

CHAPTER 1

INTRODUCTION

I. Introduction

Scyphozoans, including rhizomedusae, have been considered an integral component in the marine environment, particularly in terms of trophic levels. Besides serving as important food source for a variety of marine organisms, their predatory behavior is believed to pose a major impact on the zooplankton population and fish stock. The trophic significance of rhizomedusae, nonetheless, is not restricted to the marine environment. Rhizomedusae are subjected for human consumption. In Thailand, particularly in the Gulf, jellyfish fisheries have contributed more than 30 million bahts to the fishery industry annually. The monitoring of this valuable resource is, therefore, necessary for sustainable utilization. At the present, there has not been any certainties concerning the number of species, distribution, seasonality, and related parameters of rhizomedusae in the Gulf of Thailand. Such knowledge specifically species diversity, abundance, monthly variation in species diversity and abundance, reproduction, and governing environmental parameters are necessary to the understanding of the ecology of rhizomedusae. Furthermore, this information can be applied to the fishery management concept as well as the conservation of this particular fishery resource.

Thus, the objectives of this study are to gather information regarding:

1. the species diversity and abundance of rhizostome scyphozoan along the coasts of Chon Buri and Phetchaburi Provinces,
2. the monthly variation in the pattern of occurrence and abundance,
3. the environmental factors affecting the abundance of rhizostome scyphozoans.

II. Classification

Scyphomedusae are organisms belonging to phylum Cnidaria, formerly Coelenterata, and class Scyphozoa. The class Scyphozoa is further divided into four orders. This particular study is focused on the order Rhizostomeae, which is comprised of eight families.

Phylum Cnidaria

Class Hydrozoa

Class Scyphozoa

Order Stauromedusae

Order Coronatae

Order Semeostomeae

Order Rhizostomeae

Family Cassiopeidae

Family Catostylidae

Family Cepheidae

Family Lobonematidae

Family Lychnorhizidae

Family Mastigiidae

Family Rhizostomatidae

Family Stomolophidae

Class Anthozoa

Class Cubozoa

III. General Characteristics of Scyphozoans

Although the medusa form is present in other Cnidarian classes, namely Hydrozoa, Scyphozoa, and Cubozoa, only scyphomedusae and cubomedusae are fundamentally viewed as “true jellyfish”. Unlike the hydromedusae, which are found in both fresh and marine waters, scyphomedusae are exclusively marine. They are often large in size, ranging from 2 to 40 centimeters in diameter. In 1865, however, Agassiz recorded a *Cyanea capillata* in Massachusetts Bay with a diameter of 2.3 meters (Rifkin, 1996). Scyphomedusae are distinguished from hydro- and

cubomedusae through the lack of velum or velarium (shelf of tissue extending inward from the margin into the subumbrella space). Instead, the marginal features of scyphozoans consist of lappets, marginal tentacles, and sensory organs called rhopalia, which are located between lappets at the bell margin. There are approximately 200 species of scyphozoans inhabiting pelagic habitats, from surface to deep waters, as well as coastal waters of all oceans, from the Poles to the Tropics. Their large size and the presence of stinging nematocysts have earned them the reputation of danger and nuisance.

The class scyphozoa is subdivided into a total of four orders as follows,

1. Stauromedusae (Figure 1): This particular order is comprised of small permanently and temporarily sessile polypoid medusae, which are attached to the substrate by an aboral adhesive disc on the subumbrella or an aboral stalk (Arai, 1997).

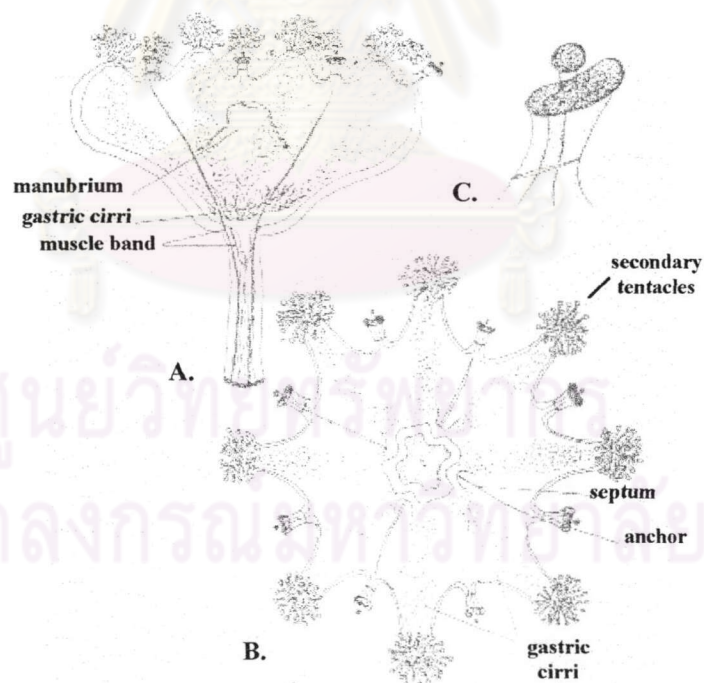


Figure 1. Stauromedusa *Haliclystus salpinx*. (A) Side view; (B) oral view; (C) anchor (Arai, 1997).

2. Coronatae (Figure 2): This order includes the bathypelagic and mesopelagic species possessing deep furrow, or coronal groove, which divides the subumbrella into two distinct regions: the central disc and the peripheral zone where there exist the pedalia (radial thickenings), lappets, and marginal tentacles (Arai, 1997).

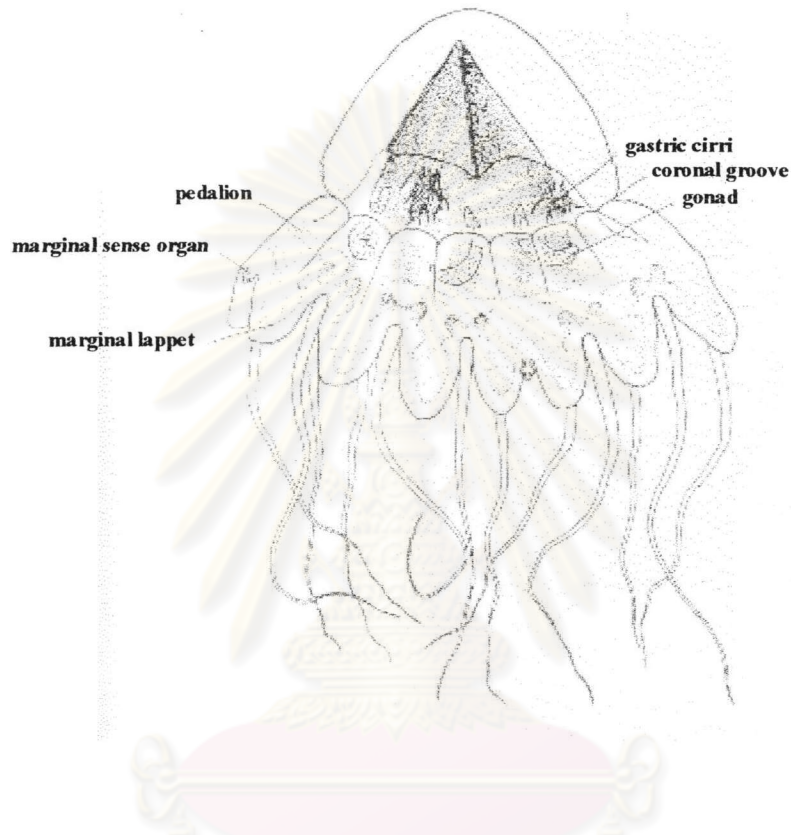


Figure 2. Young coronate scyphozoan *Periphylla periphyllo* (Arai, 1997).

3. Semaestomeae (Figure 3): The common representative of semaeostome scyphozoans is *Aurelia aurita*. These medusae usually resemble a saucer in shape and the coronal grooves and pedalia, observed in coronates, are absent. The margin is sometimes divided into lappets and is equipped with rhopalia. The single mouth is surrounded by four oral arms. Radial pouches or system of canals may be found around the stomach (Arai, 1997).

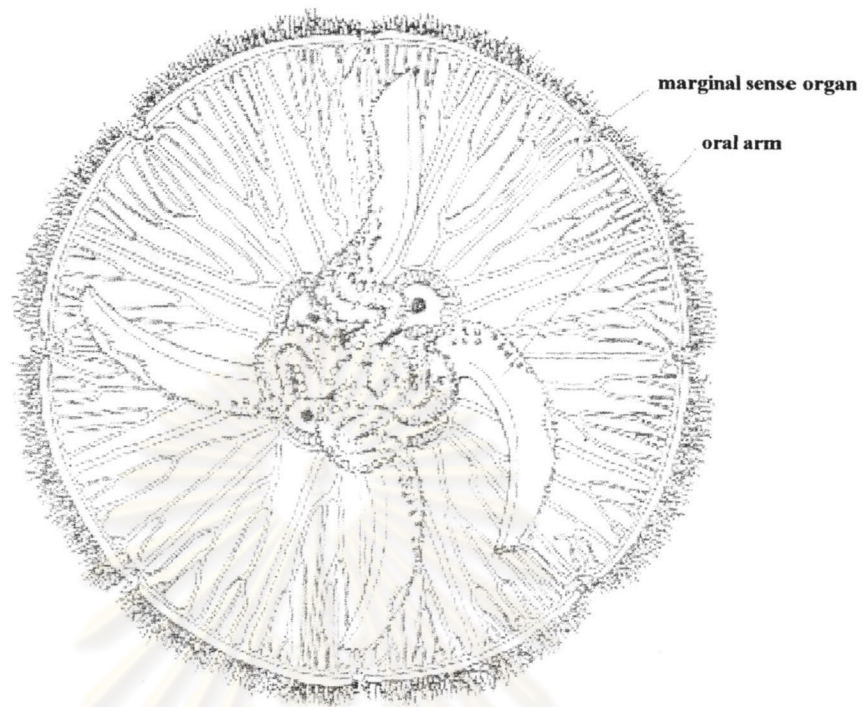


Figure 3. Semeostome scyphozoan *Aurelia aurita*; subumbrellar view of female specimen (Arai, 1997).

4. Rhizostomeae (Figure 4): Several physical characteristics distinguish rhizomedusae from jellyfish in other orders. Rhizostome medusae are recognized by the lack of tentacles along the edge of the bell and the oral arms of the manubrium that is branched, bearing deep folds into which food is passed to the mouth. They are generally found in tropical and subtropical shallow waters, and include both epipelagic and neretic forms. At the present, within order Rhizostomeae, there are 8 families, encompassing a total of 22 species (Arai, 1997). Four of the eight families of rhizomedusae are restricted to the Indo-West-Pacific regions. Few common genera are *Cassiopea*, *Rhizostoma*, *Mastigias*, and *Stomolophus* (Barnes, 1987).

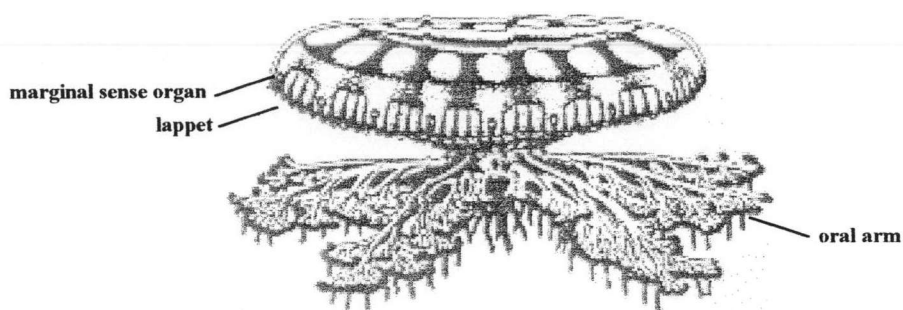


Figure 4. Rhizostome scyphozoan *Cassiopea xamachana* (Arai, 1997).

IV. Biology

A. General Biology

Cnidarians are true metazoans with two body layers, namely the epidermis and gastrodermis, and are entirely aquatic. However, they are mostly found in marine environments. They are radially symmetrical and have only one opening which functions as both the mouth and anus. They possess special stinging cell organelles called cnidae enclosing the thread-like nematocysts, the characteristics of this phylum, which they used for self-defense as well as prey capture. The excretory or respiratory systems are undeveloped and they possess no coelomic cavity.

B. Reproductive Biology and Alternation of Generations

Most scyphozoans are dioecious, having separate sexes. Nonetheless, few species are hermaphrodites. For example, the medusae of *Chrysaora hysocella* are protandrous hermaphrodites as they first produce sperm and then ova. The gonads, arise from the gastrodermis, are situated on the floor of the gastrovascular cavity. In rhizomedusae, the oocytes gradually bulge into the mesoglea of the gonad, while maintaining contact with specialized cells in the epithelium (Figure 5). Sperms, on the other hand, develop in follicles, which are formed by invagination of the epithelium into the mesoglea of the testis (Figure 6). Prior to spawning, accumulation of matured sperms may occur in the subgenital sinus or the oral arms. In *Cassiopea*

andromeda, spermatozeugmata, or sperm packages with somatic cells in the center surrounded by sperms, are formed (Arai, 1997).

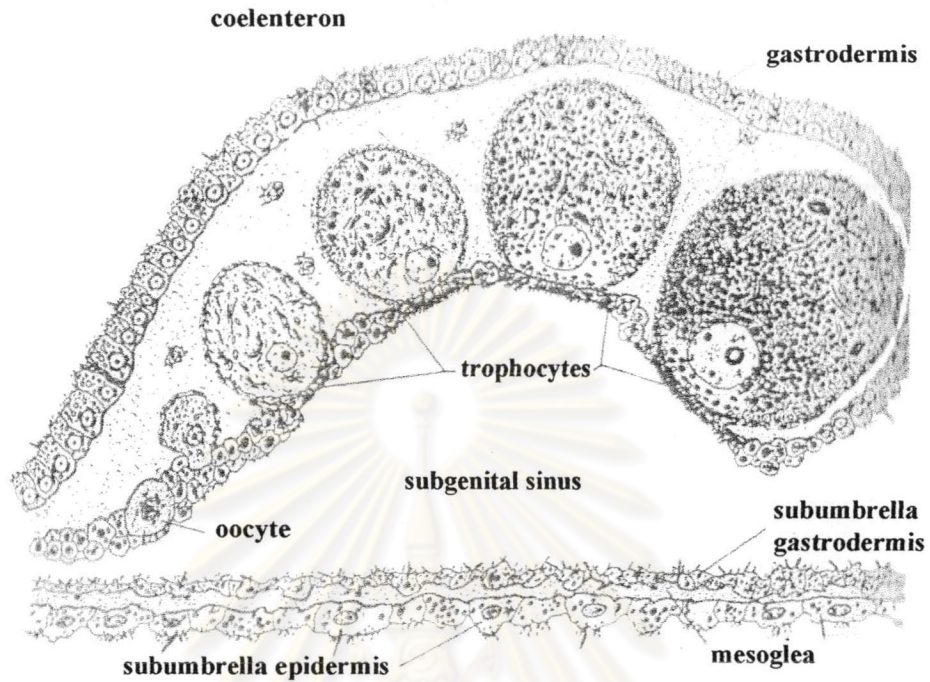


Figure 5. The ovary of *Aurelia aurita* (Arai, 1997).



Figure 6. Distal part of the testes of *Aurelia aurita* (Arai, 1997).

Modes of fertilization vary among different species of scyphozoans. Internal fertilization may occur in the gastrovascular cavity of females as observed in *Aurelia aurita* or in the femal gonads, i.e. *Cotylorhiza tuberculata*, or on the oral arms. In addition, external fertilization occurs in the seawater as observed in *Aurelia aurita*, *Chrysaora quinquecirrha*, and *Haliclystus octoradiatus* (Arai, 1997).

A typical cnidarian life cycle involves free-swimming medusoid individuals, which produce eggs and spermatozoa. External fertilization results in the zygotes that will eventually develop into planula larvae. After settlement onto suitable substratum, the planula larvae develop into the polyps, which will undergo asexual reproductions and evolve into the medusoid forms, completing the life cycle. This alternation between asexually and sexually reproducing stages is referred to as alternation of generations (Figure 7).

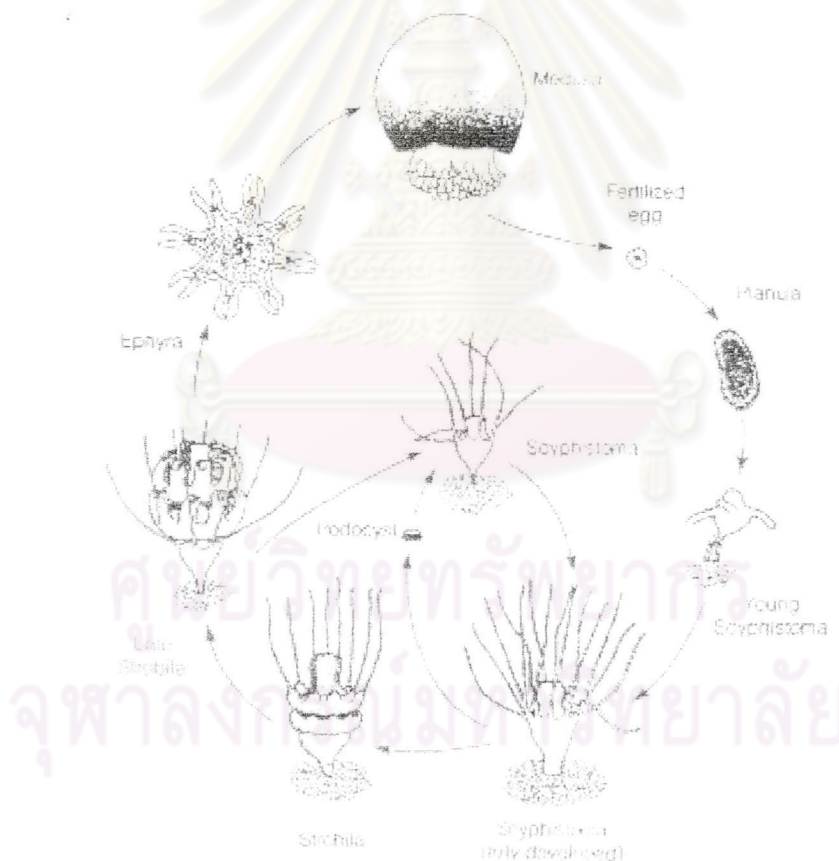


Figure 7. Life cycle of rhizostome scyphozoan *Stomolophus meleagris* (Arai, 1997).

Nonetheless, alternation between the benthic polyp stages and the medusoids are not uniformly exhibited across all three classes. For instance, in the class

Anthozoa (i.e. stony corals and sea anemones), the medusoid stages are entirely nonexistent. In the class Hydrozoa, several species lack either the polyp or medusoid stages. Furthermore, some scyphozoans (i.e. true jellyfish) possess no polyp stages at all.

Alternation of generations is observed in organisms within the class Scyphozoa. In fact, certain species may produce dormant cysts. The life cycle of *Aurelia aurita*, a well-known species of scyphozoan, includes fertilized eggs, planula larvae, scyphistoma, strobila, ephyrae, and subsequent adults. This particular kind of life cycle is typical of scyphozoans. In addition, the scyphistoma may produce further polyps by longitudinal fission, by direct budding, or by formation of stolons, cysts or planuloid buds (Arai, 1997). In Horsea Lake, England, sexual reproduction of *A. aurita* was observed over a 12-month period (from February 1994 to January 1995). Settlement of planulae was followed by strobilation, which started from December resulting in the presence of ephyrae from December to June. However, ephyrae were dominant during February. Ripe female *A. aurita* carrying fertilized eggs first appeared in May and June while planulae production occurred in September to December (Lucas, 1996).

Direct development occurs in few species of scyphomedusae. It had been observed in *Pelagia noctiluca* where the planulae develop into ephyrae without settling on the substratum. The probable advantage of direct development, independence of benthic stages, may be well adapted to oceanic species where environmental conditions are unfavorable for settlement.

Asexual reproduction in cnidarians may occur in several ways, the most common of which is budding. In colonial forms, budding usually takes place along the stolons. In comparison, budding occurs from the polyp side in solitary forms. Several medusae bud directly from the bell margin, manubrium, or tentacular bulbs. In *Cyanea*, the benthic polyp stage usually reproduces asexually via two major methods. One method involves the formation of the podocysts, which are mesogial tissue enclosed in chitinous sheath. Podocysts eventually excyst and form new polyps. Another alternative to cyst formation is strobilation, which involves transverse fission of the apical portion of the polyp. Strobilation produces ephyrae,

which are comparable to early forms of pelagic medusae. Environmental factors, which influence strobilation of polyps, include changing temperature, the extent of illumination, shifts in salinity, and feeding rate. In many instances, the settling planula forms another encysted state called the planulocyst. From their study on the effect of temperature on the benthic stages of *Cyanea* and their seasonal distribution in the Niantic River estuary in Connecticut, Brewer and Feingold (1991) discovered that both planulocysts and podocysts appeared during the warmest time of the years. Their formations appeared to be triggered by increasing temperature. Both types excysted when temperature decreased. Strobilation and liberation of ephyrae subsequently followed excystment. In the Gullmar Fjord, western Sweden, in 1984, strobilation of *Cyanea capillata* occurred in winter and early spring. Ephyrae were first observed towards the end of March and the maximum abundance was observed in June. First sexually matured female was observed in the beginning of September, which was followed by production of planulae. Subsequent settlement of planulae and development of scyphistoma occurred in October. In the laboratory, where predation factor was eliminated, strobilation did not occur until April 1985 and continued until the beginning of July (Gröndahl and Hernroth, 1987).

Alternation of generations provides many advantages as well as disadvantages for cnidarians. In general, the medusae have evolved for the better dispersal of the species (Hardy, 1971). Although some polyps are able to produce planktonic larvae via sexual reproduction, they are usually short-lived. Thus, the ciliated swimming planula, when present, may be more important in selection of favorable environment for the benthic stages than in dispersal (Arai, 1997). Through higher dispersal range, the medusae are able to exploit a wider range of food sources unavailable to the benthic forms. This allows for the sexual reproduction, which usually involves high-energy expenditure. Sexual reproduction of the medusoid forms is also necessary for genetic variability. The benthic stages, on the other hand, may have evolved as a mechanism that aids in survival of temperate and arctic species during period of low planktonic food availability. Several types of cysts may be considered as part of the benthic stage and are formed as protection against unfavorable conditions such as extreme temperature changes. They may also serve as protection against predation as well as seasonal competition for space. Above all, 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.

There are few disadvantages to alternation of generations. The benthic polyp stages are constantly prey upon by several benthic invertebrates such as the nudibranchs, which was observed in the Gullmar Fjord, western Sweden (Gröndahl and Hernroth, 1987). The free-floating-medusoid forms are evidently at the risk of being carried away by currents into areas of unsuitable conditions. As mentioned previously, the sexual reproduction of the medusae requires high energy, thus the organisms depend largely on the food concentration in the surrounding medium.

In scyphozoans, the medusoid stage serves similar function as that mentioned earlier, which is to enhance dispersal. Yet, the complex benthic stages are extremely crucial for continuity of population. In the summer, when prey population is often high, encysted stages serve to prevent mortality due to benthic predation. Excystment and strobilation, which occurs during the colder months of the year, could be viewed as a preparatory phase. As a consequence, ephyrae released during the months of spring are able to exploit the rich resources present in the surrounding water. High food availability would intensify reproductive success due to the fact that sexual reproduction of mature medusae more than likely requires relatively high energy input.

C. Feeding Biology

Scyphomedusae, among all cnidarians, are characterized by the presence of intracellular organelles called cnidae. This particular structure consists of a capsule, which contains coiled thread-like tubule that is discharged when stimulated. All scyphozoan cnidae are termed nematocysts. Nematocysts are cnidae with tubules lacking longitudinal folds or accessory hollow tubules. Equipped with toxins, the functions of cnidae are mainly for prey-capture and defense from predators. Nematocysts are distributed on all parts of the jellyfish including the exumbrella surface, oral and stomach regions, as well as the tentacles. In some species, such as *Cyanea* sp., they are arranged in specific pattern on the tentacles. Since rhizostome

scyphozoans lack a central mouth, nematocysts are generally found along the oral arms (Rifkin, 1996).

The majority of scyphozoa medusae are carnivores, although few species, such as the rhizostome *Stomolus meleagris*, are known to exhibit filter-feeding behavior. *Stomolus meleagris* is a rhizostome scyphozoan with globular umbrella, short manubrium, and lacks marginal tentacles. In addition, few may obtain a fraction of their nutritional requirement from symbionts, namely zooxanthellae. For those that are carnivores, two strategies are suggested: medusae can remain still as 'ambush' predators, or swim through the water as 'cruising predators' (Arai, 1997). It is further suggested that cruising predators tend to prey upon slower moving prey while ambush predators prey upon faster moving prey. For cruising predators, contact with prey depends largely on the fluid motion, achieved through the swimming motion of the medusa, of the immediate surrounding water. Several scyphozoans, such as *Pelagia noctiluca* (order Semaestomeae), are known to switch between the ambush and cruising modes depending on the types of preys. In *Aurelia aurita* (order Semaestomeae), the relationship between bell pulsation, fluid motion, and prey capture is observed. The swimming pattern involved the rhythmic contraction of the bell and the waving motion of the fringing tentacles. This results in water displacement and turbulence, followed by contact with prey (Arai, 1997)

Posteriori to contact with prey, the marginal tentacles contract and prey is transferred towards the mouth. In *Pelagia noctiluca*, it is observed that when prey touches a marginal tentacle, there is an immediate nematocyst discharge, followed by a tentacle contraction after 2-3 seconds (Arai, 1997). Few movements of the oral arms assist in grasping the prey. Through peristaltic and mucous movements, the prey is driven to the oral arm groove, towards the manubrium. An observation of the feeding behavior by Malej (1989) reveals that, in nature, undisturbed *P. noctiluca*, within an aggregated swarm, normally swims with tentacles trailing as long as 1.5 m. During prey capture a tentacle touching a prey contracted quickly while the other tentacles remained extended and fishing. The prey was transferred to the oral arm which bent towards the tentacle. The bell contraction did not cease completely during this prey-handling operation; however, the medusa's speed seemed to be reduced (Malej, 1989). Besides, aggregation for foraging purpose provides few advantages.

Foraging efficiency is enhanced as prey escaping from one medusa becomes more vulnerable to another. Other than reproductive benefits, foraging in groups also promotes predator avoidance and an individual medusa can spend more time feeding.

Fancett and Jenkins (1988), in their study on the predatory impact of scyphomedusae on ichthyoplankton and other zooplankton in Port Phillip Bay, Australia, measured the feeding rate of two species of scyphozoan namely *Pseudorhiza haeckeli* and *Cyanea capillata*. *P. haeckeli* is a rhizostome scyphozoan possessing mouth arms which extend further beyond the bell while *C. capillata* is a semeanostome scyphozoan with long marginal tentacles and the oral arms, spread over the surface of the prey, form a thin adhering film (Arai, 1997). In this case, feeding rate was measured in term of clearance rate, which is the volume of water from which all particles are removed over a time interval (Fancett and Jenkins, 1988). The experiment was conducted *in situ* by adding a known prey concentration to a volume of water held in an aquarium. After a period of time, through a filtering process, the number of remaining prey items was counted. A control aquarium was set up with no scyphomedusae. In general, less than 20% of the prey were consumed over a period of 15-45 minutes while prey recovery was 100% for the control. The clearance rate of the two species was independent on prey density and prey concentration. In the field, medusae are rarely observed to have full gut despite high prey abundance. Moreover, it appears to increase with size of the medusae. *P. haeckeli* was observed to have relatively higher clearance rate than *C. capillata*, with no differences in clearance rate among prey taxa. Apparently, it is suggested that this is a result of different feeding modes between the two species. *P. haeckeli* is able to filter more water per unit time. *P. haeckeli* is a rhizostomous scyphomedusan, with a central fleshy mouth bearing many small 'arms' covered with nematocysts (Fancett and Jenkins, 1988). It moves rapidly through water, pumping water downward through the arms. On the other hand, *C. capillata* swims at a relatively lower speed and, with relatively lower clearance rate, revealed differences among clearance rates for copepod taxa. In this case, prey encounter would be the determining factor governing the clearance rate. Since *C. capillata* is a slow swimmer, faster moving prey are likely able to escape, resulting in the different clearance rate for different prey items. Thus, feeding rate of scyphomedusae is affected by two factors: contact rate (resulting in selectivity) and size of both the medusae and the prey. García and Durban (1993) also observed a

similar pattern in *Phyllorhiza punctata* in their study on zooplanktivorous predation by large scyphomedusae in Laguna Joyuda. They observed that clearance rates were independent of prey densities and linearly increased with bell diameter.

In Chesapeake Bay, United States, where high biomass of medusae occurs during the months of July and August, copepod's clearance by zooplanktivorous predators resembles the seasonal pattern of gelatinous zooplankton. Clearance rate is relatively low in early to mid-May and peaks in Mid-August (Purcell *et al.*, 1994).

As mentioned earlier, filter-feeding behavior is observed in few species of scyphomedusae i.e. the rhizostome *Stomolophus meleagris*. During his study in the northeastern Gulf of Mexico, Larson (1991) attempts to determine the diet, prey selection, as well as daily ration of this particular species. Belonging to the order Rhizostomae, *S. meleagris* lacks tentacles seen in *P. noctiluca*. Instead, they have lips surrounding the mouth. The mouth has developed into oral arms, which hang from the subumbrella. As the medusa swims, these arms function as filtering sieve for zooplankton. Depending on the species of rhizomedusae, the morphology of the oral arms varies. Despite that fact, all oral arms are formed by enlargement and branching of the original ephyral lips. Branching of the distal portions of the oral arms provides for more filtering surface areas. Preys are captured by the digitata, which are finger-like structures, situated along the margins of the lips and are equipped with nematocysts. Smith (1934 & 1936), Thiel (1964), and Larson (1978) observed the feeding mechanism of *S. meleagris* and described that prey were captured by the digitata and were passed into ciliated grooves, which eventually lead to the stomach (Larson, 1991). Commonly, preys are brought into contact with the digitata by means of vortex and turbulence created by the medusa swimming motion. After filtration, the water, that initially fills the subumbrella area during bell expansion, is expelled from the cavity through bell contraction.

V. Locomotion

Larson, in 1991, stated that jellyfish can form near-shore aggregates, i.e. in bays, inlets, and leeward side of islands, as a result of wave actions or currents. This is useful in ensuring feeding and reproductive success (Rifkin, 1996). Some species

may undergo daily vertical migrations, alternating between upward swimming and sinking, oftentimes with expanded tentacles to capture prey items. Many scyphozoans are capable of active as well as passive horizontal movements. Due to the lack of velum and velarium, movement of scyphomedusae relies largely on the circular and radial muscle of the subumbrella. *Mastigias* sp., a rhizomedusa, has been observed to migrate, from one side of a lake to another, employing the sun as taxis cue (Rifkin, 1996).

In general, jellyfish swimming mechanisms involve a series of rhythmic pulsation of the bell margin accompanying by the expulsion of water out of the subumbrella area. The pulsation rate is believed to be related to environmental conditions such as temperature, food, and light concentrations (Rifkin, 1996).

Despite the belief that the polyp stage is a “sessile” stage, the polyps of few scyphozoan species are able to accomplish limited form of locomotion. The scyphistomae of stauromedusae and sarracostomedusae are capable of summersault and gliding movements along the substratum. This particular type of movement involves reversible adhesion of the basal or pedal disc and contraction of the stalk (Arai, 1997).

VI. Ecological Importance and Trophic Relationship

Being opportunistic predators, scyphomedusae utilize a variety of prey items, depending on their availability, corresponding to peak population and seasonality. Zooplankton represents a significant portion of their food source (Table 1). In comparison, although some phytoplankton maybe ingested, it represents only a small and negligible portion. The zooplankton diet of scyphozoan medusae includes fish larvae (and eggs), other medusae, chaetognaths, gastropod mollusks, copepods, nematodes, rotifers, protozoa, arthropod larvae, ctenophores, diatoms, and appendicularians.

Scyphomedusae have continuously been known as fierce predators and play an integral role in the marine food web. Their predation on fish larvae is believed to pose a major impact on the adult population of several commercial fish species.

Pseudorhiza haeckeli, a rhizomedusa, has been observed to have maximum clearance rate of 4.8% per day and 3.8% per day of copepod and fish eggs and larvae, respectively (Fancett and Jenkins, 1988).

Table 1. Prey composition of some field-caught scyphomedusae (Arai, 1997).
(*Family Rhizostomeae)

Species	Prey Size		
	< 200 μm	200 μm – 2 mm	> 2 mm
<i>Aurelia aurita</i>	Diatoms, ciliates, tintinnids, rotifers	Veligers, trochophores, barnacle larvae, copepods, cladocera, larvacea	Hydromedusae, eggs, chaetognaths, crustacea, herrings
<i>Cyanea capillata</i>		Copepods, cladocera, larvacea	Hydromedusae, ascidia, ctenophores, fish eggs, fish larvae
<i>Pelagia noctiluca</i>		Copepods, cladocera	Cumacea, amphipods, chaetognaths, euphausiids, mysids, decapods, gastropods, fish eggs, fish larvae
<i>Pseudorhiza haeckeli</i> *		Copepods, cladocera, larvacea	Decapod larvae, fish eggs, fish larvae
<i>Stomolophus meleagris</i> *	Tintinnids	Veligers, copepods, larvacea	

Apart from symbiotic relationships, scyphomedusae interact with other organisms in various ways. They are known to be associated with other planktonic organisms including fish, arthropods, nauplii, phyllosoma larvae, and pelagic

octopods. Most of these associations involve mutual benefits. The associations between the fish and medusa vary from simple opportunistic relationships, through commensalism, to ectoparasitism and predation (Arai, 1997). Scyphomedusae, despite their notorious reputations, are considered an essential source of nutrition for a wide array of predators i.e. sea turtles, *Mola mola* or sunfish, pelagic coelenterates, parasites, mesopelagic arthropods, shrimps, amphipods, sea anemones, barnacles, birds, fish, and even human.

VII. Important Environmental Parameters

A. Physical Factors

Although it is logical to assume that the distribution and survival of scyphozoa are generally affected by various physical factors, the lack of supporting data suggests that physical factors may also indirectly affect the distribution of these organisms by acting on associated organisms such as their preys. The physical factors, which affect scyphomedusae are:

1. Salinity: Scyphozoans are osmoconformers and euryhaline. They have been shown to change volume with changes in the salinity of the surrounding seawater. Indeed, they are able to tolerate a wide range of salinity. For instance, the medusae, scyphistomae, and planulae of *Rhopilema esculenta* (order Rhizostomeae) can survive in varying salinity of 8, 10, and 12 ppt (psu), respectively (Arai, 1997).
2. Temperature: Temperature has been known to affect several biological functions of most animals including scyphozoans i.e. feeding, swimming, digestion, respiration, cyst formation, strobilation, enzyme activities, and uptake of organic material which, in turn, affect the growth rate. For instance, in *Chrysoara quinquecirrha* (order Semaestomeae), acclimation in cold temperatures resulted in an increase in glucose-6-phosphate dehydrogenase (Arai, 1997). However, in the Tropics, where the temperature of the seawater fluctuates only within a small range, its effects are not significant to scyphomedusae.

3. Dissolved Oxygen: Concurrent to other factors previously mentioned in this section, scyphozoans can survive in areas of depleted oxygen level as well as in hyperoxia conditions. In some restricted areas, the bottom layers become stagnant and oxygen is depleted. Among the few animals surviving in this layer, with less than 0.5 ml O₂ per liter, are planulae larvae of *Aurelia aurita* (Arai, 1997).
4. Depth: Several environmental factors govern the habitable depth ranges occupied by scyphozoans. Such factors are temperature, light, pressure, prey density, salinity, oxygen gradients, and buoyancy. The exclusion of sulfate ions permits the organisms to achieve identical density with the surrounding waters, thus, vertical migration is allowed. In *Pelagia noctiluca* (order Semaestomeae) and *Mastigias* sp. (order Rhizostomeae), vertical migration between the surface and the chemocline occur at night (Arai, 1997). This ability is utilized by scyphozoans in exploring new habitats and exploitation of resources.
5. Pollution: Found in coastal waters all over the globe, scyphozoans are subjected to various forms of adverse environmental conditions such as eutrophication induced by nutrients derived from runoffs and domestic sewage, contamination of hydrocarbons such as DDT, and heavy metals such as copper, lead, mercury, and zinc. In many instances, eutrophication resulted in an increase in numbers of scyphozoa. The density of *Cassiopea fondosa* and *Cassiopea xamachana* was observed to be relatively higher in a lagoon where there were tourist activities compared to an undisturbed lagoon. The effects of pollution may differ depending on the life stages. Contamination by heavy metals may cause reduction of strobilation in addition to production of abnormal polyps and ephyrae. In contrast, *Rhizostoma* sp., a rhizomedusa, has been observed to be able to survive in diesel oil polluted environments (Arai, 1997).

Correspondingly, it is highly possible that these physical factors act on the different life stages of scyphozoans in affecting the distribution or abundance of the adult medusae. As in Brewer and Feingold's study (1991) mentioned in the preceding

section, temperature appears to be the governing factor for the development of the benthic stages of *Cyanea sp.* Hindered benthic development would likely lead to poor recruitment into the medusa population.

B. Biological Factors

Besides physical factors, biological factors, particularly food concentration and predators, also play an important role in the survival and abundance of scyphozoans, both the polyps stages and the medusae.

1. Food Concentration: Food concentration is believed to affect the abundance of scyphomedusae both directly and indirectly. During the summer of 1986, zooplankton bloom is believed to be the main reason for the aggregations of the scyphomedusa *Rhizostoma pulmo* in the Lebanese coastal waters. Preceding the aggregations, a blooming episode of phytoplankton is reported followed by an increase in zooplankton biomass, namely Chaetognatha, Appendicularia, Cladocera, and other meroplanktonic larvae (Lakkis, 1991). In the Gullmar Fjord, western Sweden, the maximum abundance of *Cyanea capillata* ephyrae is significantly less in comparison to the abundance of *Aurelia aurita* during 1984-1985 (Gröndahl and Hernroth, 1987). This marked difference is explained by the fact that the scyphistomae of *Aurelia* develop during the period of maximum food availability, encouraging asexual reproduction and release of ephyrae. On the contrary, *Cyanea*'s scyphistomae develop during winter and early spring where there is minimum zooplankton biomass, which affected the production of ephyrae.

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.

2. Predation: Another possible explanation for the low abundance of scyphomedusae, for example *Cyanea* sp., is the constant exposure of the scyphistomae to predation by nudibranchs coupling with the low number of planula larvae settling in the area 1985 (Gröndahl and Hernroth, 1987). According to the typical life cycle of scyphozoans, the asexual reproduction of the benthic stages produces high number of offspring. Thus, unsuccessful settlement of the planktonic larvae and predation are logical causes of low abundance of rhizomedusae.

VIII. Economical Importance

Despite the notorious reputation, jellyfish are subjected to fisheries for human consumption. In China, jellyfish are believed to possess medicinal properties that relieve pains associated with urinary bladder infections and cramps. In 1981, the value of scyphozoans exported from Asian countries, including Thailand, was US\$ 40 million, or approximately 1,200 million bahts, with the important markets being Japan and China. Most fisheries are for rhizostome medusae: *Rhopilema esculenta*, *Lobonema smithii*, *Lobonemoides gracilis*, *Rhopilema hispidum*, and *Stomolophus meleagris*. Small-scale fisheries are carried out in South Korea, West Japan, and India. In 1981, Omori reported that the main sources of jellyfish are China, Philippines, Thailand, Malaysia, and Indonesia. The potential is mainly in countries with warm coastal waters and populations of rhizostome medusae (Arai, 1987). Usually, medusae are preserved with a mixture of table salt and alum, a collagen-like protein, and dried before they are sold to the market.

In Thailand, fisheries of jellyfish have been conducted for more than 20 years. The species that are commonly harvested are *Rhopilema esculenta*, *Mastigias* spp., and *Lobonema smithii*. In addition, Boonyanej (1979) reports *Rhopilema hispidum* as a commercial species. Rhizostome jellyfish are found in abundance during March,

and also between August and September, along coastal areas of the eastern provinces including Chonburi and Rayong. Along the western coast of the Gulf of Thailand, i.e. Petchaburi, they are found between October to November. Jellyfish are collected 2 to 4 kilometers from shore. Regardless of the virtually low-cost procedure, a fishing boat may earn up to 2,000-3,000 bahts per day. Jellyfish production had decreased drastically in 1993 (Table 2). However, there has been an increase in demand along with opening of new markets in Korea, Taiwan, Malaysia, Singapore, Europe, and America. As a result, export values have been on an increasing trend in the later years (Table 2). Jellyfish fisheries are now spreading to the southern provinces of the Gulf of Thailand and the Andaman Sea, i.e. Phang Nga, Phuket, Krabi, and Pattani (Table 3). Most exported products had already been processed and dried (Sirirattanachai, 1994).

Table 2. Annual jellyfish production from 1992–1996 (Department of Fisheries, 1996).

Year	Value in 1000 Tons	Value in Million Baht
1992	103.2	52.5
1993	15.6	13.8
1994	86.1	68.5
1995	33.7	39.7
1996	30.5	36.3

Table 3. Jellyfish production in the Gulf of Thailand and the Andaman Sea in 1996 (Department of Fisheries, 1996).

	Value in Tons	Value in 1,000 Baht
Gulf of Thailand	17,956	26,479
Andaman Sea	12,540	9,842
Total	30,496	36,321

IX. Rhizostome Scyphozoans in Thai Waters

In Thailand, apart from few commercial species, the information pertaining to the species diversity of scyphomedusae is somewhat scattered. Below is the list of species of rhizomedusae (Table 4), the main focus of this particular study, that are found worldwide (Arai, 1997) and the species that are found in coastal regions of the Thai/Malaysian Peninsula, including Singapore (Cornelius, 1995).

Table 4. List of rhizomedusa species found worldwide and in Thailand (Arai, 1997 and Cornelius, 1995).

Species (Worldwide)	Species found in Thailand
Family Cassiopeidae: <i>Cassiopea andromeda</i>	✓
<i>Cassiopea frondosa</i>	
<i>Cassiopea ornata</i>	✓
<i>Cassiopea xamachana</i>	
Family Catostylidae: <i>Catostylus ouwensi</i>	✓
<i>Acromitus flagellatus</i>	✓
Family Cepheidae: <i>Cephea cephea</i>	✓
<i>Cotylorhiza tuberculata</i>	
Family Lobonematidae: <i>Lobonema smithii</i>	✓
<i>Lobonema gracilis</i>	
Family Lychnorhizidae: <i>Pseudorhiza haeckeli</i>	
Family Mastigiidae: <i>Mastigias albipunctatus</i>	
<i>Mastigias papua</i>	✓
<i>Phyllorhiza peronlesueuri</i>	
<i>Phyllorhiza punctata</i>	✓
Family Rhizostomatidae: <i>Rhizostoma pulmo</i>	
<i>Rhopilema esculenta</i>	
<i>Rhopilema hispidum</i>	✓
<i>Rhopilema nomadica</i>	
<i>Rhopilema verrilli</i>	
Family Stomolophidae: <i>Stomolophus meleagris</i>	
<i>Stomolophous nomurai</i>	

Despite their importance in the ecosystem and the fishery economy, most information regarding the species diversity of rhizomedusae are limited to few commercial species such as those mentioned earlier. In consequence, to assess the species diversity, the sole purpose of this research aims at the systematic sampling of rhizomedusa specimens present along the coast of Chon Buri and Phetchaburi Provinces, where there are intensive fisheries for jellyfish. This will serve as representative of the Eastern and Western Gulf of Thailand, respectively. Furthermore, to gain insights on the annual distribution and abundance of different species of rhizomedusae, the physical and biological environmental parameters will be monitored.



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