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research paper

Temporal and spatial patterns of abundance and occurrence of planktonic shrimps in the Songkhla Lagoon System, southern Thailand

V Lheknim *
R Yolanda

Department of Biology, Faculty of Science, Prince of Songkla University, PO Box 3 Ko Hong, Songkhla 90112, Thailand

** Corresponding author email: <vachira.l@psu.ac.th>*

ABSTRACT.—Temporal and spatial distributions of planktonic shrimps from the hyperbenthos of Thale Sap and Thale Sap Songkhla lakes in the Songkhla Lagoon system, southern Thailand, were investigated using modified Riley push nets with a mesh size of 0.5 mm between June 2017 and June 2018. Three species of Mysida and two species of Dendrobranchiata shrimps were revealed, among which *Nanomysis siamensis* was dominant, representing more than 90% of the catch throughout the year. The Songkhla Lagoon system experiences extreme changes in temperature, salinity, pH, and water levels due to seasonal monsoons. A significant difference in the planktonic shrimp assemblages between Thale Sap and Thale Sap Songkhla was observed across the sampling months. Significant differences in the assemblage structure were also evident between Thale Sap and Thale Sap Songkhla and among sampling months. Dissimilar assemblage patterns were prominent temporally during the shift from southwest to northeast monsoon seasons and from the intermediate to southwest monsoon. Lake (Thale Sap or Thale Sap Songkhla) was the most important environmental parameter affecting occurrence patterns for *N. siamensis, Mesopodopsis tenuipes*, and *Belzebub hanseni* in the Songkhla Lagoon system. Salinity governed the spatial distribution of *M. tenuipes* and *B. hanseni*. *Nanomysis siamensis* was the only species that was regularly present in high abundance in Thale Sap and Thale Sap Songkhla over the entire salinity range. This suggest that *N. siamensis* is likely a resident species of the Songkhla Lagoon system.

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Planktonic shrimps belonging to Mysidacea, Sergestidae, and Luciferidae are zooplankton that serve as a source of food for humans (Omori 1978) and play a vital role in food webs by transferring and recycling organic material and nutrients. They feed on detritus, phytoplankton, and small zooplankton and are consumed by larger crustaceans, fishes, birds, and other species at higher trophic levels (Omori 1975, 1978, Mauchline 1980, Xiao and Greenwood 1993, Mees and Jones 1997).

A large number of planktonic shrimps were observed and collected while studying variability in the recruitment abundance of *Metapenaeus* spp. in the hyperbenthos of Thale Sap and Thale Sap Songkhla lakes in the Songkhla Lagoon system of southern Thailand. Many factors can influence the abundance of these shrimps, for example, their spawning season, migrations and movements, predation, aquatic productivity, and the favorability of, and fluctuations in, hydrographic parameters. However, information on the biology and ecology of tropical, shallow-water planktonic shrimps is limited compared to subarctic and temperate species (e.g., Mauchline 1980, Fenton 1994, Yamada et al. 2007), and little is known about these species in Thailand, let alone in the Songkhla Lagoon. Tattersall (1921) provided the earliest report of mysids in this system, identifying *Rhopalophthalmus egregius* Hansen, 1910 and *Nanomysis siamensis* Tattersall, 1921, but there have been no subsequent studies on these species and no published reports of Luciferidae from the coastal waters of Thailand since Omori (1978).

Lake Songkhla is a large, shallow, well-oxygenated tropical coastal lagoon system. Water circulation and residence times in the lagoon are regulated by water levels, currents, tides, geomorphology, and freshwater inputs which can lead to marked spatial salinity gradients (Kjerfve 1994). Along the shores of the lagoon are a mix of urban settlements, fishing villages, shrimp ponds, seasonally flooded forests, rice paddy fields, and mangroves. Anthropogenic pressures associated with urbanization, industrialization, artisanal fishing, and pollution are strong. Biological studies of the Songkhla Lagoon over the last two decades have been fragmented, focusing primarily on the taxonomy and biology of a few economically important species (Sa-nguansil and Lheknim 2010, Sakai and Lheknim 2014, Rattanama et al. 2016, Hue et al. 2018).

The aim of the present study was to examine the abundance patterns of planktonic shrimps in relation to environmental conditions in two lakes in the Songkhla Lagoon system: Thale Sap and Thale Sap Songkhla. The specific objectives were to determine: (1) spatiotemporal changes in planktonic shrimp abundance over the course of a year; and (2) the influence of environmental factors on planktonic shrimp occurrence in the lagoon.

Methods

Study Sites.—The Songkhla Lagoon system (Fig. 1) is situated 7°08´N–7°48´N and 100°07´E–100°35´E on the east coast of the Thai Peninsula and covers approximately 1082 km^2. It consists of four distinct lakes (Thale Noi, Thale Luang, Thale Sap, and Thale Sap Songkhla), with the southern end connected to the Gulf of Thailand. These lakes exhibit three different water regimes (fresh, brackish, salt water) with the salinity ranging from almost zero in Thale Noi to 0–34 in Thale Sap Songkhla. This region has a tropical monsoon climate, with two monsoons per year: the northeast monsoon from October to January and the southwest monsoon from May to September. It also has an intermediate period between February and March (Evenson 1983). More than 60% of the average annual rainfall of 2000 mm falls during the peak period of the northeast monsoon, from October to January, with December usually being the wettest month and February to April being the driest (DANCED and MOSTE 1998).

The present study was carried out in Thale Sap Songkhla and Thale Sap (Fig. 1). In both lakes, the average water depth is approximately 1.0–1.5 m, with a maximum depth of about 2.5 m in the basin and 7.0–14.0 m in the channel. At the peak of the

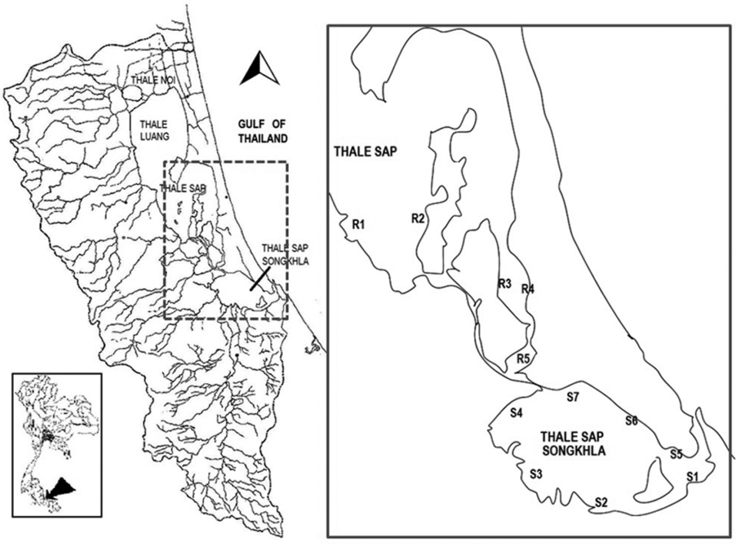

Figure 1. Map of Songkhla Lagoon system in southern Thailand, with location of Thale Sap and Thale Sap Songkhla and sampling stations R1–R5 in Thale Sap and S1–S7 in Thale Sap Songkhla.

northeast monsoon season, the average depth increases to 2.5 m in Thale Sap and remains at this level before declining to approximately 1.5 m within two months (NESDB and NEB 1988, Kuwabara 1995, DANCED and MOSTE 1998). The average tidal range at the mouth of Thale Sap Songkhla is approximately 0.5 m, with a maximum of 1.3 m, compared to only 0.03–0.10 m in Thale Sap. Tidal currents have negligible effects on physical conditions in the Songkhla Lagoon system, which is classified as a microtidal estuary (DANCED and MOSTE 1998).

The coastline vegetation at Thale Sap Songkhla is primarily a thin belt of scattered, fringing mangroves consisting of *Sonneratia caseolaris*, *Rhizophora apiculata*, *Bruguiera cylindrica*, *Nypa fruticans*, *Lumnitzera racemosa*, and *Excoecaria agallocha*. The shoreline vegetation at Thale Sap comprises mostly *S. caseolaris, Hibiscus tiliaceus*, and *Melaleuca cajuputi.* The submerged vegetation in Thale Sap is dominated by *Najas marina*, *Najas minor*, *Hydrilla verticillata*, and *Potamogeton malayanus*, whereas that in Thale Sap Songkhla has few macrophytes, with *Gracilaria tenuistipitata* and the seagrasses *Halodule pinifolia*, *Halophila beccarii*, and *Halophila ovalis* observed in some areas (Angsupanich 1996). The substratum in both lakes is mud.

Sampling Methods.—Sampling was carried out monthly from June 2017 to June 2018 at five stations in Thale Sap (R1–R5) and seven stations in Thale Sap Songkhla (S1–S7; Fig. 1), with two replicate sites at each station. No sampling was undertaken in December 2017 due to technical difficulties associated with seasonal flooding. Sampling was conducted during the day using a modified Riley's push net equipped with double nets (square, conical nets 0.45 m wide × 0.30 m high × 2 m long, with 2.0- and 0.5-mm mesh). The push net was operated by two people along a 30-m transect with three independent replicate horizontal hauls at each site. Sampling each month was completed within two consecutive days. All aquatic fauna in each net was immediately placed in separate plastic containers with distinguishing labels and fixed in 10% buffered formaldehyde with 2% rose bengal before being transported to the laboratory at Prince of Songkla University.

Environmental data were collected from each site on each sampling date. Water depth and transparency measurements (using sounding lines and Secchi disks) were obtained directly on site. Water temperature (°C), salinity (AZ 8371 Portable LCD Digital Salinity Meter), and pH (AD11 digital pH/temperature meter) were measured at a depth of 0.5 m at each site. Bed sediment representing recent deposits was collected by scooping the upper 5 cm of the sediment with a plastic spade at 50–150 cm water depth. The sediments were packed and sealed in plastic containers and transferred to a laboratory, where they were air-dried in an oven at 60 °C. Sediment samples were passed through a 0.0625-mm standard mesh sieve to separate silt and clay from the sand fractions. Total carbon and total nitrogen concentrations in the sediment samples from each replicate were determined by combustion of the dried and processed surface sediments in a CHN analyzer.

Data Collection.—Each aquatic fauna sample was sorted and identified in the laboratory to the lowest possible taxonomic unit under a stereomicroscope according to net mesh size, replicate number, sampling site, station, and location of the lake within the lagoon. Planktonic shrimps were the focus of the present study. Mysida were tentatively identified to the genus level following Mauchline (1980) and then to the species level following Tattersall (1921), Hanamura et al. (2008a), and Hanamura et al. (2011). Sergestidae were identified according to Omori (1975) and Luciferidae were identified following Naomi et al. (2006) and Vereshchaka et al. (2016).

After identification, individual counts were obtained for each species of large planktonic crustacean per haul. Planktonic shrimp abundance at each site was calculated as the number of individuals per 100 m^2 by dividing the mean individual catch per haul by the mean area covered by each push net haul, which was estimated from the distance covered (30 m $haul^{-1}$) and the width of the mouth opening of each net.

Data Analysis.—The difference in planktonic shrimp abundance was substantial between the 2.0- and 0.5-mm mesh nets in Thale Sap and Thale Sap Songkhla. The relatively lower catches associated with the 2.0-mm mesh nets were omitted from this study. Data from 0.5-mm mesh catches (June 2017 to June 2018) were analyzed for planktonic shrimp community composition differences between Thale Sap and Thale Sap Songkhla and among sampling months using a two-way permutational, multivariate analysis of variance (PERMANOVA). The independent variables were month and lake as main effects and interaction month × lake for all species combined. Abundance data (ind 100 m^{-2}) for all species in each trip were rank transformed prior to analysis to reduce the bias of highly abundant species (Conover 2012). Each factor was further investigated by one-way PERMANOVA for within-group pairwise comparisons. All procedures used Bray–Curtis dissimilarities metrics commonly employed to quantify the dissimilarity in composition between samples (Bray and Curtis 1957). Similarity Percentage (SIMPER) analysis was also applied to calculate the average contribution of each taxon to the overall Bray–Curtis dissimilarity in community composition for each lake. These procedures were used to evaluate variation in the relative abundance of planktonic shrimp taxa. Subsequently, two-way analysis of variance (ANOVA) was employed to analyze the effect of sampling month and lake on the rank-transformed abundance of each species. All multivariate statistical analyses were performed using PAST 3.24 software (Hammer et al. 2001).

To determine which environmental variables (depth, salinity, temperature, pH, percentage of silt, organic carbon) contributed to differences in planktonic shrimp occurrence, the present study applied logistic regression. The abundance proportion of each species within each sampling site of each trip was the dependent variable. A general form of the fitted Generalized Additive Models (GAMs) in the present study was as follows:

$$\eta = f(\text{lake}) + s(\text{depth}) + s(\text{salinity}) + s(\text{temperature}) + s(\text{pH}) + s(\text{percentage of silt}) + s(\text{organic carbon}),$$

where η is the predicted abundance proportion, $f()$ indicates factor descriptors, and $s()$ indicates numerical descriptors processed with smoothing splines. A stepwise regression for each planktonic shrimp species abundance proportion was applied with the environmental variables as independent factors. Iteration stopped when the absolute change in the probability of deviance between iterations was less than 0.05. Somers'D and discrimination ability "C" values of the final model were reported. All stepwise logistic regressions were performed using Statistix 10.0 (Analytical Software 2017).

Results

Environmental Measurements.—From June 2017 to June 2018, water temperature at the study sites varied between 26.0 and 33.0 °C (Table 1). The temperature in Thale Sap was close to that of Thale Sap Songkhla. Seasonal trends were evident during a period of high rainfall in January 2018, when the temperature dropped below that recorded in any other month. The mean (SE) temperature was 30.06 °C (0.10) in Thale Sap and 29.42 °C (0.12) in Thale Sap Songkhla. Across all stations and surveys, salinity varied between 0 and 29.2, with a clear seasonal trend (Fig. 2A). The overall mean (SE) salinity in Thale Sap Songkhla was 7.67 (0.44) and 3.20 (0.24) in Thale Sap in all months except between November 2017 and January 2018 (Fig. 2B). The pH varied between 6.1 and 10.3 across all sampling sites and periods (Table 1, Fig. 2C). Values of 6.4–10.3 and 6.1–9.6 were observed in Thale Sap and Thale Sap Songkhla, respectively, between June 2017 and January 2018. Sampling depth varied between 40 and 150 cm (Table 1). The water levels were recorded in July 2017 in both Thale Sap and Thale Sap Songkhla (Fig. 2D). Following an increase in water depth associated with the rainy season, the highest levels were recorded between November 2017 and January 2018. At the end of the northeast monsoon (January 2018), lake levels gradually decreased. The composition of silt in the lake sediment varied between 43.89% and 91.87% (Fig. 2E). Organic carbon in sediment varied between 341.67 and 5041.70 μmol g^{-1}. Organic carbon levels from 626.09 to 5041.70 μmol g^{-1} and from 341.67 to 2713.20 μmol g^{-1} were recorded in Thale Sap and Thale Sap Songkhla sediment, respectively (Table 1, Fig. 2F).

Planktonic Shrimps.—Planktonic shrimps collected from Thale Sap and Thale Sap Songkhla consisted of juvenile and adult members of Mysida and

Table 1. Mean (SE) and minimum–maximum record of water depth (cm), salinity, pH, temperature (°C), percent of silt in sediment, and organic carbon (µmol g^{-1}) in sediment from Thale Sap, Thale Sap Songkhla, and overall in the Songkhla Lagoon system between June 2017 and June 2018.

Species	Thale Sap			Thale Sap Songkhla			Pooled data **		
	N	Mean (SE)	Min–Max	*N*	Mean (SE)	Min–Max	*N*	Mean (SE)	Min–Max
Depth (cm)	119	120.42 (2.16)	60.00–150.00	162	120.10 (2.16)	40.00–150.00	281	109.86 (1.63)	40.00–150.00
Salinity	119	3.20 (0.35)	0.00–16.40	162	7.67 (0.63)	0.00–29.20	281	5.78 (0.41)	0.00–29.20
pH *	119	8.96	6.40–10.30	162	8.22	6.10–9.60	281	8.68	6.10–10.30
Temp (°C)	110	30.06 (0.15)	26.00–33.00	154	29.42 (0.12)	26.10–32.80	264	29.69 (0.09)	26.00–33.00
Percent silt	104	71.47 (0.84)	51.77–88.13	146	72.42 (0.73)	43.89–91.87	250	72.02 (0.55)	43.89–91.87
Organic carbon (µmol g^{-1})	120	1,769.60 (78.19)	606.09–4,265.20	167	1,279.00 (52.57)	341.67–5,041.70	287	1,484.10 (46.92)	341.67–5,041.70

* Mean of pH was calculated based on average Hydrogen ion, min–max were based on direct reading from pH meter.
** Pooled data for each parameter was calculated for average base on original data collected from Thale Sap and Thale Sap Songkhla.

Table 2. Mean (SE) and minimum–maximum individual number (ind 100 m^{-2}) of *Nanomysis siamensis*, *Mesopodopsis tenuipes*, *Rhopalophthalmus hastatus*, *Acetes indicus*, and *Belzebub hanseni* from 0.5-mm mesh net taken from Thale Sap, Thale Sap Songkhla, and pooled data in the Songkhla Lagoon system between June 2017 and June 2018.

Species	Thale Sap			Thale Sap Songkhla			Pooled data		
	N	Mean (SE)	Min–Max	*N*	Mean (SE)	Min–Max	*N*	Mean (SE)	Min–Max
Nanomysis siamensis	120	7,228.6 (1,211.7)	0–106,624.0	168	3,266.5 (985.8)	0–157,159.0	288	4,917.4 (772.5)	0–157,159.0
Mesopodopsis tenuipes	120	1.2 (1.1)	0–111.1	168	134.7 (30.1)	0–3,748.5	288	79.1 (17.9)	0–3,748.5
Rhopalophthalmus hastatus	120	5.1 (2.3)	0–194.4	168	61.0 (40.3)	0–6,691.8	288	37.7 (23.6)	0–6,691.8
Acetes indicus	120	13.9 (4.9)	0–388.7	168	166.6 (43.2)	0–4,414.9	288	103.0 (25.6)	0–4,414.9
Belzebub hanseni	120	144.6 (62.7)	0–6,330.8	168	1,372.8 (609.7)	0–99,127.0	288	861.1 (358.0)	0–99,127.0

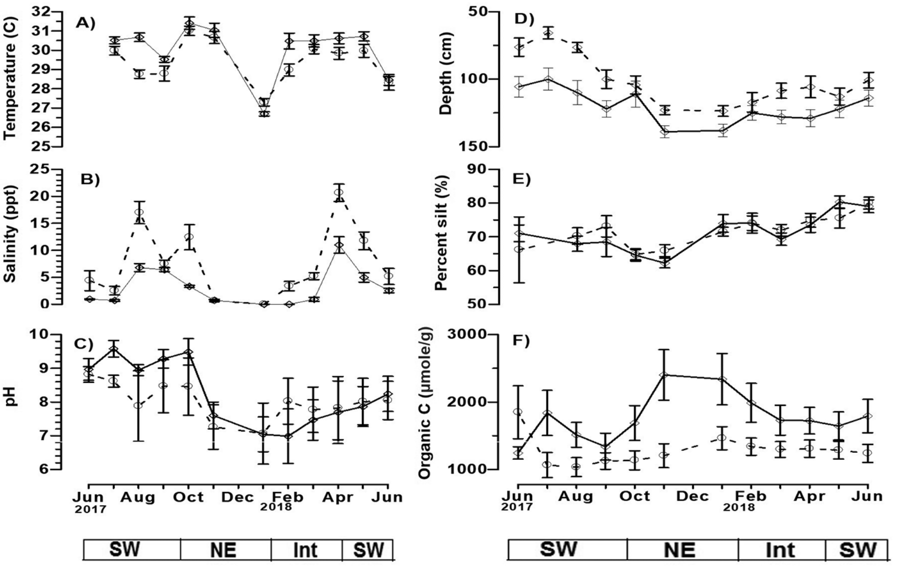

Figure 2. Mean (SE) of selected environmental variables in Thale Sap (solid line) and Thale Sap Songkhla (dashed line) of Songkhla Lagoon system in southern Thailand during the sampling period between June 2017 and June 2018. (A) Temperature (°C), (B) salinity, (C) pH, (D) depth (cm), (E) percentage of silt in sediment (%), and (F) organic carbon in sediment (μmol g^{-1}) . SW: southwest monsoon, NE: northeast monsoon, Int: intermediate period.

Dendrobranchiata. At least three species of Mysida were identified, *N. siamensis* W. Tattersall, 1921, *Mesopodopsis tenuipes* Hanamura, Koizumi, and Sawamoto, 2008 and *Rhopalophthalmus hastatus* Hanamura, Murano, and Alias, 2011. Two species of Dendrobranchiata shrimps were identified, *Acetes indicus* H. Milne-Edwards, 1830 (Sergestidae) and *Belzebub hanseni* (Nobili, 1905) (Luciferidae; previously known as *Lucifer hanseni*).

Among the mysids, *R. hastatus*, probably the largest mysid found in the Songkhla Lagoon with a body length of 7.0–12.0 mm, was rare contributing to only 0.07% and 1.21% of mysid abundance in Thale Sap and Thale Sap Songkhla, respectively. Similarly, *M. tenuipes* represented only 0.02% and 2.69% of mysid abundance in Thale Sap and Thale Sap Songkhla, respectively. *Nanomysis siamensis* made up 97.77% and 65.31% in Thale Sap and Thale Sap Songkhla, respectively (Table 2). *Acetes indicus*, a member of Sergestidae, is a common native paste shrimp in Southeast Asia. The abundance of *A. indicus* in the Songkhla Lagoon ranged from 0 to 4414.9 ind 100 m^{-2}, representing 0.19% and 3.33% of individuals in Thale Sap and Thale Sap Songkhla, respectively (Table 2). *Belzebub hanseni,* a little-known shrimp of the family Luciferidae, ranged in abundance from 0 to 99,127 ind 100 m^{-2} and comprised 1.96% and 27.44% of planktonic shrimp communities in Thale Sap and Thale Sap Songkhla, respectively (Table 2).

PERMANOVA of planktonic shrimp abundance in the Songkhla's Lagoon system indicated a significant interaction between lake and month (P = 0.0001; Table 3). Average abundance for each planktonic shrimp species at each station within each lake between June 2017 and May 2018 indicated heterogeneity and a nonsynchronous abundance pattern (Fig. 3). Proportions of species assemblage abundance differed between Thale Sap (Fig. 3A) and Thale Sap Songkhla (Fig. 3B) during the year,

Table 3. Two-way PERMANOVA tests based on the rank abundance of planktonic shrimps in Thale Sap and Thale Sap Songkhla of the Songkhla Lagoon system in southern Thailand during the sampling period between June 2017 and June 2018. Tests were based on the non-Euclidean Bray–Curtis dissimilarity measure and were carried out using 9999 permutations. Bold values indicate significant differences at $P < 0.05$.

Source	Sum of Square	df	Mean Square	*F*	*P*
Month	153,300	11	13,936.0	7.1307	**0.0001**
Lake	71,593	1	71,593.0	36.6320	**0.0001**
Month × Lake	41,561	11	3,778.3	1.9332	**0.0001**
Residual	515,960	264	1,954.4		
Total	782,420	287			

suggesting that the assemblage structure between lakes is seasonal. In Thale Sap, the major constituent was *N. siamensis*, which ranged from 98% up to 100% every month, except in April 2018 (91%; Fig. 3A). In contrast, the proportion of *N. siamensis* in Thale Sap Songkhla varied between 1% and 90%, exhibiting a decreasing trend from June 2017 to March 2018 and a subsequent increasing trend to June 2018 (Fig. 3B). Other species were present in Thale Sap (Fig. 3A), but a much greater variation in species abundance proportion was obvious in Thale Sap Songkhla (Fig. 3B).

Two-way ANOVA analyses of the rank-transformed abundance data (Table 4, Fig. 4) revealed significant lake × month interaction terms for *N. siamensis*, *M. tenuipes*, and *A. indicus* (Figs. 4A,B,E). The peak in *N. siamensis* in Thale Sap occurred during the presouthwest monsoon (May 2018), and the peak in Thale Sap Songkhla occurred during the northeast monsoon (November 2017). A peak in *M. tenuipes* was seen only in Thale Sap Songkhla during the late northeast monsoon and early intermediate season between January and March 2018. *Acetes indicus* abundance was bimodal only in Thale Sap Songkhla during the presouthwest and prenortheast monsoons (Fig. 4E). No significant interaction terms emerged for *R. hastatus* or *B. hanseni* (Table 4, Figs. 4C,F). Significantly higher abundance of *N. siamensis* was observed in Thale Sap compared with Thale Sap Songkhla (Fig. 4A).

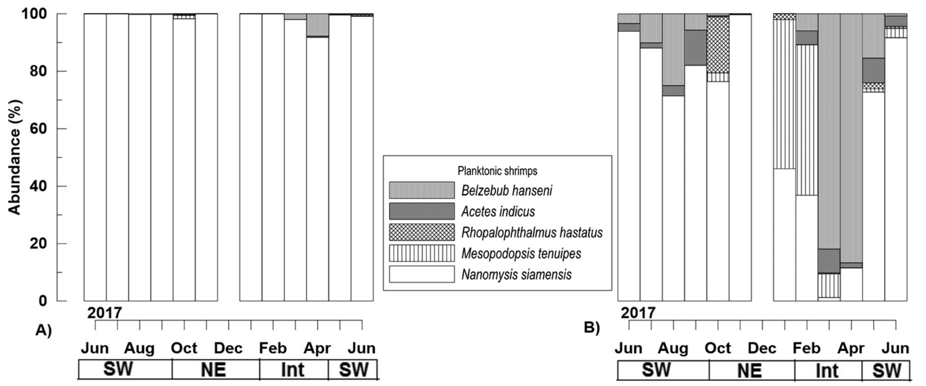

Figure 3. Monthly variations in percent abundance of planktonic shrimps in (A) Thale Sap and (B) Thale Sap Songkhla of the Songkhla Lagoon system in southern Thailand during the sampling period between June 2017 and May 2018. SW: southwest monsoon, NE: northeast monsoon, Int: intermediate period.

Table 4. Two-way ANOVA examining the month, lake, and interaction effects based on the rank abundance of *Nanomysis siamensis*, *Mesopodopsis tenuipes*, *Rhopalophthalmus hastatus*, *Acetes indicus*, and *Belzebub hanseni* taken from Thale Sap, Thale Sap Songkhla, and overall in the Songkhla Lagoon between June 2017 and June 2018. Values in bold indicate significant differences at $P < 0.05$.

Source	df	*Nanomysis siamensis*		*Mesopodopsis tenuipes*		*Rhopalophthalmus hastatus*		*Acetes indicus*		*Belzebub hanseni*	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Month	11	3.75	**0.0001**	11.87	**<0.0001**	5.52	**<0.0001**	1.40	0.1730	10.99	**<0.0001**
Lake	1	25.06	**<0.0001**	81.37	**<0.0001**	5.70	**0.0177**	54.82	**<0.0001**	35.57	**<0.0001**
Month × Lake	11	6.95	**<0.0001**	6.78	**<0.0001**	1.65	0.0863	2.07	**0.0224**	1.74	0.0650
Error	264										
Total	287										

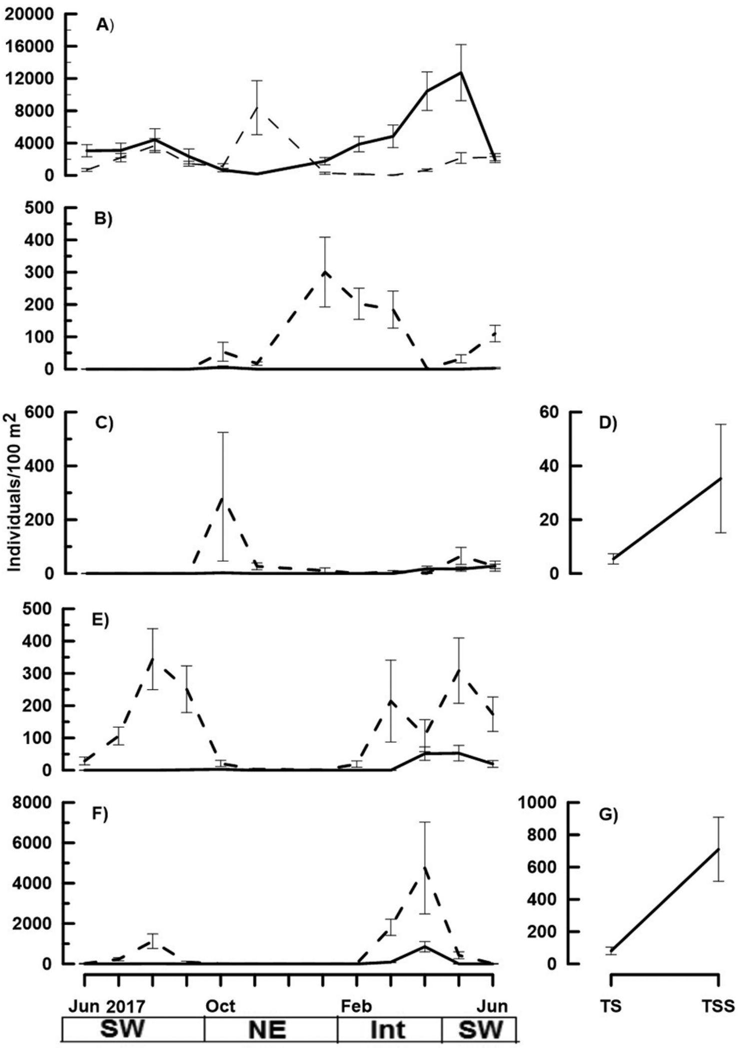

Figure 4. Mean (SE) of abundance (ind 100 m^{-2}) of planktonic shrimps in Thale Sap (TS, solid line) and Thale Sap Songkhla (TSS, dashed line) of the Songkhla Lagoon system in southern Thailand between June 2017 and June 2018. (A) *Nanomysis siamensis*, (B) *Mesopodopsis tenuipes*, (C) and (D) *Rhopalophthalmus hastatus*, (E) *Acetes indicus*, (F) and (G) *Belzebub hanseni*. SW: southwest monsoon, NE: northeast monsoon, Int: intermediate period.

Environmental Variables and Planktonic Shrimp Abundance.—Backward stepwise logistic regression models indicated significant factor descriptors and numerical descriptors that determined probability of occurrence (Table 5). Final model C-values ranged from 0.651 to 0.902 and Somers'D values ranged between 0.302 and 0.804 for each species. The factor lake was the only significant variable for *N. siamensis*, whereas depth, salinity, temperature, pH, and organic carbon were not significant in the model. For *M. tenuipes* only lake, salinity, and percentage of silt were significant, while depth, temperature, pH, and organic carbon were dropped from the model. For *B. hanseni*, both lake and salinity emerged as

Table 5. Summary GLM statistics and analysis deviance for the backward stepwise logistic regression models between selected environmental variables* and abundance proportion data of planktonic shrimps taken from Thale Sap and Thale Sap Songkhla of the Songkhla Lagoon system between June 2017 and June 2018.

Predictors	Coefficient	SE	Coefficient/SE	*P*-value
Nanomysis siamensis				
Constant	6.70028	1.25891	5.32	<0.0001
Lake	−3.25091	0.64757	−5.02	<0.0001
Deviance = 133.89	C = 0.747	Somers'D = 0.494	df = 215	*P*-value = 1.0000
Mesopodopsis tenuipes				
Constant	−8.19455	6.38257	−1.28	0.1992
Lake	6.36602	3.0802	2.07	0.0388
Salinity	−0.21639	0.05976	−3.62	0.0003
Percentage of silt	0.06633	0.02894	−2.29	0.0219
Deviance = 73.66	C = 0.902	Somers'D = 0.804	df = 213	*P*-value = 1.0000
Rhopalophthalmus hastatus				
Constant	−10.9325	8.94198	−1.22	0.2215
Lake	3.39237	4.51261	0.75	0.4522
Deviance = 10.39	C = 0.69	Somers'D = 0.38	df = 215	*P*-value = 1.0000
Acetes indicus				
Constant	−6.24999	2.02061	−3.09	0.002
Lake	1.74183	1.05998	1.64	0.1003
Deviance = 32.44	C = 0.651	Somers'D = 0.302	df = 215	*P*-value = 1.0000
Belzebub hanseni				
Constant	−6.34366	1.60268	−3.96	0.0001
Lake	2.09767	0.84223	2.49	0.0128
Salinity	0.064	0.0255	2.51	0.0121
Deviance = 85.97	C = 0.805	Somers'D = 0.611	df = 214	*P*-value = 1.0000

* All environmental variables input, including lake, depth, salinity, temperature, pH, percentage of silt, and amount of organic carbon.

significant, however, depth, temperature, pH, percentage of silt, and organic carbon were dropped from the model. No variables were predictive of the occurrence of *R. hastatus* or *A. indicus* (Table 5).

Predicted occurrence of *N. siamensis* was higher in Thale Sap than in Thale Sap Songkhla. The probability of occurrence of *M. tenuipes* significantly decreased with salinity in Thale Sap Songkhla, approaching zero at all salinities in Thale Sap (Fig. 5A). In addition, a similar decrease occurrence for *M. tenuipes* was observed with a higher percentage of silt in Thale Sap Songkhla and the occurrence approaching zero for every percentage of silt in Thale Sap sediments (Fig. 5B). For *B. hanseni*, probability of occurrence increased with salinity in both Thale Sap and Thale Sap Songkhla (Fig. 5C).

Discussion

Seasonal trends and spatial variation were observed in water temperature, salinity, pH, depth, percentage of silt in sediment, and organic carbon in the sediment of Thale Sap and Thale Sap Songkhla in the Songkhla Lagoon system. All of these parameters may play important roles in the lives of organisms within the ecosystem.

Seasonal trends in salinity in Thale Sap Songkhla were more dramatic than Thale Sap. A salinity gradient results from saltwater intrusion from the Gulf of Thailand

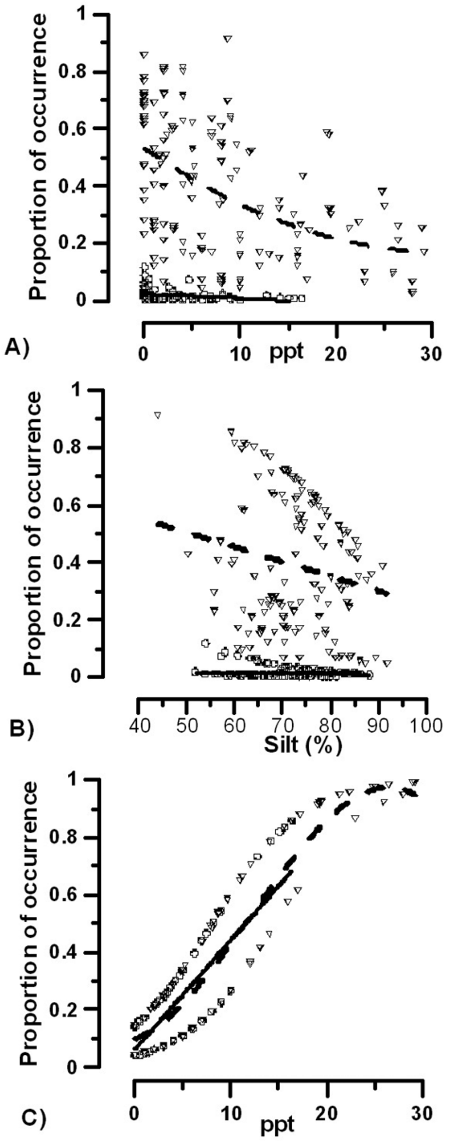

Figure 5. Predicted relationships between proportion of planktonic shrimp occurrence and statistically significant numerical environmental variables taken from Thale Sap (○ solid line) and Thale Sap Songkhla (▽ dashed line) of the Songkhla Lagoon system between June 2017 and June 2018. All predicted values have been calculated from backward stepwise logistic regression models. (A) and (B) *Mesopodopsis tenuipes*, (C) *Belzebub hanseni*.

when high tides enter the inlet to Thale Sap Songkhla and mix extensively with fresh water from Thale Luang and Thale Sap tributaries. A narrow tidal amplitude (1.2 m) and moderate altitudinal gradient of the tributary catchment (500 m above mean sea level) make the Songkhla Lagoon less responsive to variations in salinity intrusion than to annual rainfall patterns and river inflow. During the intermediate period and southwest monsoon (between February and September), the coastal water mass exerts substantial influence, reducing the riverine contribution from the watershed and increasing saline intrusion (Ganasut et al.2005). In contrast, during the northeast monsoon (between October and February), there is a higher inflow of fresh water from the surrounding areas which converts the entire lagoon into a freshwater system. As part of the government developmental plan, an extensive reservoir system has been constructed in the upper watershed of the Songkhla Lagoon Basin to regulate river flow for agriculture (DANCED and MOSTE 1998). These dams have reduced the amount of fresh water that reaches the lagoon and have markedly affected salinity patterns and associated organisms in both Thale Sap and Thale Sap Songkhla, especially during the southwest monsoon.

Five species of planktonic shrimps were collected from Thale Sap Songkhla and Thale Sap in the Songkhla Lagoon system, which remains one of the least-explored estuarine habitats for these organisms in Thailand. Three species of mysids were included in the present study: *N. siamensis, M. tenuipes*, and *R. hastatus.* However, Tattersall (1921) recorded *R. hastatus* under *R. egregius* Hansen, 1910 (Hanamura et al. 2011) and did not record *M. tenuipes* in his study from Songkhla Lagoon system. Only a few studies on mysids from lagoon habitats in tropical Asia are available for comparison. Tattersall (1915) recorded five mysids from the Chilika Lake of India [i.e., *Gastrosaccus muticus* Tattersall, 1915, *Gastrosaccus simulans* Tattersall, 1915, *Mesopodopsis orientalis* (Tattersall, 1908), *Potamomysis assimilis* Tattersall, 1908, and *Rhopalophthalmus chilkensis* O. Tattersall, 1957 as *R. egregius* (*see also* Hanamura et al. 2011)]. Punchihewa et al. (2017) recorded a single species, *Mesopodopsis zeylanica,* from the Lunawa Lagoon in Sri Lanka. The present study, which has the most comprehensive results, suggests that mysids associated with coastal lagoon habitats in tropical Asia are mainly neritic and tropical water species restricted in their geographical distributions (Hanamura et al. 2008a, 2011).

The planktonic shrimp assemblage structure in the Songkhla Lagoon showed significant interactions across habitats, significant monthly variation, and a significant difference in the assemblage structure between Thale Sap and Thale Sap Songkhla. Planktonic shrimp assemblage structures in the lagoon can be divided into Thale Sap-type and Thale Sap Songkhla-type. However, *N. siamensis* was the dominant species of planktonic shrimp and was primarily responsible for the observed difference. Shifting assemblage structure could be seen in the temporal variations possibly corresponding to the monsoon season. The temporal abundance dissimilarity of planktonic shrimps in the Songkhla Lagoon in the present study resembles the observations in zooplankton distribution patterns of Chilika Lake in India (Dhandapani 1995).

In the present study, some environmental parameters were significantly correlated with planktonic shrimp occurrence in Thale Sap and Thale Sap Songkhla. The factor “lake” primarily explained the spatial distribution of *N. siamensis*, *M. tenuipes*, and *B. hanseni*, and salinity appeared to be a secondary determining factor of the occurrence of *M. tenuipes* and *B. hanseni*. This phenomenon is reflected in the higher salinity observed in Thale Sap Songkhla and the occurrence of species that presumably prefer higher salinity levels, such as *M. tenuipes* and *B. hanseni*. Similar results have been previously reported for zooplankton communities in other lagoon systems (e.g., Dhandapani 1995, Rappé et al. 2011, Almeida et al. 2012, Mayor and Chigbu 2018, Punchihewa 2018).

Nanomysis siamensis occurred year-round and was the most dominant mysid in Thale Sap and Thale Sap Songkhla. Only three known species of *Nanomysis* (Murano

1997) are described, and *N. siamensis* was the planktonic shrimp that responded to environmental variables in both Thale Sap and Thale Sap Songkhla. The observed fluctuations in abundance were not fully synchronized between Thale Sap Songkhla and Thale Sap. During the southwest monsoon, increased saltwater intrusion and reduced freshwater inflow led to high salinity levels and low abundance of *N. siamensis* in Thale Sap Songkhla and low salinity and high abundance of *N. siamensis* in Thale Sap. By contrast, during the northeast monsoon, an increase in freshwater inflow from the watershed lowered salinity levels and produced a corresponding increase in *N. siamensis* abundance in Thale Sap Songkhla. The distribution of floodwaters, muddy-brown water, and plant debris were observed throughout Thale Sap and Thale Sap Songkhla and all were observed to outflow to the Gulf of Thailand. Seasonal changes in salinity are likely not the only explanation for the abundance patterns of *N. siamensis*. The higher density of *N. siamensis* in Thale Sap Songkhla compared to Thale Sap during the northeast monsoon can be attributed to surplus freshwater runoff and possibly suspended silts being flushed through Thale Sap by higher velocity flooding currents (Ganasut et al. 2005). Some zooplankton and mysids are influenced by tidal currents (Webber et al. 1992, Moffat and Jones 1993).

The abundance of *M. tenuipes* in the Songkhla Lagoon system peaked in association with the northeast monsoon between December 2017 and April 2018 and the relative occurrence proportion was negatively correlated with salinity and percentage of silt in the sediment, suggesting a salinity-limited distribution. Hanamura et al. (2008a) provided limited biological information on the original description for *M. tenuipes*, as a euryhaline species commonly found in the middle to upper reaches of estuaries in Southeast Asia. In addition, Hanamura et al. (2008b), in their study on the biology of *M. tenuipes* in mangroves (under the name of *M. orientalis*), reported the species in salinities ranging from 16 to 32 in the Merbok mangrove estuary of Malaysia. Our findings in the present study yielded relatively high numbers of *M. tenuipes* in Thale Sap Songkhla, where salinity was ≤20. The reason for this difference was possibly due to hydrographic and salinity regimes of Merbok mangrove estuary vs the Songkhla Lagoon system. In contrast, Hanamura et al. (2009) found no correlations between the abundance of *M. tenuipes* and temperature, salinity, and tidal cycle in the sandy beach habitat of Penang Island in Malaysia, suggesting no periodicity trend in their abundance. This previous finding should, however, be taken with caution because all information was based on the occurrence of the species from limited scientific surveys.

Rhopalophthalmus hastatus and *A. indicus* occurred sporadically in Thale Sap Songkhla and were nearly absent in Thale Sap. The probability of occurrence of *R. hastatus* in Thale Sap Songkhla of the Songkhla Lagoon system is consistent with the observation of the species in the mouth to the middle reaches of Matang and Merbok mangrove estuaries in Peninsular Malaysia (Hanamura et al. 2011). Peaks in the population of *R. hastatus* in both 2017 and 2018 were clearly associated with decreasing salinity levels, with their numbers declining during the early northeast monsoon. The significantly higher abundances of *R. hastatus* and *A. indicus* in Thale Sap Songkhla were associated with monsoon and lake, due, in part, to the extremely complicated nature of the salinity fluctuations of the lagoon system, as found in Robertson and Duke (1987) and Xiao and Greenwood (1993). The causes of such seasonality may differ between the species; *A. indicus* may arrive and depart before the end of southwest monsoon, while *R. hastatus* may use the lake between the middle and end of the monsoon. Such timing may be correlated with breeding periods, salinity, and hydrological preferences.

Belzebub hanseni is a holoplanktonic pelagic shrimp of the warm neritic waters, sometimes accounting for a substantial proportion of estuarine and coastal plankton. A positive correlation observed between *B. hanseni* occurrence and salinity for both Thale Sap and Thale Sap Songkhla was evident. The second highest abundance of *B. hanseni* in the present study was recorded with average densities up to 1372 ind 100 m^{-2} in Thale Sap Songkhla comprising 27.0% of total planktonic shrimps. Xu (2010) determined optimal salinity based on field data from the East China Sea for *B. hanseni* and reported optimal surface salinity range for *B. hanseni* between 28.9 and 34.7, with an average distribution salinity of 33.3 (SE 1.2). The observed peak of *B. hanseni* was associated with the relatively high salinity of the year, suggesting that the significantly higher abundance observed in Thale Sap Songkhla may have resulted from the salinity variation. Lower salinity in Thale Sap might reduce the survival rate of *B. hanseni* larvae, disrupting their life cycle and preventing the development of adults (Xu 2010).

The relatively low abundances of *M. tenuipes*, *R. hastatus*, *A. indicus*, and *B. hanseni* in Thale Sap compared to those in Thale Sap Songkhla were obvious. These can be attributed to the fact that all stocks of these species originated in Thale Sap Songkhla or along the coast of the Gulf of Thailand, and the species only visited the Songkhla Lagoon temporarily. The difference in abundance observed in the present study may have resulted from relatively low rainfall during the intermediate period and southwest monsoon season (February–September), causing tidal current intrusion far into the lagoon system. This suggests that these planktonic shrimps may have been associated and transported by the tidal current flowing into the Songkhla Lagoon. The tidal inflow carried high volumes of seawater with marine and coastal planktonic shrimps, such as *M. tenuipes*, *R. hastatus*, *A. indicus*, and *B. hanseni*, leading to high salinity variation between Thale Sap Songkhla and Thale Sap and prominent spatial heterogeneity in species abundance along this salinity gradient. Subsequently, low salinity intrusion into Thale Sap (Ganasut et al. 2005) leading to relatively low probability of occurrence of *M. tenuipes* and *B. hanseni* was observed. The high rainfall and flooding observed during the northeast monsoon (October–January) resulted in less salinity variation in the lagoon system; this, in turn, may have resulted in the observation of only the relatively low salinity tolerant species. More detailed studies on the life histories of these species should be conducted along the environmental gradients between Thale Sap Songkhla and Thale Sap to investigate distribution uniformity/heterogeneity, recruitment transport, and maturation of coastally spawned populations, and to identify stock sources for these organisms. In addition, further studies of their reproductive biology and environmental tolerances would improve our understanding of their temporal dynamics.

The Songkhla Lagoon is a highly productive and vulnerable ecosystem that differs greatly from the southernmost mouth of Thale Sap Songkhla toward the northernmost Thale Noi. Prior to the present study, little was known about mysids in the Songkhla Lagoon system as there were only a few specimens caught in grab samples by Angsupanich and Kuwabara (1995), and no information on mysid abundance, biomass, or life cycle in Thailand has been published. The present study revealed spatial and temporal variation in Mysida and Dendrobranchiata shrimps in Thale Sap and Thale Sap Songkhla. These data may be used to assess environmental perturbations that might affect the economic and ecological value of the lagoon provided by its ecosystem services. Planktonic shrimp populations need to be utilized and managed rationally to maintain their ecological and socioeconomic roles. Planktonic shrimps are an important food source in this region and comprise one of the main ecological subsystems in these water bodies, transferring energy from autotrophic organisms or microzooplankton to higher trophic levels and regulating sedimentation and nutrient cycling. The present study constitutes the first report on the ecology of these shrimps in the Songkhla Lagoon and demonstrates that stocks of these large planktonic crustaceans are not homogeneous or ubiquitous. Additional studies on reproduction and population dynamics of these species are required to improve our understanding of their life history within the Songkhla Lagoon system. In addition, further research on their spatial and temporal distributions at larger scales is an important prerequisite for ecosystem modeling, which may be necessary for the proper management of these coastal community resources.

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