CHAPTER 4

DISCUSSION

I. Taxonomy of Rhizomedusae

As mentioned earlier, the taxonomy of rhizomedusae was accomplished using only external physical characteristics, most of which were visible to the naked eyes. Some, however, were best viewed under the stereo microscope. Particularly, the terminal tentacles, which were delicate and easily torn during the sampling process.

Among the 6 species of rhizomedusae that were identified from this study, 3 species were relatively easy to distinguish from the rest. They were Cassiopea andromeda, Rhopilema hispidum, and Lobonema smithii. C. andromeda has distinctly flat bell and mouth arms. The color of both the fresh and preserved specimens was also readily recognizable. Fresh C. andromeda specimens were reddish brown in color while preserved specimens appeared greenish brown (Figure 12). R. hispidum was recognized through the presence of scapulae and the bell surface that was obviously rough to touch (Figure 17). L. smithii was distinguished from other species through the presence of papillae allover the bell surface and the elongated marginal lappets, which facilitate locomotion (Figure 16). Acromitus spp. was distinguished from Catostylus sp. through relatively thinner bell and the presence of filaments along the mouth arms and among mouth (Figure 13 and 15). Identification of A. flagellatus and A. hardenbergi were relatively complicated (Figure 13 and 14). These two species are distinguished from each other by the presence of terminal filaments at the tip of the mouth arms (Cornelius, 1995). As these terminal filaments, whose primary functions are defense and prey capture, are extremely thin and fragile, all of the five mouth arms must be checked thoroughly. If, in fact, all terminal filaments were lost during sampling, the identity became uncertain. According to Cornelius (1995), the validity of A. hardenbergi is yet to be confirmed.

Besides the terminal filaments, other characteristics used to identify rhizomedusae were bell shape and bell surface. According the Cornelius (1995), bell shape can be categorized into flat, round, nearly hemispherical, and hemispherical. However, the fixing and preserving solution tended to extract excess water, thus, distort the shape of the

bell in preserved specimens making it rather difficult to distinguish between nearly hemispherical and hemispherical. Likewise, bell surface is categorized into smooth and rough (finely granulated or with protuberances). Bells that were rough, with protuberances, were easily distinguished. In spite of that, bells that appeared smooth to the naked eyes can be finely granulated under the stereo microscope as in the case of *Acromitus flagellatus* and *Acromitus hardenbergi*.

In addition to the external morphologies, Mongkonsangsuree (2002) had revealed that different rhizomedusae have different types of nematocysts, which can be used in the identification process as well (Table 10 and Figure 11).

Table 10. Nematocysts of each species of rhizomedusae (Mongkonsangsuree, 2002).

Species	Type of Nematocysts	
Cassiopea andromeda	Atrichous Isorhiza (Figure 61A)	
Acromitus flagellatus Acromitus hardenbergi Catostylus townsendi Lobonema smithii	Holotrichous Isorhiza (Figure 61B)	
Rhopilema hispidum	Heterotrichous Anisorhiza (Figure 61C)	

The results from this study can be used to create an artificial key to identification for 6 species of rhizomedusae as follows,

1. Bell surface is smooth to touch. 2 3 Bell surface is rough to touch, with protuberances. 2. Bell is relatively flat, mouth arms are flat and wide. Cassiopea andromeda Bell is relatively round, nearly hemispherical. 3. Bell is granulated, with scapulae. Rhopilema hispidum Bell is rough, with papillae. Lobonema smithii 4. Mouth arms without filaments. Catostylus townsendi Mouth arms with filaments among the mouth, and along the mouth arms. 5. Mouth arms with terminal filaments. Acromitus flagellatus Mouth arms without terminal filaments. Acromitus hardenbergi

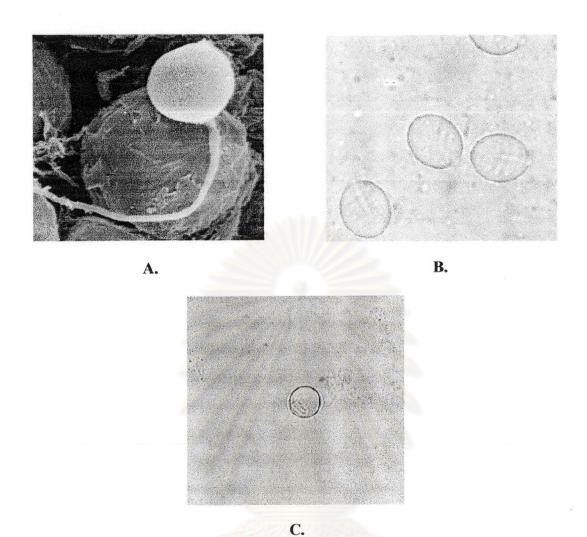


Figure 61. Types of nematocysts found in rhizomedusae; (A) Atrichous Isorhiza, (B) Holotrichous Isorhiza, and (C) Heterotrichous Anisorhiza (Mongkonsangsuree, 2002).

II. Species Diversity and Abundance

During the months when rhizomedusae were found in highest abundance, the results revealed that the abundance of rhizomedusae at Phetchaburi Province was more than 10 times higher in magnitude than that of Chon Buri Province (Figure 18). Furthermore, sampling in Chon Buri and Phetchaburi Provinces yielded 4 and 6 species of rhizomedusae, respectively (Table 6). Such differences in abundance, and species diversity, may be best explained through population dynamics, in term of reproductive strategy, coupling with the surface current pattern, food availability, fishing pressure, and environmental factors, such as salinity, in the Gulf of Thailand.

A typical cnidarian life cycle, characterized by alternation of generation, involves free-swimming medusoid individuals, which produce eggs and spermatozoa. Fertilization results in the zygotes that will eventually develop into the planula larvae. settlement onto the substratum, the planula larvae develop into the polyps, which will undergo asexual reproduction and evolve into the medusoid forms, completing the life cycle. The benthic stages, reproducing asexually, are able to give rise to numerous individuals, which will contribute largely to the recruitment and population continuity of species. Different reproductive success, specifically asexual stages, would probably contribute to the abundance of the medusae at each locale. The medusae, which are planktonic and are carried by surface current, have evolved for the better dispersal of the species (Hardy, 1971). It is highly possible that the parental stocks for Chon Buri and Phetchaburi Provinces originate in different areas, resulting in the variation in species diversity that was observed. In addition, the muddy bottom of the Inner Gulf of Thailand is rather unsuitable for the attachment and development of the benthic stages. Thus, the medusae were likely transported from outside into the Inner Gulf by current. In fact, during the month of March, the current flows northward along the western part of the middle Gulf, and eastward at the upper part of the upper Gulf (Buranapratheprat and Bunpapong, 1998). It can be assumed that the young ephyrae were carried by the current and matured when they reached the coastal water off Chon Buri Province, resulting in the high abundance as observed. If this was the case, scyphozoans larvae should be present in the zooplankton samples obtained from the western part of the Gulf, or at Phetchaburi Province, few months prior to the peak of rhizomedusae at Chon Buri Province. However, scyphozoan larvae were first observed at Phetchaburi Province in July 2000 (Figure 45). In the same manner, in November when rhizomedusae were found in highest abundance at Phetchaburi Province, the direction of flow at the most northern part of the Upper Gulf changes from eastward to westward (Buranapratheprat and Bunpapong, 1998). Zooplankton data revealed the presence of scyphozoan larvae at Chon Buri Province in July 2000 (Figure 45). Thus, it is plausible that these larvae were transported to the western part of the Gulf by current as they grew, resulting in the peak of abundance of rhizomedusae observed in November 2000.

Besides the current, a physiochemical factor, which affected the abundance of rhizomedusae, appeared to be salinity. The average salinity at Chon Buri Province fluctuated severely through out the sampling period. The highest average salinity was observed in February (31.5 \pm 0.1 psu) and the lowest was observed in June 2000 (0.3 \pm 0.0 psu). During the period of low salinity in June and July 2000, either none or less than 5 individuals \cdot 10⁴ m⁻³ of scyphomedusae was obtained from sampling (Figure 62A).

At Phetchaburi Province, on the other hand, the highest value of salinity was observed in March (32.2 ± 0.1 psu) and the lowest in October 2000 (19.9 ± 0.9 psu). The fluctuation of salinity did not appear to be related to the abundance of rhizomedusae at Phetchaburi Province (Figure 62B).

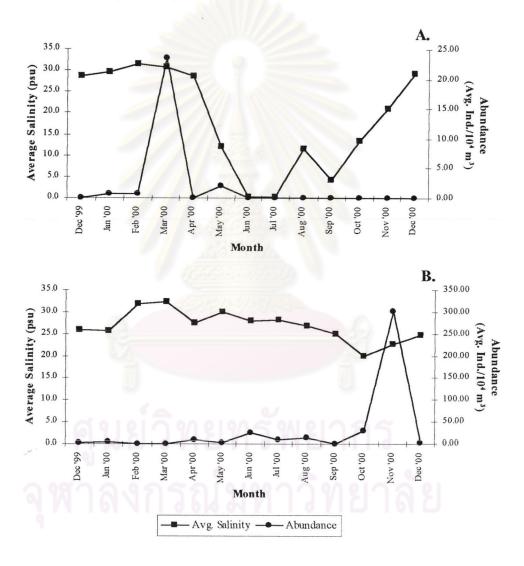


Figure 62. Average salinity and abundance of rhizomedusae at (A) Chon Buri and (B) Phetchaburi Provinces from December 1999 to December 2000.

Scyphozoans are euryhaline, and are able to tolerate a wide range of salinity. The medusae, scyphistomae, and planulae of *Rhopilema esculenta* (order Rhizostomeae) can

survive in varying salinity of 8, 10, and 12 ppt, respectively (Arai, 1997). In the study on biomass and size structure of the scyphomedusae Aurelia aurita in the northwestern Black Sea, Weisse and Gomoiu (2000) revealed that abundance and biomass of medusae were unrelated to temperature and salinity when salinity exceeded 13 ppt. Biomass was relatively low at coastal stations where salinity dropped to less than 11 ppt. Evidently, the salinity values at Chon Buri Province between June to September 2000 were much lower (near 0 psu) than the tolerable range for rhizostome jellyfish. In 1998, the salinity at the mouth of the Bangpakong River was also 0 ppt (BuraphaUniversity, 1998). The freshwater input from the Bangpakong River, situated north of the monthly sampling area, resulted in the low salinity that was observed. In order to confirm this speculation, an extra sampling was carried out further south of the usual sampling area off the coast of Chon Buri Province during August 2000. The average salinity of that particular area was 16.3 ± 0.6 psu. At the end of a tow that lasted for one hour and thirty minutes, a total of 49 specimens (1.80 individuals · 10⁴ m⁻³) of Rhopilema hispidum, an economic species, were yielded. Thus, it can be concluded that the extremely low salinity affected the presence, and magnitude of abundance, of rhizostome scyphozoans at Chon Buri Province.

A biological factor, which appeared to be related to the abundance of rhizomedusae at Chon Buri and Phetchaburi Provinces, was zooplankton concentration. During the summer of 1986, in the Lebanese coastal waters, high production rate of phytoplankton resulting in high zooplankton biomass, high temperature, salinity, and water transparency are believed to be factors responsible for aggregations of *Rhizostoma pulmo*. The outburst of zooplankton was characterized by Chaetognatha, Appendicularia, Cladocera, and other meroplanktonic larvae (Lakkis 1991). At Chon Buri Province, the highest zooplankton concentration occurred during the months of November 2000 (716,569 individuals · 10² m⁻³), where the major fraction of zooplankton were copepods, while the lowest concentration was observed October 2000 (71,703 individuals · 10² m⁻³). Preceding the peak of rhizomedusae, in February 2000, the peaks of few zooplankton prey items were observed. They are polychaetes (Figure 47), barnacle larvae (Figure 48), gastropods (Figure 51), larvaceans (Figure 57), and fish larvae (Figure 58). During the month of March 2000, where the peak of rhizomedusae abundance was observed, a large fraction of the zooplankton population was composed of fish eggs and larvae (91,494

individuals · 10² m⁻³). In April 2000, the total concentration of zooplankton had decreased dramatically. In addition the concentration of fish eggs and larvae had decreased to 23,932 individuals · 10² m⁻³ (Figure 43A). This is believed to be a result of the predatory impact by scyphomedusae. Fancett and Jenkins (1988) reported that the impact, in patches, of predation by scyphomedusae, *Cyanea capillata*, reached 2.8% day⁻¹ of fish eggs and larvae.

In comparison, at Phetchaburi Province, preceding the peak of the highest rhizomedusae abundance in November 2000, the highest zooplankton concentration was observed during October 2000 (2,734,438 individuals · 10² m⁻³). The majority of the zooplankton was decapod larvae and copepods. In fact, the peak of rhizomedusae at Phetchaburi Province followed the peak of several groups of zooplankton prey items, namely hydromedusae (Figure 44), ctenophores (Figure 46), polychaetes (Figure 47), barnacle larvae (Figure 48), gastropods (Figure 51), copepods (Figure 53), shrimps and larvae (Figure 55), crabs and larvae (Figure 56), larvaceans (Figure 57), and fish larvae (Figure 58). During the month of November 2000, and thereafter to the end of the year, the concentration of copepod and decapod larvae severely decreased (by approximately half in November) (Figure 43B). Once again, it is highly plausible that the decrease in zooplankton concentration was a direct result of the predatory impact of rhizomedusae. Fancett and Jenkins (1988) had revealed that *Cyanea capillata* and *Pseudorhiza haeckeli* can consume the maximum of 1.6% day⁻¹ and 4.8% day⁻¹ of copepods, respectively.

Although the results of this study demonstrated that salinity and zooplankton concentration are directly related to the abundance of rhizomedusae, it is possible that these factors play important roles in governing the abundance of rhizomedusae indirectly. As mentioned earlier, a typical cnidarian life cycle involved the planktonic stages as well as the benthic polyp stages. These development and survival of these stages are crucial and contribute largely to the survival and abundance of the planktonic stages. In the Gullmar Fjord, western Sweden, it was reported that the scyphistomae of *Aurelia aurita* develop during the period of maximum food availability, encouraging asexual reproduction and release of ephyrae. On the contrary, *Cyanea capillata*'s scyphistomae develop during winter and early spring where there is minimum zooplankton biomass (Gröndahl and Hernroth, 1987). Brewer and Feingold (1991) revealed that, in an

experiment, a transfer from low to high temperature induced podocysts (cysts produced by the polyps) formation in *Cyanea capillata* and transfer from high to low temperature led to excystment of podocysts as well as strobilation of polyps to form ephyrae. In the Niantic River estuary, Connecticut, field observations of the benthic stages agreed with laboratory results. In Chesapeake Bay, ephyra and polyp production of *Chrysaora quinquecirrha* was relatively lower at salinity lower than 11 ppt and higher than 25 ppt (Purcell *et al.*, 1999). Moreover, *Cassiopea xamachana*, a tropical jellyfish, has cold-sensitive scyphistomae and temperature-tolerant medusae, which are found year round (Fitt and Costley, 1998). Since this study was conducted in the tropics, where there is very little change in annual temperature, factors that affect the benthic stages, which in turn affect the abundance of rhizomedusae would be salinity, food concentration, and type of substrate available for settlement of planula larvae. As mentioned earlier, the bottom topography of the Inner Gulf is generally muddy, making it unsuitable for the attachment of polyp stages.

III. Size Distribution

The effects of surface current (Figure 63), salinity, food abundance, and reproductive strategy are much apparent when the size distribution of each species of rhizomedusae are analyzed separately.

A. Cassiopea andromeda

Cassiopea andromeda was found at both Chon Buri and Phetchaburi Provinces (Table 6). The planula larvae of the up-side-down jellyfish, Cassiopea xamachana, in South Florida are known to settle on degraded mangrove leaves, where the development and metamorphosis of the polyp stages take place (Fitt and Costley, 1998). Thus, the surrounding environment of both sampling sites, with mangrove forests along the coasts, would be ideal for settlement and development of C. andromeda larvae. It is possible than the life cycle of C. andromeda evolves within the mangrove forest. This is demonstrated in the size distribution of C. andromeda at each sampling location, where a wide range of size class was observed in the same month.

From the gonad analysis, *C. andromeda* reached sexual maturation at the size of approximately 15 cm in diameter and another maturation period at 26 cm in diameter (Table 9 and Figure 33). At Chon Buri Province, in January 2000, the largest size of *C. andromeda* obtained from sampling was 15 cm, at which sexual maturity was observed.

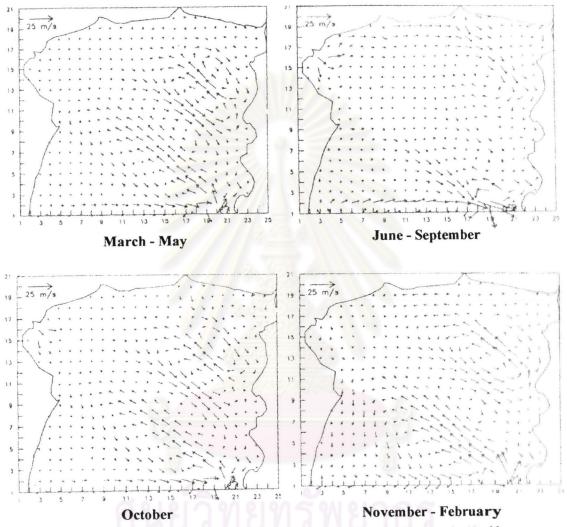


Figure 63. Water circulation in the Upper Gulf of Thailand (Sojisuporn and Putikiatikajorn, 1998).

In February and March 2000, scyphozoan larvae were observed in zooplankton samples (Figure 45) Thereafter, the size distribution of specimens was between 2 cm to 7 cm (Figure 23). At Phetchaburi, in December 1999, the sizes of specimens were smaller than 5 cm. However, in January 2000, specimens larger than 15 cm were obtained. Furthermore, in April 2000, specimens larger than 26 cm were obtained. The reproduction these of sexually matured individuals would likely resulted in the presence

of smaller size classes observed throughout the rest of the sampling period (Figure 24). The reproduction of this species at both Chon Buri and Phetchaburi Provinces did not appear to coincide with the peak of abundance of any zooplankton group. This is due to the fact that *C. andromeda* are able to attain nutrients from symbiotic algae, or zooxanthellae residing in their tissues. Thus, zooplankton concentration may not play an important role in governing the reproduction and abundance of this species.

B. Acromitus flagellatus

Similar to *C. andromeda*, *Acromitus flagellatus* was also found at both Chon Buri and Phetchaburi Provinces. *A. flagellatus* appeared to reach sexual maturation at approximately 8 cm and at 14 cm (Table 9 and Figure 34). Contrary to *C. andromeda*, monthly surface current played an important role in the abundance of *A. flagellatus* found at each sampling location.

A. flagellatus specimens were first obtained at Phetchaburi Province in January 2000 and the sizes of specimens were smaller than 8 cm (Figure 26). Thereafter, no specimens were found at Phetchaburi until April 2000. However, specimens larger than 14 cm were found at Chon Buri in February 2000. It is possible that specimens were either transported from Phetchaburi to the southern or the eastern part of the Gulf by current. Those that were transported to the eastern part of the Gulf may be trapped within the gyre that occurs between November to February. This resulted in a shift to a larger size class form January 2000 at Phetchaburi to February 2000 at Chon Buri Province. The reproduction of sexually matured individuals at Chon Buri in February 2000 resulted in the smaller size classes observed in March 2000 at Chon Buri.

According to the current pattern, specimens found at Chon Buri in March 2000 were likely transported to Phetchaburi in April 2000. This is evident in the shift of size class from 3-7 cm at Chon Buri to 8-10 cm at Phetchaburi. In addition, reproduction of sexually matured individuals, size > 8 cm, found at Chon Buri in March 2000, as well as populations further south, would result in the small individuals, sizes 4 to 8 cm, found in May 2000 at both locations. It is highly possible that this transportation of specimens back and forth, between the western and eastern sides of the Gulf, occurred throughout the rest of the year. Nonetheless, no specimens were obtained at Chon Buri after May

2000 (Figure 25). It is suspected that the freshwater input from the Bangpakong River during the rainy season, coupling with the strength of the discharge, had transported specimens to a location further south of the sampling area.

After May 2000, at Phetchaburi Province, there was a shift to a larger size class and specimens larger than 14 cm were obtained. It was expected that the reproduction of these sexually matured individuals would likely result in the smaller juveniles in June 2000. However, no specimens were found in June 2000. Nonetheless, the results of zooplankton concentration revealed a high abundance of scyphozoans larvae at Phetchaburi Province in June 2000. In fact, these larvae were smaller than the mesh size of the push net used for sampling. A shift from juveniles, 3-7 cm, to larger individuals, 9-15 cm, was observed for the rest of the sampling period (Figure 26).

C. Acromitus hardenbergi

Although A. hardenbergi was found at both sampling locations, they were found only in 2 out of the 13-months sampling period (Table 6). This was also the result of the discharge of the Bangpakong River as mentioned earlier in the case of A. flagellatus. However, at Phetchaburi Province, A. hardenbergi was found in 7 months (Table 6) and a clear shift in size classes of specimens was observed. There was an alternation between smaller juveniles (< 7 cm) and sexually matured adults that were greater than 7 cm in diameter (Table 9 and Figure 35), which were found in April and June as well as in November and December 2000 (Figure 28).

Interestingly, at Phetchaburi Province, during the months where both A. flagellatus and A. hardenbergi were found (Table 6), the abundance of A. hardenbergi was relatively lower compared to the abundance of A. flagellatus (Figure 22). However, the size of both species, within the same month, appeared to be similar (Figure 26 and 28). The explanation for the difference in the abundance of both species is possibly the fact that A. flagellatus possess terminal filaments, which are located on the tips of the mouth arms and are not present in A. hardenbergi. This structure, whose main function is prey capture, would enable A. flagellatus to compete for food better than A. hardenbergi.

D. Catostylus townsendi

Compared to A. flagellatus and A. hardenbergi, the shift in size class was not as distinct in C. townsendi (Figure 29). The analysis of gonads revealed than the sexual maturity of C. townsendi occurred at the size of approximately 6 cm and 12 cm (Table 9 and Figure 36). This data, in addition to the size class distribution, implies that sexually matured adults were found in 5 out of 6 months where C. townsendi were found at Phetchaburi Province. On the contrary, smaller juveniles were found only in August 2000. Current may be an important factor, which transport the smaller juveniles, found in August 2000 (Figure 29), to the southern part of the Gulf but not eastern part since C. townsendi were not found at Chon Buri.

E. Lobonema smithii

L. smithii were found only at Phetchaburi Province and specimens were obtained only in June and July 2000 (Table 6). In addition, the smallest size specimens (approximately 15 cm in diameter) obtained were already sexually matured (Table 9 and Figure 37). Since L. smithii is an economic species, they were subjected to intense fishery during July 2000. The data of gonad development of this particular species did not imply whether L. smithii can reproduce more than once during their life cycle since specimens were obtained in only 2 months out of the 13-months sampling period. Indeed, if they reproduce only once during their life span, fishery prior to or during reproductive periods may result in future decrease of population.

F. Rhopilema hispidum

All *R. hispidum* specimens obtained from both Chon Buri and Phetchaburi Provinces had already reached reproductive maturity (Table 9 and Figure 38). Relatively smaller specimens (≈ 15 cm in diameter) were found in July 2000 at Phetchaburi Province and larger specimens (> 15 cm in diameter) were obtained at Chon Buri in August 2000 (Figure 31 and 32). Specimens were possibly transported by current upward along the coasts of Samutsongkram and Samutsakorn Provinces and down along the coast of Chon

Buri Province during these two consecutive months. Similar to *L. smithii*, this particular species is also an economic species and are subjected to intense fishery.

In general, when comparing the sizes of the same species of rhizomedusae found at the two provinces, the size of medusae at Phetchaburi Province appeared to be larger than that of Chon Buri Province. For instance, the largest *Acromitus flagellatus* found were 12.5 cm and 16.8 cm in diameter at Chon Buri and Phetchaburi, respectively. The largest *A. hardenbergi* found were 7.9 cm at Chon Buri and 14.0 cm at Phetchaburi (Table 11).

Table 11. Summary of size distribution of rhizostome species found at Chon Buri and Phetchaburi Provinces from December 1999 to December 2000.

Species	Chon Buri		Phetchaburi	
	Min.(cm)	Max.(cm)	Min.(cm)	Max.(cm)
Cassiopea andromeda	1.9 (Mar.)	15.0 (Jan.)	1.1 (Jan.)	26.0 (Apr.)
Acromitus flagellatus	2.1 (Mar.)	16.0 (Feb.)	2.0 (Aug.)	16.8 (Jun.)
Acromitus hardenbergi	2.8 (Mar.)	10.0 (May.)	2.5 (Oct.)	14.0 (Jun.)
Catostylus townsendi	- 1744		3.0 (Aug.)	12.0 (Jun.)
Lobonema smithii	74(3)(9)		24.0 (Jun.)	53.0 (Jul.)
Rhopilema hispidum	16.1 (Aug.)	54.0(Aug.)	15.5 (Jul.)	

There are many factors, which are believed to affect the size distribution of medusae. In Namibia, the size structure of *Chrysoara hysoscella* changed with both depth and distance offshore. Medusae that were found inshore, and at the surface, were significantly smaller than at depths greater than 30 m. These medusae were also smaller than those obtained from surface waters further offshore where bigger and more mature individuals were found (Buecher *et al.*, 2001). In the northwestern Black Sea, Weisse and Gomoiu (2000) observed that there was a difference in the size structure of *Aurelia aurita* at inshore and offshore stations. Relatively smaller sized individuals were found at the inshore stations compared to those found offshore. Since the depths of both sampling areas were considerably shallow, approximately 1-3 m, it can be disregarded as affecting the size structure of rhizomedusae in both locations.

Food concentration and water circulation in the inner Gulf are belived to affect the size structure of medusae at Chon Buri and Phetchaburi Provinces. In *Aurelia aurita*, an experiment had shown that food availability governed both the maturation process as well as individual growth. While food scarcity reduces the growth rate, energy is allocated towards reproduction, which occurs at a relatively smaller size than well-fed medusae (Ishii and Båmstedt, 1998). Lucas (1996) observed a similar trend in Horsea Lake, England. Abundance of *Aurelia aurita* was limited by numerically and species-poor mesozooplankton community. However, small-size medusae were able to reach sexual maturity and reproduce. Here, medusae appeared to partition the available food resources into either somatic growth, when food was abundant, or reproduction, when food was scarce. As mentioned earlier, the general size of rhizomedusae appeared to be relatively larger at Phetchaburi compared to Chon Buri. At the same time, the zooplankton concentration at Phetchaburi was relatively higher in magnitude than at Chon Buri (Figure 43).

There was a peak in several zooplankton groups, preceding the reproductive period of each species of rhizomedusae. Prior to the reproductive period of A. flagellatus at Chon Buri Province, which occurred in March, peaks of fish larvae and gastropods were observed in February 2000. Likewise, the November reproductive period of A. flagellatus at Phetchaburi Province was preceded by the peaks of chaetognaths, polychaetes, barnacle larvae, hydromedusae, ctenophores, copepods, shrimp larvae, crab larvae, and fish larvae in October 2000. Similar, reproductive period of A. hardenbergi at Phetchaburi Province was preceded by the same peaks of zooplankton group. However, rhizomedusae at each location appeared to reach reproductive maturity at approximately the same sizes. Thus, surface current, coupling with life history of each species, was probably responsible for the different in sizes observed at both sampling locations.