Diet, Prey Selection and Daily Ration of *Stomolophus meleagris*, a Filter-feeding Scyphomedusa from the NE Gulf of Mexico

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Keywords: *Stomolophus meleagris*; scyphomedusa; feeding; prey selection; Gulf of Mexico

More than 20 prey taxa were identified from gut contents of *Stomolophus meleagris* medusae in the north-eastern Gulf of Mexico; seven taxa formed over 98% of the total. Bivalve veligers (mostly *Crassostrea virginica*) dominated, constituting 56% of the total. Other significant prey were copepod eggs, nauplii, copepodites and adults, gastropod veligers, and *Oikopleura* sp. Mean numbers of prey in the guts of *S. meleagris* medusae (bell height ranged from 1·5 to 10 cm) varied from 400 to 9300. Numbers of prey were an exponential function of medusan biomass, increasing from 700 prey at 9 g wet weight to 6000 prey at 325 g wet weight. Mean numbers of ingested prey ranged from 4000 to > 65 000 prey day $^{-1}$ medusa $^{-1}$. Bivalve veligers made up 47% of the daily ration. The daily ration was estimated to range from 20 to 100 mg C medusa $^{-1}$, depending on size of the medusa. Bivalve veligers were selected over all other kinds of prey. Fish eggs were the next preferred prey followed by harpacticoids, larvaceans and tintinnids, all with selectivities near zero. Lowest selectivity values were for copepod nauplii, and cyclopoid and calanoid copepods. Estimated *in situ* clearance rates were highly variable depending on the prey and size of the medusa, and ranged from < 1 to 1351 h $^{-1}$ medusa $^{-1}$. A description of the possible mechanism of feeding and mode of prey selection is presented. Filter-feeding in rhizostomes probably evolved in response to small prey size in tropical waters.

Introduction

Medusae are a diverse group of planktonic predators occurring in virtually all marine habitats as well as in freshwater. Their success is based in part on their ability to grow rapidly and thus be tightly coupled to ephemeral secondary production (Larson, 1986*a*). Medusae are the largest non-colonial planktonic organisms, with one species reaching a mass of nearly 100 kg (Harbison *et al.*, 1973). This large size, achieved mostly by incorporation of water into their tissues, gives them a large surface area that is formed using minimal amounts of carbon (Larson, 1986*b*). Additionally, most species have tentacles that further increase their surface area. With a substantial encounter area, many medusae can depend on the locomotion of prey to bring about encounters.

However, there is one group of medusae, the rhizostome scyphomedusae, that lacks tentacles. Instead they have lips surrounding the mouth that have undergone extensive development to form the oral arms, a sieve which filters zooplankton as the medusa swims (Uchida, 1926; Thiel, 1964).

Rhizostomes comprise about 80 species that mostly occur in inshore tropical waters (Kramp, 1970) where they are the basis of a fishery (Omori, 1981). They are often large, reaching a diameter of 50 cm or more, and have eight, gelatinous oral arms which hang from the subumbrella. The oral arms are morphologically unique at the generic or specific level, but all are formed by enlargement and branching of the four original ephyral lips (Uchida, 1926). The lips along the distal portions of the oral arms are branched, thus increasing the surface area. Regularly spaced along the margin of the lips are numerous digitata, small (30 μm wide by 0·2 to 0·3 mm long), capitate finger-like structures which have concentrations of nematocysts at their tips. Once prey are captured by the digitata, the digitata bend inward passing prey into ciliated grooves that lead proximally to a canal system extending to the stomach (Smith, 1934, 1936; Thiel, 1964; Larson, 1978).

In the few rhizostomes that have been studied, prey mostly consists of mesozooplankton, especially copepods, but many other kinds of zooplankton are also eaten (Smith, 1934; Thiel, 1964; Kikinger, 1983; Fancett, 1988). Although larger prey such as chaetognaths are occasionally consumed, the vast majority of prey are < 1 mm in length. The size of prey ingested is limited by the diameter of the canals leading to the stomach which are generally narrow (< 3 mm) in diameter. Nonetheless, elongate prey such as chaetognaths can be eaten if they are narrow enough to pass into the stomach. Although it was once thought that very large prey such as fish could be digested in the oral arms of rhizostomes, as is the case in some semaeostomes (Larson, 1986*a*), there is no evidence to support this hypothesis.

There have been few detailed studies on the trophic biology of rhizostome medusae. Smith (1934, 1936) studied prey capture and digestion in the atypical, benthic, Caribbean rhizostome *Cassiopea frondosa*, and Thiel (1964) investigated the diet of *Rhizostoma pulmo* in European waters. Most recently, Fancett and Jenkins (1988) measured clearance rates of *Pseudorhiza haeckeli* in the laboratory and extrapolated these rates to predict *in situ* predation rates, and Fancett (1988) studied *in situ* prey selectivity in this species from South Australia.

The present study documents the diet, daily ration and prey selectivity of *Stomolophus meleagris* in the north-eastern Gulf of Mexico. During summer months this medusa can be very abundant (Hedgepeth, 1954; Phillips *et al.*, 1969) and thus could be an ecologically important predator of zooplankton. Scant information is available concerning its trophic biology despite its broad distribution in inshore waters from South America to Virginia (Mayer, 1910; Larson, 1976) and in the eastern Pacific from Panama to southern California (Bigelow, 1914).

Methods

This study was conducted from June 1986 to October 1987 in the north-eastern Gulf of Mexico near the Florida State University Marine Laboratory between Carrabelle and Alligator Harbor, Florida (Figure 1). *Stomolophus meleagris* was abundant there each year from June to October, and was seen swimming at the surface where the depth was 3 to 5 m. Medusae were collected at random on 14 occasions using a dipnet (Table 1), within 5 km of the laboratory using a pontoon boat. Some specimens were immediately fixed in 10%

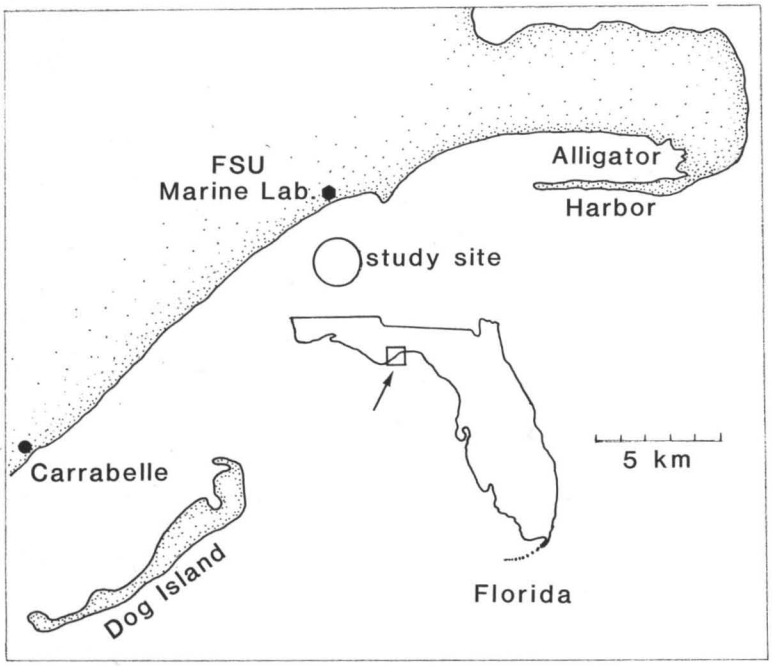

Figure 1. Map of study area.

TABLE 1. Medusae collection data

Date	Number of medusae collected for gut contents	Mean bell height (mm)	Estimated mean wet weight (g)[a]
17-6-86	20	28	19
18-6-86	18	22	10
20-6-86	9	21	9
14-7-86	5	57	120
15-7-86	21	55	110
16-7-86	12	53	100
17-7-86	13	53	100
18-7-86	15	48	80
29-6-87	16	54	105
30-6-87	17	48	80
13-7-87	6	83	330
16-9-87	8	67	190
17-9-87	5	82	325

[a]Estimated from wet weight (g) = 1·20 bell height $(cm)^{2.66}$, from unpubl. data.

formalin for later gut analysis. Others were kept alive for *ex situ* feeding and digestion experiments. These medusae were transported to the laboratory in 20-l plastic buckets. Within 1 h of capture they were placed in a 2-m diameter × 30-cm high plastic pool through which seawater at near-ambient temperature (28–30 °C) flowed. The medusae

were used for feeding experiments within 6 to 8 h of collection, although they could be kept unfed up to 4 days without significant mortality.

Gut contents were examined in a series of stages. First the oral arms and scapulets (Plate 1) were removed, and prey were searched for among the grooves and canals, using a dissecting microscope. Next, the four pleated membranes (where digestion occurs) were exposed by cutting around the stomach on the subumbrella side. The gastric surface of the pleated membranes is covered by numerous small digitate gastric cirri about 0·3 mm long. These cirri attach to prey using nematocysts and are probably responsible for digestion and absorption (Bodansky & Rose, 1922). The pleated membranes were removed by cutting around their perimeters. Prey were removed from the cirri by vigorously shaking the membranes in a bottle partially filled with water. Prey were then concentrated using a 64-μm mesh Nitex sieve. Removal of prey from the membranes resulted in the release of eggs or small fragments of the testis from the gonads in mature *S. meleagris* (>5 cm bell diameter) making counting difficult. Therefore, those samples that contained debris were diluted after shaking and the prey allowed to settle out. The supernatant was poured off and discarded; checks of this supernatant showed that it contained insignificant numbers of prey. Counting of prey was aided by using a circular, plankton-counting tray and dissecting microscope. Lengths of prey were measured using an ocular micrometer.

Digestion rates were obtained by quantifying the time-dependent decrease in numbers of prey in the guts of unfed, field-collected medusae (Larson, 1987*b*; Fancett, 1988). Upon collection, medusae were placed two per 20-l bucket in 64-μm filtered seawater so that they could not feed. Back at the laboratory, the medusae were placed in running 64-μm filtered seawater for 3 to 6 h. At intervals of 0·5 or 1 h, five to 10 animals were fixed for later gut contents analyses. 'Digestion time' was calculated from the rate of decrease in ingested prey numbers over time, defined as the time when the mean number of prey present in the guts of starved, laboratory-held medusae dropped to $\leqslant 5\%$ of ingested prey numbers observed in field-preserved specimens.

In situ zooplankton densities were measured to determine prey selectivity. Replicate vertical net tows were taken in the upper 2 m at the medusae collection sites using a 50-cm diameter, 64-μm mesh net. Longer horizontal tows were impossible because chain-forming diatoms rapidly clogged the net. Samples were fixed in 5% formalin. For enumeration, two subsamples containing >200 plankters were taken using a Stemple pipette. Replicate counts from each subsample were made with the aid of a circular counting tray and a dissecting microscope. Counts were made of the 10 dominant zooplankton groups: (1) calanoid; (2) cyclopoid; (3) harpacticoid copepods (copepodites and adults); (4) copepod nauplii; (5) barnacle larvae (nauplii and cyprids); (6) bivalve veligers; (7) gastropod veligers; (8) fish eggs; (9) tintinnids; and (10) larvaceans.

The daily (field) ration of *S. meleagris* was estimated for medusae at each collection date using the equation: $DR = GC \times 24\,h\,DT^{-1}$, where DR is the daily ration, DT the digestion time, and GC the mean number of prey in guts of field-preserved medusae (Larson, 1987*b*).

Prey selectivity was determined from an index based on the Chi square (χ^2) (Pearre, 1982). A two × two contingency table was formed based on numbers of each prey species in the ration and *in situ*. The index of selectivity '$C' = \pm(\chi^2/n)^{1/2}$, where n equals the total number of prey species, was used. Selectivity values range from −1 to +1 and represent either negative or positive or prey selectivity. Apparent prey selectivity is biased unless all prey are digested at the same rate, so differences in digestion rates were taken into account by determining selectivity from daily ration values, rather than directly from gut contents data.

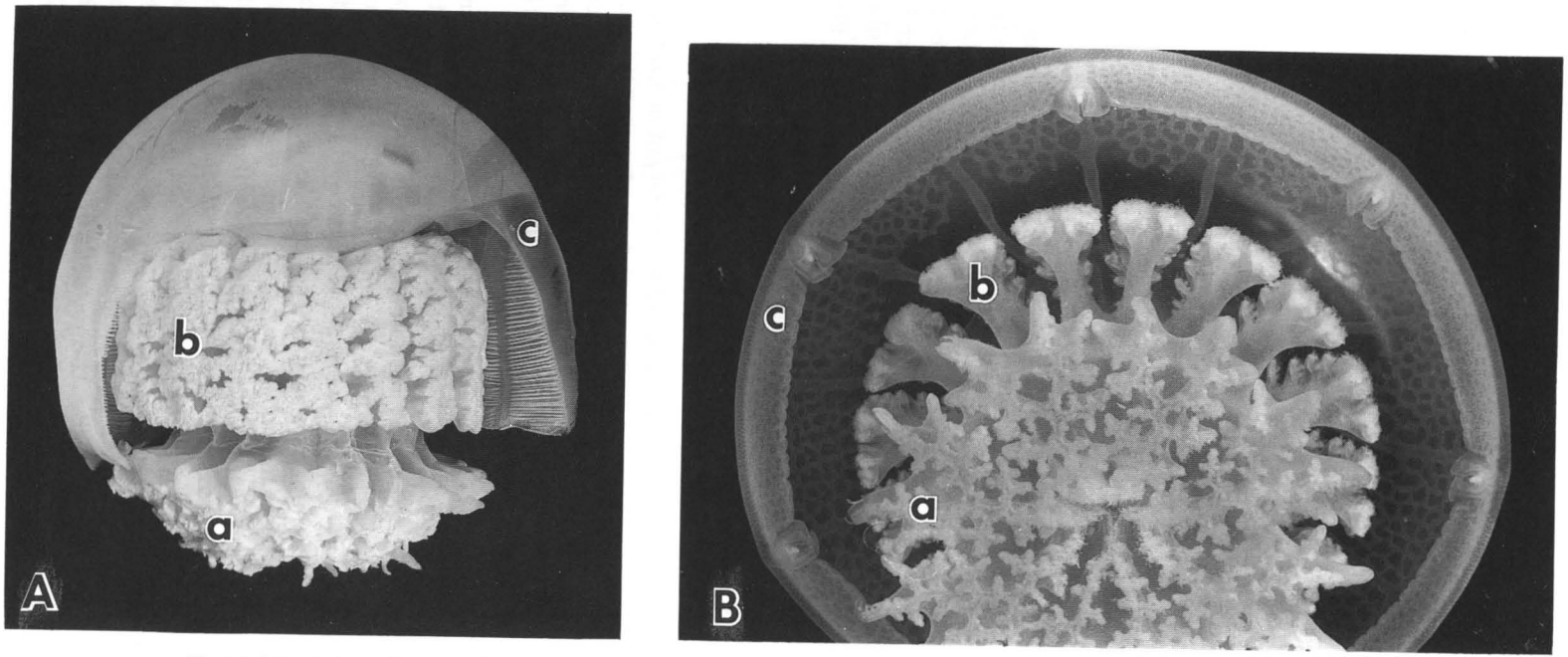

Plate 1. Morphology of *Stomolophus meleagris*. a, terminus of oral-arm cylinder; b, scapulet; c, umbrella. (A) Side view of 40-mm diameter specimen with portion of umbrella removed to show scapulets. (B) Oral view of 25-mm diameter specimen showing distal portion of oral-arm cylinder and scapulets. Note the passageways between the scapulets.

TABLE 2. Times for digestion of prey

Prey taxa	Digestion time (h)
Calanoid copepods	1·5[a]
Copepod nauplii	1·5[b]
Cyclopoid copepods	1·5[b]
Barnacle larvae	2[b]
Bivalve veligers	4[a]
Fish eggs	3[b]
Gastropod veligers	2[a]
Harpacticoid copepods	2[b]
Larvaceans	1·5[b]
Tintinnids	1·5[b]

[a]Determined from rate of decrease of numbers of ingested prey through time.
[b]Determined from time that numbers of prey in the gut reached zero.

In situ clearance rates (the rate that medusae would clear all prey from a given volume of water) were estimated from daily ration data and *in situ* prey densities (PD), where daily clearance rate = DR × PD $^{-1}$. Clearance rates were measured in the laboratory by placing five to 10 medusae that had been held in filtered seawater for 6 to 8 h, into a 840-l pool (1·8 m diameter × 0·3 m high), containing a known prey density. After 30 to 45 min, the medusae were removed and preserved for gut content analyses. *Ex situ* clearance rates (CR_{ex}) were determined from prey density (PD_{ex}) and number of prey eaten (PE_{ex}), $CR_{ex} = PE_{ex} \times PD_{ex}$.

Results

Between June and October, the mesozooplankton (>64 μm in size) was dominated by copepods (nauplii, copepodites and adults), which formed about 84% of the net zooplankton numbers. The most numerous species were *Acartia tonsa*, *Paracalanus* spp. and *Oithona* spp. Other important taxa were bivalve veligers (8%) and larvaceans (*Oikopleura* sp.) (3%). Mesozooplankton densities ranged from 18 to 500 individuals l^{-1}, with a mean of 180 individuals l^{-1}.

Medusae collected for gut contents ranged in size from 1·5 to 10 cm in bell height (overall mean = 5·2 cm) and showed a rapid growth between June and August. *In situ* observations in the top 2 m showed that most *S. meleagris* swam horizontally within 0·5 m of the surface but some were seen deeper. Medusae swam continuously, occurring almost always in patches where densities were approximately 0·1 to 10 medusae $10\,m^{-2}$. It could not be determined how such patches were maintained, but within the patches the orientation of medusae was random.

Digestion rates of *S. meleagris* depended on the prey type (Table 2, Figure 2). Some prey, e.g. *Oikopleura* sp., disappeared within 2 h of ingestion, whereas some bivalve veligers persisted even up to 6 h, although most were gone by 4 h. The rate at which prey disappeared from the gut was a hyperbolic function of time. Thus, initially the numbers of ingested prey items decreased rapidly, but thereafter more digestion-resistant prey, e.g. crustaceans and veligers, remained in the gut well after the time when the bulk had been egested.

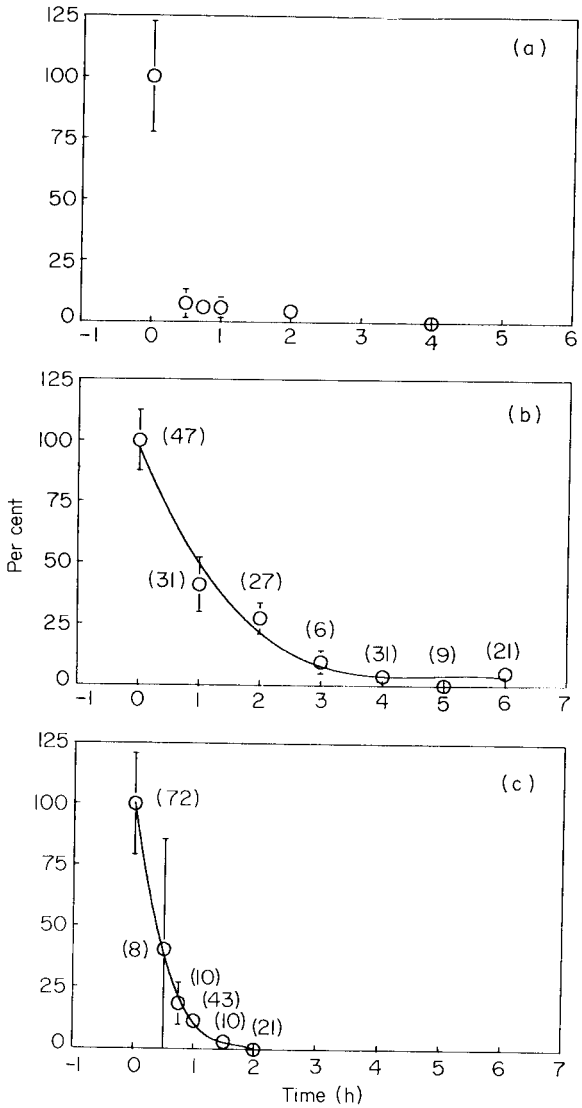

Figure 2. Plot of change in prey numbers (% of mean ± 95% confidence limits) *vs.* time in the guts of field-collected medusae placed in filtered seawater. Zero time represents time when medusae were collected. Numbers in parentheses represent number of medusae sampled. (a) Calanoid copepods; (b) bivalve veligers; (c) gastropod veligers.

Over 300 000 prey items were identified from 165 *S. meleagris* specimens (Table 3). Although prey sizes ranged from <0·1 to 10 mm long, the vast majority were from 200 to 400 μm in length. More than 20 different prey taxa were identified, but just seven formed over 98% of the total. The most abundant prey were bivalve veligers which constituted 63% of the total. They mostly consisted of oysters (*Crassostrea virginica*) which are abundant along the shore; an unidentified mytilid was also common.

Other significant prey were copepods (all stages), gastropod veligers and the larvacean *Oikopleura* sp. Ingested calanoid copepods consisted primarily of *Paracalanus* spp.

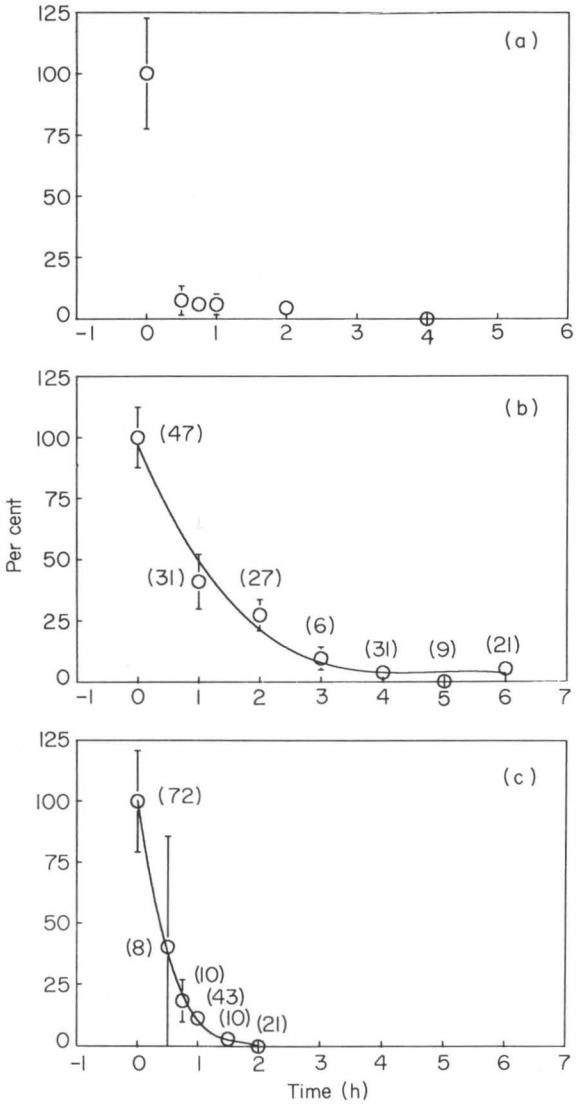

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TABLE 3. Summary of *Stomolophus meleagris* gut contents ($n = 165$ medusae)

Prey taxa	Size[a] (mm)	Number	Per cent of total
Bivalve veligers	0·15–0·4	195 900	63
Tintinnids (*Favella* sp.)	0·25–0·3	28 970	9·3
Copepod nauplii	0·1–0·15	28 420	9·1
Gastropod veligers	0·2–0·3	25 700	8·2
Calanoid copepods	0·25–1·5	13 430	4·3
Larvaceans (*Oikopleura* sp.)	0·2–0·35[b]	8850	2·8
Cyclopoid copepods	0·25–0·3	6220	2·0
Harpacticoid copepods	0·3–0·5	2670	< 1
Fish eggs	0·6–0·8	1350	< 1
Barnacle larvae	0·2–0·5	330	< 1
Tunicate larvae	0·6–0·7	136	< 1
Polychaete larvae	0·5–0·8	74	< 1
Hydromedusae	0·8–1·5	32	< 1
Brachyuran zoea larvae	0·8–1·3	20	< 1
Cladoceran (*Evadne tergestina*)	0·5–0·7	17	< 1
Chaetognaths (*Sagitta* spp.)	3–10	14	< 1
Caridean shrimp larvae	0·7–1·4	13	< 1
Brachipod larvae	ND[c]	7	< 1
Penaeid shrimp larvae	ND	5	< 1
Gammaridean amphipods	ND	1	< 1
Phoronid larvae	ND	1	< 1
Isopod juvenile	ND	1	< 1
Copepod eggs	70–80 μm	ND	ND
Algae (*Coscinodiscus* spp.)	0·2–0·25	ND	ND
		Total > 312 160	

[a] Total length.
[b] Trunk length.
[c] ND = not determined.

(mostly *P. crassirostris*) and *Acartia tonsa*. Cyclopoids were predominantly *Oithona* spp. (mostly *O. nana*). Harpacticoids consisted mostly of the pelagic *Euterpina acutifrons* and unidentified demersal species. Calanoid eggs were common in the guts, but because they were approximately the same diameter and appearance of *S. meleagris* eggs, they could not be counted.

Four types of fish eggs were ingested: (1) elliptical, probably *Anchoa hepsetus*; (2) spherical 720 to 760 μm diameter with numerous small oil globules, probably pleuronectiform eggs; (3) spherical 720 to 800 μm diameter with one to three oil droplets, probably perciform eggs; (4) spherical 700 to 800 μm lacking oil droplets, probably from an engraulid (possibly *Anchoa mitchilli*).

The large diatom *Coscinodiscus* sp. was very common in the stomach contents, but it could not be ascertained if the unpigmented cells were resuspended frustules or live cells that were partially digested. Tintinnid (*Favella* sp.) tests were also abundant in the gut samples; they ranked second (9·3% by number) in terms of their contribution to the total diet. What proportion of these were alive when ingested could not be determined because empty tests probably were present in the water column; however, in many of the ingested tests there were remains of tissue, suggesting that some live tintinnids had been ingested.

Numbers of prey observed in the gut of *S. meleagris* medusae varied from 400 to 9300 and were an exponential function of medusan biomass (Figure 3), increasing from 700

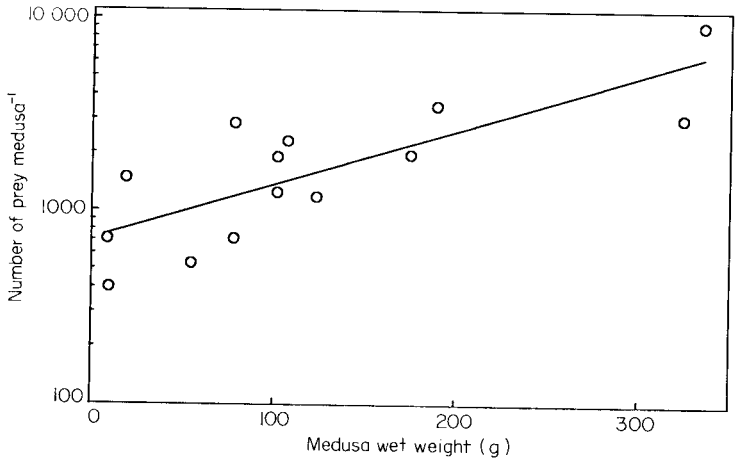

Figure 3. Plot of mean number of ingested prey per medusa *vs.* mean medusan wet weight. Each data point represents a collection of medusae.

prey at 9 g wet weight to 6000 prey at 325 g wet weight. On a weight-specific basis, the number of prey ingested per medusa decreased with increasing weight [log weight-specific number of prey ingested medusa $^{-1} = 148$ g (wet weight) $^{-0.45}$, $0{\cdot}01 < P < 0{\cdot}02$].

Based on the daily ration, mean numbers of prey estimated to be consumed per medusa per day ranged from 4000 to >65 000 (with an overall average of 20 000 prey consumed by 5·2 cm bell height medusae). Bivalve veligers made up 47% of the daily ration, and 41% consisted of five other prey comprising copepod nauplii (14%), gastropod veligers (12%), calanoid copepods (9·4%) and tintinnids (6·4%). Thus, five prey categories comprised nearly 90% of the ration.

Based on the sizes of the prey ingested by *S. meleagris*, published weights and per cent carbon values for mesozooplankton (Hirota, 1981; Nishiyama & Hirano, 1983), most prey probably had average carbon weights of from 1 to 5 μg each. Assuming mean carbon weights of prey equal to 1 μg each, the relationship between medusa biomass and daily ration equals DR (mgC) = 4·1 + wet weight (g) 0·12 (Figure 4).

Based on the relative numbers of prey in the daily ration and in plankton samples, bivalve and gastropod veligers, fish eggs, tintinnids and larvaceans formed a higher proportion of the ration than they did in the plankton (Figure 5). Harpacticoids comprised about equal proportions in the ration and in the plankton. Similar trends were shown in the selectivity levels, whereby bivalve veligers were selected over all other kinds of prey (Figure 6). Fish eggs were the next preferred prey followed by harpacticoids, larvaceans and tintinnids, all with a selectivity value of near zero. Lowest selectivity values were for copepod nauplii, and cyclopoid and calanoid copepods.

Estimates of *in situ* clearance rates proved to be highly variable depending upon medusa size and on the prey category. There were insufficient data to determine clearance rates for the complete size range of medusae; however, based on mean values, a 5·5-cm high (110 g wet weight) specimen would have clearance rates ranging from <1 to 135 l h^{-1} medusa^{-1}, depending on the prey (Table 4). Based on calculated mean rates, gastropod veligers and fish eggs were cleared from the water at the highest mean rates (135 and 130 l h^{-1} medusa^{-1}, respectively) and crustaceans were removed at the lowest rates (<1 to 7 l h^{-1} medusa^{-1}).

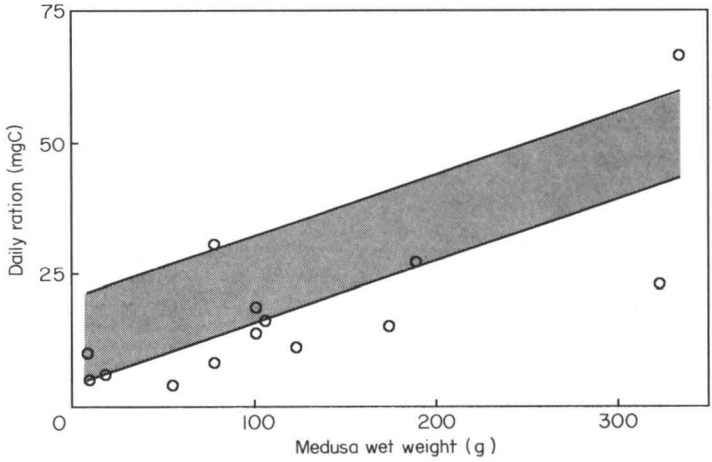

Figure 4. Scatter plot of medusa biomass *vs.* daily ration. The lower line is the line of best fit based on prey weight of 1 μg each [daily ration (mg C) = 4·1 + biomass × 0·12), $P = 0{\cdot}002$]. The upper line represents the line based on prey weight of 5 μg each.

Ex situ clearance rate studies done in the pool failed to corroborate rates obtained from the field. Clearance rates were low and highly variable; in fact some medusae had not even fed, suggesting that the medusae were not behaving normally (all field-preserved medusae contained ingested prey). This suggests that laboratory-measured feeding rates of gelatinous zooplankton could be biased.

Discussion

Although *S. meleagris* is a polytrophic planktivore, it feeds predominantly on only a few of the available prey taxa. Of more than 20 prey types identified in gut contents, most of these represented $< 1\%$ of the total prey ingested. Prey that were consumed were not necessarily those that were most abundant in the plankton, suggesting prey selection.

To understand how prey selectivity may occur in *S. meleagris* it is first necessary to describe the prey capture mechanism. The digitata, which capture the prey, are located only on the scapulets and the distal end of the oral-arm cylinder (Plate 1). In field-preserved medusae, prey found outside the stomach were seen only in these two areas, or in the canals leading from them to the stomach. Because the scapulets and the distal end of the oral arms are morphologically different and are exposed to different water motions, the prey probably contact these structures differently.

The scapulets comprise 16 ridges within the bell cavity which are arranged radially along the oral–aboral axis of the oral-arm cylinder (Plate 1). Digitata are only located on the distal edge and distal margin of the scapulets. The scapulets are positioned so that an oral–aborally directed passageway occurs between each adjacent pair. These passageways are open to the exterior at the oral end of the scapulets in the region of the bell martin. Prey encounter at the scapulets probably takes place in two ways. First, as the bell refills, prey sucked into the bell cavity probably impact the scapulets as the prey try to escape, or they impact due to turbulence within the cavity. Secondly, as the bell refills some water is

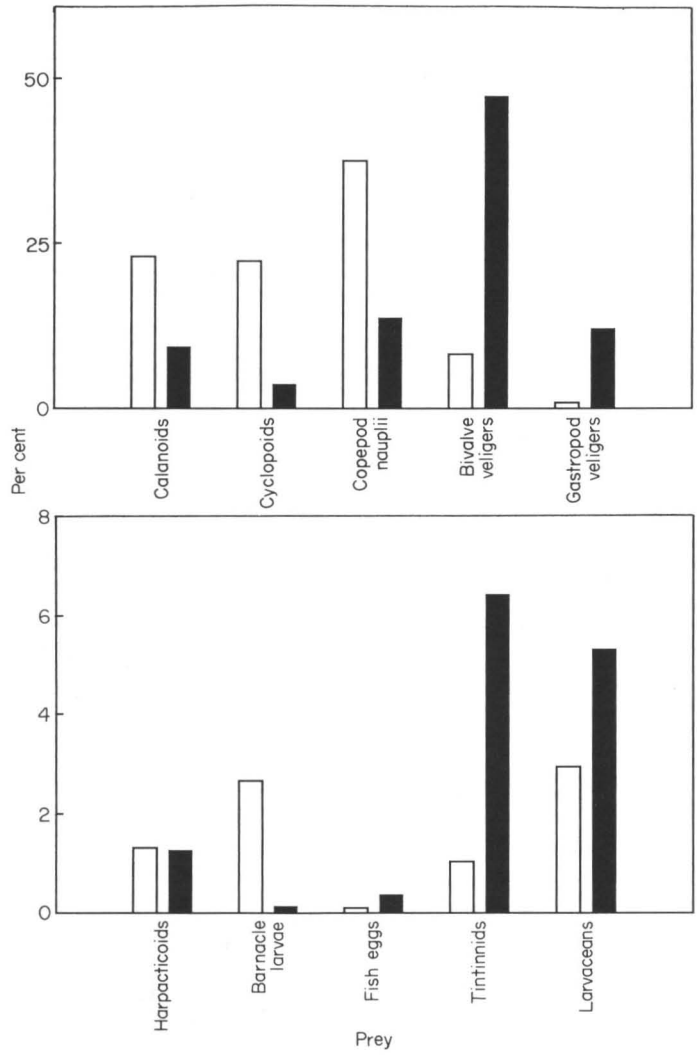

Figure 5. Histograms showing the per cent by number of individuals each prey type represents in the plankton and in the daily ration. □, Plankton; ■, daily ration.

probably forced through the passageways between the scapulets and then outwards between the digitata that line the outer scapulet margins. During this circulation, prey are probably captured by sieving and/or interception (Rubenstein & Koehl, 1977). This ' filtered ' water is then expelled from the bell cavity as the bell contracts.

Prey are also encountered on the distal (oral) surface of the oral-arm cylinder, probably as a result of inertial impact. This could happen as a result of turbulence and vortex production behind the swimming medusa. Reynolds numbers of foraging *S. meleagris* medusae are sufficiently high [1000 to 10 000 (Larson, 1987*a*)] so that flow would be turbulent (Vogel, 1981). Additionally, a torus is produced each time water is jetted from the bell (Weihs, 1976). Both turbulence and vortices probably bring prey into contact with digitata on the terminal portion of the oral arms where the prey are trapped.

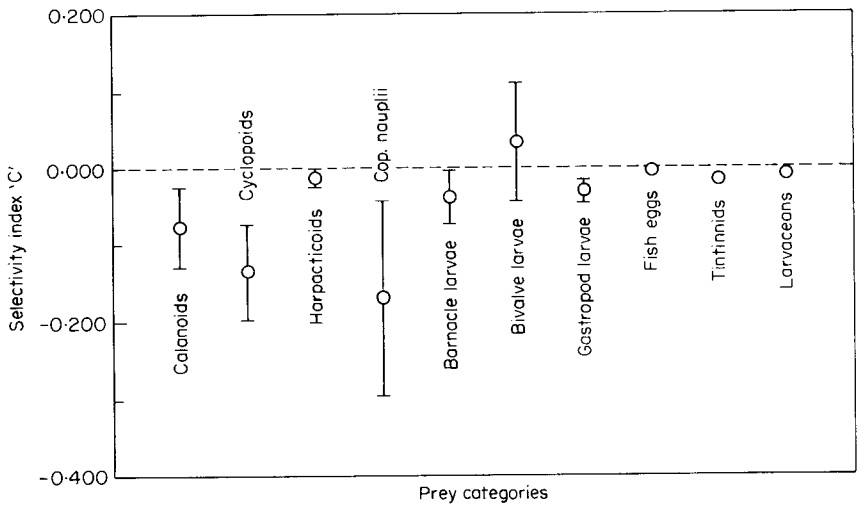

Figure 6. Selectivity values (mean $\pm 95\%$ confidence limits) of *S. meleagris* feeding on various prey based on the 'C' index (Pearre, 1982). Positive or negative selection is represented by the sign.

TABLE 4. Mean estimated *in situ* clearance rates of *Stomolophus meleagris*[a]

Prey taxa	Clearance rate ($l\,h^{-1}$ mean $\pm$ SE)	*N*
Gastropod veligers	135 ± 50	10
Fish eggs	130 ± 66	5
Bivalve veligers	53 ± 28	8
Tintinnids (*Favella* sp.)	52 ± 20	8
Larvaceans (*Oikopleura* sp.)	31 ± 16	9
Harpacticoid copepods	$7{\cdot}2 \pm 2{\cdot}4$	10
Calanoid copepods	$1{\cdot}7 \pm 0{\cdot}4$	10
Cyclopoid copepods	$1{\cdot}2 \pm 0{\cdot}4$	10
Copepod nauplii	$1{\cdot}0 \pm 0{\cdot}4$	10
Barnacle larvae	$0{\cdot}2 \pm 0{\cdot}2$	4

[a]Estimated for 5·5 cm bell height medusa.

Phillips *et al.* (1969) suggested that mucus strands are used by *S. meleagris* to capture prey; however, I have observed that large amounts of mucus are formed only in response to a disturbance such as handling, and are not normally seen *in situ*. Shanks and Graham (1988) found that mucus is secreted in response to predators.

Size-specific prey selectivity is probably the combined result of prey behaviour and the feeding mechanism of *S. meleagris*. Size selection of prey may occur at the scapulets because large or very active prey escape. Also, very small prey ($<0{\cdot}1$ mm) may pass between the digitata, which occur at intervals of about 30 to 50 μm. Similarly, there may be selection at the posterior, oral-arm region as a result of active escape by large prey and by a lack of contact with very small prey which may have insufficient inertia to impact on the digitata.

Thus, prey selectivity is probably based on a number of factors. Active, mechanosensitive or visually-acute prey might detect water movements and or see *S. meleagris* and escape before they make contact with the medusa, whilst others might escape even after contact. Relatively small prey could escape by passing through the scapulet filter, or may lack sufficient inertia to contact and be captured by digitata on the terminus of the oral arms. Data on prey selectivity and clearance rates suggest that weak or non-swimming prey, e.g. veligers, fish eggs and tintinnids, were removed at higher rates than more active prey, e.g. calanoid and cyclopoid copepods. Copepods may detect a swimming medusa as a result of fluid deformation (e.g. Haury *et al.*, 1980) or visually (e.g. Busky *et al.*, 1986). Also copepods can escape after making contact with gelatinous predators (Fancett, 1988; Larson, 1988). The low selectivity for copepod nauplii is puzzling, because similarly-sized tintinnids had higher selectivity values.

A number of other investigators have previously stressed the importance of differential escape abilities of prey as the primary factor determining prey selectivity in gelatinous predators (Greene *et al.*, 1986; Larson, 1987*c*; Purcell *et al.*, 1987; Fancett, 1988). However, there are other factors which may affect selectivity. Apparent differences in prey selectivity and *in situ* clearance rates could be highly biased by heterogeneous prey distributions. If medusae can find and exploit small prey patches, then to accurately measure prey selection would require locating and sampling these patches, something that is not easily done. This is especially true for *S. meleagris* which could have been feeding hundreds of metres from where it was collected. Thus, every study on *in situ* prey selection can only be an approximate measure.

It was estimated in this study that if prey averaged between 1 and 5 μg C each, then the overall mean daily ration would equal from 20 to 100 mg C. From respiration data in Larson (1987*a*), and assuming a respiratory quotient of 0·8 and an assimilation efficiency of 80%, a medusa of average size (45 mm bell height or 65 g wet weight) would require about 30 mg C day $^{-1}$ to meet metabolic demands. Given these assumed conditions, ingestion rates measured here were somewhat below metabolic demands. However, the rates of prey ingestion determined are probably conservative because of difficulties in counting all the prey in the gut, and the possibility that microzooplankton such as ciliates and rotifers may be eaten (Stoecker *et al.*, 1987; Bamstedt, 1990), but were not seen in the gut samples. Additionally, laboratory-measured respiration rates may be elevated because the animals were confirmed to a small chamber.

Because of a lack of quantitative data on *S. meleagris* densities, it is impossible to determine its impact on zooplankton prey populations. However, since the estimated daily consumption of bivalve larvae was so high (mean of 9000 larvae eaten per day per medusa, and an extreme average on one date of nearly 50 000 larvae eaten per day per medusa), and densities of veligers were so low (mean of 24 veligers l^{-1}), where *S. meleagris* is present in high densities it could have a significant but patchy impact on certain prey.

The evolution of filter-feeding in rhizostomes, a largely tropical group, may have been in response to the small size of zooplankton in inshore areas. These smaller species probably have relatively low swimming speeds and thus encounter rates would be decreased. However, by filtering prey, rhizostomes would not be dependent on swimming speeds of their prey to bring about encounters. Rhizostomes may be less successful in temperate and boreal regions because the relatively larger prey might avoid or escape more readily; however, other factors are probably also involved. Further studies are needed both on rhizostome feeding and on prey selection by gelatinous predators.

Acknowledgements

I would like to thank Jack Hitron and the staff at Florida State University Marine Laboratory for making their facilities available to me. Also, I thank Bruce Comyns of Gulf Coast Research Laboratory for fish egg identifications. The manuscript was improved by suggestions from two anonymous reviewers. This is contribution no. 832 of Harbor Branch Oceanographic Institution.

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