Thesis for the Degree of Master of Science

The Coexistent Mechanisms of Two Sympatric Crabs (*Hemigrapsus penicillatus* and *H. sanguineus*) in Il-Kwang, Korea

by

Hee Jin Kim

Department of Oceanography

The Graduate School

Pukyong National University

August 2007

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일광 조간대에 서식하는 동소종, 풀게 (*Hemigrapsus penicillatus*)와 무늬발게 (*H. sanguineus*)의 공존기작

Advisor: Prof. Chang Ho Moon

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Hee Jin Kim

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by

Hee Jin Kim

Approved by:

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(Chairman)

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(Member) (Member)

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(Member) (Member)

August 31, 2007

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일광 조간대에 서식하는 동소종, 풀게 (*Hemigrapsus penicillatus*)와 무늬발게 (*H. sanguineus*)의 공존 기작

김 희 진

부경대학교 대학원 해양학과

국 문 요 약

부산 일광의 암반 및 자갈로 구성된 복합조간대에 서식하는 동소적 2종(sympatric two species)인 풀게(*Hemigrapsus penicillatus*)와 무늬발게(*H. sanguineus*)는 생태적으로 동일자원에 대한 시·공간적인 강한 경쟁압에 의해 공존(共存)하기가 매우 어렵다. 그러나, 이들 2종은 현재 이들의 동소적 공존을 허용하는 어떠한 기작에 의해 현실적으로 거의 동일한 시·공간적 상황 하에서 함께 서식하고 있다. 따라서, 본 연구는 3가지 가설 - ① 주 서식지의 미세환경 차이, ② 생활사의 차이, ③ 섭식생태의 차이-을 바탕으로 이들의 공존기작을 밝히는데 목적을 두고 수행되었다.

본 연구는 부산시 일광면에 위치한 일광해수욕장 북동쪽 끝자락의 암반 및 자갈로 구성된 복합기질의 조간대이다. 평균조차는 약 90cm 정도이며 여름철 일시적인 행락객의 인위적 간섭을 제외하면 인간에 의한 간섭이 그리 크지 않은 곳이다. 연구 대상지역에 대한 표본은 2005년 11월부터 2006년 10월까지 조간대를 수직적 상·중·하로 구분한 뒤, 매월 대조시기에

50×50cm 방형구를 이용 채집하였다. 이렇게 채집되어진 샘플은 포르말린으로 고정시킨 뒤, 다음의 실험방법으로 실험하였다. ① 주서식지는 조간대의 만조선 (상부)과 간조선 (하부)을 기준으로 1m 간격을 두고 상·중·하부를 수직적으로 구분한 뒤, 채집되어진 총 개체수의 50%이상이 분포하는 곳으로 보았다. ② 생활사의 차이는 동정되어진 샘플들의 갑각 크기를 측정하여 갑각의 최소 크기가 출현하는 달을 가입시기라 판단, 포란한 개체가 출현하는 시기를 포란시기라 판단하고 두 종사이의 차이를 비교하였다. ③ 섭식생태는 게들은 먹이를 찢어 먹기 때문에 SCA (Stomach Contained Analysis)를 통한 먹이의 분석이 어려워 집게의 최대 벌려지는 크기를 이용하여 형태계측학적 차이를 알아보고, 집게의 형태학적 묘사를 통한 섭이 습성의 차이를 알아보았다. 이러한 실험 방법을 통하여 분석하여 다음과 같은 결과를 얻을 수 있었다.

동소종인 풀게 (*H. penicillatus*)와 무늬발게 (*H. sanguineus*)는 생태적으로 동일자원에 대한 시・공간적인 경쟁압을 줄이기 위하여 다음의 3가지 기작을 사용하고 있었다. 첫 번째로 주 서식지에 있어 차이를 두고 있었는데, 풀게는 중부와 하부, 무늬발게는 상부와 중부에 주 서식지를 두고 있었다. 이러한 분포는 풀게의 경우 저질을 구성하고 있는 암반과 자갈의 크기와 풀게에서만 나타나는 섭이 특징인 동종섭이 현상과의 관계가 연관되어 있는 것으로 보여 졌으며, 고정된 것이 아니라 물리적 스트레스가 강하게 작용하는 달(8월)에는 중부에서 하부로 상부에서 중부로 이동하는 경향을 보였다. 두 번째, 생활사중 종 유지에 가장 중요한 가입과 포란에 있어서도 이들은 시기와 횟수 (가입, 풀게: 1, 4, 10月 무늬발게: 3, 5月;

포란, 풀게: 6, 8, 9月 무늬발게: 8, 9月)를 달리하여 제한된 자원 이용의 경쟁을 최소화 하였다. 마지막으로, 앞의 2가지 기작뿐만 아니라 생물이 살아가는데 중요한 에너지원인 먹이 또한 제한된 자원으로 경쟁의 최소화를 위한 기작의 존재를 예상 하였으나, 종간의 뚜렷한 섭이습성의 차이를 발견 할 수는 없었지만, 먹이의 크기는 차이를 보였다. 수컷의 경우에는 풀게가 무늬발게보다 큰 먹이를 먹었지만, 암컷은 이와는 다른 경향을 보였는데, 갑각의 크기가 7.28mm 이하일 때에는 풀게가 큰 먹이를 먹었고, 7.28mm 이상일 때에는 무늬발게가 더 큰 먹이를 먹는 경향을 보였다. 이때 기준이 되는 7.28mm는 풀게가 최초로 포란하는 갑각의 크기인 8mm와 유사하였다.

이러한 결과를 바탕으로 동소종인 풀게 (*H. penicillatus*)와 무늬발게 (*H. sanguineus*)는 서식지의 차이, 포란과 가입 시기의 차이, 섭이 생태의 차이를 두고 공존함을 알 수 있었다.

Introduction

Sympatric species had demonstrated over the long haul. Gause's main work in English, in 1934, many scientists were looking at animals with the exclusion principle in mind. The implications of the principal became particularly interspecies which are called sympatric (literally "same country"), because such species might be expected to have similar niches and, therefore, be in danger of competing (Paul, 1973). Sympatric speciation occurs when reproductive isolation occurs within the rage of a population and before any differentiation of the two species can be detected. Sympatic speciation may be rare in nature (Krebs, 1994). Because such species might be expected to have similar niches therefore, be in dangerous of competing. It is evident that at any level in the structure of the biological community there is a set of complicated relations between species, which probably tend to become less important as the species become less closely allied.

These relations are of the kind which insure niche separation (Hutchinson, 1964).

Many species live in a ecosystem with competition. Diverse species are coexisting in the Il-Kwang rocky intertidal area. Many species in Il-Kwang intertidal area do not except for the competition. Sympatric two species (*Hemigrapsus penicillatus* and *H. sanguineus*) should compete for food, habitat and so many kind of natural source which they need inevitably. According to "Competition exclusive principal (Hardine 1960)", result of the competition is domination of one species in the region based on the differentiation of their realized niche (Hardine, 1960; Begon et al., 1996). Interspecific competition among these competitions is extremely violent in the same genus (Darwin, 1859). In our target species, *Hemigrapsus penicillatus and H. sanguineus,* belong to the same genus *Hemigrapsus*. So, these two grapsids are quite similar ecologically: foraging zones and vertical distributions of habitat, and both *H. penicillatus* and *H.*

sanguineus are considered opportunistic omnivores, consuming various plant and animal matter (Okamoto and Kurihara, 1989; DeGraaf and Tyrrell, 2004). Thus, their competition is more serious. Thus, according to Hardine's principal, Il-Kwang intertidal area is one species win the competition and dominated in this place. However, two close ecological relationship species of intertidal grapsid crabs (*H. penicillatus* and *H. sanguineus*) coexist in our study site of Il-Kwang rocky intertidal area. In this fact, we should have some question, How they coexist in there? what mechanisms do it possible? Because the existence of pure populations of either species, and of rocky intertidal area where both species have coexisted for extended periods of sampling time in the same area, suggests that neither historical reasons nor competitive exclusion provide a good explanation for local distribution patterns which is vertical distribution.

Hutchinson (1961) in his discussion of the ‘paradox of plankton’ pointed out that "competition exclusive principal

(Hardine, 1960)" is not suitable all kind of ecosystem. According to "competition exclusive principal (Hardine, 1960)", it is impossible that many species of phytoplankton coexist in same oceanic area, only one plankton species dominate this area, but Hutchinson (1961) found that species of phytoplankton were coexisted by difference in the nutrient absorbing ratio.

Actually, many kind of species are lived together in all kind of ecosystem, and they have variety kind of following coexistence mechanisms. For example, teleost fish are coexisted by difference in habitat and prey (Platell and Potter, 1999). Some nudibranchs are coexisted by difference in feeding behaviors and micro habitats (Lambert, 1991). Anemonefish species are coexisted by difference in host and habitat utilization, size and recruitment (Elliot and Maricsal, 2001).

Therefore, the purpose of the present study is that examine many kind of factors influencing the coexistence of two sympatric crabs (*H .penicillatus* and *H. sanguineus*) in a rocky intertidal area in Il-Kwang and we should find the mechanisms apply to sympatric species in ecosystem.

We study for coexistence mechanisms of two sympatric grapsid species (*Hemigrapsus penicillatus* and *H. sanguineus*) with basis on previous facts. First of all, we found three hypotheses: (1) Difference in main habitat; vertical distribution and various change type (2) Difference in life history; recruitment and ovigerous season (3) Difference in feeding habit; Diet type and available maximum food size. Second, we used following method for proof for these hypotheses. (1) We find how different vertical distribution (high, mid, low) in rocky intertidal area, each two species. (2) We suppose the difference in life history between two species relates to their life cycle. We use two methods for study different life history. First, we should graph the carapace width and find appearance month of the smallest individuals. Because we supposed that appearance of the smallest individuals appearance is same the recruitment. Second, we should find the ovigerous individuals in each species because we think that they could coexist difference in reproduction period. (3) It is difficult that find food items of the crab using the SCA (Stomach Contents Analysis). Because the crabs rend food with their chela and 3rd maxilliped as they eat. Therefore, we find the difference in predatism using follow two methods. First, we compare the chela gap size. The reasons of measure this part which is chela gap size speaks the maximum available size of food (Yamada and Boulding, 1998). So we measure this part and compared morphometric charaters of each species and sex. Second we draw morphological characters of chela. Because chela is main feeding organ thus, it speaks that two species are which belong to generalist or specialist (Yamada and Boulding, 1998; Seed and Hughes, 1995).

Materials and Methods

1. Study site

Il-Kwang intertidal area is located Gi-jang Il-Kwang, Busan (35°15'N, 129°14'E). There is famous sand beach of east-south seashore. There is 1km sand beach and the annual water temperature averaged 13℃. Maximum tidal range is 5m, and the total intertidal area length is 470cm, except sand beach (Fig. 1).

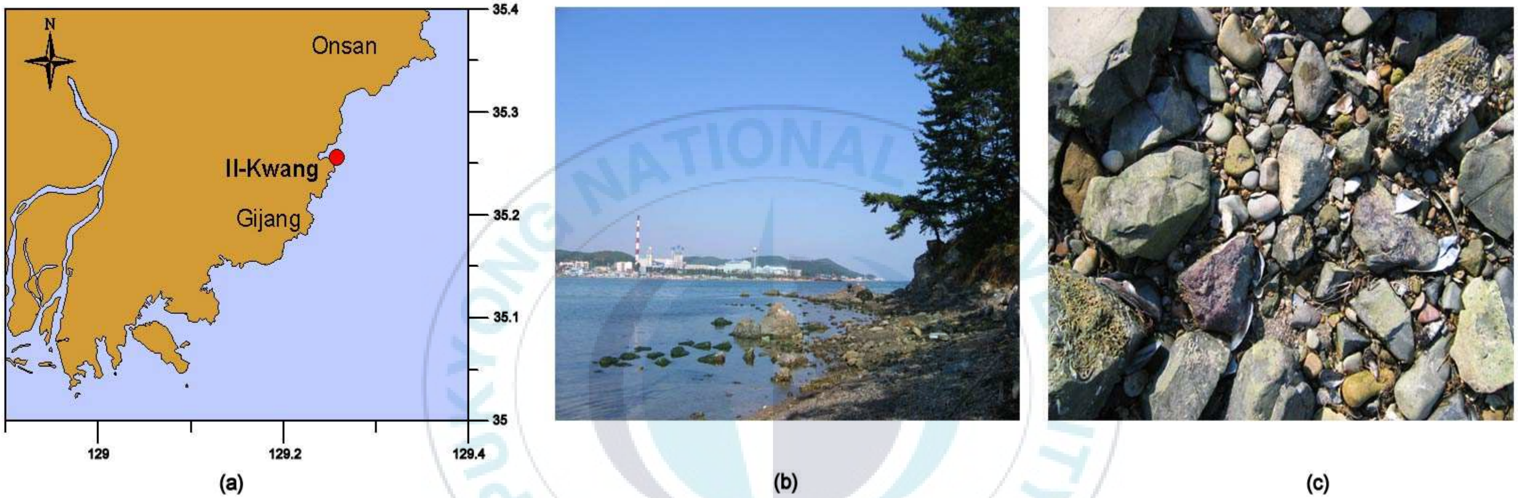

Fig. 1. Study site: (a) Map represents the location of Il-Kwang, and red circle represents the study site. (b) Landscape of the present study site during the low tide. (c) The intertidal area composed of a number of several sized boulders and rocks.

2. Materials

Hemigrapsus penicillatus and *H. sanguineus* (Fig. 2, 3), belonging the same genus, coexist in the interspace of boulders or under the rock sympatrically.

H. sanguineus is frequently the most abundant crab of rocky intertidal areas where substrates range from large boulders to small rocks, cobble and broken shell (Celestino and Hales, 1998; Lohrer and Whitlatch, 1997; Ahl and Moss, 1999; Gerard et al., 1999). They are opportunistic omnivore, it feeds on a variety of resident organisms, including macroalgae, salt march grasses and small invertebrates such as amophipods, gastropods, bivalves, barnacles and polychaetes (Lohrer and Whitlatch, 1997; McDermott, 1998c; Brousseau et al, 2000a, b).

H. penicillatus is also to collect and can be found by looking under stones in sandy or muddy places at low tide. The male chelipeds have a charactertistic patch of fur on their inner and outer surfaces neat the base of the fingers, the inner patch being larger than outer (Noèl et al., 1997). Moreover, they also belonging opportunistic omnivore (Okamoto and Kurihara, 1989).

Fig. 2. Male specimens. (a) *Hemigrapsus penicillatus* (b) *H. sanguineus*

Fig. 3. Female specimens. (a) *Hemigrapsus penicillatus* (b) *H. sanguineus*

3. Sampling

We divided the intertidal zone vertically into 3 parts (High, Mid, Low level) between high water line and low water line of intertidal area with 1m interval (Fig. 4). During low tides at the spring tides the rocky shore of the tidal creeks and the main channel are exposed. The 0.25 cm^2 quadrate (Fig. 5) which is made by stainless still was used for monthly sampling specimens along the rocky intertidal area from November 2005 to October 2006. We sampled each level of intertidal area at spring tide and replicate three times, respectively.

Crabs were collected by hand from beneath ofter extinguishing of boulders and rocks in the quadrate.

We moved these samples to laboratory for examination after fixation of the specimens with ca. 5 % neutral formalin solution.

Fig. 4. Vertical division of study area which divide into 3parts (High, Mid, Low) between high and low water line of the intertidal level area with 1 m interval.

Fig. 5. Quadrate 50×50 cm. Which used for field sampling of the crab specimens in the present study.

4. Analysis methods

Length was measured by vernier calipers, but small size individuals which were not able to measured by vernier calipers were measured with ocular micrometer attached to a stereo microscope.

(1) Main habitat

We had to count the number of crab specimen in each levels for find the main habitat in each species and sex, next we should transform these data for easy comparing of the main habitat between each species and sex. When we collected the samples, we used the quadrate which is 50×50 cm and replicated 3 times due to total dimension is 75 cm^2. We transformed these data to a square meter for graph the distribution. We graphed the distribution using the *sigma plot* 2001 to find how different their main habitat,

(2) Life history

We analysis for life history (recruitment and reproductive periods) used two methods as follows.

First, we graphed the carapace width (fig. 6, a) each month for finding the recruitment period. We graphed the carapace width size frequency and next find the smallest apparent months. Because we regard to these monthes rare Finally, we compared the month of recruitment between two species and how different they are.

Second, we pointed out of the appering ovigerous individuals months for compare the reproduction period in each species. We find the answer that how different their reproduction period, we graphed the distribution of ovigerous individuals and find the apparent months of ovigerous individuals.

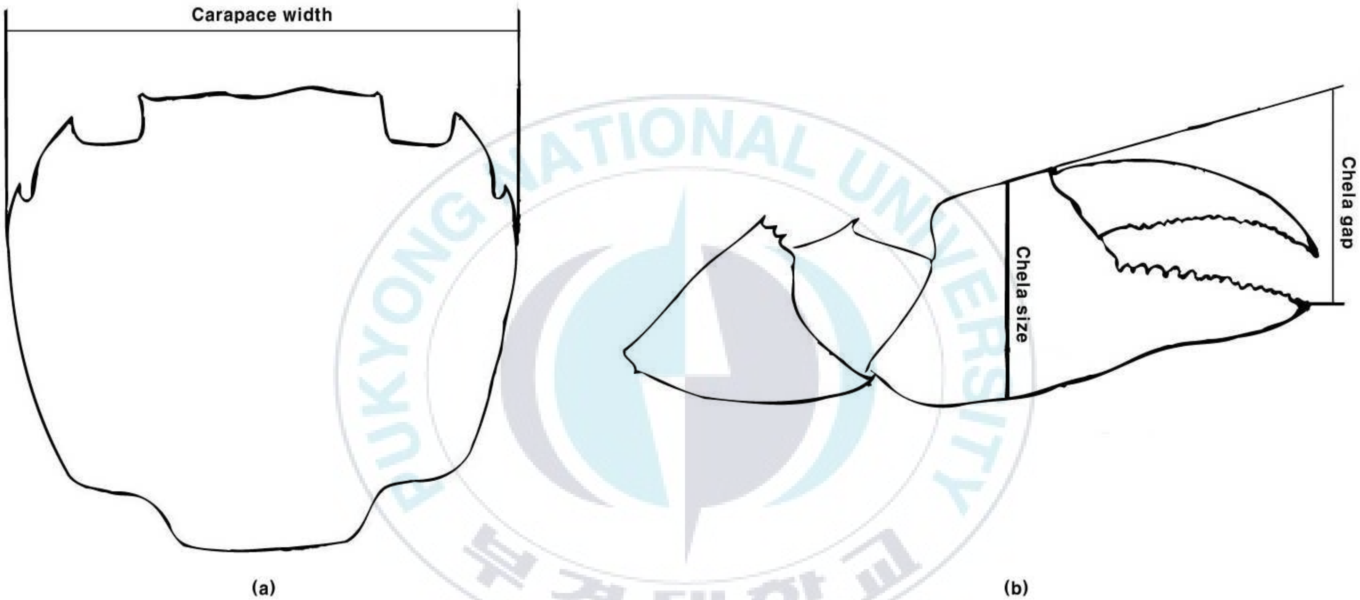

Fig. 6. Three measuring parts of morphometric characters: (a) Carapace width is used for finding recruit month. (b) Chela size and Chela gap are used for finding maximum food size.

(3) Feeding habit

In case of most species, the best way finding the food items is SCA (Stomach Contents Analysis). The crabs, however, rend food with their chela and 3rd maxilliped as they eat. Thus, SCA is not useful method in the crab species. So, we used following method for find and compare food items.

According to Smith and Palmer (1994), the chela which is major feeding organ that evolute to form of easy deal with their food. Thus, they have probability of different food items, *Hemigrapsus penicillatus* and *H. sanguineus* have a difference in morphological characters of the chela. We drew the chela and compared these morphological characters. We found how different their morphological characters. The difference in morphological characters speak they are generalist or specialist. The specialist has a strong and large dental, whereas the generalist has a weak and small dental (Yamada and Boulding, 1998).

Perhaps they are same diet type, they find other way to reduce the interspecific competition of food. The other way is difference in maximum food size (Tracy et al., 2003). Thus, we measured the chela's gap size (fig. 8, b) because of knowing difference in maximum food size (Yamada and Boulding, 1998). We measured three parts for find the difference in Chela gap size during they grown: carapace width, width and gap size. And next, we should do statistical analysis these data using *MINITAB V*. 14.

First of all, we should do the correlation analysis between the carapace width and chela width. The reason is find the relationship between crab size and chela size. Carapace width and chela width are significantly eurelated ($r=0.98$, $P<0.01$). Thus, chela width speaks to crab size. So, we tried to find the difference in maximum food size using the relationship between chela width and chela gap size.

Results

1. Main habitat

Although *Hemigrapsus penicillatus* and *H. sanguineus* lived in same intertidal area, distribution is differed by each species and sex when the intertidal area divided into 3 levels.

H. penicillatus distributed 82-100% individuals on the mid and low intertidal area during sampling period (Fig. 7, Table 1) and it was changed by season. In May–July, they mainly distributed on mid intertidal area, whereas in October–April, mainly distributed on low intertidal area. It had a little different between the sex (Fig. 8, 9). In May–September, 7–17% individuals distributed high intertidal area (Table 1). The distribution the most part was occupied with male individuals (Fig. 8). On the other hand, female particularly ovigerous specimens distribute in all the intertidal area In June, but any ovigerous individuals did not distribute in all the intertidal area in July. In August, the ovigerous individuals appeared again and mainly distributed in low level of intertidal area, and next month, in September, ovigerous individuals sharply decreased on low intertidal area, and mainly distributed on mid intertidal area (Fig. 9).

H. sanguineus mainly distributed on high and mid intertidal area (Fig. 10). Except January (the most part of individuals distribute on low intertidal area: 73.33%), 56-100% individuals distributed on high and low intertidal area (Table 1). Moreover, it was changed by season, too. In November - June, they mainly distributed on mid intertidal area. Whereas, in July – October, mainly distributed on high intertidal area. However, the highest temperature in August, they distributed in mid intertidal area. This distribution was a little difference in sex (Fig. 11, 12). August and September were brooding period (Fig. 12). In August, Female individuals mainly distributed on mid intertidal area, whereas ovigerous individuals distributed low intertidal area. In September, Female individuals mainly distributed on high intertidal area, whereas ovigerous individuals distributed in mid intertidal area. Time goes by, ovigerous individuals moved from low to mid intertidal area.

Two sympatric species had two common features. First is that size increased with decreasing of the vertical level in the intertidal area while the size of *H. penicillatus* in the low level of the rocky intertidal area showed smaller size than mid level (Table 2). Specimens of *H. penicillatus* along the rocky intertidal area were larger than *H. sanguineus* (mean carapace width of 18.23±6.1 mm, *n*=104, versus 10.6±3.6 mm, *n*=262, respectively), but less numerous.

Table 1. The percentage of distribution individual numbers in each vertical area.

		Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.
H. penicillatus	High	0.00	0.00	0.00	0.00	0.00	0.00	16.67	14.29	7.69	11.11	17.65	0.00
	Mid	8.33	0.00	20.00	10.00	0.00	22.22	50.00	85.71	76.92	22.22	35.29	27.27
	Low	91.67	0.00	80.00	90.00	100.00	77.78	33.33	0.00	15.38	66.67	47.06	72.73
H. sanguineus	High	12.50	0.00	0.00	0.00	27.78	20.00	28.95	44.44	53.33	33.33	48.48	65.38
	Mid	50.00	85.71	26.67	56.25	38.89	80.00	60.53	55.56	26.67	44.44	39.39	21.15
	Low	37.50	14.29	73.33	43.75	33.33	0.00	10.53	0.00	20.00	22.22	12.12	13.46

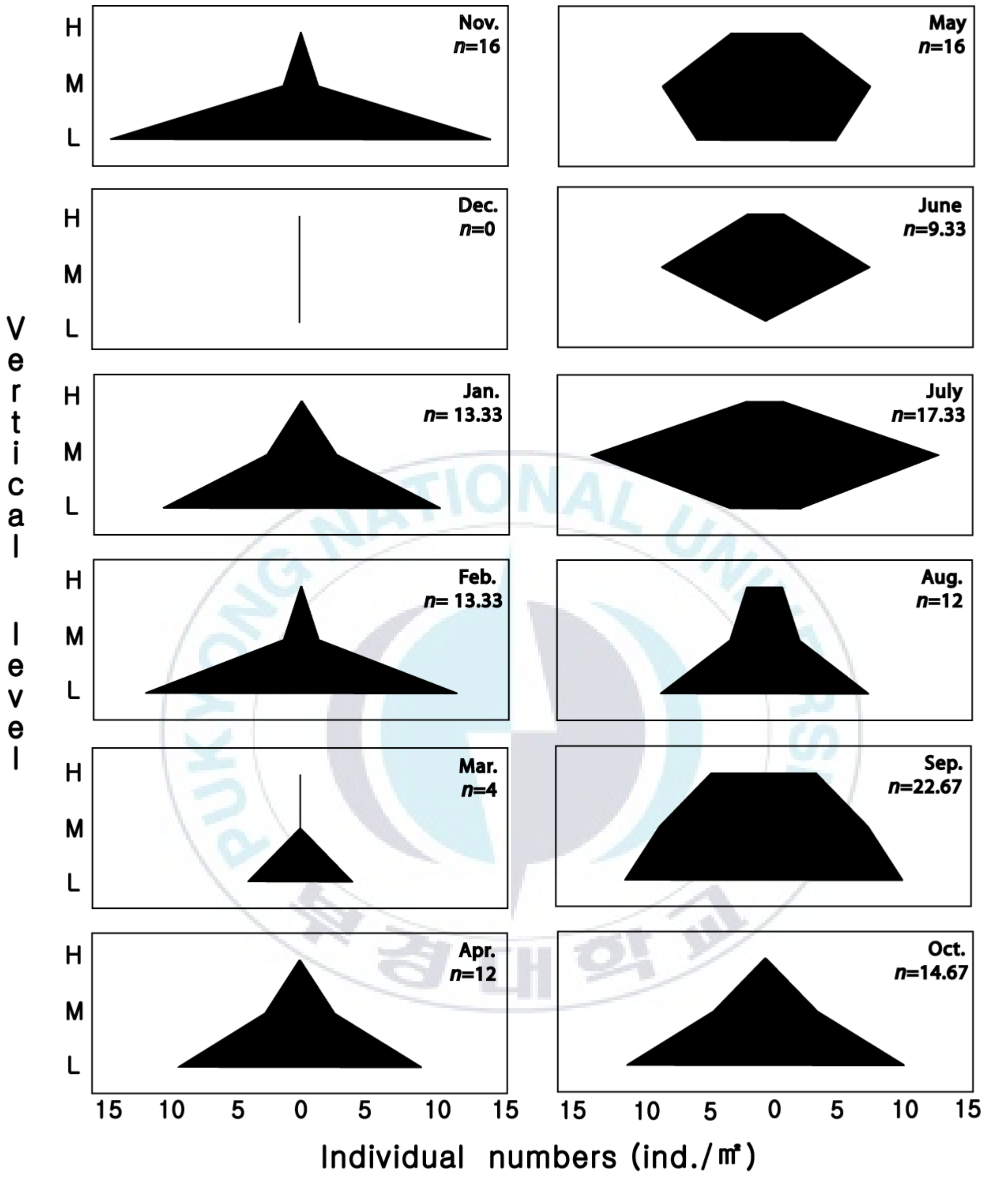

Fig. 7. The distribution of *Hemigrapsus penicillatus* during sampling months. H, M, L represent the vertical level in the intertidal area.

n = number of crabs

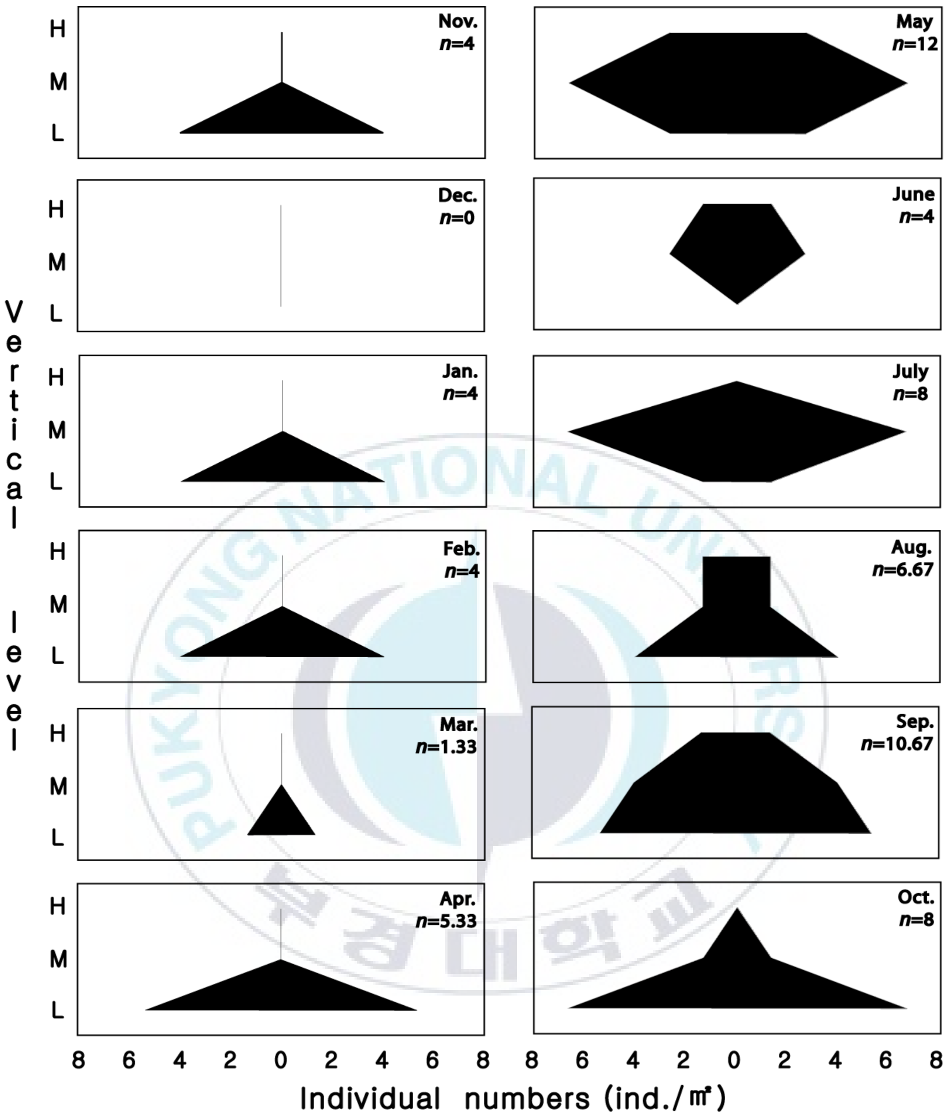

Fig. 8. The distribution of *H. penicillatus* male during sampling months. H, M, L represent the vertical level in the intertidal area.
n = number of crabs

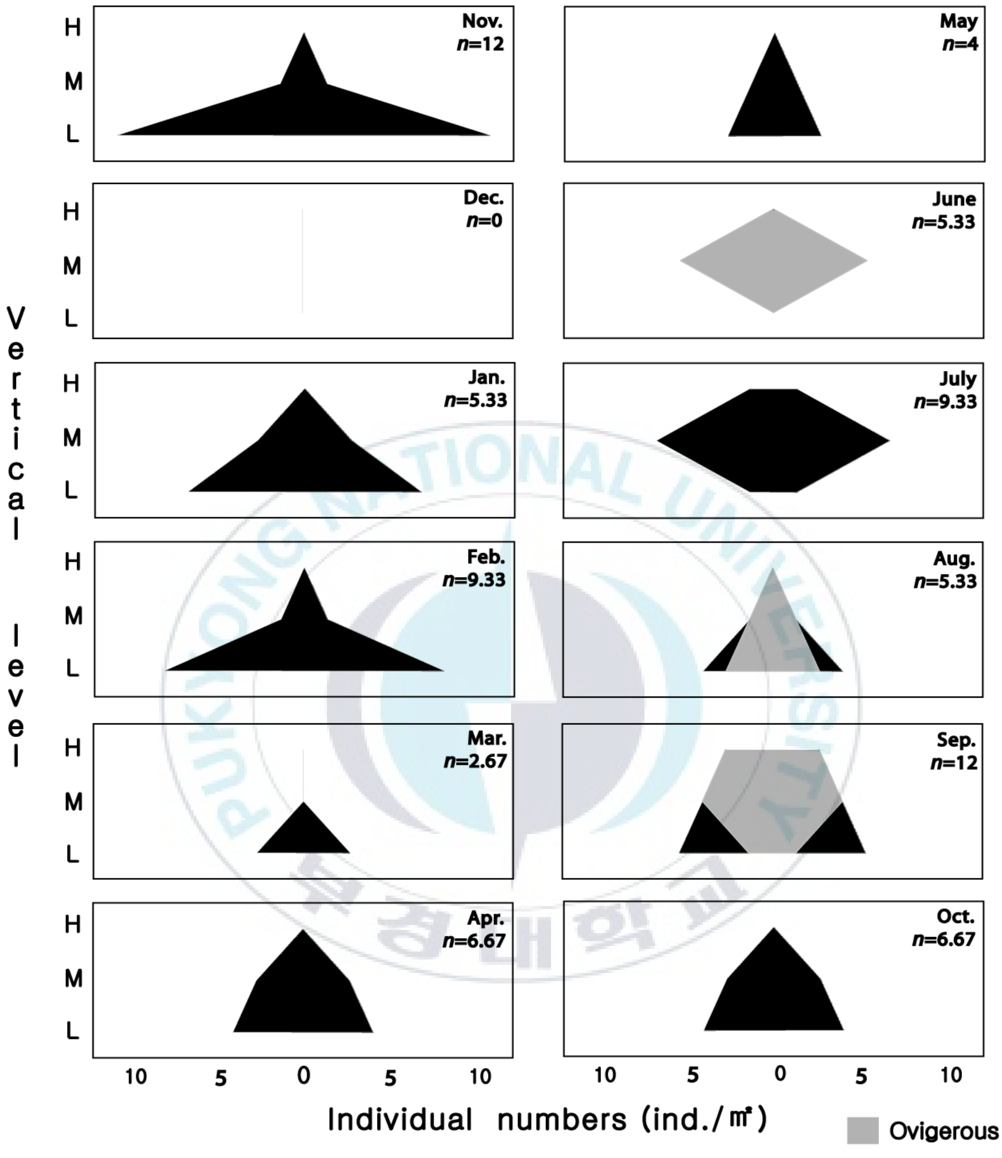

Fig. 9. The distribution of *H. penicillatus* female during sampling months. H, M, L represent the vertical level in the intertidal area.
n = number of crabs

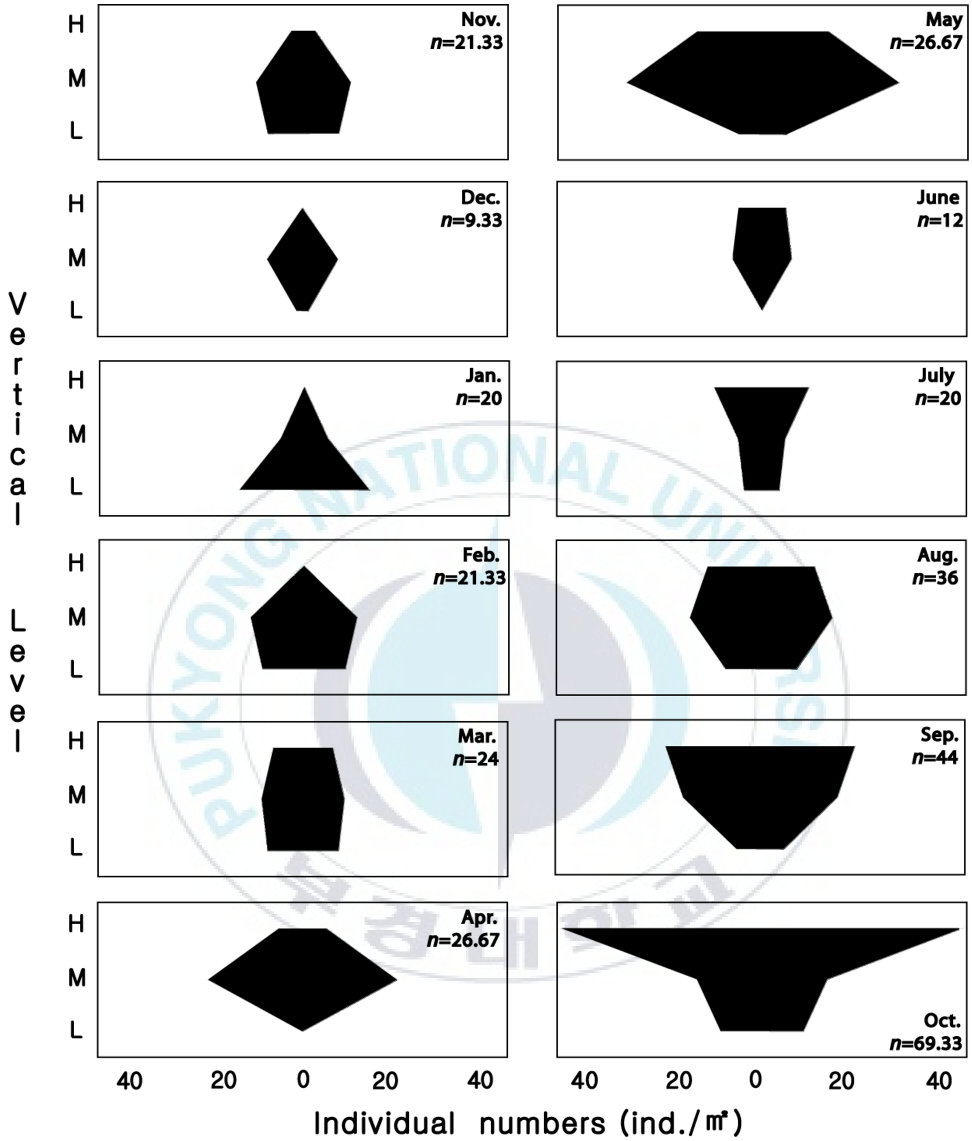

Fig. 10. The distribution of *Hemigrapsus sanguineus* during sampling months. H, M, L represent the vertical level in the intertidal area.
n = number of crabs

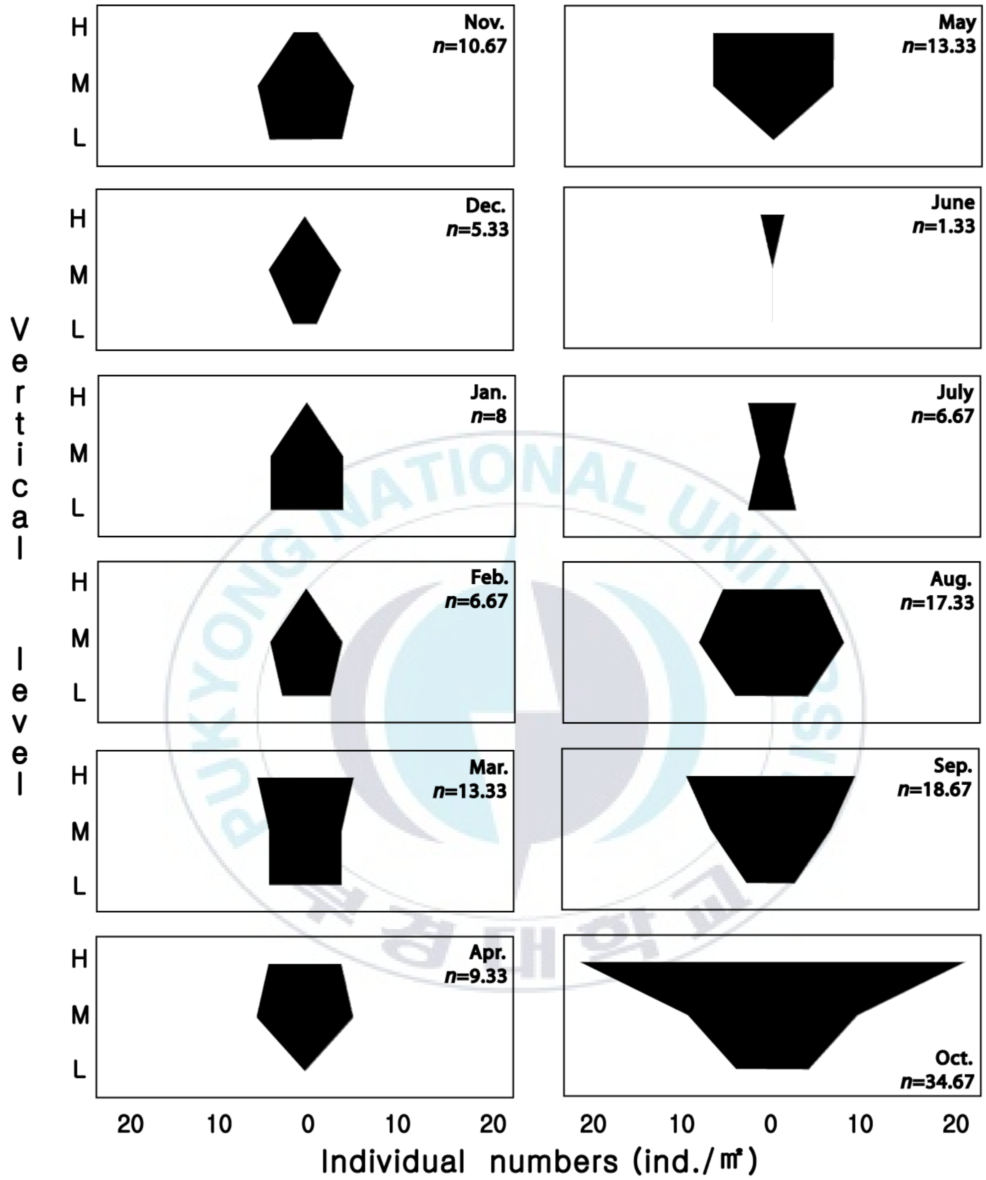

Fig. 11. The distribution of *H. sanguineus* male during sampling months. H, M, L represent the vertical level in the intertidal area.
n = number of crabs

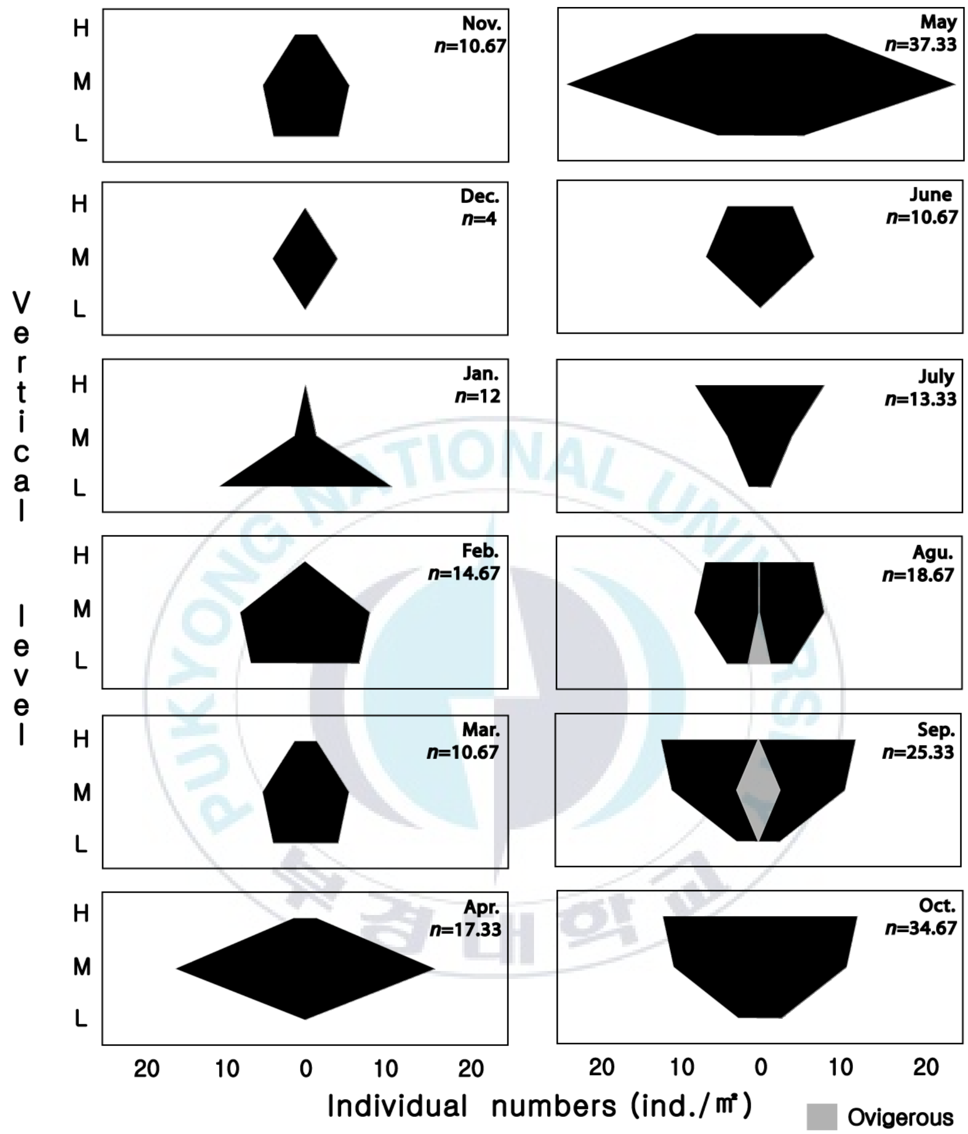

Fig. 12. The distribution of *H. sanguineus* female during sampling months. H, M, L represent the vertical level in the intertidal area.
n = number of crabs

Table 2. Density and size of the two species at the study site during the sampling period

Crab species	Abundance		Size of C.L.	
	Mean±1 S.D. (Crab m^{-2})	Significance	Mean±1 S.D. (Max) (CW mm)	Significance
Hemigrapsus penicillatus	High 0.89±1.32	P<0.0001	High 22.08±4.44 (25.91)	P<0.0001
	Mid 4.33±4.10		Mid 28.1±6.25 (28.39)	
	Low 7.33±4.84		Low 17.47±6.03 (28.02)	
Hemigrapsus snaguineus	High 10.53±12.83		High 9.9±3 (20.96)	
	Mid 13.11±7.47		Mid 11.04±3.4 (20.03)	
	Low 6.11±4.35		Low 11.72±4.5 (23.88)	

2. Life history

We should CW size frequency for find the life history in each species. We tried to explain two ways of the life history. The one is recruitment period and the other is brooding period. We compared these characters between two species. We supposed the recruit period is that appear the smallest individuals. This period differ between two species. *H. penicillatus*, in January, April, and October, the smallest individuals appeared on this site. They recruited three times a year (Fig. 15). We could find results as following in Fig. 15. 2 age class populations coexist in the same season and that the species life span is 2 years. On the other hand, *H. sanguineus*, in March and May, the smallest individuals appeared. They recruited twice a year (Fig. 16). It is also 2 age class populations coexist in the same season and that the species life span is 2 years.

We Female specimens of *H. penicillatus* were ovigerous primarily during summer from June to September except July, in June, August and September 100, 75, and 67% of the mature females were ovigerous, respectably (Fig.11). The other hand, *H. sanguineus* were ovigerous primarily during late summer August and September. In August and September 7 and 11% of the mature females were ovigerous, respectably (Fig. 14).

We should compare with the minimum and maximum CW size of ovigeous female (Table 3). *H. penicillatus*, CW size 13.68 - 24.08 mm of female specimens are ovigerous. *H. sanguineus*, CW size 15.67 – 19.12 mm of female specimens are ovigerous. According to these facts spoke to us two things. The ovigerus times are longer *H. penicillatus* than *H. sanguineus*. and the CW size interval of ovigerous possibility also showed the same pattern.

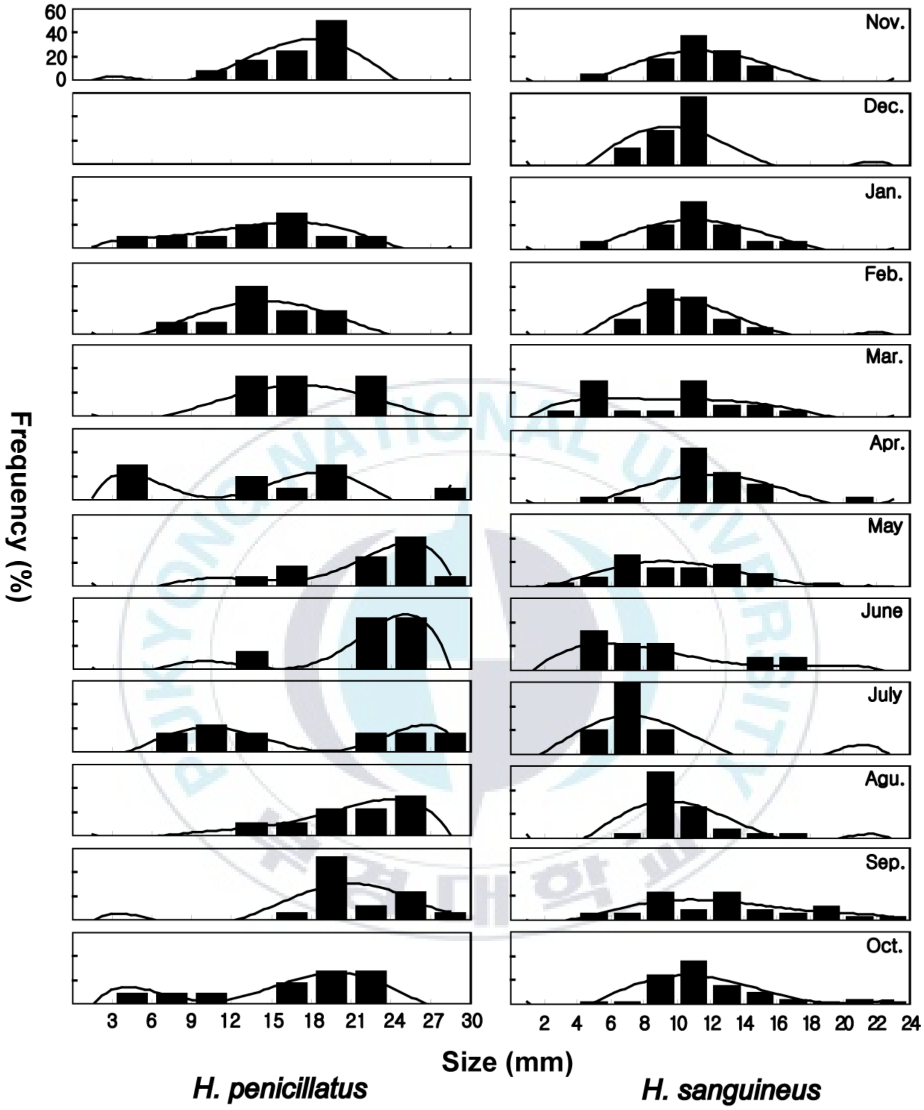

Fig. 13. The size frequency of two species. Size-frequency distributions of crabs collected from Il-Kwang rocky intertidal area.

Table 3

The size of ovigerous individuals and numbers of that in each species and month. The initial in the double parentheses speaks to the vertical area in rocky intertidal area. The size range of ovigerous individual wide *H. penicillatus*.

		June	July	Aug.	Sep.
H. penicillatus	Min size	21.25 (M)	*	13.68 (L)	16.29 (M)
	Max size	24.08 (M)		19.36(M)	23.92 (H)
	Individual numbers	4		1(M), 2(L)	2(H), 3(M), 1(L)
H. sanguineus	Min size	*	*	17.64 (L)	15.67
	Max size				19.12
	Individual numbers			1 (L)	2(M)

3. Feeding habit

We tried to find the difference in food items using two methods. The one is maximum food size and another is feeding habit.

First of all, we measured the chela gap (cG) size for find the maximum food size. cG was different with species and sex. According to Fig. 17, *H. penicillatus* is bigger than *H. sanguineus*. As compared in each species, in case of male specimens had similar steep, but *H. penicillatus* is even bigger than *H. sanguineus* as same chela width (cW). The other hand, female specimens had different steep. *H. penicilatus* $y = 0.863 + 1.29x$ and *H. sanguineus* $y = 0.664 + 1.36x$. Using this expression, calculated the crossing point. The crossing point is cW=1.7 and cG=2.976. when specimens about <1.7mm cW, *H. penicillatus* is bigger than *H. sanguineus*. Whereas about >1.7mm cW, *H. sanguineus* is bigger than *H. penicillatus*.

We tried to find the difference in feeding habit using compare the morphological characteristics of chela that is main feeding organ. The morphological characteristics of chela differ with sex rather than species. Male chela has large and powerful dentals. Whereas, female chela has small and fine dentals. Moreover female chela size is also smaller than male specimens (Fig. 18).

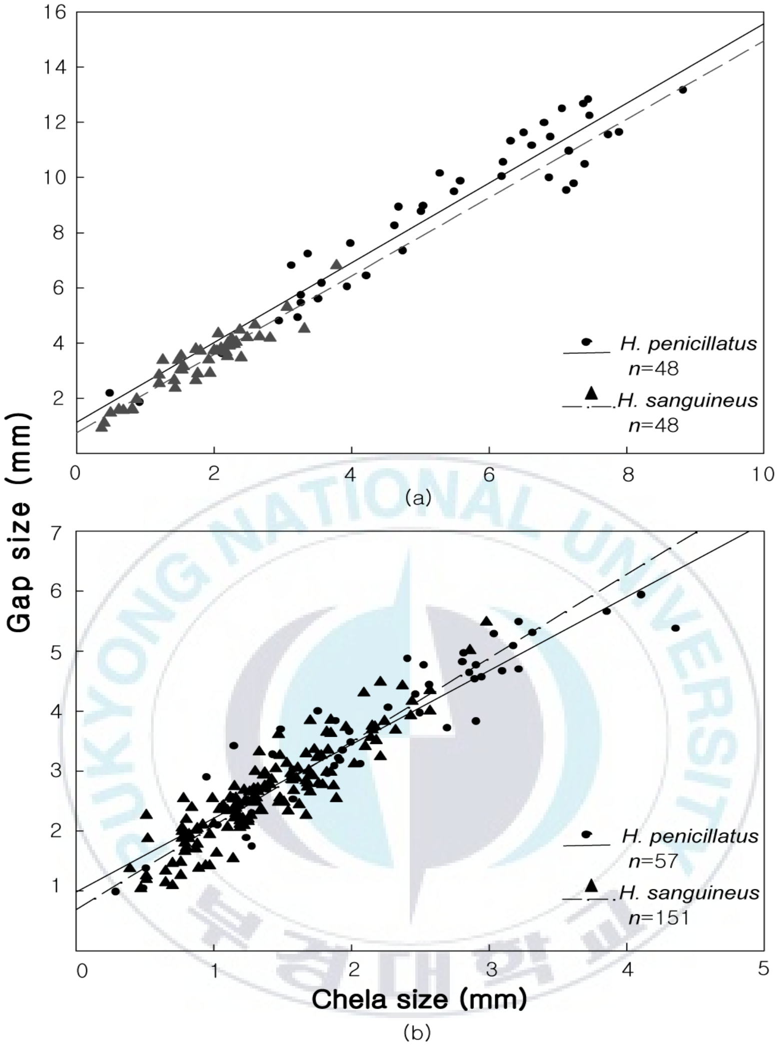

Fig. 14. The chela gap size (cG) in each species. (a) Male specimens, (b) Female specimens

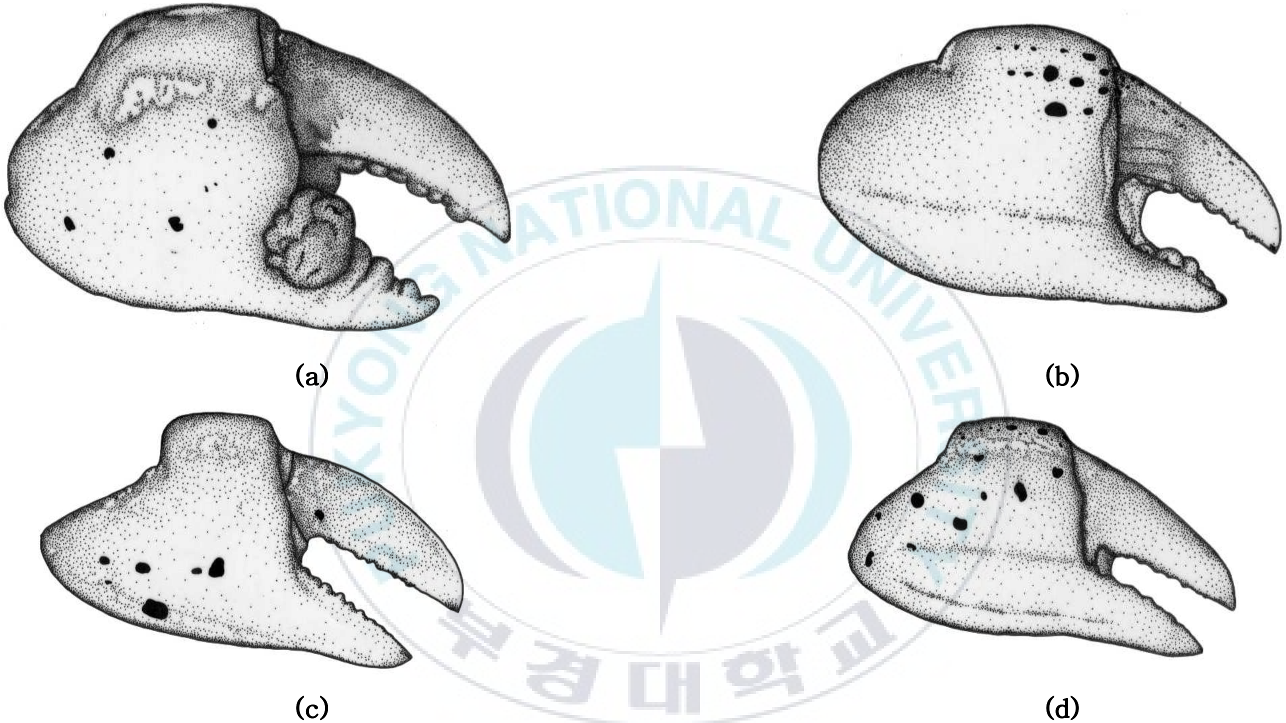

Fig. 15. The morphological characteristics of the chela.: (a) *Hemigrapsus penicillatus* male (b) *H. sanguineus* male (c) *H. penicilla* female (d) *H. sanguineus* female

Discussion

Sympatric two species *Hemigrapsus penicillatus* and *H. sanguineus* coexist in Il-Kwang rocky intertidal area and there belong to the same genus ‘*Hemigrapsus*’. Thus their competition is more serious than other species (Darwine, 1859). As time goes by, they try to develop coexistent mechanisms for living same area and using limitary resource. The purpose of this study is that we find these mechanisms don’t detective so far and adjust other kind sympatric species in general ecosystem.

We could find three kind of coexistence mechanisms in this study.

1. Difference in main habitat

"Habitat" and "Environment" are related but not synonymous terms. The habitat is the place where an organism, onymous terms. The habitat is the place where and organism, or a group of organisms, lives and is described by its geographic, physical, chemical, and biotic characteristics.

The degree of habitat complexity may influence availability of suitable shelter, affecting the survival and/or fitness of intertidal organisms in several ways. First, shelter mat reduce physical stress (e.g., heat, desiccation, freezing, osmotic fluctuations, etc.; reviewed by Newell, 1970; Conell, 1972; Peterson, 1991). Second, animals without appropriate shelter are probably more vulnerable to terrestrial and avian predators during low tide and to fish and invertebrate marine predators during high tide (Klein-Breteler, 1976; Peterson, 1991; Moksnes et al., 1998). Third, highly complex habitats may enable some mobile species to forage independently of predators, whereas organisms with limited shelter may face risks of predation that force them to curtail their foraging activities (Sih, 1987; Holbrook and Schmitt, 1998).

Often one wished to summarize the basic features of a macrohabitat without detailing any specific habitat component. Certain basic information should be recorded in any habitat analysis – the type of habitat, and the observers, time, location, and general weather conditions. A general habitat analysis should also include a brief description of the dominant physical and chemical components of the environment.

We divided three parts of intertidal area and find the main habitat of each species. Two species distribute all part of intertidal area. However, they are difference in main habitat. *Hemigrapsus penicillatus* distributed 82-100% individuals on the mid and low intertidal area. Whereas *H. sanguineus* distributed 56-100% individuals on the high and mid intertidal area, except January (mainly low intertidal area: 73.33%). This distribution was changed by season and sex.

The modeling of habitat in marine ecosystem is two kinds of things which are tolerance model (Connell and Slayter, 1977) and inhibition model (Egler, 1954). First of all, according to tolerance model, high intertidal area is physical variety is more serious than other intertidal area. So, Organisms which live in high intertidal area have large endurance from physical variety. As a result (Table 1), *H. sanguineus* distributed high and middle intertidal area. Whereas, *H. penicillatus* distributed mid and low intertidal area. Thus, *H. sanguineus* is more enduring physical stress than *H. penicillatus*. Second, inhibition model is difficult to adjust this situation. This theory interacts with succession but, our study is not a little relative succession.

The districution of *H. penicillatus* relate with the special feeding habit "Cannibalism". That is a special form of predation in which the predator and the prey are members of the same species and more serious when molting. Adults fed on the internal organs of small conspecifics after removing the carapace. This phenomenal regulates not only the population number but also distribution of small individuals (Okamoto and Kurihara,1989; Yasushi et al., 1989). Crabs with carapace width (CW) <5mm were frequently upon by larger individuals; prey size appeared to be relatived or the maximum gape of predator chela (Kurihara and Okamoto, 1987). So the <5mm CW individuals needs shelter too small to through the >5mm CW individuals with an essential condition. Sand was the dominant substrate type beneath stones along the upper transect, stones were found piled atop each other, and burial of stones was minimal. The solid rock substrate in the lower intertidal had numerous small holes and crevices, and no sand or mud was present. The mid intertidal area has the biggest rocks among the Il-Kwang rocky intertidal area (Table 5). The mean size of mid intertidal area is 30.61cm. Otherwise high intertidal area is 3.55cm and low intertidal area 13.31cm. So, mid intertidal area has many spare which size is big enough the >5mm CW individuals catch the small individuals thus, this area discomfort the small *H. penicillatus* individuals (<5mm) to live. And high intertidal area has benthic substance (3.5cm) too small to hide the <5mm CW individuals. Thus, this place is also bad for live <5mm CW individuals. Whereas, low intertidal area is suitable for the <5mm CW individuals live. Low intertidal area is bigger than high and smaller than mid intertidal area. These rocks (Table 4) make the suitable spare for hide the <5mm CW individuals from the >5mm CW individuals. The availability of shelter such as narrow gaps between boulders and stones limited cannibalism. Avoidance of large individuals by small ones, and visual approach of large individuals to small ones, as well as the presence of suitable shelter for small in maintaining the stability of the *H. penicillatus* population (Kurihara and Okamoto, 1987).

We should find this mean CW size is the most larger in all vertical intertidal area but, the biggest CW size individuals exist in low intertidal area (Table 2). The reason of this fact, the small individuals distribute more low intertidal area than mid intertidal area.

In other case of *H. sanguineus* positive relationship between cover of stone and *H. sanguineus* density were evident along both transects. Additionally, positive relationship between cover of stones and *H. sanguineus* density were evident along both transect (Andrew et al., 2000).

Mid intertidal area have so many rocks on the bottom. so, most *H. sanguineus* exist in mid intertidal area.

This distribution was varied by sex and season. *H. penicillatus* mainly distributed mid intertidal area May to July and low intertidal area August to April. Whereas, *H. sanguineus* mainly distributed high intertidal area from July to October and mid intertidal area from November to June. This variation is relatived around the air temperature (Fig. 16). In case of *H. penicillatus*, they distributed mid intertidal area from April (atmosphere temperature begin to warmer) to July (atmosphere temperature does not take over 20℃). They distributed low intertidal area during August and September which months are very hotter than other months take over 20℃ and they distribute low intertidal area from January to March (the temperature is lower than other months.). The reason of this distribution is that the low intertidal area is a little more effect atmosphere than other intertidal area. *H. penicillatus* has lower endurance of physical variation than *H. sanguineus* (Takahashi et al, 1985). Thus, they distribute low intertidal area during extreme atmosphere temperature months. Whereas *H. sanguineus* is a highly mobile grapsid crab (Takahashi et al, 1985; Diane et al., 2002) so, it is very hard to find the trend of their distribution. But, McDermott (1998a, b) spoke that in warmer months they were generally captured in the high to mid intertidal area, which had a heavy growth of the brown algae, *Fucus vesiculasus*, large numbers of acorn barnacles, *Semibalacles balanoides*, and some blue mussels, *Mytilus edulis*. We got the similar results at the Il-Kwang intertidal area. Thus we caught *H. sanguineus*in high and mid intertidal area during warm month.

This distribution is varied by sex. Two important things are in this phenomenon. First, during the ovigerous period, their distribution is same (*H. penicillatus*: June, August, and September; *H. sanguineus*: August and September) in each sex. In case of *H. sanguineus*, they are little difference in distribution usually but, we could find the same distribution during ovigerous period. The reason of this phenomenon, they should do the fertilization. In other case of *H. penicillatus*. We could find the similar distribution usually but, different in May (Fig. 16). Males went to the mid intertidal area and staid in there. Next month the female species went to the mid intertidal area and ovigerous. These results speak to us, male ahead prepare the fertilization.

Second, Each species are overlapping the ovigerous period during August and September so, they would undergo the spatial competition. They are difference in space and reduce the spatial competition in this period. *H. penicillatus* distributes low intertidal area during this period, whereas *H. sanguineus* distributes mid intertidal area in August and high intertidal area in September. They need many energy during ovigerous period thus, they are difference in distribution for reduce the competition of food and space.

Other special character of distribution is that the mean CW size of *H. penicillatus* is bigger than *H. sanguineus* whereas individual number *is H. sanguineus* bigger than *H. penicillatus* (Table 2).

Symptric two species develop different adjustment mechanisms and are separated their ecological niche. These facts are helped two sympatric species possible coexist in this study site.

Table 4

Description statistics of stone size groupings at the experimental site. Stone were categorized before measurement (n=25 per category), and circumference was measured (along longest axis) to the nearest centimeter. Note overlap between the maximum and minimum sizes in some successive categories (Andrew et al., 2000).

Stone size category	Mean ±1 S.E.	Minimum	Maximum
Rocks	17.3±0.8	11	25
Small cobbles	42.3±2.3	20	63
Large cobbles	100.6±2.6	83	124
Boulders	156.0±2.7	126	172

Table 5

Description statistics of stone size at the experimental site. We measure the stone each vertical area circumference was measured (along longest axis) to the nearest centimeter. Stone were measurement n=20 per each vertical area.

Vertical area	Mean ±1 S.E.	Minimum	Maximum
High	3.55±1.53	0.5	6.4
Mid	30.61±14.67	8	61
Low	13.31±14.39	3	25

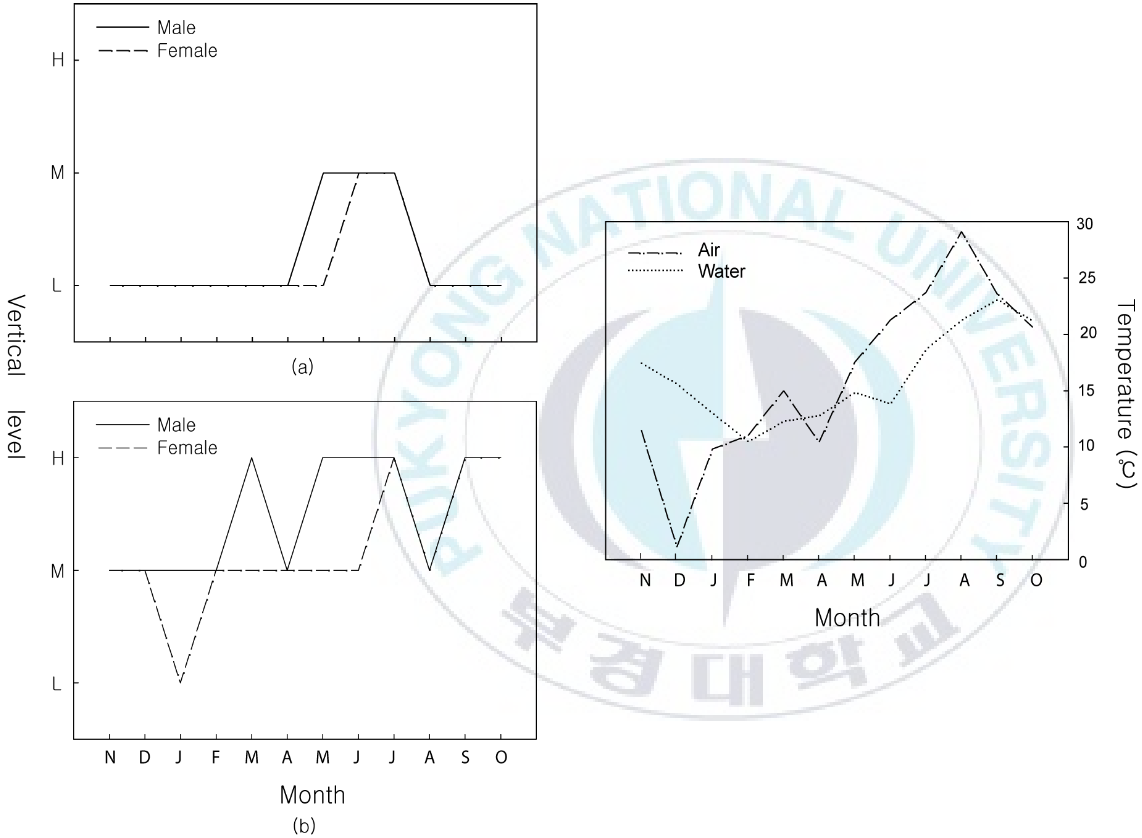

Fig. 16.

These graphs show the various distribution of two species.
(a) *H. penicillatus*
(b) *H. sanguineus*

2. Difference in life history

Life history means the development period from birth to die, simple mean is whole life all organisms in ecology. It is important recruitment and ovigerous period among the life history for maintain the species. This period individuals need to so many energy. Thus, if all species experience this period at the same time, it is hard to maintenance the species diversity. Because interspecies competition is more serious and some species win the competition dominate in ecosystem. Therefore, many species are difference in recruitment and ovigerous period and coexist with each other. Wherever a population is somewhat dependent on meteorological conditions and is geared in its fluctuations to an annual cycle by the life history of the species, we may expect apparent opportunism, and apparent replacement of one species by another, which in any year may indeed simulate competition, even if the species are not competitors and later may occur together in abundance (Hutchinson, 1964).

We suppose that *H. penicillatus* and *H. sanguineus* also coexist using this mechanisms and tried to find the life history each species through the size frequency. The results of graph, we could find the difference in life history. Okamoto & Kurihara (1987) investigated the life cycle and population dynamics of *H. penicillatus* and reported that 2 age class populations coexist in the same season and that the species life span is 2 yr. The coexistence of 2 age classes suggests the possibility of cannibalism, that is intraspecific predation, since it is well know that cannibalism is common in a wide variety of animals. Although cannibalism may be useful for regulating population density, a brake is necessary since excessive cannibalism would be disadvantageous to the survival of a species.

First, we tried to find the difference in recruitment period. *H. penicillatus* recruit three times a year, in January, April and October. Whereas, *H. sanguineus* recruit twice a year in march and May (Fig. 13). Two species are maximum age is two and each years classes coexist same space. In case of *H. penicillatus* have the cannibalism. Cannibalism is a special form of predation, in which the predator and the prey are the same species. *H.*

penicillatus with carapace width (CW) <5mm were frequently preyed upon larger individuals; prey size appeared to be related to the maximum gape of predators chela (Okamoto and Kurihara, 1987). Thus, *H. penicillatus* CW <5mm individuals are exposed serious predative pressure. Thus, they need more recruitment period and individuals for maintain the population.

Second, they are difference in ovigerous period. *H. penicillatus* broods three times a year in July, October and September. Whereas, *H. sanguineus* broods twice a year in August and September. The major environmental factor which controls the breeding in these crabs appears to be temperature (Pillay and Ono, 1978). *H. penicillatus* has numerous brood time than *H. sanguineus*. The range of CW size have brood capability is also different. The range of *H. penicillatus* is CW 13.68-24.08mm whereas *H. sanguineus* is CW 15.67-19.12mm individuals have a brood capability (Table 3). These results speak to *H. penicillatus* could brood longer and have more opportunity than *H. sanguineus* for a whole life. Thus, *H. penicillatus* has a great reproductive advantages. We should think relative this result with also cannibalism. We previously talked about *H. penicillatus* has the special feeding habit "cannibalism". Cannibalism is gave more predation pressure to <5mm CW individuals thus *H. penicillatus* need advantage of reproduction system and more and more recruitment individuals for maintain the species.

3. Difference in feeding habit

In ecosystem, all kind of organisms need the energy source to live, essentially. The energy source is food as the organisms. So, it is important thing reduce the competition of food. Thus, *H. penicillatus* and *H. sanguineus* need this mechanism reduce the feeding competition for the coexistence. We use two methods for find this mechanism. The one is difference in maximum food size and the other is difference in feeding habit.

Most crabs selectively forage on small sized molluscan prey well below the critical size that can be opened (Seed and Huges, 1995). Thus we compared the maximum chela gape (cG) and tried to find the preference food size. The cG was varied by sex and species. Generally, chela size and cG are female is smaller than male at the same CW (Paul and Nancy, 2003; Diane et al., 2001; Yasushi and Kazutosh, 1989). Greater size offered and advantage in feeding to male crabs only, with large males consuming more prey (averaged over all food type) than small males or either size of females. Both sex showed significant allometric growth of chela. The slope was significantly greater in males than female, indicating that, with increasing size, males develop disproportionately larger chelas than do females. This higher consumption rate of large males was associated with an expansion of diet breadth, leading to a significant interaction between sex, size, and prey species (Tracy et al., 2003). Moreover cG was varied by species. Each male specimens are very similar but, *H. penicillatus* is a little bigger than *H. sanguineus*. Otherwise Female specimens show the different trend. Though *H. penicillatus* is bigger than *H. sanguineus* at about <1.7mm cW but they show the opposite trend at about >1.7mm cW. The size of about 1.7mm cW is the minimum size which *H. penicillatus* female initially has the ovigerous capability. The relationship is between the carapace and chela width in *H. penicillatus* female specimens which is $y = -0.0405+0.239x$ (Fig. 17). Thus 1.7mm cW equal to the about 7.28mm CW. This size is similar to minimum size of ovigerous individual (8mm) (Noël et al., 1997). It said that *H. penicillatus* decrease the relative growth of chela at start ovigerous size and they eat possible smaller prey than *H. sanguineus*. Thus they use this mechanism reduce the feeding competition during the ovigerous season (Fig. 14).

Two functional groups of crabs emerged: generalists and specialists on hard shelled prey. The generalist has an omnivorous and possesses weak claws with small, fine denticles and mechanical advantage (MA) of the claw's lever system <0.3, while the specialists, consume hard shelled prey and possess large, powerful claws with broad, blunt molars and MA>0.3. The claws of the generalist exhibited a consistent preference for the smallest size categories, while the three specialists attacked all size classes offered (Yamada and Boulding, 1998). Differences in morphological and mechanical features of crab chelas reflect the observed difference in prey handing techniques and foraging behavior (Seed and Hughes, 1995). Thus, We tried to compare the chela morphological characters in each species by drew the chela. There has been considerable controversy in evolutionary biology about the timing of evolutionary changes during speciation. On the one extreme, the gradualists think that evolution proceeds slowly and morphological changes occur because of natural selection operating gradually (Krebs, 1994). So, we tried to find the difference in feeding habit using compared the morphological characters between two species (Fig. 15). These characters were not differed by species but differed by sex. Male specimens have a strong and large dental on chela whereas female specimens have a weak and small dental on chela. Yamada and Boulding (1998) spoke the difference in chela morphology is said how to differ their feeding habit. In case of the crab usually eats the gastropod, the specialist has large and powerful dental on their chela, otherwise the generalist has small and fine dental on their chela. According to these results, our male specimens belong to the specialist and female specimens belong to the generalist. They don't have any difference in feeding habit between species. However, they are the same species, male and female specimens are difference in feeding habit or preference food item. Why they have different chela morphological characteristics between each sex. We suppose the answer which is intraspecific competition. Female need more energy during the ovigerous season. They should reduce the feeding competition and evolute different way.

Sympatric two species are coexisted by these three mechanisms, such as difference in main habitat, life history and feeding habit. These mechanisms should be separated theirs niche and they became coexistence in same area.

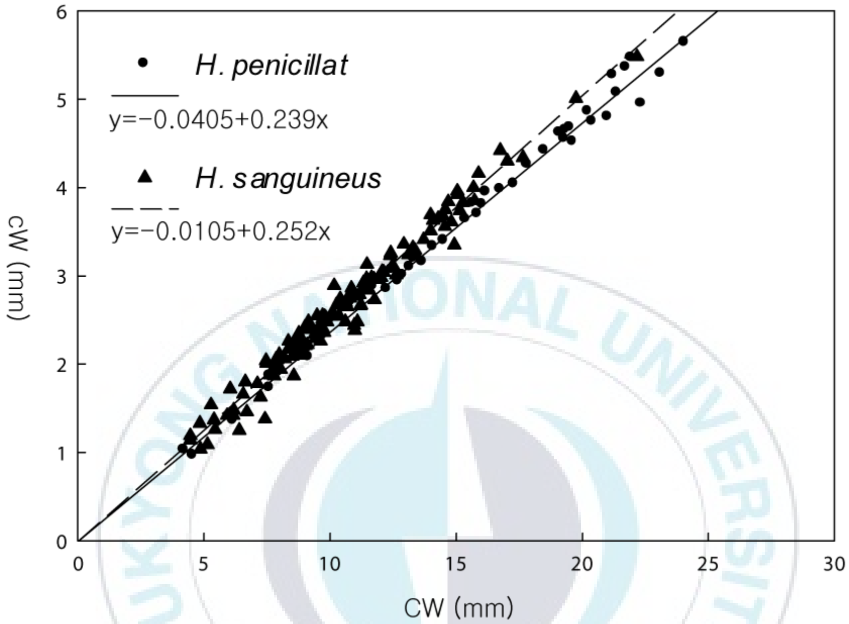

Fig. 17. The relationship between carapace width (CW) and chela width (cW): *H. penicillatus* ($P<0.001$, $r^2=99.1$) and *H. sanguineus* ($P<0.001$, $r^2=97.3$)

Summary

Two sympatric species *Hemigrapsus penicillatus* and *H. sanguineus* clearly coexist in Il-Kwang rocky intertidal area. Two species are same genus. Thus they compete with each other more serious. Competitive interactions could also be significant among co-ocurring species, affecting their densities and distribution. For example, competitively inferior individuals may not necessarily reside in their preferred habitats, but may be relegated to more marginal habitats by competitive dominants, since structurally complex habitats are potentially important to fitness, certain species may compete for them (Takahashi et al., 1985). The strengths of biological procsses (e.g., larval settlement, competition, predation, distribution of food resources) and physical factors (e.g., desication, freezing, salinity fluctuations) can be correlated with tidal height and may contribution to the vertical zonation of many rock intertidal organisms (Andrew et al, 2000). We should find this mechanisms using three hypotheses: (1) Difference in main habiat, (2) Difference in life history, and (3) Difference in feeding habit.

First of all, they have different main habitat. *H. penicillatus*

mainly distributes mid and low intertidal area. Whereas *H. sanguineus* mainly distributes high and mid intertidal area. The reason of these distribution was interaction of boulder size and cannibalism. These distribution is varied by season because of affect of surround temperature.

Second, they have different life history. We look first the recruitment period, *H. penicillatus* occurs three times a year in January, April and October. Whereas *H. sanguineus* occur two times a year in March and May. Also difference in ovigerous period. *H. penicillatus* occurs three times a year in June, August, and September. Whereas *H. sanguineus* occurs two times a year in August and September. *H. penicillatus* has greater recruitment however, *H. sanguineus* has a greater tolerance physical factors.

Third, the diet interaction of the two species raises the question of how coexistence is maintained. They have different maximum food size and feeding habit. Most crabs forage selectively on small sized molluscan prey well below the critical size that can be opened. Males develop disproportionately larger chelas than do females. And then compared in each species, male cG size is larger *H. penicillatus* than *H. sanguineus*. Otherwise, female cG size show the different pattern of male. *H. penicillatus* specimens of chela size <1.7mm are larger than *H. sanguineus* but, *H. sanguineus* specimens of chela size >1.7mm are larger than *H. penicillatus*. About 1.7mm is the cross point and minimum size of ovigerous in *H. penicillatus*. So We can find *H. penicillatus* decrease their relative growth rate of chela when they can ovigerous. Moreover, we compare diet type between two species drawing the chela morphological characters. The result of male species are specialist and female are generalist. Whereas, they don't have a difference in diet type between two species.

These mechanisms would make the niche separation between two species and can coexist in this area.

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석사과정 2년이라는 시간이 지식에 대한 목마름을 채워가는 시간일 뿐만 아니라 저에게는 내 평생에 알지 못하였던 수많은 것들에 대한 고찰의 시간 이였던 것 같습니다.

힘들고 어려운 고비마다 저의 옆에서 힘이 되어 주신 부모님께 우선 깊은 감사의 인사를 드립니다. 세상 누구보다도 무엇보다도 저에게 큰 힘이 되어주시고 저의 지지자가 되어주신 부모님 정말 감사드립니다. 두분이 계시지 않았더라면 돌덩이인 채로 세상을 살아갈 저에게 진주가 될 수 있는 기회를 주신 부모님 감사합니다. 아직 진주가 되진 못하였지만 앞으로도 꾸준히 노력하여 진주가 되어 두분의 은혜에 크게 보답하겠습니다. 부모님 정말 감사합니다.

부모님과 같은 마음으로 항상 저를 응원해 주시고 관심을 가져 주신 문창호 교수님께 우선 깊은 감사의 인사를 드립니다. 바쁘신 와중에도 논문의 시작부터 끝까지 물신양면으로 도와주신 손민호 박사님께 깊은 감사의 인사를 드립니다. 박사님의 도움이 없었다면, 석사의 문턱에 발조차 들이지 못하였을 저에게 기회를 주신 박사님께 머리숙여 깊은 감사의 마음을 전합니다. 그리고 항상 저에게 모티브를 제공해 주시며, 소리없이 앞에서 이끌어 주신 홍성윤 교수님께도 깊은 감사의 인사를 드립니다. 다음으로 부족한 시간을 내어 많은 도움을 주신 정래홍 박사님께도 깊은 감사의 말씀을 드립니다.

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고맙습니다. 감사합니다.