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PRIMARY RESEARCH PAPER

The role of monsoon-driven oceanographic variability in recruitment patterns of key intertidal space occupiers on tropical rocky shores on the west coast of Thailand, Indian Ocean

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Abstract We investigated the influences of oceanographic variables on recruitment patterns of the acorn barnacle *Chthamalus malayensis* and the rock oyster *Saccostrea cuccullata*, key space occupiers on tropical intertidal rocky shores. Recruitment data and nearshore environmental variables were obtained at spatial (regional and local) and temporal (monthly) scales on the west coast of Thailand. The relationship between the recruitment of each species and combinations of environmental variables was modeled. The climate of the study sites is influenced by the southwest and northeast monsoons of the Indochinese monsoon system. Observations showed that recruitment of both species and oceanographic variables exhibited differences at either local scale or monthly scale or both. Recruitment of both species was positively related to temperature, while barnacle recruitment was negatively related to salinity, but oyster recruitment was positively related to salinity. Barnacles showed a greater rate of recruitment when south-westerly onshore winds predominated during the southwest monsoon season, while the influence of wind patterns on rock oyster recruitment was not clear. Differential larval delivery regulated by monsoon-driven currents is, therefore, a potential determinant of barnacle recruitment. Our study highlights the roles of monsoon-influenced oceanographic processes as predictors of recruitment patterns of intertidal species in a tropical system.

Keywords Recruitment · Barnacle · Oyster · Monsoon · GLM

Introduction

Variation in recruitment can directly influence adult abundance, distribution, and interactions in marine communities (Roughgarden et al., 1985; Bertness et al., 2001). For marine broadcast spawners, the mechanisms responsible for regulating variation in recruitment can operate on a range of spatial scales (Bertness et al., 1996; Jenkins et al., 2000). At the large geographic spatial scale, larval delivery is an

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important determinant of variation in recruitment. Upwelling offshore flows can transport larvae seaward and reduce the larval supply to intertidal communities (Connolly et al., 2001; Pfaff et al., 2011) but wind-driven currents can also play a key role in the dispersal of larvae shoreward (Lagos et al., 2008; Neo et al., 2013; Mazzuco et al., 2015; Chan et al., 2022) and settlements of intertidal species are enhanced by onshore winds (e.g., Bertness et al., 1996; Mazzuco et al., 2015). Moreover, high larval production has been associated with higher primary productivity in the nearshore ocean (Leslie et al., 2005), which can be the result of upwelling and monsoonal forcing (Liu et al., 2002).

The coastal areas on the west coast of Thailand can be divided into a northern and a southern region (Fig. 1). These regions, respectively, belong to the Myanmar Shelf and the Strait of Malacca Shelf marine provinces (Brewer et al., 2015). Oceanographic processes in the waters along the west coast of Thailand are strongly influenced by monsoonal winds belonging to the Indochinese monsoon system (Khokiattiwong, 1991; Buranapratheprat & Meesuk, 2013). The northeast monsoon lasts from November to March, when north-easterly winds from Siberia and

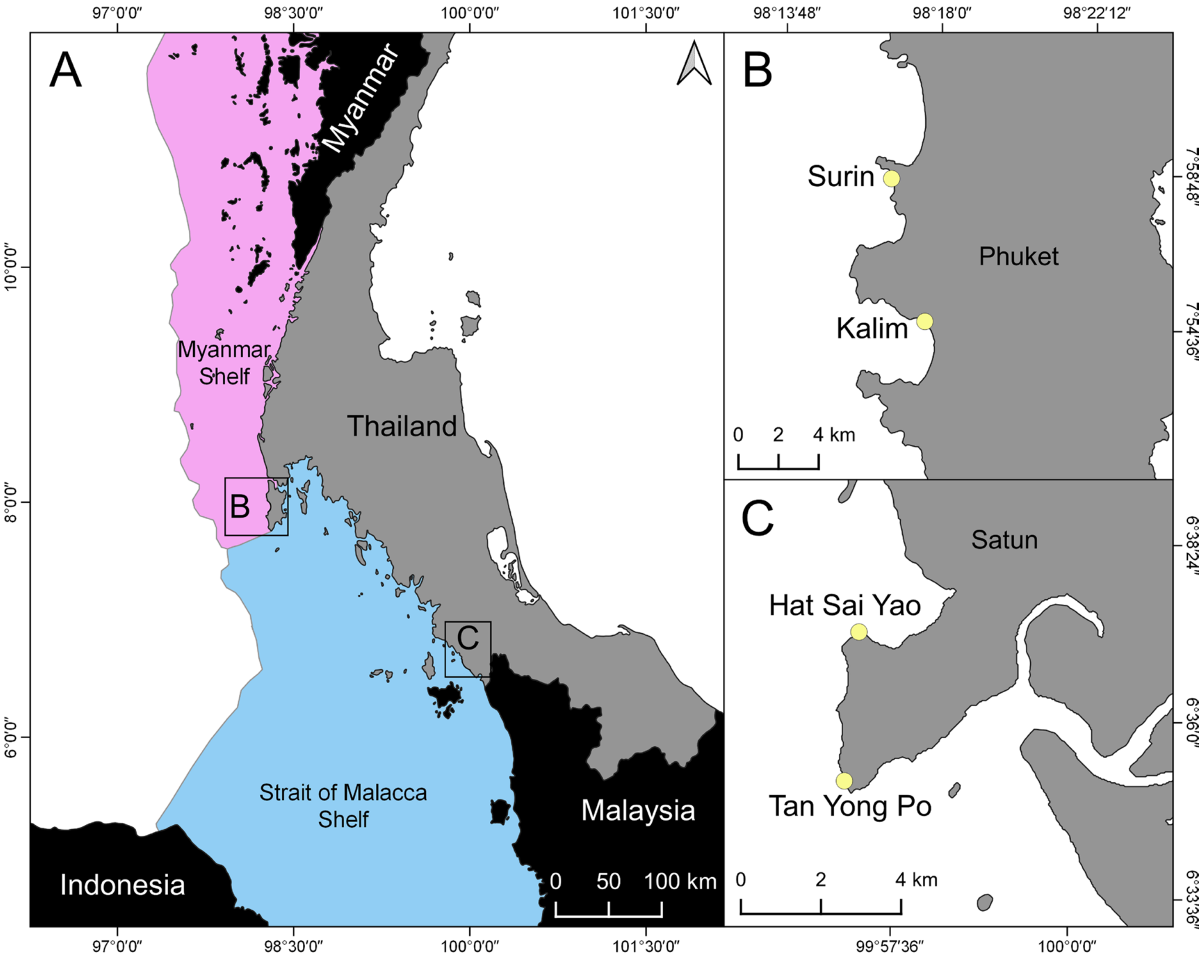

Fig. 1 **A** Map of southern Thailand. The west coast of Thailand can be divided into northern (pink) and southern (blue) regions which are parts of the Myanmar Shelf and Strait of Malacca Shelf marine provinces, respectively. The white areas are ocean. The areas in squares B and C in **A** are shown in larger scale in **B** and **C**, featuring the four study sites: two in the northern region (Phuket Province) and two in the southern region (Satun Province). The map is applied from Brewer et al. (2015)

the western north Pacific prevail. During the northeast monsoon season, there are circular clockwise currents around the upper Andaman Sea locating offshore from the Myanmar Shelf marine province which returns oceanward around the boundary between the two marine provinces (Pongparadon et al., 2015). The prevailing winds in this season generally push surface water offshore, resulting in upwellings and high primary productivity along the west coast of Thailand (Buranapratheprat & Meesuk, 2013; Hsu et al., 2014; Pongparadon et al., 2015). The southwest monsoon lasts from late May to September and is characterized by south-westerly winds from the Indian Ocean. There are two water masses from the Indian Ocean that flow toward the shore on the west coast of Thailand during this time (Pongparadon et al., 2015). There is a transition from the southwest to northeast monsoon seasons, usually in October (Cruz et al., 2013; Hsu et al., 2014). During the southwest monsoon season, south-westerly winds produce not only onshore currents, but also turbulent mixing, sedimentation in coastal areas, and heavy rainfall that lowers salinity. The prevailing southwest monsoon influences the Myanmar Shelf province through cyclonic winds and rainfall, bringing larger swells compared to the Strait of Malacca Shelf province. There are fewer large-scale storms or cyclonic activities in the Strait of Malacca Shelf province as it is more sheltered by Sumatra Island, and winds are moderate in both monsoon seasons (Brewer et al., 2015). Chan et al. (2022) suggested that the monsoon-driven currents can affect the larval supply and diversity of barnacle species in these regions. Nonetheless, the influence of monsoon-driven oceanographic variability on the reproduction of coastal marine species is poorly understood and the west coast of Thailand is a suitable trackable model system to evaluate such effects.

The acorn barnacle *Chthamalus malayensis* Pilsbry, 1916 (Thecostraca: Chthamalidae) and rock oyster *Saccostrea cucullata* (Born, 1778) (Bivalvia: Ostreidae) are dominant space occupiers, contributing more than 50% of overall biomass on rocky intertidal shores on the west coast of Thailand (Wangkulangkul & Promdam, 2018). They are recognized as ecosystem engineers that have impacts on the abundance and distribution of other species on intertidal rocky shores (Amnuaypon & Wangkulangkul, 2018). Both species have open populations, that is, they produce planktonic larvae with relatively long-distance dispersal (Ruwa & Polk, 1994; Lee et al., 2006). The development of *C. malayensis* larvae from hatching to settling requires 14–20 days (Yan and Chan, 2001), while the planktonic larval period of *S. cucullata* is three weeks to one month (Braley, 1982). Reports from elsewhere indicate that *C. malayensis* and *S. cucullata* reproduce throughout the year with several peaks of reproductive activity (Braley, 1982, 1984; Tenjing, 2020; Lee et al., 2006; Yan et al., 2006). It has been suggested that their reproduction is influenced by changes in water salinity and the abundance of plankton, which is their food source (Braley, 1982; Tsang et al., 2012), but the link between the timing of monsoons and the reproductive cycles of *C. malayensis* and *S. cucullata* remains unclear (Koh et al., 2005; Lee et al., 2006; Tenjing, 2020). Characteristics of both species make them suitable model organisms for studying the influence of monsoon-driven changes in nearshore oceanographic variables on the recruitment dynamics of intertidal species.

We aimed to examine (1) the variation in recruitment of *C. malayensis* and *S. cucullata*, as well as environmental variables (salinity, temperature, and chlorophyll *a* concentration), at spatial (regional and local) and temporal (monthly) scales; (2) the variation in wind speed between regions; (3) the relationships between recruitment and environmental variables (salinity, temperature, chlorophyll *a* concentration, and wind velocity); and (4) the effect of onshore and offshore winds on the recruitment rates of both species. We hypothesized that strong onshore winds during the southwest monsoon will enhance recruitment as it promotes larval delivery to the shore.

Materials and methods

Study sites and sampling periods

The study was conducted at four semi-exposed rocky shores on the west coast of Thailand: Kalim and Surin in the northern region and Hat Sai Yao and Tan Yong Po in the southern region (Fig. 1). The intertidal zone of all four shores is dominated (> 50% cover) by *C. malayensis* in mid to high levels of the shores and *S. cucullata* on the lower level. The tidal range is approximately 2.5 m, and the tide is semi-diurnal at all locations. Sampling was done on large boulders or rock platforms. The main rock substrate in the northern region is granitic, whereas in the southern region, the rock is sedimentary. The number of recruits attached directly to the rock were assessed instead of using recruitment collection panels, which were frequently dislodged in previous studies. The slope at all sites is comparable, with an incline of ~ 10°–20°. Sampling was done at low spring tide from September 2019 to February 2020 and from June 2020 to September 2020. Sampling was suspended from March to May 2020 due to a lockdown during the COVID-19 pandemic. The sampling period covered the southwest monsoon (September to October 2019 and June to September 2020) and the northeast monsoon seasons (November 2019 to February 2020) (Cruz et al., 2013; Hsu et al., 2014).

Sampling for barnacle and oyster recruitment

The barnacle, *C. malayensis* recruits were counted monthly for a total of ten months from photographs of thirty (5 × 5 cm) quadrats randomly placed in the barnacle zone of each site. The coverage of adult barnacles in each quadrat was estimated visually and only the quadrats with 20–30% adult coverage were used. Barnacle recruits were distinguished from adults as having a rostral-carinal diameter of 0.5–1.0 mm (Buasakaew et al., 2021). The oyster, *S. cuccullata* recruits were counted on fifteen (30 × 30 cm) permanent plots marked randomly on the rock using stainless steel screws. The oyster coverage within a 30 × 30-cm area was visually inspected and only areas with around 30–40% oyster coverage were marked. Oyster recruits were counted as individuals in a photograph that were not in the photograph of the same plot taken the previous month; therefore, oyster recruits could be determined for eight out of the ten sampling months. Oyster recruits were defined as having shell length of 0.45 to 3 mm (Braley, 1982). The numbers of replicates for *C. malayensis* (30 quadrats) and *S. cuccullata* (15 plots) were determined from personal observations. These numbers gave the least within-group variance while remaining practical to manage. All photographs were taken with a digital camera (Nikon Coolpix W300).

Sampling for environmental parameters

Monthly data of wind velocity (wind direction in degrees and wind speed in knots) in the northern and southern regions were obtained from weather stations of the Thai Meteorological Department in Phuket and Satun Provinces, respectively. On each sampling occasion, the temperature (°C) of nearshore water was measured using a pH-EC-TDS Meter COM300 (HM Digital©) at the water surface 1–2 m seaward from the waterline. Salinity (‰) was measured using a hand-held refractometer. Three replicates of 600-ml water samples were taken at each location for chlorophyll *a* analysis. The water sample was filtered through a 47-mm GF/C filter with a vacuum. The filter was folded in half twice and placed in a plastic tube which was then wrapped in aluminum foil, labeled, and stored in a freezer at − 20 °C. Before fluorometric analysis was performed, 10 ml of 90% acetone was added to each tube, and the sample was placed in the refrigerator at 4 °C for 24 h. The pigments extracted were poured into a cuvette and absorbance was measured by spectrophotometer at 750, 664, 647, and 630 nm. The cuvette was emptied and rinsed with 90% acetone before each measurement. Concentrations of chlorophyll *a* were calculated following Jeffrey & Humphrey (1975).

Statistical analyses

To determine whether the number of barnacle (*C. malayensis*) and oyster (*S. cuccullata*) recruits, water salinity, temperature, and chlorophyll a concentration varied across the study sites and sampling times, we used separate three-way ANOVA with the factor region (fixed factor: 2 levels), month (a fixed factor: 8 or 10 levels), and shore (a random factor nested in region: 2 levels). To test for variation in wind speed between regions one-way ANOVAs were done separately for north-easterly offshore and south-westerly onshore winds. In these analyses, data of wind speed for the two shores within each region were pooled.

Generalized Linear Models (GLMs) were used to determine whether there were any relationships between barnacle and oyster recruitment and the environmental variables. For this analysis, the data from all sites and months were pooled separately for oysters and barnacles. In total, there were 40 recordings for barnacles (10 months × 4 shores) and 32 for oysters (8 months × 4 shores). The GLM model with the Poisson distribution and the link function, was fitted using five environmental variables, among which salinity, temperature, chlorophyll a, and wind velocity (offshore wind speeds were assigned in minus values) were numerical, while wind type (onshore or offshore) was categorical. GLM modeling was performed using the MASS package (Ripley et al., 2021). Numerical datasets were rescaled and checked for correlation using the Spearman correlation matrix. Any highly correlated $|r > 0.8|$ variables were removed. Base models were created using all data without any interactions. Significant reciprocal interactions (represented as the × symbol) and quadratic polynomial regression for all the variables were additionally added, as preliminary results indicated very low goodness of fit for the linear regression, until the final model was created. Outliers in the final models were removed using visual inspection of the diagnostic plots. The models were compared using Akaike's information criterion (AIC), where the model with the lowest value was selected as the final model. The final models were evaluated against the base models using fitted values and Pearson residuals. The final models were then checked for overfitting using k-fold cross-validation with the boot package (Canty & Ripley, 2021). Confidence intervals and variable importance of the final models were estimated using the caret package (Khun, 2017). It was assumed that positive relationships were indicators of favorable conditions for the production of larvae.

Moreover, to examine possible effect of wind type on recruitment, the recruitment rates of both species when winds were onshore were compared to the rates when winds were offshore. This was done by a one-way PERMANOVA (wind type as a fixed factor) using the Euclidean distance measure on the raw data. Statistical significance was tested using 999 permutations. As GLM result suggests that there was no significant correlation between environmental parameters; therefore, this analysis was performed based on the assumption that effect of wind type on recruitment was not influenced by other environmental variables.

ANOVA was performed in WinGmav 5. PERMANOVAs were based on 999 permutations of the data and were performed in PRIMER v7 add-on package PERMANOVA+. GLMs were conducted in R 4.1.2 (R Studio Team, 2020).

Results

Spatial and temporal variation in recruitment

Recruitment of *C. malayensis* and *S. cucculata* occurred throughout the study period. Recruitment of *C. malayensis* responded to the interacting effects of shore nested in region and sampling month, as well as the main effects of month and shore (Table 1). At Kalim, Surin, and Tan Yong Po, the peak of *C. malayensis* recruitment was observed in June 2020, whereas at Hat Sai Yao the peak was observed in July 2020 (Fig. 2A, SNK pairwise comparison, $P < 0.05$). Recruitment of *S. cuccullata* responded to the interaction between shore and month, as well as the main effect of shore (Table 1). Recruitment did not vary significantly between months, but the highest *S. cuccullata* recruitment rate was observed at the shore at Surin, with a peak in August 2020 (Fig. 2C, SNK pairwise comparison, $P < 0.05$).

Table 1 Results from a three-way ANOVA testing for the effect of region, month, and shore nested in region on the variations in recruitment of *Chthamalus malayensis*, *Saccostrea cuccullata*, and environmental parameters at each site

Source of variation	*C. malayensis* recruitment		*S. cuccullata* recruitment		Salinity		Temperature		Chlorophyll *a*	
Source	df	*P*	df	*P*	df	*P*	df	*P*	df	*P*
Region	1	0.81	1	0.82	1	0.07	1	0.27	1	< 0.05*
Month	9	< 0.001*	7	0.25	9	< 0.05*	9	< 0.001*	9	0.89
Shore (Re)	2	< 0.001*	2	< 0.001*	2	< 0.05*	2	< 0.001*	2	< 0.001*
Re × Mo	9	0.09	7	0.17	9	0.07	9	< 0.001*	9	0.68
Sh (Re) × Mo	18	< 0.001*	14	< 0.001*	18	< 0.001*	18	< 0.01*	18	< 0.001*
Res	1160		448		80		80		80	
Total	1199		479		119		119		119	

Asterisks indicated significant effects at $P \leq 0.05$

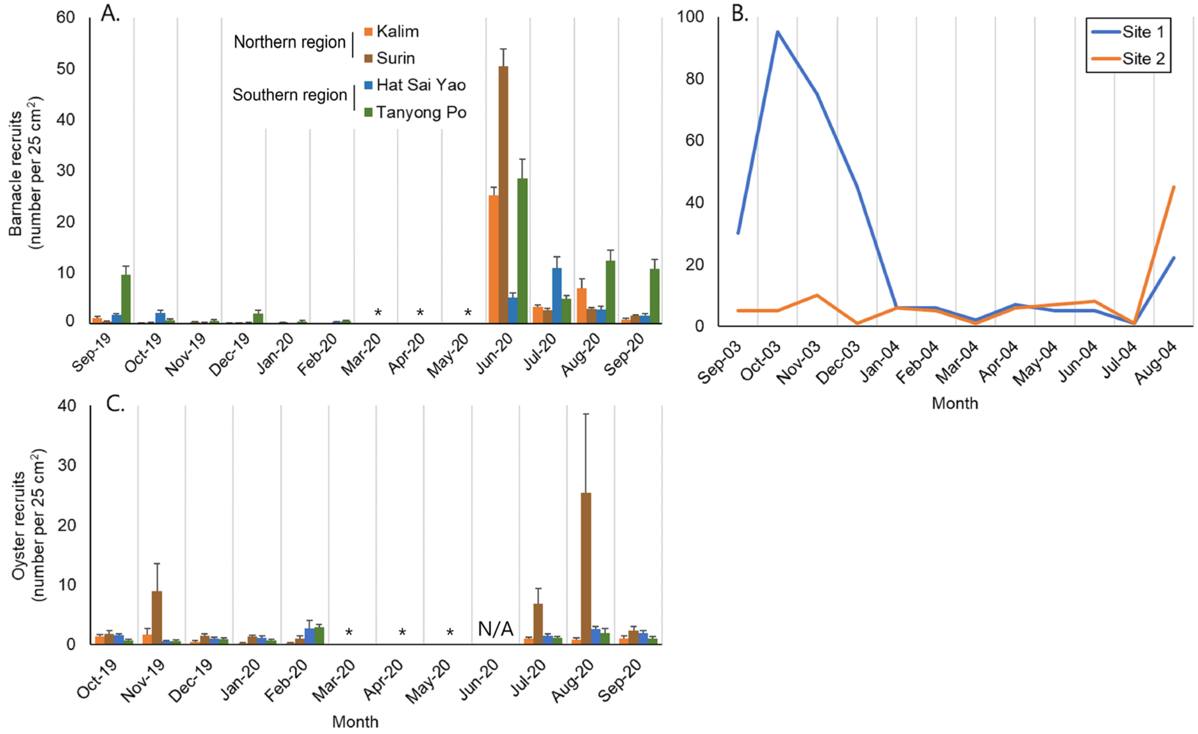

Fig. 2 Recruitment rate of **A** *Chthamalus malayensis* (Mean ± SE) on the west coast of Thailand; **B** *Chthamalus malayensis* (Mean) extracted from Lee et al. (2006) at two sites on the west coast of Malaysia; and **C** *Saccostrea cucullata* (Mean ± SE) on the west coast of Thailand. Data in **A** and **C** are from the recent study. The southwest monsoon season was from September to October 2019 and June to September 2020. The northeast monsoon season was from November to February 2020. In **A** and **C** during March to May 2020 (marked by an asterisk *), sampling was not permitted due to the COVID-19 pandemic; N/A = data were not available because field sampling was canceled in the previous month

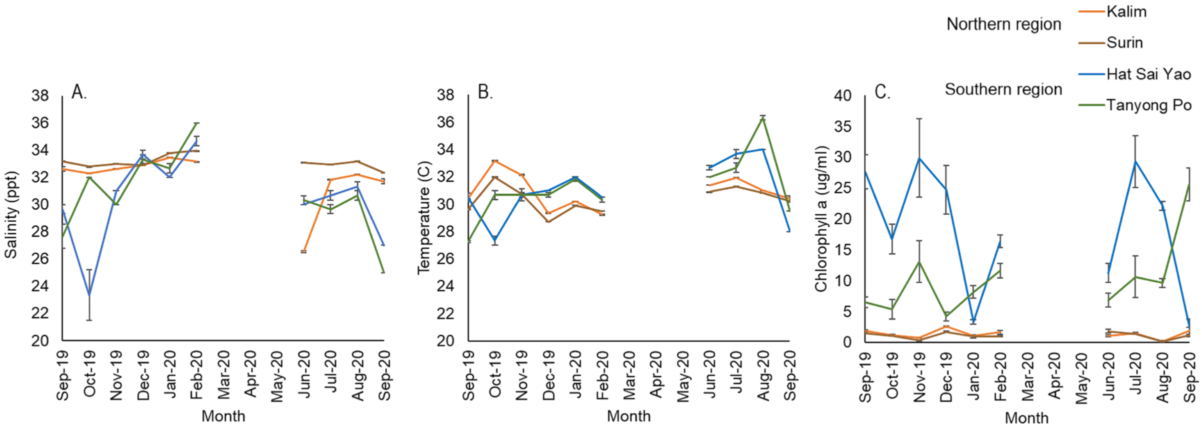

Fig. 3 Salinity, temperature, and chlorophyll *a* (Mean ± SE) of nearshore seawater measured during the study at four sites: Kalim and Surin (northern region) and Hat Sai Yao and Tan Yong Po (southern region). The southwest monsoon season was from September to October 2019 and June to September 2020. The northeast monsoon season was from November to February 2020. During March to May 2020, logistics were restricted due to the COVID-19 pandemic

Spatial and temporal variation in environmental variables

Salinity ranged from 25 to 36 ‰ (Fig. 3A). It responded to the interaction between shore and month, as well as the main effect of both factors (Table 1). The lowest salinity at each shore was observed either in September or October except at Kalim where the lowest salinity was recorded in June (2020) (Fig. 3A, SNK pairwise comparison, $P < 0.05$). The temperature of nearshore water ranged from 27 to 36.5 °C (Fig. 3B). It did not differ between regions but responded to the main effects of month and shore, and the interacting effects of region and month, as well as shore and month (Table 1). The highest nearshore water temperature was recorded at Tan Yong Po in August 2020 (Fig. 3B, SNK pairwise comparison, $P < 0.05$). Chlorophyll *a* concentration differed between regions and shores which is nested within regions (Table 1). It also responded to the interacting effects of shore and month (Table 1). Chlorophyll *a* concentration values were consistently higher in the southern region than the northern region throughout the study period (Fig. 3C). Overall, the chlorophyll *a* concentration on each shore fluctuated monthly with no obvious trend. A polar plot of monthly averages of wind direction and velocity suggested that the direction of south-westerly winds varied narrowly, whereas the direction of north-easterly winds was more widely distributed (Fig. 4). In the months when the winds were south-westerly, wind speed was greater in the northern region than the southern region ($F = 11.74$, $P < 0.01$; Fig. 4). No difference in wind speed was observed between regions when the winds were from the northeast ($F = 1.11$, $P = 0.33$; Fig. 4).

The relationship between recruitment and environmental variables.

C. malayensis

All five variables were used in the models, as the correlation between them was not significant (Table S1). The base model had an AIC of 10.882, while the final model had a much lower value of − 23.223. The final model was constructed using only 4 variables, with interactions and quadratic polynomial fitting (Eq. 1). The most important variable for the final model was Temp^2, with a score of 6.091719, followed by Sal^2, Chla × Sal^2, and Temp^2 × Windvel^2 (Table 2). To ensure that the final model was not overfitted, we performed an 18-fold cross-validation against the base model. The average of the final model estimates was 0.078 ± 0.028, while the average of the base model was 0.112 ± 0.085. Positive relationships were found between recruitment and Temp^2, as well as recruitment and Chla × Salinity^2. Meanwhile, relationships

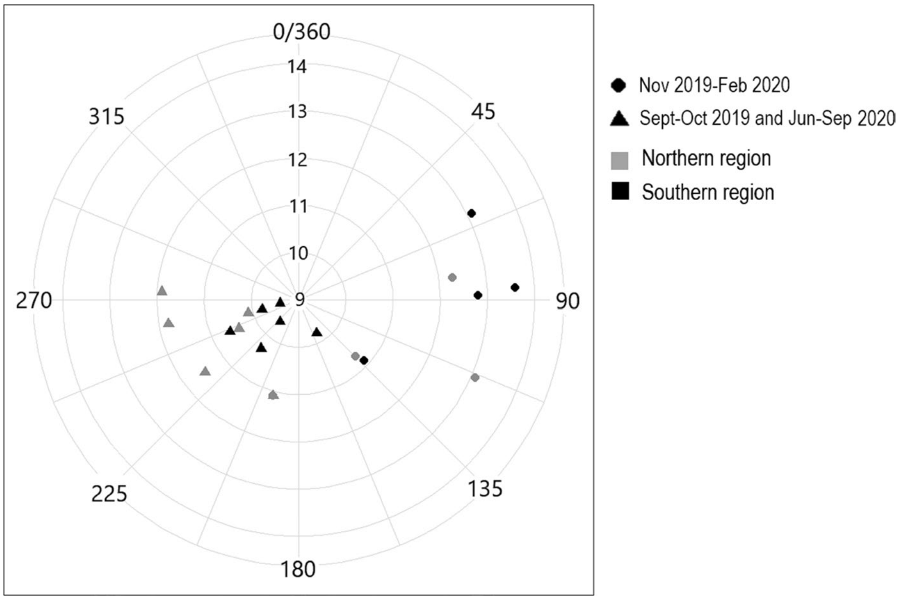

Fig. 4 Wind speed (monthly averages) as a function of wind direction. Black icons = southern region; gray icons = northern region. Months are grouped according to the monsoon season. November 2019–February 2020 were categorized as being in the northeast monsoon season. September–October 2019 and June–September 2020 were categorized as being in the southwest monsoon season

Table 2 Result from a GLM testing for the relationships between *C. malayensis* recruitment and environmental variables

Parameters	Estimate	Standard error	*P* value	95% CI	Variable importance
Intercept	− 0.36753725	0.06633620	9.268644e−06	− 0.497553815 to − 0.23752069	–
Sal	− 1.27039212	0.24699099	2.572320e−05	− 1.754485574 to − 0.78629867	5.143475
Temp	− 0.12681212	0.05226252	2.279316e−02	− 0.229244785 to − 0.02437946	2.426554
Chla	− 0.30225737	0.07652790	5.637965e−04	− 0.452249305 to − 0.15226544	3.949636
Sal^2	− 0.27375204	0.04646840	3.797975e−06	− 0.364828422 to − 0.18267565	5.891144
Temp^2	0.71324965	0.11708511	2.290902e−06	0.483767050 to 0.94273226	6.091719
Chla^2	0.09111430	0.04267107	4.272135e−02	0.007480548 to 0.17474805	2.135271
$\text{Temp}^2 \times \text{Windvel}^2$	− 0.84394112	0.15703170	1.419282e−05	− 1.151717597 to − 0.53616464	5.374336
$\text{Chla} \times \text{Sal}^2$	0.15671438	0.02727318	5.486655e−06	0.103259931 to 0.21016883	5.746099
$\text{Temp} \times \text{Chla}^2$	0.06947457	0.02038700	2.223257e−03	0.029516788 to 0.10943235	3.407788
$\text{Sal} \times \text{Windvel}^2$	1.05346019	0.21564454	5.017448e−05	0.630804660 to 1.47611573	4.885170

Estimated values, standard errors, *P* values, 95% confidence interval (CI), and variable importance for the parameters in the final model were shown

Sal salinity, *Temp* temperature, *Chla* Chlorophyll a concentration, *Windvel* wind velocity

between recruitment and Sal^2, as well as recruitment and $\text{Temp}^2 \times \text{Windvel}^2$ were negative (Table 2).

$$\begin{aligned}\text{Barnacle recruitment} = {} & \text{Sal} + \text{Temp} + \text{Chla} + \text{Sal}^2 \\ & + \text{Temp}^2 + \text{Chla}^2 + \text{Temp}^2 \times \text{Windvel}^2 \\ & + \text{Chla} \times \text{Sal}^2 + \text{Temp} \times \text{Chla}^2 \\ & + \text{Sal} \times \text{Windvel}^2. \end{aligned} \tag{1}$$

Sal salinity, *Temp* temperature, *Chla* Chlorophyll *a*, *Windvel* wind velocity.

S. cuccullata

The correlation between variables was not significant and all five variables were used in the models (Table S2). The base oyster model had an AIC of -20.479, while the final model had a value of 40.896. The final model was built using only 4 variables, with interactions and quadratic polynomial fitting (Eq. 2). The most important variable for the final model was Sal, with a score of 6.014706, followed by Temp^2, with a score of 4.342591. To ensure that the final model was not overfitted, we performed a 14-fold cross-validation against the base model. The average of the final model estimates was 0.017 ± 0.005, while the average for the base model was 0.031 ± 0.003. Relationships between recruitment and Sal and recruitment and Temp^2 were positive (Table 3).

$$\begin{aligned}\text{Oyster recruitment} = {} & \text{Sal} + \text{Temp} + \text{Chla} + \text{Windvel} + \text{Sal}^2 \\ & + \text{Temp}^2 + \text{Chla}^2 + \text{Windvel}^2 \\ & + \text{Temp} \times \text{Temp}^2 + \text{Temp} \times \text{Windvel}^2 \\ & + \text{Sal} \times \text{Windvel}. \end{aligned} \tag{2}$$

Sal salinity, *Temp* temperature, *Chla* Chlorophyll *a*, *Windvel* wind velocity.

Effect of wind type on recruitment rates

When samples were categorized according to the wind type (onshore vs offshore), recruitment of *C. malayensis* was significantly higher when the wind was westerly and onshore (Fig. 5A, Table 4). On the other hand, wind type did not significantly influence the recruitment of *S. cuccullata* (Table 4), although slightly higher numbers of recruits were observed during westerly and onshore winds (Fig. 5B).

Discussion

Variation in recruitment

Our study monitored the recruitment of two key space occupiers on intertidal rocky shores on the west coast of Thailand and evaluated their relationships with some environmental variables to investigate the mechanisms that might influence the recruitment.

Table 3 Result from a GLM testing for the relationships between *Saccostrea cuccullata* recruitment and environmental variables

Parameters	Estimate	Standard error	*P* value	95% CI	Variable importance
Intercept	− 0.1330979	0.13563169	$3.410423e^{-01}$	− 0.39893113 to 0.13273531	–
Sal	0.3128501	0.05201419	$1.801467e^{-05}$	0.21090415 to 0.41479604	6.014706
Temp	0.5594801	0.15071716	$1.893284e^{-03}$	0.26407994 to 0.85488035	3.712120
Chla	0.1267794	0.04513961	$1.261534e^{-02}$	0.03830738 to 0.21525140	2.808606
Winvel	0.1362573	0.05044255	$1.573210e^{-02}$	0.03739169 to 0.23512285	2.701237
Sal^2	0.1635798	0.04512343	$2.275002e^{-03}$	0.07513952 to 0.25202012	3.625163
$Temp^2$	0.1368572	0.03151510	$5.039243e^{-04}$	0.07508874 to 0.19862566	4.342591
$Chla^2$	− 0.0637192	0.02677940	$3.012741e^{-02}$	− 0.11620587 to − 0.01123254	2.379411
$Windvel^2$	− 0.1840946	0.13085787	$1.786053e^{-01}$	− 0.44057132 to 0.07238212	1.406829
Temp × $Temp^2$	− 0.0372753	0.01100655	$3.764742e^{-03}$	− 0.05884773 to − 0.01570287	3.386648
Temp × $Windvel^2$	− 0.5170995	0.14592379	$2.702651e^{-03}$	− 0.80310488 to − 0.23109414	3.543627
Sal × Windvel	0.2106597	0.07806272	$1.581745e^{-02}$	0.05765956 to 0.36365980	2.698595

Estimated values, standard errors, *P* values, and 95% confidence interval (CI) for the parameters in the final model were shown

Sal salinity, *Temp* temperature, *Chla* Chlorophyll a concentration, *Windvel* wind velocity

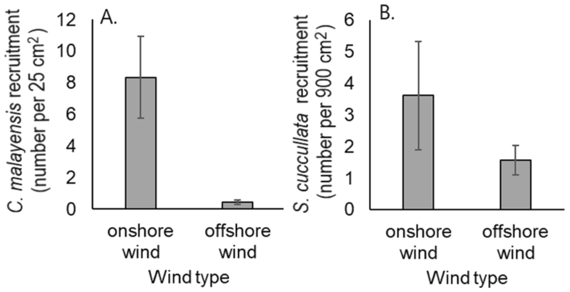

Fig. 5 Recruitment (Mean ± SE) of **A** *C. malayensis* (number of individuals. 25 cm^{-2}) and **B** *S. cuccullata* (number of individuals. 900 cm^{-2}) when winds were onshore and offshore

Table 4 Results from a univariate PERMANOVA testing for the effect of wind type on the variations in recruitment of *Chthamalus malayensis* and *Saccostrea cuccullata*

Source of variation	df	MS	Pseudo-*F*	*P* (perm)
C. malayensis				
Wind type	1	618.99	7.63	0.001*
Residual	38	81.10		
Total	39			
S. cuccullata				
Wind type	1	32.74	1.62	0.21
Residual	30	20.15		
Total	31			

Asterisks indicated significant effects at $P \leq 0.05$

The recruitment rate of *C. malayensis* and *S. cuccullata*, as well as salinity, temperature, and chlorophyll *a* varied between shores and month, while the effect of the main factor region was not observed for all variables except chlorophyll *a*. The wind speed differed between regions only when winds were southwesterly and blew onshore. The recruitment rate of *C. malayensis* showed positive correlations with temperature and the interaction between chlorophyll *a* and salinity; whereas it had negative correlation with salinity and the interaction between temperature and wind velocity. The recruitment rate of *S. cuccullata* exhibited positive correlations with all environmental variables. When comparing the recruitment rate when wind direction was onshore with the rate when it was offshore, recruitment of *C. malayensis* was greater when wind was onshore, while recruitment of *S. cuccullata* did not show such difference.

Barnacles on temperate and seasonal tropical shores usually show distinct seasonal reproductive patterns with a shorter reproductive period (Miyamoto et al., 1999; Jenkins et al., 2000; Chan & Williams, 2004), than tropical species, which breed throughout the year (Koh et al., 2005; Yan et al., 2006). In northern Europe, settlement of *Semibalanus balanoides* occurred in the spring and early summer with spatial variation in duration of the period of settlement (Jenkins et al., 2000). Chan and Williams (2004) found that the recruitment of *Tetraclita* *squamosa* and *T. japonica* on seasonal tropical shores of Hong Kong was very seasonal due to the seasonal development of the gonads. They observed pulse recruitment of local populations with some sparse recruitment which might be a result of settlement of larvae from other regions. The recruitment pattern of *C. malayensis* observed in the present study is similar to the pattern observed by a previous study conducted on the coast of the Malay Peninsula (Lee et al., 2006), in which recruitment occurred throughout the year with several peaks. However, the timing of the recruitment peaks was not the same in the two studies (Fig. 2B). At most of the sites on the west coast of Thailand, we recorded the highest recruitment rate in June 2020. This period is generally classified as the southwest monsoon season when the wind was blowing onshore from the southwest. (Cruz et al., 2013; Hsu et al., 2014). On the west coast of Malaysia (Lee et al., 2006), the highest recruitment rate was recorded in October and November, which they classified as the transitional period between monsoon seasons (Fig. 2B). The observed interaction between the effects of shore and month on barnacle recruitment implies that the important oceanographic processes that regulate monthly recruitment are influential at the scale of a few kilometers. The highly varied topography of this coastline is probably a factor in the highly localized nature of these influences. Local nearshore circulation patterns have been shown to influence the transport of barnacle larvae shoreward (e.g., Minchinton & Scheibling, 1991; Drouin et al., 2002). It is likely that different water masses arrive at each site, resulting in different larval concentrations being transported toward each particular shore. On the west Malaysian coast in the Strait of Malacca, brooding embryos were present throughout the year but hatching stage larvae were abundant around March and May (Koh et al. 2005). If the larval development of *C. malayensis* on the west coast of Thailand follows the same pattern, that is, hatching stage larvae are available during March to May, and larval period lasts ~ 20 days (Yan & Chan, 2001), the peak recruitment we observed in June might be a result of the availability of the competent larvae from local populations.

Reproduction in oysters can be continuous, semi-annual, or annual with variation in timing and duration of gonad development occurs both between and within species (Gosling, 2015; Nowland et al., 2019). Temperate oysters usually reproduce in summer when temperature is relatively high (Enríquez-Díaz et al., 2009; Lim et al., 2019; Legat et al., 2021). In tropical climate, duration of spawning is longer and at some locations spawning occur throughout the year (Nowland et al., 2019; Legat et al., 2021). Recruitment of *S. cuccullata* on the west coast of Thailand was low throughout the sampling period at all sites except Surin, where a peak in recruitment occurred in August 2020 when the south-westerly wind predominated. Although, there is a gap in the data from March to May 2020 due to the COVID lockdown, it is highly unlikely that recruitment peaked at these sites at this time since small-sized oysters were not observed on our plots either before or after the lockdown. In India, Tenjing (2020) found two major peaks of recruitment in April and September. In South Africa, Dye (1989, 1990) reported that a population of *S. cuccullata* was characterized by long periods of poor recruitment with shorter periods of good recruitment and the maintenance of the populations was determined by this period of unusually high recruitment. Since previous monitoring of another shore on the west coast of Thailand also found poor recruitment of *S. cuccullata* throughout the year without distinct peaks (personal observation), populations of *S. cuccullata* on the west coast of Thailand might exhibit a similar reproductive pattern to the South African population. Variation in recruitment at the shore scale was profound due to the presence of very high recruitment rate at Surin. In Guam (Braley, 1982), peaks of recruitment of *S. cuccullata* were observed in April and November on different shores ~ 1 km apart, suggesting a high variation at the local scale.

Although peaks of recruitment of both *C. malayensis* and *S. cuccullata* occurred during the southwest monsoon season, the highest recruitment of *S. cuccullata* occurred later in the season and with a smaller degree of synchrony among sites compared to *C. malayensis*. Recruitment of different taxa can be determined by different processes (Narváez et al., 2006; Mazzuco et al., 2015), as they may respond differently to environmental changes, such as sea surface temperature, salinity, and food supply (Narváez et al., 2006; Dudas et al., 2009). They might exhibit different larval behaviors (Mace & Morgan, 2006; Miller & Morgan, 2013) or have different planktonic larval durations (Sponaugle et al., 2002).

Variation in environmental variables

Variations in wind speed and chlorophyll *a* content in nearshore seawater at the regional scale observed in this study reflect differences in geography between the regions. The southern region displays more sheltered features and potentially receives lesser impacts from the ocean, such as weaker waves and weaker water currents, whereas the coast of the northern region has more oceanic, open-sea features. Chlorophyll *a* concentration was consistently higher in the south than the north throughout the study period. In the south, river runoff, which brings nutrients to coastal waters, and poor mixing might be responsible for the greater amount and higher variation of chlorophyll *a* observed in the southern region. Generally, salinity was more consistent in the northern region than the southern region, except in June 2020 at one shore. In the northern region, there are fewer rivers that open to the sea. The lowest salinity was recorded in the southern region during southwest monsoon months; probably due to heavy rainfall and high inputs of freshwater from large rivers during this time. The strong northward current that flows from the Strait of Malacca (Rizal et al., 2010) during the northeast monsoon months might result in the increase in salinity in the southern region observed in our study in January and February 2020. Temperatures varied monthly and locally but with no difference detected between regions. However, it was obvious that temperatures in the northern region decreased during the northeast monsoon months (December to February 2020). Buranapratheprat & Meesuk (2013) suggested that the north-easterly winds induce upwelling along the west coast of Thailand, lowering sea surface temperatures.

Relationships between recruitment and environmental variables

For broadcast spawners, larval production and the transport and delivery of competent larvae to shores are crucial processes that determine recruitment (Underwood & Fairweather, 1989). We hypothesized that a combination of environmental variables indicates favorable conditions for the production of larvae; and those onshore currents, driven by winds during the southwest monsoon season, enhance larval delivery to the shores. It is important to note that there may be a lag between changes in environmental conditions and specific responses of organisms (Mazzuco et al., 2015). Furthermore, as changes in reproductive traits are rather cumulative responses to environmental variations (Mazzuco et al., 2015), the recruitment model for each species was created from pooled datasets of sites and months and represents correlations along the whole coastline for all months.

The reproduction of chthamalid barnacles is generally influenced by temperature, photoperiod, salinity, and food supply (Barnes, 1989; O'Riordan, 1999). In our study, recruitment of *C. malayensis* exhibited a positive correlation with temperature, which is the most important predictor. The interaction between chlorophyll *a* concentration and salinity also showed a positive effect on recruitment. However, salinity alone and the interaction between temperature and wind velocity exhibited a negative effect. Although seasonality in temperature is not profound in the tropical climate of southern Thailand (ranging from 27.26 to 36.33 °C), the higher temperatures around June to September, during the southwest monsoon season, might enhance barnacle recruitment as high temperatures induce higher metabolic rates and therefore promote the development of gonads and larvae (Yan & Miao, 2004; Koh et al., 2005). In Hong Kong, higher rates of breeding activity, gonad maturation, and molting of *C. malayensis* were observed when the temperature increased (Yan & Miao, 2004) and some studies have reported a negative response of chthamalid reproduction to low salinity during monsoons (Fernando, 1999). Chan et al. (2001) also reported that low salinity may have a negative effect on some stages of the barnacle *Tetraclita* spp. life histories in Hong Kong. Although *C. malayensis* suffered higher mortality in low salinity (0‰) compared to high salinity (40‰) when exposed to thermal stress (Buasakaew et al., 2021), another study (Koh et al., 2005) found that the gonadal development of *C. malayensis* was not correlated with any change in rainfall or salinity in several locations. The peak of recruitment of *C. malayensis* in our study was in June 2020 when salinity ranged between 30 and 33‰ except at Kalim (average = 26.55‰). This range can be considered normal for these coastal waters and should not affect the survival of the larvae and recruits of *C. malayensis* (Yan, 2002). A common feature in tropical regions is an unpredictable food supply (Yan et al., 2006), but although food concentration enhances larval development in experimental settings, any direct links between the availability of food and reproductive parameters may be difficult to detect (Anil et al., 2001). In our study, when the recruitment of barnacles reached its peak in June 2020, chlorophyll *a* concentration in the southern region were low but the values rose rapidly in July 2020. Meanwhile, no effect of seasonality on chlorophyll *a* concentration was observed in the northern region.

Although the recruitment of *S. cucculata* showed positive correlations with all environmental variables in our study, the species showed consistently low recruitment throughout the study period, except on one shore. Braley (1982) found that *S. cucculata* in Guam reproduced continuously with site-specific peaks and that spawning lacked exogenous clues. However, high temperature and food supply generally support gametogenesis and larval development in oysters (Loor & Sonnenholzner, 2014; Nowland et al., 2019), while a rapid decline in salinity was reported to trigger spawning in *Saccostrea* spp. (Braley, 1982, 1984; Southgate & Lee, 1998). Local processes may be important in determining *S. cucculata* recruitment but our analysis of the data from the whole coastline was perhaps unable to find links between recruitment and environmental variables.

Although wind type did demonstrate an effect on recruitment in the recruitment models of *C. malayensis* and *S. cucculata*, the effects of wind type on recruitment rates were demonstrated as a direct effect in a separate analysis. The recruitment of *C. malayensis* was significantly greater when winds blew onshore. The results of the recruitment model for this species also suggested that wind velocity had an effect on the recruitment rate indirectly through the interaction with temperature and salinity. Onshore winds enhance settlements of intertidal species as larvae are delivered onshore by wind-driven surface currents (Bertness et al., 1996; Mazzuco et al., 2015). Onshore currents which are a result of south-westerly winds during the southwest monsoon (Rizal et al., 2012) might have carried larvae onshore, promoting the high recruitment for *C. malayensis*. Meanwhile, the north-easterly winds that blow during the northeast monsoon might transport larvae offshore similarly to upwelling systems (Pfaff et al., 2011). For *S. cucculata*, on the other hand, did not show any significant effect of wind type on recruitment, but the results of the recruitment model identified wind velocity as a predictor variable. To what extent wind-driven circulations influence recruitment of both species also depends on the production and survival of larvae. Seasonality in larval production might overshadow the importance of larval delivery to shores in this system. However, this possibility has yet to be tested.

Conclusion

This study is one of few research works conducted on southeast Asian shores that have aimed to demonstrate links between coastal marine population dynamics and monsoon-influenced oceanographic processes. The studied species were the acorn barnacle *Chthamalus malayensis* and the rock oyster *Saccostrea cucculata*. Our work suggests that the recruitment of *C. malayensis* on these shores is possibly determined by differential larval delivery regulated by wind-driven water currents. The interactions between the effects of temperature, salinity, and food supply could influence the recruitment of each species differently. Since the production and survival of larvae are important determinants of recruitment and such information are lacking for species on the west coast of Thailand, future research should investigate the effects of environmental variables and their interactions on gametogenesis and larval production to gain more understanding of the key drivers of recruitment variability on these shores.

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Data availability Data are available on reasonable request.

Declarations

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

Ethical approval This scientific research meets all the ethics and animal care regulations of Thailand.

Informed consent All authors have consented to participate in this paper and approve of the submission to Hydrobiologia.

References

Amnuaypon, P. & K. Wangkulangkul, 2018. Influence of habitat modification by rock oysters and barnacles on small-scale distribution of the tropical pulmonate limpet *Siphonaria guamensis*. Zoology and Ecology 28: 292–299.

Anil, A. C., D. Desai & L. Khandeparker, 2001. Larval development and metamorphosis in *Balanus amphitrite* Darwin (Cirripedia; Thoracica): significance of food concentration, temperature and nucleic acids. Journal of Experimental Marine Biology and Ecology 263: 125–141.

Barnes, M., 1989. Egg production in cirripedes. Oceanography and Marine Biology Annual Review 27: 91–166.

Bertness, M. D., S. D. Gaines & R. A. Wahle, 1996. Wind-driven settlement patterns in the acorn barnacle *Semibalanus balanoides*. Marine Ecology Progress Series 137: 103–110.

Bertness, M. D., S. D. Gaines & M. E. Hay, 2001. Marine Community Ecology, Sinauer Associates, Sunderland:

Braley, R. D., 1982. Reproductive periodicity in the indigenous oyster *Saccostrea cuccullata* in Sasa Bay, Apra Harbor, Guam. Marine Biology 69: 165–173.

Braley, R. D., 1984. Mariculture potential of introduced oysters *Saccostrea cuccullata tuberculata* and *Crassostrea echinata*, and a histological study of reproduction of *C. echinata*. Marine and Freshwater Research 35: 129–141.

Brewer, D., D. Hayes, V. Lyne, A. Donovan, T. Skewes, D. Milton & N. Murphy, 2015. An ecosystem characterisation of the Bay of Bengal. BOBLME-2015-Ecology-13, xvii + 287.

Buasakaew, N., B. K. K. Chan & K. Wangkulangkul, 2021. Why are barnacles common on intertidal rocks but rare in rock pools? Effect of water temperature, salinity and continuous submergence on barnacle survival in Indian Ocean rock pools. Frontiers in Marine Science 8: 1322.

Buranapratheprat, A. & A. Meesuk, 2013. Temporal variations of sea surface chlorophyll-a in the Andaman Sea based on aqua MODIS image processing. Burapha Science Journal 18: 194–201.

Canty, A. & B. D. Ripley, 2021. Boot: bootstrap R (S-Plus) function. R package version 1.3-2.8

Chan, B. K. K. & G. A. Williams, 2004. Population dynamics of the acorn barnacles, *Tetraclita squamosa* and *Tetraclita japonica* (Cirripedia: Balanomorpha), in Hong Kong. Marine Biology 146: 149–160.

Chan, B. K. K., D. Morritt & G. A. Williams, 2001. The effect of salinity and recruitment on the distribution of *Tetraclita squamosa* and *Tetraclita japonica (*Cirripedia; Balanomorpha) in Hong Kong. Marine Biology 138(5): 999–1009.

Chan, B. K. K., Y. F. Tsao, K. Wangkulangkul, K. Amjud & W. Sukparangsi, 2022. Biogeography and biodiversity of the intertidal barnacle *Tetraclita* species in the Gulf of Thailand and Andaman Sea – influences of oceanographic currents and Pleistocene glaciations. Frontiers in Marine Science 8: 2127.

Connolly, S. R., B. A. Menge & J. Roughgarden, 2001. A latitudinal gradient in recruitment of intertidal invertebrates in the northeast Pacific Ocean. Ecology 82: 1799–1813.

Cruz, F. T., G. T. Narisma, M. Q. Villafuerte, K. U. C. Chua & L. M. Olaguera, 2013. A climatological analysis of the southwest monsoon rainfall in the Philippines. Atmospheric Research 122: 609–616.

Drouin, C. A., E. Bourget & R. Tremblay, 2002. Larval transport processes of barnacle larvae in the vicinity of the interface between two genetically different populations of *Semibalanus balanoides*. Marine Ecology Progress Series 229: 165–172.

Dudas, S. E., B. A. Grantham, A. R. Kirincich, B. A. Menge, J. Lubchenco & J. A. Barth, 2009. Current reversals as determinants of intertidal recruitment on the central Oregon coast. ICES Journal of Marine Science 66(2): 396–407.

Enríquez-Díaz, M., S. Pouvreau, J. Chávez-Villalba & M. Le Pennec, 2009. Gametogenesis, reproductive investment, and spawning behavior of the Pacific giant oyster *Crassostrea gigas*: evidence of an environment-dependent strategy. Aquaculture International 17: 491–506.

Hsu, H. H., T. Zhou & J. Matsumoto, 2014. East Asian, Indochina and western North Pacific summer monsoon-an update. Asia-Pacific Journal of Atmospheric Sciences 50: 45–68.

Jeffrey, S. T. & G. F. Humphrey, 1975. New spectrophotometric equations for determining chlorophylls a, b, c_1 and c_2 in higher plants, algae and natural phytoplankton. Biochemie Und Physiologie Der Pflanzen 167(2): 191–194.

Jenkins, S. R., P. Åberg, G. Cervin, R. A. Coleman, J. Delany, P. Della Santina, S. J. Hawkins, E. LaCroix, A. A. Myers, M. Lindegarth, A. M. Power, M. F. Roberts & R. G. Hartnoll, 2000. Spatial and temporal variation in settlement and recruitment of the intertidal barnacle *Semibalanus balanoides* (L.) (Crustacea: Cirripedia) over a European scale. Journal of Experimental Marine Biology and Ecology 243(2): 209–225.

Khokiattiwong, S., 1991. Oceanographic variations in Phangnga Bay, Thailand under monsoonal effects. Phuket Marine Biological Center Research Bulletin 55: 43–76.

Khun, M., 2017. Caret: Classification and Regression Training. R package version 6.0-77. https://cran.r-project.org/package=caret

Koh, L. L., R. M. O'Riordan & W. J. Lee, 2005. Sex in the tropics: reproduction of *Chthamalus malayensis* Pilsbury (Class Cirripedia) at the equator. Marine Biology 147: 121–133.

Lagos, N. A., J. C. Castilla & B. R. Broitman, 2008. Spatial environmental correlates of intertidal recruitment: a test using barnacles in northern Chile. Ecological Monographs 78: 245–261.

Lee, W. J., R. M. O'Riordan & L. L. Koh, 2006. Spatial and temporal patterns in the recruitment of the intertidal barnacle *Chthamalus malayensis* Pilsbry (Crustacea: Cirripedia) on the equatorial shores of peninsular Malaysia and Singapore. Journal of Experimental Marine Biology and Ecology 333: 296–305.

Legat, J. F. A., A. Puchnick-Legat, S. Sühnel, A. L. M. Pereira, A. R. M. Magalhães & C. M. R. de Melo, 2021. Reproductive cycle of the mangrove oyster, *Crassostrea gasar* (Adanson, 1757), in tropical and temperate climates. Aquaculture Research 52(3): 991–1000.

Leslie, H. M., E. N. Breck, F. Chan, J. Lubchenco & B. A. Menge, 2005. Barnacle reproductive hotspots linked to nearshore ocean conditions. Proceedings of the National Academy of Sciences 102: 10534–10539.

Lim, N. L., H. M. Lee, H. D. Jeung, R. G. Noseworthy, S. Jung & K. S. Choi, 2019. Early larval development and annual gametogenesis of the brooding oyster *Ostrea circumpicta* (Pilsbry, 1904) in the shallow subtidal benthic ecosystem in Jeju Island, off the south coast of Korea. Zoological Studies 58: 29.

Liu, K. K., S. Y. Chao, P. T. Shaw, G. C. Gong, C. C. Chen & T. Y. Tang, 2002. Monsoon-forced chlorophyll distribution and primary production in the South China Sea: observations and a numerical study. Deep Sea Research Part I: Oceanographic Research Papers 49: 1387–1412.

Loor, A. & S. Sonnenholzner, 2014. Reproductive cycle of the rock oyster, *Striostrea prismatica* (Gray, 1825) from two locations on the southern coast of Ecuador. Aquaculture Research 47: 1432–1414.

Mace, A. J. & S. G. Morgan, 2006. Biological and physical coupling in the lee of a small headland: contrasting transport mechanisms for crab larvae in an upwelling region. Marine Ecology Progress Series 324: 185–196.

Mazzuco, A. C. D. A., R. A. Christofoletti, J. Pineda, V. R. Starczak & A. M. Ciotti, 2015. Temporal variation in intertidal community recruitment and its relationships to physical forcings, chlorophyll-a concentration and sea surface temperature. Marine Biology 162: 1705–1725.

Miller, S. H. & S. G. Morgan, 2013. Interspecific differences in depth preference: regulation of larval transport in an upwelling system. Marine Ecology Progress Series 476: 301–306. https://doi.org/10.3354/meps10150.

Minchinton, T. E. & R. E. Scheibling, 1991. The influence of larval supply and settlement on the population structure of barnacles. Ecology 72: 1867–1879.

Miyamoto, Y., T. Noda & S. Nakao, 1999. Zonation of two barnacle species not determined by competition. Journal of the Marine Biological Association of the United Kingdom 79(4): 621–628.

Narváez, D. A., S. A. Navarrete, J. Largier & C. A. Vargas, 2006. Onshore advection of warm water, larval invertebrate settlement, and relaxation of upwelling off central Chile. Marine Ecology Progress Series 309: 159–173.

Neo, M. L., P. L. Erftemeijer, J. K. van Beek, D. S. van Maren, S. L. Teo & P. A. Todd, 2013. Recruitment constraints in Singapore's fluted giant clam (*Tridacna squamosa*) population – a dispersal model approach. PLoS One 8: e58819.

Nowland, S. J., W. A. O'Connor, S. S. Penny & P. C. Southgate, 2019. Monsoonally driven reproduction in the tropical black-lip rock oyster *Saccostrea echinata* (Quoy & Gaimard, 1835) in northern Australia. Journal of Shellfish Research 38: 89–100.

O'Riordan, R. M., 1999. Reproductive ecology of Chthamalid barnacles. In Thompson, M. F. & R. Nagabhushanam (eds), Barnacles: The Biofoulers Regency, New Delhi: 21–50.

Pfaff, M. C., G. M. Branch, E. A. Wieters, R. A. Branch & B. R. Broitman, 2011. Upwelling intensity and wave exposure determine recruitment of intertidal mussels and barnacles in the southern Benguela upwelling region. Marine Ecology Progress Series 425: 141–152.

Pongparadon, S., G. C. Zuccarello, S.-M. Phang, H. Kawai, T. Hanyuda & A. Prathep, 2015. Diversity of *Halimeda* (Chlorophyta) from the Thai-Malay peninsula. Phycologia 54: 349–366.

Ripley, B., B. Venables, D. M. Bates, K. Hornik, A. Gebhardt & D. Firth, 2021. Package 'MASS'. http://www.stats.ox.ac.uk/pub/MASS4/

Rizal, S., I. Setiawan, T. Iskandar, Y. Ilhamsyah, M. A. Wahid & M. Musman, 2010. Currents simulation in the Malacca Straits by using three-dimensional numerical model. Sains Malaysiana 39: 519–524.

Rizal, S., P. Damm, M. A. Wahid, J. Sündermann, Y. Ilhamsyah & T. Iskandar, 2012. General circulation in the Malacca Strait and Andaman Sea: a numerical model study. American Journal of Environmental Sciences 8: 479–488.

Roughgarden, J., Y. Iwasa & C. Baxter, 1985. Demographic theory for an open marine population with space-limited recruitment. Ecology 66: 54–67.

RStudio Team, 2015. R Studio: Integrated Development for R. [Computer software]. http://www.rstudio.com

Ruwa, R. K. & P. Polk, 1994. Patterns of spat settlement recorded for the tropical oyster *Crassostrea cuccullata* (Born, 1778) and the barnacle, *Balanus amphitrite* (Darwin 1854) in a Mangrove Creek. Tropical Zoology 7: 121–130.

Southgate, P. C. & P. S. Lee, 1998. Hatchery rearing of the tropical black-lip oyster *Saccostrea echinata* (Quoy and Gaimard). Aquaculture 169: 275–281.

Sponaugle, S., R. K. Cowen, A. Shank, S. G. Morgan, J. M. Leis, J. Pineda, G. W. Boehlert, M. J. Kingford, K. C. Lindeman, C. Grimes & J. L. Munro, 2002. Predicting self-recruitment in marine populations: biophysical correlates and mechanisms. Bulletin of Marine Science 70: 341–375.

Tenjing, S. Y., 2020. Population dynamics of the edible rock oyster *Saccostrea cucullata* (Born, 1778) along the south-west coast of India. Indian Journal of Fisheries 67: 16–22.

Tsang, L. M., T. H. Wu, H. T. Shih, G. A. Williams, K. H. Chu & B. K. K. Chan, 2012. Genetic and morphological differentiation of the Indo-West Pacific intertidal barnacle *Chthamalus malayensis*. Integrative and Comparative Biology 52: 388–409.

Underwood, A. J. & P. G. Fairweather, 1989. Supply-side ecology and benthic marine assemblages. Trends in Ecology and Evolution 4: 16–20.

Wangkulangkul, K. & R. Promdam, 2018. Spatial variability in the composition of macrofauna on intertidal rocky shores along the coast of the Andaman Sea and the Gulf of Thailand, southern Thailand. Plankton and Benthos Research 13: 154–162.

Yan, Y., 2002. The ecology of the high shore barnacle: *Chthamalus malayensis* in Hong Kong. PhD Thesis. The University of Hong Kong.

Yan, Y. & B. K. K. Chan, 2001. Larval development of *Chthamalus malayensis* (Cirripedia: Thoracica) reared in the laboratory. Journal of the Marine Biological Association of the United Kingdom 81(4): 623–632.

Yan, Y. & S. Miao, 2004. The effect of temperature on the reproductive cycle of the tropical barnacle, *Chthamalus malayensis* Pilsbry (Cirripedia). Crustaceana 77: 205–212.

Yan, Y., B. K. K. Chan & G. A. Williams, 2006. Reproductive development of the barnacle *Chthamalus malayensis* in Hong Kong: implications for the life-history patterns of barnacles on seasonal, tropical shores. Marine Biology 148: 875–887.