NUTRITIONAL ECOLOGY OF AGALMA OKENI (SIPHONOPHORA: PHYSONECTAE)

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Siphonophores are among the 10 major groups of zooplankton collected by plankton tows in the upper 200 m of the Sargasso Sea (Grice and Hart, 1962; Deevey and Brooks, 1971) and they comprise 45 - 67% of the macroplankton (i.e., siphonophores, medusae, molluscs, chaetognaths, and thaliaceans) in areas of the Mediterranean (Boucher and Thiriot, 1972). Their widespread occurrence in the open ocean suggests that siphonophores are important components of oceanic ecosystems. However, most are extremely delicate and are rarely seen alive. None have been studied in their natural environment, and because of their fragility little information has been available on their metabolism and production.

METHODS

During 1973-1975, I participated in a program of 171 SCUBA dives in subtropical oceanic regions of the western North Atlantic Ocean. Most dives were made during the day in the upper 30 meters, where temperatures ranged from 23 - 29°C. Agalma okeni (Figure 1) was the most common physonect siphonophore encountered by divers, and its behavior and physiological ecology were studied in the laboratory aboard ship and in the field.

Colonies of A. okeni were individually collected in 130-980 ml glass jars and incubated at surface temperature in the laboratory aboard ship for 1 - 6 hours after enclosure. Oxygen consumption and ammonia excretion were estimated by difference from control jars of sea water which were collected at the same time as the siphonophores. The tension of dissolved oxygen was measured

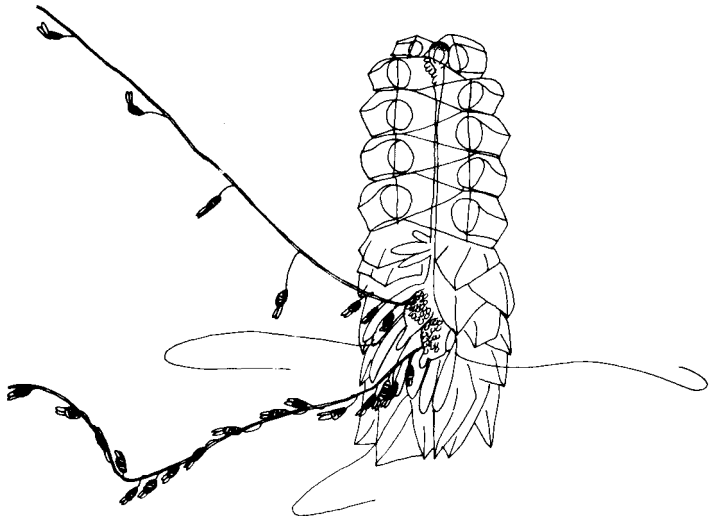

Figure 1. Colony of Agalma okeni with ten nectophores and two gastrozooids, drawn from in situ photograph. Tentacles are partially extended in fishing posture.

with a polarographic oxygen electrode (Kanwisher, 1959), and ammonia was measured by the phenol-hypochlorite method (Solorzano, 1969). Methodology has been detailed in a previous report (Biggs, in prep). Total dissolved nitrogenous excretion was determined by Kjeldahl digestion ashore. All metabolic measurements were standardized to body protein, as determined by the Lowry method (Lowry, et al., 1951), using bovine serum albumin as a reference standard.

Several colonies of A. okeni were maintained in 3.8-liter and 20-liter cylindrical aquaria for determination of short-term growth. I estimated growth rates of A. okeni by counting the increase in number of nectophores and gastrozooids in 12 colonies in captivity for 1 - 4 days. Aquaria were kept in the dark; laboratory temperatures ranged from 24 - 26°C. Water was changed every second day. Most colonies were allowed to feed on stage-2 Artemia nauplii or on Acartia and Pleuromamma spp. copepods, though three captured and ingested shrimp (Leander tenuicornis) 15 - 20 mm long. Artemia nauplii were provided at densities greater than 100/liter and copepods at greater than 20/liter.

RESULTS

Feeding and Digestion

A small colony of A. okeni which had been fed carmine-dyed Artemia nauplii egested the carmine and other undigested material within 2 - 3 hours after capture. Larger prey required longer times for digestion. For example, three colonies which had captured Leander tenuicornis and another which had captured a crab megalops in situ required 7 - 18 hours before egestion. Palpons and gastrozooids remained swollen for 18 - 48 hours.

Agalma okeni is primarily a nocturnal feeder. Tentacles were contracted in over 90 of 114 colonies observed in situ during daylight hours, while 7 colonies observed at night each had tentacles extended in fishing posture. In the laboratory, colonies would extend their tentacles only in darkness or reduced light. Since A. okeni captured prey 15 - 20 mm long on several occasions in the laboratory, vertically-migrating crustacea and fish may be an important fraction of its diet.

Respiration and Excretion

Oxygen consumption and ammonia excretion (Figure 2) can be expressed by regression equations fitted by the method of least squares:

$$\log Y = 0.87 \log X + 1.07; \; r^2 = 0.77 \qquad (1)$$

$$\log Z = 0.82 \log X - 1.21; \; r^2 = 0.79 \qquad (2)$$

where Y = oxygen consumption (μl O_2/hr); Z = ammonia excretion (μg-at NH_4^+-N/hr); X = body protein (mg BSA); r^2= coefficient of determination.

In 8 specimens of A.okeni, ranging in size from 1.3 mg to 10.1 mg body protein, ammonia excretion averaged 69% of total dissolved nitrogenous excretion (Table 1). Most other groups of planktonic invertebrates are also primarily ammonotelic (e.g., Corner and Cowey, 1968; Jawed, 1973; Mayzaud and Dallot, 1973). For colonies of A.okeni, the atomic ratio of oxygen consumed to nitrogen excreted (O:N) was 13 $\pm$ 5.5. Metabolism is apparently based on catabolism of protein, since protein catabolism (16% N and 1.04 liters O_2 needed for complete combustion of 1 g) yields an O:N ratio of about 8, while catabolism of a 50:50 mixture by weight of protein and lipid (2.02 liters O_2 needed for complete combustion of 1 g) yields an O:N ratio of about 24 (Ikeda, 1974).

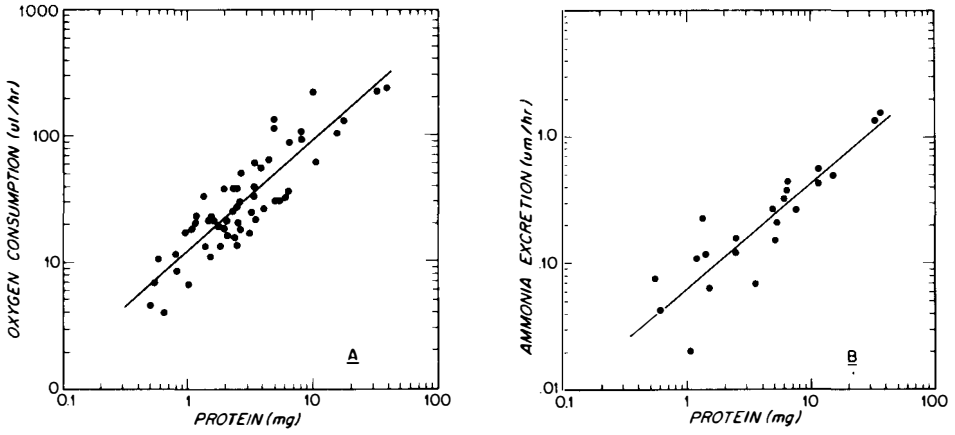

Figure 2. Oxygen consumption (A) and ammonia excretion (B) of colonies of Agalma okeni collected in situ and incubated at environmental temperatures of 23 - 29°C.

COLONY SIZE (mg protein)	AMMONIA EXCRETION (µg NH_4^+/hr)	TOTAL NITROGENOUS EXCRETION (µg NH_4^+ equivalents/hr)	$\frac{NH_4^+}{\text{TOTAL N}}$
1.3	0.4 ± 0.1	0.5 ± 0.2	0.80
2.4	1.5 ± 0.1	2.2 ± 0.2	0.68
2.5	2.6 ± 0.1	4.7	0.56
8.6	3.7 ± 0.1	5.0 ± 0.2	0.74
8.6	5.9	5.9	1.00
8.6	4.4 ± 0.2	7.7 ± 0.1	0.58
8.6	11.7 ± 0.1	13.2 ± 0.6	0.89
10.1	8.2 ± 0.2	23.6 ± 3.9	0.35

Table 1. Nitrogenous excretion by colonies of Agalma okeni collected in situ and incubated at environmental temperatures of 23 - 29°C.

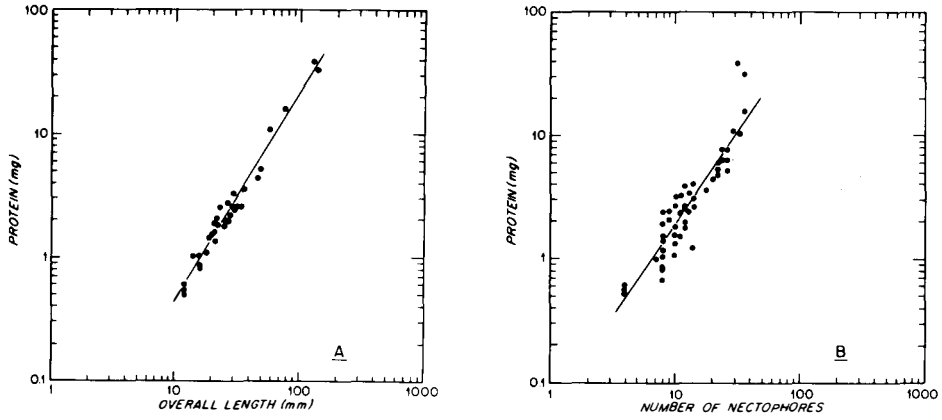

Figure 3. Protein content of colonies of Agalma okeni as a function of overall length (A) and number of nectophores (B).

Growth and Reproduction

As colonies of A. okeni grow, individual nectophores increase in size and protein content, though at any time all except 2 - 4 apical nectophores (buds) are roughly equivalent. Colonies having the same number of nectophores are similar in size, and colony biomass can be estimated from either the number of nectophores or from overall colony length (Figure 3). For example, the mean difference in size between colonies with 2 and 3 pairs of nectophores is 480 µg protein, while the mean difference in size between colonies with 6 and 7 pairs of nectophores is 600 µg protein (Figure 3).

Most colonies of A. okeni added 1 - 2 pairs of nectophores within 1 1/2 - 2 1/2 days. Five colonies maintained for 3 1/2 - 4 1/2 days added 2 - 3 pairs of nectophores (Table 2). All colonies budded a new gastrozooid and tentacle within 1 1/2 days and showed nectosome growth. Small colonies (1 or 2 pairs of nectophores) doubled in protein in 2 days, while larger colonies (4 - 6 pairs of nectophores) added 33 - 36% more protein (Table 2).

This steady increase in size was offset by accidental loss of gelatinous parts. Although the effects of laboratory confinement are difficult to assess, the faculty for autotomy is so well developed in most physonect siphonophores that shedding of nectophores and bracts probably occurs in situ as well as in the laboratory.

Colonies of A. okeni first show well-developed gonophores at about the 14 ± 2 nectophore stage (32 ± 4 mm overall length).

INITIAL SIZE — NECTOPHORES PLUS BUDS	*PROTEIN (µg)	DIET	NECTOPHORES + BUDS ADDED A	B	C	FINAL SIZE *PROTEIN (µg)
1+0	100	nauplii	-	2+1	-	300
3+1	500	nauplii; shrimp	-	3	5+1	1600
4+1	600	nauplii; shrimp	-	-	5+1	1900
5+0	700	nauplii	-	2+1	-	1100
6+0	900	nauplii	0+2	-	-	1100
6+1	1100	copepods	-	4+2	6+2	3500
6+1	1100	nauplii	-	4+1	-	2100
7+0	1100	nauplii	1	-	-	1300
7+0	1100	nauplii	1+1	-	-	1400
8+0	1400	nauplii	-	1+2	-	1900
10+1	2100	copepods	1+1	-	5	3500
13+0	2500	nauplii; shrimp	-	2+2	-	3500

*Calculated from Figure 3

Table 2. Increase in size of colonies of Agalma okeni maintained for 1 - 4 days in the laboratory (A = after 1±1/2 days; B = after 2±1/2 days; C = after 4±1/2 days).

DISCUSSION

Mackie and Boag (1963) maintained colonies of Nanomia cara (Family Agalmidae) in the laboratory at 12 - 14°C on a diet of fresh crab meat or small crustacea. They found that small colonies of N. cara budded a pair of nectophores and a gastrozooid about every three days, which approximates rates of budding observed in A. okeni.

I can now estimate the energy requirements of colonies of A. okeni. A small colony with 3 pairs of nectophores has about 1.0 mg of protein (Figure 3B) and consumes about 12 µl O_2/hr (Figure 2). Assuming an oxycaloric equivalent of 4.9 cal/ml, 3.5 calories would be consumed in respiration over a period of 2 1/2 days.

The caloric value of a Candacia sp. copepod is about 0.5 calories (Shushkina and Sokolova, 1972). If assimilation by siphonophores ranges between 70 - 90% of ingestion, a colony with 1.0 mg protein would have to ingest 8 - 10 such copepods in 2 1/2 days to balance its metabolism. Assimilation efficiencies of 70 - 90% are not unrealistic for aquatic carnivores (Welsh, 1968);

values of 80% and 88% have been reported for Sagitta hispida (Cosper and Reeve, 1975) and Euphausia pacifica (Lasker, 1966), respectively. The ctenophore Pleurobrachia pileus may have an assimilation efficiency as great as 90% (Hirota, 1972).

If siphonophores living under natural conditions increase in size at the rates I have measured in the laboratory, a colony of A.okeni with 3 pairs of nectophores would grow to the 8 or 10 nectophore stage in 2 1/2 days. This increase in size corresponds to mean production of 480 or 960 µg protein, respectively (Figure 3B). Since the caloric value of protein is about 5.5 kcal/gram (Morowitz, 1968), production represents 2.6 - 5.3 calories. Additional consumption of 6 - 15 copepods of Candacia size should support this increase in size, for a total ingestion of 14 - 25 copepods over a 2 1/2 day period. A colony of A. okeni initially three times larger, with 3.0 mg protein and 14 nectophores, would have to consume 29 - 46 copepods of similar size to balance its respiratory energy losses and increase in size to the 16 or 18 nectophore stage.

The preceding calculations suggest that growth in siphonophores like A. okeni may be quite efficient. In fish and euphausiids, the greatest fraction of ingestion goes to support respiration (Table 3). Physonect siphonophores able to grow to a colony size 2 pairs of nectophores larger in 2 1/2 days should have a higher ratio of growth to respiration,or more like chaetognaths in production efficiency (Table 3). Hirota (1972) estimated that 68% of food ingested by the ctenophore Pleurobrachia bachei was incorporated into growth and egg production. However, difficulties with organic weight determinations caused Hirota to overestimate

SPECIES	PRODUCTION	RESPIRATION	EGESTION	SOURCE
Agalma okeni				
3.0 mg protein	33%	47%	20%	
1.0 mg protein	48%	32%	20%	
Carnivorous fish	20%	60%	20%	Welsh (1968)
Euphausia pacifica	29%	59%	12%	Lasker (1966)
Sagitta elegans	35%	37%	28%	calculated from Sameoto (1972)

Table 3. A comparison of production, respiration, and egestion estimated for Agalma okeni with other marine carnivores.

production, and ctenophore growth efficiency is now believed to be less than 20% (M. R. Reeve, personal communication).

Most siphonophores are monoecious, and colonies of Agalmidae have clusters of male and female gonophores associated with each stem group. Female gonophores have 1 - 4 eggs, which measure about 0.3 - 0.7 mm in diameter (Totton, 1965). When fertilized in the laboratory at 14°C, eggs of Agalmidae require about 2 - 3 weeks to develop to the postlarva (e.g., Carré, 1969, 1971 , 1973). In tropical and subtropical environments, development is probably more rapid and might proceed in 1 - 2 weeks. If A. okeni can grow from the postlarva to the 14-nectophore adult in 1 1/2 - 2 weeks, as the data in Table 3 suggest, this physonect, like other gelatinous carnivores living in warm-water oceanic regions (Baker and Reeve, 1974) probably has a generation time of only 2 1/2 - 4 weeks. Since A. okeni is not restricted to feeding on copepod-size prey, a colony with only 1 mg protein which captured a mysid or euphausiid less than an inch long (with 5 mg protein) should gain enough energy for 1 - 2 weeks maintenance or to increase in size to within the range of reproductive capacity.

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SUMMARY

Agalma okeni was the most common physonect siphonophore encountered by SCUBA divers during the day in the upper 30 m of subtropical oceanic regions of the Western North Atlantic Ocean. In situ observations indicated that A. okeni is primarily a nocturnal feeder. A large portion of its diet may be vertically-migrating crustaceans and fish, although epipelagic copepods can be captured as well. Digestion of shrimp and megalops larvae required 7 - 18 hours.

Colonies with 1 - 10 mg body protein consumed 12±5.5 µl O_2/mg protein-hr and excreted 1.0±0.6 µg NH_4^+/mg protein-hr. The ratio of oxygen atoms consumed to nitrogen atoms excreted was 13±5.5. A small colony with 6 nectophores requires 2.8 - 5.0 calories to balance daily rates of oxygen consumption and short-term growth, while a medium-size colony with 14 nectophores requires 5.8 - 9.2 calories. Generation time in tropical and subtropical environments is probably 2 1/2 - 4 weeks.

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