LIFE CYCLE OF CULTURED PHARAOH CUTTLEFISH, *SEPIA PHARAONIS* EHRENBERG, 1831

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ABSTRACT

The pharaoh cuttlefish, *Sepia pharaonis*, were cultured in laboratory. Eggs were deposited as single eggs, round in shape and white in colour. The incubation period was 14.3 days at 28°C. Hatchlings were benthic. Mean mantle length was 0.77 cm and body weight 0.18 g. Hatchlings fed on mysids and postlarvae of penaeid shrimp. The pharaoh cuttlefish were sexually mature after 90 days and mating was observed since then. Daily growth rate was 1.37 % in mantle length and 3.40 % in body weight. Spawning occurred at the age of 110 days and one female laid from 50 to 3000 eggs. The average life span was 149.4 days due to mortality of both sex after spawning. Largest final size was 16.20 cm mantle length and 368.48 g body weight. Maximum life span was 271 days. Early maturity at a small size in culture condition revealed the alternative life strategy as short generation mode.

INTRODUCTION

The sepiid cuttlefish are decapod cephalopods with tentacles as the fifth arms pair retractile into pockets. Most of the cuttlefish are neritic with a benthic living form. The calcareous internal shell is called cuttle bone, which function is to provide buoyancy for the animal. The flesh is edible as of the other cephalopods. The cuttlebone is one of the ingredients in traditional medicine, toothpaste, cosmetics, domestic animal food and even a source of lime for cage birds and to maintain the condition of their beaks.

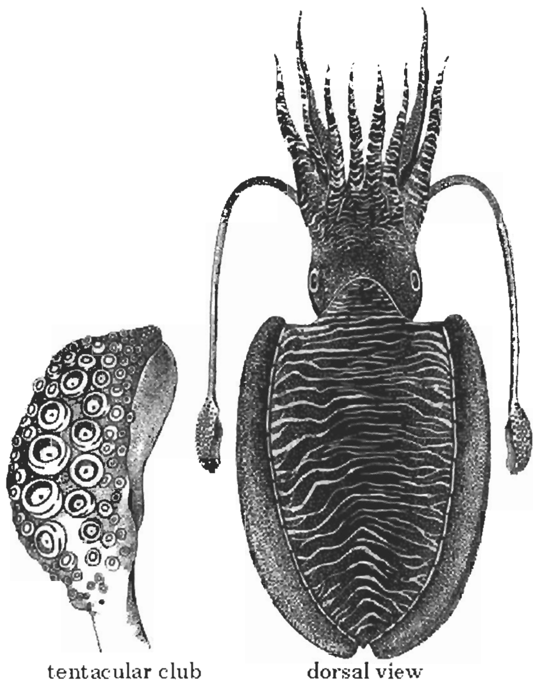

Figure 1a. The pharaoh cuttlefish, *Sepia pharaonis* Ehrenberg.

The pharaoh cuttlefish, *Sepia pharaonis* (Fig. 1a) is the sepiid with the widest distribution (Fig. 1b) in the Indo-Pacific zone, from 35° N to 30° S and 30° to 140° E. This cuttlefish is the largest of the 12 species of

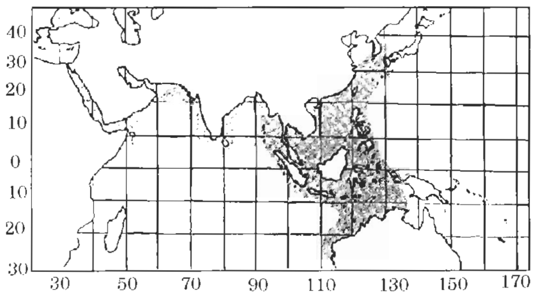

Figure 1b. The distribution of *Sepia pharaonis* (from Roper *et al.* 1984).

sepiid cuttlefish recorded in Thai waters with economic importance. The Thai name "Pla Muek Kradong Lai Sua" means tiger cuttlefish after the transverse striped pattern on the dorsum especially in the male. The species constitutes about 16 % of cephalopods landed by trawlers fishing off-shore and about 10 % of the catch in traps placed in inshore waters (Supongpan 1995).

Large scale aquaculture of the pharaoh cuttlefish has been studied in Thailand since 1978 (Nabhitabhata 1978). The low growth rate and small final size of 370 g are disadvantageous for aquaculture in term of quantitative production. However, the mentioned size is optimal for frozen products and packaging. The information obtained from this study revealed that biological insight of the life cycle should be applied in the handling of unfavourable conditions in aquaculture.

MATERIALS AND METHODS

Spawners of pharaoh cuttlefish were collected live from squid traps placed near shore in Rayong province in the eastern part of the Gulf of Thailand. The cuttlefish were transported to the hatchery and maintained in 2 m^3 concrete tanks at a male to female ratio of 1:2. They mated and spawned in the tanks attaching their egg capsules in clusters to nylon net used as an artificial substratum. Eggs were collected, aerated and left to hatch in plastic baskets of 0.5 cm mesh size. Temperature was controlled by means of a water flow through method at a rate of 1 L. min^{-1}. Light was reduced with camouflaging net to prevent algal growth. Ongrowth was conducted in 2 m^3 concrete tanks.

Hatchlings were fed live mysids (*Mesopodopsis* spp.) and the postlarvae of penaeid shrimp (*Penaeus merguiensis*). After 30 days, the cuttlefish were trained to feed on dead fish meat (*Caranx leptolepis*). Size grading and water level adjustment were performed every ten days for suitable management of feed. The density per tank had to be reduced with 25 % after each grading.

Growth was determined every 10 days in terms of gain in dorsal mantle length (ML, cm) and wet body weight (W, g). Daily growth (%) of mantle length and weight was calculated according to Choe (1966 *in* Mangold 1983) :

$DGRL = (ML_2 - ML_1) / t\ [(ML_2 + ML_2) / 2] \times 100$

and $DGRW = (W_2 - W_1) / t\ [(W_2 + W_1 / 2)] \times 100$

- where DGRL was daily growth rate in terms of mantle length (%)

DGRW daily growth rate in terms of body weight (%)

ML_1 initial mantle length (cm),

ML_2 final mantle length (cm),

W_1 initial weight (g),

W_2 final weight (g),

t = number of days (10 days period)

Gross feed conversion efficiency (%) was calculated from the amount of feed and body weight gain :

$GFCE = (W_2 - W_1) / F \times 100$

- where GFCE was gross feed conversion efficiency (%),

and F was total feed consumed in wet weight basis (g).

Growth in terms of length-weight relationship was determined by a power regression model; mantle length-age relationship by cubic regression; weight-age relationship by an exponential regression model in the early growth phase, and a quadratic regression model in the following phase:

$W = a_1 ML^{b1}$

$ML = a_2 + b_2 T + b_3 T^2 + b_4 T^3$

$W = a_3 e^{b5T}$

and $W = a_4 + b_6 T + b_7 T^2$

- where a was the constant elevation

b the slope

T the age (days).

Aspects of the biohistory were observed and recorded as drawings, still and video photography. Water quality criteria was determined by a modified bioassay experiment (Nabhitabhata *et al.* 1991; 1993 a,b) during 24 hrs period to estimate 50 % survival.

RESULTS

Eggs

Single egg capsules were attached in clusters to the substratum. The capsule was white, opaque, round in shape with tip and stalk

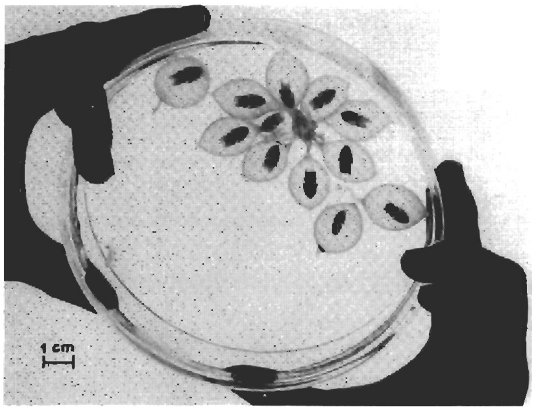

Figure 2. Pre-hatching eggs of the pharaoh cuttlefish.

(Fig. 2). The egg stalks were twined or adhered to rod and ribbon shape or flat substrata respectively. The egg capsule turned larger and it became more transparent and fragile in concert with the embryonic development, reaching its largest size near the time of hatching. The extremely rare case of two embryos in one capsule was observed in one cluster of eggs (Fig. 3). The embryonic development and hatchlings were normal.

The incubation period was 9-25 days (average 14.3 ± 3.0 days) at about 28° C. The hatching period of eggs in the same cluster of the same spawning was 3-10 days from the first to the last eggs. Most of the hatching occurred on the second and third day at night. Hatching was more than 90 % for eggs collected in nature (F1 generation) and about

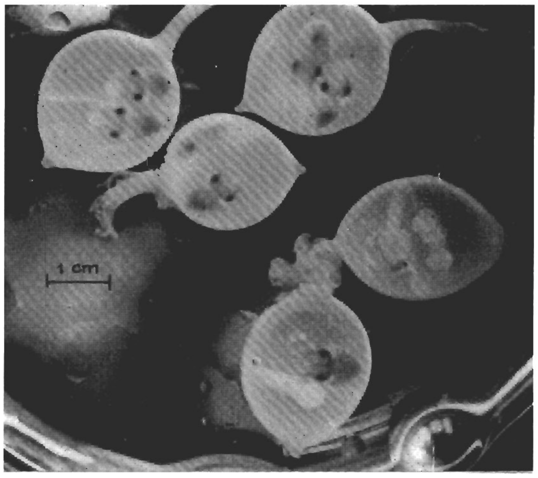

Figure 3. The "twins" or two embryos in one egg capsule.

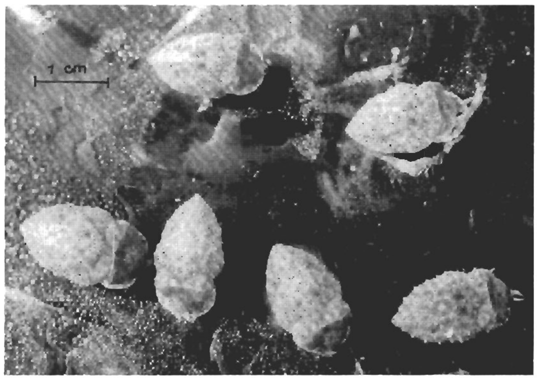

Figure 4. Hatchlings of the pharaoh cuttlefish as benthic form.

50 % for eggs of cultured specimens (F2 generation). The hatching rate of unfertilized eggs was lower (about 2 %) with abnormal development and growth of alga and fungi on the egg capsule. Brief changes of temperature and salinity as well as mechanical stimuli caused premature hatching and resulted in unhealthy hatchlings.

Hatchlings

The living mode of the hatchlings was benthic (Fig. 4). They hatched out with a small external yolk sacs which fell off during the first day. The hatchlings were capable of adhering to the substratum with the ventral surface of their mantle. Chromatophores, ink glands and tentacles were functional as well. They began feeding on the first day, 6-12 hrs after hatching. The overall morphology of the hatchling was similar to that of the adult. The length of the fins was about 70 % of the mantle length; relatively shorter than the adult. The young was observed to innately prefer crustaceans than fishes as feed. The young cuttlefish consumed an average of 10.5 postlarvae of penaeid shrimp or 13 mysid shrimps daily, up to 10 days of age. The feeding rate was 28.17±4.07 % of body weight and the feed conversion efficiency was 48.22±4.33 %. More than 90 % survived up to this stage.

Juveniles and adults

Burrowing behaviour was observed after 4 days in a sandy and small gravel substrata. The young cuttlefish was solitary, lying or burrowing in the substratum. Gregarious behaviour was occasionally observed in fleeing from an enemy and in pursuit of prey after 10 days of age. After 30 days, the fin length increased to about 80 % of the mantle. Two large black spots on the posterior dorsum could be observed. Cannibalism was extremely rare. Only one cuttlefish of this age, among thousands of individuals in 22 batches, was observed to fed on another one of the same size. It had not been observed whether the eaten one had already died before being seized or not. The feeding behaviour was in three steps: attention, positioning and seizure with the tentacles. After 30-50 days, they changed to use arms only in seizure of dead feed without the positioning step. The cuttlefish emerged from the substratum to seize their prey. The prey was held by the arms and first bitten at the joint part of the carapace between head and body. The hard structure of the prey was left uneaten.

After 60 days, the normal colour pattern of the cuttlefish turned into dark brown with scattered small black rings on the dorsum

Table 1. Growth of pharaoh cuttlefish, *Sepia pharaonis*, in terms of dorsal mantle length (cm).

Age	Mantle length	Length increment				Daily growth
(days)	(cm)	(cm)	(cm / day)	(%)	(% / day)	(%)
0	0.77	-	-	-	-	-
10	1.09	0.32	0.03	41.56	4.16	3.44
20	1.5	0.41	0.04	37.62	3.76	3.17
30	1.95	0.45	0.05	30.00	3.00	2.61
40	2.56	0.61	0.06	31.28	3.13	2.71
50	2.9	0.34	0.03	13.28	1.33	1.24
60	3.53	0.63	0.06	21.72	2.17	1.96
70	4.42	0.89	0.09	25.21	2.52	2.24
80	5.13	0.71	0.07	16.06	1.61	1.49
90	5.88	0.75	0.08	14.62	1.46	1.36
100	6.21	0.33	0.03	5.61	0.56	0.55
110	7.16	0.95	0.1	15.30	1.53	1.42
120	7.85	0.69	0.07	9.64	0.96	0.92
130	8.41	0.56	0.06	7.13	0.71	0.69
140	8.78	0.37	0.04	4.40	0.44	0.43
150	9.51	0.53	0.05	6.04	0.60	0.59
160	9.62	0.31	0.03	3.33	0.33	0.33
170	10.51	0.89	0.09	9.25	0.92	0.88
180	12.04	1.53	0.15	14.56	1.46	1.36
190	12.5	0.46	0.05	3.82	0.38	0.38
200	13.01	0.51	0.05	4.08	0.41	0.40
210	13.94	0.93	0.09	7.15	0.72	0.69
Mean ±se	-	0.63±0.06	0.06±0.01	15.32±2.54	1.53±0.25	1. 37±0.21

and dark brown colour on both fins. The fin length was about 95 % of mantle. After 90 days, sex dimorphism could be recognized in the colour pattern. The male had brown-white transverse stripes or a tiger pattern on the dorsum. The female did not change colour pattern. The male tiger pattern was very clear after 120 days.

Growth

Hatchlings of pharaoh cuttlefish grew from 0.77 cm in mantle length and 0.18 g of wet body weight to 1.09 cm and 0.42 g respectively in the first 10 days. The daily growth rate was 3.44 % in length and 8.00% in weight. Length increased 4.16 % day^{-1} and weight 13.33% day^{-1}, which were the highest rates during their growth. The daily growth was 2 % the higher in length and 7 % in weight during the first 40 days. For the overall life cycle of 210 days, the average daily growth rate was 1.37 % in mantle length and 3.40% in body weight. The cuttlefish were mature after 90 days at a length of about 6 cm (30 g). The first spawning was observed at a length of about 7 cm (50 g), generally at 10 cm (100 g). Maximum cultured length was 16.20 cm (368.48 g) for the male, and 15.50 cm (350.0 g) for the female.

Growth of the pharaoh cuttlefish was allometric. The relationship between mantle length and weight was

$W = 7.070 \times 10^{-4} ML^{2.591}$ ($n = 1854$, $r^2 = 0.974$)

The growth in terms of mantle length-age relationship was

$ML = 7.730 + 0.300 T + 3.584 \times 10^{-3} T^2 - 1.1089 \times 10^{-5} T^3$ ($n = 1854$, $r^2 = 0.917$)

The early growth phase from hatching to 60 days of age or about 4.0 cm mantle length was exponential

$W = 0.196 e^{0.061T}$ ($n = 1203$, $r^2 = 0.795$)

The adult growth phase was from 50 to 260 days of age and fitted by the model

$W = 6.433 \times 10^{-2} T + 5.224 \times 10^{-3} T^2 - 16.583$ ($n = 936$, $r^2 = 0.763$)

Table 2. Growth of the pharaoh cuttlefish, *Sepia pharaonis*, in terms of wet body weight (g).

Age	Body weight	Weight increment				Daily growth
(days)	(g)	(g)	(g / day)	(%)	(% / day)	(%)
0	0.18	-	-	-	-	-
10	0.42	0.24	0.02	133.33	13.33	8.00
20	0.89	0.47	0.05	111.91	11.19	7.18
30	1.87	0.98	0.10	110.11	11.01	7.10
40	3.94	2.07	0.21	110.70	11.07	7.13
50	4.77	0.83	0.08	21.07	2.11	1.91
60	8.18	3.41	0.34	71.49	7.15	5.27
70	14.62	6.44	0.64	78.83	7.87	5.65
80	19.94	5.32	0.53	36.39	3.64	3.08
90	32.20	12.26	1.23	61.48	6.15	4.70
100	36.68	4.48	0.45	13.91	1.39	1.30
110	53.25	16.57	1.66	45.17	4.52	3.68
120	64.47	11.22	1.12	21.07	2.11	1.91
130	86.30	21.83	2.18	33.86	3.39	2.90
140	92.30	6.00	0.60	6.95	0.70	0.67
150	118.88	26.58	2.66	28.80	2.88	2.52
160	139.96	21.08	2.11	17.73	1.77	1.63
170	191.03	51.07	5.11	36.49	3.65	3.09
180	221.67	30.64	3.06	16.04	1.60	1.48
190	236.67	15.00	1.50	6.77	0.68	0.65
200	265.00	28.33	2.83	11.97	1.20	1.13
210	275.00	10.00	1.00	3.77	0.38	0.37
Mean ±se	-	13.09±2.84	1.31±0.28	46.56±8.84	4.66±0.88	3.40±0.53

Mating and spawning

The pharaoh cuttlefish began to form mating pairs after 90 days and the first mating was observed. The mature male selected his mate and displayed tiger colour pattern. He approached her with his first-arm pair raised up. If the female accepted, she allowed him to touch her with his arms, and form a swimming pair. The process of copulation began with the male hovering above the female, caressing her dorsum with his arms in a parallel position. Their heads were in the same direction. The male grasped her arms by his arms and twisted to a head-to-head position for copulation (Fig. 5). The spermatophores were transferred by the fourth arm of the male and fixed to the seminal receptacle in the buccal region of the female. Copulation might last from less than 1 minute to more than 30 minutes. The male released the female after that and continued escorting her.

The mated male defended his mate from other males. The defence behaviour constituted spreading of the arms, displaying the dark tiger colour pattern and turning his head to the opponent. The mated male attacked by approaching the opponent with rapid fin movements. The ink might be ejected to the opponent. If this activity failed, the mated male darted to the offender, seized and bit him at the side of mantle. Biting was a rare case against a strong offender. The mated male mostly succeeded except when the opponent was much larger in size.

Spawning was observed after 110 days of age or about 1-3 weeks after mating. The spawning behaviour began when the female swam around touching the substrata with the tip of her arms in order to investigate the surface for attachment of the egg capsules. The site was selected carefully at sites, which only could be reached by her arms. The female swam towards the substratum and attached one egg capsule using her arms (Fig. 6). Then she swam backwards, hovered for a while, probably for coating another egg in her arm pouch and then swam forward again to attach the egg capsule. The process of spawning of one egg capsule took about one minute. The wild females were able to spawn 500-3000 egg capsules. The females from cultured batches were comparatively smaller in size and spawned about 50-200 comparatively smaller egg capsules. The eggs were laid in one cluster or more every day or every other day if they were interrupted. Mating was observed between spawning of each cluster. After spawning of each cluster, the female was lying on the bottom, protected by her mate. However, she was ready to eat and would grab passing prey or dead feed. The spawning period ranged from 1 to 24 days

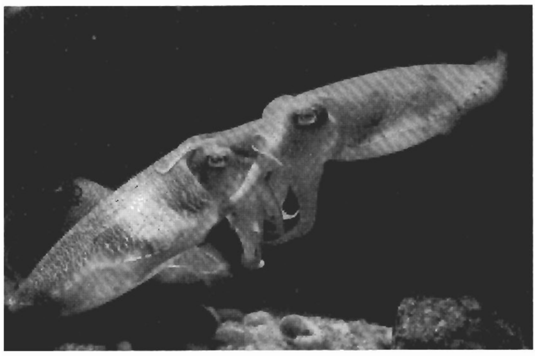

Figure 5. Mating behaviour of the pharaoh cuttlefish in the culture tank.

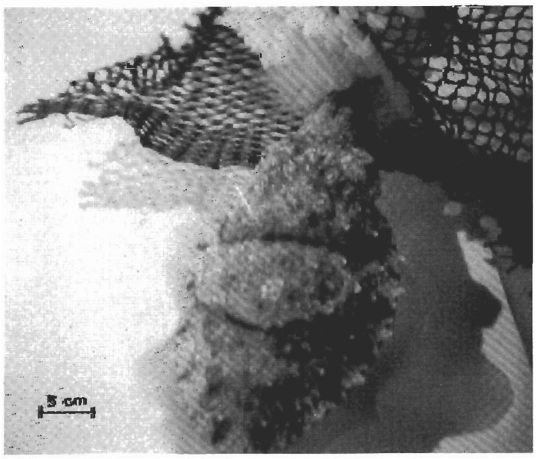

Figure 6. Spawning behaviour. The female pharaoh cuttlefish attached her egg capsules to an artificial substratum.

depending on her own size, hence number of egg production and her own health. The male escorted and protected her during spawning. The other females were allowed to approach and spawn at the same site and time. The healthy male turned to form pair with another selected female after the last spawning of his mate. The mating and spawning were observed in the early morning and late afternoon.

Mortality

The life span of the pharaoh cuttlefish was tied to reproduction due to the death of both sexes 1-3 weeks after spawning. The life span ranged from 112-271 days with an average 149.4 ± 34.8 days for both sexes. The average life span of cultured males and females was 158.9 ± 50.2 and 147.3 ± 35.1 days respectively. The reproductive period was estimated at 29.53 % of the life span with 16.11 % for the spawning period. The juvenile to adult phase was 60.40 % of the total life span; to the time of first spawning it was 73.83 %.

Infection with unknown bacteria in the mantle caused high mortality in 24-48 hrs (Fig. 7). The first symptom appeared as a black streak on the anterior dorsum of the mantle. The skin was wrinkled towards the streak. The normal colour pattern turned paler and later yellowish. The mantle rot began and spread sideways from the streak, continuing to both fins. The colour of the fins disappeared. This disease was called "white collar disease" according to the look of the infection. The mantle rot continued enlarging and caused the cuttlebone to be exposed. At that stage the cuttlefish was unable to swim, the tentacles fell out from their pockets, and it soon died. Immersion of the cuttlefish in 5 mg terramycin L^{-1} and transfer to new tanks stopped the disease from spreading. The treatment did not work on cuttlefish at the stage of exposed cuttlebone.

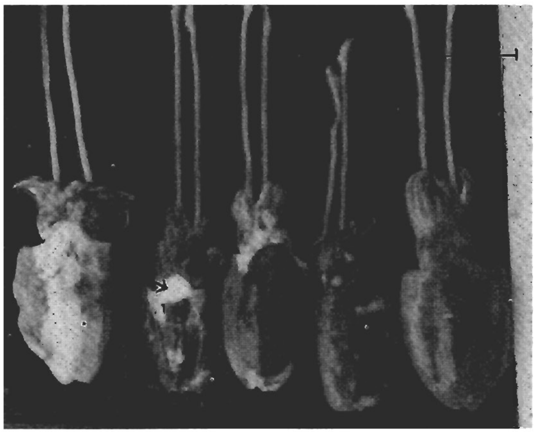

Figure 7. Bacterial "white collar disease" infection at various stages. Arrow indicates exposed cuttlebone.

Ecology

The eggs of the pharaoh cuttlefish did not hatch in salinities below 20 and above 40 ‰. The hatching was more than 80 % in 24-36 ‰ and the optimum range for 50 % hatching was 22.5-37.5 ‰. Salinity lower than 30 ‰ tended to cause abnormal development. The hatchlings could survive for more than 24 hrs in 21.4-39.4 ‰. They all died in 16 and 44 ‰. About 50 % of the hatchlings survived at pH 5.94-6.37 but died at pH 4.0 and 9.0.

The optimum density for culture was 500 ind. $m.^{-2}$ during the first 10 days. During the next 10-days periods the density was reduced to 250 and 125 ind. m^{-2} after size grading. These densities promoted growth and survival in culture tanks.

DISCUSSION

The size and the shape of the egg capsule was comparable to other sepiid cuttlefish (Table 3). The external characters of the coating and colour were different and useful for field recognition. The incubation period of the pharaoh cuttlefish was relatively shorter even though the temperature was not much different, about 5 °C in *S. subaculeata*. The hatching period of the eggs of *S. pharaonis* in this study was about 3-10 days which was much shorter than 2-3 months (60-90 days) in *S. officinalis* (Forsythe *et al.* 1994) probably due to the

Table 3. Comparison on some biohistoric aspects of *Sepia* spp. Reference: a -Choe (1966), Choe & Ohshima (1963), Ohshima & Choe (1961); b -Roper *et al.* (1984); c -Forsythe *et al.* (1994); d -present study; e - Chotiyaputta (1982). (*S. subaculeata* = *S. lycidas*).

aspect	*S. esculenta*[a]	*S. subaculeata*[a]	*S. officinalis*[c]	*S. pharaonis*[d]
egg - colour	white particulated	white particulated	black	white
- number	-	-	3082	1500
- incubation (d)	29-42	29-31	42	14
- temperature (°C)	15.5-23.6	23.5-24.0	16-18	28
hatchling size (cm; g)	0.87; 0.15	0.57; 0.06	0.50; 0.15	0.77; 0.18
shoaling behaviour	occasional	no	occasional	occasional
initial density (ind/m2)	-	600	250-300	500
age of maturity (d)	-	-	105-180	90
size of maturity (g)	-	-	600-1600	30
age of 100 g weight (d)	110	65	160	140
feed efficiency (%)	17-43	25-31	40-50	19-66
length weight relationship (slope)	-	-	2.6 - 2.9	2.2 - 2.6
comparative size (M:F)	-	-	M<F	M>F
sex ratio (M:F) cultured	-	-	-	M>F
max wild size (cm, g)	18; 1600	23; 1300	45; 4000	36; 4200 26; 1400[c]
max cultered size (cm; g)	9; 130	17; 350	27; 2900	16; 370

difference in temperature and species. The male cuttlefish in this study was larger than the females whereas the opposite was observed in *S. officinalis*. The benthic form of young pharaoh cuttlefish corresponded to that of the adult. The same mode of life indicated absence of true larval stage as found in *S. officinalis* (Boucad-Camou *et al.* 1985). The morphological change during growth was in less pronounced compared with the pelagic squids e.g. *Sepioteuthis lessoniana* (Nabhitabhata 1996). The adhering behaviour to the substratum of the hatchlings with the ventral surface of the mantle resembled adhering with the dorsum in idiosepiid squid, *Idiosepius thailandicus* (Nabhitabhata 1998).

The young sepiid cuttlefish innately recognized and fed on mysid shrimps (Messenger 1977). It was also true in pharaoh cuttlefish (Nabhitabhta 1978). The attempt to feed young *S. pharaonis* and *S. officinalis* with live feeds other than crustaceans and fishes did not succeed (Nabhitabhata 1978; Toll & Strain 1988). The hatchlings were able to survive without feed for 3-7 days. The reason could be that they still had yolk reserves and the digestive activities would begin after 3 days as in *S. officinalis* (Boucaud-Camou & Roper 1995). After 30 days, they were able to take dead feed. When they grew older it was easier to train them to accept the dead feed. Nixon (1985) claimed that the ability to become trained indicated adulthood (after 5-6 weeks in *S. officinalis*). At that age they were able to take a wider spectrum of prey. Wells (1962) stated that the ability to learn was correlated with the development of the vertical lobe of central nervous system. This lobe was the important part of the learning system and memory retention in the adult. Training the pharaoh cuttlefish to fed on dead feed after 30 days (2-3 cm mantle length) is the critical stage for aquaculture. The cuttlefish starved to death if they did not accept dead feed. The survival, hence production, highly decreased during this period (Nabhitabhata 1978). Boucad-Camou *et al.* (1985) found that the post-embryonic life ended in *S. officinalis* and the juvenile-adult phase began when the digestive glands matured. This enabled the cuttlefish to feed on a more varied diet. Other metabolic and physiological changes occurred in blood composition at the same time. In overall view, the success of the weaning period to dead prey depended on the timing and good skills of the farmer.

The pharaoh cuttlefish used the arms when feeding on dead feed and the tentacles when live prey was seized. Such change of feeding behaviour has also been observed in other sepiid cuttlefish. *S. officinalis* (DeRusha *et al.* 1989), *Sepiella inermis* (Nabhitabhata 1997). The feeding of one *S. pharaonis* stimulated other cuttlefish in the same tank to feed. DeRusha *et al.* (1989) noted similar stimulation in *S. officinalis.* Such stimulation accelerated the acceptance of dead feed in training of cultured batches.

The feeding rate of *S. esculenta* was 17-43 % and of *S. subaculeata* it was 25-31 % (Choe 1966), which is similar to *S. pharaonis*' rate of 18-63 % (Nabhitabhata *et al.* 1996). The feed conversion efficiency was 40-50 % in *S. officinalis* (Clarke *et al.* 1989; Nixon 1985), which agreed to 48.22 % in this study but was higher than the 35.97 % found in *S. lycidas* (Natsukari 1991). However, the difference was probably related to the temperature which was not mentioned in the latter study.

Habitually *S. subaculeata* would swim in pairs but not in groups (Choe 1966). This behaviour seems to be common among sepiid cuttlefish. Normally, the present pharaoh cuttlefish was not gregarious but occasionally they hunted in a group moving in the same direction. Chikuni (1983) also referred to *S. pharaonis* as being moderately aggregative.

We found that *S. pharaonis* was moderately attracted to light (50 % response in short periods). This agrees with fishermen's observations. This species is not a major catch during light luring fisheries in Thailand. In contrast Prabhakaran Nair *et al.* (1985) reported that *S. pharaonis* was strongly phototactic. Interspecific differences are also known. Choe (1966) reported that *S. esculenta* was remarkable phototactic while *S. aculeata* was not.

Cannibalism was extremely rare in pharaoh cuttlefish but it was a major cause of mortality in *S. officinalis* (Forsythe *et al.* 1991) Cannibalism accounted for up to 44 % of the deaths in one reared batch (Henry & Boucaud-Camou 1991).

Choe (1966) reared *S. esculenta* and *S. subaculeata* from an initial density of 600 ind. m^{-2} to about 2 cm mantle length. Forsythe *et al.* (1994) reared *S. officinalis* at 250-300 ind. m^{-2} for 4-6 weeks. The initial density in this study was 500 ind. m^{-2}, which was decreased to about 200 after 4 weeks (about 2 cm mantle length). At 50 days of age (about 5 cm mantle length), Natsukari (1991) reared *S. lycidas* at a density of 37.5 ind. m^{-2}, which was much lower than the 110-150 ind. m^{-2} used in this study for the same size. No matter how different the rearing density was, all general agreement exists that the horizontal space is the more

Table 4. Growth in terms of mantle length (cm) and weight (g) of various species of *Sepia*. Reference. : a -Choe (1966), Choe & Ohshima (1963), Ohshima & Choe (1961); b - Pascual (1978 : Forsythe & Van Heukelem 1987); c - Henry & Boucaud-Camou (1991); d - Coelho et al. (1991); e -present study. Numbers in parenthesis indicate precise numbers of days.

Age	*S. esculenta*[a]		*S. subaculeata*[a]		*S. officianalis*[b]		*S. pharaonis*[e]	
(days)	(cm)	(g)	(cm)	(g)	(cm)	(g)	(cm)	(g)
	ML	W	ML	W	ML	W	ML	W
0	0.57	0.06	0.87	0.15	0.5	0.15	0.77	0.18
10	0.8	0.2	-	-	-	0.35 (15)	1.09	0.42
20	1.2 (19)	0.4	1.7 (21)	0.8	-	-	1.50	0.89
30	2.2 (29)	1.9	2.3 (26)	2.0	-	0.8	1.95	1.87
40	2.4 (39)	2.3	4.7	18.0	-	1.8 (45)	2.56	3.94
50	2.5 (45)	2.4	5.8 (47)	27.0	-	-	2.90	4.77
60	4.0	16.0	8.5 (58)	65.0	2.4 (56)[c]	4.2	3.53	8.18
70	4.8 (65)	18.0	11.0	150.0	-	9.5	4.42	14.62
80	6.1 (78)	35.0	13.0 (85)	190.0	4.3 (81)	12.0[d]	5.13	19.94
90	7.2 (88)	52.0	-	-	-	17.0	5.88	32.20
100	-	-	-	-	-	26.0 (105)	6.21	36.68
110	-	-	17.0	350.0	-	-	7.16	53.25
120	-	-	-	-	-	38.0	7.85	64.47
130	9.0	130.0	-	-	-	54.0 (135)	8.41	86.30
140	-	-	-	-	-	-	8.78	92.30
150	-	-	-	-	-	80.0	9.31	118.88
160	-	-	-	-	-	100 (165)	9.62	139.96
170	-	-	-	-	-	-	10.51	191.03
180	-	-	-	-	-	140.0	12.04	221.67
190	-	-	-	-	-	190.0 (195)	12.50	236.67
200	-	-	-	-	-	-	13.01	265.00
210	-	-	-	-	-	210.0	13.94	275.00

important than the volume, since the cuttlefish were bottom oriented. High density culture might generate bacterial infection as observed in *S. officinalis* (Forsythe *et al.* 1991) and *S. pharaonis* in this study. Overcrowding, overfeeding and careless management might be responsible for an increase of bacteria. Oral or immersion treatment with antibiotics seemed to be effective for both species of cuttlefish, but the dose should be different for different species and stages of growth.

Growth in aquaculture of pharaoh cuttlefish was not much different compared to other species (Table 4) except the *S. subaculeata* had a higher growth rate. However fast they grew, the cultured cuttlefish of every species died after spawning. The pharaoh cuttlefish grew differently when raised from spawners of different populations (Table 5). The Andaman type tended to grow much faster than the Gulf of Thailand type, about 2 folds in length and 4-5 folds in weight. Growth variation was also observed in cultured batches of the same population. The difference was about 4 folds between the maximum and the minimum growth rate.

Table 5. Comparison of growth of two types of *Sepia pharaonis* from different waters. (Gulf type -Gulf of Thailand, Pacific Ocean ; Andaman type -Andaman Sea, Indian Ocean).

	Gulf type		Andaman type	
Age (days)	Length(cm)	Weight (g)	Length(cm)	Weight (g)
0	0.77	0.18	0.75	0.09
10	1.09	0.42	1.78	1.06
20	1.50	0.89	2.90	3.90

Sexual maturity occurred after 3.5-6 months in *S. officinalis* (Forsythe *et al.* 1994), which was nearly the same as in *S. pharaonis*. However, the age at first spawning of *S. officinalis* was 6.6-12.6 months (average 9.6 months), which was 4 months later than in *S. pharaonis*. The average life span was about 330 days in *S. officinalis* and 140 days in *S. pharaonis*. Forsythe *et al.* (1994) suggested that there should be a general trend of shorter life span with increasing temperature although there was no statistically significant relationship.

Roper *et al.* (1984) quoted the maximum size of *S. pharaonis* to be 35 cm length and 4200 g total weight. Chotiyaputta (1982) found the maximum size of this species to be 26 cm and 1400 g in the Gulf of Thailand. However, the size of the cuttlefish from the nature was much higher than from culture where the maximum size was only about 16 cm and 370 g. The same kind of difference has also been shown in other species (Table 4). The least difference was reported in *S. officinalis* (Forsythe *et al.* 1994) even though small cultured females of 11-25 cm also occurred in this specie (Nixon 1987).

Chikuni (1983) reported one spawning season of the pharaoh cuttlefish in Japan. Chotiyaputta (1981, 1982) stated two peaks of spawning in the Gulf of Thailand. Nabhitabhata *et al.* (1993c) also found that spawning peaked two times in nature. Observations on relative large (1500 g) and small (400 g) spawners and two annual spawnings of pharaoh cuttlefish raised the question if there were two different life strategies on the basis of semelparity, viz. a short generation strategy and a long generation strategy where two groups of the same batch use different strategies (Fig. 8). One group of the pharaoh cuttlefish grew for about 6 months in the short generation mode, spawned in August and died soon after. In the meantime, the other group (following the long generation strategy), probably migrated further offshore where it grew to a larger size without reproducing. At an age of one year they then migrated inshore, spawned in the next February, and died. The proposed hypothesis is based on semelparity. However, further studies on age and growth, including comparisons of wild and cultured stocks are necessary to gain more evidence for the hypothesis. The hypothesis might suite other sepiid cuttlefish as well. Boletzky (1983), Bachayokho (1983), and Le Goff & Daguzan

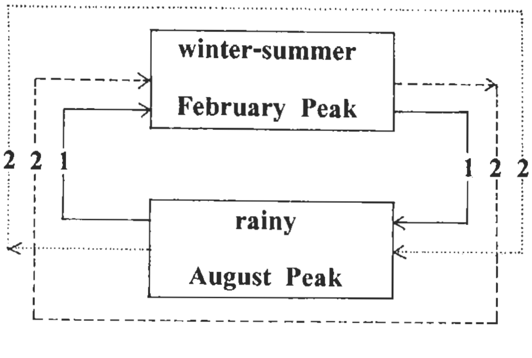

Figure 8. Possible life history of *Sepia pharaonis* corresponds to spawning season in the eastern coast of the Gulf of Thailand; 1- short generation strategy, 2- long generation strategy.

Table 6. Combination of factors effect on the age at spawning and final size. (Tagged numbers indicate proposed factor). Reference: 1 -modified after Mangold (1987), Mangold and Froesch (1977); 2 -aquaculture condition in present study ; 3 -Nabhitabhata (1997).

Factor	Early spawning small size	Late spawning large size
feeding		
- availability[1]	restricted	*ad libitum*
- nutritive value[2]	low	high
day length[1]	short	long
light intensity[1]	low	high
temperature[1]	high	low
salinity[3]	low	high
density[2]	high	low
sex competition[2] (visual, chemical stimuli etc.).	high	low
burrowing in the substratum[2]	absent	present

(1991) have proposed a comparable hypothesis for East Atlantic *S. officinalis* based on distribution, reproduction and growth estimates.. The life span of this species should be about one year in the short generation mode and about two years in the long generation mode. Bachayokho (1983) seemed to assume that the cuttlefish spawned two times annually with two spawning peaks, hence they were iteroparous. Boletzky (1983) stated that maturation was attained earlier in male than in female, whereas reproductive activity apparently covered a much longer time. Boucaud-Camou & Boismery (1991) proposed only long generation mode of semelparous 2 years life span for both males and females. Males reached maturity earlier than females; the cuttlefish of 0 and 1 year class were juveniles. The two life strategies enabled the cuttlefish to earn the alternation or flexibility to deal with different life conditions and habitat as well as the enhancement of the opportunity of genetic exchange among populations. Probably more than one factor trigged the choice between the two strategies. Calow (1983) stated that the shift from somatic to reproductive production of molluscs depended upon the relationship between resource availability for production, size, and the relative survivorship of the small offspring and large adults. Many abiotic and biotic factors had been reported to effect the age of spawning and final size (Table 6) in the wild and under culture conditions.

Availability of feed, which might be restricted in nature, could cause a shift to the short generation strategy. In our culture, the pharaoh cuttlefish were fed twice daily with fish meat until saturation to reduce the cost for large scale production. Crustaceans might have been better. Stomach content of captured cuttlefish was composed of 72.55 % crustaceans and 11.76% fishes (Chotiyaputta 1980). DeRusha *et al.* (1989), noted that *S. officinalis* had reduced growth rate when they were reared on non-living feed.

Environmental factors (day length, light, temperature, and salinity) were not considered to have obvious effects in this study since they were partially controlled or managed in the culture tanks. Boletzky (1975) suggested that the spawning behaviour of *S. officinalis* might have been induced by the unnatural light conditions in the laboratory. We did not observe any change in captured *S. pharaonis* from the time they were brought in until they died after the last spawning. We also avoided unnatural and artificial light.

This study agrees with Forsythe *et al.* (1994) that no substratum was necessary for normal growth and survival of *S. pharaonis* and *S. officinalis*, even under high density conditions. Without a substratum, the tank cleaning was greatly facilitated. A disadvantage of the open tank environment was that sudden human appearance might cause stress.

From an aquacultural point of view, long generation, larger size and late maturity would yield higher production (of course short generation with large size would be the best if possible). Undesirable factors should be eliminated. Two of these factors might be managed. First, the nutritive value of the feed could to be enhanced by adding crustaceans or direct enrichment to the routine fish meat. Second, sexual confrontation or encounter should be avoided by monosex culture.

REFERENCES

Bachayokho, M. 1983. Biology of the cuttlefish *Sepia officinalis hierredda* off the Senegalese coast. Pages 204-263 *in* : Caddy, J.F. (ed.). Advances in Assessment of World Cephalopod Resources. FAO Fisheries Technical Paper 231, 457 pp.

Boletzky, S.v. 1975. Spawning behaviour independent of egg maturity in a cuttlefish (*Sepia officinalis* Linnaeus). - The Veliger **17**(3) : 247-248.

Boletzky, S.v. 1983. *Sepia officinalis.* Pages 31-52 *in* Boyle, P.R. (ed.) Cephalopod Life Cycles vol. I Species Accounts. Academic Press, London, 475 pp.

Boletzky, S.v. 1987. Fecundity variation in relation to intermittent or chronic spawning in the cuttlefish, *Sepia officinalis* L. (Mollusca, Cephalopoda). - Bulletin of Marine Science **40**(2) : 382-387.

Boucaud-Camou, E. & C.F.E. Roper. 1995. Digestive enzymes in paralarval cephalopods. - Bulletin of Marine Science **57**(2) : 313-327.

Boucaud-Camou, E. & J. Boismery. 1991. The migrations of the cuttlefish (*Sepia officinalis* L) in the English Channel. Pages 179-189 *in* : Boucad-Camou, E. (ed.). The Cuttlefish, First International Symposium on the Cuttlefish *Sepia*. Centre de Publications de l'Université de Caen, Caen, 358 pp.

Boucaud-Camou, E., M. Yim & A. Tresgot. 1985. Feeding and digestion of young *Sepia officinalis* L. (Mollusca : Cephalopoda) during post-hatching development. - Vie Milieu 35(3/4) : 263-266.

Calow, P. 1983. Life-cycle patterns and evolution. Pages 649-678 *in* : Russell-Hunter, W.D. (ed.). The Mollusca vol. 6 Ecology. Academic Press, Orlando, 690 pp.

Chikuni, S. 1983. Cephalopod resources in the Indo-Pacific region. Pages 264-305 *in* : Caddy, J.F. (ed.). Advances in Assessment of World Cephalopod Resources. FAO Fisheries Technical Paper 231, 457 pp.

Choe, S. 1966. On the eggs, rearing, habits of the fry, and growth of some Cephalopoda. - Bulletin of Marine Science **16**(2): 330-348.

Choe, S. & Y. Ohshima. 1963. Rearing of cuttlefishes and squids. - Nature 197(4364) : 307.

Chotiyaputta, C. 1980. Biological study on cuttlefish, *Sepia pharaonis* Ehrenberg in the Gulf of Thailand. - Technical Paper 16/1980, Invertebrates Section, Marine Fisheries Division, Department of Fisheries, 11 pp. (In Thai).

Chotiyaputta, C. 1981. Biology of the cuttlefish, *Sepia pharaonis* Ehrenberg. - Annual Report 1981, Invertebrates Section, Marine Fisheries Division, Department of Fisheries, 7 pp. (In Thai with English Abstract).

Chotiyaputta, C. 1982. Biological study on cuttlefish, *Sepia pharaonis* Ehrenberg. - Technical Paper No. 4/1982, Invertebrates Section, Marine Fisheries Division, Department of Fisheries, 6 pp. (In Thai).

Clarke, A., P.G. Rodhouse, L.J. Holmes & P.L. Pascoe. 1989. Growth rate and nucleic acid ratio in cultured cuttlefish *Sepia officinalis* (Mollusca:Cephalopoda). - Journal of Experimental Marine Biology and Ecology **133** : 229-240.

Coelho, N.M.L., T. Modesto & F. Soares. 1991. *Sepia officinalis* : potential for aquacultura and restocking? Pages 348-349 *in* : Boucad-Camou, E. (ed.). The Cuttlefish, First International Symposium on the Cuttlefish *Sepia*. Centre de Publications de l'Université de Caen, Caen, 358 pp.

DeRusha, R.H., J.W. Forsythe, F.P. DiMarco & R.T. Hanlon. 1989. Alternative diets for maintaining and rearing cephalopods in captivity. - Laboratory Animal Science **39**(4) : 306-312.

Forsythe, J.W. & W.F. Van Heukelem. 1987. Growth. Pages 135-156 *in* : Boyle, P.R. (ed.). Cephalopod Life Cycles vol. II Comparative Reviews. Academic Press, London, 441 pp.

Forsythe, J.W., R.H. DeRusha & R.T. Hanlon. 1994. Growth reproduction and life span of *Sepia officinalis* (Cephalopoda : Mollusca) cultured through seven consecutive generations. - Journal of the Zoological Society of London **233** : 175-192.

Forsythe, J.W., R.T. Hanlon & R.H. DeRusha. 1991. Pilot large-scale culture of *Sepia* in biomedical research. Pages 313-323 *in* : Boucad-Camou, E. (ed.). The Cuttlefish, First International Symposium on the Cuttlefish *Sepia*. Centre de Publications de l'Université de Caen, Caen, 358 pp.

Henry, J. & E. Boucaud-Camou. 1991. Rearing *Sepia officinalis* L. outdoors realisation of a low-cost dismantable installation. Page 349 *in* : Boucad-Camou, E. (ed.). The Cuttlefish, First International Symposium on the Cuttlefish *Sepia*. - Centre de Publications de l'Université de Caen, Caen, 358 pp.

Le Goff, R. & J. Daguzan. 1991. Growth and life cycles of the cuttlefish *Sepia officinalis* L. (Mollusca : Cephalopoda) in South Brittany (France). - Bulletin of Marine Science **49**(1-2) : 341-348.

Mangold, K. 1983. Food, feeding and growth in cephalopods. Pages 81-93 *in* Stone, D.M. (ed.). Proceedings of the Workshop on the Biology and Resource Potential of Cephalopods. - Memoirs of the National Museum of Victoria No. 44, 311 pp.

Mangold, K. 1987. Reproduction. Pages 157-200 *in* : Boyle, P.R. (ed.). Cephalopod Life Cycles vol. II Comparative Reviews. Academic Press, London, 441 pp.

Mangold, K. & D. Froesch. 1977. A reconsideration of factors associated with sexual maturation. Pages 541-555 *in* : Nixon, M. & J.B. Messenger (eds.).The Biology of Cephalopods. Academic Press, London, 615 pp.

Messenger, J.B. 1977. Prey-capture and learning in the cuttlefish, *Sepia*. Pages 347-376 *in* : Nixon, M. & J.B. Messenger (eds.). The Biology of Cephalopods. Academic Press, London, 615 pp.

Nabhitabhata, J. 1978. Rearing experiment on economic cephalopod-II : cuttlefish *Sepia pharaonis* Ehrenberg. - Technical Paper 1978, Brackishwater Fisheries Section, Rayong Brackishwater Fisheries Station, Brackishwater Fisheries Division, Department of Fisheries, 62 pp. (In Thai with English Abstract).

Nabhitabhata, J. 1996. Life cycle of cultured big fin squid, *Sepioteuthis lessoniana* Lesson. - Phuket Marine Biological Center Special Publication **16**: 83-95.

Nabhitabhata, J. 1997. Life cycle of three cultured generations of spineless cuttlefish, *Sepialla inermis* (Ferussac & díOrbigny, 1848). - Phuket Marine Biological Center Special Publication **17**(1): 289-298.

Nabhitabhata, J. 1998. Distinctive behaviour of Thai pygmy squid, *Idiosepius thailandicus* Chotiyaputta, Okutani & Chaitiamvong, 1991. - Phuket Marine Biological Center Special Publication **18** (1): 25-40.

Nabhitabhata, J., S. Kbinrum & Y. Soodmee. 1991. Effect of pH on survival rate of cephalopods hatchlings. - Technical Paper No. 17/1991, Rayong Coastal Aquaculture Station, Coastal Aquaculture Division, Department of Fisheries, 13 pp. (In Thai with English Abstract).

Nabhitabhata, J., N. Kakhai., J. Suriyawarakul & P. Nilaphat. 1996. Feeding and cost of seed production of cephalopods, *Sepioteuthis lessoniana* Lesson; *Sepia pharaonis* Ehrenberg; *Sepiella inermis* Fer. & díOrb. - Technical Paper No. 1/1996, Rayong Coastal Aquaculture Station, Coastal Aquaculture Division, Department of Fisheries, 25 pp.

Nabhitabhata, J., P. Nilaphat, J. Kongrot & S. Ratanasoot. 1993a. Effect of salinity on survival rate of pharaoh cuttlefish hatchlings, *Sepia pharaonis* Ehrenberg. - Technical Paper No. 11/1993, Rayong Coastal Aquaculture Station, Coastal Aquaculture Division, Department of Fisheries, 18 pp. (In Thai with English Abstract).

Nabhitabhata, J., W. Phudtaraksa, P. Nilaphat, & G. Phetrasatian. 1993b. Effect of salinity on hatchling rate of pharaoh cuttlefish , *Sepia pharaonis* Ehrenberg. - Technical Paper No. 10/1993, Rayong Coastal Aquaculture Station, Coastal Aquaculture Division, Department of Fisheries, 13 pp. (In Thai with English Abstract).

Nabhitabhata, J., P. Sangkasem, W. Phudtaraksa, V. Sriakaphrom, S. Chenkitkarn, Y. Soodmee, P. Nilaphat, G. Phetrasatian, J. Kongrot & S. Ratanasoot. 1993c. On mass production of cephalopods seeds for releasing as stock enhancement, 1990-1992. - Technical Paper No. 9/1993, Rayong Coastal Aquaculture Station, Coastal Aquaculture Division, Department of Fisheries, 27 pp. (In Thai with English Abstract).

Natsukari, Y. 1991. Cuttlefish fisheries in Japan. Pages 345-348 *in* : Boucaud-Camou, E. (ed.). The Cuttlefish, First International Symposium on the Cuttlefish *Sepia*. - Centre de Publications de l'Université de Caen, Caen, 358 pp.

Nixon, M. 1985. Capture of prey, diet and feeding of *Sepia officinalis* and *Octopus vulgaris* (Mollusca : Cephalopoda) from hatchling to adult. - Vie Milieu **35** (3/4) : 255-261.

Ohshima, Y. & S. Choe. 1961. On the rearing of young cuttlefish and squid. - Bulletin of the Japanese Society of Scientific Fisheries **27** (11) : 978-986.

Prabhakaran Nair, K., P. A. Thomas, G. Gopakumar, S. G. Vincent & T. A. Omana. 1985. Some observations on the hatching and post-hatching behaviour of the cuttlefish *Sepia pharaonis* Ehrenberg. Pages 157-159 *in* : Silas, E.G. (ed.). Cephalopod Bionomics, Fisheries and Resources of the Exclusive Economic Zone of India. - Central Marine Fisheries Research Institute Bulletin 37, 195 pp.

Roper, C.F.E., M.J. Sweeney & C.E. Nauen. 1984. FAO Species Catalogue Vol. 3 Cephalopods of the World An Annotated and Illustrated Catalogue of Species of Interest to Fisheries. Synopsis No. 125, Vol. 3, 277 pp.

Silas, E.G., R. Sarvesan, K. Prabhakaran Nair, Y. Appanna Sastri, P.V. Sreenivasan, M.M. Meiyappan, Kuber Vidyasagar, K. Satyanarayana Rao & B. Narayana Rao. 1985. Some aspects of the biology of cuttlefishes. Pages 49-70 *in* Silas, E.G.(ed.). Cephalopod Bionomics, Fisheries and Resources of the Exclusive Economic Zone of India. - Central Marine Fisheries Research Institute Bulletin 37, 195 pp.

Supongpan, M. 1995. Cephalopod resources in the gulf of Thailand. Pages 190-220 *in* : Nabhitabhata, J. (ed.). Biology and Culture of Cephalopods. Contribution No. 18, Rayong Coastal Aquaculture Station, Coastal Aquaculture Division, Department of Fisheries, 231 pp. (In Thai).

Toll, R.B. & C.H. Strain. 1988. Freshwater and terrestrial food organisms as an alternative diet for laboratory culture of cephalopods. - Malacologia 29(1): 195-200.

Wells, M.J. 1962. Early learning in *Sepia*. Symposia of the Zoological Society of London No. 8: 149-169.