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A Note on the Feeding, Growth, and Reproduction of the Epipelagic Scyphomedusa *Pelagia noctiluca* (Forskål)

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Abstract *Pelagia noctiluca* is a common circumtropical, epipelagic scyphomedusa. It captures prey either on the exumbrella, tentacles, or oral arms. Ciliary activity and muscular contractions transport the prey proximally toward the stomach where the elongate gastric cirri attach to it and digestion begins. Prey of *P. noctiluca* medusae collected in inshore waters of Puerto Rico consisted of a wide variety of zooplankton (e.g., hydromedusae, ctenophores, copepods, chaetognaths, and fish eggs). The ability of *P. noctiluca* to feed on both large and small prey species is adaptive in the open ocean where prey are taxonomically variable and of a broad size range. *Pelagia noctiluca* medusae were maintained in the lab for more than 20 days. A biomass doubling occurred in 14 days. The medusae consumed food equaling 60% of their wet weight per day. Growth efficiency was 10%. Starvation weight loss was >50% in 7 days. Because *P. noctiluca* often occurs in dense swarms, they can consume large amounts of prey in a short time period. Since they also become sexually mature at a small size and have direct development, they can have a significant impact on prey populations.

KEY WORDS: Scyphomedusa, *Pelagia,* feeding, growth, reproducton.

Introduction

Pelagia noctiluca is a small, brightly colored, epipelagic scyphomedusa which is often seen in large numbers throughout warm oceans (it can also be carried into colder waters by currents). Sanders and Sanders (1963) reported *P. noctiluca* strandings along the Texas gulf coast where the medusae were seen ". . by the thousands in a belt about 9 feet broad extending for miles. . . ."; Russell (1970) recorded a number of large swarms near the British Isles; and Angel et al. (1982) found dense nighttime surface swarms at 42°N, 17°W. Recent blooms of *P. noctiluca* in the Mediterranean have had a significant financial impact on the tourist industry and have spurred research into the sudden population increases shown by this species (Malej, 1982; Rottini-Sandrini et al., 1983; Anonymous, 1984).

Although *P. noctiluca* is both ecologically important and has economic significance, little is known about its trophic biology. Delap (1907) observed that when *P. noctiluca* occurred in Valencia Harbor, the adult medusae fed on salps, and laboratory-maintained ephyrae ate hydromedusae. Bozler (1926) examined the reactions of this medusa to various chemical components of their food and found that *Pelagia* was highly responsive to proteins. Malej (1982) examined gut contents of *P. noctiluca* collected in the Adriatic Sea and found planktonic cnidarians, planktonic crustaceans, larvaceans, doliolids, and fish eggs. Additionally, Harbison (pers. comm., 1986) has seen this medusa off Florida with their guts filled with salps.

This paper presents the first detailed account of prey capture, growth, and egg production of *P. noctiluca*.

Methods

Pelagia noctiluca medusae were collected from shelf waters off the south coast of Puerto Rico during March 1976. Medusae were carefully dipped from surface waters with a bucket. Some specimens were immediately fixed in 5% formalin for later analysis of gut contents. Others were brought to the lab and kept alive in outdoor tanks where a normal light cycle occurred. These specimens were kept in 2-L plastic bags suspended in an aquarium. Water was changed daily. Water temperatures in the lab were 27–29°C. Ova from spawning females were collected by sieving the water through 100-μm Nitex cloth. *P. noctiluca* medusae were fed pieces of *Cassiopea* sp. Food was weighed, after careful blotting, and any uneaten food was removed daily and also weighed. Medusae were weighed at intervals of a week or less.

Results

In Situ Observations

On March 12, 1976, a small shoal of *P. noctiluca* was seen about 2 miles offshore from La Parguera, on the south coast of Puerto Rico. Medusae were most abundant in an area ~200 m^2, where they reached densities of 20–50 medusae m^{-2}. Most of the medusae were seen at the surface, but others could be seen in the upper 1–3 m. Individuals were mostly oriented vertically, swimming with their tentacles contracted.

Gut Contents

Fifty field-preserved medusae were examined for contained prey. Medusae ranged in size from 10 mm to 40 mm bell diameter, with a mean of ~30 mm. The following prey were found: hydromedusae, siphonophores, ctenophores, polychaetes, copepods, ostracods, cumaceans, isopods, amphipods, chaetognaths, and fish eggs. Fish eggs were the most abundant prey with up to 10 eggs found per medusa. The mean abundances of the most numerous prey were: 2 copepods, 1 cumacean, 1 chaetognath, and 3 fish eggs. Other prey occurred at densities of <1 per medusa. Only 2 medusae were found without prey. Non-prey items found in the guts were: macroalgae, seagrass, and pieces of cane charcoal. No plankton samples were taken and thus prey selectivity could not be determined.

Laboratory Behavior

About 30 medusae were observed in the lab. During the first 24 h, the medusae were apparently disturbed; swimming was vertical (either downward or upward) and bell pulsation rates were high (130–170 pulsations min^{-1}); tentacles remained contracted. After 24 h, a few medusae began to swim horizontally, with their tentacles extended, and pulsation rates decreased (120–150 pulsations min^{-1}). After 2 days, some specimens had resorbed so much umbrella mesoglea (due to excessive activity) that they could hardly swim. After 3–4 days, many medusae had died (due to starvation induced tissue resorption). After 5 days, 4 medusae in the best condition were selected for feeding and growth experiments.

Feeding Behavior

When a piece of food (*Cassiopea*) was placed with a *P. noctiluca* specimen, it was either caught on the exumbrella, tentacles, or oral arms (all of these areas have many visible nematocyst warts—small atrichous nematocysts 4–7 μm were especially abundant, but larger atrichs 12 × 15 μm and very large holotrichs 30 × 30 μm and a few eurytele nematocysts also were found). If food was caught on the exumbrella, it was usually swept to the bell margin; the margin then bent inward; and the adjacent oral arm contracted and bent outward toward the margin. Once the lip margin of the arm contacted the food, it rapidly began to creep (due to ciliary activity) over the food moving it proximally within the oral arms. Under 10× magnification, the oral arms appeared to be highly excitable—with much spontaneous twitching, bending, and contracting, especially in the region of the lips.

Food touched to a tentacle caused an immediate contraction. The stiff tentacle with attached food then bent inward and the adjacent oral arm bent outward toward the food.

When food was transferred from the tentacle or exumbrella to the oral arms, swimming (which is otherwise continuous) stopped, owing to complete inhibition of bell pulsations on the side of the umbrella nearest the food. On the opposite side of the bell, pulsations were weak, but rapid. Once transfer was complete, swimming resumed.

Digestion

Once the food was moved as far as possible to the proximal portions of the oral arms, it became attached to the elongated (to 2 cm) gastric cirri (these cirri contain atrichous nematocysts (12 × 17 μm) which apparently attach the cirri to the food). Within 10 min, the cirri had completely covered the food, obscuring it from view.

During digestion, carmine particles were injected into the coelenteron so that the circulation of gastric fluids could be seen through the transparent subumbrella. Particles moved peripherally along the roof of the stomach in the tentacular and rhopalar radii. On the floor of the stomach, movement was oriented proximally along the gastric septa. As digestion progressed, particles moved distally along the abaxial portion of the oral arms and were ejected at the arm tips. Digestion was rapid, considering the size of the meal, taking 8–10 h for the medusa to completely digest a piece of *Cassiopea* equal to ½ its body weight.

Growth Experiment

Medusae showed rapid growth during the first week of the experiment, with a mean weight gain of ~55% (range = 53–66%) (Figure 1). However, between 7 and 14 days, one specimen died and another began losing some weight and later died; the other two continued to grow. After 14 days, the remaining 2 specimens (both female) were then starved to determine starvation weight loss. After 6 days of starvation, the 2 specimens weighed approximately the same as they did at the beginning of the experiment.

During the period when the medusae were fed, they consumed food equal to 40–90% (mean = 65%) of their biomass per day. Growth efficiency (biomass increase/food consumed), on a wet weight basis, equaled ~10% (range = 7–12%).

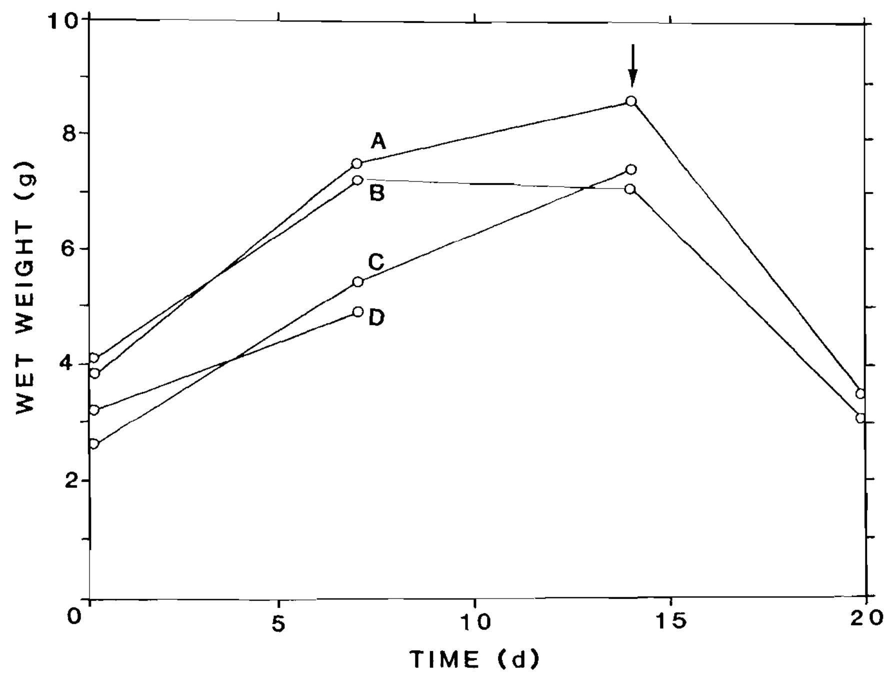

FIGURE 1. Growth and degrowth of *Pelagia noctiluca* in the laboratory. Wet weight for 4 *P. noctiluca* specimens as a function of time (arrow = time at which medusae were starved). Specimens A and B were females for which egg production was measured.

Egg Production

During the 2-week period of time when the medusae were fed, the 2 female medusae released ova nightly. Ova production occurred only when medusae were fed and stopped shortly after food was withheld. On average, 40 (range 10–90) ova (250–300 μm diameter) ova were released per day.

Discussion

Pelagia noctiluca is apparently an opportunistic predator, feeding on zooplankton of a broad size and taxonomic range. Such a strategy is adaptive in the open ocean where potential prey are highly diverse in taxonomic makeup and cover a broad size range. Since the medusae can consume prey equivalent to >50% of their body weight (wet weight) per day, they could have a significant impact on prey populations when the medusae are abundant.

Production and maintenance of a large standing stock of *P. noctiluca* are indicative of favorable trophic conditions since medusae quickly stop reproducing and lose weight when starved. Although temporary jellyfish swarms may be accounted for by hydrological conditions (Vucetic, 1983; Hamner and Schneider, 1986), maintenance of a large population can only occur when sufficient food is available.

Growth rates of *Pelagia noctiluca* are less than have been reported for other gelatinous predators (Arai, 1980; Reeve and Walter, 1978) but are similar to growth rates of some scyphomedusae (Larson, unpublished). Growth efficiencies for *P. noctiluca* are comparable to those for 2 other scyphomedusae (i.e., *Chrysaora quinquecirrha* and *Drymonema dalmatinum*) (Larson, unpublished). Fraser (1969) estimated that growth efficiencies for single specimens of *Aurelia aurita* and *Cyanea capillata* were 37%. Higher growth efficiencies for *P. noctiluca* may occur *in situ* because of reduced metabolic rates. Davenport and Trueman (1985) have shown that active metabolism of *P. noctiluca* can be twice that of the basal level.

Pelagia noctiluca may be the dominant medusa (in terms of biomass) in the epipelagic zone of warm oceans. Because of its opportunistic feeding habits, high ingestion and digestion rates, rapid growth, and high fecundity, it can quickly reach bloom proportions if sufficient food is available. The impact of this predator on prey populations requires investigation.

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