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Ecology of Pinnidae (Mollusca: Bivalvia) from the Gulf of Thailand

Cheewarat Printrakoon[1]*, Peter D Roopnarine[2], Thamasak Yeemin[3]

[1] Animal Systematic Special Unit, Department of Zoology, Faculty of Science, Kasetsart University, Bangkok 10900, Thailand

[2] Department of Invertebrate Zoology and Geology, California Academy of Sciences, San Francisco, California 94118, USA

[3] Department of Biology, Faculty of Science, Ramkhamhaeng University, Bangkok 10240, Thailand

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Abstract

The ecology of the family Pinnidae was studied by sampling three pinnid species from 36 sampling sites across four different microhabitats in the Gulf of Thailand. The species spatial distributions were mostly uniform, with some populations having random distributions. Species abundances differed between sandy and coral habitats according to non-metric multi-dimension scaling analyses. Although the Gulf of Thailand is a relatively small geographic area, habitats are varied enough to provide variable shell densities. Small islands are important distribution areas, and coral reefs provide both direct and indirect shelter which support high abundances, densities and increased shell size. The highest density was recorded in sand beds within coral reefs. Low density and small shell size in sand beaches might be related to high mortality in shallow water or to adaptations for survival in shallow waters. A clear correlation between sediment composition and species abundance was found in *Pinna atropurpurea*; abundance increased with the sand content of the sediment. For *P. deltodes*, abundance increased as the rock fraction of the sediment increased. These results suggest that adaptations in Pinnidae, such as shell size, shell morphology, and the exposure of the shell above the sediment-water interface, are responses for survival in different habitats.

Key words: density, distribution, pinnid shell, shell adaptation, the Gulf of Thailand

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1 Introduction

The Gulf of Thailand hosts a diverse array of shallow marine habitats, including nearshore coral reefs, mangrove forests and seagrass beds, which play an essential role in commercial harvesting of fish, molluscs and crustaceans (Office of Natural Resources and Environment Policy and Planning, 2004). Species of the bivalve molluscan family Pinnidae are distributed throughout the gulf and among these habitats. There are about 55 known species of recent pinnid species in the world (Schultz and Huber, 2013), concentrated mostly in tropical regions, including the Indo-Pacific, Indo-west Pacific (Rosewater, 1961; Morris and Purchon, 1981; Purchon and Purchon, 1981; Idris et al., 2008, 2011; Xue et al., 2012; Schultz and Huber, 2013), Australia (Butler and Keough, 1981; Butler, 1987; Beer and Southgate, 2006; Macreadic et al., 2014), Mediterranean (Richardson et al., 1999; Šiletić and Peharda, 2003; Katsanevakis, 2006; Coppa et al., 2010; Nebot-Colomer et al., 2016), tropical American waters (Turner and Rosewater, 1958) and Mexico (Cendejas et al., 1985; Arizpe, 1995). Two genera have been described from the Gulf of Thailand, *Pinna* Linnaeus and *Atrina* Gray, 1842. Both are harvested commercially in most regions for consumption of the large posterior adductor muscle (Rosewater, 1961; Nielson, 1976; Amornjaruchit, 1988; Swennen et al., 2001; Yu et al., 2004), known locally as “hoi jorb” or “hoi song ploo”. No study to date, however, has examined ecological properties of pinnid distribution in Thailand, which is essential for both evaluating the conservation status of the species, and potentially improving the fisheries productivity and sustainability. The main objective of this study is to provide an initial ecological baseline of Pinnidae in Thailand, including species densities, habitats and distribution, and dead shell proportions. We also report on individual masses, state of the byssal threads, and nature and size of particles to which individuals are attached.

Few data are available regarding the distribution and ecology of Pinnidae in Thailand. Most data are literature reports and checklists. For example, Amornjaruchit (1988) surveyed markets and interviewed villagers in the 22 coastal provinces of Thailand for economically important molluscan shellfish. Three species of Pinnidae were recorded: *Pinna bicolor* Gmelin, 1791, *Atrina vexillum* Von Born, 1778 and *A. pectinata* Linnaeus, 1767. These species are commonly recorded from the Gulf of Thailand, in particular the eastern region (Kurozumi et al., 1989; Sanpanich, 2011). Swennen et al. (2001) listed five pinnid species from the southern Gulf of Thailand; two *Pinna* species, *P. bicolor* Gmelin, 1791 as uncommon in the Pattani Bay, in seagrass beds at depth of 0.5 to 1 m below low tide level, and *P. incurve* Gmelin, 1791, com-

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*Corresponding author, E-mail: fscicrp@ku.ac.th, cheewarat040@gmail.com mon amongst catches of fishing boats off Pak Bang and Saiburi. Three species of *Atrina* were listed, *A. inflata* Dillwyn, 1817, *A. lamelata* Habe, 1961 and *A. vexillum*, in depths ranging from 12 to 22 m, near Pattani. Rosewater (1961) previously assigned all three species to the single species *A. vexillum*. Nielson (1976) listed *P. bicolor* and *A. vexillum* among 91 bivalves species recorded at the Phuket Marine Biological Centre, informing the pinnids as inhabiting shale patches on sandy beaches, and the reef flat. Tantanasiriwong (1979) also presented a checklist of Pinnidae among littoral and sublittoral marine bivalve mollusks from Phuket. *Pinna bicolor* was collected from muddy sand between tide marks, down to a depth of 8 m, whereas *A. pectinata* Linnaeus, 1767 and *A. vexillum* were record as embedded in sand landward of coral reefs. Carr (1991) recorded *P. bicolor* in depths of 0–5 m from the Phang Nga Bay, east of the Phuket Island. Recently, Silina (2012) reported that local variation of factors such as seasonal temperature, salinity and sediment load clearly influence the growth and longevity of *A. vexillum* in the southern gulf. Schultz and Huber (2013) reported up to ten pinnid species distributed in Thailand, including *P. attenuata* Reeve, 1858, *P. incurve*, *P. atropurpurea* Sowerby I, 1825, *P. muricata* Linnaeus, 1758, *A. vexillum*, *A. chinensis* Deshayes in Cuvier, 1841, *A. exusta* Gmelin, 1791, *A. inflata*, *A. pectinata*, *A. penna* Reeve, 1858 and *Streptopinna saccata* Linnaeus, 1758.

Pinnid bivalves generally have large fragile fan shaped valves, with umbones pointed and situated at the extreme anterior end of the shell. The posterior end of the shell is wide and gaping, reflecting the asymmetry of the adductor muscles, where the anterior muscle is generally much smaller than the posterior (Swennen et al., 2001; Schultz and Huber, 2013). Species range from the intertidal to subtidal, and may be found variously buried partially in sand, mud or gravel substrates, or attached to submerged hard substrates by a thick, silky byssus (Abbott and Dance, 2000; Schultz and Huber, 2013). The genera *Pinna* and *Atrina* can be distinguished easily, with *Pinna* having a nacreous layer on the valve's interior, divided by a sulcus into dorsal and ventral lobes, whereas *Atrina* has a nacreous layer not divided into two parts (Swennen et al., 2001). Here we report on both the ecology of the pinnid species, *P. atropurpurea*, *P. deltodes* and *A. vexillum* in the Gulf of Thailand, and compare the intergeneric ecologies of *Pinna* and *Atrina*.

2 Materials and methods

2.1 *Study area*

Pinnid species were studied in three areas of the Gulf of Thailand, referred to different municipal and territorial waters (Office of Natural Resources and Environment Policy and Planning, 2004), and specimens were collected from six zones (Fig. 1). The first zone is the innermost region of the upper Gulf of Thailand including the Sichang Island (Zone A; 1–3): Ngo Cape (13°07′54.98″N, 100°48′57.27″E), Hintasin (13°07′55.56″N, 100°49′5.10″E) and Randokmai Island (13°09′6.00″N, 100°50′2.65″E) (Fig. 1A); and the Lan Island (Zone B; 4–6): Sak Island (12°56′45.64″N, 100°47′25.77″E), Yuon Cape (12°54′49.13″N, 100°47′12.23″E), Tharai Bay (12°54′33.72″N, 100°47′01.81″E) (Fig. 1B) of Chonburi Province.

The second zone (Zone C and D) are the two islands of Trat

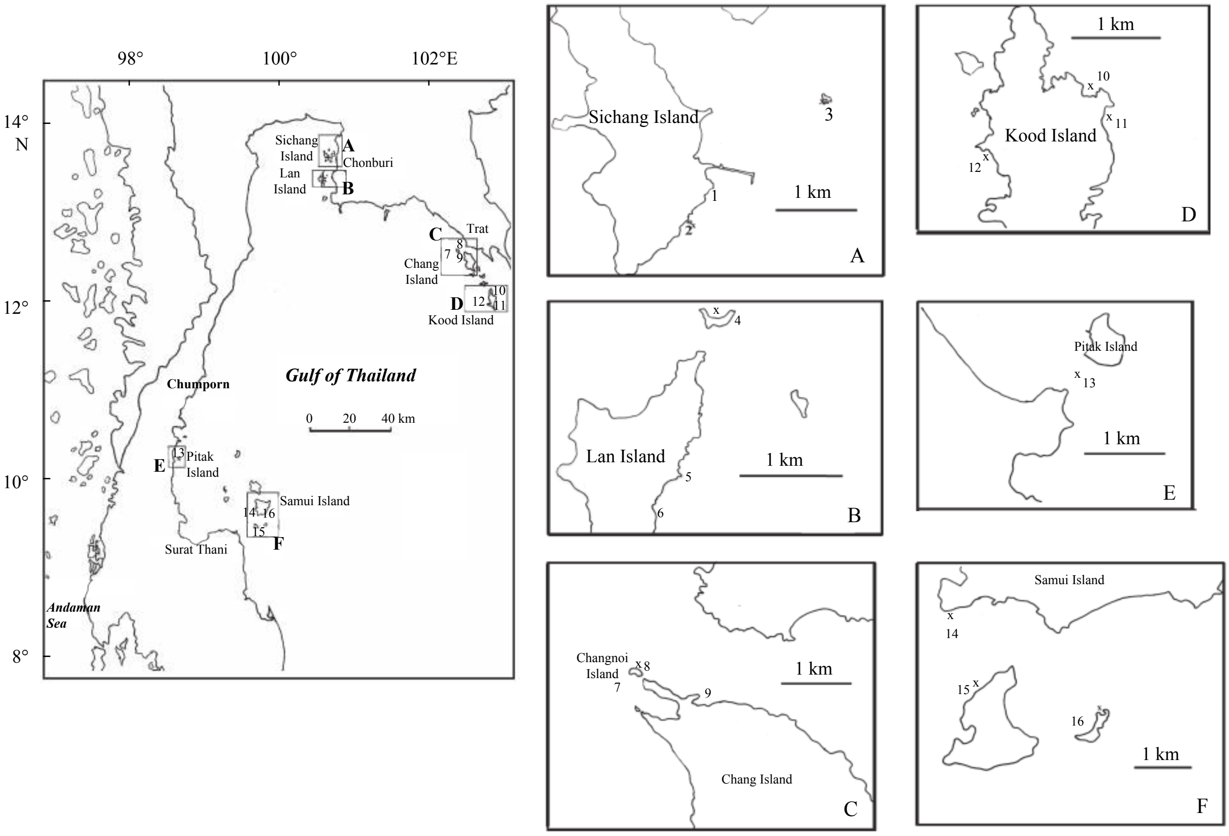

Fig. 1. Ecological study sites of Pinnidae: the Sichang Island (A) and Lan Island (B) of Chonburi Province; the Chang Island and Changnoi Island (C), and the Kood Island (D) of Trat Province; sand beach, in front of the Pitak Island of Chumporn Province (E); and the Samui Island and neighbors Island of Surat Thani Province (F).

Province at the eastern end of the upper Gulf of Thailand including Changnoi Island (7 and 8): western coast of Changnoi (12°09′31.71″N, 102°14′42.92″E) and eastern coast of Changnoi (12°09′41.00″N, 102°14′58.90″E), and the Chang Island (9): Sabbarot Bay (12°08′36.99″N, 102°17′10.11″E) (Fig. 1C); and the Kood Island (10–12): Sai Bay (11°38′28.02″N, 102°36′41.53″E), Kluai Bay (11°41′09.17″N, 102°36′19.94″E) and Praw Bay (11°35′29.0″N, 102°33′30.4″E) (Fig. 1D) near the Cambodian border. The southern area comprised a sandy beach stretching from Bang Num Chet (13) (10°02′88.6″N, 99°10′94.3″E) (Fig. 1E) on the mainland to the Pitak Island, a small island of Chumporn Province, and Samui Island (14): Thongtanod Bay (9°24′56.7″N, 99°56′18.3″E) which belongs to Surat Thani Province. The Samui Island has two small connected islands, Kraten Island (9°23′06.80″N, 99°56′17.36″E) (15) and Mudsum Island (9°22′29.88″N, 99°58′37.00″E) (16) to the south, representing sites in the southern Gulf of Thailand (Fig. 1F). Each zone was characterized by habitat types present at sub-sampling sites (Table 1), and all zones are summarized in Table 2.

2.2 *Sampling*

The study was conducted during March to May of 2010–2015. Three transect lines were set perpendicular to the shore at each study site and extended from the Mean Low Water mark for approximately 30 m. Lines were separated by 20 m interval, and covered an area of approximately 1 800 m^2. Percent cover along each transect was calculated following English et al. (1997). Dominant coral species, defined in terms of areal coverage, were recorded for coral habitats. Live and dead pinnids were counted and collected from 30 (1 m^2) quadrats distributed equidistantly along each transect before calculated density. Water depth was also recorded for each quadrat, classifying burial depth as shallow (0–3 m), medium (3–6 m) or deep (>6 m).

2.3 *Statistical analyses*

Pinnid densities were compared among habitat types (coral reef, coral and rocky rubble, sandy sub-tidal bed, and sandy beach) and localities with one-way analysis of variance (ANOVA). Abundances were compared among plots to determine the manner in which the species were distributed across the submerged landscape. Morisita's index (I_δ) of dispersion was used to illustrate spatial distribution, and chi-square (χ^2) tests were applied to determine if the spatial distributions were random, uniform or clumped (Morisita, 1962). Water temperature, pH, salinity and conductivity were also measured three times at each quadrate using a YSI 556 MPS Handheld Multi-parameter instrument. All live and dead pinnid specimens collected were transferred to 70% alcohol.

Initial taxonomic identifications made in the field were tested by additional examination in the laboratory using monographic treatments of the Pinnidae, Turner and Rosewater (1958), Rosewater (1961), Swennen et al. (2001), Idris et al. (2008), and particularly the recent treatment by Schultz and Huber (2013). Basic shell morphometric data, including valve length and height, and byssus characters, were collected by using Vernier calipers (0.01 mm precision), and pinnid size was compared among the four habitat types. The physical character of the localities was compared by principle components analysis on the physical and chemical data. Pinnid compositions were compared among localities with non-metric multidimensional scaling (NMDS) analysis of inter-locality Bray-Curtis distances. The Bray-Curtis distance accounts for both similarity/dissimilarity of species composition, as well as the abundance of each species and also combined with sediment composition to analyse abundance factors. All analyses were conducted with the PRIMER software (Clarke and Warwick, 1994).

Burial depth (cm) was measured for each individual by measuring the distance from the buried umbonal region to the ex-

Table 1. Sixteen studied sites of ecological studies of Pinnidae

No.	Site name	Locality	Area description
1	Ngo Cape	Sichang Island, Chonburi Province	small semi-enclosed coastline, area of cable line construction of the southeast of Sichang Island, electricity supplied from mainland
2	Hintasin	Sichang Island, Chonburi Province	semi-enclosed coastline of stump the southeast of Sichang Island, create narrow channel to Island
3	Randokmai Island	Sichang Island, Chonburi Province	enclosed coastline by rocks of small island, middle between Sichang Island and mainland
4	Sak Island	Lan Island, Chonburi Province	semi-enclosed coastline of small island, the northern of Lan Island
5	Yuon Cape	Lan Island, Chonburi Province	small semi-enclosed coastline near headland of the eastern of Lan Island
6	Tharai Bay	Lan Island, Chonburi Province	opened coastline beach, area of electricity cable line construction from the mainland to Lan Island, strong sea wave
7	Western coast of Changnoi	Changnoi Island, Trat Province	semi-enclosed coastline of the western coast of Changnoi Island, this site faced the Gulf of Thailand
8	Eastern coast of Changnoi	Changnoi Island, Trat Province	opened coastline of the eastern cost of Changnoi Island, this site faced mainland
9	Sabbarot Bay	Chang Island, Trat Province	semi-enclosed coastline of the northeast of Chang Island, this site faced mainland, opposite ferry port
10	Sai Bay	Kood Island, Trat Province	semi-enclosed coastline of the northeast of Kood Island, this site faced mainland
11	Kluai Bay	Kood Island, Trat Province	small semi-enclosed coastline beach of Kood Island, covered by small scattered patches of seagrass *Cymodocea serrulata*, *Halodule uninervis* and *Halophila beccarii*
12	Praw Bay	Kood Island, Trat Province	opened coastline of the southwest of Kood Island, this site faced the Gulf of Thailand, dense coral reef
13	Bang Num Chet beach	Pitak island, Chumporn Province	sand beach expanded from eroded cliff, walked way from mainland to Pitak Island when neap tides
14	Thongtanod Bay	Samui Island, Surat Thani Province	semi enclosed coastline, the southern west of Samui Island, this site faced mainland and strong sea wave
15	Kraten Island	Samui Island, Surat Thani Province	opened coastline of small island, the southern of Samui Island, this site faced mainland
16	Mudsum Island	Samui Island, Surat Thani Province	enclosed coastline by coral reef of small island, the southern of Samui Island, surrounded by Samui Island, Kraten Island and mainland, sand bed back reef

Table 2. Site composition (%, mean±SE) and dominant coral species of habitat profile in transect line

Site name	Rock/%	Live coral/%	Dead coral/%	Sand bed/%	Others/%	1 to 3 dominant coral species with percentage area cover
Ngo Cape	26.27±0.25	23.83±2.98	15.7±0.96	25.73±0.68	8.47±2.34	*Platygyra sisnensis* 1.03%, *Favites abdita* 0.83%, *Porites lutea* 0.66%
Hintasin	33.87±6.15	14.53±4.71	24.93±44.67	26.67±7.78	0.0±0.0	*Porites lutea* 20.03%, *Favites abdita* 1.12%, *Platygyra sisnensis* 1.07%
Randokmai Island	29.15±1.03	15.37±2.51	26.76±5.62	27.02±6.68	1.7±1.09	*Porites lutea* 5.03%, *Favites abdita* 3.53%, *Platygyra sisnensis* 1.85%
Sak Island	12.3±6.08	25.74±2.42	48.85±2.08	8.81±2.15	4.3±0.82	*Porites lutea* 10.66%, *Symphyllia agaricia* 1.85%, *Pavona decussata* 1.84%
Yuon Cape	12.2±1.73	12.88±2.78	45.75±0.4	26.9±4.0	2.27±2.55	*Porites lutea* 2.34%, *Favites abdita* 0.68%, *Platygyra daedalea* 0.48%
Tharai Bay	16.16±0.41	21.1±1.93	20.34±0.77	39.27±2.11	3.13±0.55	*Porites lutea* 6.14%, *Favites abdita* 0.72%, *Platygyra sisnensis* 0.57%
Western coast of Changnoi	5.57±0.81	31.82±6.38	43.3±4.91	18.27±6.3	1.04±1.81	*Porites lutea* 9.75%, *Pavona decussate* 5.96%
Eastern coast of Changnoi	0.0±0.0	30.77±8.11	55.6±11.36	8.23±4.21	5.4±4.12	*Porites lutea* 13.57%, *Pavona decussate* 8.38%, *Turbinaria mesenterina* 2.57%
Sabbarod Bay	4.47±0.95	25.89±5.59	45.98±5.33	15.3±10.3	8.36±1.53	*Porites lutea* 9.65%, *Platygyra sisnensis* 3.86%, *Favia matthaii* 3.58%
Sai Bay	2.0±0.5	22.74±7.32	53.71±2.93	18.31±7.48	3.23±3.03	*Porites lutea* 7.38%, *Pavona decussate* 3.41% *Fungi* sp. 1.83%
Kluai Bay	6.13±1.27	0.0±0.0	0.0±0.0	77.87±5.68	16.0±6.56	
Praw Bay	7.86±0.22	24.87±0.21	47.74±0.59	11.68±1.1	7.85±0.93	*Diploastrea heliopora* 13.41%, *Symphyllia racta* 2.14%, *Favia favus* 1.20%
Thongtanod Bay	0.0±0.0	24.3±1.91	49.47±0.97	3.38±0.27	22.85±1.37	*Porites lutea* 5.75%, *Pachyseris rugosa* 3.17%, *Pavona frondifera* 2.11%
Kraten Island	8.14±7.13	23.31±2.24	39.07±9.0	6.17±4.08	23.31±3.49	*Porites lutea* 3.24%, *Symphyllia agaricia* 2.56%, *Favia speciosa* 2.45%
Mudsum Island	0.0±0.0	0.0±0.0	0.0±0.0	96.48±0.95	3.52±1.42	
Bang Num Chet beach	8.57±2.56	0.0±0.0	0.0±0.0	83.68±4.86	7.75±2.31	

posed posterior region of the valve. This transition area of shell is readily apparent on valves because of textural differences and the presence of epibiont organisms on the exposed posterior portion. Linear regression analysis was used to determine the relationship between shell length and burial depth, byssus thread characters among species.

Additionally, the exposed portions of valve surfaces or sediment water interface was compared among habitat types (coral reef, coral and rocky rubble, sandy sub-tidal bed, and sandy beach) of *P. atropurpurea* and *A. vexillum* with one-way analysis of variance (ANOVA). Independent *t*-tests were used to compare coral, and the mixed rock-coral habitats of *P. deltodes*.

3 Results

3.1 *Distribution*

A total of 293 live and dead pinnid specimens were recorded at the sampled localities with *P. atropurpurea* being the most abundant (119 individuals), followed by *A. vexillum* (103 individuals) and *P. deltodes* (71 individuals). All three species (Fig. 2) were recorded in sediment of coral reefs and all mixed rock and coral sites (Figs 3a, b). *Pinna deltodes* lives on open sediment, grouped together between rock and coral rubble, with up to five individuals per group (Figs 3c, d). *Pinna atropurpurea* and *A. vexillum* occurred in sand beach and sand bed (Figs 4a–d), where both species are commonly buried in sand habitats and include sand substrate under coral, rock and coral (Figs 4a, b).

3.2 *Abundance of pinnid species*

All species are most abundant at shallow depths of less than 40 m, in water depth of 1–4 m and ranging 10–30 m from the shoreline (Figs 5 and 6). *Pinna deltodes* was most abundant at the Randokmai Island, where 18 individual were found (Fig. 5c).

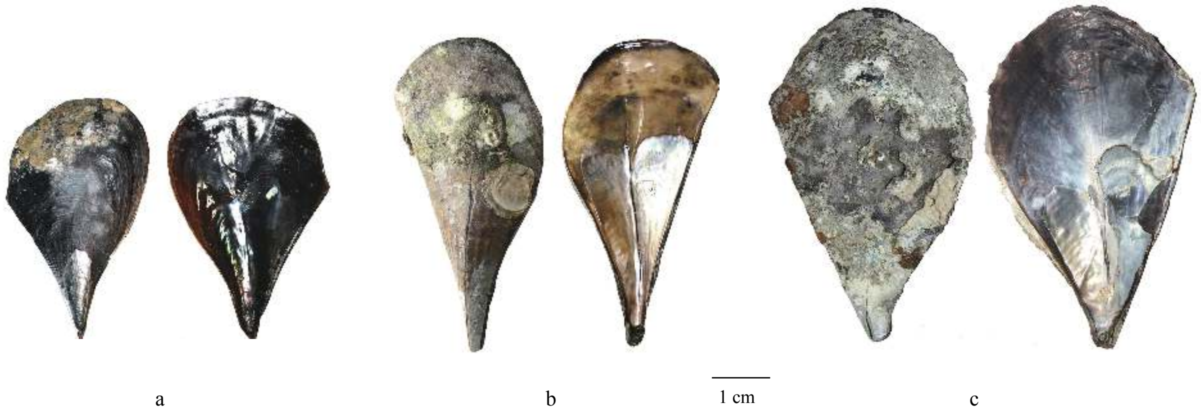

Fig. 2. Three pinnid species from the Gulf of Thailand: *Atrina vexillum* (a), *Pinna atropurpurea* (b) and *Pinna deltodes* (c).

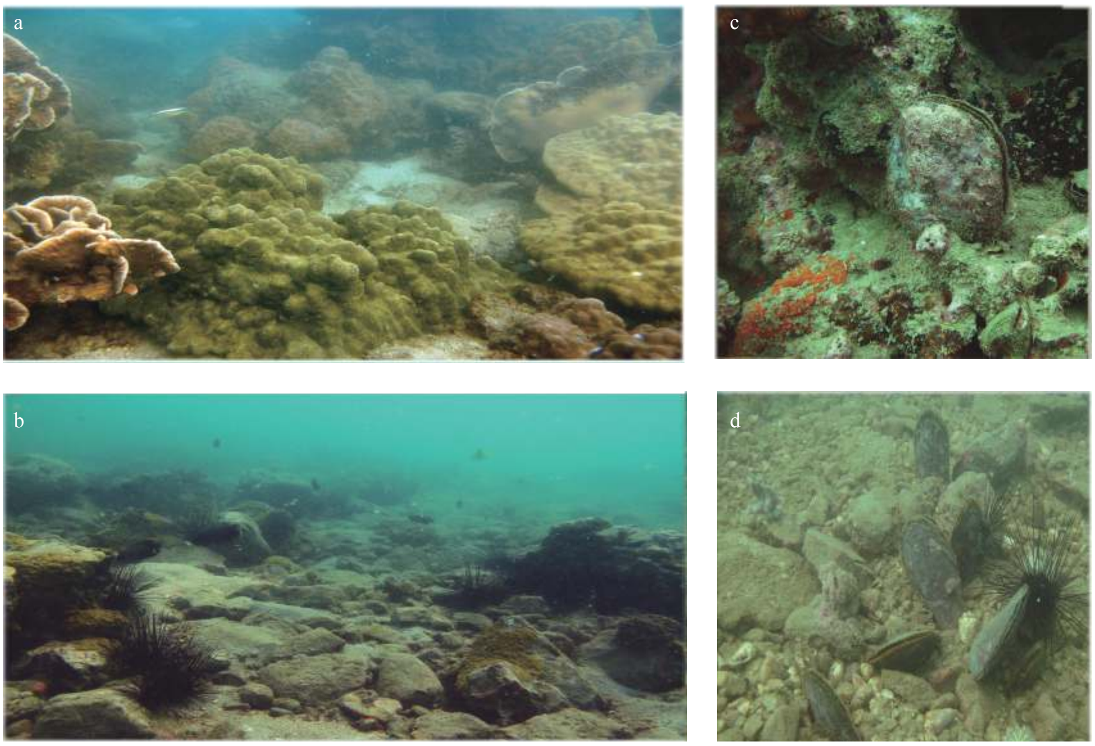

Fig. 3. Underwater photos of coral reef (a) and coral and rock rubble (b). *Pinna deltodes* was common species that buries in substrate under or between coral stones (c) and stone or rock (d).

Fig. 4. Overview pictures of sand bed under water (a) and sand beach during low tide (b). Two *P. atropurpurea* buried in sand bed substrate that above surface shell was place for epibiont attachment (c) and one living closed shell of *A. vexillum* nearly completed buried in sediment of sand beach (d).

Pinna atropurpurea was most abundant at Mudsum (sand habitat, 66 individuals, Fig. 5f), whereas the abundance of *A. vexillum* did not differ among habitats, and was greatest at the coral reef at the Sai Bay (15 individuals, Fig. 6g).

Spatial distribution patterns of each species are shown in Table 3. All the species appeared to distribute uniformly at most

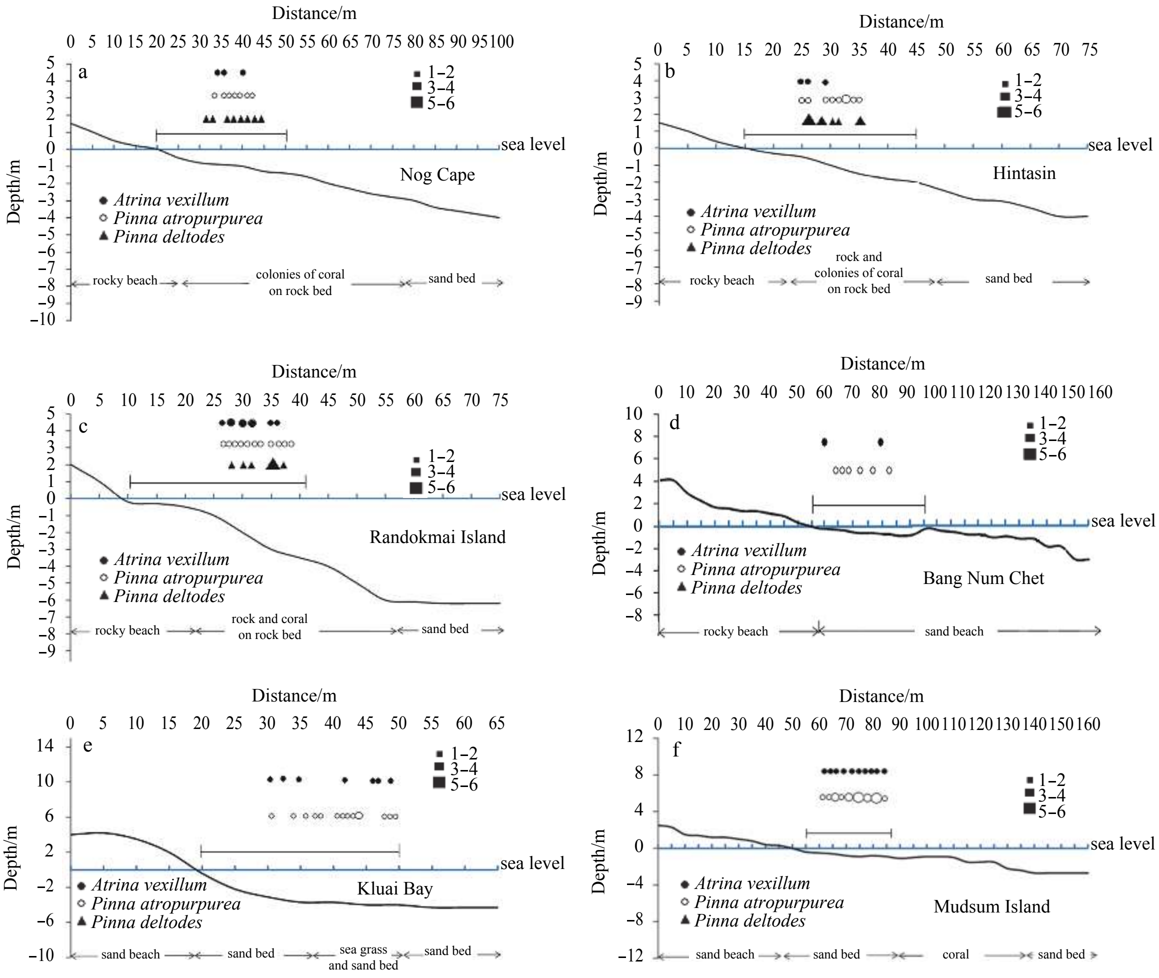

Fig. 5. Distribution pattern of pinnid habitat profile from land to 30 m off shore. Three abundance classes distributions (1–2, 3–4 and 5–6 individuals) were from rock and coral rubble (a–c), sand beach (d) and sand bed (e–f).

sites (Morisita's index, $0 \leqslant I_\delta < 1$), although this could be influenced by low abundances at many sites. A zero index at the Yuon Cape, coral and rock rubble, Bang Num Chet, and sand beach, indicated that only one single individual was present in each experimental plot. Although the Randokmai Island, coral and rock rubble, and Mudsum Island, sand bed had I values indicating uniform distributions, those figures did not differ significantly from random (χ^2=9.51 ($\chi^2_{0.95}$, *df*=6) and χ^2=10.78 ($\chi^2_{0.95}$, *df*=3)), respectively. No specimens occurred at the Praw Bay and Tharai Bay, and a single specimen occurred at the Kraten Island (Table 3).

Non-metric multidimensional scaling (MDS) similarities among the 36 sites clustered them into four groups (Fig. 7). Group 1 (G I) comprises coral reef sites of the Sak Island and Ngo Cape, from the Lan Island, Chonburi Province, where only one species, *P. deltodes* occurred, with 94.4% similarity among sites within the group. Group 2 (G II) comprise nine coral reef sites, including the east and west coasts of Changnoi and Sai Bay from Trat Province, where only *A. vexillum* was present, with 85.0% similarity among sites within the group. Group 3 (G III) is a large group consisting of 16 sites from mix coral and coral rubble habitats that show varied abundances of *A. vexillum*, *P. atropurpurea* and *P. deltodes*. Three main subsets were reported with 71.33% similarity within the group. Group 4 (G IV) comprises six sites, including two sand habitats where *A. vexillum* and *P. atropurpurea* co-occurred, but *P. deltodes* was absent in these sites (88.51% similarity within group). Abundances of pinnid dead shells found in each habitat were also compared (Table 4). Coral reefs showed the lowest percentage of dead shells, in contrast to sand beaches. Sand beaches contained large numbers of dead shells, including *P. atropurpurea* (36.36%) and *A. vexillum* (27.57%). Notably, *A. vexillum* consistently had the lowest numbers of dead shells. *Pinna deltodes* from rock and coral rubble habitats had greater numbers of death shells at (33.50%) compared to coral reefs (18.19%).

3.3 *Density*

Densities of the dead and live pinnid based on locality varied from not zero (absent) (open coastline at the Tharai Bay and Praw Bay, with strong wave action), to a maximum 2.67 ind./m^2 at the Mudsum Island, where the locality is a sheltered coastline with sand beds (Table 5).

The most common pinnid species, *A. vexillum,* had its highest density at the Sai Bay, coral reef ((0.50±0.16) ind./m^2), but that did not differ significantly from other sites (*F*=2.391, *p*=0.07, *df*=464). *Pinna atropurpurea* had its highest density ((2.20±0.36) ind./m^2) at the Mudsum Island, a sand bed habitat, and this density was significantly greater than those at other localities (*F*=17.634, *p*=0.009, *df*=464). *Pinna deltodes* was recorded only from coral and rock rubble and coral reef habitats, and the three localities of greatest densities were from coral and rock rubble of

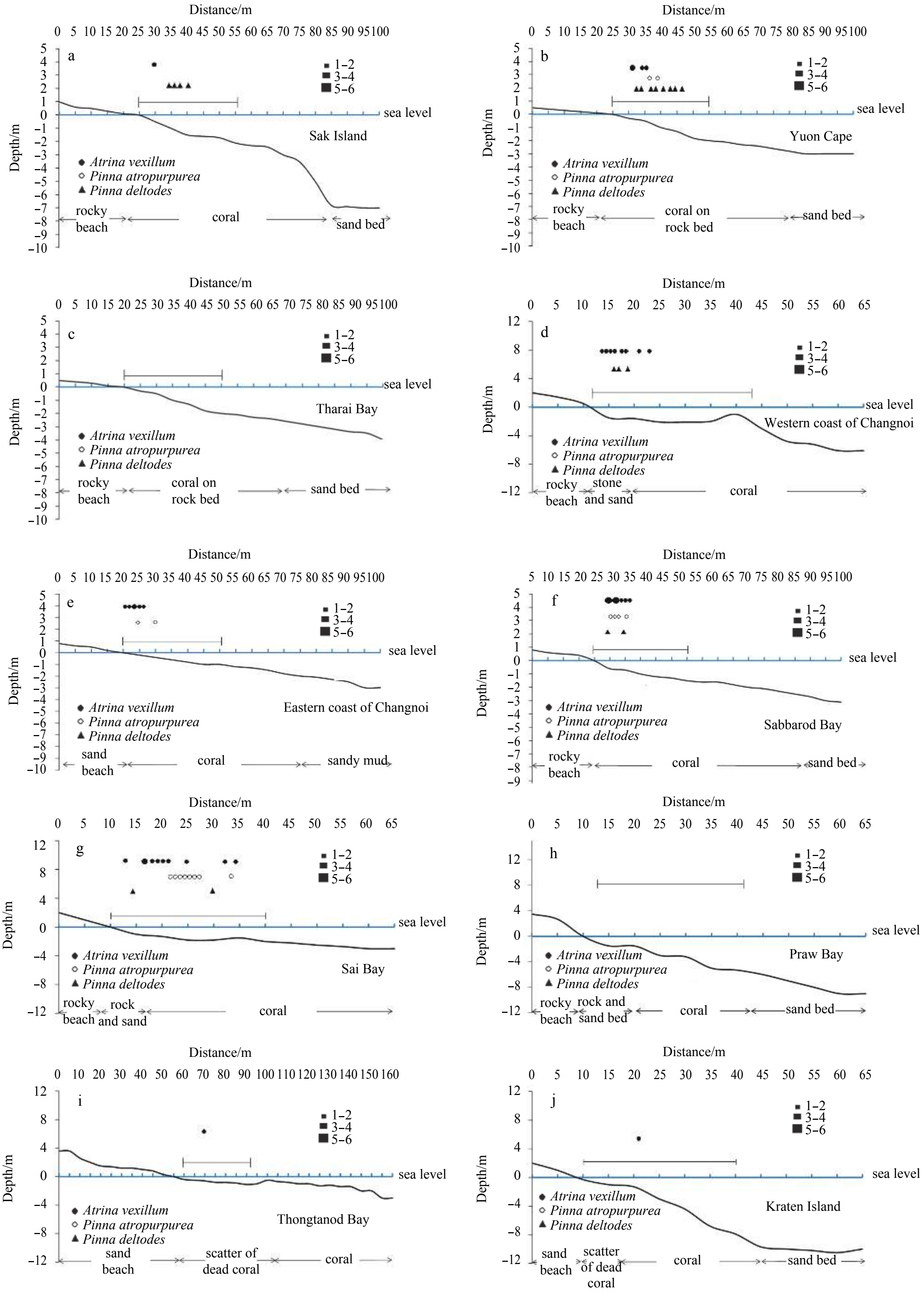

Fig. 6. Distribution pattern of pinnid habitat profile from land to 30 m off shore from coral reef (a–j). Three abundance classes distributions (1–2, 3–4 and 5–6 individuals) were reported.

Table 3. Distribution pattern in each sampling site by Morisita's index dispersion and chi-square test

Habitat	Site	Morisita indχ (I_δ)	Chi-square (χ^2) at 0.95 levels (df=N–1)	Interpretation
1	Ngo Cape	0.024	52.894	uniform
1	Hintasin	0.026	58.812	uniform
1	Randokmai Island	0.03	9.506	uniform, non-significant from random
2	Sak Island	0.047	83.285	uniform
2	Yuon Cape	0	75	uniform
2	Tharai Bay	not found specimen	not available	uniform
2	Western coast of Changnoi	0.019	75.266	uniform
2	Eastern coast of Changnoi	0.036	79.363	uniform
2	Sabbarot Bay	0.031	70.6	uniform
2	Sai Bay	0.004	69.095	uniform
2	Praw Bay	not found specimen	not available	uniform
2	Thongtanod Bay	not available, only one specimen	not available	uniform
2	Kraten Island	not available, only one specimen	not available	uniform
3	Kluai Bay	0.002	58.063	uniform
3	Mudsum Island	0.01	10.775	uniform, non-significant from random
4	Bang Num Chet beach	0	82	uniform

Note: 1 represents coral and rock rubble, 2 coral reef, 3 sand bed, and 4 sand beach.

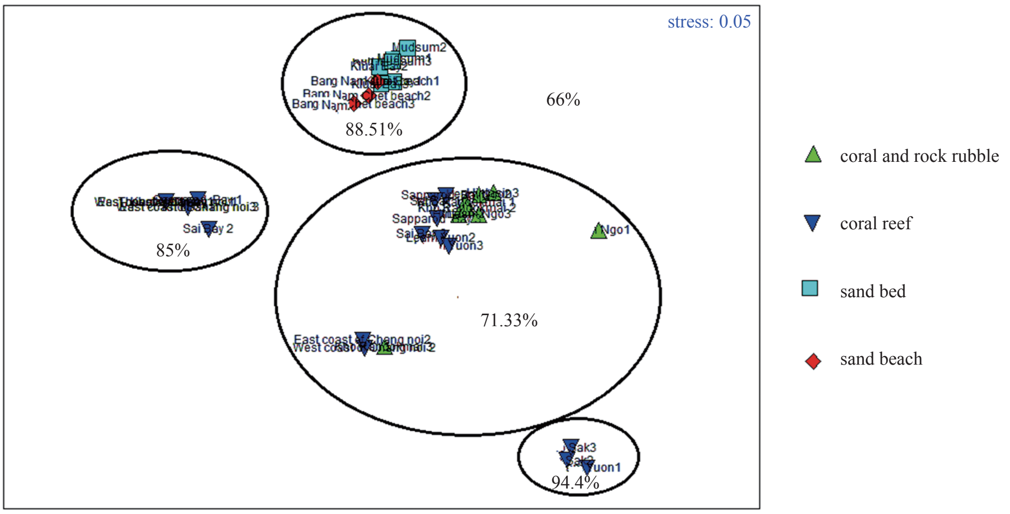

Fig. 7. MDS analysis of Pinnidae abundance, based on species and abundance similarity matrix (fourth root transferred) from 36 localities and four habitats. Four groups (GI–GIV) were separated at similarity levels 66% (stress=0.05).

the Sichang Island, Chonburi Province, and the inner Gulf of Thailand. The Randokmai Island ((0.60±0.15) ind./m^2), Hintasin ((0.57±0.22) ind./m^2) and Ngo Cape ((0.43±0.16) ind./m^2) differed significantly because of low densities. These are coral habitats from Trat Province, and the latter two from Surat Thani Province (F=3.486, p=0.01, df=377).

Atrina vexillum was significantly most abundant at coral reef habitats ((1.90±0.56) ind./m^2 (F=4.446, p=0.005, df=116)), whereas *P. atropurpurea* was most dense at sand habitats, including sandy beaches ((0.37±0.01) ind./m^2) and particularly sand beds ((2.90±0.48) ind./m^2) (F=13.961, p=0.009, df=116). *Pinna deltodes* was most dense at rock and coral habitats ((1.60±0.42) ind./m^2), and was greatest at coral habitats ((0.77±0.17) ind./m^2), although this did not differ significantly between the two sites (t=1.89, p=0.07, df=58) (Fig. 8).

3.4 *Shell size frequency, shell burial and byssus thread characteristic*

Shell length of *P. deltodes* did not differ significantly among habitat types (t=2.98, p=0.10) (Fig. 9). However, individuals from coral reefs and mixed coral and rock of species *P. atropurpurea* (Fig. 10) and *A. vexillum* (Fig. 11) were significantly larger than those from sand beaches (F=5.50, p=0.002 and F=18.53, p=0.001, respectively).

Maximum sizes of those species in coral reefs and mixed coral and rock habitats ranged from 36 to 40 cm, but those in sandy habitats ranged from 21 to 25 cm, with averages of (22.11±1.15) cm (mean±SE) for *P. atropurpurea* (Fig. 10) and (15.61±0.77) cm for *A. vexillum* (Fig. 11).

In terms of byssus thread characteristics, *P. deltodes* had significantly fewer threads (13.95±4.36, F=3.74, p=0.03) and were significantly shorter ((5.34 ±0.74) cm, F=5.98, p=0.003) than oth-

Table 4. Percentage (%) of pinnid dead shell from each habitat (dead shell/total shell) (n=total dead shell)

Habitat Species	Coral	Rock and coral	Sand bed	Sand beach
	n=56	n=20	n=26	n=9
Atrina vexillum	3.57	5.04	3.85	22.57
	n=22	n=42	n=0	n=0
Pinna deltodes	18.19	33.5	not available	not available
	n=12	n=53	n=87	n=11
Pinna atropurpurea	16.66	20.75	24.15	36.36

Table 5. Density (ind./m^2, mean±SE) and distribution of Pinnidae in each locality by classified in four habitat types

Site name	Density/ind.·m^{-2}			
	A. vexillum	*P. deltodes*	*P. atropurpurea*	Total
Ngo Cape	0.10±0.05^{abc}	0.43±0.16^{b}	0.40±0.14^{ab}	0.97±0.26
Hintasin	0.13±0.08^{abc}	0.57±0.22^{b}	0.37±0.13^{ab}	1.07±0.27
Randokmai Island	0.43±0.18^{bc}	0.60±0.15^{b}	0.47±0.20^{ab}	1.43±0.37
Sak Island	0.07±0.07^{ab}	0.17±0.07^{ab}	0.0±0.0	0.23±0.09
Yuon Cape	0.17±0.11^{abcd}	0.27±0.08^{ab}	0.07±0.05^{a}	0.50±0.12
Tharai Bay	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Western coast of Changnoi	0.40±0.13^{abcd}	0.10±0.06^{a}	0.0±0.0	0.53±0.17
Eastern coast of Changnoi	0.30±0.14^{abcd}	0.0±0.0	0.07±0.05^{a}	0.37±0.15
Sabbarod Bay	0.40±0.16^{abcd}	0.10±0.07^{a}	0.17±0.08^{a}	0.67±0.25
Sai Bay	0.50±0.16^{d}	0.07±0.05^{a}	0.17±0.07^{a}	0.70±0.17
Kluai Bay	0.37±0.10^{abcd}	0.0±0.0	0.70±0.16^{b}	1.07±0.19
Praw Bay	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Thongtanod Bay	0.03±0.03^{a}	0.0±0.0	0.0±0.0	0.03±0.03
Kraten Island	0.03±0.03^{a}	0.0±0.0	0.0±0.0	0.03±0.03
Mudsum Island	0.47±0.14^{cd}	0.0±0.0	2.20±0.36^{c}	2.67±0.39
Bang Num Chet beach	0.07±0.04^{ab}	0.0±0.0	0.20±0.07^{b}	0.27±0.08
F value	2.391	3.486	17.443	
p value	0.07	0.01	0.009	

Note: Superscripts a, b and c represent ANOVA Duncan's multiple range test uses harmonic mean sample.

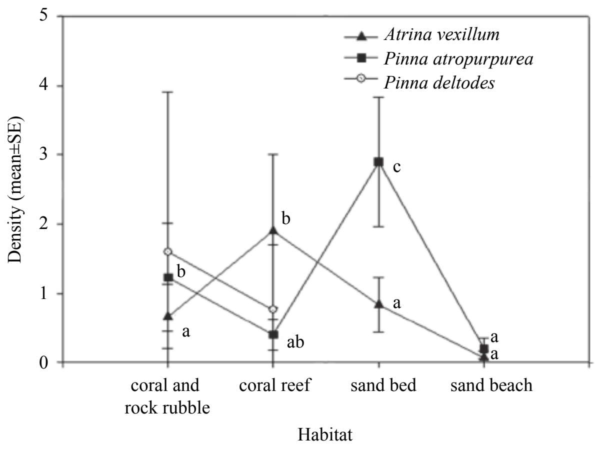

Fig. 8. Density of Pinnidae based on four main habitats in the Gulf of Thailand. a, b and c represent ANOVA Duncan's multiple range test uses harmonic mean sample.

er species, although the diameter of the byssus mass and the burial depth was not significantly different among members of the family. Whereas *A. vexillum* showed significant difference in mass of byssus thread, measured by diameter bundle ((0.58±0.02) cm, F=0.27, p=0.04) (Table 6). The correlations between shell length and boring length of all pinnids showed the same trends of positive correlation by linear regression and coefficient of determination (r^2). Significant correlations were found in *A. vexillum* and *P. atropurpurea*. The strongest correlation was between shell length and boring length in *A. vexillum* (r^2=0.79, p=0.000 1) and linear equation; y=0.770 4x+0.719 8 (Fig. 12b). This was followed by *P. atropurpurea* (r^2=0.34, p=0.001) with linear equation; y=0.304x+6.857 (Fig. 12a). The linear regression of shell length and boring length in *P. deltodes* was not significant (r^2=0.27, p=0.06) with linear equation; y=0.438 0x+2.785 3 (Fig. 12c). In terms of correlations between shell length and characteristics of byssus threads, the shell length of *A. vexillum* was positively correlated with byssus thread length and the number of byssus threads by linear equation; y=0.412 9x–0.084 0 (Fig. 12e) and y=19.371 5x–235.341 (Fig. 12h). However, only byssus thread length was significantly correlated with shell length (r^2=0.24, p=0.000 3). Shell length of the genus *Pinna* was not significantly correlated to any byssus thread characteristics.

Exposed valve portions were compared among habitat types. Populations of *P. atropurpurea* and *A. vexillum* from sand beaches showed significantly shorter distances from the sediment-water interface than species in other habitat types. The shortest open shell area for epibiont attachment was (1.288±0.219) cm for *A. vexillum* (F=5.83, p=0.002, df=49) and (2.38±1.64) cm for *P. atropurpurea* (F=41.08, p=0.000 1, df=73) (Fig. 13).

3.5 *Environmental parameters*

Seawater temperature ranged 30.30–35.23°C, with maximum temperatures at three coral sites: Trat Province, western and eastern coast of Changnoi and Sabbarot Bay of Chang Island

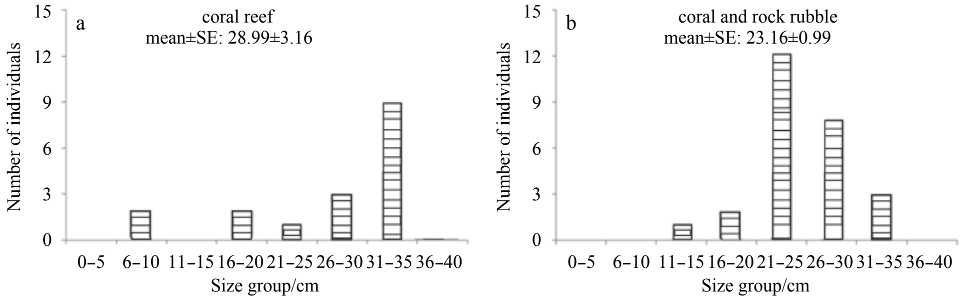

Fig. 9. Size frequency distribution and mean shell length (mean±SE, cm) of *P. deltodes*.

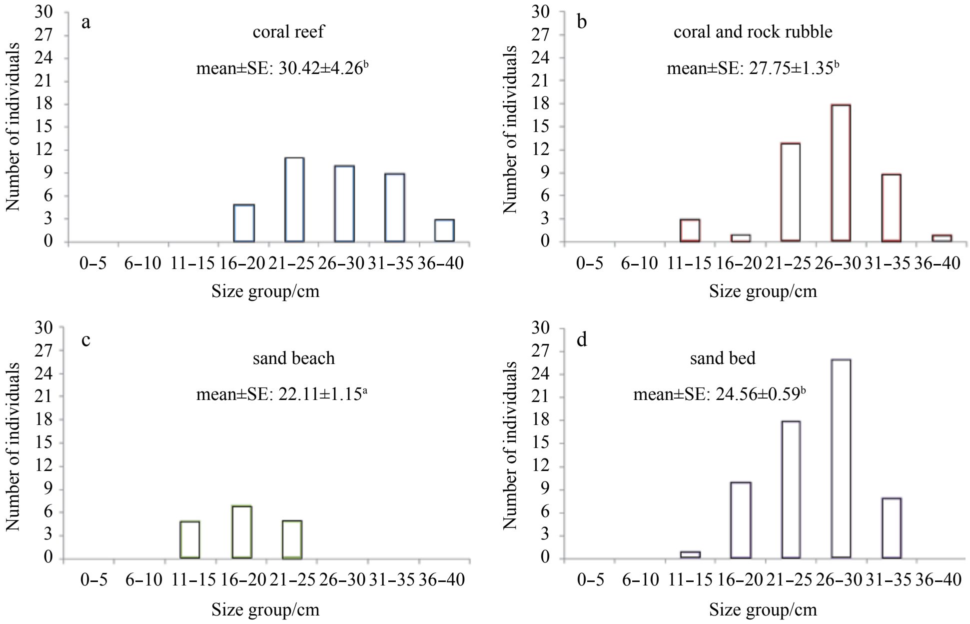

Fig. 10. Size frequency distribution and mean shell length (mean±SE, cm) of *P. atropurpurea* from four habitats. Superscripts a, b and c represent ANOVA Duncan's multiple range test uses harmonic mean sample.

(Table 5). Water pH was alkaline, ranging 7.80–8.63, conductivity ranged from 47.87 to 66.93 ms/cm and salinity varied between nearly normal and high, 30.99–36.49. (Table 7). Maximum salinity and conductivity were recorded in the south of Thailand, the Thongtanod Bay having the highest salinity (36.49±1.33) and Mudsum having the highest conductivity ((66.93±0.04) ms/cm). The Sabbarot Bay had the highest levels of suspended solids, (36.18±16.75) mg/L whereas the lowest was recorded at the Thongtanod Bay, (16.55±1.71) mg/L (Table 7).

When each sampling site was linked to five environmental variables that showed low coefficient correlation as Fig. 14, the maximum was 0.500 at salinity and suspended solid (Fig. 14). High abundance of *P. atropurpurea* was correlated to sites with high percentage of sand composition in sediment. In sand habitats, sand bed and sand beach showed higher than 60% of sand composition (d symbol categories) found high *P. atropurpurea* abundance (large area of bubble circles) (Fig. 15A). However, percentage of sand sediment could not explain any pattern in *A. vexillum* abundance because high abundance of *A. vexillum* (large area of bubble circles) was found in all range of sediment composition (a to d symbol categories) (Fig. 15B). High abundance of *P. deltodes* was mainly found at 10%–29% sand composition (b symbol categories) (Fig. 15C).

Because *P. deltodes* was specifically found in coral reef and coral and rock rubble habitats, several factors such as rock composition and coral type were used to find correlated pattern. Most likely *P. deltodes* abundance increased (increasing size of bubble circle) when sites had more than 20% of rock composition (c to d symbols categories). Whereas *P. deltodes* prefer any sites that composed of 20%–60% dead coral and 10%–30% lived coral (Fig. 16). Where the percentages of rock, dead coral or lived coral were similar to sand composition could not be used to explain the abundance of *A. vexillum* (Fig. 17).

4 Discussion and conclusions

Atrina vexillum, a species with a very broad shell, is an *Atrina* species that has a broad distribution (from the Red Sea to the Philippines, including the Gulf of Thailand) (Schultz and Huber, 2013; Silina, 2012). Although *A. pectinata* and *A. chinensis* were report on the coast of western Thailand in the recent review on Pinnidae (Schultz and Huber, 2013), it was absent in this study because the habitats surveyed did not include muddy sand. The species diversity found in the Gulf of Thailand was lower than that reported in Sungai Pulai, South Western Johor coast, Malaysia (seven species) where higher diversity was recorded in seagrass habitats, with species consisted of *P. muricata*, *P. bicolor*, *P. incurve*, *P. deltodes*, *P. atropurpurea*, *A. pectinata* and *A. vexillum* (Idris et al., 2008). Many large pinnid species around the

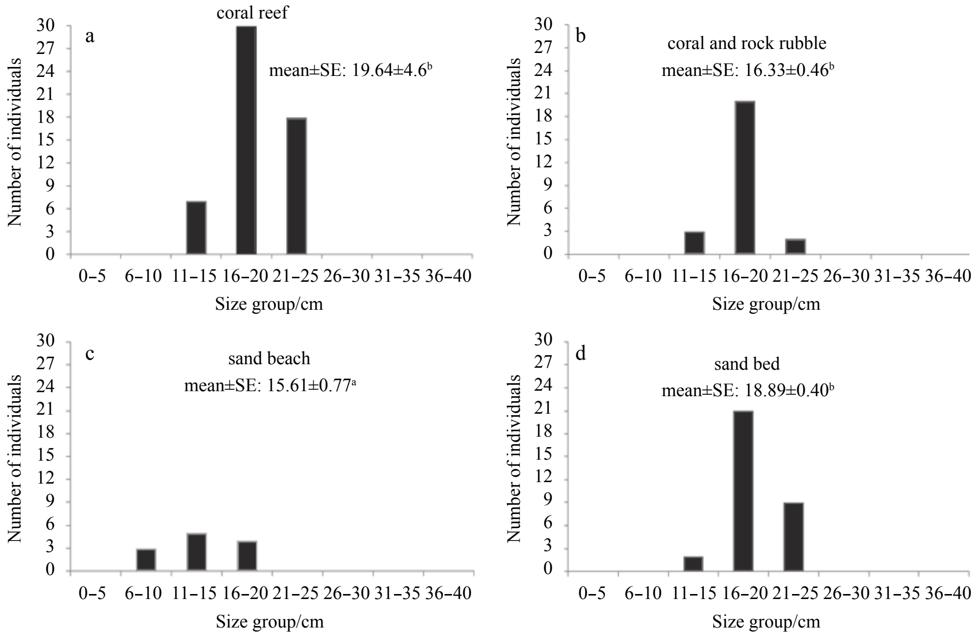

Fig. 11. Size frequency distribution and mean shell length (mean±SE, cm) of *A. vexillum* from four habitats. Superscripts a, b and c represent ANOVA Duncan’s multiple range test uses harmonic mean sample.

Table 6. Byssus thread characteristic and burial depth of Pinnidae from Thailand (random n=30)

Characteristic	*A. vexillum*	*P. atropurpurea*	*P. deltodes*	p-value
No. of attachment byssus threads	114.57±25.57^{b}	104.16±17.97^{b}	13.95±4.36^{a}	0.026
Byssus thread length/cm	7.37±0.29^{b}	7.39±0.31^{b}	5.34±0.74^{a}	0.003
Diameter of byssus thread mass/cm	0.588±0.024^{a}	0.826±0.038^{b}	0.734±0.47^{ab}	0.096
Burial depth/cm	14.36±3.112^{a}	13.96±2.85^{a}	13.94±3.71^{a}	0.076

Note: Superscripts a, b and c represent ANOVA Duncan’s multiple range test uses harmonic mean sample.

Table 7. Environmental parameters in each studies site

Site name	Water temperature/°C	Water pH	Salinity	Suspended solid/mg·L^{-1}	Conductivity/ms·cm^{-1}
Ngo Cape	30.33±0.21	8.04±0.08	31.87±0.34	22.23±1.25	48.79±0.62
Hintasin	30.30±0.66	7.99±0.18	33.63±0.4	29.42±0.15	48.17±0.85
Randokmai Island	30.33±0.55	7.99±0.13	32.50±0.30	24.41±1.65	47.98±0.56
Sak Island	31.08±0.74	7.88±0.19	31.99±0.79	24.76±1.86	47.87±0.42
Yuon Cape	31.44±0.76	7.90±0.09	31.84±0.49	25.89±0.23	48.39±0.51
Tharai Bay	31.11±1.23	7.96±0.06	31.95±0.40	23.41±1.43	48.52±0.62
Western coast of Changnoi	35.56±0.21	8.21±0.04	32.27±0.21	20.32±8.47	51.19±0.01
Eastern coast of Changnoi	35.27±0.12	8.23±0.23	31.37±0.51	21.76±11.41	52.77±0.25
Sabbarot Bay	35.2 3±0.06	8.20±0.02	31.0±0.2	36.18±16.57	52.07±0.45
Sai Bay	30.41±0.29	8.57±0.06	31.91±0.15	29.77±13.29	54.18±0.50
Kluai Bay	31.12±0.26	8.55±0.02	32.20±0.12	34.64±1.69	55.30±0.44
Praw Bay	30.30±0.24	8.57±0.04	30.99±0.11	24.93±12.10	52.38±0.07
Thongtanod Bay	31.36±0.16	7.80±0.06	36.49±1.33	16.55±1.71	61.34±0.24
Kraten Island	31.19±0.14	7.88±0.0	36.07±0.01	20.77±3.54	61.23±0.13
Mudsum Island	31.19±0.14	7.88±0.00	36.07±0.01	20.77±3.54	66.93±0.04
Bang Num Chet	32.17±0.21	8.63±0.11	34.18±0.22	16.59±3.22	59.16±0.16

world are found in islands and some pinnid species occur between the islands in the gulf. These species include *P. carnea*, which usually occurs between the islands of Bermuda (Yonge, 1953), and *P. nobilis* which is commonly found on islands within the Mediterranean, such as Antioco Island in the Gulf of Oristano (Addis et al., 2009), Djerba Islands in the Gulf of Gabes (Rabaoui et al., 2010), Columbretes Island (García-March and Márquez-Aliaga, 2007) and areas around the island of Majorca and the Balearic Islands in Spain (Hendriks et al., 2013). The islands in the Gulf of Thailand were one of important habitats for pinnid populations which mostly occur close to islands. The Gulf of Thailand is a semi-enclosed extension of the South China Sea. The current systems in the gulf include a surface current pattern during the northeast monsoon that moves from the South China

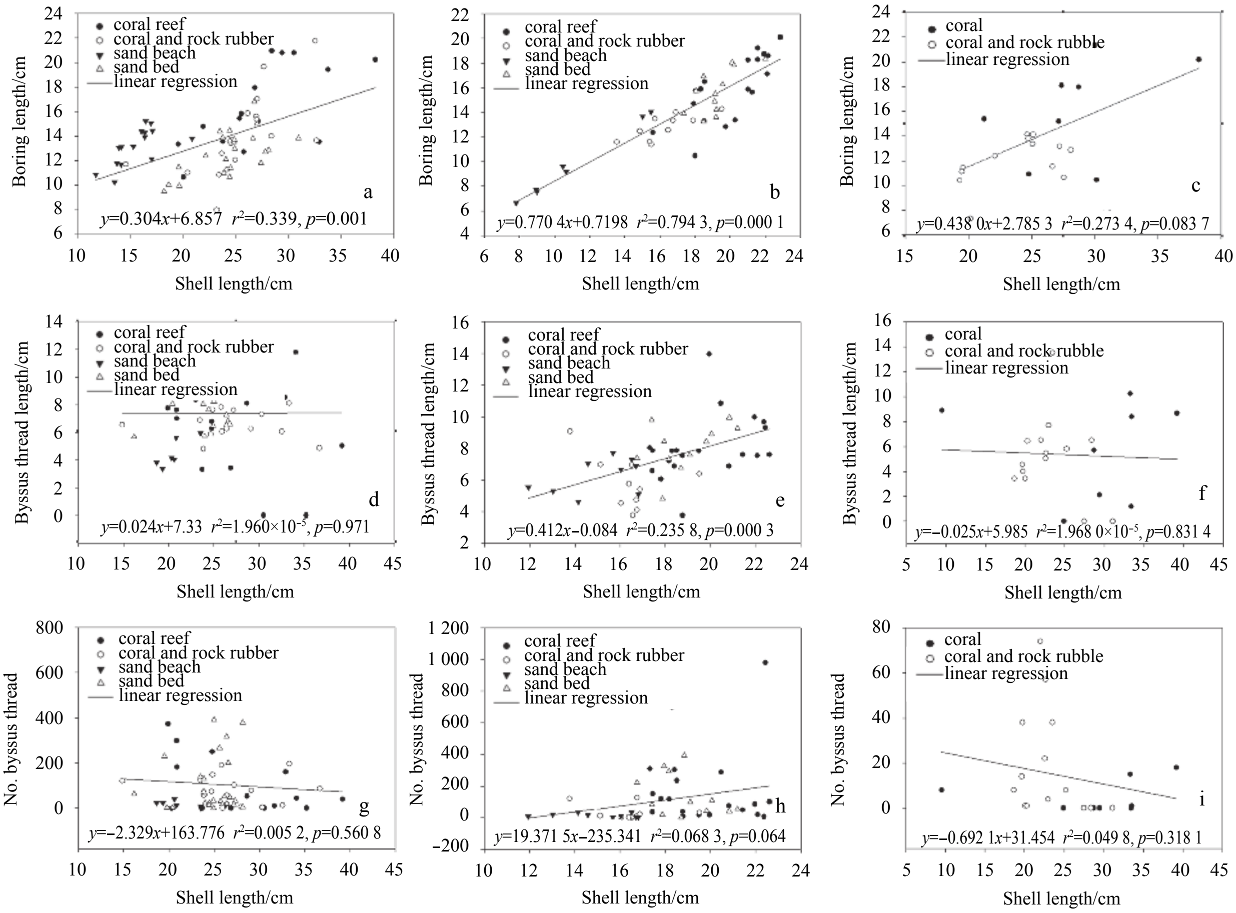

Fig. 12. Mean for the relationship between shell length (cm) (x-axis) and boring length in sediment (cm) (y-axis) of pinnids, all data in plot; *P. atropurpurea* (a) and *A. vexillum* (b) by four habitats and *P. deltodes* (c) by two coral associated habitats; and the relationship between shell length (cm) (x-axis) and byssus thread characteristics of *P. atropurpurea* (d, g), *A. vexillum* (e, h) and *P. deltodes* (f, i).

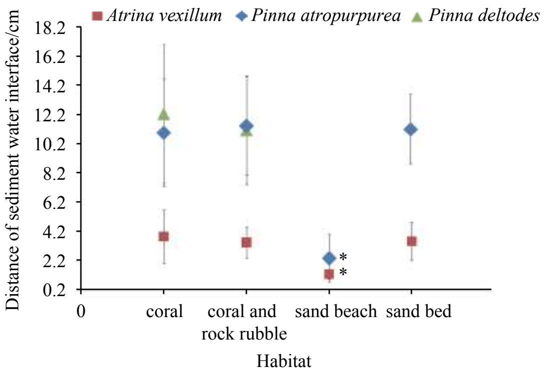

Fig. 13. Mean and SE of distance of sediment-water interface (cm) of three Pinnidae from each habitat. * Significant different at 95% confident level.

Sea, past China and down to the Gulf of Thailand from December to May (Chansang et al., 1999; Yanagi et al., 2001). There is also a southwest monsoon that moves along the Sunda Shelf, from Peninsular Malaysia up to the Gulf of Thailand from June to November (Chansang et al., 1999; Yanagi et al., 2001). Then islands in the Gulf of Thailand are sheltered habitats with a high abundance of pinnid species. However, two sites in the Gulf of Thailand (Tharai Bay and Praw Bay) were with abundance of no pinnid species in spite of the presence of ideal habitat characteristics, such as an open coastline facing strong sea waves. This finding was similar to that of Rabaoui et al. (2008) who also found no pinnids in expected sites on the Tunisian coast. They proposed that the absence may have been due to recent habitat modifications due to environmental conditions.

Pinnidae were found at varying depths in the sub-tidal or intertidal zone (Butler and Brewster, 1979; Butler and Keough, 1981; Butler, 1987; Katsanevakis, 2006; Rabaoui et al., 2008, 2010). Shallow intertidal water depth (no more than 4 m) was preferred by pinnid species in this study. This study demonstrated that the Gulf of Thailand provides details on microhabitats and the distribution of pinnids at a species level. Interestingly, pinnids were found in sites with four different habitats, including sand beaches, sand bed coral reefs and coral mixed with rock. This could explain the distribution flexibility of this family which occur over a broad habitat range. The finding could support Katsanevakis (2006) who asserted that habitats for *Pinna* are not specific; they do not require only seagrass meadows, and they can exist in bare soft sediment as well.

A clumped distribution pattern has been found in pinnids from many places around the world. These species include *P. nobilis* (Coppa et al., 2010; García-March et al., 2007a) and *P. rudis* (Nebot-Colomer et al., 2016) from the Mediterranean Sea, and *P.*

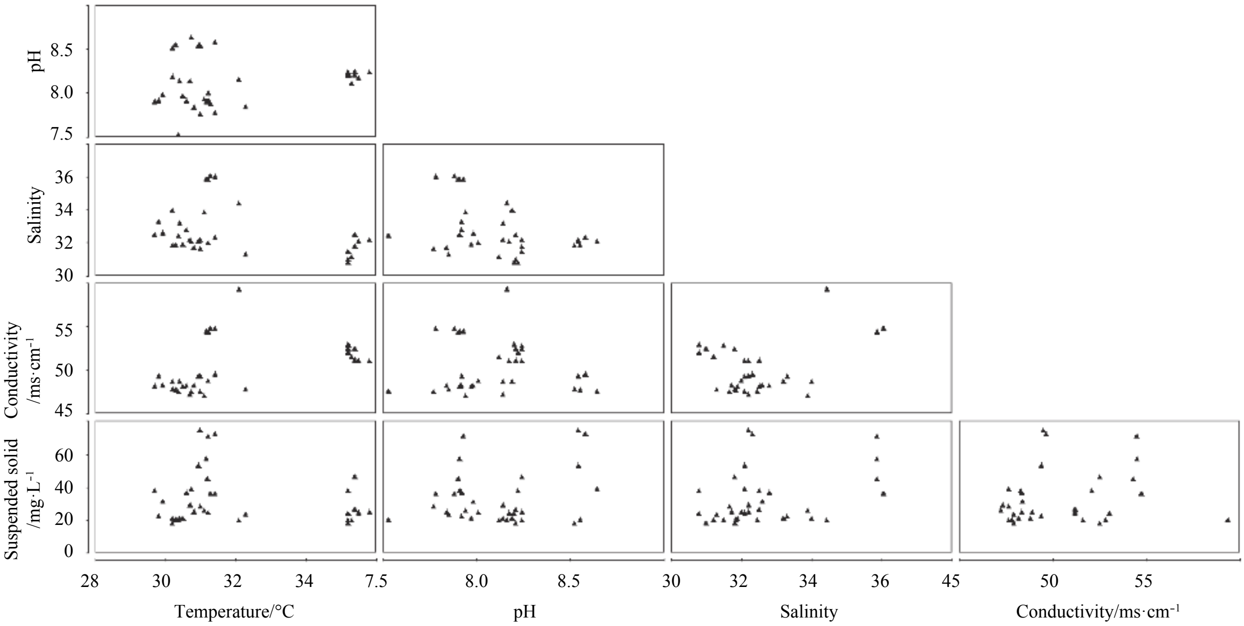

Fig. 14. Pairwise scatter plots of the environmental variables (low correlation with the maximum coefficient 0.500 between salinity and conductivity).

bicolor from South Australia and South Western Australia (Butler and Keough, 1981; Butler, 1987). Pinnid individuals tend to be attracted to particular locations within an environment. Aggregation patterns in pinnids may be explained by higher survival in particular habitats (Begon et al., 1996).

The distribution of the three pinnid species this study surveyed were uniform in distribution following the Morisita's index, meaning that pinnid populations presented with one or more individuals per plot. A maximum of five individuals were found per plot, although some sites had none or only one individual per plot. Generally, a regular or uniform dispersion is a common pattern in forests and monoculture plantations where there is competition between individuals or positive antagonism that promotes uniform spacing in land reference (Odum, 2004). This uniform pattern was demonstrated in most coral reef habitats, which demonstrates a successful adaptation to competition in limited sediment space for pinnid larvae. Other sites, such as Mudsum which had sand beds and reefs and the Randokmai Island which had coral and rock rubble, presented uniform patterns that were not significantly different from a random distribution. These habitats provided a homogenous space or stable area as sediment for larvae to settle. This may support the random distribution of pinnid species occurring in the open and in huge gaps of sediment. This case was similar to studies of *P. nobilis* which found that random distribution occurred in sea beds dominated by meadows of seagrass in the Moraira Bay (García-March et al., 2007b) and Lake Vouliagmeni (Katsanevakis, 2006). Katsanevakis (2006) suggested that dispersion of pinnids was related to quadrate size. Random distribution of pinnids occurred in small quadrats in small-scale samples whereas aggregated distribution was found in large-scale samples. The positive correlation of dispersion indices with quadrat area may be related to the corresponding scale of patchiness in an environment. Our study could attribute the flexible distribution of pinnid populations to differences in sediment space and habitats required by larvae. Then clumping in pinnids is not gregarious behaviour because in some habitats, a random distribution pattern was shown, indicating possible ecological reasons behind population distribution.

Pinnidae abundance in sand habitats, such as sand beds and sand beaches, were significantly different from pinnids in coral habitats. It is possible that sand habitats provided particularly substrate for supporting the abundance of *A. vexillum* and *P. atropurpurea* that different from coral. Yonge (1953) described the habits that Pinnidae always live embedded vertically in soft substrata with enough underlying gravel to provide byssus threads attachment.

Density of pinnids in the Gulf of Thailand varied from site to site, with some sites containing no individuals and others containing 2.67 ind./m^2 (maximum density found). Although, the Gulf of Thailand is geographically small, the high density values found in this area are indicative of healthy populations. The figures found in this study are much higher than other species in the Pinnidae family in regions that developed during a similar time frame (approximately 2000 BC) (Šiletić and Peharda, 2003; Katsanevakis, 2006; Idris et al., 2008; Rabaoui et al., 2008; Caronni and Navone, 2010; Fryganiotis et al., 2013; Hendriks et al., 2013). The density of Mediterranean *Pinna*, such as *P. nobilis*, ranged from 0.002 to 0.20 ind./m^2 in seagrass and rocky substrate (Šiletić and Peharda, 2003; Katsanevakis, 2006; Rabaoui et al., 2008; Caronni and Navone, 2010; Fryganiotis et al., 2013; Hendriks et al., 2013). Another Mediterranean species, *P. rudis*, ranged from 0.0 to 6.89 individuals per 100 m^2 (Nebot-Colomer et al., 2016). Thai pinnids, mainly from corals and sands habitats, showed higher density than pinnids in the seagrass habitat of Sungai Pulai, South Western Johor coast of Malaysia in the South China Sea region (less than 0.02 ind./m^2) and the seven pinnid species reported by Idris et al. (2008). The difference in density can be explained by larvae survival and accumulation differences. Nebot-Colomer et al. (2016) suggested that areas with the highest densities commonly indicate an optimum area for larval growth and settlement.

Pinnidae are suspension-feeding bivalves that often depend on the local productivity of phytoplankton as a food source (Newell, 2004). Among many environmental factors, the growth

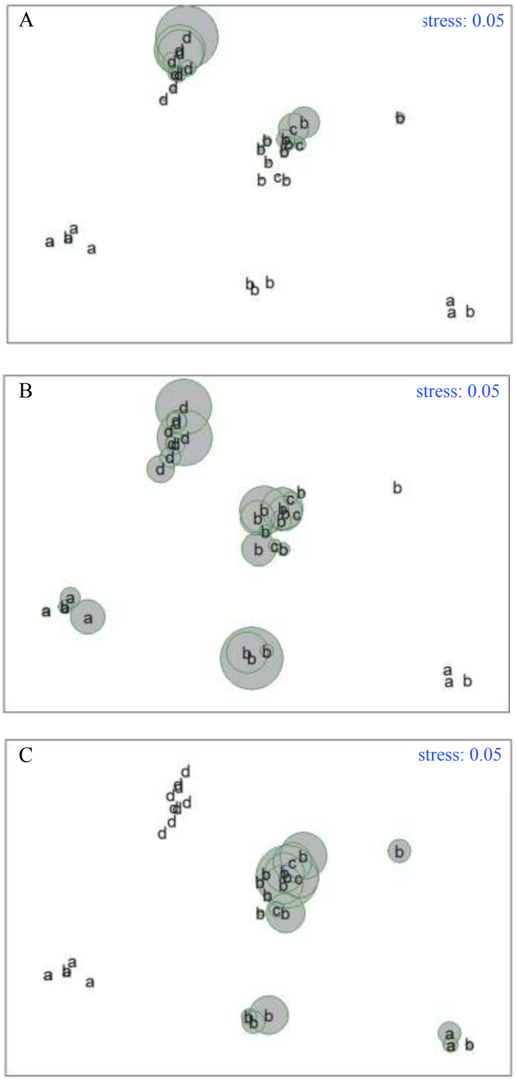

Fig. 15. MDS ordination of Bray-Curtis matrix of similarities from fourth root transferred species abundance based on between 36 localities. Four classes of sand composition percentage were categories: a<10%, b=11%–29%, c=30%–59%, d>60%. Circles of increasing size represent increasing pinnid abundance in *P. atropurpurea* (A), *A. vexillum* (B) and *P. deltodes* (C) (stress value 0.05).

and survival of *Pinna* juveniles is influenced by the presence of chlorophyll *a* and particle organic matter (Acarli et al., 2011; Silina, 2012). Many researchers suggest that food availability is an important factor influencing the density in Pinnidae populations (Wu and Shin, 1998; Šiletić and Peharda, 2003; Silina, 2012). The Gulf of Thailand receives discharges from four main rivers (in the northern part of the gulf) which contribute important sources of nutrients for phytoplankton photosynthesis (Buranapratheprat et al., 2008). In this area, Chalermwat and Lutz (1989) reported extensive aquaculture, especially for shellfish. Shellfish, including green mussel, oyster and blood clam, are intensely farmed in this area. In addition to food availability, warm water temperatures (particularly warm bottom temperatures throughout the year, i.e., 30–35°C in the Gulf of Thailand; Yeemin, unpublished data) may also help the settlement of pinnid larvae. Growth of newly settled young pinnid is rapid in shallow waters and in the summer months (Butler and Brewster, 1979; Richardson et al., 1999; Katsanevakis 2006; Silina, 2012). Highly productive and suitable environments contribute to the density of pinnids in Thai coastal areas and may be selected by pinnids as habitats in the future.

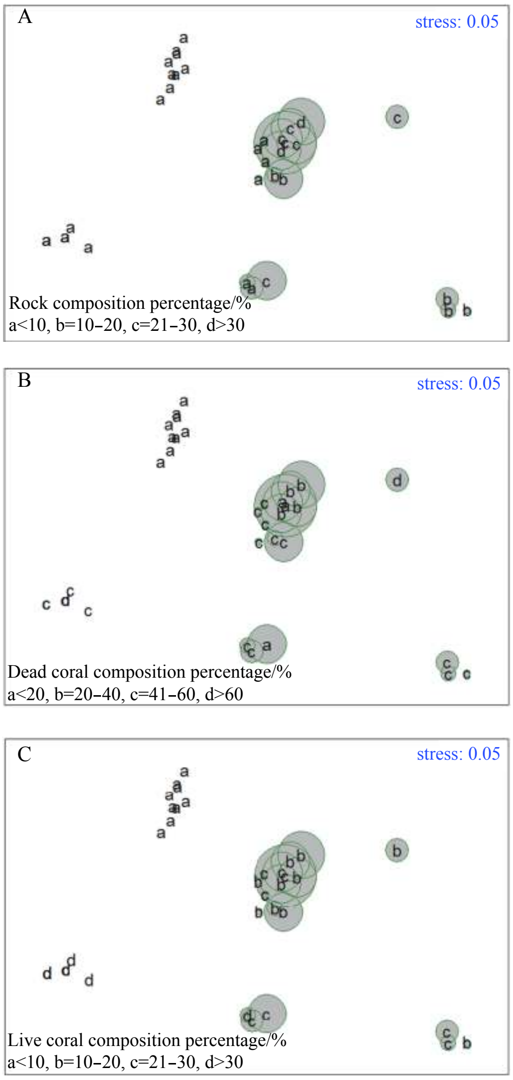

Fig. 16. MDS ordination of Bray-Curtis matrix of similarities from fourth root transferred from *P. deltodes* species abundance under three factors of sediment composition (%): rock (A), dead coral (B) and live coral (C) composition in different categories level (a–d). Circles of increasing size represent increasing abundance of *P. deltodes* (stress value 0.05).

Effective wave sheltering was an important factor in explaining the high density of pinnids in small-scale populations. Mostly pinnid populations that were assessed tended to be denser in sheltered locations than in more exposed ones (García-March et al., 2007a). For example, *P. nobilis* appear in denser populations when they are sheltered from the hydrodynamic forces of wave action (Hendriks et al., 2011). The same trend is seen in populations of *P. rudis*, which use caves as sheltered habitats and are highly concentrated in these areas compared to low densities in other habitats (e.g., rock, sand and seagrass) (Nebot-Colomer et al., 2016). High densities of *P. nobilis* found in Mediterranean waters indicated that this species may favour settlement of larvae at low wave period and intensity in heterogeneous sediment (Richardson et al., 1999; Katsanevakis, 2006; Rabaoui et al., 2008).

The highest densities of pinnids in the Gulf of Thailand oc-

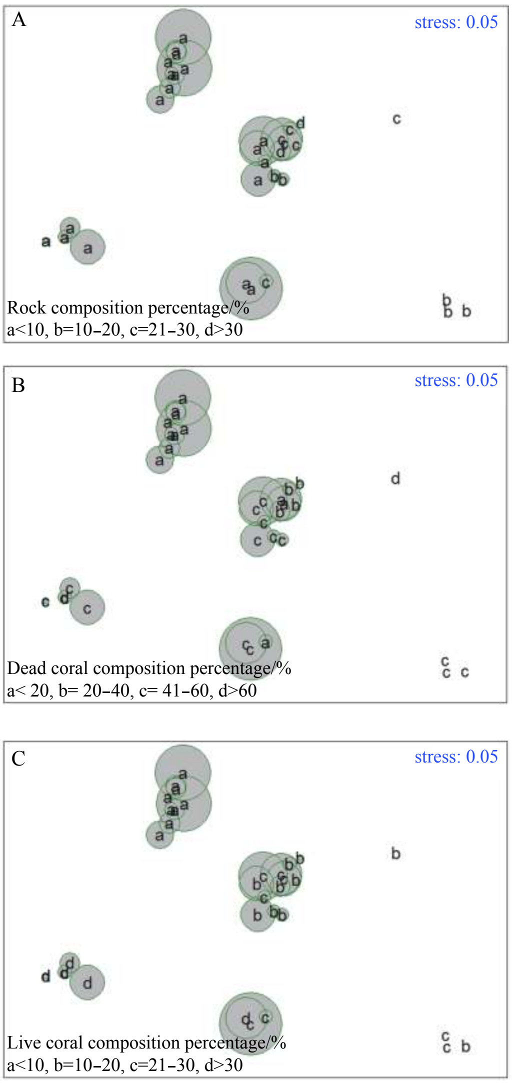

Fig. 17. MDS ordination of Bray-Curtis matrix of similarities from fourth root transferred from *A. vexillum* species abundance under three factors of sediment composition (%): rock (A), dead coral (B) and live coral (C) composition in four different categories (a–d). Circles of increasing size represent increasing abundance of *A. vexillum* (stress value 0.05).

curred in sand beds, back reef, and the enclosed coastlines of coral reefs or small islands. These habitats using coral reef as barrier to face strong sea wave and large area of sand beds behind reef provide suitable substrate for fan mussel larvae settlement. It might be concluded that pinnid population use indirect benefit of the coral reef to form a community. However, no information has been reported about the relationship between water speed and coral size (García-March et al., 2007b). The large sand beds in this study are similar to habitat characters reported for *P. bicolor* from the Gulf St. Vincent off the coast of Edithburgh, South Australia. These *P. bicolor* populations had a maximum density of 2.8–2.6 ind./m^2.

The low pinnid density found in sand beaches may be related to the high mortality rates found in this study. This habitat had the highest number of dead pinnid shells any other habitats. The cause of mortality in sand beach habitats can be explained by their shallow depths; it is particularly difficult to live in very shallow waters (less than 1 m of water depth) in this area. Some uprooted dead shells and injured shells might be the consequences of hydrodynamic stress from seawater and predators attracted at low tide. Many researches demonstrated the depth and predators as the main factors for pinna mortality. The correlation of depth with environmental factors can be explained by habitat distribution and food productivity (Katsanevakis, 2006, 2007). A significant correlation between fan shell density and depth was demonstrated by Rabaoui et al. (2010). They found no presence of *P. nobilis* in waters shallower than 0.3 m; below this depth, density increased with depth. Moreover, García-March et al. (2007a, b) showed that hydrodynamic stress was reduced in deeper areas, and it controlled the density of *P. nobilis* in the Moraria Bay in the western Mediterranean.

Another possible reason for shell death in sandy beach habitats is the increase in predation pressure (Šiletić and Peharda, 2003). Benthic predators observed in our study were mainly the long-spine sea urchin (*Diadema setosum*) and crabs. These were found in high numbers in the study sites attached to the posterior shell. This was similar to a report of the mortality from transplanted *P. bicolor* predominantly caused by crabs and fish (Wu and Shin, 1998). Shell damage by predators can expose soft tissues and increase sensitivity to other causes of death (Dietl and Alexander, 2005). Mortality in shallow waters can also be caused by the harvesting of larger individuals by humans (Katsanevakis, 2006, 2007; Rabaoui et al., 2008). The high visibility of these shells may partly explain the low density in this habitat compared to others in the Gulf of Thailand.

The shell morphology and behaviour of Pinnidae species could be the cause of differences in mortality. The lower mortality of *Atrina* species than *Pinna* species from all habitats in this study may be explained by the natural round shape and the shorter hinge line with a broad byssal sinus (Yonge, 1953; Stanley, 1970; Schultz and Huber, 2013). In terms of behaviour, *Atrina* species bury themselves more completely and deeply in the sediment than *Pinna* species (Yonge, 1953; Richardson et al., 1999; García-March et al., 2007a). This not only decreases the opportunity of predator contact but also reduces the chance of being washed out to sea by waves and desiccated during low tide (Neubauer et al., 2013). Stanley (1970) found that *A. rigida* buried themselves more deeply than *P. carnea*. Stanley (1970) also found that *A. rigida* was more effective at anchoring themselves in the sediment and had a deeper burrowing mechanism, since its periodic muscular contraction was apparent during ontogeny.

The general size of pinnid specimens in the Gulf of Thailand ranged from 11 to 40 cm. The genus *Pinna* was similar in size to *P. bicolor* from Australia (Butler and Brewster, 1979). Butler and Brewster (1979) reported size-class by the modal length and estimated the age of *P. bicolor* by size: year-old shells should be 20 cm, two-year-old shells should be 26 cm and three-year-old shells should be 35 cm or longer. It is common for this family to show variable success in recruitment and a growth rate which decreases with age (Butler and Brewster, 1979; Idris et al., 2008; Silina, 2012).

Size frequency distribution of the three pinnid populations in our study among the four habitats showed that the largest shell lengths were from coral or coral associated areas such as coral and rock rubble and sand bed back reef. The sand beach habitat had a high frequency of the smallest shell size (11–25 cm). There are two main reasons why different shell sizes would be found in different habitats. First, shell size in the family Pinnidae may be related to the growth curve of the animal or the physical factors in the study site (Richardson, 1999; Šiletić and Peharda, 2003; Rabaoui et al., 2008; Idris et al., 2011; Silina, 2012). Second, larger size of the same species may result from older individuals staying longer under fewer disturbances. García-March et al. (2007a) showed that large individuals of *P. nobilis* survived by being completely hidden by the leaves of *Posidonia oceanica* in Mediterranean water. While pinnids from sand beaches may have a higher frequency of younger shells than other habitats, small shell size may also be selected by the mortality pressure as previous discussion. For example, Katsanevakis (2007) and García-March et al. (2007a) demonstrated that natural mortality was strikingly size-dependent in *P. nobilis*, suggesting that the likelihood of mortality increased as fan mussels grew in size. Rabaoui et al. (2008) suggested that the high frequency of small *P. nobilis* individuals in sandy and shallow sites on the Tunisian coast may be because the site is a recruitment area for juveniles. In this study, small shell size may improve survival rates in sand beaches at low tide. This case was similar to the study on transplanted *P. bicolor*, Wu and Shin (1998) demonstrated that young and small individuals were protected from high flow speeds. Another possible advantage of small shell size is the short distance in the sediment-water interface on posterior side which may protect from predation or prevent the shell mantle being exposed to air. It was demonstrated in both *Atrina* and *Pinna* at the sand beaches site. Pinnidae has the capacity to withdraw the mantle and squeeze the shell edges together. Mantle retraction and flexible margins are advantageous in surviving marginal injuries (Yonge, 1953) and speeding up the regeneration of damaged shells (Dietl and Alexander, 2005).

Members of Pinnidae always live vertically embedded in soft substrata, using byssus threads to attach themselves to gravel (Rosewater, 1961; Yonge, 1953) and in crevices or cement themselves to substratum (Schultz and Huber, 2013). Survival of byssates living in each habitat probably depends on adjustments of their thread character or the development of boring mechanisms (Printrakoon and Tëmkin, 2008; Pearce and La Barbera, 2009).

This study demonstrated that members of Pinnidae increase their boring depth when shell length increases to prevent dislodgment from sediment in the same trend of all pinnids in all habitat types. However, *Atrina* shows more effective byssus threads in the burrowing mechanism by increase length and number of byssus threads when shell size increases. This makes *Atrina* a stronger, deeper borer than *Pinna* which may also make it less susceptible to mortality.

Composition of sediment characteristics was an important factor in determining the species type and abundance of Pinnidae in this study. Our results concurred with those of Addis et al. (2009) who suggested that settlement and distribution of *Pinna* in estuarine and unvegetated sea floors would be determined by sediment. *Pinna* have been reported as living primarily in sandy sediment (Stanley, 1970). Populations of *P. atropurpurea* in subtidal areas use byssus threads to attach themselves to soft muddy sand in the Indo-Pacific region (Schultz and Huber, 2013). A high abundance of *P. atropurpurea* occurred in habitats with very high soft sediment composition (more than 60%), particular sand habitats (sand beds and sand beaches), throughout the Gulf of Thailand. *Pinna* individuals need more sand since it is the appropriate substrate for the settlement and survival of larvae. Since *Pinna* shell is very large, elongated and thin, it can only be buried in the sediment to about half the shell's length (Stanley, 1970).Therefore, sandy sediment may enhance a stable vertical position without uprooting the shell.

Generally, *P. deltodes* prefers hard substratum of either rock-strewn reefs of coral blocks and head (Scheltema, 1983; Schultz and Hubber, 2013). Moreover, Schultz and Hubber (2013) reported that *P. deltodes* individuals shallowly buried themselves in sand among these hard substrates, coral and rock reef. Idris et al. (2008) reported that rocky shore areas from the south part of Peninsular Malaysia were the habitat for *P. deltodes*.

Rock and coral habitats of the Gulf of Thailand are an appropriate habitat for this species which prefer sites with more than 20% rock composition. This study revealed that *P. deltodes* used the shortest byssus threads and the lowest number of byssus threads for sediment attachment than any member of Pinnidae. Some of *P. deltodes* live behind rock or orientate themselves at narrow angles to bottom instead of boring deeper into sand sediment. Interestingly, Schultz and Huber (2013) reported finding some specimens oriented horizontally under coral blocks. The byssus of this species allows attachment to a variety of surrounding broken rocks or coral fragments (Printrakoon, pers. obs.). Similar to *P. nobilis*, one of the largest mollusc species, typically occurs in association with *Posidonia oceanic* meadows. This fan mussel utilizes the rhizomes and shoots of *P. oceanic* to attach their numerous byssus filaments to anchor themselves and live partially buried upright in the sand (Coppa et al., 2010; Hendriks et al., 2011).

In this study, *A. vexillum* was found buried in various sand sediment compositions. Its shell is round with a short posterior end, which is advantageous for burial in small spaces or shallow sediment (Yonge, 1953; Schultz and Huber, 2013) of various habitats including sand, coral sand and sandy mud in seagrass flats. Its versatile shape explains why *A. vexillum* was commonly found in all sites and also the highest density was specifically found in small limited sediment gap under coral reef habitat.

In summary, the Gulf of Thailand is an important place for Pinnidae populations, and it provides varied habitats that benefits high density and biomass. Coral reefs are one of the most important marine habitats in shallow tropical seas, and they provide a number of important ecosystem services (Moberg and Folke, 1999). Coral reefs are mainly found fringing islands in the Gulf of Thailand. This habitat and the seagrass provide direct and indirect shelter for Pinnidae. In terms of production, reefs provide structure and act as focal points for secondary producers. Also, shelter from hydrodynamic forces in reefs enhanced by increasing sedimentary fluxes may increase food supplies to support large filter-feeder bivalves (Moberg and Folke, 1999). However, habitat destruction and over-exploitation of pinnids as a food source may be an important factor limiting pinnid population density in the future. The database constructed during the course of this study will assist in understanding the ecology of the family Pinnidae and will inform management and conservation efforts in the future.

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References

Abbott R T, Dance S P. 2000. Compendium of Seashells. California: Odyssey Publishing

Acarli S, Lök A, Yigitkurt S, et al. 2011. Culture of Fan mussel (*Pinna nobilis*, Linnaeus 1758) in relation to size on suspended culture system in Izmir Bay, Aegean Sea, Turkey. Kafkas Universitesi Veteriner Fakultesi Dergisi, 17(6): 995–1002

Addis P, Secci M, Brundu G, et al. 2009. Density, size structure, shell orientation and epibiontic colonization of the fan mussel *Pinna nobilis* L. 1758 (Mollusca: Bivalvia) in three contrasting habitats in an estuarine area of Sardinia (W Mediterranean). Scientia Marina, 73(1): 129–141

Amornjaruchit S. 1988. Economically important molluscan shellfish of thailand. In: McCoy EW, Chongpeepien T, eds. Bivalve mollusc culture Research in Thailand. Thailand: Department of Fisheries, Bangkok, 1–18

Arizpe C O. 1995. Mortality, growth and somatic secondary production of the bivalve, *Pinna rugosa* (Sowerby), in suspended and bottom culture in Bahia de La Paz, Mexico. Aquaculture Research, 26(11): 843–853

Beer A C, Southgate P C. 2006. Spat collection, growth and meat yield of *Pinna bicolor* (Gmelin) in suspended culture in northern Australia. Aquaculture, 258(1–4): 424–429

Begon M, Harper J, Townsend C. 1996. Ecology: Individuals, Populations and Communities. 3rd ed. Oxford: Backwell Science Ltd

Buranapratheprat A, Yanag T, Niemann O K, et al. 2008. Surface chlorophyll-a dynamics in the upper gulf of Thailand revealed by a coupled hydrodynamic-ecosystem model. Journal of Oceanography, 64(5): 639–656

Butler A J, Brewster F J. 1979. Size distributions and growth of the Fan-shell pinna bicolor Gmelin (Mollusca: Eulamellibranchia) in South Australia. Australian Journal of Marine and Freshwater Research, 30(1): 25–39

Butler A J, Keough M J. 1981. Distribution of pinna bicolor Gmelin (Mollusca: Bivalvia) in South Australia with observations on recruitment. Transaction of Research Society of Science, 105(1): 29–39

Butler A J. 1987. Ecology of *Pinna bicolor* Gmelin (Mollusca: Bivalvia) in gulf st vincent, south Australia: density, reproductive cycle, recruitment, growth and mortality at three sites. Australian Journal of Marine and Freshwater Research, 38(6): 743–769

Caronni S, Navone A. 2010. Density and size of the fan mussel *Pinna nobilis* (Linnaeus, 1758) in two differently protected zones of Tavolara-Punta Coda Cavallo Marine Protected Area. Biologia Marina Mediterranea, 17(1): 294–295

Carr D. 1991. Distribution of bivalves and gastropods in Phang-Nga Bay, South Thailand. Phuket Marine Biological Center Research Bulletin, 56: 11–22

Cendejas J M, Carvallo M G, Juarez L M. 1985. Experimental spat collection and early growth of the pen shell, *Pinna rugosa* (Pelecypoda: Pinnidae), from the Gulf of California. Aquaculture, 48(3–4): 331–336

Chalermwat K, Lutz R A. 1989. Farming the green mussel in Thailand. World Aquacult, 20: 41–46

Chansang H, Satapoomin U, Poovachiranon S. 1999. Maps of coral reefs in Thai's waters, vol 1. Gulf of Thailand. Coral Reef Management Project. Phuket, Thailand: Department of Fisheries

Clarke K R, Warwick R M. 1994. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. Plymouth: Plymouth Marine Laboratory

Coppa S, Guala I, De Lucia G A, et al. 2010. Density and distribution patterns of the endangered species *Pinna nobilis* within a *Posidonia oceanica* meadow in the Gulf of Oristano (Italy). Journal of the Marine Biological Association of the United Kingdom, 90(5): 885–894

Dietl P G, Alexander R R. 2005. High frequency and severity of breakage-induced shell repair in western Atlantic Pinnidae (Bivalvia). Journal of Molluscan Studies, 71(3): 307–311

English S, Wilkinson C, Baker V. 1997. Survey Manual for Tropical Marine Resources. 2nd ed. ASEAN-Australia Marine Science Project. Australia: Living Coastal Resources, Australian Institute of Marine Science, Townsville Mail Centre, Australia

Fryganiotis K, Antoniadou C, Chintiroglou C. 2013. Comparative distribution of the fan mussel *Atrina fragilis* (Bivalvia, Pinnidae) in protected and trawled areas of the north Aegean Sea (Thermaikos Gulf). Mediterranean Marine Science, 14(1): 119–124

García-March J R, Márquez-Aliaga A. 2007. *Pinna nobilis* L., 1758 age determination by internal shell register. Marine Biology, 151(3): 1077–1085

García-March J R, García-Carrascosa A M, Catero A L P, et al. 2007a. Population structure, mortality and growth of *Pinna nobilis* Linnaeus, 1758 (Mollusca, Bivalvia) at different depths in Moraira Bay (Alicante, western Mediterranean). Marine Biology, 150(5): 861–871

García-March J R, Pérez-Rojas L, García-Carrascosa A M. 2007b. Influence of hydrodynamic forces on population structure of *Pinna nobilis* L., 1758 (Mollusca: Bivalvia): the critical combination of drag force, water depth, shell size and orientation. Journal of Experimental Marine Biology and Ecology, 342(2): 202–212

Hendriks I E, Cabanellas-Reboredo M, Bouma T J, et al. 2011. Seagrass meadows modify drag forces on the shell of the fan mussel *Pinna nobilis*. Estuaries and Coasts, 34(1): 60–67

Hendriks I E, Tenan S, Tavecchia G, et al. 2013. Boat anchoring impacts coastal populations of the pen shell, the largest bivalve in the Mediterranean. Biological Conservation, 160: 105–113

Idris M H, Arshad A, Bujang J S, et al. 2008. New distribution record of two pen shells (Bivalvia: Pinnidae) from the Seagrass Beds of Sungai Pulai, Johore, Malaysia. Journal of Biological Sciences, 8(5): 882–888

Idris M H, Arshad A, Amin S M N, et al. 2011. Age, growth and length-weight relationships of *Pinna bicolor* Gmelin (Bivalvia: Pinnidae) in the seagrass beds of Sungai Pulai Estuary, Johor, Peninsular Malaysia. Journal of Applied Ichthyology, 28(4): 597–600

Katsanevakis S. 2006. Population ecology of the endangered fan mussel *Pinna nobilis* in a marine lake. Endangered Species Research, 1(1): 51–59

Katsanevakis S. 2007. Growth and mortality rates of the fan mussel *Pinna nobilis* in Lake Vouliagmeni (Korinthiakos Gulf, Greece): a generalized additive modelling approach. Marine Biology, 152(6): 1319–1331

Kurozumi T, Kosuge T, Tsuchiya M. 1989. List of shallow-water marine molluscs in the Sichang Island, the Gulf of Thailand. Galaxea, 8: 295–310

Macreadic P, Kimbro D, Fourgerit V, et al. 2014. Effects of Pinna clams on benthic macro-fauna and the possible implementation of their removal. Journal of Molluscan Studies, 80(1): 102–106

Moberg F, Folke C. 1999. Ecological goods and services of coral reef ecosystems. Ecological Economics, 29(2): 215–233

Morisita M. 1962. Iσ-index, a measure of dispersion of individuals. Researches on Population Ecology, 4(1): 1–7

Morris S, Purchon R D. 1981. The marine shelled mollusca of West Malaysia and Singapore Part 3, Bivalvia. Journal of Molluscan Studies, 47(3): 322–327

Nebot-Colomer E, Vázquez-Luis M, García-March J R, et al. 2016. Population structure and growth of the threatened pen shell, *Pinna rudis* (Linnaeus, 1758) in a Western mediterranean marine protected area. Mediterranean Marine Science, 17(3): 785–793

Neubauer T A, Harzhauser M, Mandic O. 2013. Phenotypic evolution in a venerid bivalve species lineage from the late Middle Miocene Central Paratethys Sea: a multi-approach morphometric analysis. Biological Journal of the Linnean Society, 110(2): 320–334

Nielson C. 1976. An illustrated checklist of the bivalves from P.M.B.C. beach with a reef flat at Phuket, Thailand. Phuket Marine Biological Center Research Bulletin, 9: 1–7

Newell R I E. 2004. Ecosystem influences of natural and cultivated populations of suspended-feeding bivalve molluscs: A review. Journal of Shellfish Research, 23(1): 51–61

Odum E P, Barrett G W. 2004. Fundamentals of Ecology. 5th ed. Stamford: Cengage Learning

Office of Natural Resources and Environment Policy and Planning. 2004. Thailand's Coastal Resources and Environmental Profile. Bangkok, Thailand: Ministry of Natural Resources and Environment, 201

Pearce T, La Barbera M. 2009. Biomechanids of byssal threads outside the Mytilidae: *Atrina rigida* and Ctenoidesmitis. Journal of Experimental Biology, 212(10): 1449–1454

Printrakoon C, Tëmkin I. 2008. Comparative ecology of two parapatric populations of *Isognomon* (Bivalvia: Iognomonidae) of Kungkrabaen Bay, Thailand. The Raffles Bulletin of Zoology, 18: 75–94

Purchon R D, Purchon D E A. 1981. The marine shelled Mollusca of west Malaysia and Singapore: Part 1. General Introduction and an account of the collecting Station. Journal of Molluscan Studies, 47: 290–312

Rabaoui L S, Tlig-Zouari S, Hassine K B, et al. 2008. Distribution and habitat of the fan mussel *Pinna nobilis* Linnaeus, 1758 (Mollusca: Bivalvia) in the northern and eastern Tunisian coasts. Cahier de Biologie Marine, 49: 67–78

Rabaoui L S, Tlig-Zouari S, Katsanevakis S, et al. 2010. Modelling population density of *Pinna nobilis* (Bivalvia) on the eastern and southeastern coast of Tunisia. Journal of Molluscan Studies, 76(4): 340–347

Richardson C A, Peharda M, Kennedy H, et al. 2004. Age, growth rate and season of recruitment of *Pinna nobilis* (L) in the Croatian Adriatic determined from Mg: Ca and Sr: Ca shell profiles. Journal of Experimental Marine Biology and Ecology, 299(1): 1–16

Rosewater J R. 1961. The family pinnidae in the indo-pacific. Indo-Pacific Mollusca, Philadelphia, 1(4): 175–226

Sanpanich K. 2011. Marine bivalves occurring on the east coast of the Gulf of Thailand. Science Asia, 37: 195–204

Scheltema A. 1983. *Pinna deltodes* Menke newly described and differentiated from *P. bicolor* Gmelin (Bivalvia, Pterioida). Journal of the Malacological Society of Australia, 6(1–2): 37–52

Schultz P W W, Huber M. 2013. Revision of the worldwide recent Pinnidae and some remarks on fossil European Pinnidae. Acta Conchyliorum13. Club Conchylia: Öhringen, 1–164

Šiletić T, Peharda M. 2003. Population study of the fan shell *Pinna nobilis* L. in Malo and Veliko Jezero of the Mljet National Park (Adriatic Sea). Scientia Marina, 67(1): 91–98

Silina A V. 2012. Growth of Bivalve *Atrina vexillum* in the Gulf of Thailand. Journal of Shellfish Research, 31(4): 989–995

Stanley S M. 1970. Relation of shell form to life habits of the Bivalvia (Mollusca). Memoir 125. Boulder: The Geological Society of America, Inc

Swennen C, Moolenbeek R G, Ruttanadakul N, et al. 2001. The Molluscs of the Southern Gulf of Thailand. Bangkok: The Biodiversity Research and Training Program, 4: 70–71

Tantanasiriwong R. 1979. A checklist of Marine bivalves from Phuket Island, adjacent mainland and offshore islands, Western Peninsula Thailand. Phuket Marine Biological Center Research Bulletin, 27: 1–15

Turner R D, Rosewater J. 1958. The family Pinnidae in the Western Atlantic. Johnsonia Monographs of the marine mollusks of the Western Atlantic. Cambridge, MA: Department of Mollusks, Museum of Comparative Zoology, 328–385

Wu R S S, Shin P K S. 1998. Transplant experiments on growth and mortality of the fan mussel *Pinna bicolor*. Aquaculture, 163(1–2): 47–62

Xue Dongxiu, Wang Haiyan, Zhang Tao, et al. 2012. Morphological and Genetic Identification of the Validity of the Species *Atrina chinensis* (Bivalvia: Pinnidae). Journal of Shellfish Research, 31(3): 739–747

Yanagi T, Sachoemar S I, Takao T, et al. 2001. Seasonal variation of stratification in the Gulf of Thailand. Journal of Oceanography, 57(4): 461–470

Yonge C M. 1953. Form and Habitat in *Pinna carnea* Gmelin. Philosophical Transactions of the Royal Society B: Biological Sciences, 237(648): 335–374

Yu Xiangyong, Mao Yong, Wang Meifang, et al. 2004. Genetic heterogeneity analysis and RAPD marker detection among four forms of *Atrina pectinata* Linnaeus. Journal of Shellfish Research, 23(1): 165–171