ว.วิทย. มข. 50(2) 162-171 (2565) KKU Sci. J. 50(2) 162-171 (2022)

ผลของความหนาแน่นต่ออัตราการเจริญเติบโต การสะสมหินปูน การลงเกาะและการตายของสาหร่ายชนิด *Halimeda macroloba* Decaisne

The Effect of Density on Growth, $CaCO_3$ Accumulation, Recruitment, and Mortality Rates of *Halimeda macroloba* Decaisne

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Received: 10 December 2021 | Revised: 17 August 2022 | Accepted: 31 August 2022

บทคัดย่อ

Halimeda macroloba Decaisne (Chlorophyta, Ulvophyceae) เป็นสาหร่ายสีเขียวขนาดใหญ่ ที่มีการแพร่กระจายกว้างทั้งในระบบนิเวศเขตร้อนและเขตกึ่งร้อน สาหร่ายชนิดนี้ไม่เพียงแค่เป็นผู้ผลิตขั้นต้นเท่านั้น แต่ยังเป็นผู้ผลิตแคลเซียมคาร์บอเนตที่สำคัญให้แก่ระบบนิเวศชายฝั่ง ความหนาแน่นของประชากรสาหร่ายที่ลดลงจะส่งผลกระทบต่อระบบนิเวศและปริมาณทรายแคลเซียมคาร์บอเนต แต่อย่างไรก็ตามการศึกษาเกี่ยวกับผลของความหนาแน่นต่อพลวัตประชากรและการผลิตแคลเซียมคาร์บอเนตยังมีค่อนข้างน้อย ดังนั้นในการศึกษาครั้งนี้มีวัตถุประสงค์เพื่อศึกษาผลของความหนาแน่นของสาหร่ายชนิด *H. macroloba* ที่แตกกต่างกันสามระดับ คือ ความหนาแน่นต่ำ (10 แทลลัสต่อแปลง) ความหนาแน่นปานกลาง (19 แทลลัสต่อแปลง) และความหนาแน่นสูง (38 แทลลัสต่อแปลง) ต่ออัตราการเจริญเติบโต การลงเกาะและการตายบริเวณเกาะลิดี จังหวัดสตูล โดยสาหร่ายที่ติดเครื่องหมายทุกแทลลัสในแต่ละแปลงจะถูกติดตามตรวจสอบเป็นระยะเวลาสองเดือนตั้งแต่เดือนธันวาคม 2562 ถึง มกราคม 2563 เพื่อศึกษาอัตราการเจริญ การลงเกาะและการตายของสาหร่าย และตรวจวัดอัตราการเจริญเติบโตและการสะสมหินปูนของสาหร่ายด้วยวิธี Alizarin Red-S marking technique ผลการศึกษาพบว่า ความหนาแน่นไม่ได้ส่งผลต่ออัตราการลงเกาะและการตายของสาหร่าย *H. macroloba* แต่ความหนาแน่นส่งผลต่ออัตราการเจริญเติบโตและการสะสมหินปูน โดยอัตราการเจริญเติบโตและการสะสมหินปูนของสาหร่ายจะต่ำในแปลงที่มีความหนาแน่นสูง ซึ่งในการศึกษาครั้งนี้พบอัตราการเจริญเติบโตและการสะสมหินปูนเฉลี่ยสูงที่สุดในแปลงที่มีความหนาแน่นต่ำเท่ากับ 37.27±3.21 และ 36.72±0.7 มิลลิกรัมต่อแทลลัสต่อวัน ตามลำดับ ผลการศึกษาครั้งนี้เป็นข้อมูลพื้นฐานที่ทำให้เข้าใจเกี่ยวกับผลของความหนาแน่นต่ออัตราการเจริญเติบโตและการสะสมหินปูนของสาหร่ายชนิด *H. macroloba* การศึกษาเพิ่มเติมเกี่ยวกับปัจจัยทางนิเวศวิทยาและสรีรวิทยาจะสามารถช่วยให้เกิดความเข้าใจผลของความหนาแน่นต่ออัตราการเจริญเติบโตและและการผลิตแคลเซียมคาร์บอเนตในระบบนิเวศทางทะเลบริเวณเกาะลิดี จังหวัดสตูล

ABSTRACT

Halimeda macroloba Decaisne is a macrophytic green alga (Chlorophyta, Ulvophyceae) widely distributed in the tropical and sub-tropical marine ecosystems. It plays important role not only primary producers, but also potential calcium carbonate producer in the coastal ecosystems. The loss of this calcified *Halimeda* might have negative effects on ecosystem, decreasing the $CaCO_3$ sands. Little is known of the effects of density on the population dynamics and $CaCO_3$ contribution. Thus, the objective of the present study was to investigate the effects of population density on growth, $CaCO_3$ accumulation, recruitment, and mortality rates. Three different density treatments were selected in a natural population of *H. macroloba*. A natural density of 19 thalli quadrat^{-1} was used as the medium-density treatment, and the low- and high-density treatments had respectively 10 thalli quadrat^{-1} and 38 thalli quadrat^{-1}. Each individual was tagged and monitored for two months (December 2019 to January 2020) in order to determine the recruitment and mortality rates. Alizarin Red-S marking was used to indicate the growth and $CaCO_3$ accumulation of *H. macroloba*. Our results revealed that no significant difference in recruitment and mortality rates were observed among the three treatments. However, the growth and $CaCO_3$ accumulation rates in the low-density treatment appeared to be higher than those of high-density treatments. The area of the low-density treatment showed the highest growth rate and $CaCO_3$ accumulation rate with 37.27±3.21 mg thallus^{-1} day^{-1} and 36.72±0.7 mg $CaCO_3$ thallus^{-1} day^{-1}, respectively. In conclusion, this work provides basic knowledge of population density of macrophytic green alga *H. macroloba* in relation to its growth and $CaCO_3$ accumulation. Further investigation on other ecological and physiological parameters would help understanding the effect of density on growth and $CaCO_3$ production in marine ecosystem of Lidee Island, Satun Province.

คำสำคัญ: ความหนาแน่น *Halimeda* การแข่งขันภายในประชากร ประชากร

Keywords: Density, *Halimeda*, Intraspecific competition, Population

INTRODUCTION

The successful establishment of marine algal populations can be influenced by endogenous processes such as competition and predation, and exogenous processes such as environmental factors of light, temperature, and water current (Borlestean et al., 2015). A factor known to influence the growth, survival, and mortality of these populations is density and both positive and negative relationships with growth, recruitment, and mortality have been reported (Vadas et al., 1992; Flores-Moya et al., 1996). Several studies have found that increasing density in a population tends to limit growth and reproduction (Reed, 1990; Ang and De Wreede, 1992; Viejo and Åberg, 2001; Arenas et al., 2002) and prevents the settlement of algal propagules (Hruby and Norton, 1979). Algae also had higher mortality rates in crowded stands (Vadas et al., 1990). Conversely, some studies have shown that survival rates were not affected by population density (Viejo and Åberg, 2001). So, the effects of density on algal growth, survival, and mortality are not consistent across algal species and life stages and may be affected by biological and environmental factors.

No previous field experimental study has looked at density dependence on population dynamics in calcified algae such as *Halimeda*. These algae are considered a key component of carbon budgets and can accumulate around 0.15 Gt $CaCO_3$ year^{-1}, contributing around 2 kg $CaCO_3$ m^{-2} year^{-1} (Perry et al., 2016). The vulnerability of these algae has previously been considered when populations decreased under the influence of climate change (Hoegh-Guldberg et al., 2007).

In Thai waters, *Halimeda macroloba* Decaisne (Sarai-Bai-Ma-Kud) belongs to Chlorophyta, class Ulvophyceae. It is a dominant and common species, widespread from shallow subtidal to intertidal zones. *H. macroloba* grew by 0.021 g dry weight thallus^{-1} day^{-1} and produced 1-2 new segments thallus^{-1} day^{-1} (Mayakun and Prathep, 2019). *H. macroloba* is known as a carbonate contributor that utilizes bicarbonate for calcification and precipitates aragonite crystals in its intercellular spaces (van Tussenbroek and van Dijk, 2007; Mayakun et al., 2020). The annual $CaCO_3$ production of this species in Thai waters was around 291.94-908.11 g m^{-2} yr^{-1}, and the sediment production rate was around 2.5 g m^{-2} yr^{-1} (Mayakun and Prathep, 2019). However, the abundance of *H. macroloba* can be affected by factors such as competition, density, predation, temperature, and light. The loss of *H. macroloba* populations will negatively affect ecosystem. Therefore, it is useful to determine the factors that regulate *H. macroloba* population dynamics. Here, the effects of population density on the growth rate, recruitment, and mortality of *H. macroloba* were investigated and it was hypothesized that low-density treatments would show higher growth rates and recruitment rates, and lower mortality rates compared to high-density treatments.

MATERIALS AND METHODS

Study site

The experiment was carried out at Lidee Island (6° 46'58" N, 99° 46'10" E), Mu Ko Phetra National Park, Satun Province, Southern Thailand (Figure 1 a-c). The climate presents two seasons; a rainy season from May to October, dominated by the southwest monsoon and a dry season from November to April, dominated by the northeast monsoon. The substrate was plain sand. *H. macroloba* was the conspicuous species. The natural density was around 74.70±8.05 thalli m^{-2} or 19 thalli quadrat^{-1} (personal observation) (Figure 1d). In this area, *H. macroloba* has a high standing stock of around 62,400-414,660 thalli covering 3000 m^2 (Mayakun and Prathep, 2019).

Field experimental set-up

Three density treatments were used in this study: high, medium, and low. The natural density of ~ 74 thalli m^{-2}, or 19 thalli quadrat^{-1}, was used as the medium-density treatment; the high-density treatments contained twice the number of *H. macroloba*, around 38 thalli quadrat^{-1}, and the low-density treatment containned half the number of *H. macroloba*, around 10 thalli quadrat^{-1}. Mature calcified *H. macroloba* individuals with four levels of segments were counted in each density treatment. Each density of *H. macroloba* was identified in the natural meadow. There was no manipulation of the density either by transplantation or thinning. Plots of each density measuring 50×50 cm were randomly marked out in the *H. macroloba* meadow. Three plots of each density were used, and replicates were around 1-2 m apart. All nine plots were located at similar depths to reduce confounding factors.

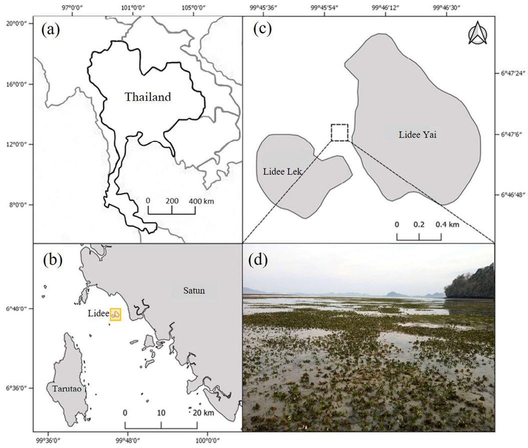

Figure 1 The location of Lidee Islands, Phetra Islands National Park, the Andaman Sea, Satun Province, Thailand (a, b). Location of our study site (c). *Halimeda macroloba* meadow in our study site (d).

The effects of density on the growth rate, recruitment, and mortality of *H. macroloba* were investigated from December 2019 to January 2020. Unfortunately, data could not be collected during February 2020 owing to the northeast monsoon, and after February 2020 the study could not be continued as planned because of the COVID-19 pandemic and the subsequent lockdown of the province that prohibited travel to the site from our province. However, two months of data collection was enough to investigate the growth rate of *H. macroloba* because it grows fast, producing 1-2 new segments day^{-1} (Mayakun et al., 2020).

Growth rate

Growth rate was determined in each treatment plot. Two to three selected mature *H. macroloba* individuals with no epiphytes were stained with Alizarin Red-S in each month. Selected thalli were covered with transparent plastic bags containing ~ 500 mL of seawater that were attached to the base of each thallus with wire ribbon. A concentrated solution of 1 g of Alizarin Red-S per 100 mL of seawater was injected into the bags, which were checked for leakage of the coloring agent. After 12-14 h, the bags were removed. Fifteen days later, the dyed thalli were collected and brought back to the laboratory at the Division of Biological Science, Prince of Songkla University. The stained thalli without their holdfast were cleaned of epiphytes and bleached in a 5-10% sodium hypochloride solution for 20-30 min. The segments were separated into two parts: old, stained segments, and new, unstained segments. The numbers of segments in each group were counted, dried at 65 °C in a drying oven to constant dry weight, and then weighed. Growth rate was calculated from the dry weight in mg thallus^{-1} day^{-1} of the unstained, new segments (Mayakun et al., 2020).

$CaCO_3$ accumulation rate

After calculated growth rate, the dried, new segments were decalcified in 5% hydrochloric acid until gas bubbles disappeared and then rinsed with tap water. The decalcified segments were dried at

65 °C and then weighed to determine their somatic weight. The $CaCO_3$ accumulation rate was calculated as difference weight of before and after decalcification (mg $CaCO_3$ thallus^{-1} day^{-1}) (Mayakun et al., 2020).

Recruitment and mortality

To investigate recruitment and mortality of *H. macroloba*, all individuals in each treatment were tagged at the base with ribbon. The numbers of tagged plants in the high-, medium-, and low-density treatments were 38, 19, and 10 thalli quadrat^{-1}, respectively. Tagged individuals and new recruits in each treatment were observed and counted monthly.

Environmental factors

Light intensity and water temperature under the canopy of *H. macroloba* in each treatment were determined monthly using a HOBO data logger (Onset Computer Corporation, USA).

Statistical analysis

A Repeated Measures Analysis of Variance (RM-ANOVA) was used to test the effects of density on growth, recruitment, and mortality. Mauchly's test of sphericity indicated that the assumption of sphericity had been violated. In this analysis, the Greenhouse-Geisser method was used to collect the degrees of freedom. The homogeneity of variances was analyzed by Levene's test. The data were log x transformed to meet the assumption of normal distribution. Tukey's HSD was used to test the differences between each treatment. Pearson correlation analyses were used to correlate: light intensity with growth rate, $CaCO_3$ accumulation rate, and mortality. All data were analyzed using SPSS v. 13.0 for Windows.

RESULTS AND DISCUSSION

The light intensity under the *H. macroloba* canopy during this study varied significantly (F = 3.179, p = 0.016). The highest light intensity, around 961.32±83.06 µmol photons m^{-2} s^{-1}, was recorded in the low-density treatment. Light intensity in the medium- and high-density treatments was 866.285±112.09 and 881.15±109.46 µmol photons m^{-2} s^{-1}, respectively (Figure 2). Water temperature varied from around 30 to 31 °C but showed no significant difference among treatments (F = 2.819, p = 0.064).

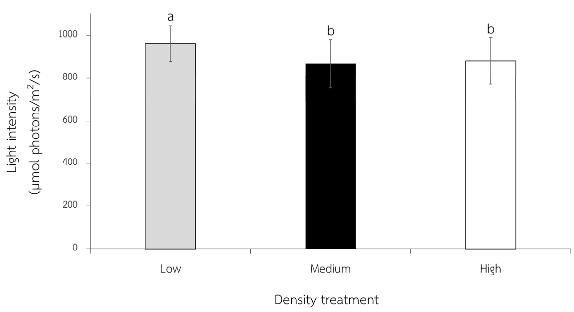

Figure 2 Light intensity in the three different density treatments (mean ± SE). Different letters above the bars indicate differences in light intensity among treatments that are significant at p < 0.05.

Growth rate differed significantly among density treatments (F = 46.784, p < 0.001; Table 1). The highest mean growth rate, around 37.27±3.21 mg thallus^{-1} day^{-1}, was found in the low-density treatment. The growth rates in the medium-density and the high- density treatments differed significantly at 19. 41±4. 43 and 13.00±2. 1 mg thallus^{-1} day^{-1} (F = 5.084, p = 0.048), respectively (Figure 3). *H. macroloba* in the low-density treatment also produced the highest number of new thalli within 30 days, around 3 thalli quadrat^{-1} or 0.1±0.02 thallus day^{-1}. In the medium-density and the high-density treatments, *H. macroloba* produced around 1 thallus quadrat^{-1} or 0.05±0.01 thallus day^{-1}.

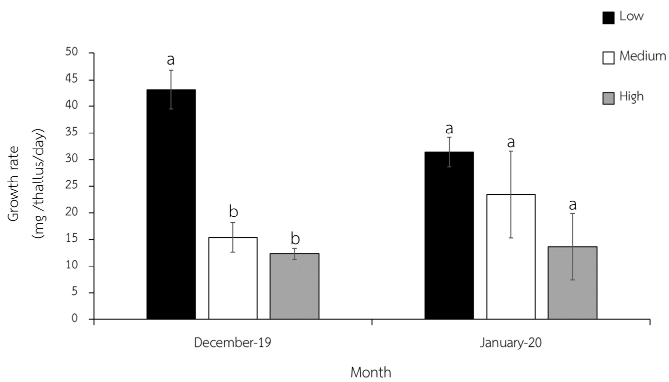

Figure 3 Growth rates of *Halimeda macroloba* in the three different density treatments (mean ± SE) (n = 3).

$CaCO_3$ accumulation rate was significantly different among density treatments (F = 189.110, p < 0.001; Table 1). The highest accumulation rate was found in the low-density treatment with approximately 36.72±0.7 mg $CaCO_3$ thallus^{-1} day^{-1}. The $CaCO_3$ accumulation rates were lower in higher density, around 14.88±3.62 and 9.83±2.74 mg $CaCO_3$ thallus^{-1} day^{-1} in the medium-density and the high-density treatments, (F = 6.931, p= 0.025) respectively (Figure 4)

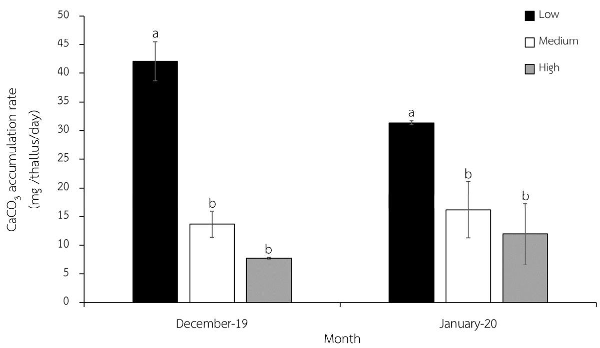

Figure 4 $CaCO_3$ accumulation rates of *Halimeda macroloba* in the three different density treatments (mean ± SE) (n = 3).

Since *H. macroloba* produced the highest growth and $CaCO_3$ accumulation rates in the low-density treatment, both rates were apparently influenced by density. In the low-density treatment, the greater light intensity could promote photosynthesis and there would be less competition for light from other *H. macroloba* individuals (Dean et al., 1989). Our results showed that there were positive correlations between light intensity and the growth (r = 0.538, n = 18, p = 0.021) and $CaCO_3$ accumulation rates (r = 0.512, n = 18, p = 0.03) (data not shown). Algae in the high-density treatment might be more shaded by neighbors that could reduce available light and affect photosynthesis (Dean et al., 1989; Reed, 1990). Additionally, intraspecific competition for space, nutrient, and light among individual *H. macroloba* might be less complicated in the low-density treatment than in the high-density treatment. Our results indicated similar effects of density to those found in a study of *Ascophyllum* by Viejo and Åberg (2001), who reported that growth rate decreased when the population density increased. They also suggested that light limitation in crowded populations might be the key factor influencing algal growth. The light intensity of around 900 µmol photons m^{-2} s^{-1} recorded in the low-density treatment in the present study, was previously suggested to be the favorable condition for photosynthesis and calcification of *H. macroloba* (Prathep et al., 2018). Dean and Jacobsen (1984) indicated that reduced light intensity can limit the growth of *Macrocystis* juveniles. Our results, however, are not consistent with those of Lazo and Chapman (1998) who showed that the elongation of *Ascophyllum nodosum* occurred faster in high-density populations. These positive and negative effects of density dependence in algal populations might be influenced by the physical environment and might also be species-specific.

There was no significant difference in the recruitment rate among density treatments (F = 2.405, p = 0.176; Table 1). However, the highest recruitment rate was found in the low-density treatments in December 2019, at around 91.72-96.16% while the lowest recruitment rate was found in the high-density treatment in December 2019, at around 72.34-87.38% (Figure 5). There was also no significant difference in the mortality rate among density treatments (F = 0.213, p = 0.687; Table 1). The highest mean mortality rate, around 71.78-79.68%, was found in the low-density treatment while the mean mortality rates in the medium-density and high-density treatments were 63.99-75.29% and 60.97-84.53%, respectively (Figure 6). Additionally, our results showed that there was no positive correlation between light intensity and mortality (r = 0.003, n = 18, p = 0.989) (data not shown).

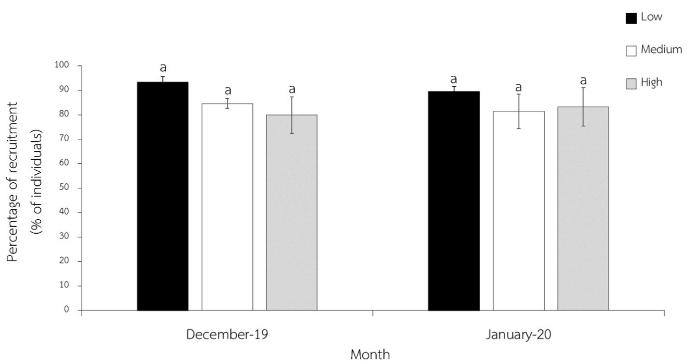

Figure 5 The percentage recruitment of *Halimeda macroloba* in the three different treatments (mean ± SE) (n = 3).

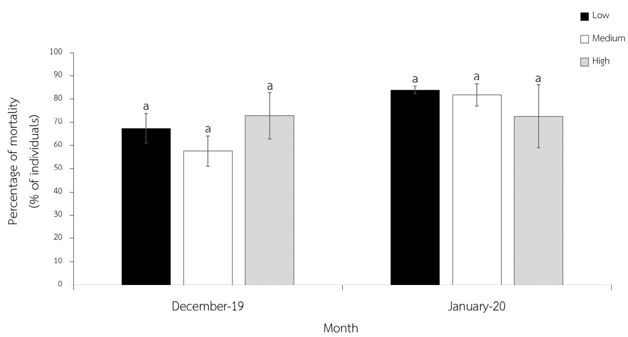

Figure 6 The percentage mortality of *Halimeda macroloba* in the three different treatments (mean ± SE) (n = 3).

Recruitment and mortality are one of the processes regulating algal population structures but no density dependent effects on recruitment and mortality were observed in our study, where the recruitment rate was quite high in all density treatments (Table 1). Since algal numbers can be boosted and abundance increased through asexual reproduction (Walters et al., 2002; Mayakun and Prathep, 2019), perhaps the parental thalli exploited the available space for lateral spread through the substrate by producing new recruits from rhizoidal runners or filaments of the holdfast. Certainly, sexual reproduction was rarely observed in our study site, and therefore the higher recruitment rate in the low-density treatments might be a response to the greater space available for new recruits (Ang and De Wreede, 1992; Conitz et al., 2013). With regard to mortality, there was no evidence that the mortality rate of *H. macroloba* increased in dense stands. However, the effects of density on population dynamics might vary depending on extrinsic factors such as grazing, substrate and desiccation (Reed, 1990) and on intrinsic factors such as age, growth condition, or morphology (Hruby and Norton, 1979). In the present study, although the factors that affected recruitment and mortality were not completely clear, the significance of density dependence on growth in a monospecific patch of *H. macroloba* was supported. The effects of herbivory, desiccation, shading and microhabitat on recruitment and mortality rates of *H. macroloba* in the study area remain to be clarified and would be an interesting topic for further examination.

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Table 1 The effects of population density on the growth, $CaCO_3$ accumulation, recruitment, and mortality of *Halimeda macroloba.* A repeated measures ANOVA was applied to two months of data (December 2019 – January 2020).

Source of variation	Growth			$CaCO_3$ accumulation			Recruitment			Mortality		
	df	MS	*F*	df	MS	*F*	df	MS	*F*	df	MS	*F*
Density treatment	2	948.411	46.784^{***}	2	1225.832	189.11^{***}	2	303.638	2.405^{ns}	2	99.717	0.213^{ns}
Error	8	20.272		8	6.482		10	126.267		10	467.41	

*p < 0.05; **p < 0.01; ***p < 0.001; ns not significant.

CONCLUSIONS

The growth rate and $CaCO_3$ accumulation of *Halimeda macroloba* tended to be related with the density of its population. It appeared that the growth rate of *H. macroloba* decreased when growing in the high population density. On the contrary, recruitment and mortality rates were not related with the population density. However, long-term data collection and further analysis of other ecological and physiological factors needs to be explored to make clear understanding the phenomenon of density-dependent factor in regulating algal populations.

ACKNOWLEDGEMENTS

This research was financially supported by the Development and Promotion of Science and Technology Talents Project to S.P. and PSU Basic Research Grant from Prince of Songkla University (grant no. SCI6302020S to J.M.). This work was partly supported by the National Research Council of Thailand (NRCT, grant no. RDG6130002 to J. M.). Thanks to Mr. Thomas Duncan Coyne for assistance with the English.

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