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NAME: Mr. Charuay Sukhsangchan

THIS THESIS HAS BEEN ACCEPTED BY

____________________ **THESIS ADVISOR**

(Associate Professor Shettapong Meksumpun, Ph.D.)

____________________ **THESIS CO-ADVISOR**

(Mrs. Mala Supongpan, Ph.D.)

____________________ **DEPARTMENT HEAD**

(Assistant Professor Sunan Patarajinda, M.S.)

APPROVED BY THE GRADUATE SCHOOL ON ____________________

____________________ **DEAN**

(Associate Professor Gunjana Theeragool, D.Agr.)

THESIS

BEHAVIOR AND LIFE HISTORY OF PAPER NAUTILUS (*Argonauta hians* Lightfoot, 1786) IN THE ANDAMAN SEA, THAILAND

CHARUAY SUKHSANGCHAN

A Thesis Submitted in Partial Fulfillment of
the Requirements for the Degree of
Doctor of Philosophy (Marine Science)
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Charuay Sukhsangchan 2009: Behavior and Life History of Paper Nautilus (*Argonauta hians* Lightfoot, 1786) in the Andaman Sea, Thailand. Doctor of Philosophy (Marine Science), Major Field: Marine Science, Department of Marine Science. Thesis Advisor: Associate Professor Shettapong Meksumpun, Ph.D. 127 pages.

Argonauta hians were collected as bycatch of purse-seiners and from local fish markets around the Andaman Sea, Thailand. The animals were distributed between 7˚ 30′ 24″ – 8˚ 13′ 22″ N and 97˚ 01′ 50″ – 98˚ 55′ 48″ E. Most of the collected females were mature as evidenced by the presence of fertilized eggs within their shells. Embryonic development was observed in 15 stages. Embryos hatched with a mantle length of approximately 0.6 ± 0.103 mm and went through the planktonic life phase for at least four days. Mantle length-weight relationship in mature females could be expressed as a power regression model, $W = 1.6 \times 10^{-3}L^{2.3827}$, $R^2 = 0.888$. The relationship between mantle length and fecundity in this study was estimated to be Fe = 267.85ML-4427.8, $R^2 = 0.437$, $p<0.05$, while the relationship between weight and fecundity was estimated to be Fe = 537.81W+572.76, $R^2 = 0.4997$, $p<0.05$. Length at 50% maturity of *A. hians* was at 20.14 mm, while at 27.5 mm, 100% of the females were mature. The relationship between the proportion of mature female and total number of female followed by length could be analyzed by $P_L = \frac{1}{1+e^{(8.7031-0.4321L)}}$. Stomach contents of *A. hians* contained three major groups, namely crustaceans, cephalopods and fish. *Argonauta hians* cultivation was limited; paralarvae could be maintained for four days only. Cultivation of the adult females was also restricted to one month, although they feed routinely and develop new shell rib. Behavior (locomotion, feeding and defense) of *A. hians* was also studied.

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Charuay Sukhsangchan

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES (Continued)

Figure **Page**

LIST OF FIGURES (Continued)

LIST OF FIGURES (Continued)

Figure **Page**

Appendix Figure

LIST OF FIGURES (Continued)

LIST OF ABBREVIATIONS

a	=	arm	st	=	stalk
bde	=	blastoderm	yo	=	yolk
bm	=	buccal mass	ys	=	yolk sac
cho	=	chorion	s	=	sucker
chr	=	chromatophore	r	=	retina
e	=	eye	pe	=	perivitelline space
eys	=	external yolk sac	ol	=	optic lobe
f	=	funnel	m	=	mantle
g	=	gill	iys	=	internal yolk sac
h	=	head	is	=	ink sac
l	=	lens			

BEHAVIOR AND LIFE HISTORY OF PAPER NAUTILUS (*Argonauta hians* Lightfoot, 1786) IN THE ANDAMAN SEA, THAILAND

INTRODUCTION

Thailand is located in Southeast Asia between the latitude of 05°37′-20° 27′ N and the longitude of 93°22′-105°37′ E (Arparcuppakul, 2004). Thailand has an area close to two oceans, the Gulf of Thailand of the Pacific Ocean to the East and the Andaman Sea of the Indian Ocean to the West. The coastal area covers approximately 420,280 km^2, of which 304,000 km^2 to the Gulf having the coastline of 1,875 km., and 116,280 km^2 to the Andaman Sea having the coastline of 740 km. (Songjitswat, 2005). The Gulf of Thailand (Pacific Ocean) is shallow with the average depth of not over 90 meters whilst the Andaman Sea (Indian Ocean) is deep with the maximum depth of more than a thousand meters. The western part of Thailand consists of six provinces namely Ranong, Phang-nga, Phuket, Krabi, Trang and Satun. Although this area is directly influenced by the southwest monsoon, the water of the Andaman Sea is very clear and transparent due to its topography of deep-sloped sea bottom. The marine floras and faunas in this area therefore are specific (Nateewathana, 1993).

Cephalopods are in Phylum Mollusca but their natural history is different from those of mollusks. Cephalopods have active nerve and have evolved themselves similar to the vertebrates. They can learn and recognize new subjects. Many species of cephalopods are economically important and every year many cephalopods are caught in Thailand. The fishery statistic (2004) indicated the total caught of 184,836 tonnages valuing 10,645,800,000 Baht. The most economically popular cephalopods in Thailand are cuttlefishes, squids and bigfin reef squids, of which a lot of information on such as biology and taxonomy have been studied. However, there are more than 60 species of cephalopods found in Thailand (Nabhitabhata, 1999) and some species are in bigger sizes than those in the economic group and some species may look different but better for aquariums such as the *Argonauta*.

Argonauta are usually by-caught in purse-seiners. They are a member of the Family Argonautidae and closely relate to octopods but live epipelagically, predominantly in more than 100 meters deep and at all epipelagic depths. Argonauts feed on heteropods, pteropods and small fishes (Nixon and Young, 2003). Okutani (1960) reported that the female *A. boettgeri* hunted on the pteropod (*Cavoilnia tridentata).* Argonauts exhibit extreme sexual dimorphism in size. Males are dwarf and much smaller than females (Roper *et al*., 1984; Nesis, 1987).

Argonauta has a slender body, narrow head, and unequal arm length. Mantle length of a female *A. hians* can reach up to 50 mm while those of males are only 20 mm (Norman, 2000). *Argonauta* has eight arms, each with two rows of suckers. The numbers of suckers on the arms vary between the species. The dorsal arms in female are with laterally enlarged membrane. The male third left arm is hectocotylized, which is comparatively huge and detachable. At copulation, the hectocotylus becomes detach and active autonomously as spermatophore carrier in the mantle cavity of the female (Hanlon and Messenger, 1996).

The unique characteristic of *Argonauta* is that the female develops a calcareous structured shell, which is thin and laterally compressed. The lateral sides of shell are with radial ribs. The shell center is pressed in or bent outwards into a prominent horn (Nateewathana, 1997). The shell provides protection and floatation for the female and functions as a site of attachment for her eggs. Egg case is a single chamber with a flat keel fringed by two rows of tubercles (Beesley *et al*., 1998).

Thailand is still lacking information on *Argonauta*. All information reported only on the species found in Thai waters. Nateewathana (1997) reported collections of *Argonauta hians* found in local markets on the Andaman side. Therefore, this research aims to study on distribution, biology, life history, behavior and stomach content of the *Argonauta hians* for further managing the utilization of paper nautilus either for biodiversity preservation in Thai water.

OBJECTIVES

1. To study the distribution of *Argonauta hians* in the Andaman Sea, Thailand

2. To study the behavior of *Argonauta hians* in laboratory

3. To study the life history of *Argonauta hians* from the Andaman sea, Thailand

LITERATURE REVIEW

Cephalopod comes from the words “cephalo” meaning head and “poda” meaning foot, so cephalopod is the animal that has head close to foot. Norman and Reid (2000) reported that cephalopods had lived in this world for more than 500 million years, the studies on fossil called them “ammonites”. Cephalopods have evolved more advanced than other invertebrates. The ratio of brain to the body is similar to those of humans (Nabhitabhata *et al*., 1996).

Nateewathana (1993) reported that species of cephalopods found were different due to the geology and habitats. Thai waters comprise of the Gulf of Thailand of the South China Sea, Pacific Ocean and the Andaman Sea of the Indian Ocean. The recent cephalopods reported in this list were of 68 species belonging to 28 genera in 18 families (Nabhitabhata, 1999).

Taxonomy

Nixon and Young (2003) reported taxonomy of *Argonauta* (*Argonauta hians*) as follows;

Phylum Mollusca
Class Cephalopoda Cuvier, 1797
Subclass Coleoidea Bather, 1888
Order Octopodida Leach, 1817
Family Argonautidae Cantraine, 1841
Genus *Argonauta* Linnaeus, 1758
Species *Argonauta hains* Lightfoot, 1786

Family Argonautidae has only one genus of *Argonauta* (Voss and Williamson, 1971) consisting about 7 species; which are *Argonauta hians* (Lightfoot, 1786), *A. argo* (Linnaeus, 1758), *A. boettgeri* (Maltzan, 1881), *A. cornuta* (Conrad, 1854), *A. nodosa* (Lightfoot, 1786), *A. nouryi* (Lorois, 1852) and *A. pacifica* (Dall, 1871). In Thai waters 3 species are reported: *A. hians*, *A. argo* and *A. boettgeri*. *Argonauta argo* is the largest one in this group and its shell size can reach up to 300 mm whilst *A. hians* is the smallest and its shell size about 50 mm (Nateewatthana, 1993; Nixon and Young, 2003).

Argonauta has 8 arms; each arm is equal in length. The male third left arm is hectocotylized, which is comparatively huge and detachable (Figure 1). Female secretes in a shell with an enlarged web of dorsal arms, functioning as an elaborate egg case and this is how the name *Argonauta* is derived (Figure 2).

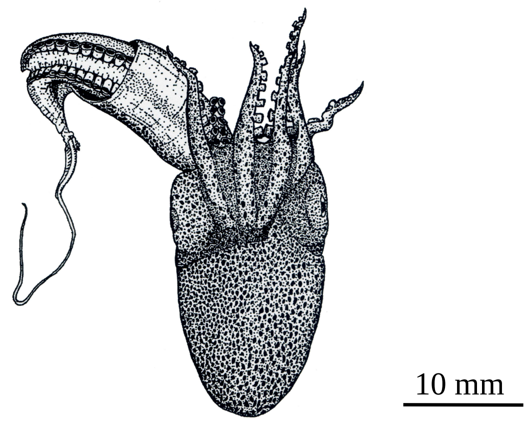

Figure 1 Male *Argonauta* with hectocotylus arm
Source: O'shea (1999)

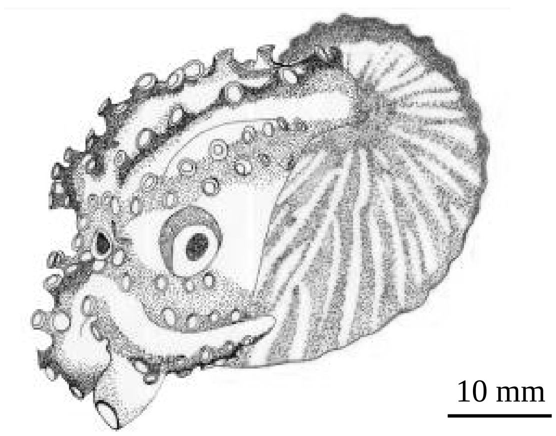

Figure 2 Female *Argonauta* has a shell cover or eggcase

General Characteristics

Cephalopods are bilateral symmetric. Foot changes to tentacle or arm (longer arm called tentacle). Squids and cuttlefishes have ten arms called decapods, of which the fifth pair is longer so called tentacles. Octopods and *Argonauta* have only eight arms and are classified as Octopodidae. The siphon of cephalopods is on the ventral side to control the direction. Cephalopods use the fins to stabilize control (Voss and Williamson, 1971). Sometimes cephalopods live in the water column and move along with the current like plankton (Yoosukh, 1998). The outer layer of cephalopods is the mantle used for covering internal organs. Cephalopods have no shell except for *Nautilus* and *Argonauta*.

Chromatophores are spreaded on the body and head (Figure 3). They are concentrated on dorsal side or ventral side and consist of three color pigments such as black, red and yellow. They are small-sized flat cells controlled by nerves (Kreuzer, 1984). Active chromatophores do change the skin colors of cephalopods. In reproductive season, male cephalopods will change their colors to attach females or sometimes to oppress other males (Phanichpong, 1985).

The heart of cephalopods consists of two auricles and one ventricle. There is a pair of ctenidia gills in mantle cavity. *Loligo* sp. and *Sepioteuthis* sp. have 20-80 filaments on each side of the gills; whereas octopods have 6-13 filaments (Nesis, 1987; Figure 4). Squids have no cilia on the gills so they can live only in clear water environment.

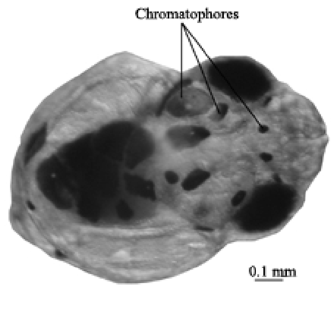

Figure 3 Chromatophores on the dorsal side of paralarva of paper nautilus

Normally female cephalopods are bigger than male, which appears also in *Argonauta* (Norman, 2000). Food and energy is very important to produce her eggs and sexual cells. The shell length of a female *Argonauta argo* can reach up to 45 cm or more than 10 cm of mantle length (Norman, 2000). The mantle length of female *A. hians* can reach up to 50 mm whilst that of male is only 20 mm (Norman, 2000)

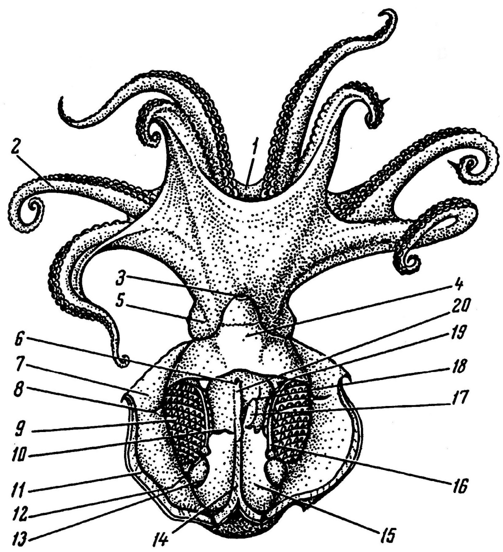

Figure 4 General internal morphology on ventral view 1. Web, 2. Arm, 3. Funnel opening, 4. Funnel, 5. Eye, 6. Anus, 7. Mantle, 8. Gill mesentery, 9. Gill, 10. Kidney opening, 11. Section of mantle wall, 12. Branchial gland, 13. Branchial heart, 14. Mantle septum, 15. Visceral mass, 16. Branchial vein, 17. Penis, 18. Genital opening, 19. Funnel retractor muscle, 20. Intestione

Source: Nesis (1987)

In *A. argo* there are 30 pairs of suckers on the first dorsal arm (Okutani *et al*., 1987). The dorsal arms in female have laterally enlarged membranes. The unique characteristic of *Argonauta* is that the female secretes in a shell under the enlarged web of dorsal arms. The calcareous-structured shell is thin and laterally compressed. Egg case is a single chamber not separated by septum unlike chambered nautilus (Nesis, 1987) with a flat keel fringed by two rows of tubercles (Beesley *et al*., 1998). The lateral sides of shell are with radial ribs. The shell center is pressed in or bent outwards into a prominent horn (Nateewathana, 1997). The shell provides protection and floatation for female and is a site of attachment for her eggs (Nixon and Young, 2003) (Figure 5).

Figure 5 Lateral side of shell of *A. hians* female

Male *Argonauta* are dwarf and 10-15 times much smaller than female (Norman, 2000; Roper *et al*., 1984). Their total length is approximately 2 cm, its mantle length approximately 1.1 cm and they lack of the promiscure shell. The males look like octopods, are finless, and have likewise 8 arms. The hectocotylus of *Argonauta* consists of three parts; a basal spermatophore reservoir, a central section bearing suckers and distally, and a long lash-like 'penis' (Beesley *et al*., 1998). At copulation, the hectocotylus is detached and active autonomously as spermatophore carrier in the mantle cavity of the female (Hanlon and Messenger, 1996).

Digestive System

Digestive system of *Argonauta* consists of chitinous-structured jaws or beaks (Figure 6). Teeth or radula are inside a buccal membrane and buccal mass (Figure 7-8). They graze food before passing to the stomach. The radula can renew after removal (Yoosukh, 1998). An ink sac is present which contains compounds of melanin pigment and alkaloid (Aungtonya *et al*., 2007). This compound solution can change the water quality locally to high alkalinity and provide bad condition for aquatic animal. The solution inhibits chemoreceptor of aquatic animal such as fish; therefore, after a cephalopod releases its ink into the water column to avoid predator, the ink chemical will attach to the nerve system of enemy. It causes the predator move slower or be unable to see for a while (Wells, 1962). The cephalopod then can escape (Chotiyaputta, 1993). Salivary glands are located on three places; sublingual, anterior and posterior. The posterior one is smaller than the others and the anterior glands in cephalopods could produce toxic (Nixon and Young, 2003; Chotiyaputta, 1993; Norman and Reid, 2000).

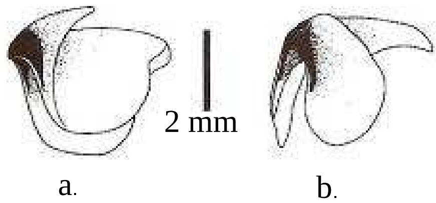

Figure 6 Beaks of *A. hians*; a. Upper beak and b. Lower beak

Source: Nateewathana (1997)

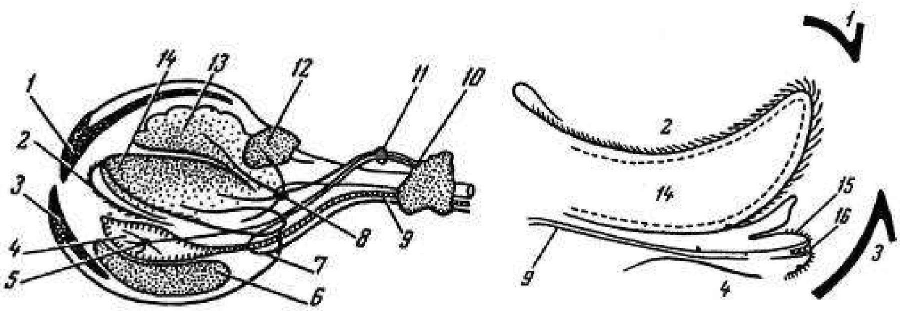

Figure 7 Mouth composition; buccal mass 1. Upper mandible 2. Radula, 3. Lower mandible, 4. Salivary papilla, 5. Subradular ganglion, 6. Sublingual salivary gland, 7. Posterior salivary gland, 8. Inferior buccal ganglion, 9. Posterior salivary gland duct, 10. Superior buccal lobe, 11. Interbuccal and cerebro-subradular connectives, 12. Anterior salivary gland, 13. Buccal palp, 14. Muscular radula support, 15. Salivary papilla teeth, 16. Teeth on inverted end of salivary duct

Source: Nesis (1987)

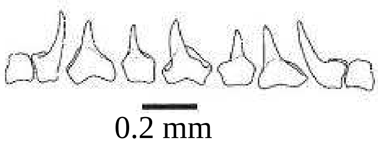

Figure 8 Radula of *A. hians* with 7 transverse rows of unicuspid teeth and 2 marginal plates

Source: Nateewathana (1997)

Food and Feeding

Cephalopods are carnivorous and selective feeding animal (Norman, 2000); feeding and digestive process changes during the life cycle of them (Boucher-Rodoni *et al*., 1987). Prey items are almost certainly different during growth, at least in their size. However, Octopus like to feed on fishes, crustaceans and other cephalopods. Feeding behavior of cephalopods consists of 3 processes; attention, positioning and seizure (Messenger, 1977; Nabhitabhata, 1993). Several kinds of species are active at night, in the sea as well as in the laboratory such as *Octopus vulgaris* (Boucher-Rodoni *et al*., 1987). *Nautilus* is a nocturnal feeder, hunt by smell and touch; prey being capture by the many tentacles (Haven, 1972).

Stomach contents of *Nautilus macrocephalous* consist of crustacean molt, appendages of large spiny lobster (*Panulirus longipes*), hermit crabs and crab (Nixon, 1987). In stomach contents of *Grimpoteuthis glacailis* had a large pieces of polychaetes, In stomach contents of *Chunioteuthis ebersbachi* was filled with small crustacean and in *Octopus vulgaris* feeds mostly upon crabs, mollusk and bony fish (Nixon, 1987). Oceanic octopus such as *Tremoctopus violaceus* the stomach contents contained shells of pteropod mollusks and fish (Thomas, 1977).

Nixon and Young (2003) reported that *Argonauta* fed on heteropods, pteropods and small fishes. Female *A. boettgeri* hunted on the pteropods (*Cavoilnia tridentate*; Okutani, 1960). *Argonauta* fed on small fishes by biting the head off and eating the body (Beebe, 1926) and gonad or center of bell jellyfish (Heeger *et al.*, 1992).

Nervous System

Nervous system of cephalopods has developed the most advanced compared with other invertebrates. They have brains which are separated into two parts of posterior part or supraesophageal ganglion, and ventral part or subesophageal ganglion (Nixon and Young, 2003; Chotiyaputta, 1993). The supraesophageal ganglion consists of cerebral, buccal, and optic ganglions while subesophageal ganglion consists of pedal, branchial, and visceral ganglions (Nixon and Young, 2003; Wells, 1962; Hanlon and Messenger, 1996).

Kreuzer (1984) reported that the brains of pelagic squids are more developed than those of bottom squids because they usually more often use their eyes to look for preys and enemies. The size of cephalopod's brain ranking from bigger one to smaller one is that of squid, cuttlefish, and octopus respectively. Upper brain and lower brain are able to memorize the past activities (of the last 3 weeks) and able to improve the future behavior (Nabhitabhata, 1993).

All behaviors of cephalopod are the result of developing brain such as defensive behavior. This behavior starts from raising the tentacles, blowing water, changing color, ejecting ink and finally swimming away (Sukhsangchan *et al*., 2005).

Receptors

Cephalopod eyes are the same as vertebrates consisting of retina, lens, iris and cornea. There is no cone cell but rod cell at retina. The eyes of cephalopod are the largest eyes in the world with a diameter of about 20 cm (Pechenik, 1996). Cephalopod eyes are unable to tell color shade but the retina is able to check and identify wave length (Kreuzer, 1984; Nabhitabhata *et al*., 1996). The eyes of *Argonauta* are large, round and silvery. They are placed laterally thus give wide visual field. The eye size compared with the mantle length is for a 2.5 mm male, the eye size is about 40% of mantle length; whereas, for a 95 mm female shell diameter, the eye size is about 17% of mantle length (Nixon and Young, 2003).

Circulation System

The blood circulation system of cephalopod consists of three heart one over each gill (brachial heart) and one central heart, brachial glands and blood vessels and is close circuit; The blood is transparent or pale blue resulted by haemocyanin compound and blood from the body is actively pumped to the gills in order to add oxygen before circulating back to the body (Norman, 2000).

Reproductive System

Cephalopods are dioecious (the species is distinctly male or female). Females have ovary and oviduct. Males have testis, a seminal vesicle, a spermatophoric sac, and a gonad appearing at posterior end (Figure 9). Male cephalopods collect sperm in spermatophores located in a specific arm call (hectocotylized arm). For example, in *Loligo* spp. it appears at the fourth left arm while in *Argonauta* the third left arm is modified. This arm is longer than other arms, which develops within a sealed pouch. During copulation, hectocotylized arm is detached and passed to female. The male then die (Norman, 2000). Eggs are fertilized in the mantle cavity and developed inside in early stage, after that female will laid her eggs in the egg case (Hanlon and Messenger, 1996; Norman and Reid, 2000; Sukhsangchan and Nabitabhata, 2007).

The female cephalopod becomes mature 2-3 month after hatching. Cephalopods in natural environment mate in the morning or at night or in twilight time (Nabhitabhata, 1993), whilst in the laboratory cephalopods mate at any time and lay their eggs about one week later. Fertilized eggs are covered with gelatinous matrix from nidamental gland, accessory nidamental gland and oviducal gland (Nabhitabhata, 1993).

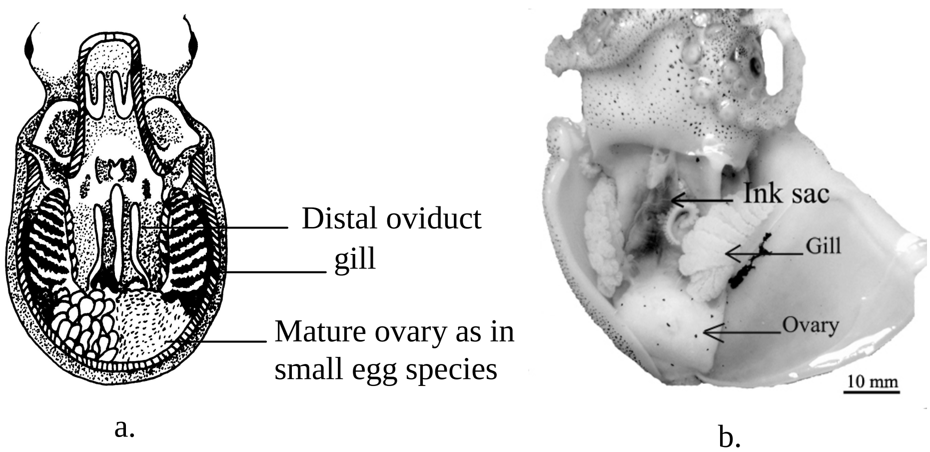

Figure 9 Internal structure of octopods**;** a. female *Octopus* b. Female*s A. hians*
Source: Carpenter and Niem (1998)

Cephalopod's eggs are separated into two types: 1) the aggregated egg and 2) the single egg. Both eggs types are encapsulated, but in the aggregated form an egg capsule contain many embryos. In the single type, the capsule contains only one embryo and each egg connected to the others by a stalk. The single egg looks like a grape and is found at bottom floor or inside the shell in Argonaut (Nilaphat, 2001).

The eggs of *Argonauta*'s are solitery (Figure 10). After reproduction the female of *Argonauta* spawn into the egg case. The eggs of *Argonauta* are small telolecithal eggs or uneven distribution of yolk in the cytoplasm of egg. Paralarvae of *Argonauta* will develop in the egg case until hatching, normally at nighttime (Morton, 1968; Nixon and Young, 2003).

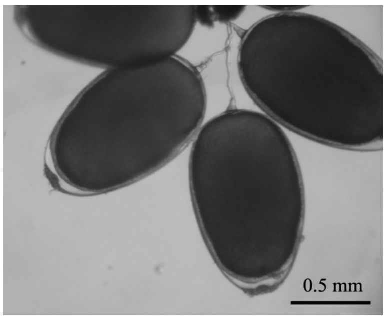

Figure 10 *A. hians* eggs with stalk

Embryonic development of cephalopods is different among each species/groups; for example, *Sepia pharaonis* has 19 stages while *Sepioteuthis lessoniana* provides only 12 stages (Chumdang, 1998). Arnold *et al.*, (1972) reported that the embryonic development of *Euprymna scolopes* implicates 30 stages. The period of hatching for cephalopods was controlled by the temperature and the optimum temperature was 20-30 degree Celsius. For Octopus, the optimum temperature was 28 degree Celsius (Phanichpong, 1985; Segawa, 1987). Nabhitabhata (1993) reported that the embryonic development of cephalopods could be identified into 10 stages as follows;

Stage 1 Egg was not transparent.

Stage 2 Egg was transparent and the cleavage cell at the top of the egg could be seen.

Stage 3 Blastoderm covered about half of the egg.

Stage 4 Head and eyes appeared.

Stage 5 Tentacles appeared.

Stage 6 Eyes became red.

Stage 7 Head separated from the body.

Stage 8 Eyes changed to black color.

Stage 9 Yolk reduced to the same size as the head

Stage 10 Yolk reduced to be smaller size than the head, moved and hatched.

The new hatching some organs of juvenile are active after hatching; for example, ink sac can release ink, and chromatophores are active by changing color (Nabhitabhata, 1993).

Habitat

Cephalopods can be found worldwide but they live in different habitats depending on the species. Cuttlefishes live near the bottom floor, bigfin reef squids live in water column and squids live in the coral reef (Supongpan *et al*., 1988). Hanlon and Messenger (1996) reported that several species of octopuses lived in tidal zones, but finned octopods and vampire squids lived in the deep ocean usually below 3000 m. Many cephalopods cannot live either in dirty water, where there are a lot of particles because they cannot get rid of the particles on their gills, or in freshwater (Nixon and Young, 2003). Cuttlefishes can live around continental shelf or continental upper edge and sometimes they migrate to the coastal zones of the Atlantic Ocean in Europe, West of Africa, the Indian Ocean and West of the Pacific (Kreuzer, 1984).

Argonauta are cosmopolitan species found in tropical and subtropical oceans and they live epipelagically. The different species can be found at the water depth from 50 up to 350 meters (Figure 11; Nixon and Young, 2003). Temperature is an important factor for the appearance of *A. argo* (Norman, 2000; Guerra *et al*., 2002; Nixon and Young 2003).

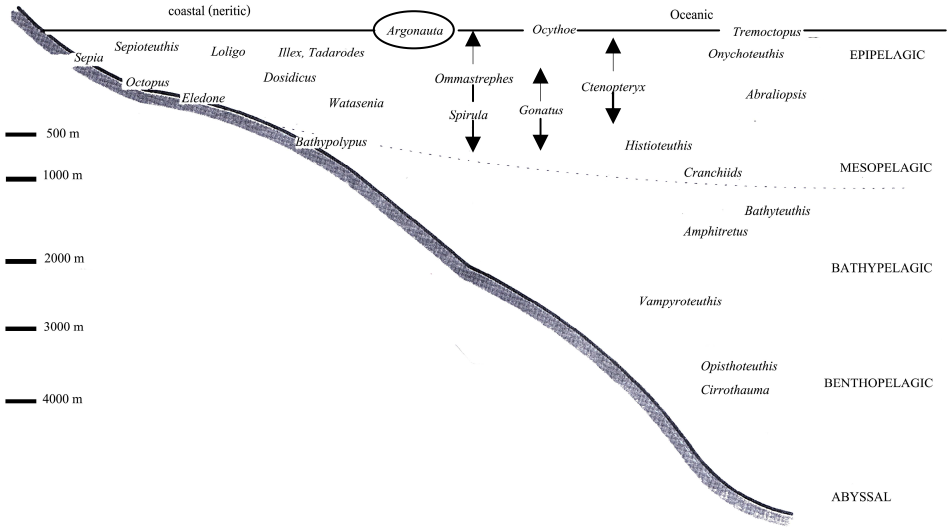

Figure 11 Distribution map of cephalopods within depth
Source: Hanlon and Messenger (1996)

Argonauta hians and *A. boettgeri* can be found solitary attaching to floating substances or in groups of 20-30 in the water. Collections of Day (2003) provide detailed GPS data of *Argonauta* collections. *Argonauta hians* and *A. argo* were catched in tropical and subtropical open seas (*A. hians* 21.32 N, 106.40 E; *A. argo (*1.45 S to 43.0 N, 28.47 W to 124.26 E) while *A. boettgeri* (31.92 N 140.30 E) was found in tropical and subtropical zones of the Indo-Western Pacific.

Cephalopod Culture

Biologists believed that cephalopods were difficult to culture because they were sensitive to the water quality including temperature, pH, and dissolved oxygen. However, cephalopods can be cultured in close circuit system. Nabhitabhata (1993) reported that the first process, in order to study squid culture, was clean and clear water of more than 5 mg/l dissolved oxygen, pH 7.0-8.5 and 25-35 ppt. of salinity. Cephalopods feed on living animals but in the cultivation cuttlefish could be fed with frozen shrimps or fresh fishes (Sukseelaung, 1995).

Nabhitabhata (2000) reported that squid culture was started in 1928 but it was not popular because the cephalopods in the sea were still abundant. In Thailand, squid culture started in 1977 by Boonpragaub *et al*. with studies on the biology of *Sepiella inermis*. After that Nabhitabhata (1978a, b) tried to culture *Sepioteuthis lessoniana*, *Sepia pharaonis* and *Sepiella inermis* (Nabhitabhata *et al*., 1984a) in the laboratory. Nabhitabhata (1984b) reported that bigfin reef squids could be cultured in developed net in the sea. The squid culture in a pond could be done in several areas but the result was different among each species; for example, *S. inermis and S. pharaonis* was easier to culture than *S. lessoniana* (Nabhitabhata *et al*., 1985).

Nabhitabhata (2000) reported that from the past recent years, more than 14 species of cephalopods could be cultured in Thailand, of which only for four species (*S. lessoniana, S. pharaonis, S. inermis* and *E. hyllebergi*,) the whole life cycle is documentated.

Nilaphat (2001) reported that culturing *Euprymna* had high growth rate in the first 20 days both in length and weight, especially the length in day 10 to 20. After 50 days the growth rate decreased. The reproduction occurred after 90 days and they died after laying eggs. In Argonaut still lack of information to cultivate, the paralarvae were able to survive for about 4 days in laboratory tank (Sukhsangchan and Nabhitabhata, 2007).

Behavior

Although cephalopods are the member of mollusc but their morphology, physiology and ecology are more fish-like than any other molluscan, they have the largest brain of all invertebrates and their behavior is comparable in many aspects with that of the higher vertebrates (Wells, 1962; Packard, 1972).

Cephalopod behavior has been studied in five different ways such as; *in vitro* studies, *in situ* direct observation, shipboard research, indirect methods and new technique (Hanlon and Messenger, 1996). Behavior of cephalopod is driven by sense organs, effectors and the brain. Sense organs of cephalopod include the mechaloreceptors, chemoreceptor and photoreceptors while effectors are consisting of muscles, chromatophore organs, reflecting cells, photophore, ink sac, arm appendages and the buccal mass. The brain of cephalopod is advance, routine handle much more information, its central nerves system (CNS) is substantially larger and the ganglions more dilicate than other mollusks (Hanlon and Messenger, 1996). Usually, behavioral studies of cephalopod includes 1) the changing of color change and body patterns, 2) feeding and foraging 3) defending, 4) reproducing, 5) communicating, and 6) learning and adapting.

Cephalopods are living prey carnivorous. They feed on whatever they can detect by sighting or touching. The most important part uses for capturing prey in octopods or some pelagic octopods such as argonaut are their web. This web can be extended from each of the first arm during feeding (Hanlon and Messenger, 1996).

The defending behavior of Cephalopods can be divided into primary defensive and secondary defensive strategies. Primary defensive strategy aims to decrease the chances of predator encountered while secondary defensive strategy is usually used when the cephalopods are detected by predator. The strategy aims to interfere the approaching or attacking sequences of the predator. The secondary strategy also aims to force the predator to release its prey during capture or consumption (Hanlon and Messenger, 1996).

Octopods are solitary animals except the time during mating while they will show a little agonistic or courtship behavior before mating. So far, mating behavior of 16 octopods species has been observed including *O. cyanea, O. vulgaris or O.briareus* ect. The mating duration varied by species and ranged from half to two hours. Mating behavior of *O.vulgaris* copulated in two ways. Male either leap upon a female and mounting her mantle or station near female and extend the hectocotylus arm toward female.

Some of the different involve the relatively abrupt changes in behavior that call learning. Learning behavior in cephalopod has been developing by sight and touch (Wells, 1962). However, knowledge on learning behavior is limited from many reasons including the difficulty to study adult cephalopod *in situ* and various cephalopods are not easy to keep, alone rare, in an aquarium, even though new techniques are making culture more feasible (Hanlon, 1990).

MATERIALS AND METHODS

Materials

1. Materials for collecting specimens

    1.1 Plastic bags, plastic boxes and foam boxes

    1.2 Air pump set

    1.3 Fixation solution: formalin 10% and alcohol 70%

2. Materials for hatchery maintenance

    2.1 Fiber glass aquaria. Size 300, 500 and 1,000 liters

    2.2 Small aquarium. Size 24 x 46 x 28 cm

    2.3 Air pump set

    2.4 Salinity refractometer of Optik^{R} Handeld Refractometer model S-100

    2.5 Thermometer of Maxima-Minima-Thermometer

    2.6 pH meter of Oakton model pHTestr 30

    2.7 Food for paralarvae of *Argonauta* such as *Penaeus* spp. and *Acetes* spp.

    2.8 Food for adult such as small fishes (wild fish larvae), shrimps (*Litopenaeus vannamei*, *Parapeneopsis* sp.) and polychaetes (*Perinereis* sp.)

3. Materials in laboratory

    3.1 Binocular stereo microscope “SZ-ST Olympus”

    3.2 Scanning electron microscope “JSM 5600 LV”

    3.3 Balance meter (3 point) of Mettler Toledo model AB204-S

    3.4 Vernier caliper

    3.5 Petri dish

    3.6 Beaker

    3.7 Forceps

    3.8 Needles

    3.9 Scissors

3.10 Knives
3.11 Trays
3.12 Digital camera “Sony model DSC-W7”
3.13 Recorder camera “Sony model DCR-DVD605E”

Methods

1. Distribution

Study on distribution of *Argonauta hians* by field survey and fisherman’s questionnaire of each individual province along the Andaman Sea and then plot the latitude and longitude position in the map.

Specimen Collecting

a. Dead specimen

- Collect the specimen from fish markets of each province around the Andaman Sea every month throughout the year.
- Preserve the specimens in formalin 10% and change to alcohol 70%.

b. Live specimen

- Collect the live specimens from purse-seiners operating in the Andaman Sea (Figure 12).
- Maintain the live specimens onboard in PVC tanks with aeration supplies. Then, transport to the hatchery at Phuket Marine Biological Center (PMBC).

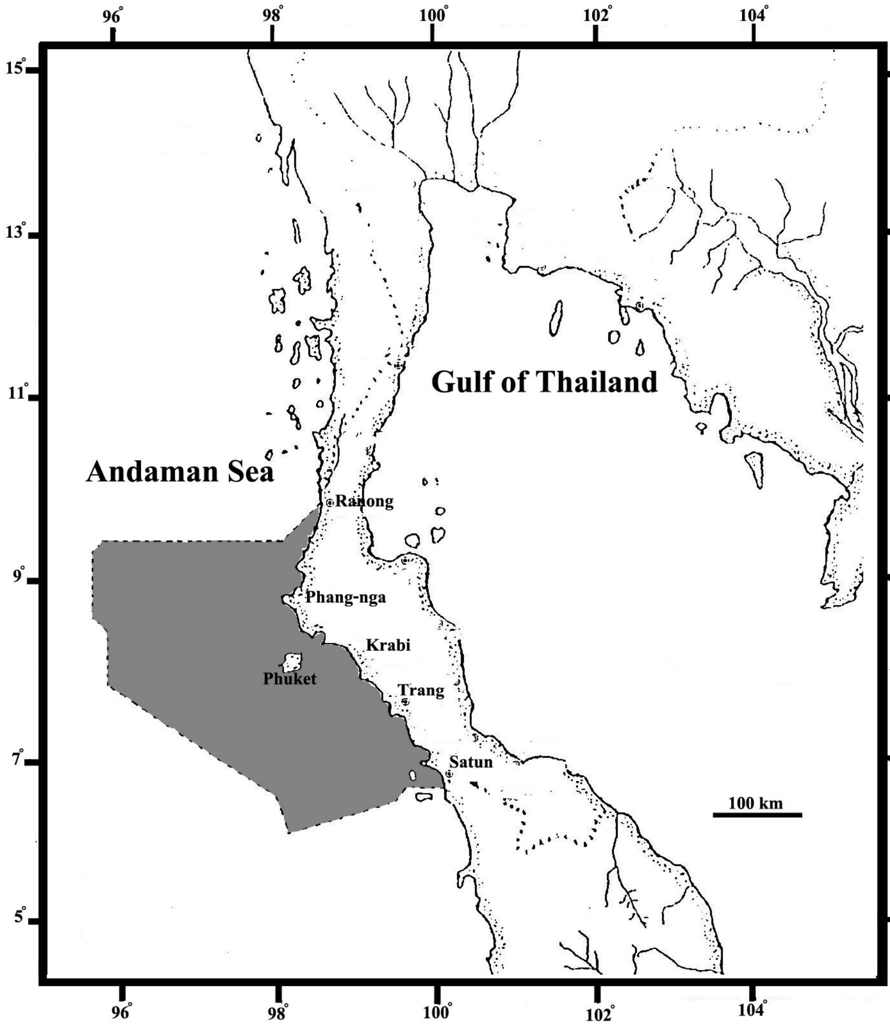

Figure 12 Map of area collection

2. Paper nautilus cultivation

2.1 Prepare the fiber glass aquaria , size 300, 500 and 1,000 liters, by clean and set air supply and for cultivating the live specimen

2.2 Prepare live and fresh food for *Argonauta* such as shrimp, mysis, polychaete and small fish.

2.2 Control water quality including pH, salinity and temperature to the optimum condition for *Argonauta*

3. Behavior and Life History

3.1 Measurements on morphometric data such as number of sucker, length of arms, shell length, radula and beak

3.1.1 Beak measurement (Figure 13). Beak measurements were taken according to the definition of Clarke (1986).

3.1.1.1 Upper beak

- Length of the rostrum: rl
- Length of the rostral tip to inner margin of wing: rw
- Length of hood: hl
- Width of the wing: ww
- Wing to crest length: wcl
- Length of the crest: cl
- Jaw angle width: jw

3.1.1.2 Lower beak

- Length of the rostral tip to inner posterior corner of lateral wall: rc
- Length of the rostral tip to inner margin of wing: rw
- Length of the rostral: rl
- Length of the wing: wl
- Jaw angle width: jw

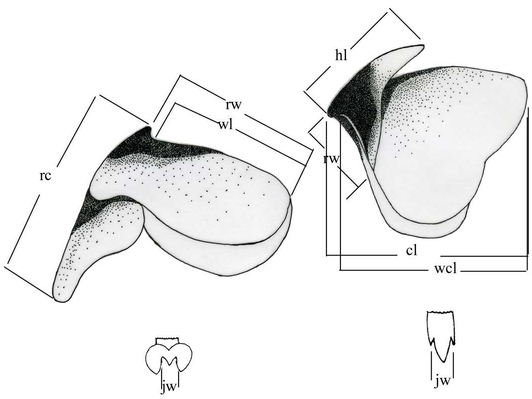

Figure 13 Beak Morphology

Source: Clarke (1986)

3.1.2 Body measurement in mm

3.1.2.1 Total length (TL) measured from posterior end to anterior end in mm

3.1.2.2 Mantle length (ML) measured from posterior end to middle of the eye in mm (Figure 14)

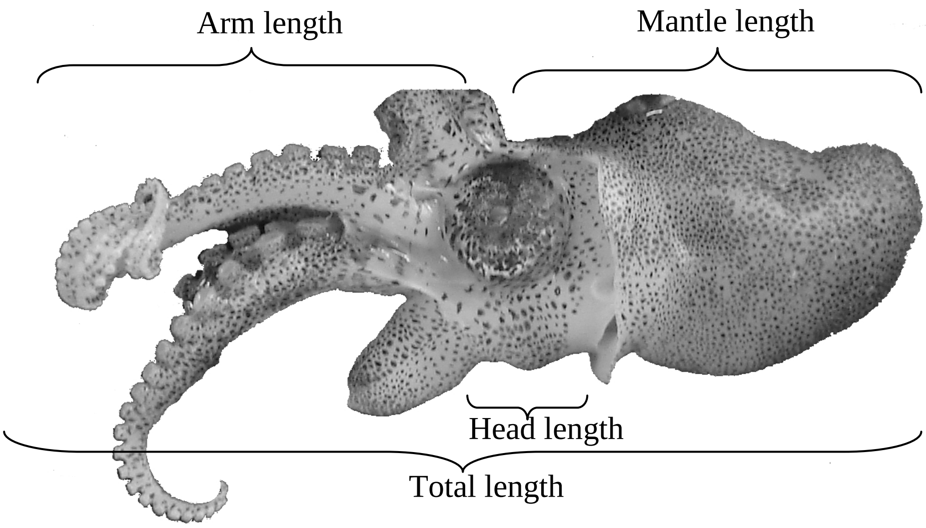

Figure 14 Measurement of *A.hians*

3.1.3 Shell measurement in mm (Figure15-16)

3.1.3.1 Shell length (SL)

3.1.3.2 Shell width (SW)

3.1.3.3 Shell height (SH)

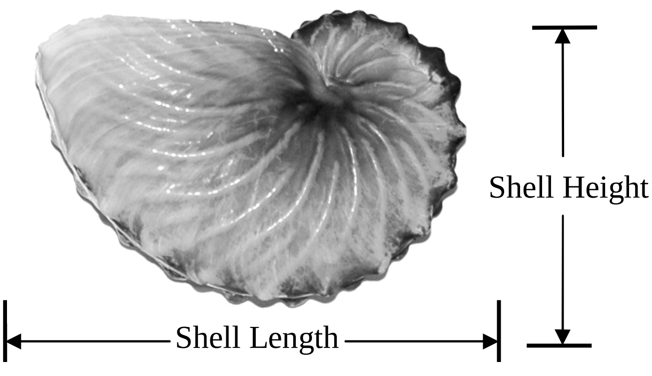

Figure 15 Shell length and shell height measurement

Figure 16 Shell width measurement

3.2 Study the behavior of *Argonauta* such as feeding, defensive and locomotion was recorded in small aquarium by digital camera and video camera.

3.3 Study on life history

3.3.1 Fecundity following Holden and Raitt (1974) as of formula;

$$F = \frac{n.G}{g} \qquad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots..(1)$$

When F = Fecundity

n = Number of egg's random

G = Weight (g)

g = Weight of ovary's random (g)

3.3.2 Gonadosomatic index following King (1995) as of formula;

$$GI = 100\frac{GM}{TM} \qquad \text{…………………... (2)}$$

When GI = Gonad index

GM = Gonad mass (g)

TM = Total mass of the animal (g)

3.3.3 Length at 50% maturity. Bakhayokho (1983) reported that size at first maturity was the smallest size of mature female and the ratio of mature female was separated by middle length following Thappanand (2000) as of formula;

$$P_L = \frac{N_{fmL}}{N_{ftL}} \qquad \text{……………………..(3)}$$

When P_L = Proportion of mature female

N_{fmL} = Number of adult female

N_{ftL} = Total number of adult female

3.3.4 Embryonic development observed under stereo binocular and recorded by digital camera and video camera

3.3.5 Length-weight relationship following Rounsefell and Everhart (1953); Brown (1957) as of formula;

$$W = qL^b \qquad \text{………………………(4)}$$

When W = Weight (g)

L = Mantle length (mm)

q = Y-intercept

b = Slope

3.4 Stomach content

Specimens of *Argonauta* were fixed in 10% formalin and preserved in 70% alcohol. They were measured to the nearest millimeter of mantle length (mm ML).

Stomach fullness was determined to five points according to the definition of Lipinski and Linkowski (1988): 0 = stomach empty, 1 = traces of food, 2 = less than half filled, 3 = more than half filled and 4 = full

The contribution of prey item to the diet was determined using the index of relative importance (IRI) of Pinkas *et al*., (1971). This analysis combines the frequency of occurrence, numerical abundance and volume displacement of prey items as of formula;

$$IRI = F(N+V) \qquad \text{..........................(5)}$$

When F is the percentage of frequency of occurrence (the number of stomachs in which a specific prey item was found, divided by the total number of non-empty fish stomach); N is the percentage of numerical abundance (the total number of the specific prey item divided by the total of all prey items) and V is the percentage of volume displacement (the volume of a specific prey item divided by the total volume of all prey).

Research Area

Main Research Centers

1. Department of Marine Science, Faculty of Fisheries, Kasetsart University
   - Study on morphology, biology and data analysis
2. Phuket Marine Biology Center
   - Study on behavior, embryonic development and specimen culture

Research Period

March 2006 – July 2007

Benefits

1. To know the distribution of *Argonauta hians* in the Andaman Sea, Thailand

2. To know the life history and behavior of *Argonauta hians* from the Andaman Sea, Thailand

3. To know the biology, morphometric and behavior of *Argonauta hians*

RESULTS AND DISCUSSION

Distribution

Argonauta hians was collected around the Andaman Sea, about 20 nautical miles offshore from purse seiner, between the sea surface and the depth of more than 80 meters. They were distributing between 7˚30′ 24″ – 8˚ 13′ 22″ N and 97˚ 01′ 50″ – 98˚ 55′ 48″ E in the area of Phangnga, Phuket and Krabi Provinces (Figure 17).

Field survey and fisherman’s questionnaire on the distribution of *A. hians* reveled that the specimens can be found along the western coastal of Thailand except Ranong, Trang and Satun Provinces. One possibility that causes the lack of existence of *A. hians* might caused by the shallower water of average depth of sea bottom around Ranong, Trang and Satun Provinces when compare to the other four provinces (Phongsuwan, 1999). Areas of fishing ground in Phangnga, Phuket and Krabi Province are mostly beyond the continental shelf line (over 100 metres depth), while fishing ground of Ranong, Trang and Satun are usually shallower. However, the fishermam’s questionare reported can found the specimens of *A.hians* in the area of Malaysian Waters which closed up with Satun Province.

Nesis (1982) reported *Argonauta* found in epipelalgic zone but not only at the surface in tropical and subtropical area. Chun (1975) reported can collected the specimens of male and female of *Argonauta hians* from vertical net in deep water in the area of the South Equatorial Current. However, *Argonauta* could also live in deeper water of 300-350 meters (Nixon and Young, 2003). Guerra *et al.*, (2002) reported that in the North-eastern Atlantic *A. argo* appeared near the surface at 42˚15′ N–08˚48′ W. All of specimens collected during the research period in the Andaman Sea found only one species and they were females and mostly 92 % mature. Demicheli *et al*., (2006) reported the mass standing of *A.nodosa* can be found along the Uruguayan coast (southwestern Atlantic Ocean) between January and April 2004 and in Uruguay waters have been mentioned for three species of argonaut such as *A.argo*, *A.hians* and *A.nodosa*. Guerra *et al*.,(2002) reported the specimen of mature female of *A. argo* found near the surface at dusk, in the Ria de Aldan (42˚15′ N–08˚ 48′ W) in the north-western Atlantic.

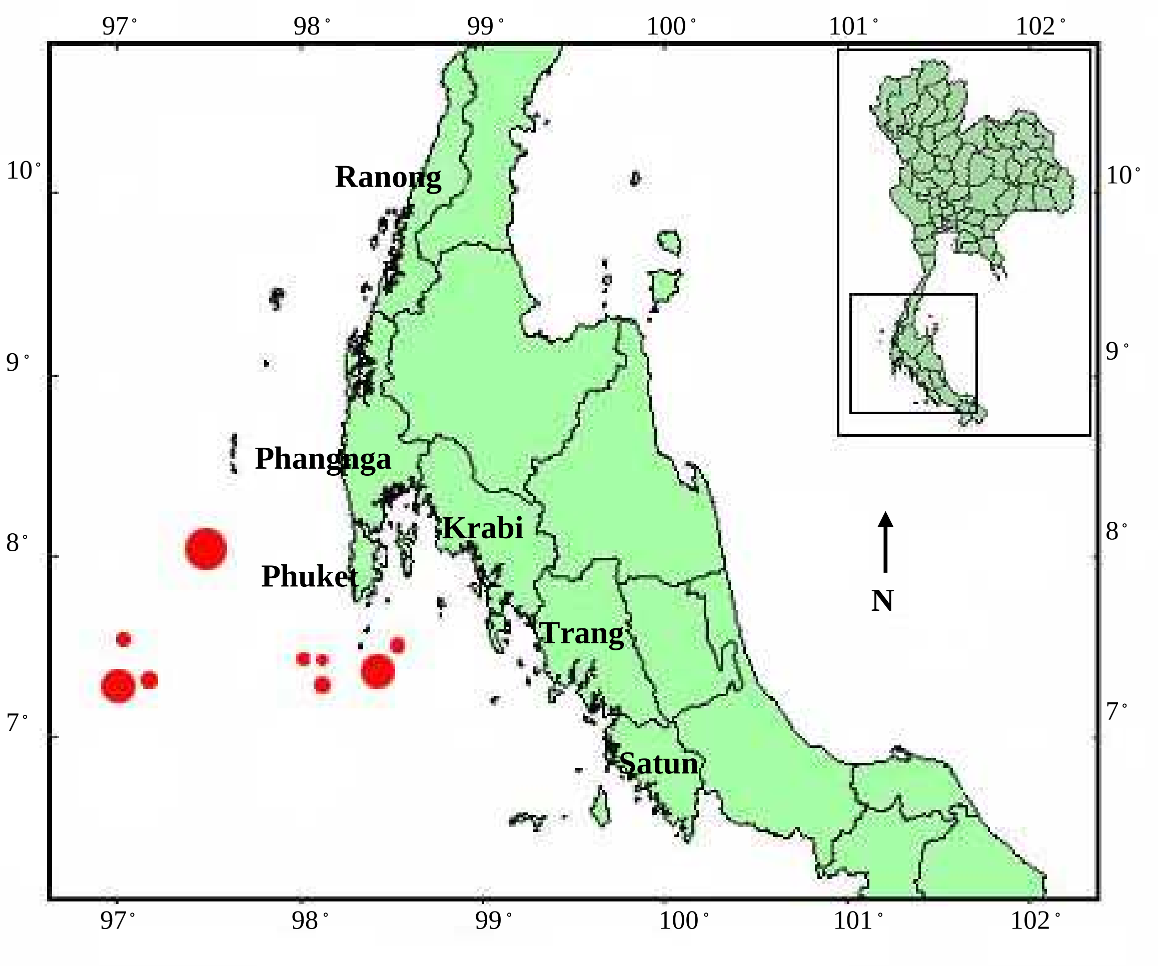

Figure 17 Distribution of *A.hians* in the Andaman Sea, Thailand

Embryonic Development

Egg Capsules

The egg capsules were single and connected to each other by stalks (Figure 18). The average length of egg capsules of *A. hians* was 1.06±0.11 mm (0.77-1.46 mm, weight 0.0024 g), which was the same size as *A. boettgeri* of about 0.85-1.1 millimeter

(Nesis, 1977). Normally, female argonauts began to reproduce at young stage, *A. boettgeri* at 14-15 mm mantle length and *A. hians* at 18-20 mm (Beesley *et al*., 1998).

The mantle length of *A. hians* was collected in this study were around 14.8-52.2 (30.99±6.47) mm which could be assumed that the collected specimen had partially spawned.

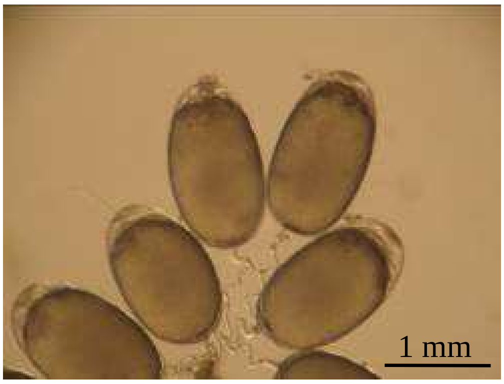

Figure 18 Egg capsules of *A. hians*

The number of eggs inside the shell of *A. hians* was 6,276-17,936 (12,048±4,432). In contrast to this Laptikchovsky and Salman (2003) estimated a potential fecundity of 18,000 eggs for *A. hians*. Average weight of the egg cluster inside the egg case was 3.09±1.26 g. The oval-shaped eggs were telolecithal. The egg capsules inside the egg case had various embryonic stages, which could be separated visually by colors (Figure 19). The eggs in the early stages (stage 1-6) of development were yellow or white, and situated in the outer part of egg case close to the shell aperture. Eggs of stages (7-12) were situated in the middle part, while the late stages (13-15) could be found in the inner part of the shell chamber. According to my observation, most of the embryos hatched at night. The mantle lengths of hatchlings were approximately 0.6±0.103 mm with the total length of 1.0 mm and relatively almost equal to the short arm length. The embryos can not be separated male or female and all of embryos at the first pair of arms were not laterally enlarged and shell. However, in *A. argo* can separate into male or female at the mantle length of

2 mm. In male the pouch of the hectocotylus arm will appear at 2.5 mm ML. while in female, the shell sac is visible at 4 mm ML (Nixon and Young, 2003). The hatchlings were planktonic, suspending in the water column by means of water jetting from funnels. They were able to survive for about 4-7 days without feeding.

In the laboratory the adult females died after egg hatching by sinking to the bottom and crawling out of the shell. This observation varies to the description of Beesleys *et al*. (1998) and Nesis (1977) that females argonauts reproduce very early and continue growing and reproduce for a long period of time. Further study is necessary to verify if *Argonauta* could be maintained for further reproductive cycles.

Figure 19 Eggs in the egg case

Embryonic Development

Embryonic development of *A. hians* (at time of collection) could be characterized to 15 stages (Figure 20-34). The time of fertilization and spawning could unfortunately not be observed (Table 1).

Table 1 Embryonic development of *A. hians*

Observed Stage	Description	Develop period (hrs.)	Days after fertilization
1	earliest stages obtained, oval in shape, chorion cover yolk (Figure 20)	-	-
2	blastoderm covering about 15% of the egg (Figure 21)	50	2 days 2 hrs.
3	blastoderm covering about 30% of the egg (Figure 22)	12	2 days 14 hrs.
4	blastoderm covering about 50% of the egg (Figure 23)	7	2 days 21 hrs.
5	blastoderm covering about 75% of the egg (Figure 24)	2	2 days 23 hrs.
6	blastoderm covering about 90% of the egg (Figure 25)	2	3 days 1 hrs.
7	another organ primordial observed, the vegetal pole developing into yolk sac and the animal pole developing into mantle and appendages, head forming, pale orange spots developing into eyes, primordial of arms observed (Figure 26)	9-10	3 days 10-11 hrs.
8	orange eyes and gills observed, arms were observed with suckers, mantle round on the animal pole, internal yolk sac observed (Figure 27)	3	3 days 13-14 hrs.

Table 1 (Continued)

Observed Stage	Description	Develop period (hrs.)	Days after fertilization
9	mantle fully developed, funnel protruding, head enlarging into 2 lobes, optic lobes developing into eyes with lens color changed from orange to black, internal yolk sac forming 2 lobes, arms developed (Figure 28)	2-7	3 days 15-21 hrs.
10	about 10 orange and black chromatophores observed on dorsum (Figure 29)	51-55	5 days 18 hrs. – 6 days 4 hrs.
11	arm length increasing from previous stages, size of external yolk sac decreased to about 40% of head (Figure 30)	23-27	6 days 17 hrs. - 7 days 8 hrs.
12	yolk transferring from external into internal yolk sac and decreasing in size to be about 25% of head, 3-4 chromatophores on ventral mantle and head patterning in straight line (Figure 31)	9-14	7 days 2 hrs. -7 days 22 hrs.
13	external yolk decreasing to about 15% of head, size of internal yolk sac observed about 50% of mantle width, chromatophores scattered (Figure 32)	12-15	7 days 14 hrs. - 8 days 13 hrs.

Table 1 (Continued)

Observed Stage	Description	Develop period (hrs.)	Days after fertilization
14	external yolk sac about 10% of head (Figure 33)	3-8	7 days 17 hrs. - 8 days 21 hrs.
15	internal yolk sac about 50% of mantle width, hatching started, hatchling (Figure 34)	24-27	8 days 17 hrs. - 10 days
	Total	204-239	

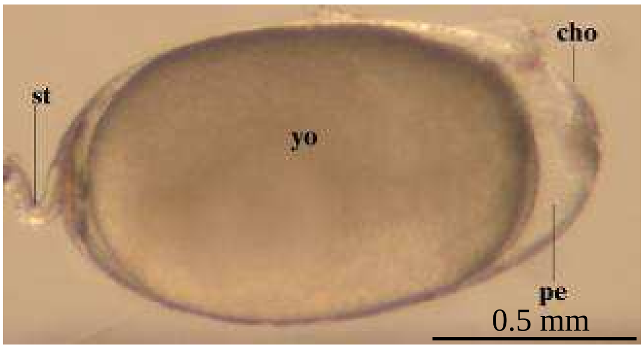

Figure 20 Observed stage 1

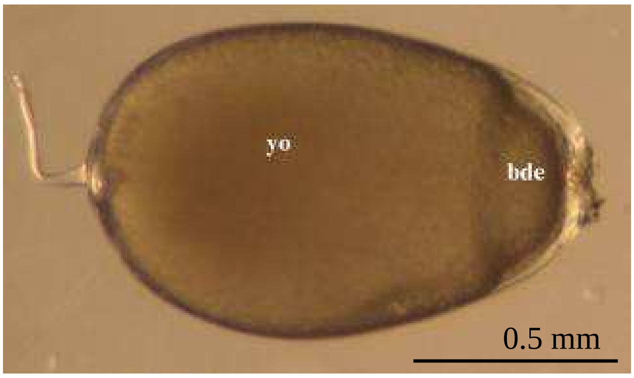

Figure 21 Observed stage 2

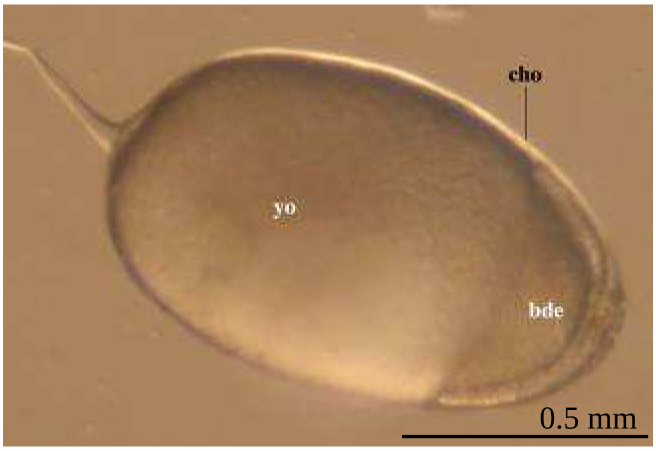

Figure 22 Observed stage 3

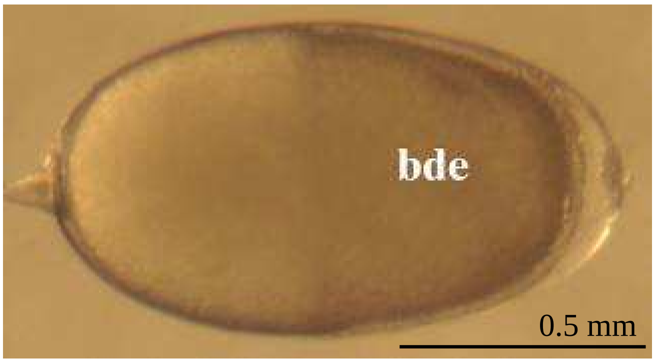

Figure 23 Observed stage 4

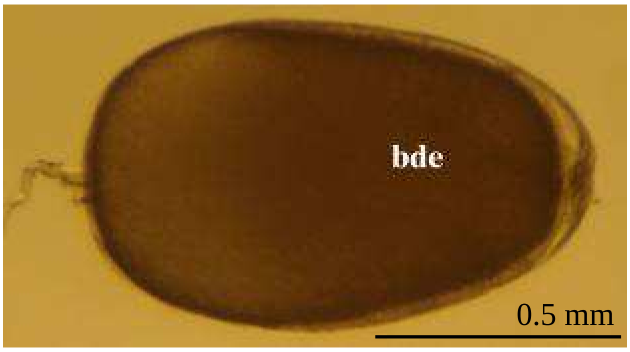

Figure 24 Observed stage 5

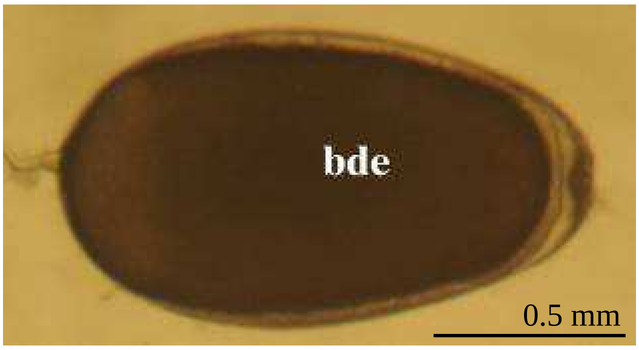

Figure 25 Observed stage 6

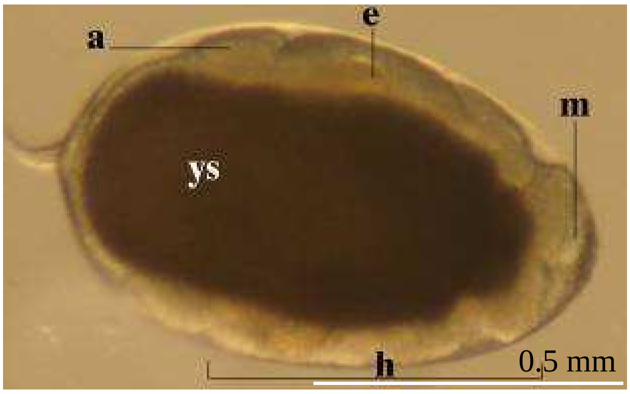

Figure 26 Observed stage 7

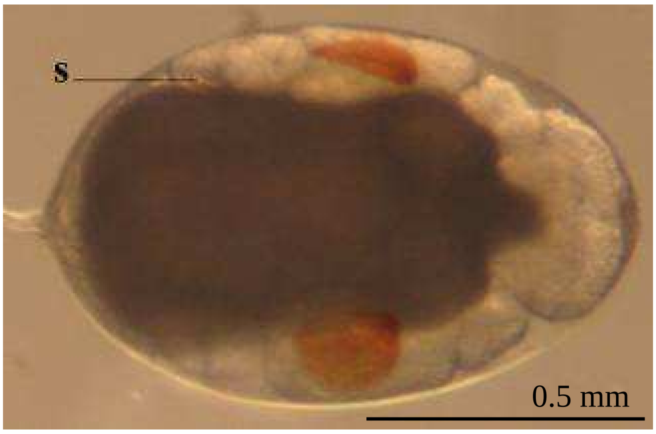

Figure 27 Observed stage 8

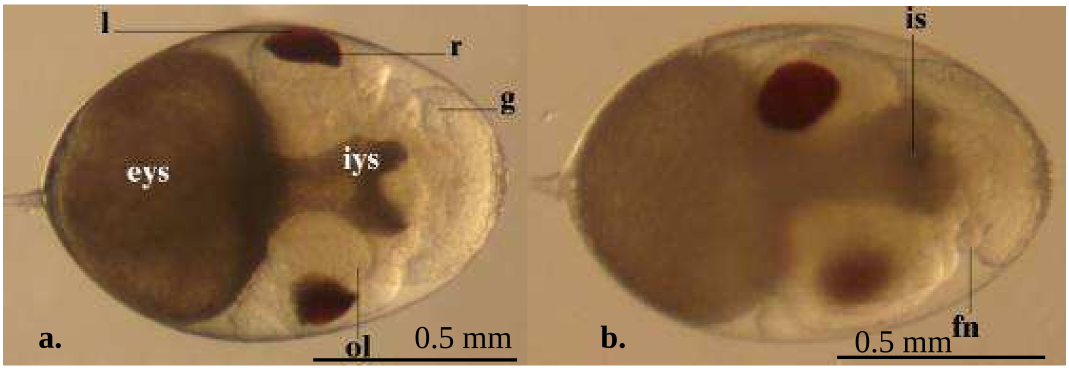

Figure 28 Observed stage 9; a -dorsum and b -laterum

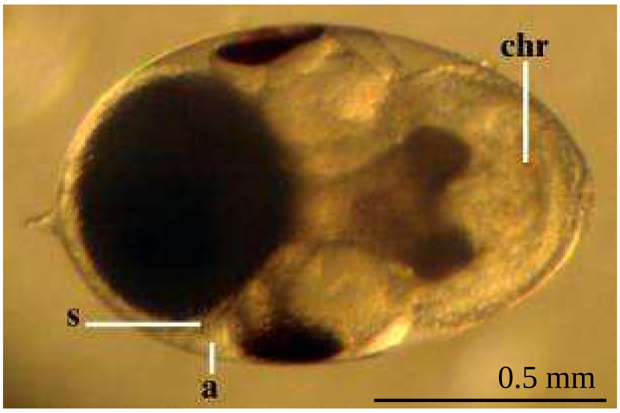

Figure 29 Observed stage 10

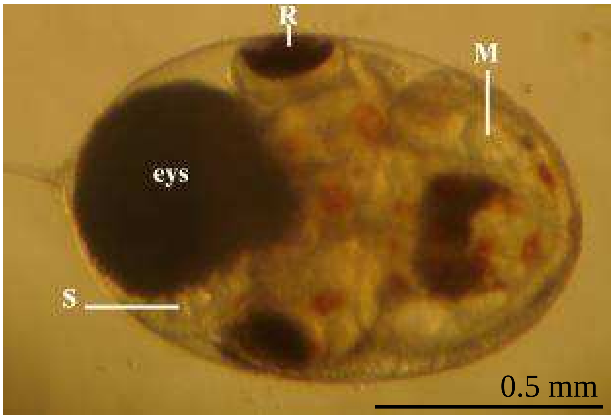

Figure 30 Observed stage 11

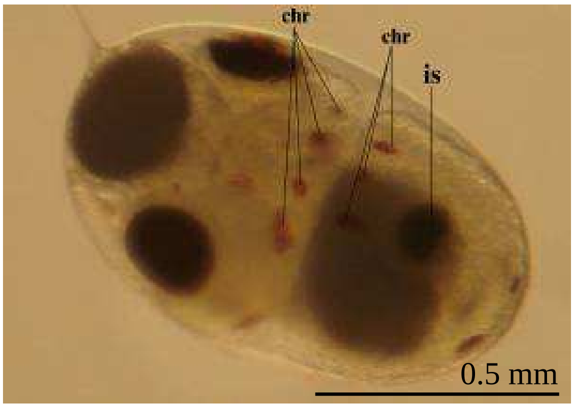

Figure 31 Observed stage 12

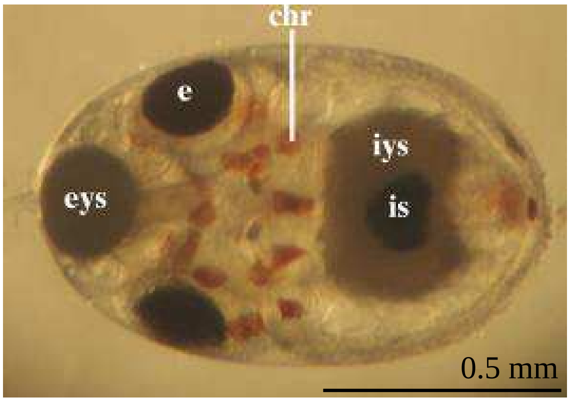

Figure 32 Observed stage 13

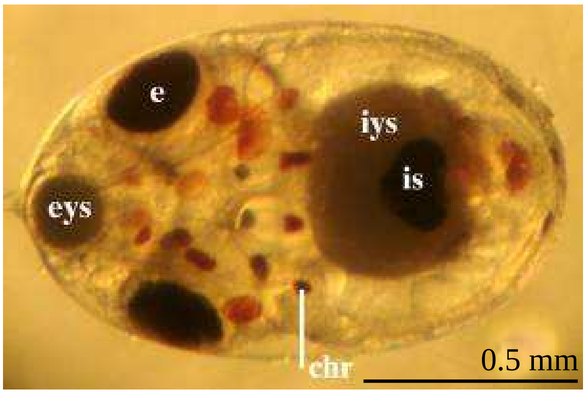

Figure 33 Observed stage 14

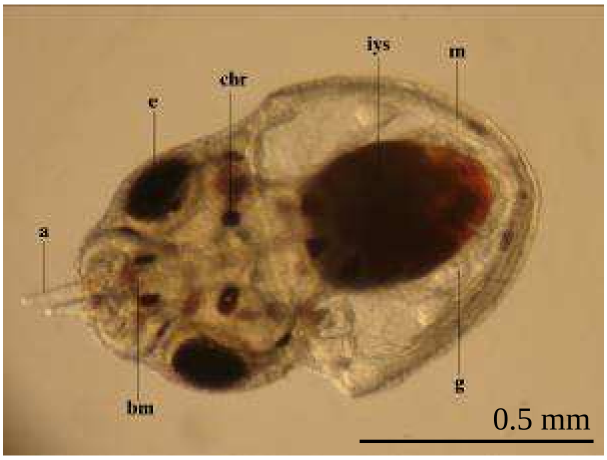

Figure 34 Observed stage 15

Morphology and Biology

Shell

Shell of *A. hians* was calcareous, thin, planospiral, and lateral compressed, with only one chamber and no septum (Figure 35). This shell is found only in the female and forms the brood chamber (Nixon and Young, 2003). The number of lateral side with radial ribs was 10-36 (24±4.9), and the number of keels with two rows of tubercles was 15-33 (22±3.6). Shell length was 12.6-52 (20.6±5.3) mm, shell height was 9-50.5 (23.8±6.3) mm and shell width was 14.7-77.3 (37.1±10.9) mm.

Figure 35 Inner shell of *A. hians*

The largest shell length was 52 mm while the smallest shell was only 12.6 mm long. The largest shell of argonauts found in *A. argo* which can reach a diameter of 300 mm (Nixon and Young, 2003). Average shell size of individuals was statistically different from samples collected in different months (appendix table 9). Samples collected in January revealed a maximum shell size of 50.58 ± 8.8 mm while sample collected in September exhibited the minimum size of 31.74 ±5.68 mm (Figure 36-37).

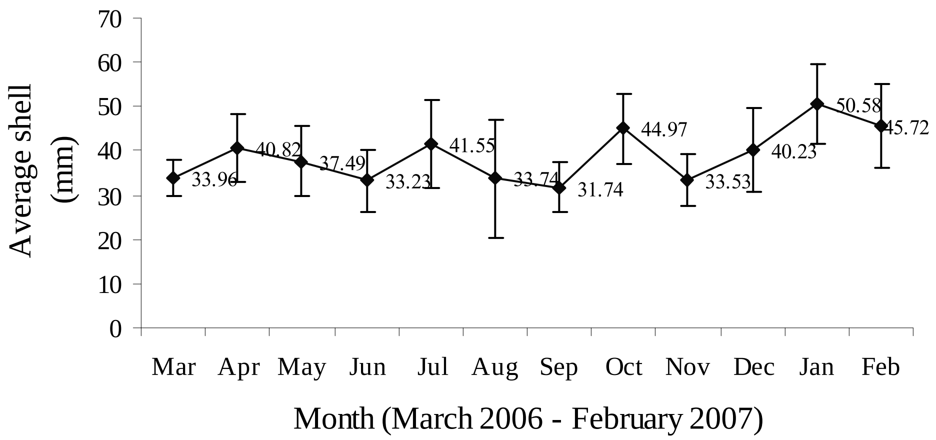

Figure 36 Shell length of *A. hians* collected year round from the Andaman Sea, Thailand

Figure 37 Shell of *A. hians*

Arm suckers

Arm suckers of *Argonauta* from SEM showed it has eight arms and each arm had two rows of suckers (Figure 38). The number of suckers on the first left arm was the highest with the average of 132.0±10.7 (range 101-149) on the left and 131.3±11.0 (range 103-146) on the right arm. On the second arm, the numbers of suckers were averagely 80.3±7.4 (range 64-98) on the left and 81.2±7.9 (range 68-100) on the right arm. On the third arm pair, the numbers were 76.6±7.7 (range 61-99) on the left and 77.0±8.0 (range 59-98) on the right. The numbers of suckers on the forth arm pair were the lowest with the average of 39.7±3.0 (range 34-46) on the left and 39.7±3.0 (range 34-44) on the right arm.

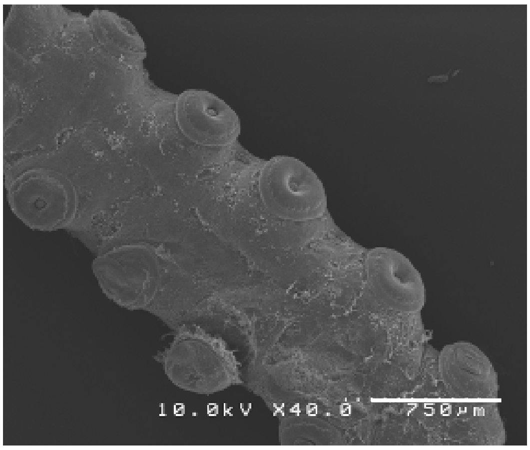

Figure 38 Suckers on the arm2 of *A. hians*

Suckers were stalkless round shape or borne on relatively long peduncles. The sucker had no chitinous rings likes those of other Octopods and *Vampyroteuthis* (Beesley *et al*., 1998). The sucker had a tissue that could be removed from the sucker; these tissue stout cones around the margin of infundibulum became visible. The cone had sharp tip; its base breadth and height were in the same length and the cone was ten times larger than the pegs. Pegs were small and spread over the tissue and were short. The breadth and height were also similar in length and after tissue was removed from the sucker, a hole on the sucker could be seen. This hole was smooth and its diameter was the same as its depth (Figure 39-40).

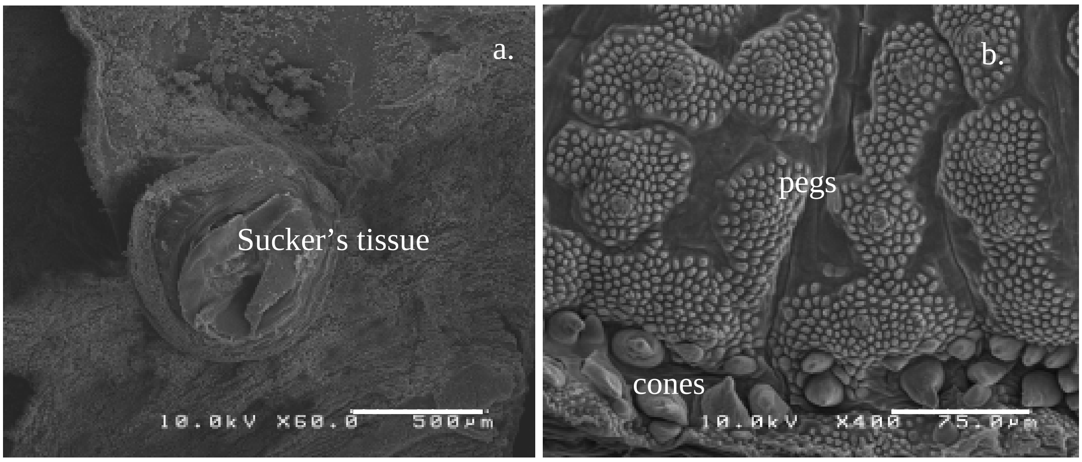

Figure 39 Sucker; a and b showed sucker, pegs and cones on the first arm

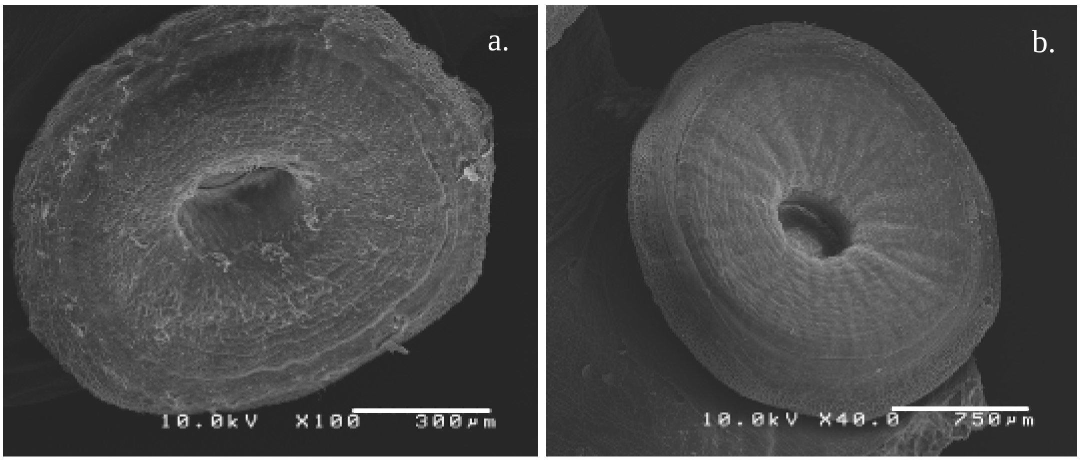

Figure 40 Sucker; a and b showed hole on the sucker of the second arm after removing the tissue

The hectocotylus which found in mantle cavity of female consisted of three parts: 1 basal, 2 central and 3 tips or distally (Sukhsangchan and Nabhitabhata, 2007). The basal part is spermatophoric reservoir, which is not found in the mantle cavity. This might suggest that during reproductive period when male insert the hectocotylus arm inside cavity of female, the arm might break apart between basal part and central part. The central part bears two rows of stalkless suckers which were connected to other suckers with a web. The suckers were obviously not covered by tissue as given for the arms in females. The suckers in the middle zone were the largest (compare with the other suckers on hectocotylus arm) and those near the connection zone towards the tip were the smallest. These suckers had no chitinous rings as given for the suckers on the other arms. The tip part ended in a long lash “penis” like tube with an opening for carrying the spermatophore (Figure 41-42). Since copulation could not be observed so far, we could only speculated about the spermatophore disposal. The presence of a functional intact hectocotylus in the mantle cavity of female (sometimes up to seven arms) indicate that males deposit this arm during reproduction. Some specimens of hectocotylus arm from mantle cavity of female can slowly moving (at the tip part) and this result is the same with Voss and Williamson (1971) reported that the still live hectocotylus was able move slowly like a “Gecko tail”.

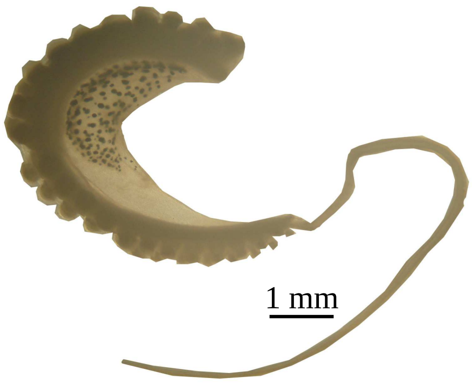

Figure 41 Hectocotylus arm from mantle cavity

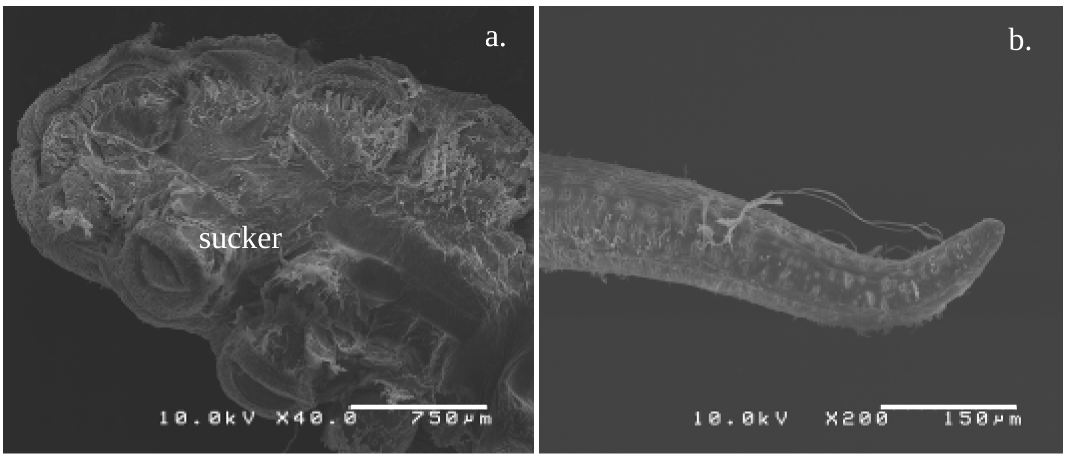

Figure 42 Hectocotylus arm; a is the central part and b is the tip part

Arms of paralarvae were short and sub-equal in length. Each arm had three suckers on the base similar to those of *A. argo* (Naef, 1928: Figure 43). The first dorsal arm of paralarvae was not laterally enlarged. Nixon and Young (2003) reported shell sac of female will appear when mantle length reaches up 4 mm. Naef (1928) reported that the arm parts presented did not yet directly relate to the shell at later stage. Body and head of the paralarvae was covered with small cones (Figure 44).

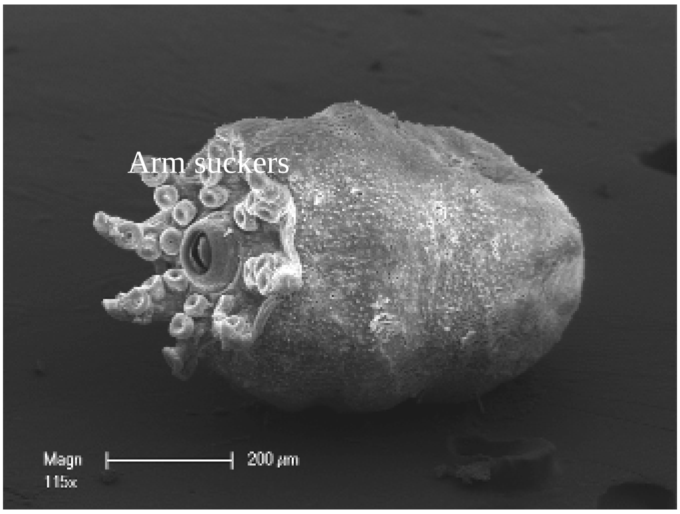

Figure 43 Dorsal side of paralarva of *A. hians* in stage 15

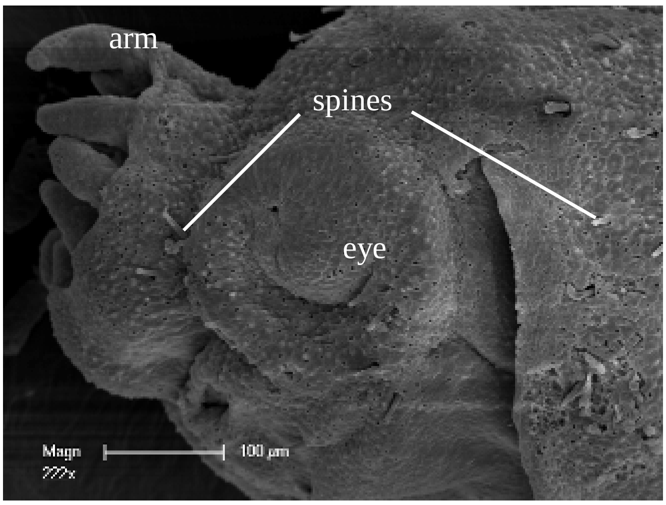

Figure 44 Spine on the head and body of paralarva in stage 15 (lateral side)

Beaks and Radula

Beaks of paralarvae were different from those of adults because they possess serrated teeth at the tip, which disappear during development (Figure 45). The beaks of the adults was wide and flattened interiorly, providing a small indistinct rostrum, sharp shoulder and broad low flat hood with no notch near the wide crest (Figure 46). Possible reasons of the Beak characteristic difference in adult and paralarva including the ability to build chitinous structure to cover old beak in adult which make beak thicker than paralarva and secondly, the serrate teeth of paralarva erode during the biting. The characteristic of adult’s beak was similar to the report of *Ocythoe* and *Vitreledonella* (Clarke, 1986).

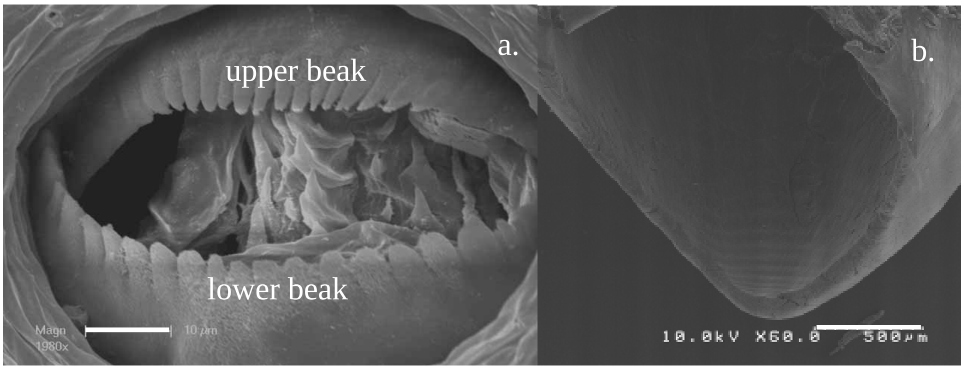

Figure 45 Beak; a is paralarvae’s beak and b is adult female’s beak

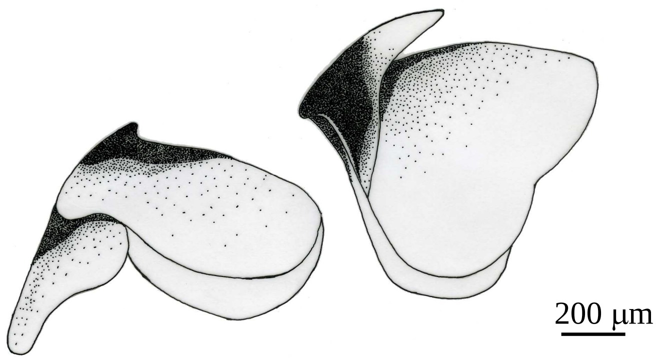

Figure 46 Beak of female’s adult on the left is lower beak and on the right is upper beak

Nixon and Young (2003) reported that the buccal mass of *Argonauta argo* was relatively large with anteroposterior lengths of 48% and 21% in relation to 15 mm and 83 mm mantle length respectively. The beaks of *Argonauta* consists of strong upper and lower mandible.

The radula formed relatively large part of the buccal complex, consisting of 7 transverse rows of unicuspid teeth and 2 marginal plates. They were chitin-protein complex and ribbon-like band (Figure 47). Nixon (1988) reported that the teeth of *Argonauta* argo were relatively stout and cone-shaped and having no lateral cusp. Teeth of *Argonuata hians* were unequal in length in the order of rachidian teeth>marginal teeth>2nd lateral teeth>1st lateral teeth. Rachidian teeth had width base and were higher than other teeth whilst the marginal teeth had narrow base and were more tapered than the other teeths and the result similar with Nateewatthana (1997).

Figure 47 Radula of *A. hians*

Relationships of dimensions in *Argonauta*'s beaks were estimated as following figure 48-56, n = 393.

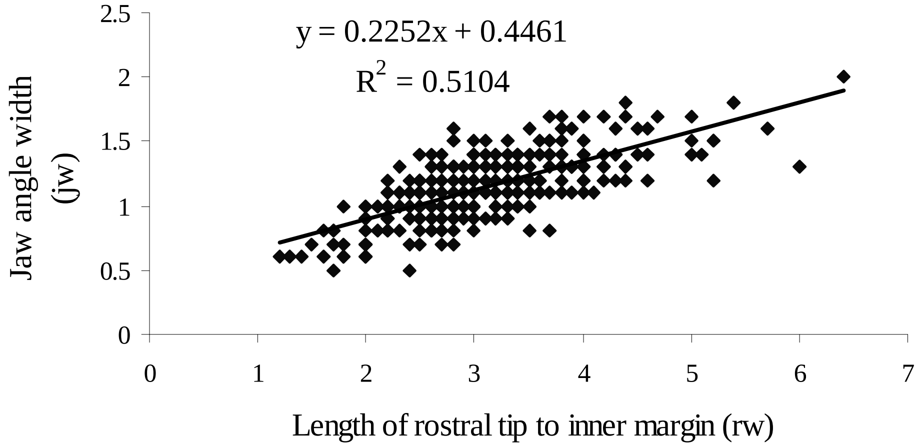

Figure 48 Relationship between the length of rostral tip to inner margin and jaw angle width of the upper beak

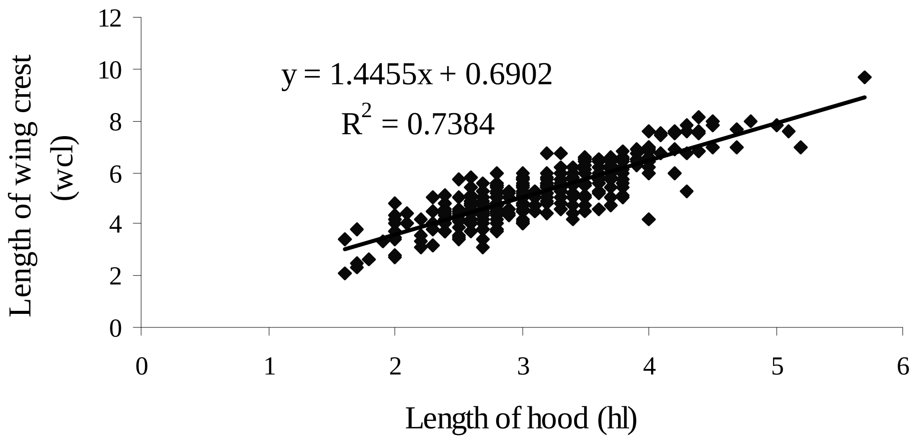

Figure 49 Relationship between the length of hood and length of wing crest of upper beak

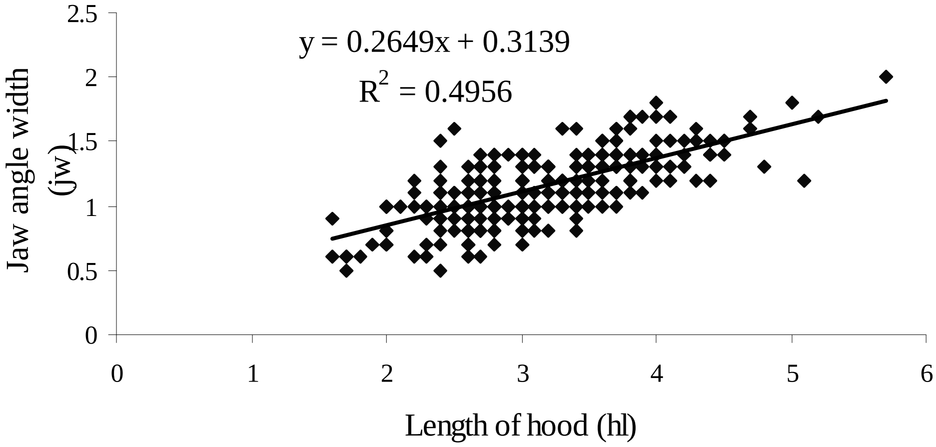

Figure 50 Relationship between the length of hood and jaw angle width of upper beak

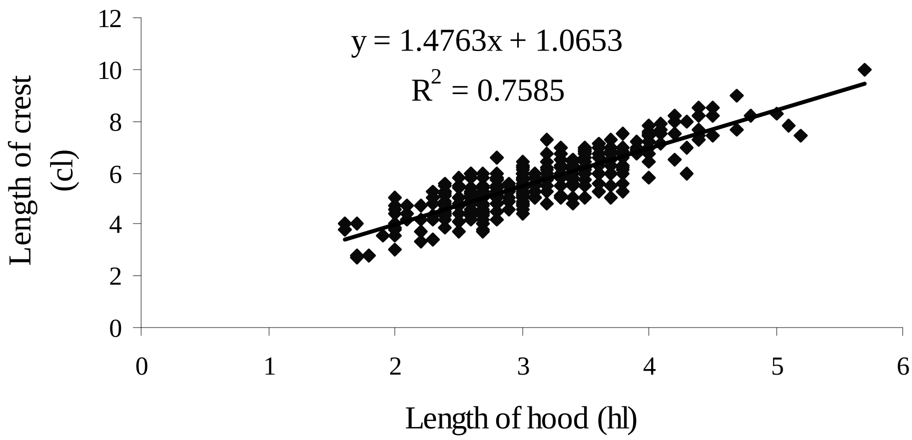

Figure 51 Relationship between the length of hood and length of crest of upper beak

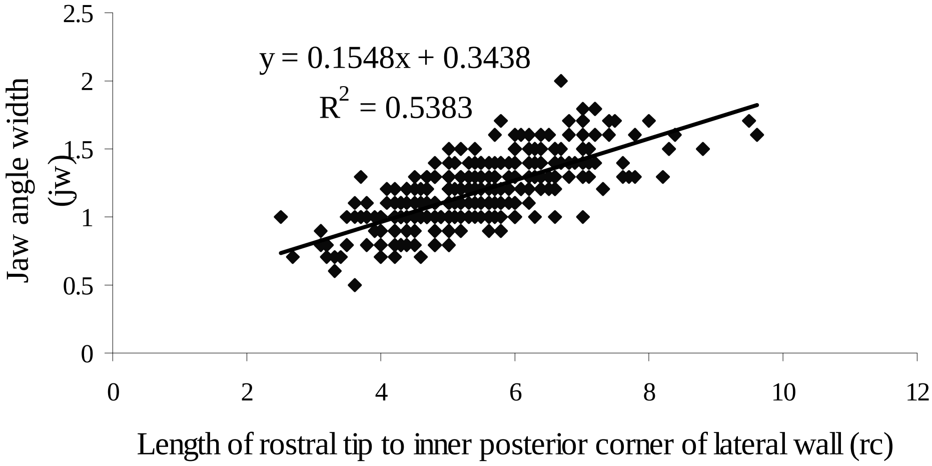

Figure 52 Relationship between the length of rostral tip to inner posterior corner of lateral wall and jaw angle width of lower beak

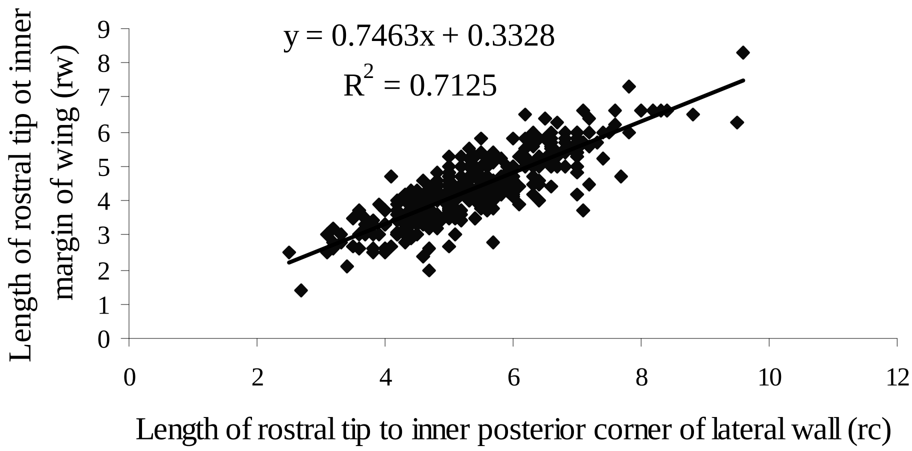

Figure 53 Relationship between the length of rostral tip to inner posterior corner of lateral wall and length of rostral tip of inner margin of lower beak's wing

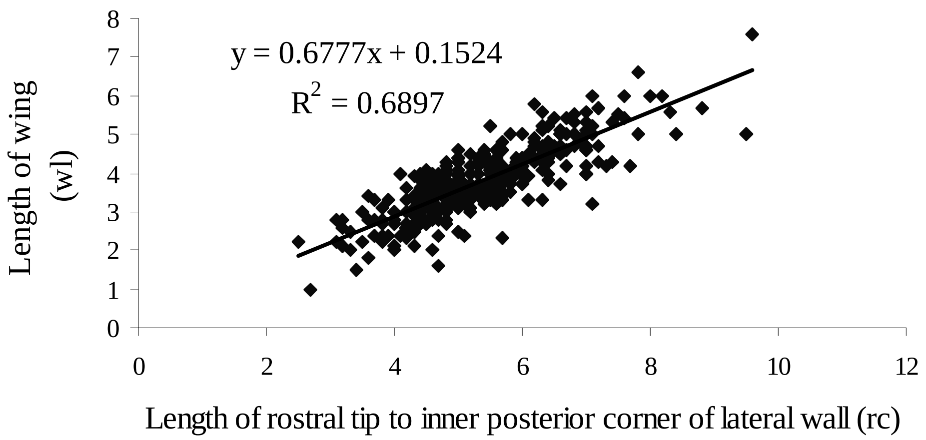

Figure 54 Relationship between the length of rostral tip to inner posterior corner of lateral wall and length of lower beak's wing

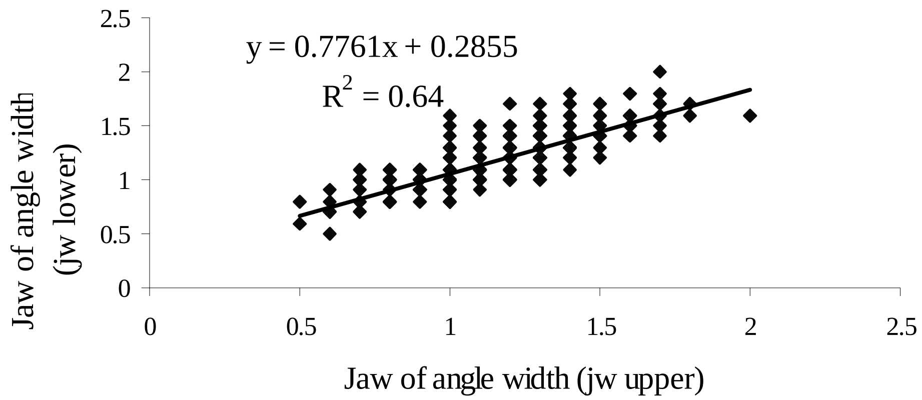

Figure 55 Relationship between the jaw of angle width (upper beak) and jaw of angle width (lower beak)

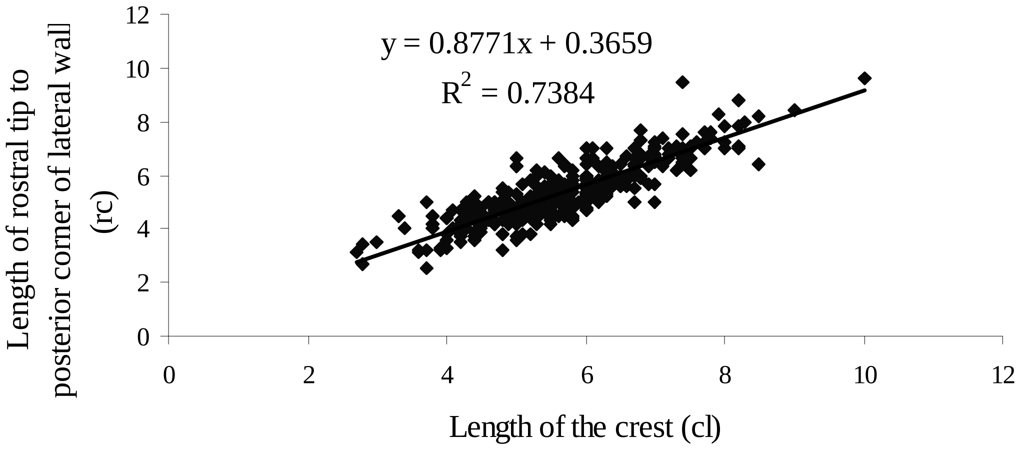

Figure 56 Relationship between the length of the crest (upper beak) and length of the rostral tip to inner posterior corner of lateral wall (lower beak)

Chromatophore

The number of chromatophore on the surface of seventy-five paralarva of *Argonauta hians* (Figure 57) was characterized. The chromatophores firstly appeared in the embryonic stage 10 on the dorsal side and spread out with further development to the whole body and head. At hatch the amounts of chromatophore vary between the dorsal and ventral side, dorsally more chromatophores were present. Average number of chromatophores on the dorsal side is 21.23±4.37 while the average number on the ventral side is 13.93±2.53, whilst on the head the amount of chromatophore on both sides did not differ.

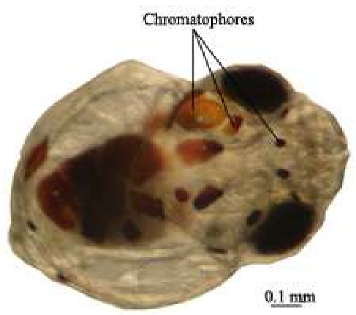

Figure 57 Chromatophore on dorsal side of paralarva stage 15

Mantle length-weight relationship

The average mantle length of the studied females was 30.99±6.47 mm (range 14.8-52.2), and the average body weight was 6.36±3.61 g (range 1.12-26.28). Mantle length-weight relationship could be expressed as a power regression model (Figure 58) as $W = 1.6 \times 10^{-3}L^{2.3827}$, $R^2 = 0.888$, n=389.

While length-weight relationship in male and female of *Octopus dollfusi* was $W=0.001L^{2.6028}$ and $W=0.0018L^{2.4546}$ respectively (Boonwanich *et al.*, 2004).

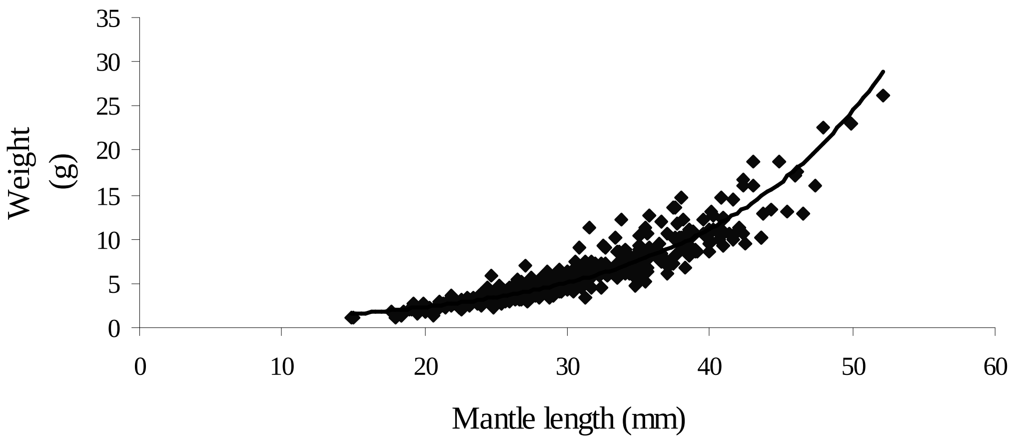

Figure 58 Mantle length-weight relationship of *A. hians*

Relationships of shell length, height and width

The relationships of shell length, shell height and shell width could be expressed as linear regression models (Figure 59-61) as follows:

SH = 0.6054(SL) + 0.605 (R^2=0.8861, n=389)

SH = 1.4791(SW) – 4.9766 (R^2=0.6259, n=389)

And SL = 2.3552(SW) – 7.5161 (R^2=0.6565, n=389)

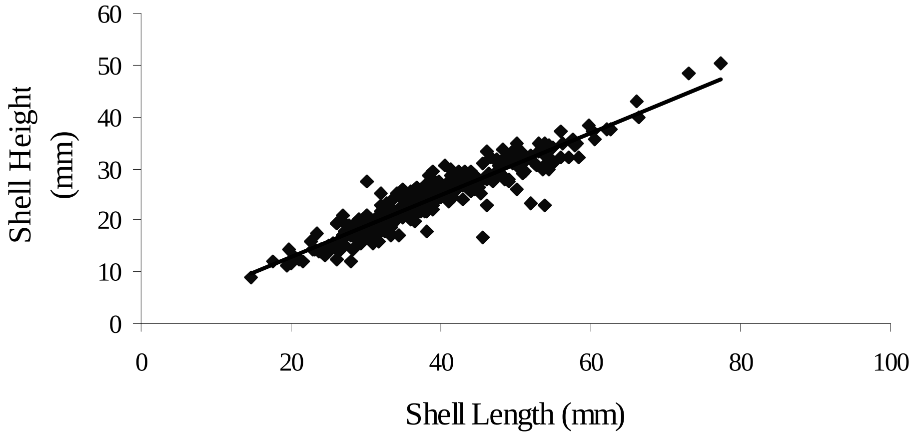

Figure 59 Relationship of shell length and shell height of *A. hians*

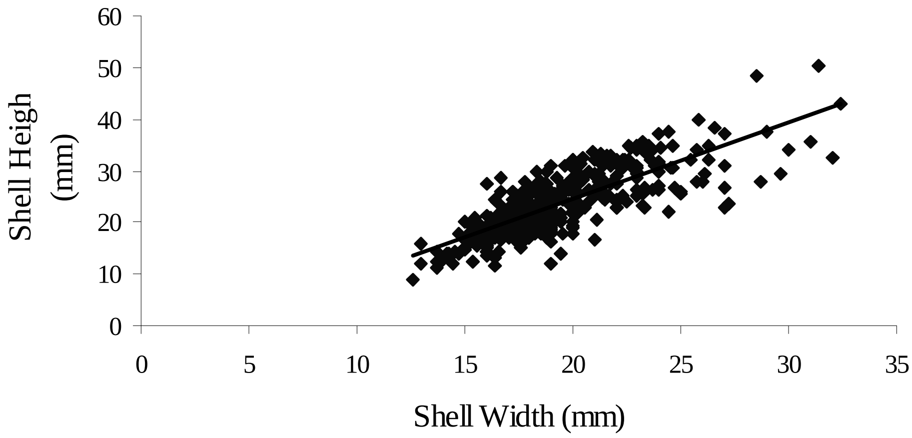

Figure 60 Relationship of shell width and shell height of *A. hians*

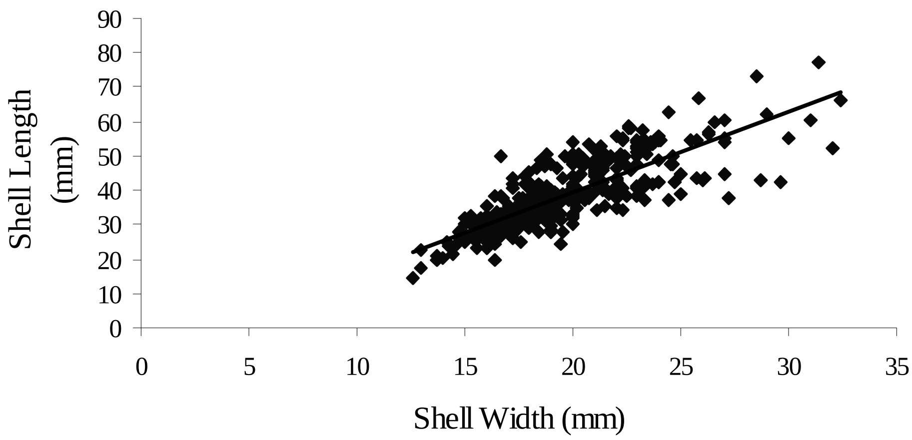

Figure 61 Relationship of shell width and shell length of *A. hians*

Gonadosomatic Index (GSI)

The gonadosomatic index of *A. hians* could be measured from the weight of the ovary. This serves as parameter for the evaluation of breeding cycle. After eggs are released the GSI would decrease (Thapanand, 2006). The GSI of *A. hians* reached the highest peak in June (15.86) and lowest in August (5.88). However, the GSI was likewise high in almost other months (Figure 62) indicating that *Argonauta* could reproduce all year round.

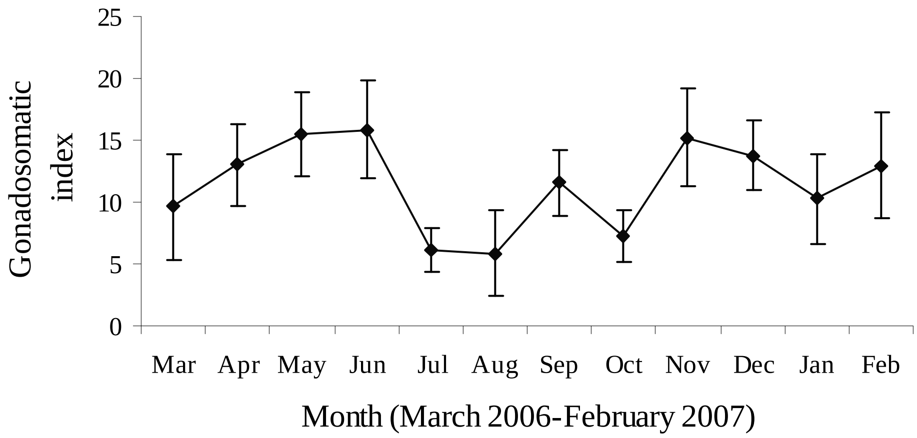

Figure 62 Gonadosomatic index of *A. hians*

Fecundity

Fecundity of females ranged from 266 to 16,530 eggs/batch (Figure 63). As of the result from statistic test, the fecundity differs seasonally. At confident interval 95% the highest fecundity was in January (mean batch size consists of 6,912 ±3,393) whereas the lowest was in March (mean batch size consists of 819±495). Boonwanich *et al*., (2004) reported fecundity of *Cistipus indicus* and *Octopus dollfusi* was 32-281 (106±74.95) and 6,895 respectively. Silva *et al*., (2002) reported in common octopus (*Octopus vulgaris*) the total fecundity ranged between 70,060 and 605,438 oocytes and the breeding season extended from February to October, with spawning peaks in April-May and August.

From the graph of fecundity (Figure 64), it could be assumed that the higher reproduction cycles were in December, January and February while they drop during rainy season (May-October). The fecundity graph and the gonadosomatic index graph were showing the similar aspect which might indicated their relationship in some context.

Figure 63 Eggs of *A. hians*

High fecundity rate might be correlated to the high abundance of prey during rainy season. This implicates enough diets to grow. The animals use winter season to develop sex cells and reproduce (Thailand has 3 season such as winter season: October-January, summer season: January-May and rainy season: May-October).

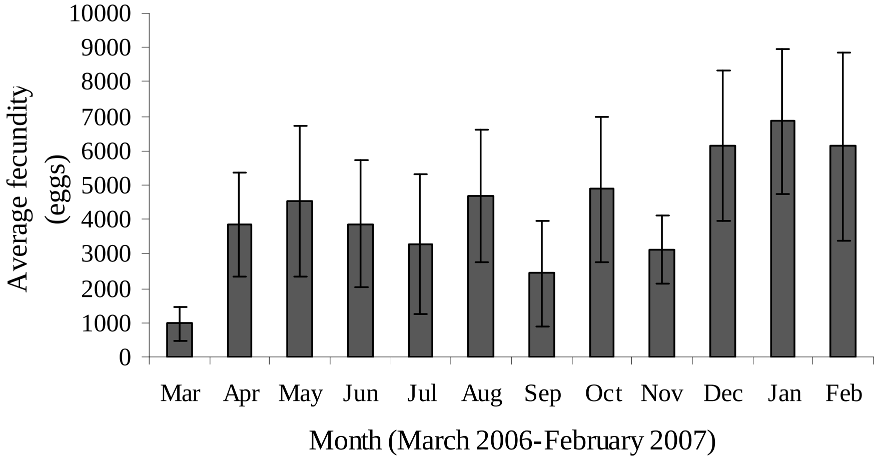

Figure 64 Fecundity of *A. hians* by month

Relationship between mantle length and fecundity

Relationship between mantle length and fecundity of the *A. hians* in this study (Figure 65) was estimated as Fe=267.85ML-4427.8 R^2=0.437, p<0.05, n=338.

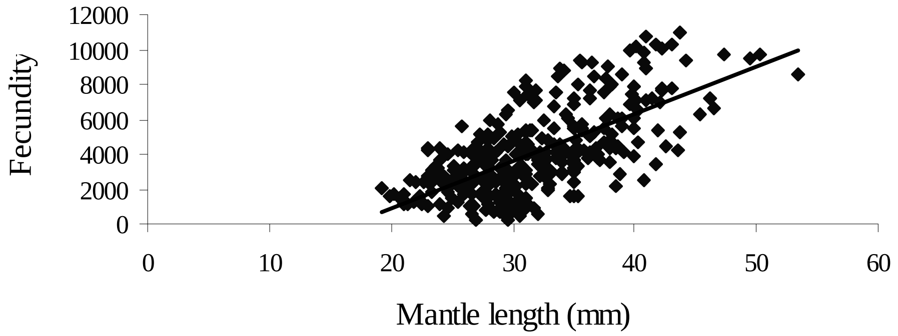

Figure 65 Relationship of mantle length and fecundity of *A. hians*

Relationship between weight and fecundity

Relationship between weight and fecundity was estimated as Fe=537.81W+572.76 R^2=0.4997, p<0.05, n=338 (Figure 66).

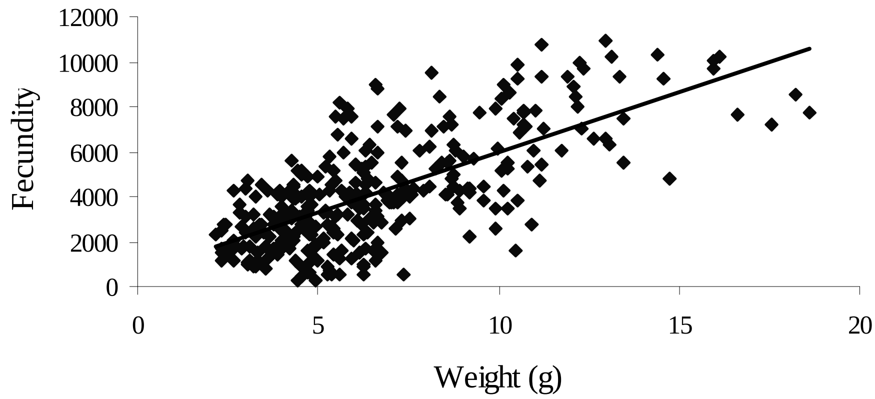

Figure 66 Relationship of weight and fecundity of *A. hians*

Length at 50% maturity

Length at 50% maturity was estimated from 368 specimens. All the specimens were separated as immature and mature stages. There were 30 immature specimens with the mantle length between 14.5 and 26.5 mm, while 338 specimens were mature. Length at 50% maturity was 20.14 mm and proportion of mature female at 100 percent was 27.5 mm.

Relationship between proportion of mature female and total number of female followed by length expressed as the power regression and analysed by the least square analysis was estimated as $P_L = \frac{1}{1+e^{(8.7031-0.4321L)}}$ (Figure 67).

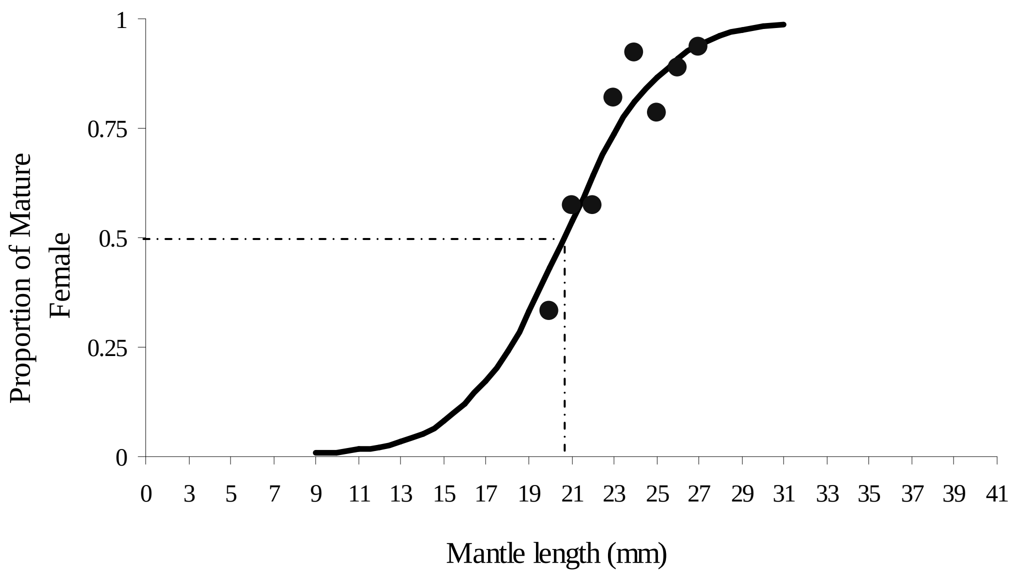

Figure 67 Length at 50% maturity of *A. hians*

Stomach content

Stomach contents from 101 females argonaut (mantle length 19.7-46.0 mm, weight 3.29-18.25 g) were studied. Food digested in various degrees could be found in the stomachs of more than 50 specimen (Figure 68). The quantity of food in the stomachs showed that 43% (index 0) was almost empty, 23% was full (index 4), 13% was traces of food and more than half filled (indices 1 and 3) and 11% was less than half filled (index 2).

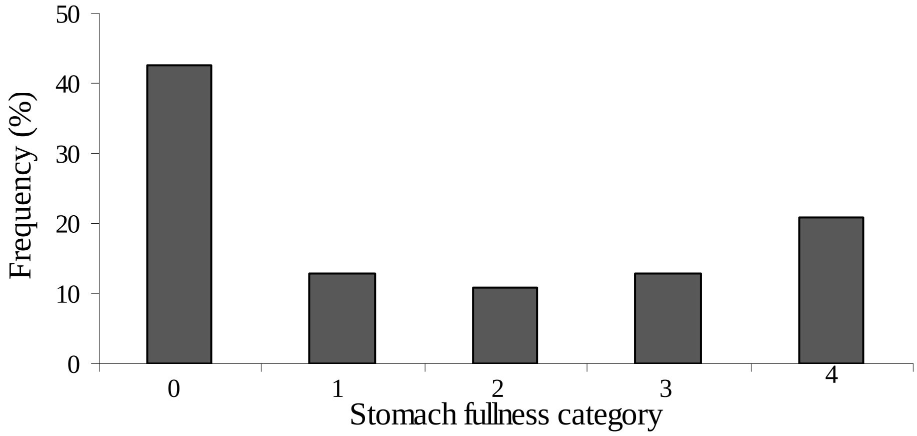

Figure 68 Frequency of occurrence of stomach fullness categories

Of all identified, three groups of food sources dominated the diet of *A. hians.* Mainly crustaceans (IRI was 1,612.48) but also cephalopods (IRI was 1,281.34) and fish (IRI was 280.61) (Figure 69). This finding contrast with Heeger *et al*., (1992) who reported the feeding preference of *A. argo* at the north of Bohol Island in the Philippine archipelago that fed on jellyfish (*Phyllorhiza punctata*). However, the finding is similar to Robson (1932) who reported small fish and crustacrans preferences for argonaut. While, the stomach content in the other octopods such as *Cistopus indicus* in Thai waters has a little bit different, were found the starfish, clam and crab (Darunchu, 2001).

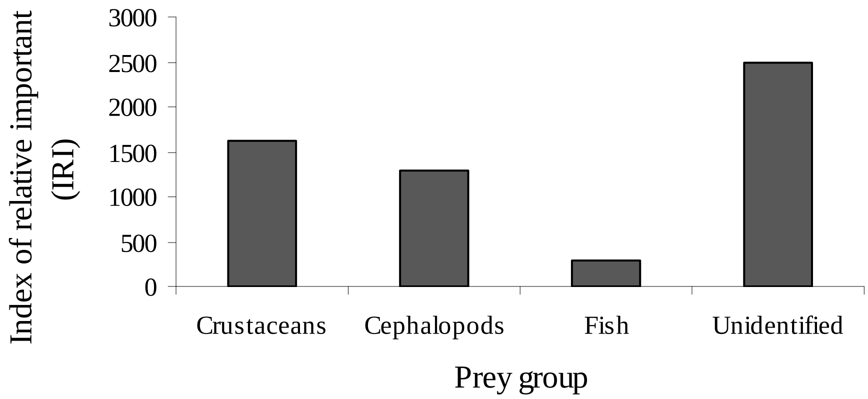

Figure 69 Overall frequencies of prey groups in diet of *A. hians*

All of appendages of all organisms could not be identified to the lowest taxon excepted in cephalopods fragment appendages because all of them were too small and normally finely fragmented. Appendages of crustacean collected were from mandibles, eyes, legs and various other fragment; appendages of fish collected were from scale and bone. Besides, there were appendages of unidentified group collected from stomach of *A. hians* ; those tissues could not be identified since they had already been digested and had no trace to identify into any group. However, the appendages of cephalopod can identified to order Teuthida from the fragment appendages of sucker, beak, sucker ring and arm

The differences of prey groups in documented diets probably reflected the combined influences of broad distribution and diverse sampling locations, as well as some possible seasonal factors and annual differences of the abundance of preys. However, the cannibalism might be important as a supplement to the diet when the other food sources were scare (Lipinski and Linkowski, 1988).

The relationship between stomach content and mantle length

A. hians are able to feed on any food which is not related to mantle length. However the relationship between food and mantle size can be roughly divided into three clusters (Crustacens, cephalopods and fish) at the 92% similarity (figure 70-71).

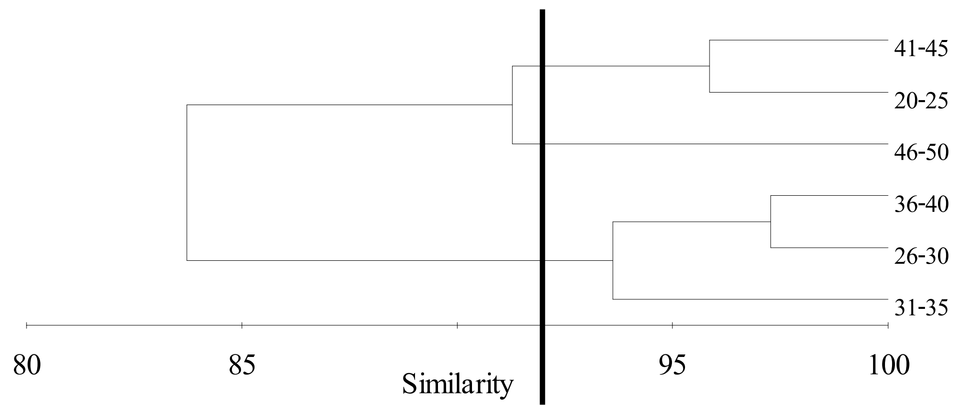

Figure 70 The cluster similarity of relationship between food and mantle length of *A. hians*

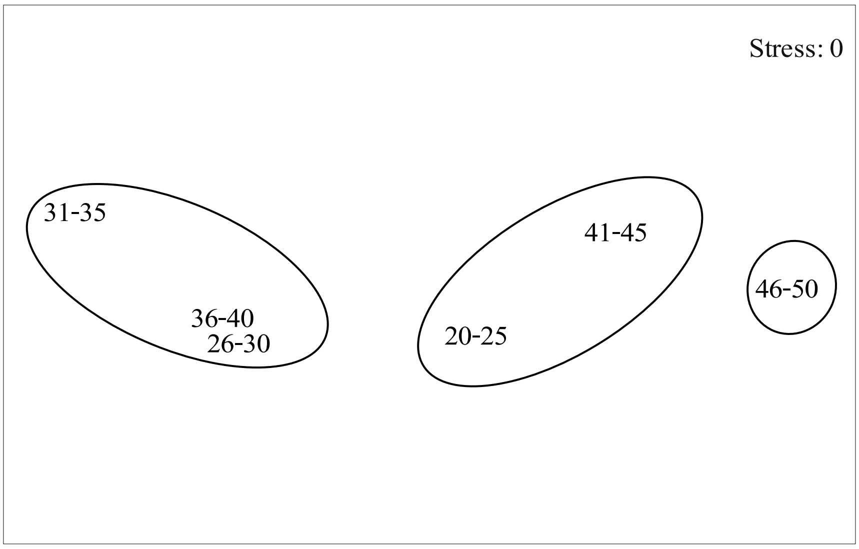

Figure 71 Grouping of similarity of food and mantle length at 92 % similarity

Paper nautilus cultivation

After collecting the specimens of *Argonauta* from the sea through purse seine operators in the Andaman Sea, Thailand, the specimens were brought to the laboratory at Phuket Marine Biology Center for culturing. All of specimens were females and 92% were adults. So when leaving the specimens in the fiber glass tanks for one or two days paralarvae had hatched in the tank. After hatching, the females and paralarvae were separated for culturing in the quality-controlled water in the tanks.

Water quality for culturing the *Argonauta* was controlled in similar condition to cephalopod culture (Nabhitabhata, 1993); salinity at 30-33 psu, pH at 7.0-8.5 and temperature at 25-28 degree Celsius. Females of *Argonauta* were cultured in the fiber glass tank of one tonnage size and they could live longer than 30 days in the tank fed by three kinds of food; small fishes, polychates (*Perinereis* sp.) and shrimps (*Litopenaeus vannamei*, *Parapaeneopsis* sp.). The *Argonauta*es usually ate polychaetes much more than the other food and this was reported in the feeding behaviour topic. In the laboratory tank the *Argonauta* always stayed at the bottom and sometimes they swam up in the water column. They always used the web of the first dorsal arm to cover their shell.

The longest-life *Argonauta* in the laboratory tank died after living in the tank for 30 days. Shell's observed found the rim was thin and pale color, which was different from other zones, measured 3 millimetres (Figure 72). Assumably, the *Argonauta* could grow in the laboratory tank and build its shell from the first dorsal arm because on this arm there was a secretary gland used to build the shell.

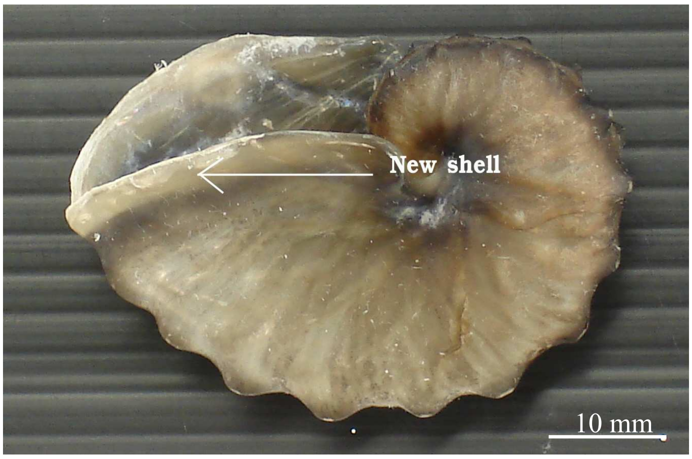

Figure 72 Show white band on the shell assumable appearing according to the growth rate

Although the researcher offered different food spectra as brine shrimp's eggs, brine shrimp's larvae, mysis, blue swimming crab's nauplius, sea urchin's eggs, sea urchin's larvae, rotifers, white shrimp's nauplius, copepod and true oyster's larvae it failed to rear the paralarve. Always 4 days after hatch, when their inner yolk sac was digested, they sank to the aquarium bottom and died. Only a small percentage of paralarvae in the tank tried to catch the brine's shrimp eggs. However, this behavior is vary to observations of Nabhitabhata (1978a) where paralarvae of cephalopods prefer to feed on live and bigger prey. It could be concluded that in this experiment, the culture of both adults and paralarvae of *Argonauta* was not success. It was because the culture was done in a short period of time; adult females and paralarvae could be kept in the tank for only 30 days and 4 days respectively. The researcher could observe only the behaviour but not the feeding rate, growth rate and food conversion efficiency. For the further researches, it is suggested that researchers should collect samples of paralarvae directly from the sea by plankton net since after hatching paralarvae of *Argonauta* were in planktonic stage. Study on stomach contents of paralarvae in order to maintain and prepare the optimum diets in the laboratory is required.

Behavior

Locomotion

In captivity *A. hians* swam and hovered in the water column at night and crawled on the bottom at the day time. The forward and backward swimming, vertical movement and hovering manoeuvrability was enabled by the water jetting propulsion from the funnel. The direction was controlled by turning the protruded funnel to the opposite site. Young (1960) reported that *A. argo* was neutrally buoyant, aided by a bubble of gas trapped in the upper of the shell. This method of vertical movement seems to be a general within the group of chambered cephalopods (*Naulitus*, *Spirula*, *Argonauta*) (Norman, 2000) and could also be assumed for *A. hians*. During swimming, all arms of *A. hians* were folded backward and their distal parts were inserted into the shell opening (Figure 73). The webs of the dorsal arms were spread out to cover the whole surface of the shell (Figure 74) showing brilliant white iridescence. Similar behavior of web spreading was also observed in *A. argo* (Young, 1960). In ritual position, arm suckers and beaks were protruded and exposed outward (Figure 75). Swimming direction seemed to be irregular and sometimes the animals bumped onto the aquarium wall.

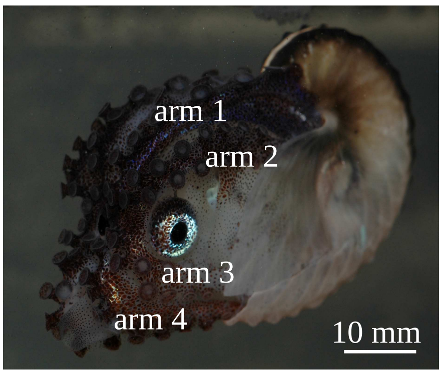

Figure 73 All arms of *A. hians* were folded backward and distal parts inserted into shell opening

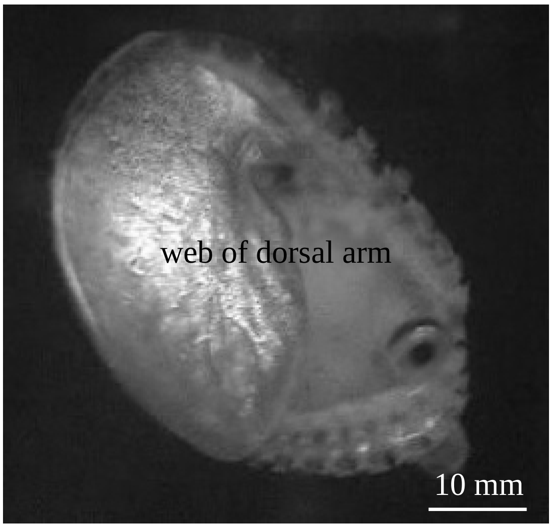

Figure 74 Shell of *A. hians* covered by the web of dorsal arms

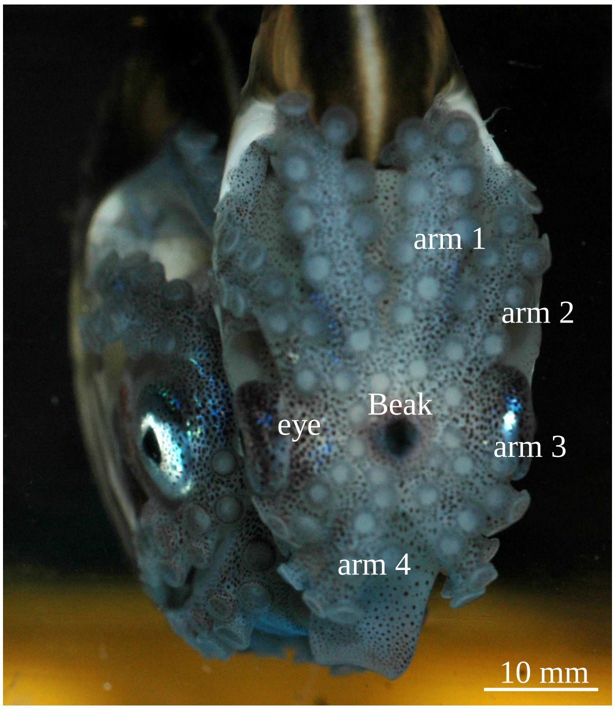

Figure 75 *A. hians* arm suckers and beaks exposed during swimming and attachment

A. hians also used their arm suckers around the buccal region attaching to attach to substratum, side-wall and bottom of the aquarium. This behavior could likewise be observed in wild, where wild *Argonauta* attached to drifting substrated or animals such as jellyfish (Heeger *et al*., 1992; Norman, 2000) as well as to each other in a string (Voss and Williamson, 1971). They also walked or crawled on the bottom with ventral part of mantle and shell pointing upwards and dorsal part was close to bottom, thus nearly upside-down position (Figure 76). Young (1960) suggested that the primary function of shell was to coordinate the posture and locomotion of *Argonauta*. The nearly upside-down walking posture revealed that the gas bubble used for buoyancy was trapped at the ventral part of shell and its position might be closed to the shell opening.

Figure 76 *A. hians* in walking or crawling position on the bottom of a aquarium

Feeding

Feeding behavior of *A. hians* took place in three steps as given for *Sepia* (Messenger, 1977): 1) attention, 2) positioning and 3) seizure. Benthic polychaetes were seized by using the protruded part of arms, and holding its prey by using the suckers at the basal part of arms, while arm tips were kept inside its shell. Preys were seized from the head and then *A. hians* postured body-side-down, turning its mouth from the bottom and starting to ingest while still lying on the bottom. If polychaetes as *Perinereis* sp. were seized in the middle part, *A. hians* used its beaks to divide the prey into two parts and ingested each part separately (Figure 77).

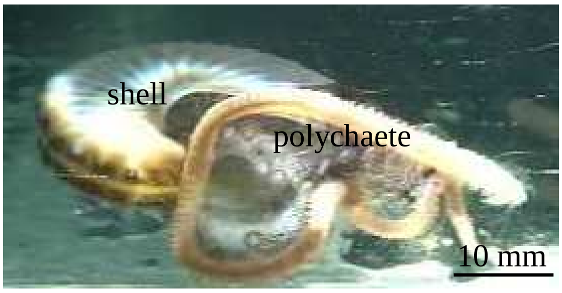

Figure 77 *A. hians* laying lateral on the bottom of the aquarium during ingesting a benthic polychaete

Feeding behavior against small fish and shrimp as *Litopenaeus vannamei* or *Parapaeneopsis* sp. were similar to those of the benthic polychaetes. *A. hians* swam and hovered towards the prey and seizure attempt was taken using the base of all arms. If seizure failed, it swam backward and attempted again. Seized preys were bitten from its head direction before ingestion (Figure 78).

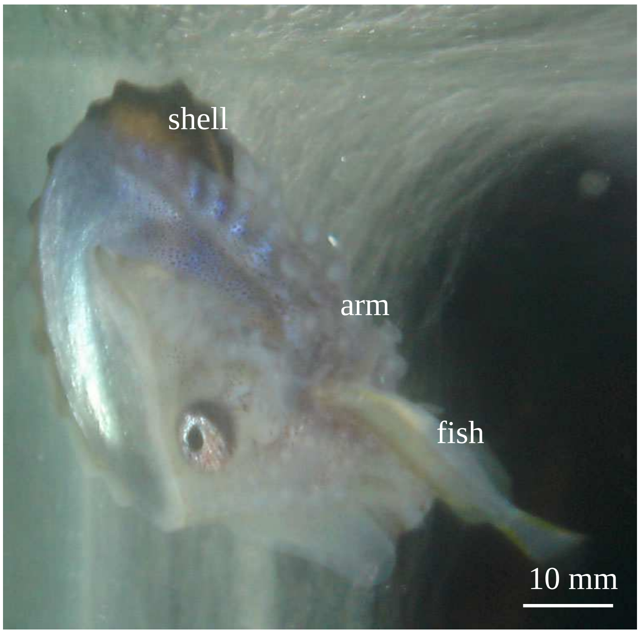

Figure 78 *A. hians* ingesting a small fish

In captivity *A. hians* mostly fed on benthic polychaetes than other provided food. Since, they usually crawled on the bottom of the aquaria than swimming, this increase the opportunity to encounter on such prey type. Such benthic prey catching might occur only in captivity. The present stomach content analysis as well as several observations indicate that *Argonauta* fed on pelagic prey such as pteropods (*Cavolinia tridentate;* Okutani, 1960) or jellyfishes (*Phyllorhiza punctata*; Heeger *et al.*, 1992). Attempts to offer the crawling *A. hians* other benthic food spectra such as small fish or shrimp mostly failed.

Defense

Defense observations in this study were interpreted as secondary defenses behavior following the definition of Hanlon and Messenger (1996). The animals exposured always itself towards the reflecting glass of the aquaria. Deimatic displays of cephalopods were characterized by the sudden appearance of bold light/dark chromatic components, usually with spreading of arms, web or fins to create the illusion of largeness (Hanlon and Messengers, 1996). In *A. hians*, the color pattern on arms turned to dark red when stimulated visually by present prey or aquarium cleaning procedures. This behavior could was also observed in *A. argo*, those purple-red chromatophores of the funnel, neck and mantle expanded when the animal was disturbed (Young, 1960). However, the deimatic response of the quickly withdrawn silver iridescent web as observed in *A. argo*, failed for *A. hians*. This present study agreed to Nixon and Young (2003) that the range of color patterns was limited, reflecting in the small size of chromatophore lobe in brain comparing to other octopods. The adjustment to deimatic behavior was the forcible blowing of water from funnel at intruders (Hanlon and Messenger, 1996) which was also observed in *A. hians* in this study.

Protean behavior was that behavior which was sufficiently unsystematic in appearance to prevent a reactor predicting in detail the position or actions of the actor and one of the most typical response was the Blanch-Ink-Jet manoeuvre that was performed when attack was imminent (Hanlon and Messenger, 1996). Erratic jetting, in combination with pale color pattern was performed by *A. hians* when escaping backwards from foreign inserted objects into the aquaria. As soon as these objects approached towards the animals, ink ejecting was accompanied. Ink could be ejected several times a day. However, inking might cause stress and weakness in addition to the limited condition of living in captivity. Although not verified statistically, many specimens died one day after ink ejection even when the water was cleaned and the ink removed.

CONCLUSION

Argonauta hians were distributing along the coastline of Thailand in the Andaman Sea between 7°30' 24" – 8° 13' 22" N and 97° 01' 50" – 98° 55' 48" E. This species could be captured all year round from the water surface to more than 80 meters deep.

Egg capsules of *Argonauta hians* were single shape connected to one another by stalks. The oval-shaped eggs were telolecithal and its size was about 1 mm. Females spawn inside their shells. The eggs developed into at least 15 stages before hatching to paralarva. The hatching phase was planktonic and suspending in the water column by mean of water jetting from the funnel. At hatch sex could not be determined. The paralarvae arms were short, equal in length and each arm bear only three suckers. The first dorsal arm of paralarvae had no laterally large web and at this stage they had no shell either.

Morphology of *Argonauta hians* was observed in shell and body. Shell of *Argonauta* was calcareous-structured, thin and fragile. The shell was a single chamber with flat keel fringed by two rows of tubercles. Lateral sides of shell were with radial ribs. The middle of the shell was pressed in or bent outwards into a prominent horn.

Argonauta hians had a slender body, a narrow head and unequal developed arms (eight totally), each beared two rows of suckers. The number of suckers on the first dorsal arm were the highest and degraded towards the fourth arm pair. The suckers were stalkless round shape or borne with relatively long peduncles. On the surface of sucker there was no chitinous ring, the surface tissue rather beared cones and pegs covering around the tissue.

The third left arm of males was hectocotylized and consisted of three parts: 1) basal part, 2) central part and 3) tip part or distally. The tip ended in a long lash-like "penis" which could move slowly like a "Gecko tail". Within the mantle cavity of females several (up to seven) hectocotyli could be found.

Beaks of paralarvae were different from those of adult, by possessing serrated teeth at the tip part, both upper and lower of paralarvae while disappear in adult.

Chromatophores were spread over the body and head. They firstly appear in the embryonic stage 10 and spread out until hatch stronger on the dorsal than on the ventral side.

Mantle length-weight relationship could be expressed as a power regression model as; $W = 1.6 \times 10^{-3} L^{2.3827}$. The relationships of shell length, height and width could be expressed as linear regression model as; SH=0.6054(SL) + 0.605, SH =1.4791(SW) – 4.9766 and SL=2.3552(SW) – 7.5161 respectively.

Gonadosomatic index (GSI) was terminated, with a maximum in June and minimum in August. Fecundity occurred in the first and last quarter of the year. Relationship between mantle length and fecundity could be expressed as linear model as; Fe = 267.85ML - 4427.8, $R^2 = 0.437$, $p<0.05$ and the relationship between weight and fecundity could be expressed as linear model as; Fe = 537.81W + 572.76, $R^2 = 0.4997$, $p<0.05$

Length at 50% maturity is 20.14 mm for *Argonauta hians*, the proportion of mature female at 100 percent was 27.5 mm. The relationship between the proportion of mature female and total number of female followed by length could be analyzed as;

$$P_L = \frac{1}{1+e^{(8.7031-0.4321L)}} .$$

Stomach contents of *A. hians* comprised of three main diet groups, crustaceans, cephalopods (order Teuthida) and fish.

Argonauta culture could not be completed in this observation because the adults and paralarvae did not survive longer than 30 days and 4 days respectively. This issue therefore should be studied more detailed in future.

Within the observations of the cultivated species we focused on three behavior pattern: 1). Locomotion behavior: *A hians* swam and hovered in the water column at night and crawled on the bottom in the day time. When situated on the aquaria bottom, they were orientated in opposite direction or upside down position compared normal swimming posture. 2). Feeding behavior: In cultivation *A. hians* mostly fed on benthic polychaetes rather than on shrimps and fishes. 3). Defensive behavior: As other cephalopods also *A. hians* provide a variable repertoire for defense mechanisms such as camouflage or ink ejecting.

RECOMMENDATIONS FOR FURTHER WORK

While this extensive study has manage to cover most possible aspect, there are some limitation that needed to be clarify in further study which included:

1. In this study, information of male's biology is lacked due to the improper capturing gears. While male specimens are small, the mesh size used to capture should be small enough to be able to collect them. Further studies should design the suitable gear for the male collection.

2. This research had try to cultivate the paralarvae but there were some limitation on the suitable technique or food. The future research should avoid the unsuccessfully techniques as described in this study and design the appropriated one.

3. While stomach content should be identified to the lowest taxa, in this study, there are some limitation on the *in situ* preservation. Some specimen collected in this study were not preserved correctly which result in some digested of stomach contents. Further study should prepared the appropriated method to preserve the specimen as soon as collected.

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APPENDIX

Appendix Table 1 Length-weight data

ML (mm)	W (g)	ML (mm)	W (g)	ML (mm)	W (g)	ML (mm)	W (g)
32	6.252	23.1	2.389	24.7	5.783	32.4	7.182
29	5.317	29	5.224	31.2	3.427	30.7	5.986
29.5	5.386	20.7	2.311	23	2.895	28	3.899
29.6	4.43	25	3.377	31	5.574	18.4	1.339
30	6.235	23.2	3.247	35	5.643	20	1.835
30	4.965	29	3.662	21	2.494	20.6	1.448
41	9.209	29.5	5.283	23.7	2.801	45.4	13.087
29.5	5.945	37.2	7.009	19.5	1.649	52.2	26.279
29.3	5.613	34.6	7.796	26	3.776	31	5.244
29	5.571	24.4	3.47	24	2.422	27.7	3.569
30.4	6.601	29.2	5.377	21.5	2.313	30.5	4.743
30.5	7.367	41	12.082	22.4	2.499	34	6.551
29.8	5.27	31	5.821	24	3.313	31.2	5.705
21.7	2.675	26	4.196	33.6	5.951	48	22.633
31	6.136	21.8	2.424	23.3	2.681	28.6	5.029
29.4	6.234	27	7.001	18.5	1.764	28.6	4.806
28.6	6.313	33.5	6.107	23	2.661	27.5	3.977
29.2	4.383	21	2.304	38.4	8.92	26	3.085
27.5	5.658	38.6	8.062	36.2	8.888	26.5	3.98
26.6	4.716	26	3.992	35	6.506	29.8	4.905
28.4	4.791	27.4	4.735	31	5.912	28.7	3.289
24.4	4.538	30.7	5.333	32.6	6.686	29	4.713
31	6.753	24	3.626	32.8	6.64	27.7	3.744
27	4.919	20.3	2.322	26	4.199	25.5	3.598
42.5	9.584	22.2	2.704	29.7	5.423	29.6	4.646
36.6	7.466	22	2.807	38	8.731	31.7	4.567
38.5	9.172	32.5	6.669	26.4	3.151	27	4.522

Appendix Table 1 (Continued)

ML (mm)	W (g)	ML (mm)	W (g)	ML (mm)	W (g)	ML (mm)	W (g)
38	9.21	25.2	4.243	41	10.59	26.7	3.262
38	10.224	30.4	5.418	35	10.46	20	1.88
23	3.427	27	4.33	30	4.308	22.7	2.185
32	6.239	41.7	14.38	35	6.37	30.3	5.163
27.5	4.224	42.3	10.707	24.5	2.847	32.7	7.172
40	9.593	35	6.439	34	6.143	29.4	4.336
32.7	7.108	34.8	4.69	33.2	6.504	26	2.915
22.5	3.093	28	4.312	40.7	9.931	34.2	6.662
35	8.502	25.4	3.216	31.3	7.37	25.4	2.699
35.8	7.904	35	8.147	35	7.201	29.6	3.972
37	6.098	41	12.315	30	5.496	32.8	5.969
33.8	7.361	21	2.855	32.7	6.116	28	4.069
28.3	5.955	33.5	7.219	37	10.547	29.6	4.088
31.1	5.753	27.2	3.027	29	4.245	32.2	6.188
33.8	6.022	39	8.66	42.3	16.605	26.8	3.064
33	6.627	35	6.602	31.6	5.522	29.5	4.951
31	6.737	32.4	4.492	18.3	1.345	28	4.311
36.3	8.703	24.6	3.478	32.6	8.929	30.4	3.998
40	8.606	24.6	3.346	33.8	6.618	28	3.468
34.5	6.308	29.5	4.839	18	1.124	28	3.918
38.3	6.817	24	2.831	23	3.014	33	6.261
32.7	6.031	31.4	6.016	24.8	2.245	31	4.664
31.5	6.301	27.7	3.971	35	9.221	35	7.299
41.4	10.671	31	6.033	20.9	1.976	27.8	3.896
23.8	3.23	23.4	3	22.4	2.272	26.6	3.746
35	5.791	22.4	2.484	22.5	2.043	29.4	4.032
24.7	3.227	40.22	12.63	31.6	5.732	44.92	18.776

Appendix Table 1 (Continued)

ML (mm)	W (g)	ML (mm)	W (g)	ML (mm)	W (g)	ML (mm)	W (g)
29	3.901	38.1	12.202	31	6.598	35.72	12.748
28	4.844	24.96	4.392	32.7	6.129	37.53	13.444
26.8	4.715	29.58	5.423	31.92	7.065	49.9	23.124
33.3	10.229	32.47	9.152	24.7	3.256	37.44	13.489
33.6	8.566	27.99	3.903	35.34	7.279	35.1	7.543
38.8	10.895	24.23	3.001	30.51	6.624	47.33	15.983
31	4.77	34	7.534	25.93	4.277	41.94	10.806
36.4	7.568	25.5	3.668	25.49	4.246	33.72	12.158
41.7	9.919	28.4	4.712	29.44	6.441	39.17	8.525
46	17.134	24	3.938	33.45	5.536	35.7	8.408
33.3	6.335	25	3.314	25.81	4.283	31.03	6.187
34.7	5.645	36.3	8.768	36.61	8.346	35.65	10.533
38	9.898	33.2	6.109	34.31	8.093	29.98	5.157
26.6	3.815	28.2	3.748	33.47	8.643	39.7	10.411
35.4	6.518	25.2	4.658	34.94	7.304	40.85	11.174
38	14.757	31	5.395	35.47	11.217	35.54	6.799
29.3	4.388	23	3.06	35.14	7.467	44.24	13.332
31	4.535	28	4.226	32.91	6.367	43.77	12.97
34.6	6.911	27.3	4.415	40.12	13.147	36.57	11.908
35	9.299	19	1.96	39.95	11.006	27.99	4.037
30.3	4.756	25	3.341	37.8	10.162	40.29	11.118
37.7	11.725	24.7	3.546	38.9	10.305	46.59	12.966
43.6	10.146	34	8.749	23.16	2.804	30.86	9.145
35.4	5.17	17.6	1.753	21.25	2.443	31.65	7.445
37.6	8.216	20	2.261	19.97	2.63	32.3	5.874
38.6	10.989	14.8	1.219	18.92	1.922	15	1.223
42	11.224	23.4	3.275	21.34	2.637	21.6	2.921

Appendix Table 1 (Continued)

ML (mm)	W (g)	ML (mm)	W (g)	ML (mm)	W (g)	ML (mm)	W (g)
37	6.923	27.6	4.129	27.31	4.424	19.2	2.657
39	8.816	25.6	3.91	28.77	5.302	23	2.914
35.6	6.338	29.7	4.773	29.97	6.249	23.8	3.574
43	16.136	28	5.272	29.55	5.911	24.4	3.357
36.6	8.273	28.8	4.778	39.98	10.666	21.8	3.648
28.11	5.683	26	4.623	40.71	10.504	32	6.246
36.9	7.65	30.2	4.723	38.2	10.106	29.3	5.488
34.3	6.071	30.5	6.161	31.91	7.185	27.7	4.531
25.72	2.907	30.4	5.524	39.58	12.241	39.95	9.949
26.4	4.935	37.54	9.936	28.86	5.602	36.4	9.494
26.6	4.022	35.71	9.052	26.48	5.436	40.78	14.59
35.1	8.698	43.65	10.26	37.47	7.319	46.15	17.589
40.12	10.766	26.8	5.207	30.75	6.58	37.62	10.096
30.45	5.509						

Appendix table 2 Gonadosomatic Index (GSI) data

Month	GSI	s.d.
Mar-06	9.62	4.29
Apr-06	13.03	3.33
May-06	15.48	3.33
June-06	15.86	3.96
July-06	6.14	1.75
Aug-06	5.88	3.54
Sep-06	11.6	2.66
Oct-06	7.26	2.04
Nov-06	15.24	3.96

Appendix table 2 (Continued)

Month	GSI	s.d.
Dec-06	13.79	2.84
Jan-07	10.25	3.56
Feb-07	12.97	4.3

Appendix table 3 Fecundity data

Fecundity	ML (mm)	W (g)	Fecundity	ML (mm)	W (g)	Fecundity	ML (mm)	W (g)
556	32.0	6.25	2739	23.1	2.39	3696	35.0	7.20
700	29.0	5.32	5313	29.0	5.22	7533	30.0	5.50
500	29.5	5.39	1479	20.7	2.31	2912	32.7	6.12
266	29.6	4.43	2506	25.0	3.38	3800	37.0	10.55
933	30.0	6.24	2255	23.2	3.25	7640	42.3	16.61
1138	30.0	4.97	2574	25.4	3.22	2317	31.6	5.52
952	41.0	9.21	6896	35.0	8.15	3489	32.6	8.93
2109	29.5	5.95	7052	41.0	12.32	8955	33.8	6.62
559	29.3	5.61	1690	21.0	2.86	4380	23.0	3.01
1238	29.0	5.57	4100	33.5	7.22	4161	35.0	9.22
1168	30.4	6.60	4703	27.2	3.03	4932	32.4	7.18
503	30.5	7.37	5644	39.0	8.66	4004	30.7	5.99
525	29.8	5.27	3654	35.0	6.60	4055	28.0	3.90
1504	31.0	6.14	3146	32.4	4.49	6268	45.4	13.09
980	29.4	6.23	2405	24.6	3.35	891	31.0	5.24
1663	28.6	6.31	3627	29.5	4.84	783	27.7	3.57
1177	29.2	4.38	3640	24.0	2.83	1046	30.5	4.74
1584	27.5	5.66	5380	31.4	6.02	2803	34.0	6.55
627	26.6	4.72	4006	27.7	3.97	7462	31.2	5.71
667	28.4	4.79	5394	31.0	6.03	4128	28.6	5.03
454	24.4	4.54	3142	23.4	3.00	2347	28.6	4.81

Appendix Table 3 (Continued)

Fecundity	ML (mm)	W (g)	Fecundity	ML (mm)	W (g)	Fecundity	ML (mm)	W (g)
1486	31.0	6.75	1608	22.4	2.48	3517	27.5	3.98
269	27.0	4.92	4550	31.2	3.43	1743	26.0	3.09
4420	42.5	9.58	2643	23.0	2.90	4092	26.5	3.98
4158	36.6	7.47	8175	31.0	5.57	2638	29.8	4.91
2225	38.5	9.17	4264	35.0	5.64	847	28.7	3.29
4324	38.0	9.21	3287	23.7	2.80	1594	29.0	4.71
2602	29.0	5.45	3146	26.0	3.78	1685	27.7	3.74
3503	38.0	10.22	2765	24.0	2.42	1267	25.5	3.60
2759	23.0	3.43	2520	21.5	2.31	909	29.6	4.65
3625	32.0	6.24	1425	22.4	2.50	931	31.7	4.57
1884	27.5	4.22	1152	24.0	3.31	2732	27.0	4.52
3836	40.0	9.59	7586	33.6	5.95	2287	26.7	3.26
3743	32.7	7.11	1845	23.3	2.68	1605	28.0	3.94
1122	22.5	3.09	4250	23.0	2.66	2347	22.7	2.19
7152	35.0	8.50	4309	38.4	8.92	2142	30.3	5.16
4273	35.8	7.90	3765	36.2	8.89	2590	32.7	7.17
4005	37.0	6.10	5473	35.0	6.51	2083	29.4	4.34
4233	33.8	7.36	1258	31.0	5.91	1764	26.0	2.92
3689	28.3	5.96	1976	32.8	6.64	8805	34.2	6.66
4042	31.1	5.75	1683	26.0	4.20	3085	29.6	3.97
4590	33.8	6.02	2413	29.7	5.42	2047	32.8	5.97
3092	33.0	6.63	6296	38.0	8.73	3211	28.0	4.07
2863	31.0	6.74	1075	26.4	3.15	2014	29.6	4.09
7175	36.3	8.70	1578	41.0	10.59	2785	32.2	6.19
5534	40.0	8.61	7729	43.0	18.64	1018	26.8	3.06
6001	34.5	6.31	1582	35.0	10.46	1827	29.5	4.95
488	38.3	6.82	2277	30.0	4.31	2216	28.0	4.31
4104	32.7	6.03	2432	35.0	6.37	1729	30.4	4.00

Appendix Table 3 (Continued)

Fecundity	ML (mm)	W (g)	Fecundity	ML (mm)	W (g)	Fecundity	ML (mm)	W (g)
4171	31.5	6.30	3488	34.0	6.14	1095	28.0	3.47
7225	41.4	10.67	9635	33.2	6.50	4233	28.0	3.92
3167	23.8	3.23	2563	40.7	9.93	2284	33.0	6.26
3186	35.0	5.79	4016	31.3	7.37	3127	31.0	4.66
2940	35.0	7.30	3314	28.0	4.04	7610	31.9	7.07
1782	27.8	3.90	4681	40.3	11.12	4012	24.7	3.26
1731	26.6	3.75	6597	46.6	12.97	7948	35.3	7.28
2565	29.4	4.03	4319	30.9	9.15	7095	30.5	6.62
926	24.7	3.23	6960	31.7	7.45	3007	25.9	4.28
1400	29.0	3.90	6553	40.2	12.63	4217	25.5	4.25
4417	29.6	4.32	7973	38.1	12.20	6324	29.4	6.44
1455	28.0	4.84	5394	31.5	11.21	6768	33.5	5.54
3369	26.8	4.72	1405	29.6	5.42	5630	25.8	4.28
5480	33.3	10.23	2869	28.0	3.90	8446	36.6	8.35
4059	33.6	8.57	2444	24.2	3.00	6240	34.3	8.09
2800	38.8	10.90	3007	34.0	7.53	7531	33.5	8.64
2315	31.0	4.77	2202	25.5	3.67	5510	34.9	7.30
4110	36.4	7.57	4931	28.4	4.71	9335	35.5	11.22
3455	41.7	9.92	2558	24.0	3.94	4226	35.1	7.47
11664	46.0	17.13	2324	25.0	3.31	4800	32.9	6.37
4534	33.3	6.34	4980	36.3	8.77	10189	40.1	13.15
1584	34.7	5.65	2929	33.2	6.11	7861	40.0	11.01
7871	38.0	9.90	2748	28.2	3.75	9014	37.8	10.16
1577	35.4	6.52	3044	25.2	4.66	8585	38.9	10.31
4823	38.0	14.76	2649	31.0	5.40	1566	20.0	2.63
2439	29.3	4.39	1083	23.0	3.06	1113	21.3	2.64
4025	31.0	4.54	4290	28.0	4.23	5181	27.3	4.42
4072	34.6	6.91	4000	27.3	4.42	4848	27.9	4.99

Appendix Table 3 (Continued)

Fecundity	ML (mm)	W (g)	Fecundity	ML (mm)	W (g)	Fecundity	ML (mm)	W (g)
5657	35.0	9.30	1530	25.0	3.34	5748	28.8	5.30
4016	30.3	4.76	1800	24.7	3.55	5076	30.0	6.25
6082	37.7	11.73	4440	34.0	8.75	6541	29.6	5.91
9512	49.5	8.13	2409	23.4	3.28	7850	40.0	10.67
4224	43.6	10.15	2379	27.6	4.13	9832	40.7	10.50
3323	35.4	5.17	3867	26.8	4.39	5197	38.2	10.11
11023	37.6	8.22	2624	25.6	3.91	5756	35.7	9.05
6068	38.6	10.99	2849	29.7	4.77	5254	43.7	10.26
7009	42.0	11.22	3267	28.0	5.27	4805	35.1	8.70
3796	37.0	6.92	4249	28.8	4.78	7098	40.1	10.77
6838	39.6	10.58	2541	26.0	4.62	7106	31.9	7.19
6027	39.0	8.82	2875	30.2	4.72	9932	39.6	12.24
5370	35.6	6.34	3923	30.5	6.16	7691	26.5	5.44
10253	43.0	16.14	3192	30.4	5.52	4678	37.5	7.32
5287	36.6	8.27	4158	32.3	5.87	3344	30.8	6.58
5988	28.1	5.68	2033	19.2	2.66	4722	30.5	5.51
4335	36.9	7.65	2429	22.0	3.26	6091	40.0	9.95
4125	34.3	6.07	2784	24.4	3.36	7694	36.4	9.49
5505	35.7	8.41	1309	21.8	3.65	9287	40.8	14.59
5252	31.0	6.19	3428	32.0	6.25	7234	46.2	17.59
9200	35.7	10.53	3098	29.3	5.49	8339	37.6	10.10
1969	30.0	5.16	3399	26.8	5.21	11784	37.5	9.94
7482	39.7	10.41	4951	27.7	4.53	10013	42.3	15.96
10716	40.9	11.17	1808	26.4	4.94	7490	37.5	13.44
4192	35.5	6.80	2935	26.6	4.02	5513	37.4	13.49
9360	44.2	13.33	4219	31.6	5.73	4017	35.1	7.54
9707	50.2	12.36	4661	31.0	6.60	9676	47.3	15.98
10945	43.8	12.97	3690	33.8	6.97	5354	41.9	10.81

Appendix Table 3 (Continued)

Fecundity	ML (mm)	W (g)	Fecundity	ML (mm)	W (g)	Fecundity	ML (mm)	W (g)
9289	36.6	11.91	3669	32.7	6.13	8485	33.7	12.16
4105	39.2	8.53	4519	29.2	5.38	4406	38.6	8.06
3239	29.0	3.66	8892	41.0	12.08	2037	26.0	3.99
2790	29.5	5.28	7875	31.0	5.82	7806	27.4	4.74
3700	37.2	7.01	4105	26.0	4.20	4263	30.7	5.33
6019	34.6	7.80	3750	33.5	6.11	4309	24.0	3.63
2431	24.4	3.47	1116	21.0	2.30	1694	20.3	2.32
5937	32.5	6.67	3360	25.2	4.24	5181	28.0	4.52

Appendix table 4 Shell morphological data

SL	SW	SH	SL	SW	SH	SL	SW	SH
3.5	1.83	2.1	2.06	4.8	2.9	2	3.04	1.9
3.14	1.65	2	1.87	4.7	2.76	2.87	4.3	2.8
3.31	1.65	1.9	1.85	3.87	2.7	2.57	5.44	3.4
2.98	1.73	1.8	1.78	4.4	2.8	1.9	2.8	1.2
3.6	1.8	2	1.9	4	2.5	2.2	4.36	2.73
3.33	1.745	2.03	1.85	4.02	2.47	1.56	3	1.72
5	1.67	2.6	2.24	4.75	3.16	2.46	4.76	3.07
3.5	1.7	2.07	1.67	2.94	1.77	2.02	3.92	2.4
3.65	1.76	1.96	1.83	4.1	2.6	2	3.3	2
3.2	1.76	1.82	1.6	2.85	1.92	1.9	2.96	1.9
3.7	1.8	2.17	1.67	3.84	2.88	1.7	3.1	1.7
3.4	1.85	2.1	1.54	2.67	1.64	2	3.8	2.17
3.3	1.75	1.87	1.53	3	1.83	1.84	2.8	1.84
2.6	1.54	1.22	1.57	2.83	1.75	2.06	3.7	2.3
3.3	1.85	1.8	1.7	3.12	1.92	1.82	3.1	1.9
3.57	1.855	2.05	1.75	3.58	2.25	2.72	3.78	2.35

Appendix Table 4 (Continued)

SL	SW	SH	SL	SW	SH	SL	SW	SH
3.4	1.8	2	1.72	4.07	2.44	1.63	2.87	1.72
3.16	1.76	1.58	2.1	4.5	2.65	1.6	2.7	1.7
3.43	1.88	1.71	1.7	3	1.91	1.7	3.16	2
3.1	1.6	1.55	1.83	3.53	2.23	2.32	4.07	2.55
3.33	1.73	1.72	1.88	5.06	3	1.9	2.87	1.64
3.1	1.73	1.65	1.8	3.63	2.2	2.3	3.83	2.5
3.6	1.87	2.05	1.74	3.36	2.07	2.2	3.92	2.43
3.3	1.82	1.8	1.56	2.56	1.55	1.8	2.9	1.7
2	5.4	3.1	1.9	3.7	2.3	1.74	2.9	1.86
1.9	4.77	3.1	1.67	2.7	1.7	1.9	3.14	1.83
1.88	4.9	2.76	2	4.75	2.85	1.66	2.83	1.44
1.92	3.97	2.5	1.77	3.06	2.02	1.47	2.63	1.4
2.12	5.13	2.93	1.9	3.5	2.58	1.95	2.8	1.8
1.65	3.04	1.8	2.3	4.07	2.64	1.87	3.15	1.94
2	4.44	2.77	1.66	3.04	1.96	1.93	3.88	2.44
1.6	3.56	2.14	1.72	2.6	1.95	1.7	2.72	1.8
2.07	5.36	3	1.9	2.8	1.8	1.94	2.41	1.4
1.83	4.62	2.3	1.8	3	1.88	1.61	2.87	1.72
1.5	3	1.68	2	4.1	2.63	2	4.87	3.2
1.85	4.85	2.8	1.86	3.35	2.14	2	4.8	3.04
1.8	4.53	2.53	1.64	3.84	2.45	1.9	4	2.43
1.88	4.15	2.5	2.2	3.88	2.3	1.78	4.16	2.45
1.8	4.23	2.65	2.44	3.7	2.2	1.72	4.38	2.6
1.85	3.61	2.36	3	5.5	3.4	1.95	3.9	2.66
1.74	3.46	2.5	2.63	5.62	3.5	2.23	3.4	2.5
1.8	3.76	2.4	2.61	4.33	2.94	2.14	4	2.46
1.81	4.03	2.57	2.6	4.3	2.8	2.4	4.23	2.64
2.03	4.39	2.57	2	3.8	2.22	1.9	3.24	1.95
1.93	4.65	2.85	1.6	3	2.74	2.32	5.2	2.33

Appendix Table 4 (Continued)

SL	SW	SH	SL	SW	SH	SL	SW	SH
2.85	7.3	4.85	1.64	2.7	1.7	2.02	3.5	2.41
2.57	4.36	2.77	1.56	2.9	1.6	2.18	3.97	2.74
2	3.18	1.92	1.8	3.33	1.87	2.3	5.12	2.94
1.9	3.58	2.24	1.47	2.8	1.77	2.7	5.5	3.1
1.6	2.7	1.7	1.74	3.08	1.9	2.25	3.84	2.4
2.5	3.88	2.56	1.73	2.8	1.7	1.94	3.68	2.17
1.9	3.8	2.52	1.67	2.84	1.67	2.5	4.46	2.6
2.45	4.78	3.07	1.7	3.3	1.84	2	3.24	1.8
2.07	3.95	2.4	1.63	3.2	1.85	2.2	3.78	2.45
2.17	3.87	2.5	1.66	3.2	2.15	2.7	5.38	2.28
1.94	3.32	2.1	1.5	2.47	1.47	2.11	3.4	2.04
2.15	3.55	2.42	1.62	3.18	1.84	1.93	3.44	2.1
2.3	4.14	2.88	1.64	2.44	1.33	2.2	4.1	2.4
1.94	3.12	2	1.42	2.5	1.4	2.7	4.46	2.66
3.74	5.76	3.69	1.7	3.54	2.14	2.33	3.7	2.3
1.72	3.23	2.24	2	3.87	2.32	2.27	5.78	3.45
1.37	1.95	1.13	1.64	3.05	1.77	2.96	4.23	2.96
2.37	4.2	2.64	1.6	2.72	1.52	2.34	5.06	3.34
2.07	3.77	2.64	1.85	4.1	2.38	2.02	3.74	2.16
1.64	2	1.18	1.6	2.72	1.7	2.4	4.26	2.7
1.26	1.47	0.9	1.6	3.24	1.9	2.38	5.4	3.08
1.3	1.75	1.2	1.68	3.8	2.27	2.4	5.44	3
1.9	2.85	1.87	1.66	3.2	1.77	2.2	4.3	2.4
1.76	2.5	1.5	1.6	2.94	1.56	2.3	5.27	3.07
2.14	4.25	2.82	1.9	3.45	2.2	2	5.05	3.2
1.6	2.32	1.44	1.5	2.7	1.68	2.14	4.13	2.58
1.43	2.37	1.4	1.9	3.25	2.1	2.9	6.2	3.76
1.5	2.6	1.5	1.6	3.22	1.9	2.2	4.65	2.92
2.2	3.84	2.3	1.53	3.25	1.95	1.88	3.8	1.78

Appendix Table 4 (Continued)

SL	SW	SH	SL	SW	SH	SL	SW	SH
2.2	3.48	2.3	1.66	2.87	1.72	1.72	4.16	2.6
1.74	2.85	1.7	1.63	3.16	1.96	2.44	6.26	3.74
1.37	2.1	1.22	1.9	3.83	2.28	2	3.9	2.41
1.6	2.3	1.43	1.7	3.34	1.86	1.65	2.9	2
1.44	2.17	1.2	4.2	1.9	2.5	2.12	4.5	2.77
3.2	5.2	3.25	1.7	3.1	1.88	1.8	3.28	2.24
3.14	7.73	5.05	1.63	3	1.75	2.3	4.78	2.98
1.75	3.24	1.94	1.57	3.2	1.94	1.88	3.5	2.26
1.6	2.85	1.74	1.6	2.94	1.68	2.11	4.7	2.85
1.8	2.95	1.7	1.65	3.3	1.87	2.27	4.56	3.08
1.85	3.79	2.17	1.72	3.1	1.94	1.98	3.77	2.38
1.7	3.4	2.16	1.9	3.3	2	2.2	5.6	3.2
3.1	6.05	3.57	1.86	3.33	2.15	2.2	4.95	3.13
1.6	3.18	1.83	2.4	4.87	3.18	2.3	5.43	3.05
1.76	3.27	2	2.47	4.25	2.66	2.46	5	3.48
1.9	3.3	2.1	1.55	2.7	2.1	2.13	4.95	3.27
2.14	5.1	3.1	1.68	2.96	2.03	2.24	4.98	3.23
2.23	5.5	3.12	1.68	3	2.08	2.1	4.22	2.89
2.23	5.44	3.23	1.7	3.3	2.3	2.37	5.36	3.4
2.4	5.6	3.7	1.83	4.13	3	1.86	3.2	2.53
2.33	5.47	3.4	1.77	3.8	2.6	1.92	3.72	2.56
2.26	5.85	3.2	1.78	3.57	2.29	2.04	4.8	3.12
2.36	5.42	3.22	1.74	3.55	2.2	2.1	3.94	2.5
2	3.66	2.6	1.76	3.52	2.2	1.9	3.46	2.18
2.33	4.3	2.67	1.74	3.36	2.4	2.16	4.92	3.3
2.55	5.43	3.2	1.83	3.83	2.74	2.18	4.97	3.3
2.85	3.45	2.07	2.03	3.87	2.76	2.26	5.8	3.48
1.7	2.97	1.82	2	4.2	2.8	2.66	5.96	3.83

Appendix Table 4 (Continued)

SL	SW	SH	SL	SW	SH	SL	SW	SH
1.95	4.37	2.7	1.96	3.8	2.6	2.3	5	3.4
1.5	3.2	2	2	3.9	2.8	2.3	5.38	3.5
1.8	3.64	2.38	1.62	3	2.1	2.58	6.65	4
1.74	3.2	2.07	2.23	4.05	3.05	2.4	5.48	3.14
1.64	3	1.8	2.02	4.05	2.6	2.41	5.43	3.45
2.05	4.7	2.83	1.84	3.27	2.34	2.3	5.25	3.1
1.83	3.7	2.35	1.8	3.46	2.57	3.24	6.6	4.3
1.7	3.2	1.9	2.03	3.88	2.94	2.63	5.7	3.23
1.75	3.5	2.08	1.95	3.7	2.44	2.1	4.55	1.65
1.8	3.7	2.36	1.8	3.32	2.22	2.7	6.03	3.7
1.5	2.72	1.68	2.05	4.91	3.24	2.32	5.44	3.41
1.72	3.24	1.94	2.1	4.6	3.33	1.96	5	3.1
1.75	3.4	2.1	2.1	4.66	3.2	2.14	4.62	2.8
1.45	2.4	1.44	2.1	4.4	2.94	1.64	2.76	1.75
1.7	3.06	2	2.35	5.3	3.5	2.22	5.08	3.12
1.7	3.1	1.88	2.04	4.46	2.88	1.9	3.85	2.48
2.14	4.56	2.77	2.12	4.07	2.7	1.86	3.94	2.5
1.3	2.26	1.6	2.32	5.77	3.58	1.9	3.74	2.6
1.5	2.57	1.5	2.18	4.95	3.1	1.37	1.96	1.45
1.4	2.06	1.26	2.1	5.15	3.23	1.63	2.78	1.9
1.6	2.9	1.8	5.2	2.3	3.34	1.57	2.72	1.8
1.7	3.22	2.03	1.68	2.8	1.72	1.98	3.69	2.63
1.67	3.3	2.1	1.55	2.7	1.7	1.97	3.9	2.74
1.75	3.2	2.27	1.58	2.74	1.9	2.03	5.08	2.9
1.7	3.46	2.13	1.56	2.35	1.76	2.13	5.3	3.34
1.75	3.78	2.43	1.56	2.6	1.92	2.17	4.88	3.22
1.8	3.6	2.57	2.83	3.4	2.46	2.09	4.82	3.38
1.65	3.35	2.4	1.87	3.47	2.26	1.85	3.85	2.64
2	3.9	2.2						

Appendix table 5 Beak morphological data

Upper beak					Lower beak			
rw	hl	wcl	cl	jw	rc	rw	wl	jw
0.28	0.36	0.53	0.6	0.15	0.55	0.38	0.33	0.14
0.34	0.27	0.53	0.6	0.13	0.5	0.36	0.35	0.12
0.23	0.24	0.51	0.53	0.13	0.52	0.34	0.33	0.11
0.25	0.23	0.45	0.5	0.1	0.44	0.33	0.32	0.12
0.32	0.3	0.52	0.55	0.12	0.54	0.35	0.34	0.12
0.32	0.3	0.47	0.51	0.1	0.5	0.37	0.34	0.13
0.45	0.38	0.64	0.68	0.14	0.6	0.47	0.4	0.16
0.34	0.35	0.56	0.6	0.13	0.5	0.41	0.36	0.11
0.28	0.28	0.5	0.54	0.1	0.55	0.42	0.38	0.1
0.27	0.3	0.46	0.47	0.07	0.5	0.36	0.33	0.09
0.25	0.3	0.5	0.6	0.12	0.47	0.39	0.36	0.11
0.27	0.3	0.55	0.57	0.1	0.45	0.4	0.39	0.1
0.3	0.27	0.48	0.53	0.1	0.48	0.34	0.31	0.11
0.18	0.26	0.37	0.43	0.06	0.4	0.26	0.2	0.07
0.3	0.28	0.55	0.57	0.12	0.56	0.4	0.37	0.11
0.28	0.33	0.57	0.59	0.1	0.5	0.45	0.43	0.1
0.32	0.3	0.57	0.6	0.14	0.47	0.36	0.3	0.12
0.28	0.26	0.44	0.5	0.08	0.43	0.3	0.25	0.1
0.18	0.2	0.48	0.5	0.1	0.46	0.35	0.32	0.11
0.27	0.2	0.42	0.46	0.1	0.43	0.32	0.26	0.11
0.3	0.26	0.51	0.53	0.1	0.46	0.38	0.33	0.1
0.23	0.23	0.5	0.53	0.1	0.48	0.34	0.31	0.1
0.28	0.32	0.54	0.57	0.13	0.57	0.43	0.38	0.13
0.31	0.3	0.45	0.5	0.11	0.46	0.4	0.37	0.1
0.42	0.36	0.65	0.7	0.14	0.7	0.54	0.46	0.14
0.39	0.36	0.65	0.67	0.13	0.66	0.53	0.47	0.14
0.37	0.4	0.65	0.72	0.14	0.66	0.56	0.51	0.14
0.46	0.41	0.67	0.71	0.12	0.74	0.52	0.43	0.17

Appendix Table 5 (Continued)

Upper beak					Lower beak			
rw	hl	wcl	cl	jw	rc	rw	wl	jw
0.3	0.32	0.55	0.58	0.13	0.54	0.5	0.46	0.13
0.38	0.39	0.69	0.72	0.13	0.7	0.56	0.51	0.15
0.27	0.27	0.47	0.52	0.13	0.44	0.41	0.36	0.12
0.32	0.35	0.55	0.61	0.13	0.52	0.47	0.4	0.13
0.29	0.28	0.48	0.53	0.11	0.5	0.39	0.35	0.12
0.43	0.32	0.67	0.73	0.12	0.69	0.55	0.48	0.14
0.34	0.4	0.6	0.64	0.14	0.63	0.5	0.47	0.13
0.28	0.24	0.46	0.51	0.1	0.46	0.36	0.31	0.11
0.34	0.35	0.61	0.66	0.1	0.6	0.42	0.37	0.13
0.41	0.39	0.64	0.69	0.11	0.63	0.51	0.46	0.15
0.33	0.37	0.57	0.65	0.11	0.6	0.46	0.41	0.14
0.36	0.35	0.55	0.6	0.12	0.64	0.53	0.46	0.13
0.3	0.3	0.45	0.48	0.11	0.54	0.35	0.32	0.12
0.3	0.31	0.52	0.56	0.1	0.58	0.45	0.41	0.11
0.32	0.32	0.54	0.62	0.11	0.56	0.44	0.4	0.11
0.33	0.3	0.55	0.58	0.12	0.5	0.44	0.38	0.11
0.36	0.35	0.6	0.64	0.11	0.61	0.44	0.39	0.12
0.37	0.39	0.65	0.67	0.14	0.63	0.57	0.51	0.13
0.34	0.39	0.65	0.69	0.14	0.57	0.46	0.42	0.13
0.34	0.32	0.6	0.67	0.13	0.64	0.52	0.44	0.13
0.33	0.35	0.64	0.68	0.13	0.59	0.47	0.43	0.11
0.3	0.32	0.55	0.58	0.11	0.5	0.5	0.44	0.13
0.34	0.34	0.57	0.6	0.1	0.55	0.45	0.4	0.13
0.4	0.44	0.81	0.85	0.12	0.64	0.58	0.52	0.14
0.25	0.28	0.45	0.53	0.1	0.47	0.38	0.3	0.12
0.38	0.38	0.54	0.61	0.13	0.57	0.42	0.38	0.12
0.26	0.3	0.46	0.51	0.1	0.38	0.26	0.23	0.11

Appendix Table 5 (Continued)

Upper beak					Lower beak			
rw	hl	wcl	cl	jw	rc	rw	wl	jw
0.33	0.34	0.57	0.65	0.13	0.56	0.42	0.37	0.14
0.25	0.25	0.44	0.5	0.11	0.47	0.38	0.35	0.11
0.27	0.29	0.46	0.49	0.1	0.47	0.34	0.3	0.11
0.28	0.25	0.42	0.47	0.1	0.47	0.34	0.3	0.1
0.28	0.28	0.48	0.55	0.11	0.47	0.44	0.4	0.11
0.34	0.32	0.52	0.58	0.11	0.54	0.49	0.45	0.11
0.38	0.36	0.64	0.71	0.13	0.63	0.57	0.52	0.13
0.4	0.37	0.6	0.68	0.14	0.77	0.47	0.42	0.13
0.3	0.3	0.48	0.5	0.11	0.46	0.33	0.3	0.1
0.31	0.24	0.48	0.55	0.11	0.5	0.41	0.35	0.13
0.4	0.38	0.68	0.75	0.14	0.66	0.54	0.46	0.13
0.32	0.33	0.56	0.6	0.11	0.56	0.44	0.35	0.11
0.26	0.3	0.54	0.57	0.11	0.57	0.42	0.4	0.1
0.2	0.21	0.44	0.47	0.1	0.43	0.33	0.3	0.1
0.34	0.38	0.57	0.62	0.12	0.63	0.6	0.56	0.14
0.33	0.3	0.57	0.6	0.11	0.53	0.41	0.37	0.11
0.22	0.22	0.42	0.47	0.1	0.5	0.27	0.25	0.1
0.42	0.4	0.64	0.72	0.13	0.68	0.55	0.53	0.13
0.25	0.3	0.51	0.56	0.1	0.52	0.37	0.31	0.11
0.31	0.27	0.5	0.54	0.11	0.61	0.39	0.33	0.12
0.32	0.26	0.58	0.6	0.13	0.59	0.5	0.44	0.14
0.26	0.28	0.48	0.57	0.1	0.5	0.39	0.31	0.11
0.25	0.27	0.43	0.47	0.09	0.42	0.3	0.26	0.09
0.23	0.25	0.41	0.44	0.11	0.52	0.37	0.3	0.1
0.21	0.27	0.46	0.51	0.08	0.43	0.28	0.25	0.1
0.34	0.28	0.6	0.66	0.12	0.58	0.47	0.4	0.11
0.26	0.28	0.5	0.57	0.1	0.51	0.44	0.37	0.1
0.26	0.33	0.54	0.58	0.12	0.58	0.42	0.37	0.11

Appendix Table 5 (Continued)

Upper beak					Lower beak			
rw	hl	wcl	cl	jw	rc	rw	wl	jw
0.29	0.3	0.57	0.61	0.11	0.56	0.47	0.42	0.1
0.26	0.3	0.4	0.49	0.09	0.54	0.43	0.35	0.1
0.52	0.41	0.67	0.77	0.15	0.76	0.62	0.54	0.13
0.44	0.42	0.69	0.75	0.13	0.62	0.55	0.48	0.15
0.4	0.39	0.65	0.68	0.13	0.66	0.53	0.47	0.13
0.3	0.27	0.44	0.5	0.1	0.48	0.36	0.3	0.1
0.27	0.28	0.48	0.54	0.13	0.52	0.43	0.35	0.12
0.2	0.24	0.45	0.49	0.1	0.44	0.37	0.29	0.1
0.31	0.3	0.57	0.64	0.12	0.56	0.44	0.4	0.11
0.34	0.42	0.76	0.82	0.14	0.7	0.57	0.46	0.14
0.26	0.28	0.46	0.52	0.11	0.45	0.3	0.27	0.11
0.33	0.37	0.57	0.6	0.11	0.59	0.43	0.4	0.12
0.24	0.28	0.47	0.51	0.09	0.45	0.42	0.33	0.1
0.39	0.37	0.64	0.7	0.13	0.65	0.52	0.46	0.12
0.29	0.28	0.52	0.55	0.11	0.54	0.53	0.43	0.14
0.28	0.25	0.43	0.47	0.1	0.47	0.4	0.36	0.1
0.27	0.23	0.38	0.43	0.09	0.44	0.4	0.36	0.1
0.29	0.27	0.42	0.46	0.11	0.5	0.42	0.35	0.1
0.32	0.35	0.45	0.55	0.11	0.6	0.5	0.44	0.11
0.25	0.25	0.45	0.5	0.1	0.46	0.37	0.33	0.11
0.32	0.3	0.53	0.57	0.12	0.47	0.44	0.38	0.1
0.27	0.3	0.52	0.55	0.12	0.57	0.38	0.34	0.1
0.37	0.34	0.47	0.55	0.13	0.6	0.47	0.42	0.13
0.21	0.26	0.47	0.49	0.1	0.42	0.3	0.26	0.1
0.22	0.21	0.4	0.42	0.1	0.37	0.32	0.24	0.1
0.32	0.32	0.57	0.6	0.11	0.53	0.4	0.34	0.12
0.29	0.28	0.47	0.5	0.1	0.53	0.4	0.35	0.12
0.23	0.26	0.44	0.51	0.1	0.5	0.35	0.32	0.1

Appendix Table 5 (Continued)

Upper beak					Lower beak			
rw	hl	wcl	cl	jw	rc	rw	wl	jw
0.3	0.32	0.56	0.6	0.13	0.6	0.5	0.44	0.11
0.35	0.33	0.53	0.58	0.11	0.55	0.44	0.4	0.12
0.25	0.24	0.43	0.48	0.11	0.48	0.36	0.32	0.11
0.24	0.26	0.47	0.5	0.12	0.47	0.41	0.35	0.13
0.2	0.2	0.37	0.39	0.07	0.33	0.3	0.25	0.07
0.26	0.3	0.4	0.5	0.08	0.42	0.34	0.3	0.1
0.23	0.23	0.4	0.42	0.1	0.38	0.3	0.24	0.1
0.22	0.24	0.44	0.52	0.09	0.38	0.33	0.27	0.1
0.23	0.27	0.43	0.45	0.1	0.39	0.39	0.33	0.1
0.26	0.27	0.38	0.43	0.12	0.46	0.36	0.29	0.1
0.28	0.3	0.56	0.6	0.13	0.48	0.4	0.31	0.11
0.25	0.26	0.44	0.5	0.09	0.45	0.33	0.27	0.1
0.24	0.24	0.4	0.44	0.09	0.39	0.3	0.24	0.09
0.23	0.24	0.4	0.44	0.11	0.37	0.33	0.28	0.1
0.36	0.4	0.64	0.75	0.14	0.7	0.48	0.4	0.13
0.35	0.37	0.66	0.7	0.14	0.67	0.53	0.42	0.14
0.36	0.37	0.47	0.5	0.15	0.63	0.56	0.43	0.15
0.3	0.33	0.54	0.58	0.12	0.48	0.33	0.28	0.11
0.35	0.3	0.42	0.47	0.12	0.5	0.44	0.33	0.12
0.33	0.32	0.52	0.57	0.12	0.57	0.28	0.23	0.11
0.28	0.31	0.52	0.56	0.13	0.51	0.4	0.33	0.12
0.27	0.3	0.41	0.46	0.1	0.5	0.37	0.34	0.1
0.33	0.36	0.52	0.56	0.1	0.56	0.38	0.32	0.11
0.23	0.27	0.46	0.5	0.1	0.47	0.26	0.24	0.1
0.4	0.4	0.68	0.74	0.13	0.66	0.5	0.45	0.1
0.57	0.47	0.77	0.9	0.16	0.84	0.66	0.5	0.16
0.35	0.3	0.52	0.6	0.1	0.57	0.45	0.35	0.16
0.17	0.27	0.38	0.4	0.08	0.44	0.29	0.27	0.1

Appendix Table 5 (Continued)

Upper beak					Lower beak			
rw	hl	wcl	cl	jw	rc	rw	wl	jw
0.3	0.28	0.54	0.58	0.1	0.56	0.4	0.38	0.09
0.2	0.24	0.45	0.47	0.07	0.42	0.3	0.26	0.07
0.3	0.27	0.5	0.54	0.1	0.5	0.36	0.31	0.1
0.28	0.25	0.34	0.54	0.16	0.48	0.48	0.33	0.14
0.3	0.4	0.42	0.58	0.12	0.62	0.58	0.44	0.13
0.26	0.28	0.56	0.6	0.1	0.54	0.47	0.36	0.15
0.32	0.3	0.54	0.62	0.11	0.53	0.55	0.43	0.1
0.3	0.3	0.5	0.52	0.14	0.46	0.4	0.32	0.11
0.32	0.25	0.5	0.55	0.1	0.42	0.37	0.27	0.1
0.33	0.32	0.54	0.64	0.12	0.57	0.45	0.37	0.13
0.25	0.24	0.4	0.46	0.11	0.5	0.47	0.4	0.14
0.27	0.4	0.64	0.7	0.14	0.7	0.5	0.42	0.18
0.23	0.28	0.44	0.48	0.08	0.43	0.42	0.34	0.08
0.16	0.18	0.26	0.28	0.06	0.34	0.21	0.15	0.07
0.3	0.34	0.42	0.48	0.1	0.55	0.54	0.41	0.14
0.28	0.27	0.42	0.5	0.13	0.63	0.42	0.33	0.1
0.13	0.16	0.34	0.4	0.06	0.36	0.26	0.18	0.05
0.12	0.17	0.25	0.28	0.06	0.27	0.14	0.1	0.07
0.14	0.17	0.23	0.27	0.06	0.31	0.25	0.22	0.09
0.23	0.28	0.45	0.5	0.1	0.43	0.33	0.25	0.1
0.15	0.2	0.27	0.36	0.07	0.32	0.27	0.21	0.08
0.27	0.3	0.5	0.57	0.1	0.47	0.4	0.37	0.12
0.21	0.21	0.4	0.44	0.1	0.37	0.3	0.24	0.1
0.25	0.24	0.4	0.43	0.12	0.43	0.33	0.21	0.1
0.2	0.16	0.21	0.38	0.09	0.42	0.39	0.23	0.09
0.33	0.3	0.47	0.57	0.12	0.46	0.35	0.28	0.1
0.31	0.24	0.37	0.43	0.15	0.5	0.48	0.4	0.12
0.2	0.24	0.37	0.45	0.09	0.4	0.37	0.28	0.09

Appendix Table 5 (Continued)

Upper beak					Lower beak			
rw	hl	wcl	cl	jw	rc	rw	wl	jw
0.17	0.17	0.38	0.4	0.05	0.33	0.28	0.2	0.06
0.16	0.2	0.34	0.4	0.08	0.38	0.25	0.22	0.08
0.17	0.2	0.28	0.3	0.08	0.35	0.27	0.22	0.08
0.35	0.37	0.6	0.68	0.14	0.73	0.57	0.42	0.12
0.47	0.52	0.7	0.74	0.17	0.95	0.63	0.5	0.17
0.28	0.27	0.56	0.58	0.12	0.43	0.35	0.29	0.11
0.24	0.26	0.48	0.5	0.07	0.43	0.34	0.33	0.1
0.27	0.3	0.52	0.55	0.09	0.45	0.4	0.37	0.1
0.3	0.32	0.56	0.6	0.1	0.5	0.43	0.39	0.12
0.34	0.31	0.53	0.58	0.11	0.5	0.46	0.43	0.09
0.5	0.45	0.8	0.85	0.14	0.82	0.66	0.6	0.13
0.25	0.24	0.51	0.56	0.09	0.45	0.43	0.41	0.1
0.3	0.3	0.5	0.55	0.11	0.43	0.42	0.39	0.1
0.28	0.28	0.45	0.5	0.1	0.44	0.3	0.29	0.09
0.21	0.25	0.36	0.41	0.1	0.4	0.33	0.3	0.08
0.25	0.28	0.38	0.45	0.11	0.46	0.37	0.34	0.1
0.29	0.28	0.53	0.57	0.1	0.48	0.44	0.4	0.1
0.3	0.27	0.48	0.54	0.1	0.49	0.35	0.32	0.1
0.3	0.3	0.51	0.54	0.1	0.49	0.4	0.35	0.1
0.27	0.3	0.45	0.52	0.1	0.5	0.38	0.33	0.1
0.25	0.29	0.46	0.5	0.1	0.43	0.3	0.27	0.1
0.27	0.31	0.53	0.56	0.09	0.5	0.43	0.38	0.1
0.27	0.27	0.53	0.55	0.12	0.52	0.34	0.33	0.11
0.27	0.27	0.47	0.5	0.08	0.45	0.4	0.36	0.1
0.25	0.27	0.49	0.52	0.1	0.48	0.46	0.4	0.08
0.24	0.27	0.44	0.5	0.1	0.47	0.42	0.38	0.1
0.22	0.26	0.4	0.43	0.08	0.4	0.33	0.3	0.1
0.2	0.26	0.4	0.45	0.08	0.43	0.4	0.34	0.11

Appendix Table 5 (Continued)

Upper beak					Lower beak			
rw	hl	wcl	cl	jw	rc	rw	wl	jw
0.29	0.33	0.55	0.58	0.12	0.57	0.4	0.33	0.12
0.3	0.3	0.55	0.57	0.1	0.55	0.5	0.43	0.11
0.25	0.3	0.5	0.54	0.1	0.46	0.4	0.33	0.11
0.23	0.26	0.47	0.5	0.1	0.46	0.4	0.36	0.1
0.31	0.31	0.5	0.55	0.13	0.54	0.4	0.33	0.12
0.25	0.26	0.44	0.48	0.11	0.46	0.35	0.3	0.11
0.26	0.27	0.46	0.53	0.1	0.5	0.4	0.36	0.11
0.3	0.32	0.5	0.53	0.1	0.56	0.5	0.44	0.1
0.26	0.28	0.5	0.53	0.08	0.47	0.4	0.37	0.1
0.26	0.25	0.46	0.5	0.1	0.47	0.38	0.35	0.1
0.34	0.32	0.54	0.6	0.12	0.52	0.42	0.36	0.11
0.24	0.27	0.5	0.53	0.1	0.5	0.37	0.34	0.1
0.23	0.28	0.5	0.57	0.1	0.5	0.43	0.36	0.1
0.23	0.27	0.45	0.51	0.1	0.46	0.4	0.34	0.1
0.28	0.28	0.44	0.48	0.1	0.51	0.3	0.24	0.1
0.25	0.25	0.42	0.48	0.11	0.43	0.4	0.34	0.11
0.27	0.26	0.49	0.52	0.11	0.46	0.36	0.34	0.1
0.3	0.3	0.5	0.6	0.1	0.56	0.45	0.4	0.1
0.3	0.27	0.5	0.54	0.1	0.46	0.42	0.38	0.1
0.3	0.3	0.58	0.63	0.11	0.6	0.43	0.37	0.1
0.22	0.25	0.45	0.48	0.09	0.48	0.4	0.35	0.09
0.26	0.27	0.47	0.5	0.1	0.45	0.4	0.34	0.09
0.28	0.29	0.44	0.49	0.09	0.5	0.43	0.41	0.1
0.25	0.26	0.45	0.5	0.1	0.43	0.4	0.34	0.11
0.26	0.27	0.5	0.53	0.1	0.47	0.44	0.37	0.1
0.28	0.28	0.5	0.54	0.1	0.49	0.41	0.36	0.1
0.25	0.3	0.58	0.62	0.11	0.5	0.46	0.4	0.12
0.26	0.29	0.53	0.55	0.1	0.51	0.41	0.35	0.11

Appendix Table 5 (Continued)

Upper beak					Lower beak			
rw	hl	wcl	cl	jw	rc	rw	wl	jw
0.35	0.33	0.67	0.7	0.1	0.71	0.37	0.32	0.13
0.35	0.33	0.6	0.63	0.12	0.58	0.43	0.37	0.12
0.36	0.38	0.66	0.67	0.12	0.64	0.4	0.38	0.13
0.3	0.28	0.5	0.52	0.1	0.58	0.42	0.38	0.09
0.3	0.3	0.6	0.63	0.1	0.7	0.42	0.4	0.1
0.35	0.36	0.62	0.63	0.13	0.63	0.47	0.45	0.13
0.6	0.48	0.8	0.82	0.13	0.78	0.73	0.66	0.13
0.37	0.34	0.55	0.57	0.08	0.52	0.45	0.4	0.1
0.32	0.25	0.57	0.58	0.09	0.48	0.45	0.42	0.09
0.34	0.3	0.57	0.6	0.1	0.6	0.47	0.43	0.1
0.25	0.31	0.5	0.6	0.1	0.51	0.35	0.32	0.1
0.3	0.33	0.5	0.55	0.1	0.5	0.46	0.38	0.11
0.32	0.37	0.63	0.73	0.1	0.62	0.65	0.58	0.12
0.3	0.3	0.48	0.53	0.1	0.5	0.4	0.32	0.13
0.34	0.32	0.44	0.48	0.13	0.5	0.44	0.4	0.13
0.4	0.38	0.57	0.63	0.12	0.62	0.5	0.43	0.14
0.42	0.38	0.65	0.67	0.12	0.5	0.48	0.37	0.13
0.37	0.42	0.75	0.8	0.15	0.72	0.45	0.43	0.14
0.39	0.33	0.62	0.67	0.16	0.64	0.53	0.45	0.15
0.34	0.43	0.53	0.6	0.12	0.66	0.6	0.5	0.15
0.3	0.3	0.53	0.6	0.14	0.51	0.42	0.36	0.14
0.46	0.34	0.62	0.65	0.16	0.64	0.5	0.48	0.15
0.3	0.38	0.56	0.6	0.14	0.6	0.41	0.39	0.15
0.33	0.43	0.76	0.8	0.15	0.7	0.54	0.5	0.17
0.36	0.36	0.46	0.53	0.11	0.62	0.51	0.49	0.11
0.32	0.4	0.7	0.74	0.13	0.7	0.55	0.5	0.13
0.35	0.37	0.65	0.67	0.16	0.62	0.53	0.47	0.16
0.38	0.34	0.6	0.63	0.13	0.55	0.43	0.38	0.12

Appendix Table 5 (Continued)

Upper beak					Lower beak			
rw	hl	wcl	cl	jw	rc	rw	wl	jw
0.52	0.51	0.76	0.78	0.12	0.76	0.66	0.6	0.14
0.33	0.36	0.58	0.6	0.14	0.58	0.52	0.5	0.14
0.3	0.27	0.31	0.37	0.14	0.5	0.47	0.44	0.13
0.3	0.28	0.43	0.53	0.14	0.56	0.37	0.33	0.14
0.54	0.5	0.78	0.83	0.18	0.8	0.66	0.6	0.17
0.25	0.3	0.4	0.44	0.11	0.5	0.37	0.33	0.12
0.33	0.3	0.47	0.48	0.12	0.38	0.34	0.28	0.11
0.29	0.34	0.52	0.56	0.13	0.57	0.43	0.37	0.12
0.26	0.3	0.48	0.53	0.13	0.42	0.34	0.26	0.12
0.37	0.35	0.65	0.69	0.14	0.67	0.5	0.46	0.15
0.25	0.27	0.44	0.5	0.12	0.36	0.37	0.34	0.11
0.38	0.38	0.6	0.63	0.13	0.61	0.53	0.45	0.16
0.44	0.35	0.63	0.67	0.13	0.55	0.42	0.36	0.13
0.3	0.3	0.55	0.58	0.12	0.44	0.34	0.31	0.11
0.43	0.38	0.64	0.7	0.16	0.72	0.64	0.57	0.18
0.4	0.39	0.67	0.7	0.17	0.68	0.58	0.55	0.16
0.38	0.37	0.64	0.7	0.16	0.5	0.53	0.46	0.15
0.37	0.38	0.62	0.66	0.17	0.67	0.54	0.5	0.2
0.22	0.22	0.36	0.42	0.12	0.41	0.27	0.24	0.12
0.5	0.41	0.74	0.75	0.17	0.71	0.57	0.5	0.14
0.44	0.4	0.7	0.76	0.18	0.72	0.56	0.47	0.16
0.44	0.4	0.62	0.67	0.17	0.7	0.58	0.5	0.17
0.38	0.38	0.5	0.56	0.17	0.66	0.57	0.5	0.15
0.42	0.47	0.7	0.77	0.17	0.72	0.6	0.57	0.18
0.5	0.45	0.7	0.74	0.15	0.68	0.6	0.5	0.17
0.4	0.4	0.76	0.78	0.15	0.74	0.6	0.53	0.16
0.3	0.35	0.5	0.6	0.11	0.53	0.5	0.43	0.12
0.4	0.35	0.56	0.62	0.14	0.57	0.46	0.42	0.13

Appendix Table 5 (Continued)

Upper beak					Lower beak			
rw	hl	wcl	cl	jw	rc	rw	wl	jw
0.51	0.44	0.68	0.74	0.14	0.75	0.6	0.55	0.17
0.26	0.27	0.44	0.45	0.13	0.41	0.47	0.4	0.11
0.23	0.28	0.47	0.52	0.1	0.47	0.2	0.16	0.1
0.33	0.35	0.5	0.57	0.12	0.63	0.45	0.41	0.13
0.22	0.27	0.38	0.44	0.11	0.48	0.42	0.34	0.11
0.26	0.28	0.44	0.52	0.14	0.52	0.36	0.3	0.12
0.29	0.28	0.42	0.48	0.1	0.5	0.38	0.35	0.1
0.2	0.26	0.45	0.48	0.07	0.47	0.32	0.28	0.1
0.34	0.35	0.55	0.62	0.13	0.58	0.43	0.38	0.14
0.28	0.28	0.55	0.58	0.13	0.48	0.46	0.43	0.11
0.25	0.27	0.4	0.42	0.12	0.43	0.36	0.31	0.1
0.27	0.24	0.42	0.47	0.1	0.42	0.36	0.3	0.11
0.28	0.3	0.53	0.6	0.12	0.5	0.42	0.35	0.1
0.18	0.23	0.32	0.34	0.07	0.4	0.33	0.27	0.09
0.31	0.29	0.52	0.56	0.09	0.5	0.4	0.33	0.09
0.27	0.3	0.5	0.55	0.08	0.48	0.43	0.41	0.11
0.18	0.23	0.45	0.48	0.06	0.32	0.26	0.21	0.08
0.26	0.25	0.39	0.41	0.09	0.47	0.34	0.31	0.11
0.24	0.26	0.46	0.5	0.1	0.42	0.3	0.26	0.1
0.37	0.33	0.6	0.65	0.11	0.56	0.47	0.4	0.11
0.24	0.24	0.37	0.39	0.05	0.32	0.28	0.26	0.08
0.21	0.25	0.35	0.37	0.08	0.25	0.25	0.22	0.1
0.17	0.19	0.33	0.36	0.07	0.31	0.3	0.28	0.08
0.25	0.28	0.37	0.42	0.07	0.42	0.37	0.33	0.11
0.24	0.28	0.5	0.53	0.11	0.44	0.36	0.31	0.12
0.25	0.31	0.45	0.53	0.08	0.44	0.4	0.38	0.08
0.26	0.28	0.48	0.53	0.08	0.48	0.32	0.27	0.08
0.27	0.27	0.38	0.4	0.08	0.44	0.35	0.3	0.1

Appendix Table 5 (Continued)

Upper beak					Lower beak			
rw	hl	wcl	cl	jw	rc	rw	wl	jw
0.32	0.32	0.5	0.55	0.1	0.52	0.43	0.37	0.09
0.28	0.28	0.5	0.55	0.09	0.46	0.38	0.33	0.11
0.29	0.26	0.49	0.52	0.09	0.46	0.35	0.31	0.1
0.3	0.3	0.5	0.56	0.11	0.51	0.38	0.34	0.1
0.27	0.34	0.52	0.55	0.09	0.6	0.46	0.4	0.1
0.33	0.26	0.48	0.54	0.09	0.56	0.4	0.33	0.11
0.35	0.32	0.52	0.58	0.08	0.6	0.49	0.42	0.11
0.2	0.22	0.33	0.37	0.06	0.32	0.32	0.28	0.07
0.22	0.26	0.4	0.44	0.08	0.43	0.3	0.27	0.08
0.2	0.27	0.43	0.44	0.06	0.46	0.24	0.2	0.07
0.24	0.27	0.34	0.38	0.1	0.45	0.37	0.32	0.08
0.24	0.28	0.4	0.45	0.1	0.42	0.31	0.26	0.08
0.3	0.28	0.47	0.5	0.08	0.42	0.4	0.36	0.1
0.26	0.28	0.48	0.52	0.09	0.44	0.35	0.28	0.1
0.28	0.26	0.45	0.48	0.07	0.47	0.42	0.37	0.1
0.3	0.3	0.45	0.5	0.12	0.53	0.5	0.43	0.1
0.3	0.26	0.5	0.58	0.1	0.5	0.44	0.36	0.08
0.33	0.32	0.56	0.6	0.11	0.5	0.43	0.36	0.1
0.22	0.24	0.48	0.53	0.08	0.44	0.38	0.35	0.09
0.3	0.29	0.43	0.46	0.09	0.5	0.38	0.35	0.08
0.26	0.28	0.5	0.53	0.08	0.49	0.4	0.33	0.1
0.39	0.33	0.57	0.62	0.11	0.58	0.44	0.38	0.1
0.4	0.34	0.58	0.64	0.12	0.6	0.45	0.4	0.1
0.34	0.37	0.58	0.67	0.13	0.64	0.46	0.4	0.12
0.31	0.26	0.54	0.6	0.12	0.55	0.47	0.41	0.11
0.35	0.3	0.47	0.54	0.12	0.55	0.42	0.38	0.14
0.27	0.31	0.47	0.5	0.11	0.37	0.35	0.33	0.13
0.4	0.34	0.6	0.63	0.13	0.52	0.53	0.42	0.15

Appendix Table 5 (Continued)

Upper beak					Lower beak			
rw	hl	wcl	cl	jw	rc	rw	wl	jw
0.3	0.37	0.6	0.63	0.15	0.53	0.44	0.4	0.14
0.25	0.35	0.47	0.5	0.11	0.44	0.38	0.35	0.11
0.25	0.27	0.42	0.45	0.14	0.48	0.42	0.36	0.13
0.31	0.33	0.46	0.5	0.12	0.47	0.4	0.35	0.13
0.27	0.34	0.44	0.5	0.13	0.66	0.44	0.37	0.12
0.3	0.33	0.48	0.51	0.11	0.57	0.4	0.33	0.1
0.34	0.42	0.6	0.65	0.13	0.58	0.47	0.4	0.14
0.4	0.37	0.54	0.6	0.11	0.56	0.52	0.46	0.12
0.31	0.29	0.5	0.53	0.14	0.6	0.46	0.42	0.14
0.38	0.28	0.48	0.54	0.12	0.53	0.52	0.44	0.12
0.3	0.36	0.65	0.7	0.13	0.57	0.54	0.46	0.14
0.39	0.37	0.58	0.6	0.13	0.53	0.44	0.4	0.12
0.32	0.36	0.56	0.6	0.14	0.52	0.5	0.45	0.13
0.36	0.38	0.61	0.67	0.12	0.7	0.6	0.5	0.15
0.44	0.38	0.65	0.7	0.12	0.67	0.63	0.54	0.14
0.43	0.35	0.66	0.7	0.14	0.68	0.5	0.47	0.14
0.37	0.36	0.57	0.6	0.15	0.7	0.53	0.47	0.16
0.24	0.27	0.43	0.48	0.11	0.38	0.34	0.31	0.1
0.22	0.2	0.4	0.44	0.1	0.36	0.3	0.28	0.1
0.3	0.2	0.43	0.47	0.1	0.42	0.3	0.26	0.1
0.22	0.2	0.35	0.38	0.1	0.4	0.25	0.21	0.1
0.2	0.26	0.4	0.42	0.1	0.35	0.35	0.3	0.1
0.22	0.22	0.31	0.33	0.11	0.45	0.34	0.33	0.12
0.24	0.24	0.37	0.42	0.11	0.47	0.42	0.35	0.12
0.33	0.28	0.5	0.53	0.13	0.48	0.42	0.38	0.13
0.3	0.31	0.45	0.53	0.13	0.46	0.46	0.4	0.12
0.3	0.32	0.48	0.55	0.11	0.45	0.38	0.33	0.11
0.4	0.37	0.58	0.63	0.14	0.65	0.64	0.54	0.16

Appendix Table 5 (Continued)

Upper beak					Lower beak			
rw	hl	wcl	cl	jw	rc	rw	wl	jw
0.39	0.32	0.52	0.57	0.13	0.64	0.45	0.43	0.14
0.34	0.32	0.55	0.61	0.12	0.66	0.55	0.47	0.12
0.31	0.36	0.6	0.66	0.13	0.56	0.52	0.46	0.13
0.31	0.34	0.5	0.55	0.11	0.55	0.58	0.52	0.14
0.3	0.32	0.49	0.6	0.13	0.53	0.47	0.44	0.13
0.35	0.35	0.51	0.6	0.13	0.57	0.51	0.48	0.13
0.3	0.28	0.47	0.53	0.14	0.53	0.46	0.42	0.13
0.4	0.43	0.67	0.7	0.15	0.68	0.57	0.53	0.14
0.38	0.3	0.5	0.52	0.11	0.45	0.37	0.35	0.11
0.27	0.3	0.57	0.58	0.11	0.45	0.42	0.39	0.13
0.34	0.34	0.55	0.58	0.13	0.58	0.45	0.35	0.17
0.3	0.31	0.47	0.5	0.14	0.48	0.41	0.37	0.13
0.25	0.26	0.42	0.46	0.11	0.44	0.43	0.4	0.11
0.38	0.4	0.69	0.74	0.14	0.64	0.52	0.48	0.16
0.34	0.37	0.61	0.67	0.14	0.6	0.45	0.4	0.13
0.37	0.34	0.57	0.61	0.14	0.7	0.6	0.56	0.17
0.46	0.44	0.75	0.77	0.14	0.7	0.58	0.53	0.15
0.34	0.36	0.57	0.6	0.12	0.66	0.52	0.45	0.13
0.35	0.38	0.51	0.53	0.11	0.6	0.46	0.41	0.15
0.42	0.41	0.75	0.79	0.13	0.83	0.66	0.56	0.15
0.34	0.37	0.65	0.68	0.13	0.68	0.54	0.5	0.14
0.38	0.44	0.68	0.73	0.15	0.71	0.57	0.52	0.14
0.4	0.4	0.66	0.74	0.14	0.65	0.58	0.47	0.13
0.64	0.57	0.97	1	0.2	0.96	0.83	0.76	0.16
0.43	0.44	0.76	0.82	0.14	0.88	0.65	0.57	0.15
0.3	0.32	0.58	0.6	0.13	0.59	0.48	0.43	0.13
0.52	0.45	0.78	0.82	0.15	0.71	0.66	0.6	0.15
0.45	0.43	0.78	0.8	0.16	0.78	0.6	0.5	0.16

Appendix Table 5 (Continued)

Upper beak					Lower beak			
rw	hl	wcl	cl	jw	rc	rw	wl	jw
0.43	0.39	0.63	0.68	0.14	0.66	0.58	0.5	0.14
0.32	0.37	0.5	0.55	0.13	0.6	0.58	0.5	0.15

Appendix table 6 The number of chromatophore on the surface of paralarva of *A. hians*

Side / No.	Dorsal (D)			Ventral (V)		
	head	body	sum(D)	head	body	sum(V)
1	12	11	23	11	5	16
2	7	9	16	16	3	19
3	7	14	21	8	3	11
4	12	6	18	13	3	16
5	10	13	23	10	4	14
6	13	16	29	12	5	17
7	12	11	23	12	4	16
8	10	13	23	10	3	13
9	10	15	25	9	3	12
10	19	17	36	10	4	14
11	9	14	23	12	3	15
12	11	10	21	6	4	10
13	12	9	21	12	4	16
14	9	12	21	9	4	13
15	9	7	16	10	5	15
16	11	13	24	11	6	17
17	12	13	25	10	4	14
18	9	10	19	7	3	10
19	8	5	13	6	3	9
20	6	4	10	4	3	7

Appendix table 6 (Continued)

Side / No.	Dorsal (D)			Ventral (V)		
	head	body	sum(D)	head	body	sum(V)
21	12	13	25	14	4	18
22	8	5	13	7	3	10
23	13	16	29	13	4	17
24	11	13	24	12	3	15
25	12	7	19	11	3	14
26	10	15	25	11	7	18
27	6	6	12	8	3	11
28	9	7	16	8	4	12
29	12	8	20	6	3	9
30	8	13	21	7	4	11
31	5	11	16	5	3	8
32	9	14	23	10	4	14
33	12	13	25	7	4	11
34	9	11	20	10	2	12
35	11	10	21	15	3	18
36	12	8	20	12	4	16
37	17	14	31	10	7	17
38	11	10	21	8	3	11
39	9	10	19	10	4	14
40	8	12	20	11	3	14
41	7	11	18	11	3	14
42	7	9	16	12	3	15
43	9	12	21	10	3	13
44	10	11	21	10	4	14
45	10	12	22	10	3	13
46	13	11	24	13	3	16
47	9	11	20	10	3	13
48	7	8	15	10	3	13

Appendix Table 6 (Continued)

Side / No.	Dorsal (D)			Ventral (V)		
	head	body	sum(D)	head	body	sum(V)
49	13	14	27	13	3	16
50	8	12	20	10	3	13
51	11	14	25	10	5	15
52	13	10	23	11	4	15
53	10	11	21	10	3	13
54	8	10	18	9	3	12
55	10	11	21	14	4	18
56	8	9	17	9	3	12
57	10	11	21	10	3	13
58	12	19	31	12	6	18
59	11	11	22	10	3	13
60	11	9	20	9	4	13
61	13	13	26	13	3	16
62	10	10	20	11	3	14
63	12	9	21	14	3	17
64	11	5	16	10	3	13
65	13	13	26	10	3	13
66	12	19	21	12	3	15
67	11	13	24	9	4	13
68	13	11	24	10	7	17
69	9	9	18	13	4	17
70	11	10	21	11	3	14
71	13	10	23	11	3	14
72	10	11	21	12	3	15
73	12	7	19	11	3	14
74	10	8	18	12	3	15
75	11	9	21	9	3	12
Average	10.40	10.95	21.23	10.32	3.61	13.93

Appendix table 7 Cephalopods in Thai waters (Nabhitabhata, 1999)

Group	Gulf of Thailand	Andaman Sea
Family Nautilidae		
Nautilus pompilius	-	√
F. Spirulidae		
Spirula spirula	-	√
F. Sepiidae		
Sepia aculeata	√	√
Sepia arabica	-	√
Sepia brevimana	√	√
Sepia kobiensis	√	√
Sepia latimanus	√	√
Sepia lycidas	√	√
Sepia pharaonis	√	√
Sepia prashadi	-	√
Sepia recurvirostra	√	√
Sepia stellifera	√	√
Sepia inermis	√	√
Metasepia tullbergi	√	-
F. Sepiadariidae		
Sepiadarium kochii	√	√
F. Sepiolidae		
Sepiaola trirostrata	√	-
Inioteuthis maculosa	√	√
Euprymna berryi	√	√
Euprymna hyllebergi	√	√
Euprymna morsei	√	√
Euprymna stenodactyla	√	√

Appendix Table 7 (Continued)

Group	Gulf of Thailand	Andaman Sea
F. Idiosepiidae		
Idiosepius biserialis	-	√
Idiosepius pygmaeus	√	√
Idiosepius thaiandicus	√	√
F. Loliginidae		
Loligo beka	-	√
Loligo chinensis	√	√
Loligo duvauceli	√	√
Loligo edulis	√	√
Loligo "edulis" (new subspecies)	√	-
Loligo (Doryteuthis) sibogae	√	√
Loligo singhalensis	√	√
Loligo sumatrensis	√	√
Loliolus (Loliolus) affinis	√	√
Lolliguncula panamaensis	√	-
Sepioteuthis lessoniana	√	√
F. Enoploteuthidae		
Abralia armata	√	√
Abralia (Asteroteuthis) andamanica	-	√
Abralia (Stenabralia) lucens	-	√
F. Onychoteuthidae		
Onychoteuthis banksi	√	√
F. Architeuthidae		
Architeuthis sp.	√	√
F. Histioteuthidae		
Histioteuthis celetaria pacifica	-	√

Appendix Table 7 (Continued)

Group	Gulf of Thailand	Andaman Sea
F. Ommastrephidae		
Nototodarus hawaiiensis	-	√
Sthenoteuthis oualaniensis	-	√
F. Thysanoteuthidae		
Thysanoteuthis rhombus	√	√
F. Chiroteuthidae		
Chiroteuthis imperator	-	√
F. Cranchiidae		
Liocranchia reinhardi	-	√
F. Octopodidae		
Octopus aegina	√	√
Octopus cyanea	√	√
Octopus dollfusi	√	√
Octopus exannulatus	√	√
Octopus globosus	-	√
Octopus horridus	√	-
Octopus luteus	-	√
Octopus marginatus	√	√
Octopus membranaceus	√	√
Octopus neglectus	√	√
Octopus cf. niveus	-	√
Octopus ornatus	√	√
Octopus parvus	√	-
Octopus rex	√	√
Octopus siamensis	-	√
Octopus cf. vulgaris	-	√
Cistopus indicus	√	√

Appendix Table 7 (Continued)

Group	Gulf of Thailand	Andaman Sea
Hapalochlaena maculosa	√	√
F. Argonautidae		
Argonauta argo	√	√
Argonauta boettgeri	-	√
Argonauta hians	√	√
F. Alloposidae		
Alloposus mollis	-	√

Appendix table 8 Length at 50% maturity data

ML (mm)	immaturity	maturity	sum	P_L	$Ln(\frac{1}{P_L})-1$	
14.5	3	0	3	0.0000		
15.5	1	0	1	0.0000		
17.5	2	0	2	0.0000		
18.5	5	0	5	0.0000		
19.5	4	2	6	0.3333	0.6931	
20.5	3	4	7	0.5714	-0.2877	Number for
21.5	3	4	7	0.5714	-0.2877	calculate
22.5	2	9	11	0.8182	-1.5041	formula
23.5	1	12	13	0.9231	-2.4849	relationship
24.5	3	11	14	0.7857	-1.2993	
25.5	2	16	18	0.8889	-2.0794	
26.5	1	14	15	0.9333	-2.6391	
27.5	0	26	26	1.0000		
28.5	0	18	18	1.0000		
29.5	0	31	31	1.0000		

Appendix Table 8 (Continued)

ML (mm)	immaturity	maturity	sum	P_L	$Ln(\frac{1}{P_L})-1$
30.5	0	30	30	1.0000	
31.5	0	16	16	1.0000	
32.5	0	16	16	1.0000	
33.5	0	18	18	1.0000	
34.5	0	22	22	1.0000	
35.5	0	13	13	1.0000	
36.5	0	13	13	1.0000	
37.5	0	12	12	1.0000	
38.5	0	10	10	1.0000	
39.5	0	9	9	1.0000	
40.5	0	10	10	1.0000	
41.5	0	5	5	1.0000	
42.5	0	6	6	1.0000	
43.5	0	3	3	1.0000	
44.5	0	1	1	1.0000	
45.5	0	1	1	1.0000	
46.5	0	2	2	1.0000	
47.5	0	1	1	1.0000	
49.5	0	1	1	1.0000	
50.5	0	1	1	1.0000	
53.5	0	1	1	1.0000	
	30	338	368		

Appendix Table 9 Group of similarity shell length of individual month

		Subset for alpha = 0.05					
Month	N	1	2	3	4	5	6
7	51	31.7431					
4	35	33.2257	33.2257				
9	50	33.5260	33.5260				
6	30	33.7400	33.7400				
1	24	33.9583	33.9583				
3	31		37.4903	37.4903			
10	36			40.2250			
2	35			40.8200	40.8200		
5	17			41.5471	41.5471	41.5471	
8	31				44.9677	44.9677	
12	29					45.7172	
11	25						50.5840
Sig.		.357	.070	.078	.062	.060	1.000

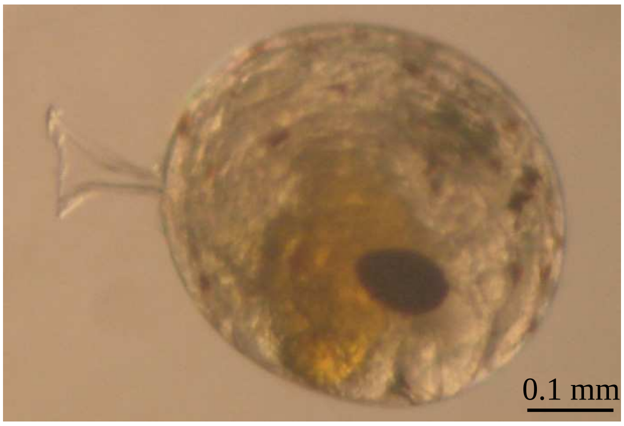
Laboratory Equipment

Appendix figure 1 Fiber glass size 300 liters

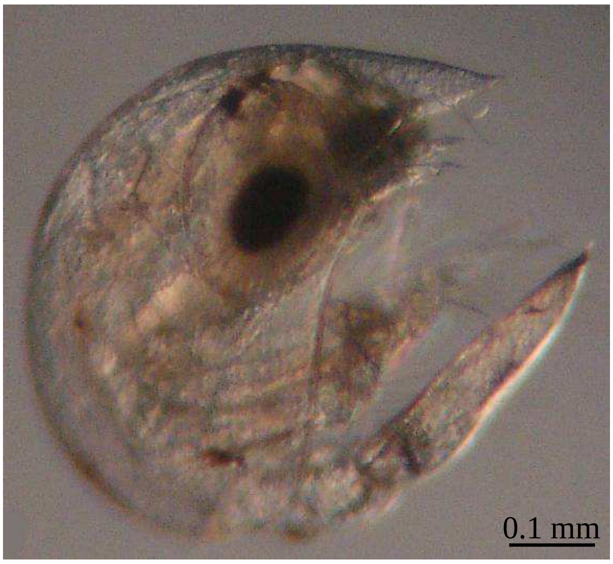
Appendix figure 2 Fiber glass with aeration system

Appendix figure 3 Case net for stocking specimen in the sea

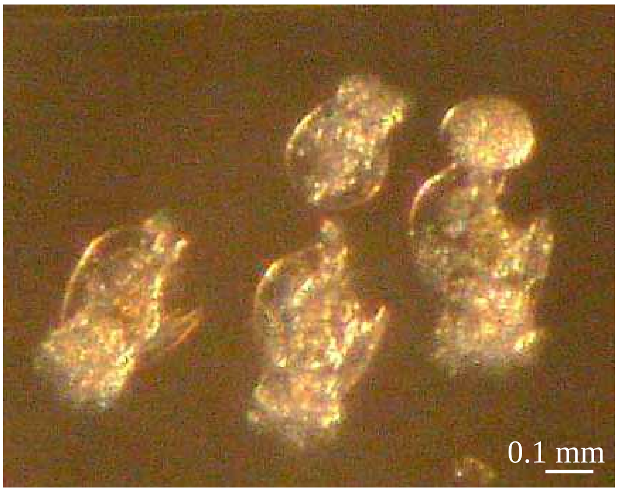
Food for paralarvae



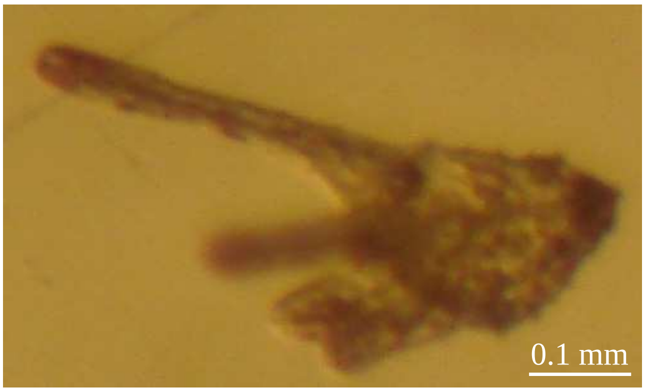
Appendix figure 4 Mole crab’s egg



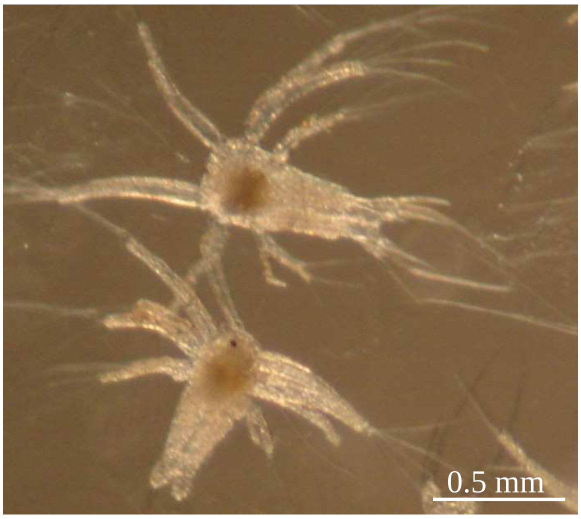
Appendix figure 5 Mole crab's nauplius



Appendix figure 6 Rotifer



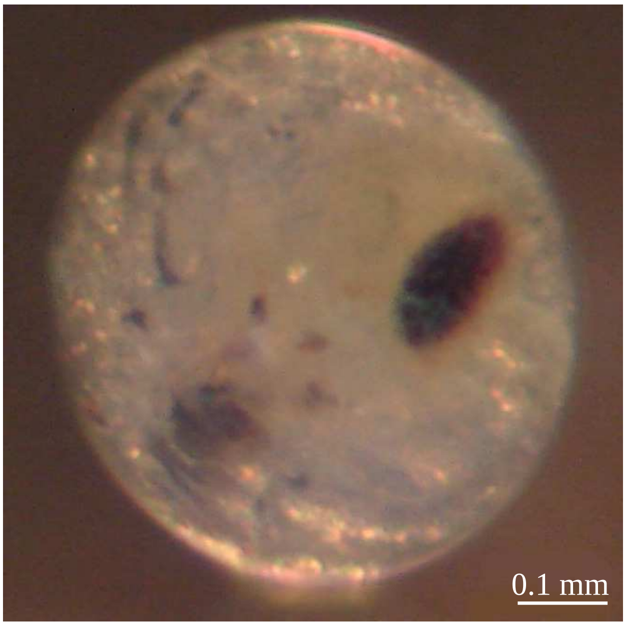
Appendix figure 7 Sea urchin’s larva



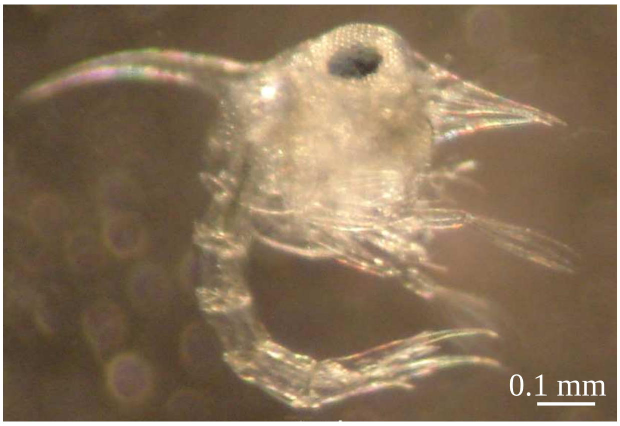
Appendix figure 8 White shrimp’s nauplius

Appendix figure 9 Mysid

Appendix figure 10 Copepod

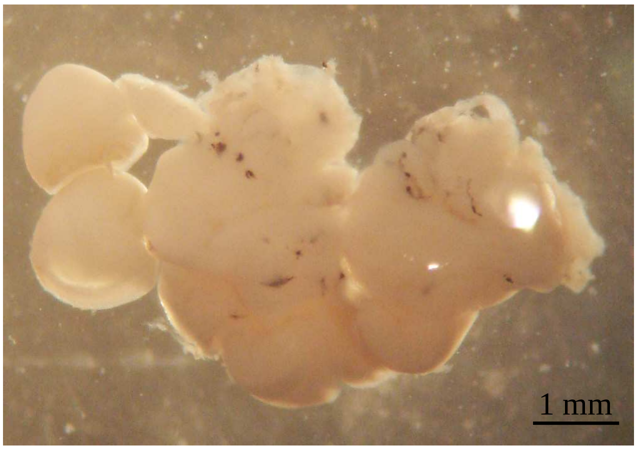


Appendix figure 11 Blue swimming crab’s egg

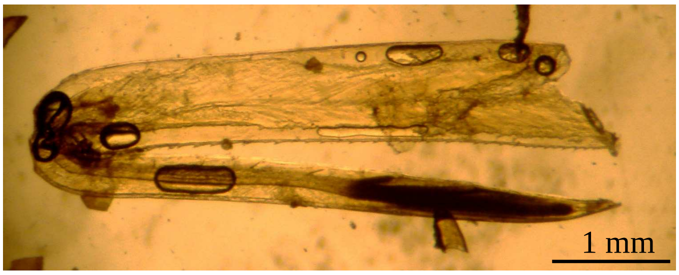


Appendix figure 12 Blue swimming crab's zoea

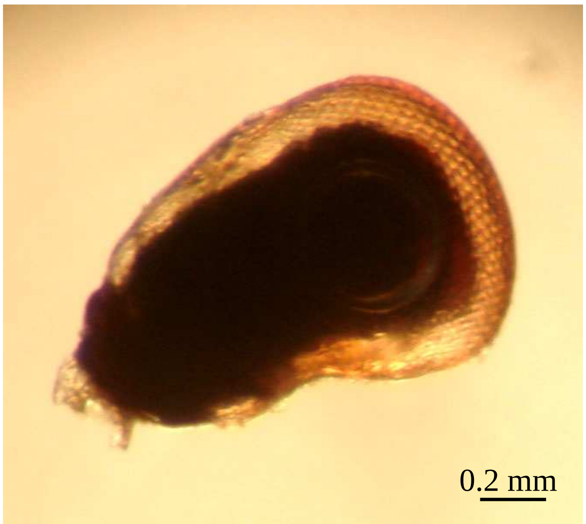
Stomach content



Appendix figure 13 Cephalopod's suckers

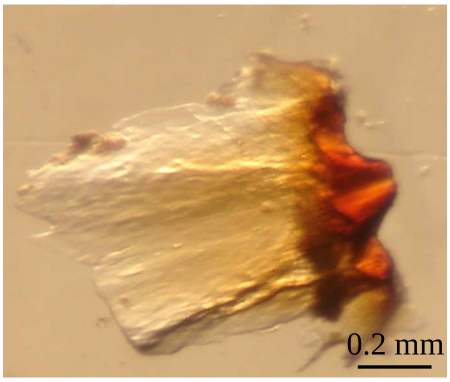


Appendix figure 14 Crustacean's leg



Appendix figure 15 Crustacean's eye

Appendix figure 16 Fish scale



Appendix figure 17 Cephalopod's beak

CURRICULUM VITAE

NAME	: Mr.Charuay Sukhsangchan
BIRTH DATE	: October 2, 1973
BIRTH PLACE	: Pathumthani Province, Thailand
EDUCATION	

YEAR	INSTITUTION	DEGREE/DIPLOMA
1997	Kasetsart University	B.S.(Fisheries)
2000	Kasetsart University	M.S.(Marine Science)
2009	Kasetsart University	Ph.D.(Marine Science)

POSITION.TITLE	: Lecturer
WORK PLACE	: Department of Marine Science, Faculty of Fisheries Kasetsart University

PUBLICATIONS

Sukhsangchan, C and J. Nabhitabhata. 2006. **External Morphology and Embryonic Development of Muddy Paper Nautilus, *Argonauta hians* Lightfoot, 1786, from Andaman Sea, Thailand**. JSPS-NRCT International Symposium, Joint Seminar 2006 "Innovative Technology for the Sustained Development of Fishery and Aquaculture. Kasetsart University, Bangkok, Thailand.

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