J. Exp. Mar. Biol. Ecol., 1982, Vol. 62, pp. 39–54
Elsevier Biomedical Press

FEEDING AND GROWTH OF THE SIPHONOPHORE *MUGGIAEA ATLANTICA* (Cunningham 1893)

JENNIFER E. PURCELL[1]

Department of Biological Sciences and the Marine Science Institute, University of California, Santa Barbara, CA 93106, U.S.A.

Abstract: The siphonophore *Muggiaea atlantica* (Cunningham 1893) was the most abundant planktonic non-crustacean predator during October, 1980 in the surface waters at Friday Harbor, Washington. During the day, only 2% of the gastrozooids ("stomachs") of hand-collected siphonophores contained prey, while 7% contained prey at night. Daily in situ prey consumption, calculated from gut contents and digestion rates, was estimated to be 5.5 to 10.5 prey · siphonophore^{-1} · day^{-1}. The ingested carbon and nitrogen was adequate to meet the estimated daily metabolic demands of a siphonophore, but little surplus remained for growth. Prey density significantly affected feeding and growth of siphonophores in laboratory experiments. Feeding increased linearly with prey densities up to 30 prey · l^{-1}, increasing slightly at greater densities, and was greater when higher proportions of large prey were available. Growth, measured as the production of eudoxids (sexually reproducing stage), increased with increasing prey availability. Carbon content of eudoxids increased most rapidly at the highest prey densities, and decreased in starved eudoxids. The minimum maturation time of eudoxids at high laboratory prey densities was 6 days, and was estimated to be > 11 days in situ.

INTRODUCTION

Recent work on the feeding ecology of siphonophores has dealt primarily with large, oceanic species (Biggs, 1976, 1977; Purcell, 1980, 1981a,c), which have gastrozooid ("stomach") chains and tentacles which extend many centimeters to meters in length. Experimental studies with the large oceanic siphonophores are plagued by the physical constraints of the experimental containers, and the small numbers of any species generally available at one time. In contrast, the small size (total length < 10 cm) and abundance of the neritic siphonophores, such as *Sphaeronectes gracilis* and *Muggiaea atlantica*, make them amenable to laboratory experimentation.

In situ predation has been quantified and compared with prey size distributions to determine size-selective predation by chaetognaths and ctenophores (Anderson, 1974; Hirota, 1974; Pearre, 1974, 1981) and combined with prey digestion rates to estimate daily predation rates (Anderson, 1974; Newbury, 1978; Szyper, 1978). Siphonophore species differ in the range of prey sizes consumed in situ (Purcell, 1980, 1981a). Selection has been demonstrated for the larger prey sizes within the size range of consumed prey of some siphonophore species (Purcell, 1981c; Purcell & Kremer, pers.

[1] Present address: Woods Hole Oceanographic Institution, Woods Hole, MA 02543, U.S.A.

0022-0981/82/0000-0000/$02.75

comm.). Daily predation rates calculated for the siphonophores *Rhizophysa eysenhardti* and *Rosacea cymbiformis* were far greater than the minimum needed to balance metabolic demands (Purcell, 1981b,c), while daily predation by *Sphaeronectes gracilis* was approximately equal to metabolism (Purcell & Kremer, pers. comm.).

The purpose of this study is to estimate the daily predation, and carbon and nitrogen budgets of the siphonophore *Muggiaea atlantica* (Cunningham 1893), and to examine the effect of prey density upon feeding and growth of this siphonophore. In situ prey consumption was quantified during day and night for *M. atlantica*, compared to the size distribution of prey populations to determine feeding selectivity, and combined with digestion rates of prey to yield estimates of daily predation. The only previous observations on growth of siphonophores have been made on the physonect siphonophore *Agalma okeni* in the laboratory (Biggs, 1976). Growth in *Muggiaea atlantica* was monitored at different food levels by counting the number of eudoxids (sexual stage) produced, and by measuring the increase in carbon of the eudoxids.

Materials and Methods

Specimens of the siphonophore *Muggiaea atlantica* were collected throughout October, 1980 off the docks of the Friday Harbor Laboratories, Friday Harbor, Washington. Siphonophores were dipped undamaged from the surface water (to 0.5 m) as they were carried past the docks by the prevailing current. Horizontal plankton net tows were made within 150 m of the dock immediately following siphonophore collections, using a 70-μm mesh, 0.5-m diameter net with flowmeter at 0 to 3 m depth, to assess abundances of copepods, siphonophores, and other soft-bodied predators, and to collect prey used in laboratory experiments. Ambient water temperatures were 8 to 10 °C.

FEEDING

Some siphonophores were preserved immediately after collection for examination of consumed prey. The contents of gastrozooids were identified and measured at 100 to 200 × magnification through the semitransparent gastrozooids. Copepod prey were measured according to cephalothorax length.

Live siphonophores were maintained in 4-l plastic containers filled with filtered sea water. These containers stood in a running sea water bath at 8 to 10 °C, and were covered with black plastic to eliminate phototactic responses of siphonophores or copepods. Copepods which passed through 420-μm mesh netting but which remained after siphoning water out through 149-μm mesh were used as prey in experiments. This procedure exposed the copepods to as little trauma as possible.

The time required for siphonophores to egest copepods from the gastrozooids was estimated in two ways. (1) Siphonophores were collected in situ, and some preserved immediately as a reference. The remaining specimens were kept in filtered water, and some were preserved at 1- to 2-h intervals following collection. This method allows

estimation of the maximum digestion time for natural prey. (2) After siphonophores were starved for 12 h following collection, they were allowed to feed at high prey densities for 2 h. The siphonophores then were transferred to filtered water and some specimens were preserved immediately and at 2-h intervals thereafter. The gastrozooids in both methods were examined for prey as described before.

Daily in situ predation rates per siphonophore were calculated by summing the results of the following equation for three prey types; (1) nauplii, (2) copepods ≤ 0.35 mm, and (3) copepods > 0.35 mm. Day and night were assumed to be 12 h each.

$$\sum_{1}^{3} (\%\text{ of prey (av. no. prey} \cdot \text{siphonophore}^{-1})\ 24\text{ h/digestion time})$$

Carbon and nitrogen ingestion by the siphonophores were calculated from the preceding estimate of daily prey consumption. The dry weights of the various copepods and nauplii were estimated according to regression equations determined by Durbin & Durbin (1978) which relate length to dry weight in *Acartia clausi*: for copepodites and copepods, weight = 9.63 (cephalothorax length)$^{3.059}$; and for nauplii, weight = 19.04 (total length)$^{2.849}$. These regressions were calculated for preserved copepods, therefore weights were estimated to be 30% low (Durbin & Durbin, 1978), and a correction of 30% was used in the present study. Unpreserved copepods (*Pseudocalanus* sp.) collected during the present study measured 0.6 mm cephalothorax length and 2.5 μg copepod^{-1} dry weight, which corresponds to 2.6 μg copepod^{-1} dry weight calculated by the above regression. Dry weight was converted to carbon and nitrogen by multiplying by 48.8% carbon and 8.6% nitrogen measured for *Pseudocalanus* sp. in the present study.

The ingestion rate of siphonophores over a range of prey densities was investigated in three laboratory experiments. Two-fold serial dilutions of concentrated prey were prepared and added in 30-ml aliquots to 4-l containers, each having one siphonophore starved for 12 h. The proportions of prey differed among the experiments, but varied little within each experiment: Expt. A: $87.8 \pm 5.8\%$, $12.2 \pm 5.8\%$ nauplii and copepods, respectively; Expt. B: $61.8 \pm 8.5\%$, $38.2 \pm 8.5\%$; Expt. C: $41.2 \pm 6.4\%$, $58.8 \pm 6.4\%$. After feeding for 3.5 h, the siphonophores were preserved and the gastrozooids examined for prey as before. The uneaten prey were preserved and counted. Initial prey densities were determined from the number of prey captured by the siphonophores plus the uneaten prey. Electivity indices were calculated from the proportions of the various prey available and from the proportions consumed by the siphonophores, according to Chesson (1978). "Selection", as used herein, does not imply choice by the predator, but merely that prey were consumed in different proportions than were available in the environment.

GROWTH

Most polygastric colonies of calycophore siphonophores continually break off units from the end of the gastrozooid chain. These freed units (eudoxids) contain a gelatinous float, one gastrozooid and tentacle, and an immature gonophore. Once released, they continue to feed, grow, mature, and produce additional gonophores. The production of eudoxids by a siphonophore colony is an easily quantifiable measure of growth (asexual reproduction), although new units are added at the opposite end of the gastrozooid chain, and the size of each unit increases along the length of the chain.

The effects of food concentration on siphonophore growth (eudoxid production) and on eudoxid growth (increase in carbon content) were examined over 7 days. Six siphonophores were kept in individual 4-l containers in each of three experimental conditions: no food (starved), low food (≈ 10 prey $\cdot$ l^{-1}), and high food (≈ 20 prey $\cdot$ l^{-1}). Siphonophores were transferred to containers with fresh sea water and prey every other day: some freshly-collected prey were added on alternate days. Exact food concentrations were not precisely maintained, but food provided at high levels was twice that at low levels. The number of gastrozooids were counted from undisturbed siphonophores at the beginning of the experiment and after 7 days. Eudoxids were pipetted from each container and counted once per day. The eudoxids were maintained in groups at three food levels; low, high, plus very high (double high prey levels), and starved. Eudoxids were pipetted into fresh sea water with prey every other day.

At daily intervals some eudoxids were starved for 8 to 12 h, placed in groups of 4 to 8 on pieces of pre-ashed, pre-weighed glass fiber filters, dried for 48 h in a 60 °C oven, weighed to the nearest 1 μg on a Cahn electrobalance, and analysed for the carbon and nitrogen contents (Perkin Elmer 240B Elemental Analyser). Eudoxids and polygastric siphonophores collected in situ were starved for 12 h, and individually dried, weighed, and analysed for CHN. Groups of 20 copepods of similar size were treated as above.

RESULTS

Muggiaea atlantica was abundant at Friday Harbor, Washington throughout October, 1980, with densities of the polygastric colonies ranging from 0.6 to 2.7 siphonophores $\cdot$ m^{-3}. The abundance of polygastric siphonophores in 13 plankton tows was 1.4 ± 0.8 specimens $\cdot$ m^{-3} (mean $\pm$ SD), and for reproductive eudoxids was $8.0 \pm 3.8 \cdot$ m^{-3}, an average of 5.9 eudoxids to each dioecious polygastric colony. There were no significant differences between daytime and nighttime abundances of polygastric or eudoxid stages ($P > 0.75$, single classification analysis of variance (ANOVA), Sokal & Rohlf, 1969). This is in contrast to samples over a 0 to 225 m depth range, which show greater densities of both stages of *M. atlantica* during the day off California and Baja California (Alvarino, 1980). The ratio of male to female gonophores in the

present study averaged 1.2 : 1. In Friday Harbor, polygastric and eudoxid stages of *M. atlantica* were the most abundant non-crustacean zooplankton predators in the surface waters during October, outnumbering other planktivores including ctenophores (*Pleurobrachia* sp.: $0.1 \pm 0.2 \cdot m^{-3}$), medusae (primarily *Phialidium* sp. and *Aequorea* sp.; $0.7 \pm 0.5 \cdot m^{-3}$), and chaetognaths (*Sagitta* sp.; $1.3 \pm 0.9 \cdot m^{-3}$). Copepod densities averaged $9120.9 \pm 3726.5 \cdot m^{-3}$, with no significant difference between day and night (ANOVA, $P > 0.5$). Abundant copepod genera included *Acartia*, *Calanus*, *Metridia*, *Oithona*, and *Pseudocalanus*.

FEEDING

In situ feeding was quantified for 2604 gastrozooids of 117 siphonophores. *Muggiaea atlantica* consumed prey 0.1 to 0.9 mm in length, including all stages of calanoid copepods, and some cyclopoid and harpacticoid copepods. A larvacean had been consumed by one specimen. Both the mean percentage of siphonophores with prey, and the mean percentage of gastrozooids with prey were greater at night. Of 84 siphonophores collected at night, $64.7 \pm 14.8\%$ of the colonies, and $6.9 \pm 3.8\%$ of the 1818 gastrozooids contained prey, while of 33 siphonophores collected during the day, only $34.2 \pm 23.1\%$ of the colonies and $2.0 \pm 0.9\%$ of the 786 gastrozooids contained prey. The number of prey captured per siphonophore was significantly greater at night than in the day (ANOVA, $P < 0.01$).

In siphonophores collected to determine digestion rates, 13% of the gastrozooids initially contained prey. The number of prey remains in the gastrozooids was reduced by 97% in 3 h, and no prey remains were seen 4.5 h beyond collection of the siphonophores. A total of 40 siphonophores (929 gastrozooids) were examined. These results suggest a maximum digestion time of 4.5 h at ambient temperatures of 8 to 10 °C.

For 45 siphonophores (1193 gastrozooids) fed for 2 h in the laboratory digestion experiment, 32% of the 207 gastrozooids preserved initially contained prey. The number of prey remains was reduced by 33% after 2 to 4 h digestion, and by 98% after 4 to 6 h digestion (including the 2-h feeding period). Small prey (≤ 0.35 mm) were egested from the gastrozooids in 2 to 4 h, and all were egested within 8 h. These digestion times for small copepod prey equal egestion times of 2 to 4 h at 26 °C of brine shrimp nauplii by other small siphonophores (Biggs, 1976).

Electivity indices were calculated from the percentages of prey available in the environment, and from the percentages of prey consumed (which were adjusted for different digestion times according to prey size). The most extreme corrections for digestion were assumed, which would tend to overestimate the proportions of nauplii consumed and to underestimate the proportions of large copepods consumed. In spite of the extreme corrections, selection was negative for nauplii, and was positive for copepods (Table I). Electivity for large copepods was somewhat greater than for small copepods (Table I).

Daily in situ predation rates were estimated from the numbers and sizes of prey found

in the gastrozooids of *M. atlantica*, combined with the digestion rates of different sizes of prey. Gastrozooids contained an average of 0.6 prey · siphonophore^{-1} during the day, and 1.5 prey · siphonophore^{-1} at night. The percentages of the identifiable prey in the gastrozooids were 27.6% nauplii, 42.0% small copepods ≤ 0.35 mm, and 30.4%

TABLE I

Electivity indices for prey of *Muggiaea atlantica*, calculated from the average percentages of prey available in the environment and prey consumed in situ during day and night: electivity indices were calculated using the adjusted percentage of prey consumed, assuming that digestion times for nauplii, copepods ≤0.35 mm, and copepods >0.35 mm were 2, 4, and 6 h, respectively; electivity values, which lie between 0 and 1, $> \underline{\alpha}$ indicate positive selection (+), and those $< \underline{\alpha}$ indicate negative selection (−).

	Prey available (%)	Prey consumed (%)		Electivity $\underline{\alpha} = 0.333$
		in the gastrozooids	adjusted for digestion	
Nauplii ≤0.35 mm	82.6	42.1	60.5	0.137 −
Copepods ≤0.35 mm	10.9	24.6	23.5	0.403 +
Copepods >0.35 mm	6.5	33.3	16.0	0.460 +

large copepods > 0.35 mm. An average of 1.7–3.4 nauplii, 2.6–5.2 small copepods, and 1.2–1.9 large copepods were captured by each siphonophore per day, which totalled 5.5–10.5 prey · siphonophore^{-1} · day^{-1}. Siphonophore density averaged 1.4 polygastric colonies · m^{-3}. Thus 7.5–14.4 prey · day^{-1} · m^{-3} were consumed by *M. atlantica*. At average prey densities of 9121 prey · m^{-3}, only 0.1–0.2% of the available prey were consumed by the siphonophore, disregarding predation by eudoxids. The above estimates depend upon the ranges of prey digestion times.

The dry weight of prey ingested by *M. atlantica* was calculated to be 6.7 to 10.9 μg · siphonophore^{-1} · day^{-1}, which is equivalent to 3.3 to 5.3 μg C and 0.6 to 0.9 μg N · siphonophore^{-1} · day^{-1}. Food was assumed to be assimilated with 80% efficiency, which is comparable to values measured for other gelatinous zooplankton predators (e.g. Reeve *et al.*, 1978; Purcell, 1981b). Thus, assimilated carbon and nitrogen were calculated to be 2.6 to 4.2 μg C · siphonophore^{-1} · day^{-1}, and 0.5 to 0.8 μg N · siphonophore^{-1} · day^{-1}.

Respiration and excretion (NH_4) for the siphonophore *Sphaeronectes gracilis* were 3% · day^{-1} of the carbon and nitrogen contents of the siphonophore at 13 °C at prey densities of 5 prey · l^{-1} (Purcell & Kremer, pers. comm.). These weight-specific metabolic measurements for *S. gracilis* were used to estimate metabolism in *M. atlantica*, and adjusted for a 5 °C temperature differential, by assuming that metabolism doubles with each 10 °C rise in temperature (a Q_{10} of 2). Thus, respiration and excretion for *Muggiaea atlantica* were estimated to require 2.9 μg C · siphonophore^{-1} · day^{-1}, and 0.7 μg N · siphonophore^{-1} · day^{-1}, approximately 2.3% of the carbon and nitrogen contents of the siphonophore. Since both siphonophore species are similar in size and have

similar activity, these estimates of metabolism for *M. atlantica* are believed to be reasonable. Calculated metabolism for *M. atlantica* was within the estimated range of in situ carbon and nitrogen ingestion, suggesting that the siphonophores had little surplus available for growth.

Feeding of *M. atlantica* in laboratory experiments was examined at prey densities similar to and much greater than field prey densities (Fig. 1). In Expt. A, where the

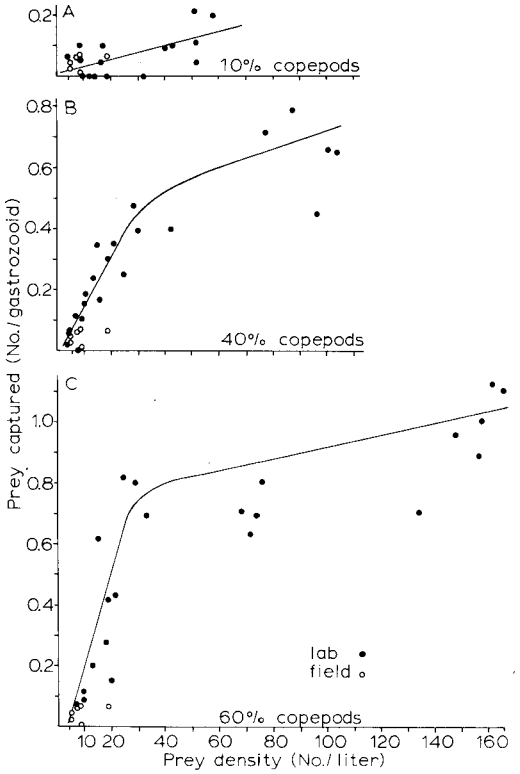

Fig. 1. Prey capture by *Muggiaea atlantica* over a range of prey densities in laboratory experiments which differed in the proportions of nauplii and copepods available: each point represents one siphonophore; linear regressions were calculated: for Expt. A, $y = 0.002x + 0.064$ ($r = 0.63$, $P < 0.01$); and for points below 30 prey $\cdot l^{-1}$ in Expt. B, $y = 0.015x - 0.013$ ($r = 0.90$, $P < 0.01$) and in C, $y = 0.025x - 0.067$ ($r = 0.70$, $P < 0.05$); the mean in situ feeding for siphonores on 6 days is plotted (○) on each graph for comparison.

proportions of nauplii and copepods were very similar to those in situ (83.1 ± 6.5% nauplii, and 17.6 ± 6.1% copepods), feeding was indistinguishable from feeding in situ (Fig. 1A). Feeding increased at higher prey densities (Fig. 1A); the slope of the line was significantly different than zero slope ($P < 0.005$, comparison of slopes and elevations of linear regressions, Zar, 1974).

In Expts. B and C, which had much greater proportions of copepods than in A,

feeding increased linearly at prey densities < 30 prey $\cdot l^{-1}$ (Fig. 1B,C). The slopes of lines B and C were not significantly different, but the elevations of the lines (intercepts) were significantly different ($P = 0.05$). More prey were captured in Expt. C where higher proportions of large prey were available than in Exp. B. An average of > 1 prey per gastrozooid was consumed by siphonophores at very high prey densities in Expt. C. Feeding increased much less rapidly at prey densities above $30 \cdot l^{-1}$ in Expts. B and C, suggesting a partial saturation in feeding (Fig. 1B,C).

TABLE II

Electivity indices for small and large prey of *Muggiaea atlantica* from three laboratory experiments (A, B, C): small prey include nauplii and copepods ≤ 0.35 mm, and large prey were copepods > 0.35 mm; for explanations of electivity see caption of Table I; the number of replicates for A, B, C are 17, 22, 21, and the number of prey consumed equal 15, 195, 347, respectively.

Prey size	Prey available (%)	Prey consumed (%)	Electivity $\underset{\sim}{\alpha} = 0.500$
Small			
A	95.8	80.0	0.178 –
B	86.6	66.6	0.223 –
C	56.5	38.0	0.321 –
Large			
A	5.2	20.0	0.822 +
B	12.4	33.3	0.777 +
C	43.5	62.0	0.679 +

Electivity indices consistently were negative for small prey and positive for larger prey (Table II). Small prey were not distinguishable as nauplii or copepods after 1 h digestion, and so were considered together. Some small prey could have been egested during the 3.5-h feeding period, based on gut clearance estimates of 2 to 4 h. Hence, the percentages of prey observed in the gastrozooids may have slightly underestimated the capture of small prey, and may have biased the electivity indices similarly. Selection of large prey within the size-range of prey consumed is typical of tentaculate predators, and is related to prey diameter and prey swimming speed, which increase with prey length (Anderson, 1974; Purcell, 1981c; Dodson & Cooper, pers. comm.; Purcell & Kremer, pers. comm.).

Daily predation rates in the laboratory experiments of 3.5-h duration were calculated for prey densities < 10 prey $\cdot l^{-1}$ for comparison to in situ predation rate estimates. In Expts. A at < 10 prey $\cdot l^{-1}$, 7 prey $\cdot$ siphonophore$^{-1} \cdot$ day^{-1} would have been consumed, which is comparable to estimates of 5.5 to 10.5 prey $\cdot$ siphonophore$^{-1} \cdot$ day^{-1} in situ where the composition of prey populations was similar. Daily predation in Expts. B and C at prey densities $< 10 \cdot l^{-1}$ would have been 17.8 and 22.8 prey $\cdot$ siphonophore$^{-1} \cdot$ day^{-1}, respectively. Thus differences in the size composition of prey popu-

lations at similar densities radically altered the number of prey captured by siphonophores.

GROWTH

Growth of the siphonophores at three food levels was quantified by the number of eudoxids produced by the gastrozooid chain. The number of gastrozooids per siphonophore colony was unchanged from the beginning to the end of the experiment at all food levels, although colonies had produced an average of 57, 40, and 16 eudoxids at high, low, and starved food levels, respectively. Total eudoxid production over 6 days in the laboratory was greater for siphonophores with a greater initial number of gastrozooids (Fig. 2). Growth of the gastrozooid chain is primarily one-dimensional, so the relation-

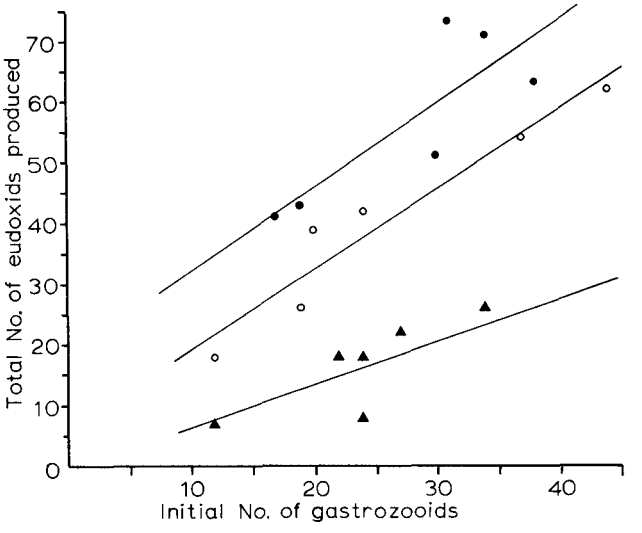

Fig. 2. Total number of eudoxids produced at three food levels by siphonophores having different initial numbers of gastrozooids: each point represents the total eudoxids produced by each siphonophore during 6 days in the laboratory; linear regressions: high food (●) $y = 1.37x + 18.3$ ($r = 0.82$, $P < 0.05$); low food (○) $y = 1.30x + 6.05$ ($r = 0.96$, $P < 0.01$); starved (▲) $y = 0.86x - 4.2$ ($r = 0.82$, $P < 0.05$).

ship between eudoxid production and the number of gastrozooids would be predicted to be linear. The slopes of the lines at three prey densities were not significantly different. Elevations of the lines were different overall ($P \ll 0.001$), and each line was different from the others (high vs. low, $P < 0.05$; low vs. starved, $P < 0.001$). Eudoxid production increased linearly with greater gastrozooid chain length, and it was greater when more food was available.

Eudoxid production was constant over 6 days in siphonophores fed in the laboratory, but decreased in starved siphonophores and ceased after 5 days (Fig. 3). The cumulative number of eudoxids increased linearly with time at high and low prey densities. The

slopes of the two lines were significantly different ($P < 0.005$). Eudoxids were produced at a greater average rate (11.0 · siphonophore^{-1} · day^{-1}) in high prey densities than at low prey densities (7.4 · siphonophore^{-1} · day^{-1}). The nutritional state of the siphonophores strongly affected the rate of asexual reproduction.

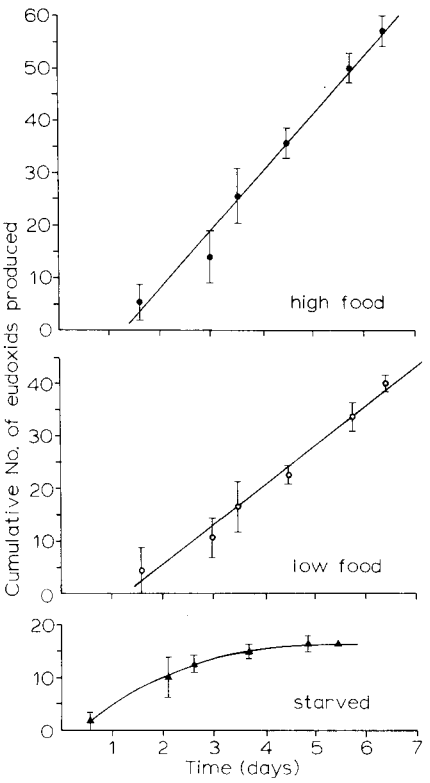

Fig. 3. Cumulative number of eudoxids produced per siphonophore during 6 days in the laboratory at three food levels: each point represents the mean number of eudoxids produced by six siphonophores ± SD; linear regressions: high food $y = 11.04x - 13.7$ ($r = 0.88$, $P \ll 0.01$); low food $y = 7.44x - 9.2$ ($r = 0.73$, $P \ll 0.01$).

The growth of eudoxids, measured by the change in carbon content, also was dependent upon nutrition (Fig. 4). Starved eudoxids lost carbon during the experiment. The carbon content of eudoxids at three prey densities increased exponentially over 5 days in the laboratory. The slopes of the lines were significantly different overall ($P < 0.05$). Comparison between pairs of lines showed the slopes to differ only between very high and low prey densities ($P < 0.05$). On the 5th day, some male gonophores of eudoxids kept at the highest prey density resembled mature, opaque gonophores seen in field-collected eudoxids. The carbon content of mature eudoxids collected in situ (Fig. 4, Table III) varied considerably due to size differences of the eudoxids. The

smallest carbon content of a mature field-collected eudoxid was assumed to be the minimum size at which eudoxids mature. Fig. 4 demonstrates that eudoxids kept at very high prey densities reached this minimum size within 6 days. Extension of the lines calculated for growth at lower prey densities indicates that those eudoxids would have required from 9 to 11 days to mature (Fig. 4). Eudoxids at lower prey densities in situ probably require longer than 11 days to mature.

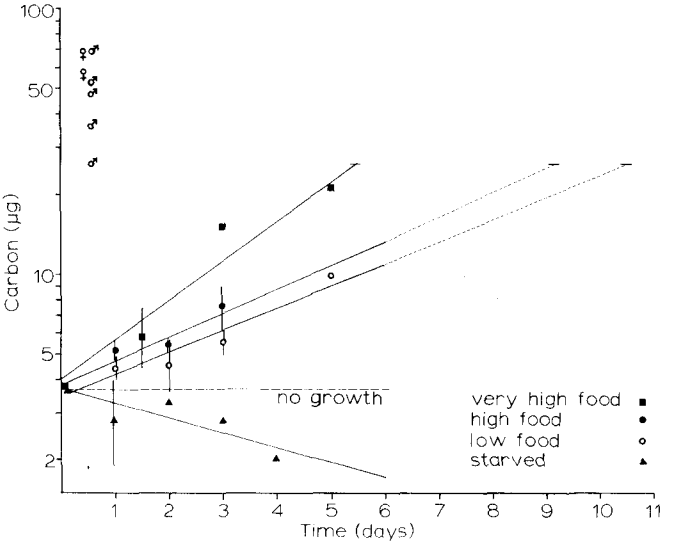

Fig. 4. Growth of eudoxids of *Muggiaea atlantica* during 5 days in the laboratory at four food levels: points represent one measurement of 4–8 eudoxids, or the mean ± SD of three or more measurements; the number of eudoxids and the number of measurements (e,m) are: ■ (32,8); ● (102,13); ○ (86,14); ▲ (49,9); correlations to the lines were significant ($P < 0.01$): ■ $r = 0.74$, $\log y = 0.147x + 0.608$; ● $r = 0.85$, $\log y = 0.058x + 0.606$; ○ $r = 0.94$, $\log y = 0.063x + 0.564$; ▲ $r = -0.85$, $\log y = -0.050x + 0.564$; these lines have been extended (– – – –) to estimate the time to reach the minimum size of mature eudoxids; the carbon content of mature eudoxids collected in situ are represented by male and female symbols.

The dry weights, and carbon and nitrogen contents of polygastric colonies and eudoxids of *M. atlantica* are summarized in Table III. The percentages of carbon and nitrogen of the dry weight for *M. atlantica* are low compared to those of crustacean zooplankton (e.g. copepods, 48.8% C and 8.6% N in this study), but are similar to those measured for the siphonophore *Sphaeronectes gracilis* (Purcell & Kremer, pers. comm.), and to other gelatinous zooplankton (e.g. Reeve, 1980). Carbon content (y) increased with the number of gastrozooids (x) in 34 siphonophore colonies according to the equation: $\log y = 0.013x + 1.778$, $r = 0.77$, $P \ll 0.01$. The values of dry weight, carbon and nitrogen in Table III are means of colonies having 10 to 35 gastrozooids, which explains the large standard deviations. The percentage of carbon in polygastric colonies was considerably less than the percentage carbon of mature eudoxids, while the percentages of nitrogen were similar. Mature eudoxid dry weight was five to six

TABLE III

Dry weights, and carbon and nitrogen contents of *Muggiaea atlantica* polygastric and eudoxid stages: numbers represent means ± SD for >2 samples.

	N	Size (mm)	Dry weight (μg)	Carbon (%)	Carbon (μg)	Nitrogen (%)	Nitrogen (μg)	C/N
Polygastric	34	6–9	1656.00 ± 588.00	7.51 ± 1.72	130.46 ± 46.06	1.68 ± 0.25	29.55 ± 11.47	4.54 ± 0.54
Eudoxids								
Laboratory, ≤6 h old	9	2	67.50	5.88	3.72	0.63	0.59	6.32
Field								
immature females	17	2–4	262.70 ± 99.90	14.02 ± 4.77	33.78 ± 12.72	1.98 ± 0.94	5.19 ± 3.01	7.16 ± 2.01
immature males	4	2–4	286.00 ± 43.41	14.12 ± 5.22	39.27 ± 13.92	1.71 ± 0.67	4.75 ± 1.77	8.32 ± 0.48
mature females	2	4–5.5	350.00	10.46	33.10	1.16	7.74	6.94
mature males	5	4–5.5	420.20 ± 60.23	13.54 ± 2.75	58.92 ± 20.12	2.23 ± 0.46	9.65 ± 3.23	6.17 ± 1.20

times that of newly-released eudoxids, with up to 16-fold increases in carbon and nitrogen. This was probably a result of gamete development in the eudoxids.

Maturing field-collected eudoxids often had an additional developing gonophore. Female gonophores contained 30.2 ± 7.0 eggs (n = 10 gonophores examined). Neither the total number of gonophores produced by each eudoxid, nor the total number of eudoxids produced by each polygastric siphonophore colony during their life spans are known. No estimates of the production of *M. atlantica* populations can be made until more is known about reproductive capacity, life spans, and survival.

Discussion

The ecological importance of predation by gelatinous zooplankton has been studied for few species: for the ctenophores *Pleurobrachia bachei* (Hirota, 1974), *P. pileus* (Anderson, 1974; Greve, 1977), *Mnemiopsis leidyi* (Miller, 1970; Miller & Williams, 1972; Kremer, 1979), and *M. mccradyi* (Reeve & Baker, 1975; Reeve *et al.*, 1978); for the scyphomedusa *Aurelia aurita* (Möller, 1979, 1980); and for the siphonophores *Rhizophysa eysenhardti*, *Rosacea cymbiformis*, and *Sphaeronectes gracilis* (Purcell, 1981b,c; Purcell & Kremer, pers. comm.).

These studies suggest that when gelatinous predators are very abundant, prey populations can be significantly affected. The present results indicate that *Muggiaea atlantica* consumed only 0.1 to 0.2% of the available prey daily, even when abundances of the siphonophore were high. Parsons *et al.* (1969) estimated daily copepod production to be 6.5% of the standing stock during spring months near the location of the present study. It seems that *M. atlantica* may have removed only a small portion of the copepod populations, although no data exist on copepod production during the present study.

The calculations of in situ predation by *M. atlantica* depend upon the accuracy of several measurements: (1) estimation of prey digestion times; (2) identification of partially digested prey in the gastrozooids: (3) conversion of prey size to dry weight and carbon; and (4) determination of prey and siphonophore densities from plankton tows. The approximations inherent in each of these factors probably involve less error than extrapolation from laboratory data to field conditions. For instance, ingestion by the ctenophores *Mnemiopsis leidyi* and *M. mccradyi* measured in the laboratory at prey densities found in situ was not adequate to sustain the ctenophores (Miller, 1970; Miller & Williams, 1972; Reeve, 1980). Reeve (1977, 1980) and Purcell & Kremer (pers. comm.) conclude that laboratory conditions may reduce feeding.

Polygastric colonies of *Muggiaea atlantica* were estimated to consume 7.5 to 14.4 prey $\cdot$ day^{-1} $\cdot$ m^{-3}, ignoring predation by eudoxids with average densities of 8 $\cdot$ m^{-3}. A daily ration of 2 prey $\cdot$ day^{-1} is representative for several species of chaetognaths (Mironov, 1960; Nagasawa & Marumo, 1972; Kuhlmann, 1977; Feigenbaum, 1979). Accordingly, chaetognaths would have consumed only 2.8 prey $\cdot$ day^{-1} $\cdot$ m^{-3} at average densities observed in the present study. Since

ctenophores and medusae were not abundant, I conclude that *M. atlantica* was the most important non-crustacean planktonic predator of copepods in surface waters throughout this study. However, no concurrent abundance data are available over the 200-m depth range of Friday Harbor, and other soft-bodied predators may have been more important overall than *M. atlantica*. *M. atlantica* was seasonally abundant in Saanich Inlet during May and June (0.3 siphonophores $\cdot$ m^{-3}) and during September–December (0.2 to 2.3 siphonophores $\cdot$ m^{-3}) in 1978 and 1979, with 90% of the population occurring above 50 m (C. Mills, pers. comm.). The periods of abundance of *M. atlantica* coincide with peak abundances of zooplankton during spring and fall in the area (Stephens *et al.*, 1969).

In laboratory feeding Expts. B and C, the prey capture rate per siphonophore as a function of prey density (the functional response), was similar to a Type 1 functional response as described by Holling (1959, 1965). Prey capture by *M. atlantica* increased linearly with prey density, in contrast to the curvilinear or sigmoidal patterns of Type 2 and 3 responses of Holling. Prey capture differed from all three types of functional response in that feeding did not appear to remain at a constant maximum beyond some critical prey density, at densities tested in the present study. Further evidence from experiments over longer feeding periods or at still higher prey densities might demonstrate a more typical functional response. Feeding by tentaculate ctenophores increased linearly up to a critical prey density around 5×10^5 copepods $\cdot$ m^{-3}, a much higher density than observed for siphonophores in the present study. This high critical prey density for ctenophores may be due to very rapid prey digestion by ctenophores. With prey populations similar to those in the field, *M. atlantica* showed no satiation, even at prey densities 10 times those in the field. Satiation probably does not occur in situ at environmental prey densities.

The rates of eudoxid production by *M. atlantica* and of growth in the eudoxids increased with increasing density of prey. The nutritional state of other soft-bodied zooplankters has been shown to affect their growth: the pteropod *Clione limacina* grew faster on large, preferred prey (Conover & Lalli, 1972); and the larvae and adults of two species of ctenophores grew faster at higher prey densities (Reeve *et al.*, 1978; Stanlaw *et al.*, 1981). The growth coefficient (k), calculated from the equation $W_T = W_O e^{kT}$, equalled 0.20 and 0.35 for eudoxids of *Muggiaea atlantica* at prey densities of ≈ 10 and 20 prey $\cdot$ l^{-1}. These values are quite comparable to laboratory measurements on other gelatinous zooplankton: $k = 0.35$ for small colonies of the siphonophore *Agalma okeni* (Biggs, 1976); and $k = 0.26$ to 0.60 for ctenophores at prey densities of 10 to 100 copepods $\cdot$ l^{-1} (Reeve *et al.*, 1978).

Sexual-reproductive capacity of *Muggiaea atlantica* also may depend upon nutrition of the siphonophores. In Friday Harbor, gonophores were 5.9 times more numerous than polygastric colonies in the field, and contained an average of 30 eggs per female gonophore. Eudoxids of *M. atlantica* from Southern California, where prey densities were much less (≈ 275 prey $\cdot$ m^{-3}; 70-μm mesh, 0.5-m diameter net), were only 2.5 to 3 times more numerous than polygastric colonies, and gonophores contained an average

of only 18 eggs (Purcell, unpubl. data). Additionally, the higher temperature in Southern California (13 °C) may have caused the gonophores to mature more quickly at smaller sizes, and, therefore, to be less fecund.

Prey density influenced feeding rates of the siphonophore *M. atlantica*, and in turn, growth and reproduction. This study was the first step in examining the interaction of siphonophore and prey populations. Further research will be designed to determine population dynamics of *M. atlantica* and copepods, and generation time and reproductive capacity of the siphonophores.

ACKNOWLEDGEMENTS

I greatly appreciate the use of facilities at the Friday Harbor Laboratories, assistance in field sampling by W. K. Fitt, and comments by A. L. Alldredge, S. D. Cooper, W. K. Fitt, B. H. Robison, and S. Pearre, Jr. upon the manuscript. This research was supported by NSF Grant OCE 76-23432 to A. L. Alldredge, and by an International Women's Fishing Association Fellowship and a Sigma Xi Grant-in-aid to the author.

REFERENCES

ALVARIÑO, A., 1980. Reproduction seasons and day/night bathymetric distribution of three species of Diphyinae (Siphonophorae), off California and Baja California. In, *Developmental and cellular biology of coelenterates*, edited by P. Tardent & R. Tardent, Elsevier/North-Holland Biomedical Press, Amsterdam, pp. 33–38.

ANDERSON, E. A., 1974. Trophic interactions among ctenophores and copepods in St. Margaret's Bay, Nova Scotia. Ph.D. thesis, Dalhousie University, 85 pp.

BIGGS, D. C., 1976. Nutritional ecology of *Agalma okeni* (Siphonophora; Physonectae). In, *Coelenterate ecology and behavior*, edited by G. O. Mackie, Plenum Press, New York, pp. 201–210.

BIGGS, D. C., 1977. Field studies of fishing, feeding, and digestion in siphonophores. *Mar. Behav. Physiol.*, Vol. 4, pp. 261–274.

CHESSON, J., 1978. Measuring preference in selective predation. *Ecology*, Vol. 59, pp. 211–215.

CONOVER, R. J. & C. M. LALLI, 1972. Feeding and growth in *Clione limacina* (Phipps), a pteropod mollusc. *J. Exp. Mar. Biol. Ecol.*, Vol. 9, pp. 279–302.

DURBIN, E. G. & A. G. DURBIN, 1978. Length and weight relationships of *Acartia clausi* from Narragansett Bay, R. I. *Limnol. Oceanogr.*, Vol. 23, pp. 958–969.

FEIGENBAUM, D., 1979. Daily ration and specific daily ration of the chaetognath *Sagitta enflata*. *Mar. Biol.*, Vol. 54, pp. 75–82.

GREVE, W., 1977. Interspecific interaction: the analysis of complex structures in carnivorous zooplankton populations. *Helgol. Wiss. Meeresunters.*, Vol. 30, pp. 83–91.

HIROTA, J., 1974. Quantitative natural history of *Pleurobrachia bachei* in La Jolla Bight. *Fish. Bull.*, Vol. 72, pp. 295–335.

HOLLING, C. S., 1959. Some characteristics of simple types of predation and parasitism. *Can. Entomol.*, Vol. 91, pp. 385–398.

HOLLING, C. S., 1965. The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. Entomol. Soc. Can.*, Vol. 45, pp. 3–60.

KREMER, P., 1979. Predation by the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island. *Estuaries*, Vol. 2, pp. 97–105.

KUHLMANN, D., 1977. Laboratory studies on the feeding behaviour of the chaetognaths *Sagitta setosa* J. Muller and *S. elegans* Verril with special reference to fish eggs and larvae as food organisms. *Meeresforschung*, Vol. 25, pp. 163–171.

MILLER, R.J., 1970. Distribution and energetics of an estuarine population of the ctenophore, *Mnemiopsis leidyi*. Ph.D. thesis, North Carolina State University, Raleigh, 78 pp.

MILLER, R.J. & R.B. WILLIAMS, 1972. Energy requirements and food supplies of ctenophores and jellyfish in the Patuxent River Estuary. *Chesapeake Sci.*, Vol. 13, pp. 328–331.

MIRONOV, G.N., 1960. The food of plankton predators II. Food of *Sagitta*. *Tr. Sevastop. Biol. Stn. Akad. Nauk Ukr. SSR*, Vol. 13, pp. 78–88.

MÖLLER, H., 1979. Significance of coelenterates in relation to other plankton organisms. *Meeresforschung*, Vol. 27, pp. 1–18.

MÖLLER, H., 1980. Population dynamics of *Aurelia* medusae in Kiel Bight, Germany (FRG). *Mar. Biol.*, Vol. 60, pp. 123–128.

NAGASAWA, S. & R. MARUMO, 1972. Feeding of a pelagic chaetognath, *Sagitta nagae* Alvariño in Suruga Bay, central Japan. *J. Oceanogr. Soc. Jpn.*, Vol. 28, pp. 181–186.

NEWBURY, T.K., 1978. Consumption and growth rates of chaetognaths and copepods in subtropical oceanic waters. *Pac. Sci.*, Vol. 32, pp. 61–78.

PARSONS, T.R., R.J. LEBRASSEUR, J.D. FULTON & O.D. KENNEDY, 1969. Production studies in the Strait of Georgia. Part II. Secondary production under the Fraser River Plume, February to May, 1967. *J. Exp. Mar. Biol. Ecol.*, Vol. 3, pp. 39–50.

PEARRE, S., JR., 1974. Ecological studies of three West-Mediterranean chaetognaths. *Inv. Pesq.*, Vol. 38, pp. 325–369.

PEARRE, S., JR., 1981. Feeding by chaetognatha: the relation of prey size to predator size in several species. *Mar. Ecol. Prog. Ser.*, Vol. 3, pp. 125–134.

PURCELL, J.E., 1980. Influence of siphonophore behavior upon their natural diets: evidence for aggressive mimicry. *Science*, Vol. 209, pp. 1045–1047.

PURCELL, J.E., 1981a. Dietary composition and diel feeding patterns of epipelagic siphonophores. *Mar. Biol.*, Vol. 65, pp. 83–90.

PURCELL, J.E., 1981b. Feeding ecology of *Rhizophysa eysenhardti*, a siphonophore predator of fish larvae. *Limnol. Oceanogr.*, Vol. 26, pp. 424–432.

PURCELL, J.E., 1981c. Selective predation and caloric consumption of the siphonophore *Rosacea cymbiformis* in nature. *Mar. Biol.*, Vol. 63, pp. 283–294.

REEVE, M.R., 1977. The effect of laboratory conditions on the extrapolation of experimental measurements to the ecology of marine zooplankton V: a review. In, *Proceedings of the symposium of warm water zooplankton*. National Institute of Oceanography, Goa, pp. 528–537.

REEVE, M.R., 1980. Comparative experimental studies on the feeding of chaetognaths and ctenophores. *J. Plankton Res.*, Vol. 2, pp. 381–393.

REEVE, M.R. & L.D. BAKER, 1975. Production of two planktonic carnivores (chaetognath and ctenophore) in South Florida inshore waters. *Fish. Bull.*, Vol. 73, pp. 238–248.

REEVE, R.M., M.A. WALTER & T. IKEDA, 1978. Laboratory studies of ingestion and food utilization in lobate and tentaculate ctenophores. *Limnol. Oceanogr.*, Vol. 23, pp. 740–751.

SOKAL, R.R. & F.J. ROHLF, 1969. *Biometry*. W.H. Freeman & Co., San Francisco, 776 pp.

STANLAW, K.A., M.R. REEVE & M.A. WALTER, 1981. Growth, food, and vulnerability to damage of the ctenophore *Mnemiopsis mccradyi* in its early life history stages. *Limnol. Oceanogr.*, Vol. 26, pp. 224–234.

STEPHENS, K., J.D. FULTON & O.D. KENNEDY, 1969. Summary of biological oceanographic observations in the Strait of Georgia 1965–1968. Fish. Res. Board Can. Tech. Report No. 110.

SZYPER, J.P., 1978. Feeding rate of the chaetognath *Sagitta enflata* in nature. *Estuarine Coastal Mar. Sci.*, Vol. 7, pp. 567–575

ZAR, J.H., 1974. *Biostatistical analysis*. Prentice-Hall, Inc., Englewood Cliffs, New Jersey, 620 pp.