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Studies for the Sustainable Management of Oyster Farms in Pukman Bay, Korea: Estimation of Carrying Capacity from Food Availability

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To develop a sustainable management model for oyster farming in Pukman Bay, Korea, we estimated the carrying capacity for oyster farming using food availability data. Optimal culture densities were calculated to be 124-133 individuals per unit flux area (m^2) and 310-330 individuals per string. The present annual production is approximately 1,038 tons/year, which is 87% of the estimated maximum yield of 1,193 tons/year. Therefore, considering annual fluctuations and a critical buffer to reduce ecological impacts, the current level is within optimal conditions. During periods of increased water temperature, energy demand was largely met by high primary production. The food supply significantly decreased as the harvest season approached, and 10 out of 21 oyster farms had a deficient food supply for at least 1 month. Therefore, these farms (39% of the farms within the bay) exceeded optimal densities.

Key words: Pacific oyster, Food availability, Carrying capacity, Pukman Bay

Introduction

The behavior, growth, and survivorship of filter-feeding invertebrates are strongly influenced by the quantity and composition of their food, planktonic matter (Bayne, 1983; Pechenik, 1987; Strathmann, 1987; Baldwin and Newell, 1995). To maximize sustainable yield, food availability should be maintained at appropriate levels in areas of intensive aquaculture. Food availability is difficult to predict, as it can fluctuate daily and seasonally (Van Valkenburg et al., 1978; Berg and Newell, 1986; Malone et al., 1986; Litaker et al., 1987). Despite these difficulties, much effort has been spent on developing strategic management systems to ensure maximum sustainable yield from filter-feeding marine-bivalve farms (Hoffmann et al., 1992; Margaret et al., 1993; Hoffmann et al., 1994; Powell et al., 1994).

Few studies of oyster, scallop, and marine ascidian farms have predicted carrying capacity from food availability, except in a self-purification capacity (Choi et al., 1991). According to this approach, energy flow should be considered when estimating carrying capacity in aquaculture areas (Bernard, 1974; Dame, 1976; Rodhouse, 1978, 1979; Kim, 1980).

The aim of the present study was to provide fundamental information for the management of coastal filter-feeder aquaculture areas, especially in Pukman Bay, one of the foremost oyster aquaculture areas in Korea. We estimated the carrying capacity from food availability data using a numerical model. To do this, we calculated food requirements and evaluated food availability in terms of the aquaculture operations in the bay.

Materials and Methods

Seawater was sampled monthly at eight sites in Pukman Bay, Korea, from July 1995 to April 1996. Pacific oysters, *Crassostrea gigas*, from 21 farms were sampled (Fig. 1) at three depths (upper, middle, and lower). In total, nine samples were collected from each farm.

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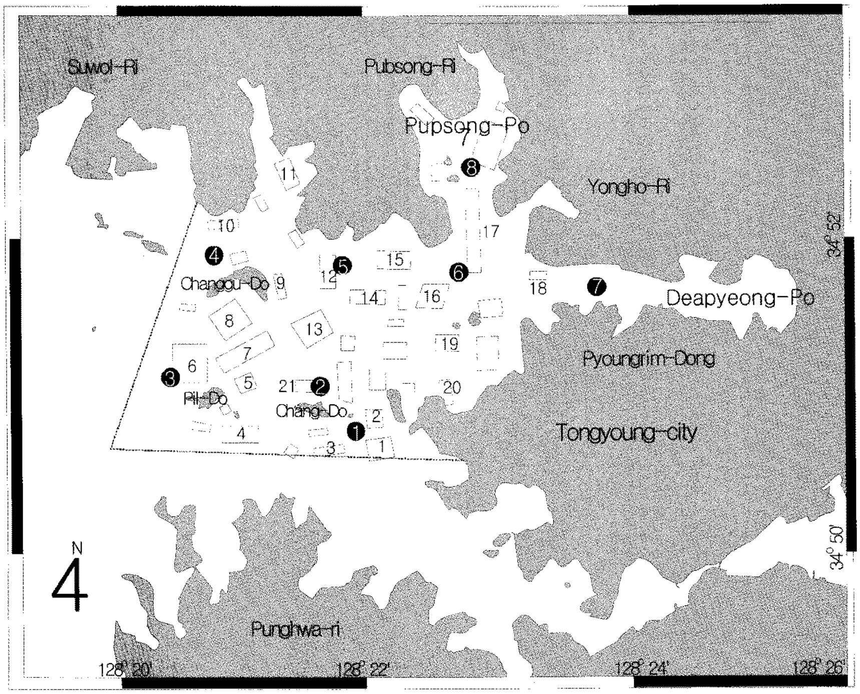

Fig. 1. Map of sample sites and oyster farms. Sample sites were distributed throughout the area to reduce geographical bias. All licensed oyster farms were included for estimation of carrying capacity in Pukman Bay, Korea, in 1995-1996.

Theoretical equations

We used a numerical equation to estimate food availability. The food requirement within aquaculture waters is the total food intake of all cultured oysters. The total number of animals at each farm was calculated as follows:

$$N_0 = \frac{\Sigma L}{H_s} \times C \times \overline{n_c} \tag{1}$$

where ΣL is the sum of long-line length (m), H_s is the string interval (m), C is the number of clusters per string, and $\overline{n}_c$ is the number of animals per cluster.

Individual filtration rate (FR) was calculated using equation (2) (Kim, 1995):

$$FR = Exp(0.208 - 4.324T) \cdot DW^{0.223} \text{ (L/h)} \tag{2}$$

where T is ambient water temperature (°C) and DW is oyster dry weight. The equation can be transformed to calculate instant filtration rate (ΔFR), as shown in equation (3):

$$\Delta FR = FR / 60 \text{ (L/min)} \tag{3}$$

In coastal areas, marine food supply is closely associated with tidal currents. Therefore, the flux areas for oyster growth are restricted to areas of tidal flux, which is related to tidal velocity. Considering the semi-diurnal tidal cycle (372 min), instant current velocity (U_i) can be calculated as follows:

$$U_i = Vx \times \sin(\pi \times \frac{i}{372}) \text{ (m/min)} \tag{4}$$

where Vx and i are the momentary maximum current velocity and measured time at each farm, respectively. Therefore, the tidal square (S) that directly affects a given oyster farm can be obtained as follows:

$$S = L \times H \text{ (m}^2\text{)} \tag{5}$$

From the equation above, the instant filtration efficiency (rF_i) of cultured oysters can be calculated using equation (6), which accounts for the volumetric ratio between the total volume of water passing through the oyster farm and the volume of water filtered by the cultured oysters:

$$\begin{aligned} &rF' = U_i \times S / (\Delta FR \times N \times 10^{-3}) \\ &rF' \geq 1 \rightarrow rF_i = 1 \\ &rF' < 1 \rightarrow rF_i = rF' \end{aligned} \tag{6}$$

Considering the semi-diurnal tide cycle, the total filtered volume per farm (V_F) can be calculated as follows:

$$V_F = \left(\sum_{i=0}^{372} \Delta FR \cdot rF_i\right) \times \frac{24}{t_p} \times N \times 10^{-3} \ (\mathrm{m^3/d}) \qquad (7)$$

where 24 is the number of hours in the day and t_p is the tidal period, from neap tide to spring tide.

The total energy intake (E_I) is calculated using the intake of primary production (PP) by cultured oysters in farmed waters, as follows:

$$E_I = V_F \times PP \times 10^{-3} \quad (\mathrm{Mcal/d}) \qquad (8)$$

The weight growth of cultured oysters in time t (W_t) is calculated by von Bertalanffy's growth equation, as follows:

$$W_t = W_{\max}(1 - e^{-k(t-t_0)})^3 \ \ (\mathrm{g}) \qquad (9)$$

When estimating the total yield of each oyster farm, the total number of oysters cultured on each farm must be calculated. For various reasons, the number of animals decreases over time. Therefore, total mortality (z) should be considered in determining the number of animals over time t (N_t):

$$N_t = N_0 \cdot e^{-z \cdot t} \qquad (10)$$

where N_0 is the initial number of oyster spats on a farm. Because we sampled the animals monthly, the daily growth rate (ΔW) was calculated as follows:

$$\Delta W = (W_{t+1} - W_t)/30 \quad (\mathrm{g/d}) \qquad (11)$$

According to Kim (1980), trends in the energy content (E_k) of oyster tissue change once 0.5 g of meat weight is reached. This is shown in equation 12:

$$\begin{aligned} &DW < 0.5 \ (g) \rightarrow E_k = 4 - DW + 1.2(DW)^2 \\ &DW \geq 0.5 \ (g) \rightarrow E_k = 3.375 + DW - 0.314(DW)^2 \\ &\qquad\qquad\qquad\qquad + 0.0435(DW)^3 \end{aligned} \qquad (12)$$

The energy efficiency of growth (rG) is negatively correlated with water temperature (Kim, 1980):

$$rG = 0.75 - 0.028 \ T \qquad (13)$$

Therefore, energy requirement at time t (E_R) is the sum of individual requirements, which can be calculated from growth efficiency (rG) and instant growth rate (ΔW):

$$E_R = (\Delta W \times dr \times E_k / rG) \times N_t \times 10^{-3} \ (\mathrm{Mcal/d}) \qquad (14)$$

where dr is the ratio of oyster dry weight to wet weight.

With respect to food availability, carrying capacity (CC) reflects the adequacy of the food supply for cultured oysters. CC is the ratio of ingested energy (E_I) to the energy required for growth (E_R):

$$CC = \frac{E_I}{E_R} \qquad (15)$$

Culture density is one of the most important factors affecting productivity. Culture productivity tends to decrease exponentially with increasing culture density. Thus, the maximum surplus capacity (K) can be calculated as follows:

$$\frac{dK}{dN} = -MK \qquad (16)$$

where N is the number of animals per harvest and M represents the density-dependent elimination efficiency. When N is 0 (i.e. no oysters), K_0 can account for the total natural carrying capacity of the flux area. At a given density, N, the surplus carrying capacity can be calculated using the integral of the exponential decrease in K_0:

$$K_N = K_0 \cdot e^{-MN} \qquad (17)$$

K_N indicates the surplus capacity in the flux rate after the cultured animals have fed. If oyster growth is positively correlated with carrying capacity, maximum oyster production (W_N) can substitute for K_N, and the theoretical maximum production of oysters (W_K) for K_0 is as follows:

$$W_N = W_K \cdot e^{-MN} \qquad (18)$$

Therefore, the yield biomass (Y) in a flux area can be calculated as follows:

$$Y = W_N \cdot N \qquad (19)$$

Results and Discussion

Unit flux area

The number of suspended oysters was estimated using equation (1). This value was used to estimate culture density (data not shown). A cumulative flow meter recorded measurements for 24 hours at each farm; the velocity of the tidal current (V_x) was then calculated as follows:

$$\begin{aligned} &V_x = V_{day} \times \frac{6.2}{24} \\ &V_x = \int_0^x H \cdot \sin x \cdot dx = 2H \\ &V_x = \frac{V_x}{2} \times \frac{\pi}{372} \\ &\rightarrow = V_{day} \times \frac{6.2}{24} \times \frac{1}{2} \times \frac{\pi}{372} \\ &\rightarrow = V_{day} \times 0.00109 \ (\mathrm{m/min}) \end{aligned} \qquad (20)$$

Table 1. Hydrographic measurements and estimated flux area at each oyster farm in Pukman Bay

#Farm code	Total flux per day (m/d)		Mean flux (m/d)	Instantaneous maximum Current (m/min)	Flux area (m^2)
	Neap tide	Spring tide			
1	619.63	2,540.49	1,580.06	1.72	31,020
2	236.50	975.33	605.92	0.66	23,000
3	860.40	3,527.64	2,194.02	2.39	36,300
4	957.10	2,514.69	1,735.89	1.89	57,500
5	725.67	1,669.04	1,197.36	1.31	37,000
6	9,256.32	21,289.53	9,256.32	10.09	127,160
7	3,028.43	6,475.92	4,752.18	5.18	112,500
8	468.78	821.59	645.18	0.70	98,010
9	83.95	151.11	117.53	0.13	28,500
10	413.50	781.17	597.34	0.65	31,350
11	609.21	913.81	761.51	0.83	57,000
12	297.29	634.46	465.87	0.51	84,000
13	260.10	546.21	403.16	0.44	88,275
14	309.32	1,168.24	738.78	0.81	51,000
15	361.49	1,445.98	903.74	0.99	36,750
16	331.06	1,575.87	953.46	1.04	32,300
17	145.53	582.12	363.83	0.40	158,205
18	225.60	902.40	564.00	0.61	19,800
19	81.22	348.12	214.67	0.23	26,520
20	183.93	367.85	275.89	0.30	16,900
21	381.57	1,717.07	1,049.32	1.14	35,530

Table 2. Initial number of oyster spats and total mortality (*Z*) at each farm in Pukman Bay

#Farm code	Initial number of animals (×1000)	Total mortality (Z)
1	5,922.0	0.0676
2	2,862.2	0.1116
3	6,468.0	0.1733
4	10,465.0	0.0971
5	7,104.0	0.0415
6	27,479.8	0.0613
7	26,100.0	0.0415
8	22,809.6	0.0191
9	2,736.0	0.1014
10	7,600.0	0.1077
11	13,933.3	0.1077
12	12,600.0	0.0099
13	12,358.5	0.0904
14	6,346.7	0.1189
15	5,635.0	0.0351
16	3,876.0	0.231
17	21,166.4	0.1226
18	3,207.6	0.3466
19	2,320.5	0.0673
20	2,535.0	0.1034
21	9,413.1	0.0179

Table 3. Estimated parameters for Bertalanffy growth curves at each farm in Pukman Bay

#Farm code	W_{max}	k	t_n
1	9.22	0.2746	-1.31
2	4.57	0.3475	-0.36
3	9.22	0.2746	-1.31
4	9.22	0.2746	-1.31
5	4.34	0.3919	-1.96
6	10.14	0.1205	-4.55
7	4.34	0.3919	-1.96
8	10.02	0.1014	-7.60
9	5.29	0.1932	-3.99
10	4.89	0.5345	-0.89
11	4.89	0.5349	-0.89
12	10.00	0.2473	-3.02
13	4.95	0.1520	-3.65
14	9.65	0.1823	-3.67
15	8.91	0.4843	-0.49
16	12.04	0.2280	-2.35
17	11.05	0.2303	-1.36
18	10.01	0.2818	-0.87
19	4.80	0.3825	-1.90
20	4.80	0.3825	-0.67
21	6.89	0.2602	-2.11

where V_{day} is the daily volume of tidal flux, V_x is the volume of tidal flux during the π cycle, and H is the instantaneous maximum velocity of the tidal current. The field survey was carried out on July 23 and 24, 1996, during the neap tide and on July 31 and August 1, 1996, during the spring tide. V_x was calculated from the mean flow rate of the neap and spring tides (Table 1). Flux area, the initial number of animals, and total mortality (*Z*) are listed in Tables 1 and 2.

Estimation of carrying capacity in Pukman Bay

Growth of cultured oysters was estimated using equation (9). All parameters for the growth curve (W_{max}, k, and t_0) are listed in Table 3. Energy requirements (E_R) on a farm scale were estimated from the energy efficiency and growth rates of each farm's

Table 4. Estimated energy requirements (E_R) at each farm (Mcal/d) in Pukman Bay

#Farm	Month									
	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
1	759.0	1,458.0	865.0	715.0	305.0	189.0	124.0	97.0	82.0	81.0
2	172.0	397.0	226.0	168.0	64.0	35.0	21.0	14.0	11.0	9.0
3	746.0	1,289.0	688.0	512.0	197.0	110.0	65.0	45.0	34.0	31.0
4	1,303.0	2,428.0	1,400.0	1,124.0	466.0	280.0	179.0	135.0	111.0	107.0
5	1,167.0	1,458.0	529.0	374.0	129.0	69.0	37.0	28.0	19.0	18.0
6	2,641.0	4,031.0	1,883.0	1,776.0	834.0	614.0	452.0	463.0	441.0	562.0
7	4,286.0	5,356.0	1,945.0	1,376.0	472.0	253.0	135.0	101.0	71.0	66.0
8	2,183.0	3,266.0	1,544.0	1,481.0	709.0	537.0	409.0	436.0	434.0	581.0
9	252.0	503.0	135.0	112.0	45.0	28.0	20.0	15.0	13.0	15.0
10	1,797.0	3,137.0	650.0	384.0	105.0	44.0	21.0	11.0	7.0	5.0
11	3,297.0	5,753.0	1,191.0	703.0	192.0	81.0	38.0	21.0	12.0	9.0
12	3,081.0	6,909.0	2,055.0	1,778.0	750.0	455.0	340.0	263.0	247.0	293.0
13	1,336.0	4,589.0	593.0	497.0	204.0	134.0	91.0	76.0	68.0	76.0
14	944.0	1,946.0	555.0	465.0	191.0	113.0	82.0	62.0	57.0	65.0
15	2,077.0	5,066.0	1,351.0	945.0	308.0	142.0	80.0	46.0	33.0	29.0
16	763.0	2,647.0	416.0	287.0	103.0	54.0	30.0	21.0	17.0	16.0
17	3,387.0	14,923.0	2,801.0	2,299.0	957.0	581.0	366.0	290.0	258.0	285.0
18	444.0	1,639.0	252.0	158.0	49.0	22.0	10.0	6.0	4.0	3.0
19	402.0	1,322.0	195.0	128.0	43.0	22.0	12.0	8.0	6.0	6.0
20	348.0	1,483.0	240.0	163.0	57.0	29.0	15.0	10.0	8.0	7.0
21	2,072.0	7,862.0	1,084.0	953.0	400.0	262.0	178.0	146.0	130.0	142.0

Table 5. Estimated total volume of seawater filtered by cultured oysters (V_F) at each farm in Pukman Bay (Kton/d)

#Farm	Date									
	1995. Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	1996. Jan.	Feb.	Mar.	Apr.
1	95.7	176.7	113.2	102.0	28.1	12.8	6.7	7.1	10.6	24.0
2	32.7	64.0	40.8	35.7	9.5	4.2	2.1	2.1	3.0	6.5
3	94.1	156.2	90.0	73.0	18.1	7.4	3.5	3.3	4.5	9.1
4	164.2	294.3	183.0	160.1	42.8	19.0	9.7	9.9	14.4	31.6
5	194.7	268.4	142.9	136.2	36.1	17.3	7.3	11.1	13.2	36.0
6	709.6	943.2	494.5	468.7	123.9	59.4	25.0	38.2	45.1	122.3
7	715.2	986.2	525.0	500.5	132.5	63.6	26.8	40.9	48.6	132.2
8	689.7	927.4	496.0	482.2	131.2	65.1	28.4	44.8	55.0	155.0
9	68.8	105.2	42.7	39.3	9.5	4.1	2.3	2.1	2.9	7.8
10	190.2	311.1	127.9	116.8	27.7	11.7	6.5	5.9	7.9	20.9
11	348.8	570.5	234.4	214.2	50.9	21.4	12.0	10.8	14.5	38.3
12	405.3	687.7	313.7	310.6	85.5	32.6	23.1	19.2	35.1	109.9
13	364.1	568.4	194.6	178.4	44.6	20.7	9.9	10.2	14.7	36.1
14	170.5	258.7	106.0	94.5	23.4	8.1	5.1	3.9	6.3	17.9
15	150.3	282.2	131.2	128.5	34.6	12.8	8.8	7.1	12.5	38.1
16	93.3	154.2	52.9	39.1	8.7	3.0	1.1	1.0	1.6	4.0
17	473.7	924.8	365.2	307.4	77.4	30.4	12.1	12.9	22.1	62.3
18	55.3	89.3	29.7	20.1	4.0	1.2	0.4	0.3	0.5	1.0
19	62.4	119.9	47.6	40.8	10.5	4.3	1.8	2.0	3.5	10.3
20	52.0	107.2	43.2	36.8	9.3	3.7	1.5	1.6	2.7	7.8
21	312.6	543.2	203.4	202.1	54.5	27.1	14.0	15.5	23.8	62.7

oysters (Table 4). Individual filtration rate was estimated using parameters of water temperature and tissue weight (Kim, 1980) and was then integrated into a farm-scale filtration volume (V_F) (Table 5). Monthly water temperatures are shown in Fig. 2.

Table 6 shows the primary production data that was calculated from chlorophyll-a content and light intensity, using a numerical model (Jeong et al., submitted). The value for the energy equivalent of carbon was 15.8 Kcal/g of carbon, as described by Platt (1971). Total energy intake (E_I) on a farm scale was estimated using primary production data and total filtration volume of cultured oysters (V_F) (Table 7).

As a result of tidal flow in coastal areas, the productivity of oyster farms is strongly associated with

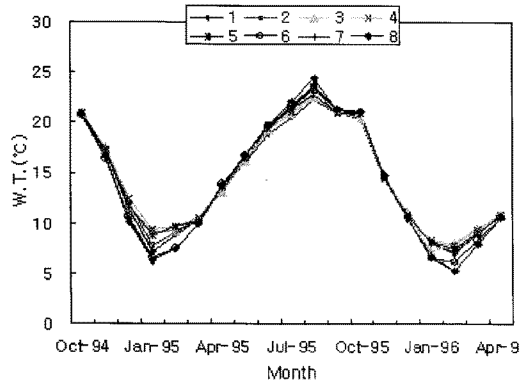

Fig. 2. Monthly variation in water temperature from Oct. 1994 to Apr. 1996. Clear seasonal variations are observed. Slight differences with respect to geographical location were observed during winter.

the input and output processes of primary production (Strohmeier et al., 2008). Oyster farm productivity may be defined as the combined effects of the oysters' biological processing activities and interacttions with environmental factors. Food availability is one of the main environmental factors directly influencing the growth of cultured animals (Winter, 1978; Bayne and Newell, 1983; Soniat and Ray, 1985). This directly affects carrying capacity (i.e., the asymptotic population biomass is supported by an ecosystem under the limitations of food, shelter, etc.) and the effects of predation and exploitation (Kashiwai, 1995). Carrying capacity is, therefore, synonymous with general productivity, or the productive capacity of an ecosystem (Perry and Schweigert, 2008).

We estimated the optimal culture density from primary production data. The combination of primary production and flux area restricts culture productivity. Productivity should increase linearly with culture density; however, above a certain level, productivity becomes saturated and then drastically decreases with increasing culture density. Therefore, we must estimate the optimal density for maximum sustainable productivity of marine farms.

The total number of oysters (N_{total}) per farm can be estimated as follows:

$$N_{total} = \frac{L_{total}}{S} \times N_s \qquad (21)$$

where L_{total} is the long-line length, S is the string interval, and N_S is the mean number of oysters per string. This can be transformed to unit culture density (N_U) per culture area (U) as follows:

$$N_U = \frac{N_{total}}{U} \text{ (individuals/m}^2\text{)} \qquad (22).$$

Tissue weight (W) exponentially decreased with increasing N_U (Fig. 3). Different patterns of W existed at each layer, as shown below:

Upper layer $W = 17 \cdot e^{-0.008N}$ (23)

and

Lower layer $W = 7.64 \cdot e^{-0.0075N}$ (24)

Table 6. Estimated primary productivity (mgC/m^3/d) at each site in Pukman Bay

Month \ Station	1	2	3	4	5	6	7	8
Oct. 1994	227.8	129.4	52.3	35.0	49.8	49.8	146.8	97.1
Nov.	173.4	132.2	78.3	30.8	44.2	43.3	128.6	104.9
Dec.	185.7	114.9	70.2	36.0	39.4	34.1	119.7	129.4
Jan. 1995	181.2	110.9	72.6	40.8	36.5	35.8	126.6	128.2
Feb.	214.8	80.5	47.2	45.2	37.9	38.1	115.3	111.8
Mar.	61.1	38.7	31.8	31.3	31.5	33.7	58.5	54.8
Apr.	162.9	174.3	60.2	128.4	50.4	119.2	111.8	103.8
May	306.2	254.1	99.5	147.8	64.9	138.9	172.8	170.1
Jun.	433.2	242.1	113.9	157.5	68.8	202.7	153.0	172.2
Jul.	383.4	147.4	110.1	126.2	74.0	135.0	133.4	216.1
Aug.	305.1	87.3	87.2	129.6	81.2	148.3	103.7	186.0
Sep.	220.7	150.8	70.6	109.9	88.4	113.1	132.0	187.7
Oct.	168.6	143.5	75.9	77.7	88.5	113.9	139.0	143.6
Nov.	130.5	105.7	51.0	55.7	60.8	89.5	99.0	106.3
Dec.	61.2	94.8	45.1	45.1	49.1	61.6	119.4	194.7
Jan. 1996	76.1	101.7	46.4	45.1	51.8	65.2	117.3	192.9
Feb.	100.2	135.5	62.9	58.2	61.0	77.2	142.9	232.9
Mar.	119.8	107.7	72.2	53.1	52.5	69.7	62.9	69.4
Apr.	161.5	169.3	124.8	68.8	72.7	81.7	85.6	99.2

Table 7. Estimated energy intake (E_I) at each farm (Mcal/d) in Pukman Bay

#Farm	Month									
	1995. Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	1996. Jan.	Feb.	Mar.	Apr.
1	5,798.0	8,517.0	3,946.0	2,717.0	579.0	124.0	81.0	112.0	201.0	614.0
2	1,978.0	3,087.0	1,423.0	952.0	195.0	40.0	25.0	33.0	57.0	165.0
3	5,698.0	7,529.0	3,139.0	1,944.0	373.0	72.0	42.0	53.0	85.0	233.0
4	9,949.0	14,188.0	6,383.0	4,266.0	883.0	184.0	116.0	157.0	273.0	807.0
5	3,387.0	3,697.0	1,594.0	1,634.0	290.0	123.0	54.0	111.0	151.0	710.0
6	12,345.0	12,990.0	5,517.0	5,622.0	997.0	424.0	184.0	379.0	515.0	2,411.0
7	12,442.0	13,583.0	5,857.0	6,003.0	1,067.0	454.0	197.0	407.0	554.0	2,608.0
8	11,998.0	12,772.0	5,533.0	5,784.0	1,057.0	464.0	208.0	446.0	628.0	3,057.0
9	1,372.0	2,154.0	742.0	483.0	83.0	29.0	17.0	20.0	24.0	85.0
10	3,791.0	6,369.0	2,220.0	1,435.0	244.0	83.0	47.0	54.0	66.0	227.0
11	6,951.0	11,679.0	4,071.0	2,631.0	448.0	153.0	85.0	99.0	121.0	417.0
12	4,760.0	8,821.0	4,381.0	4,340.0	821.0	253.0	189.0	185.0	291.0	1,263.0
13	8,478.0	7,839.0	4,638.0	4,046.0	745.0	309.0	159.0	219.0	250.0	966.0
14	2,003.0	3,318.0	1,481.0	1,321.0	225.0	62.0	42.0	37.0	53.0	206.0
15	1,766.0	3,619.0	1,833.0	1,796.0	332.0	99.0	72.0	68.0	104.0	438.0
16	1,989.0	3,614.0	945.0	704.0	123.0	30.0	11.0	13.0	17.0	51.0
17	10,101.0	21,678.0	6,527.0	5,531.0	1,094.0	296.0	124.0	157.0	244.0	804.0
18	1,887.0	2,624.0	882.0	456.0	68.0	37.0	12.0	13.0	5.0	16.0
19	1,330.0	2,811.0	851.0	734.0	149.0	42.0	18.0	24.0	39.0	133.0
20	1,109.0	2,513.0	773.0	661.0	132.0	36.0	15.0	19.0	30.0	101.0
21	7,278.0	7,492.0	4,848.0	4,583.0	910.0	406.0	225.0	331.0	405.0	1,679.0

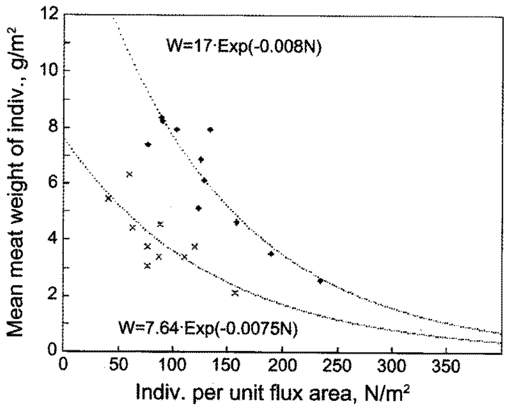

Fig. 3. Relationship between culture density (N_U) and mean meat weight per unit flux area. A significant difference was observed in intercept but not in slope of the regression.

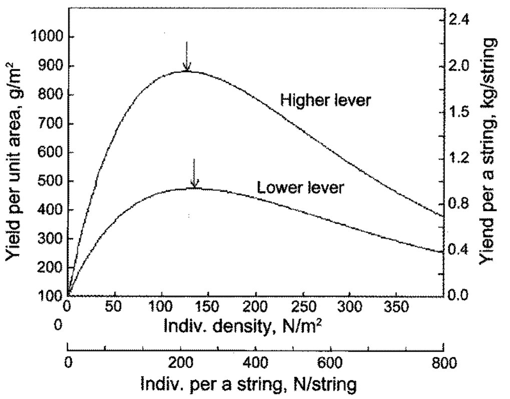

Fig. 4. Relationship between culture density and unit yield. Arrows indicate maximum yield at each level.

When these values are substituted into equation (19), given the range of N=1-400, the biomass in each culture area can be estimated (Fig. 4). The optimal N_U was estimated as 125-133 individuals per m^2. At 0.5-m intervals, and with string lengths of 5 m, the optimal culture density should be 310-330 animals per string. Therefore, maximum production could be 0.9-1.95 kg per string. Maximum productivity for the bay was estimated at 1,193 tons/year. Present oyster production is approximately 1,038 tons/year, which is 87% of the estimated maximum production.

In Pukman Bay, productivity showed a number of geographical and hydrological trends. Over a total potential area of 1,090 ha, a region of relatively high productivity was located in the outer part of the bay (A, 1.8-2.0 kg/string, 550 ha), whereas the inner part of the bay was a region of relatively low productivity (B, 1-1.2 kg/string, 540 ha) (Fig. 5). Approximately 18.2% of the potential aquaculture area is currently licensed for marine farming. Considering yearly fluctuations and critical buffers to reduce ecological impacts, we conclude that the farmed area should not

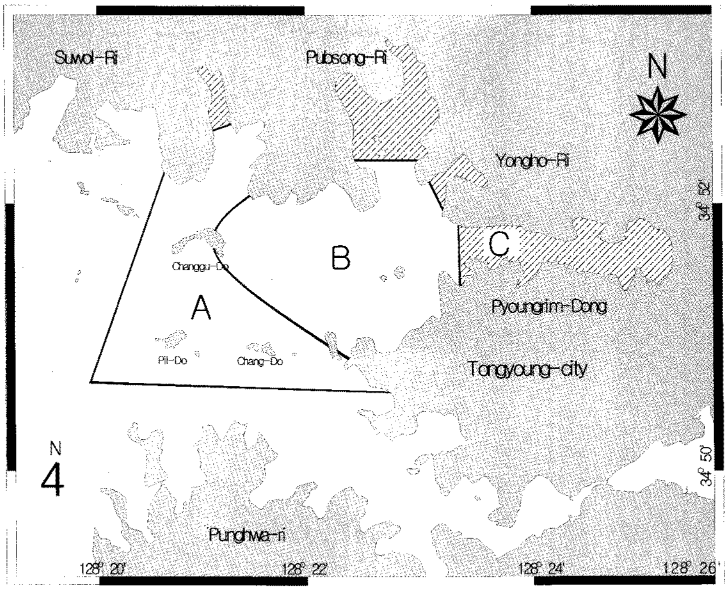

Fig. 5. Oyster productivity within Pukman Bay (calculated from carrying capacity). Three regions of productivity were designated: (A) high-yield area with good tidal circulation and high food availability; (B) low-yield area mainly confined to the inner part of the bay; and (C) area unavailable for oyster farming because of shallow depth and heavy pollution load from nearby inhabited areas.

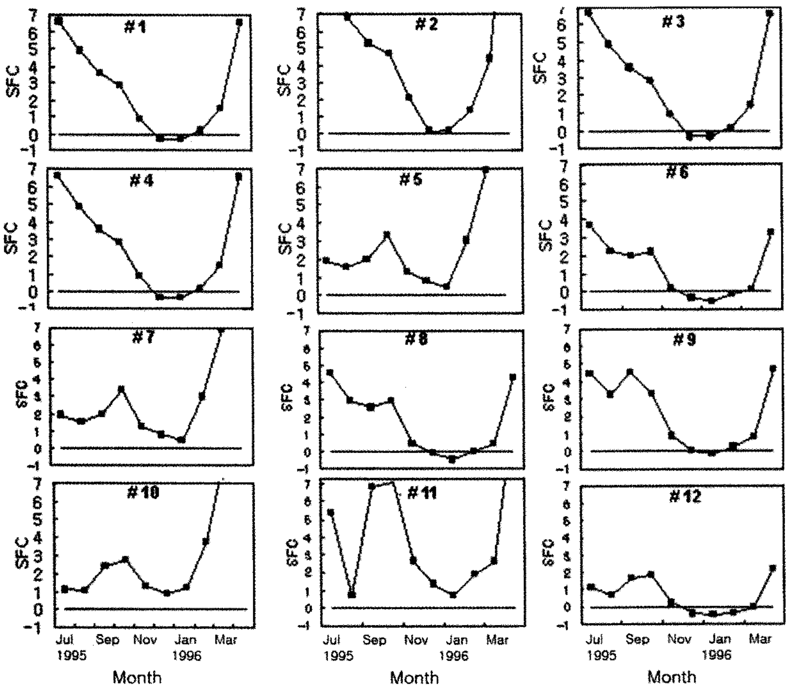

Fig. 6. Evaluation of food availability using the surplus food coefficient (SFC) at each oyster farm in Pukman Bay. Values lowered than zero indicate food deficiency, as estimated from metabolic cost and primary production.

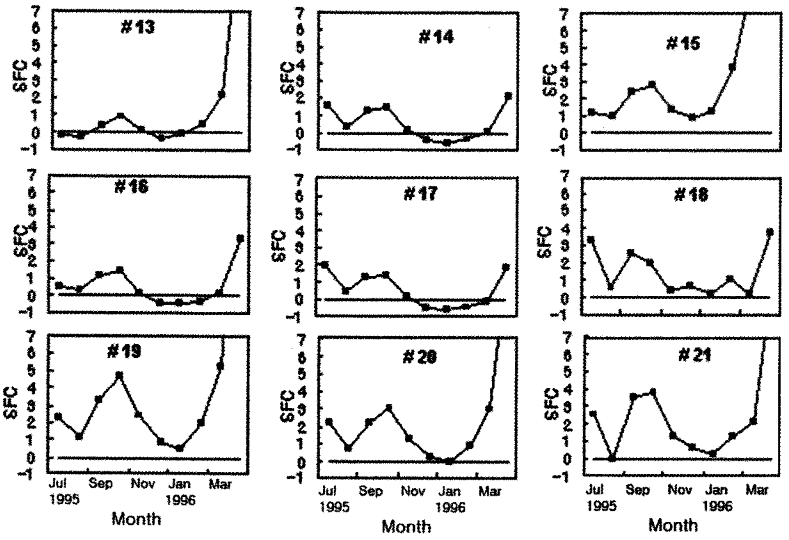

Fig. 6. Continued.

Table 8. Estimated survival rate from food coefficient at each farm in Pukman Bay

#Farm	Month									
	1995. Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	1996. Jan.	Feb.	Mar.	Apr.
1	1.00	1.00	1.00	1.00	1.00	0.66	0.65	0.65	0.65	0.65
2	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
3	1.00	1.00	1.00	1.00	1.00	0.66	0.65	0.65	0.65	0.65
4	1.00	1.00	1.00	1.00	1.00	0.66	0.65	0.65	0.65	0.65
5	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
6	1.00	1.00	1.00	1.00	1.00	0.69	0.41	0.41	0.41	0.41
7	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
8	1.00	1.00	1.00	1.00	1.00	0.86	0.51	0.51	0.51	0.51
9	1.00	1.00	1.00	1.00	1.00	1.00	0.85	0.85	0.85	0.85
10	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
11	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
12	1.00	1.00	1.00	1.00	1.00	0.56	0.56	0.56	0.56	0.56
13	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
14	1.00	1.00	1.00	1.00	1.00	0.55	0.51	0.51	0.51	0.51
15	0.85	0.71	0.71	0.71	0.71	0.70	0.70	0.70	0.70	0.70
16	1.00	1.00	1.00	1.00	1.00	0.55	0.37	0.37	0.37	0.37
17	1.00	1.00	1.00	1.00	1.00	0.51	0.34	0.34	0.34	0.34
18	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
19	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
20	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
21	1.00	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95

be extended.

Estimation of surplus food coefficient from food availability

Since oysters are sessile filter-feeders, their feeding behavior is passive, largely relying on the tidal current. The energy content of ambient water (i.e., primary production) is crucial for the sustainable management of oyster farms. The essential energy requirement (E_R) was estimated using equation (14), the minimum criterion for growth.

Food availability is a major factor in oyster growth and is affected by seston concentration, composition, and transport rate (Incze and Lutz, 1980; Frechette et al., 1989; Blanco et al., 1996). In the present study, food availability is represented by the relationships between ingested energy (E_I), flux area, and primary production (*PP*).

In our study, the ratio between food requirements and food supply is the surplus food coefficient (*SFC*).

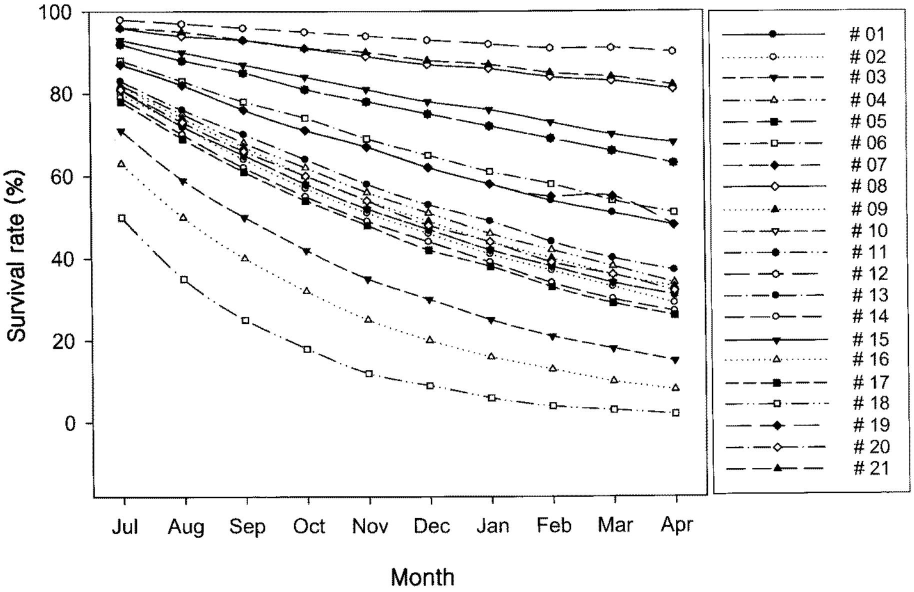

Fig. 7. Monthly mortality at each oyster farm in Pukman Bay. Mortality occurred year-round. Mortality rates at some farms could be expected to reduce profitability.

This is a simple index that indicates saturation of food supply for cultured oysters. We evaluated *SFC* monthly at each farm (Fig. 6). *SFC* values lower than zero indicate food scarcity. If food supply is deficient for more than 1 month, mortality or defects in oyster quality (e.g., the condition known as "watery oyster") can result. At farms 6, 16, and 17, the food supply was severely deficient (reduced by >50%) for several months, which could have negatively affected productivity of these farms.

Table 8 shows estimated survival rate, as calculated from *SFC* data. The estimated survival rates indicate that mortality resulting from deficient food supply occurred during the high-growth period. According to the measured survival rates (Fig. 7), however, mortality occurred throughout the year. This mortality could be due to other reasons, such as disease or environmental damage. At farms with high mortality, the maximum rate was observed after spawning (July to September). Excessive growth of fouling organisms can also lead to high mortality as a result of food competition. In Pukman Bay, mussels were the major fouling organisms in the inner regions of the bay where high mortality occurred, especially at farm 18.

December is the main harvesting period for oysters in the bay, and in this month there were extremely low survival rates at farms 16 and 18 (2% and 20% survival, respectively). This high mortality (i.e., greater than approximately 60%) can destroy the commerciality of oyster farms (Ventilla, 1984). In Pukman Bay, the most unprofitable oyster farms were mainly located in Area B (Fig. 5). Among other farms, survival rates ranged from 42% to 93%, with the highest survival rate at farm 12.

The food supply was deficient during winter, which is an active growth period for cultured oysters. This may be attributed to changes in environmental conditions and increased endogenous metabolic costs of growth (Bayne and Svensson, 2005). At farms 14, 17, and 18, there were relatively prolonged periods of food deficiency, which can result in growth stagnation and mortality, or loss of oyster quality.

The productivity of oysters is affected by several factors, including environmental changes, disease, and oyster metabolism (Mackin, 1962; Ray, 1987; Allen and Turner, 1989). Of these, food availability is a major factor to be considered when establishing an oyster farm. Food availability is coupled with phytoplankton dynamics, which in turn rely on high tidal amplitudes that re-suspend organic material and therefore increase food availability (Strohmeier et al., 2008). For these reasons, oyster farms are often densely arranged in coastal areas, which can lead to systematic problems arising from the close proximity. When considering the interactions between food availability and mortality in studies of population distribution and density (Powell et al., 1994), food availability must be taken into account in order to achieve maximum sustainable production; i.e., the carrying capacity should be estimated to determine the appropriate number and/or arrangement of oyster farms in a given area.

In conclusion, 10 of the 21 oyster farms in Pukman Bay have deficient food supplies for periods longer than 1 month each year. These "over-dense" oyster farms account for approximately 39% of the total oyster farms in Pukman Bay; however, the total area currently used for oyster farming is within the optimal range. With appropriate management, productivity may reach the maximum level predicted in this study.

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