2013	38		0.403	0.197	0.673		0 < b < 1
			P-B	1995	2013	38		0.519	0.163	0.925		0 < b < 1
h	Japanese horse mackerel	the Pacific stock	OLS	1970	2013	34	2	0.669	0.200	1.138	6.24 (10 ⁻³)	b = 1
	<i>Trachurus japonicus</i>		Deming	1970	2013	34		2.908	1.895	4.921		1 < b < 4
			P-B	1970	2013	34		1.697	1.280	2.874		1 < b < 2
i	Japanese horse mackerel	the Tsushima Warm	OLS	1973	2012	40	2	0.845	0.386	1.303	6.23 (10 ⁻⁴)	b = 1
	<i>Trachurus japonicus</i>	Current stock	Deming	1973	2012	40		2.386	1.611	4.230		1 < b < 4
			P-B	1973	2012	40		1.765	1.095	2.773		1 < b < 2
j	Yellowback seabream	the Japan Sea and	OLS	1980	2012	33	2	0.556	0.236	0.875	1.27 (10 ⁻³)	0 < b < 1
	<i>Dentex tumifrons</i>	the East China Sea	Deming	1980	2012	33		1.064	0.800	1.378		b = 1
		stock	P-B	1980	2012	33		0.963	0.665	1.249		b = 1
k	Blue mackerel	the East China	OLS	1992	2012	21	3	0.399	-0.172	0.970	1.60 (10 ⁻¹)	b = 0 (< 1)
	<i>Scomber australasicus</i>	Sea stock	Deming	1992	2012	21		1.951	0.985	3.294		1 < b < 3
			P-B	1992	2012	21		1.457	0.928	2.943		1 < b < 2

Continued

l	Alaska pollock <i>Theragra chalcogramma</i>	Northern Japan Sea stock	OLS	1980	2010	21	3	1.282	0.882	1.683	3.62 (10 ⁻⁷)	b = 1
			Deming	1980	2010	21		1.898	1.601	2.841		1 < b < 2
			P-B	1980	2010	21		2.192	1.545	3.292		2 < b < 3
m	Chub mackerel <i>Scomber japonicus</i>	the Pacific stock	OLS	1970	2013	34	3	0.669	0.200	1.138	6.24 (10 ⁻³)	b = 1
			Deming	1970	2013	34		2.908	1.895	4.921		2 < b < 4
			P-B	1970	2013	34		1.697	1.280	2.874		b = 2
n	Chub mackerel <i>Scomber japonicus</i>	the East China Sea stock	OLS	1973	2012	40	3	0.346	0.108	0.585	5.52 (10 ⁻³)	0 < b < 1
			Deming	1973	2012	40		0.612	0.045	0.961		0 < b < 1
			P-B	1973	2012	40		0.787	0.519	1.058		b = 1
o	Round-nose flounder <i>Eopsetta grigorjewi</i>	Japan sea stock	OLS	1993	2011	19	3	0.520	-0.825	1.865	4.26 (10 ⁻¹)	0 < b < 1
			Deming	1993	2011	19		11.976	5.516		-	
			P-B	1993	2011	19		3.740	1.023	8.426		1 < b < 8
p	Pointhead flounder <i>Cleisthenes pinetorum</i>	Japan sea stock	OLS	1997	2012	16	3	0.290	-0.485	1.064	4.36 (10 ⁻¹)	0 < b < 1
			Deming	1997	2012	16		3.429	-5.356	666.734		-
			P-B	1997	2012	16		1.815	0.681	3.520		b > 1
q	Japanese amberjack <i>Seriola quinqueradiata</i>		OLS	1994	2012	19	3	0.790	0.279	1.300	4.58 (10 ⁻³)	b = 1
			Deming	1994	2012	19		1.467	0.990	5.142		0 < b < 6
			P-B	1994	2012	19		1.310	0.827	2.084		0 < b < 3
r	Red sea bream <i>Pagrus major</i>	Western Japan sea and East China Sea	OLS	1986	2011	26	3.5	0.979	0.413	1.545	1.55 (10 ⁻³)	b = 1
			Deming	1986	2011	26		2.246	1.605	2.476		b = 2
			P-B	1986	2011	26		2.010	1.303	3.757		1 < b < 4
s	Red sea bream <i>Pagrus major</i>	Eastern Seto Inland Sea stock	OLS	1977	2012	36	3.5	0.354	0.234	0.475	9.39 (10 ⁻⁷)	0 < b < 1
			Deming	1977	2012	36		0.396	0.243	0.475		0 < b < 1
			P-B	1977	2012	36		0.413	0.283	0.555		0 < b < 1
t	Red sea bream <i>Pagrus major</i>	Central and western Seto Inland Sea stock	OLS	1977	2012	36	4	-0.119	-0.605	0.368	6.24 (10 ⁻¹)	-1 < b < 1
			Deming	1977	2012	36		-8.253	-22.165	12.006		-
			P-B	1977	2012	36		2.017	0.373	3.993		0 < b < 4
u	<i>Bastard halibut</i> <i>Paralichthys olivaceus</i>	Seto Inland Sea stock	OLS	1994	2011	18	4	-0.409	-2.230	1.413	6.41 (10 ⁻¹)	-3 < b < 2
			Deming	1994	2011	18		-26.918	-63.031	951.519		
			P-B	1994	2011	18		14.300	-	-		-
v	Japanese pufferfish <i>Takifugu rubripes</i>	Ise and Mikawa Bays stock	OLS	1993	2012	20	4	-0.917	-1.567	-0.267	8.31 (10 ⁻³)	-2 < b < 0
			Deming	1993	2012	20		-2.167	-9.660	-1.453		-
			P-B	1993	2012	20		12.391	-	-		-
w	Alaska pollock <i>Theragra chalcogramma</i>	the Pacific stock	OLS	1981	2012	32	6	-0.369	-1.135	0.397	3.33 (10 ⁻¹)	b < 0
			Deming	1981	2012	32		-9.198	-147.568	5290.808		-
			P-B	1981	2012	32		5.307	-	-		-
x	Snow crab <i>Chionoecetes opilio</i>	Northern Pacific stock	OLS	1997	2012	15	6	0.414	-0.372	1.200	2.78 (10 ⁻¹)	-1 < b < 2
			Deming	1997	2012	15		2.886	-0.035	9.856		-
			P-B	1997	2012	15		2.686	0.645	4.055		1 < b < 4

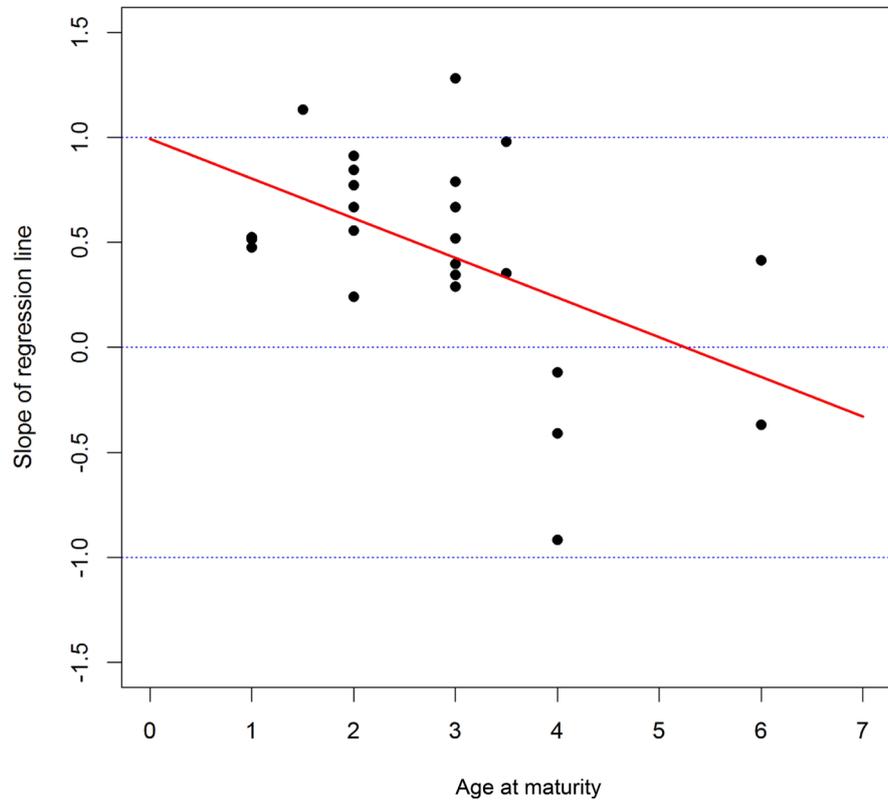


Figure 5. The relationship between the slope of the regression lines and the age at maturity. The regression line estimated is $b = 0.992 - 1.89 m$.

4. Discussion

4.1. Clockwise or Anticlockwise Loops in the SRR

Sakuramoto explained the mechanism that a clockwise loop or an anticlockwise loop in SRR were necessary detected [23]. In this paper, we again explained the mechanism that must appear loops in SRR. The plot of the S-R relationship merely implies the plot of the R-R relationship. Therefore, loops necessarily appear in SRR. The SRR appears to be a complex relationship. Loops should appear for all SRRs. This paper elucidated this fact using 24 stocks that live around Japan. We believe that the same results will be obtained for other stocks that live in other areas.

When the age at maturity was low, clockwise loops were dominant, and when the age at maturity was high, anticlockwise loops were dominant. However, with regard to the direction of the loop, two exceptions were observed. For the Seto Island Sea stock of Japanese Spanish mackerel and the Pacific stock of Blue mackerel, anticlockwise loops were dominant, although the ages of these stocks at maturity were low, *i.e.* 1.5 years old and 2 years old, respectively. In the case of the Seto Island Sea stock of Japanese Spanish mackerel, the first seven lines appear to show clockwise loops (See **Figure 4(d)**). Hasegawa *et al.* [24] noted the possibility that even when the age at maturity is low, the SRR could show anticlockwise loops when strong species interactions can be assumed to exist. Further, the direction of the loops would be strongly influenced by the cycle of en-

environmental conditions. When the length of the cycle of environment conditions was short, an anticlockwise loop would likely occur. In almost all cases, the present results were coincided well with the theory proposed by Sakuramoto [12] [23], with only two exceptions.

The time series data available is also an important factor to construct the loops. When the time series data is short, it is difficult to construct a loop such as the cases of a and x in **Figure 4**. On the contrary, when the time series data is too long, two or more than two loops are constructed and it is difficult to distinguish into each loop, such as the case in m in **Figure 4**. In this case, it is better to plot in each period of time such as the case done for Pacific bluefin tuna [12]. In the case for Pacific bluefin tuna [12], the 60-year time series data available were separated into four periods and detected the three anti-clock loops.

4.2. Slope of the Regression Lines in SRR

Sakuramoto noted that the slopes of the regression lines adapted for SRR were determined by the age at maturity and the length of the cycle of environmental factors [12] [23]. When the age at maturity is low, the slope estimated by a simple regression method in which $\ln(R_{t+m})$ is plotted against $\ln(SSB_t)$ shows a positive value, although the slope is statistically less than unity. When the age at maturity is high, the slope of the regression line is close to zero. Furthermore, the age at maturity becomes higher, and the slope of the regression line becomes negative. Sakuramoto showed that the slope of the Pacific stock of Japanese sardines was close to unity, although it was statistically less than unity. This finding is very important because it shows that a density-dependent effect is easily detected for stocks which have a low age at maturity. In contrast, the results of this paper show that no relationship between recruitment and SSB could be easily detected for stocks which have a high age at maturity. For instance, the SSR of Pacific bluefin tuna showed no relationship between R and SSB, and the plots were widely scattered without any trend [12] [13]. The Beverton and Holt model or hockey stick model is usually applied as the SSR for Pacific bluefin tuna, and the management procedure has been widely discussed. However, this paper suggests that the Beverton and Holt model or hockey stick model is not appropriate for this stock, and so a discussion based on those SRR model would not be fruitful.

In general, 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. All the management procedures that are constructed based on the density-dependent effect should be revised, because the density-dependent effect observed in SRR is not valid.

5. Conclusions

The results elucidated in this paper can be summarized as follows:

- 1) Loop shapes emerged in SRR for almost all 24 stocks investigated in this paper.
- 2) When the age at maturity was low, clockwise loops were dominant, and when the age at maturity was high, anticlockwise loops were dominant.
- 3) The slope of the regression line for SRR had a negative correlation with the age at maturity. When the age at maturity was low, the slope was positive but less than unity. When the age at maturity became high, the slope decreased to zero, and as the age at maturity increased further, the slope became negative.

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