Reference: *Biol. Bull.* **176**: 272–281. (June, 1989)

The Annual Pattern of Feeding, Growth, and Sexual Reproduction in *Cyanea* (Cnidaria: Scyphozoa) in the Niantic River Estuary, Connecticut

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Abstract. The seasonal occurrence, population dynamics, feeding, growth, reproduction, and timing of planular deposition was determined for a semelparous annual population of *Cyanea* medusae in the Niantic River estuary, Connecticut, which was sampled for 14 years. The annual pattern was highly predictable. Their ephyrae appear shortly after ice-out in late February, medusae with gonads occur in late April–early May, and are reproductive (bearing planulae on their oral folds) by late May–early June. At this time (early to mid-June), the medusae deteriorate, disappearing from the plankton in late June–early July. Population size, similarly, exhibits small variation, showing only a 5-fold difference in abundance. With deterioration, the frequency of feeding medusae declines; otherwise, they are opportunistic predators on seasonally numerous zooplankton, including fish. Growth shows two phases: first, a three month period of rapid exponential growth when medusae mature; and second, a one and one half month period of decline in average size of individuals as the larger medusae die. Medusae exhibit a sequence of "organ" loss prior to death: first, the tentacles, then the oral folds, and last, the gonads. Coincident with the disappearance of these organ-deficient medusae from the water column, their planulae first appear attached to shells in the benthos. The deterioration of medusae, and in particular the loss of planulae-bearing oral folds, may be requisite for the mass release of their planulae.

Introduction

The general biology, ecology and life history of the Scyphozoa are well-known, (*e.g.*, Agassiz, 1862; Mayer, 1910; Thiel, 1959, 1962; Russell, 1970). Jellyfish, such as *Cyanea*, are found in coastal seas worldwide. They possess a benthic polyp stage (larva) which reproduces asexually to give rise to ephyrae; these grow into dioecious, planktonic medusae (adults) that produce planulae (motile stereogastrulae), and the latter settle to the benthos to form polyps, completing the cycle. Studies of the asexual reproduction by polyps both in the laboratory (*e.g.*, Custance, 1964; Spangenberg, 1965; Sugiura, 1965; Kakinuma, 1975; Cargo and Rabenold, 1980; Calder, 1982) and in the field (*e.g.*, Thiel, 1962; Gröndahl and Hernroth, 1987; Gröndahl, 1988; Brewer, unpubl.) show the effect of food and seasonal temperature on this process. On the other hand, most past studies of scyphozoan medusae have been taxonomic and zoogeographical (*e.g.*, Mayer, 1910; Kramp, 1961), or have focused on their local seasonal and spatial distributions (see below), and the details of their sexual reproduction and ecology remain obscure.

The awareness that scyphozoan medusae may have a major impact on the dynamics of plankton communities (*e.g.*, Phillips, *et al.*, 1969; Shushkina and Musayeva, 1983; Feigenbaum and Kelly, 1984) and especially on fish populations (*e.g.*, Möller, 1979, 1980a, b, 1984; van der Veer, 1985) has stimulated a renewed interest in jellyfish; that they, and other gelatinous plankton, eat fish is established (reviewed in Purcell, 1985). Larson (1986a) examined growth and production rates of gelatinous plankton in pelagic food webs; Shenker (1985), Larson (1986b), and Schneider (1988) provide data on the chemical composition of medusae necessary for such studies. Fancett (1988) showed that *Cyanea* is a selective predator on fish, and an evaluation of their influence on the abundance of both ichthyoplankton and zooplankton is given by Fancett and Jenkins (1988). Larson

Received 22 September 1988; accepted 29 March 1989.

(1987a) describes the predatory impact of hydromedusae and ctenophores on commercially important zooplankton. The effect of different density combinations of hydro- and scyphomedusae and their larval fish prey has been experimentally examined in the field by de Lafontaine and Legget (1988) using *in situ* enclosures.

Field studies of several years duration help to determine the significance of such predator-prey relationships as well as to understand the life history of the predator species concerned. Few long-term field investigations of *Cyanea* have been done. Exceptions are the studies of seasonal abundance by Russell (1931) in the Plymouth area, van der Maaden (1942) and Verwey (1942) along the Dutch coast, and by Rasmussen (1973) in the Isefjord, Denmark; and more recently, in its role as a predator, by NUSCo (1986) in the Niantic River, Connecticut, and by Hernroth and Gröndahl (1983), Gröndahl and Hernroth (1987), and Gröndahl (1988) off the west coast of Sweden. Earlier, Fish (1925) reported the seasonal occurrence of *Cyanea* in the Woods Hole region of Massachusetts for the years 1893–1907, during two years of which they were absent. A difficulty for long-term studies of these medusae is their large year-to-year variation in abundance (*e.g.*, van der Maaden, 1942; Verwey, 1942; Rasmussen, 1973).

This study of *Cyanea* was done on a circumscribed estuarine population in the Niantic River, Connecticut; here, medusae occur from early spring to early summer every year (Marshall and Hicks, 1962). I sampled medusae at this site for 14 years to determine the annual timing of sexual maturation (appearance of gonads) and of reproduction (presence of blastulae and/or planulae on the oral folds); the extent to which population size varies from year to year; their diet, feeding frequency, and seasonal food preferences; the average growth rate of medusae; and when planulae are released by medusae which marks the beginning of the asexual benthic phase of their life cycle.

Materials and Methods

The site of this study was the estuary of the Niantic River, Waterford, Connecticut, described in Marshall (1960), Marshall and Wheeler (1965), and in McGill (1972). It is a typical coastal estuary except that its mouth into Long Island Sound (Niantic Bay) is restricted to a narrow channel by a railroad embankment. Sampling for medusae, and recording of surface temperature, was done between February and July, 1973–1986, at weekly or fortnightly intervals.

Medusae were collected from docks at Smith Cove (on the western margin of the Niantic River) using a dip net, and on each sample date a relative measure of abundance of medusae was obtained by counting the number seen during a 30-min period (1981–1986). In the laboratory, their size, state of reproduction, condition (intact or deteriorating), and the contents of their gastrovascular cavity, was determined. The maximum diameter of each medusa (3220 individuals) was measured to the nearest 1.0 mm by lying specimens on their aboral surface in a dish of only enough seawater to flatten them. To determine the relationship between diameter and wet weight, the volume (ml) of 41 medusae, 42 to 215 mm diameter, was determined by liquid displacement and expressed as wet weight (g) (Omori and Ikeda, 1984; McCauley, 1984); the wet weights were used to calculate k, the exponent for exponential growth (Omori and Ikeda, 1984) to obtain the instantaneous growth rate ($k = 1/T\ [\ln W_T - \ln W_0]$, where T is time [days] and W_0 and W_T are the initial wet weight and wet weight at time T, respectively). For each sample, and using up to 50× magnification as necessary, the number of medusae with undeveloped gonads, with testes or ovaries, and with or without blastulae or planulae on the oral folds, was recorded. Food items in 2060 individuals collected in 1980–1986 were identified.

Two methods were used to determine the timing of planula release. First, a plankton net (diameter = 24 cm; mesh = 76 mμ) was used to collect planulae in the water column during the period when medusae were reproducing. Second, sampling for planulae attached to benthic substrate occurred weekly or fortnightly between 7 April and 9 September 1981, to obtain planulocysts (newly settled planulae); these were counted, at 50×, on shells obtained by dredging the channel of the Niantic River (depth at MLW = 4 m) with a 9.1-m otter trawl. On most dates, a 3-gallon bucket of shells was gathered for examination (total = 3039 shells).

Results

Cyanea medusae exhibit four stages of development: immaturity, sexual maturation, reproduction (presence of blastulae), and deterioration as shown in Figure 1 for the years 1973–1986. Maturation occurs 43 days (range, 28–58 days) after the initial presence of medusae; gonads usually appear during the latter half of April. From then through the first half of May, fertilization and ensuing embryogenesis brings development to the blastula stage after an additional 17 (10–24) days; planulae (not shown in Fig. 1) appear on oral folds of female medusae an average of 11 (5–15) days later. Intact medusae brooding blastulae and planulae are present for 18 (11–25) days. Deteriorating medusae, which bear planulae until they lose their oral folds, occur for another 25 (11–39) days. Deterioration of medusae occurs in the same sequence each year: first, the tentacles disintegrate; next, the oral folds are lost; this is followed by deterioration of the gonads; and finally, after the necrosis of the rest of the sub-

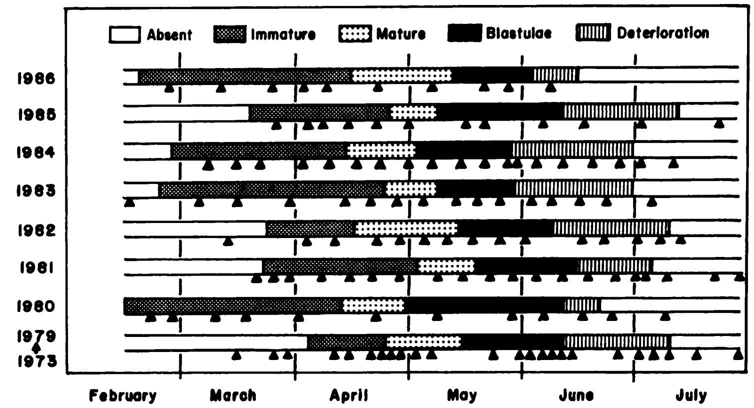

Figure 1. The seasonal occurrence and characteristics of *Cyanea* medusae in the Niantic River estuary, 1973–1986. Solid triangles indicate sample dates. Sampling was less frequent, 1973–1979, and the pattern shown represents the average for those years.

and exumbrellar epithelium, only the mesoglea remains. Even in an early deteriorated state, the medusae cannot feed (see below). Medusae, in one or another stage, occur for about 4 months each year before they disappear. The average last date to find deteriorated medusae in the plankton is 29 June.

The small annual variation in the occurrence of the different medusa stages is paralleled by the nearly constant population size of *Cyanea*. The comparison of their peak annual abundance (Fig. 2) shows that the maximum abundance of medusae (always occurring between late April and mid-May) alternates between relatively large populations in even years (1982, 1984, 1986) and relatively low populations in the odd years (1981, 1983, 1985). However, the largest population (recorded in 1986) was only 4.2 times that of the smallest (1985).

The content of their gastrovascular cavity (Fig. 3) is as predictable as is the temporal occurrence of their different stages and the range in their population size. From March through the first half of May, an average of at least 65% of medusae have copepods in their gastrovascular cavity; during the first half of this period many also contain *Palaemonetes* and *Mysis*, replaced by amphipods (mostly gammarids, but a few caprellids) during the second portion of this period. In the latter half of May, when many medusae also contain *Nereis* in their gastrovascular cavity, the percentage that are feeding is halved (from 85% to 41%); this coincides with the deterioration of medusae. This decline in proportion of feeding medusae continues, until in July it is usual to find the gastrovascular cavity empty. Most of the medusae which are still feeding late in the season contain veliger larvae. Less than 2% of medusae contain 12 other species of zooplankton (Cnidaria [ephyrae, *Sarsia, Nemopsis, Rathkea*]; nemertean larvae; Rotifera; polychaete larvae; crustacean larvae [nauplii, megalops, cypris]; Isopoda; and Ostracoda). On the other hand, a consistent proportion (18.9 ± 7.6%) contain fish eggs, yolk-sac larvae, fry, or adults (*Ammodytes, Fundulus, Gasterosteus, Syngnathus*). The percentage of these medusae containing fish eggs was 29%; yolk-sac larvae, 35%; fry, 18.7%; and adults, 17.4%.

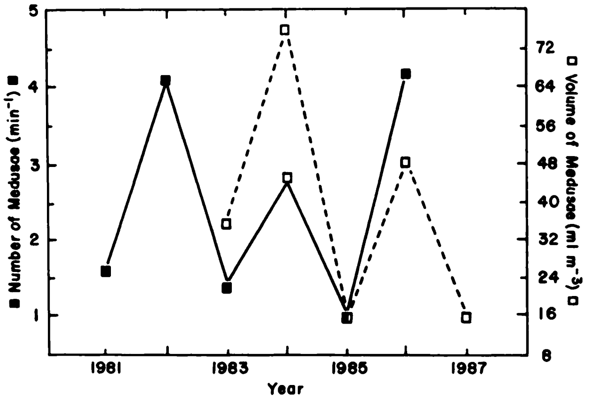

Figure 2. The relative number (this study) and volume (NUSCo, 1988) of *Cyanea* medusae in the Niantic River estuary, 1981–1987. (See Discussion for NUSCo data.)

The growth of medusae follows the same pattern each year (Fig. 4). From their first appearance until the second half of May their growth is exponential. During this time, the fastest growth was 5.6 mm diameter week^{-1}; the slowest was 2.8 mm week^{-1}; and the overall average was 5.0 mm week^{-1}. Wet weight, determined from the relationship shown in Figure 5, was used to calculate the instantaneous daily growth rate (k): $k = 0.13$, 0.02, and 0.06 for the fastest and slowest growth, and the overall average, respectively. The period of exponential increase ends in June, when the average size of medusae declines

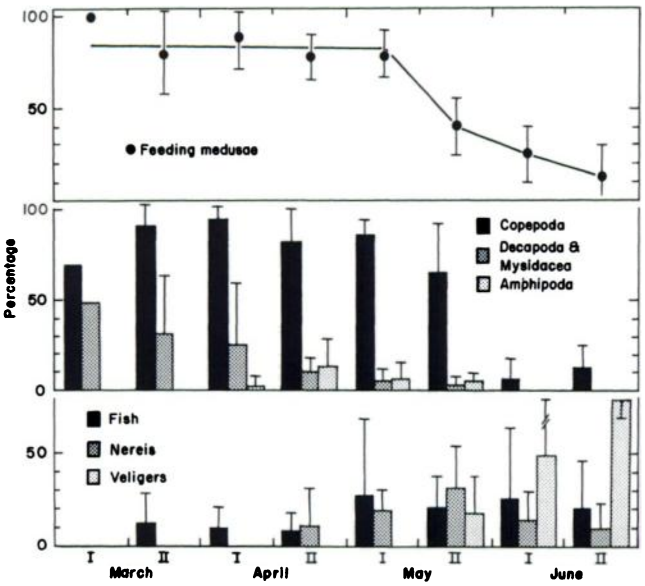

Figure 3. The percentage (±S.D.) of feeding medusae (1980–1986) in the Niantic River estuary, and the average percentage (±S.D.) which contained the indicated taxon in their gastrovascular cavity in the half-month shown.

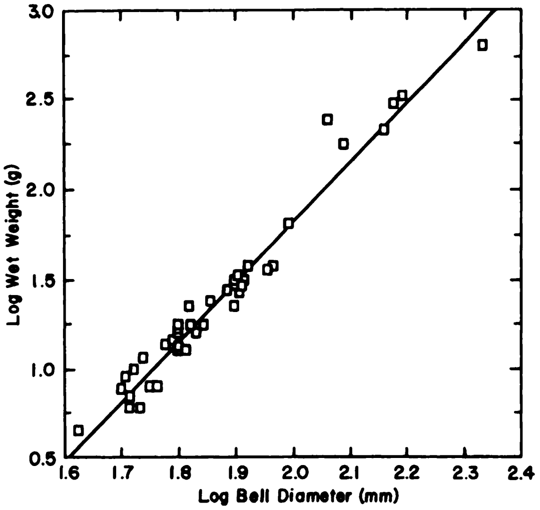

Figure 5. Log-log plot of the relationship between wet weight and bell diameter for *Cyanea:* log wet weight (g) = 3.34 log bell diameter (mm) − 4.85 ($R^2 = 0.964$, $F = 1047$, $P = 0.0001$).

due to death of larger individuals (Fig. 6). The overall average temperature (and range) at which deterioration occurs is 19.1 ± 2.3°C (16.7°C to 23.3°C).

The onset of reproduction (females with blastulae) is also shown in Figure 6. This occurs earliest in the largest medusae, but even the smallest medusae mature and reproduce before all individuals eventually disappear (between 7 July and 13 July in 1982). The average size (all years) of the earliest 10% of medusae which reproduce is 124 ± 16 mm, and that for the latest 10% of reproducing medusae is 39 ± 7 mm; but the average age of the smaller

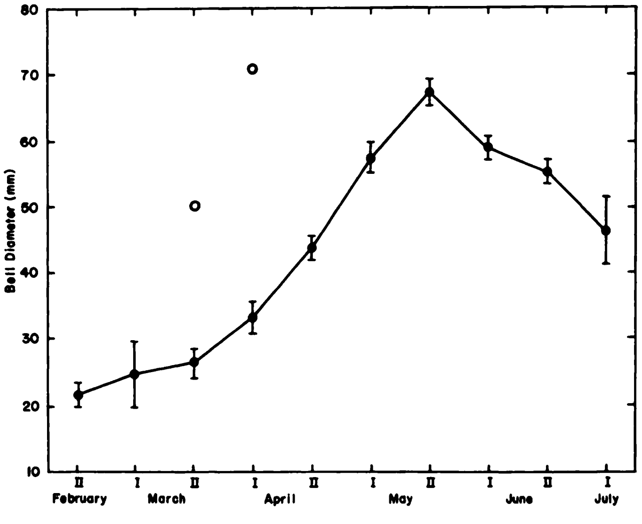

Figure 4. The growth (mean ± 0.95 c.l.) of *Cyanea* medusae in the Niantic River estuary, by half-month interval, from 1973 to 1986. Medusae in 1985 (open circles) are not included in the calculations.

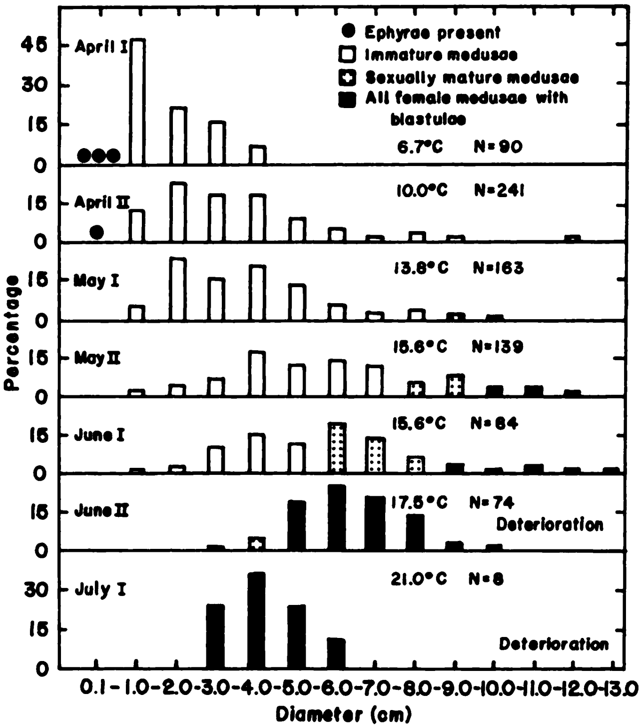

Figure 6. The size frequency distribution for *Cyanea* medusae collected in 1982. The frequency of individuals in each size class from samples in each half of a month are combined. The state of maturity, reproduction (females with blastulae), and condition are indicated. The temperature shown is the average for the half-month periods, and N is sample size.

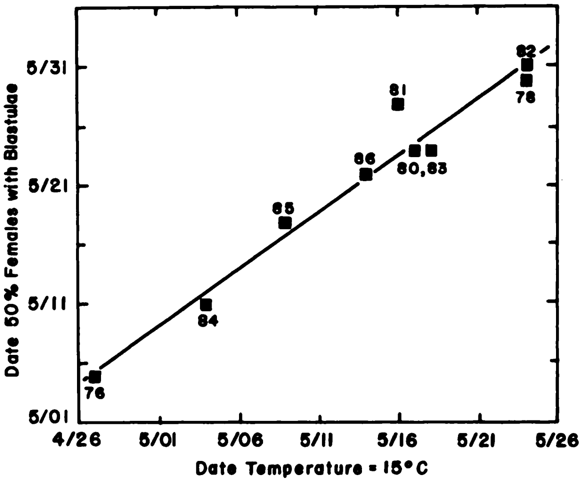

Figure 7. The relationship between temperature and the onset of reproduction (appearance of blastulae on the oral folds) in *Cyanea*. Numbers beside the points indicate the year.

medusae is up to 45.0 ± 10.6 days older than the larger ones. The sex ratio of *Cyanea* is 1:1 (n = 1239).

Sexual development and the onset of reproduction, shown in Figures 1 and 6, is correlated with the increase in temperature during May (and late April). The date that 50% of females bear blastulae on their oral folds is plotted in Figure 7 against the date that the surface water temperature attains 15°C for the nine years that the data permit such calculations ($R^2 = 0.96$, $F = 156$, $P \ll 0.001$). The average female produces blastulae 8 ± 2 days after the surface water temperature reaches 15°C; the blastulae then develop to form planulae.

The attachment of planulae to hard substrate in the benthos occurs predominantly after medusae deteriorate, and particularly after they disappear from the water column (Fig. 8). The proportion of shells bearing attached planulae of *Cyanea* (distinguished from those of other Scyphozoa because they uniquely encyst prior to forming a polyp) increases significantly ($P < 0.001$) at this time over that for the two samples immediately prior to the total disappearance of medusae; the difference among the five later samples is non-significant ($0.10 < P < 0.50$). The number of planulocysts found on shells just before the medusae disappear averages 6 ± 0.7; after the disappearance of medusae, the number averages 168 ± 107. Planulocysts were not observed on six sample dates prior to their first appearance shown in Figure 8, nor were planulae found in the plankton during this period even when a net was passed beneath aggregations of gravid medusae.

Discussion

The population of *Cyanea* medusae in the Niantic River estuary is remarkably stable, both in the annual timing of its growth, maturation, and reproduction, and in its annual abundance from year to year. These data on relative abundance are consistent with those obtained using standard oceanographic methods (Fig. 2). The Northeast Utilities Environmental Laboratory has recorded medusa volume in their plankton tows in the Niantic River since 1983 (NUSCo, 1984), and in three out of the four years that our sampling has overlapped, the regressions comparing our results are highly significant (1983, $R^2 = 0.959$; 1984, $R^2 = 0.962$; 1986, $R^2 = 0.828$); in 1985, the fit was poor ($R^2 = 0.297$). In 1985, the size of medusae did not fit the pattern observed in other years (Fig. 4), and the numbers I obtained then might not correspond to their volume measurements. Their data on volume have the same alternating pattern of peak abundance and show a five-fold difference between the largest population and the smallest (from data in NUSCo, 1988), and is close to what I obtained (a 4-fold difference). The density of medusae, estimated (NUSCo, 1987) by converting volume to numbers from size frequency data, shows a similar range (from 1 to 4 medusae m^{-3}) during the years 1983–1984.

There are few other long-term studies of scyphozoan abundance. Rasmussen (1973) reports relative abundance of *C. capillata* in the Isefjord (Denmark) between 1950 and 1962, by indicating the years that were exceptionally low (3 years) or high (5 years); the remaining five years presumably representing an undefined "normal" abundance. van der Maaden (1942) gauges abundance along the coast of Holland, between 1933 and 1937, by counts of stranded individuals. These data show about a 35-fold difference between the lowest and highest numbers for *C. capillata* and *C. lamarcki,* but the extent to which these reflect population size off shore is not clear.

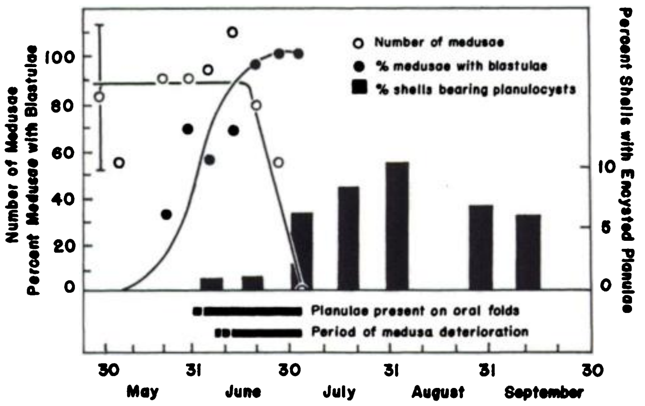

Figure 8. The relative numbers of *Cyanea* medusae in the plankton, the proportion with blastulae on their oral folds, the period when planulae were present and the medusae were deteriorating, and the frequency of attached, encysted planulae on shells during 1981. Number of medusae is number $\text{min}^{-1} \times 50$; the average ± S.D. for April is shown.

There is a 13-fold range in relative abundance, *in situ,* for *C. lamarcki* in the Plymouth area during 1925–1930 (Russell, 1931). Jellyfish abundance, *in situ,* is reported by Cargo and Schultz (1967) for *Chrysaora quinquecirrha* in Chesapeake Bay between 1960 and 1966. For this species, there is about a 100-fold difference between the lowest and highest peak population, but for the years 1962–1966, the maximum difference is only 6-fold, and was about the same ten years later (Cargo and Rabenold, 1980). Had the present study been of longer duration, the interannual peak populations might have differed to a greater extent. Nonetheless, these abundances generally indicate that variation in numbers of jellyfish among years is often less than the spatial and temporal range observed within a given season (*e.g.,* Thiel, 1962). The populations above (except for *C. lamarcki*) exhibit peak populations which alternate between low and high relative abundance for periods of at least four consecutive years as in this study, but with occasional two-year runs of similar abundance.

The succession of items appearing in the diet of *Cyanea* indicates that it is an opportunistic predator, and that apparently copepods are particularly important. During the time of maximum growth of *Cyanea,* the peak densities of *Pseudocalanus minutus, Acartia hudsonica* (both in mid-March), and *Temora longicornis* (in mid-April) occur; and the population of *Centropages hamatus* is increasing during this period, peaking in mid-June (NUSCo, 1984). The trophic significance of crustacean zooplankton in the diet of medusae is noted by Fraser (1969), Clifford and Cargo (1978), and Möller (1980, 1984). But the prevalence of copepods in the gastrovascular cavity may give a false impression of the trophic ecology of this medusa. Fancett (1988) shows that *Cyanea* exhibits a negative selection for copepods and a strong positive selection for fish (eggs, yolk-sac larvae). The proportion of medusae containing fish in the present study varied widely in different samples (occasionally reaching 100%), but on all dates, at least some medusae had fed on them. The positive relationship ($P = 0.0004$) between growth of medusae (this study) and the density of winter flounder (*Pseudopleuronectes americanus*) larvae (from NUSCo, 1987) is shown in Figure 9; in addition, NUSCo (1986) found a significant negative correlation between the abundance of *Cyanea* and density of winter flounder larvae from 1983 through 1985. If these indicate cause and effect (both medusae and flounder larvae may be independently influenced, directly or inversely, by other factors) then fish, though less frequently encountered in medusae than copepods, are important in the diet of *Cyanea* in the Niantic River. An intensive study of the trophic relations of this population of *Cyanea* using more rigorous methods (*e.g.,* Larson, 1987b; Fancett, 1988) is required to resolve this question or its predatory status, in general. Others report that ctenophores are important in the diet of scyphozoa (reviewed in Larson, 1978; Larson, 1986c). In the Niantic River estuary, *Pleurobrachia* is present with *Cyanea* early in the season, but only in low numbers, so it is probably not a significant prey item. *Mnemiopsis* often is abundant, but this usually is after *Cyanea* has disappeared late in the season; in the three years when their populations overlapped, the numbers of *Cyanea* were declining and individuals were in a deteriorated condition incapable of efficient feeding.

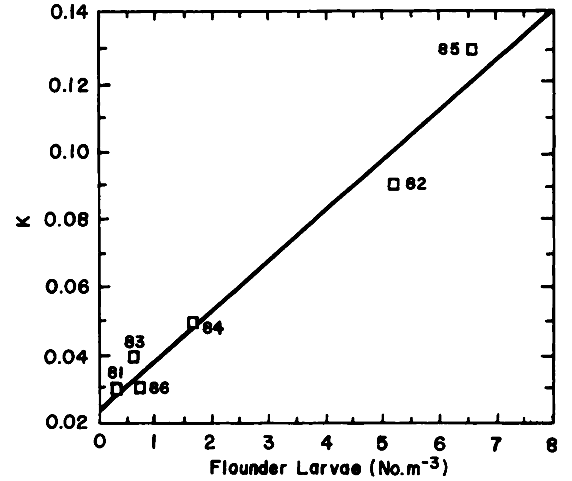

Figure 9. The relationship between instantaneous daily growth rate of *Cyanea,* k, and density of winter flounder larvae in the Niantic River estuary. Numbers beside the points indicate the year.

The average value for daily instantaneous growth rate of the different annual populations of *Cyanea* ($k = 0.06$) is low compared to those reported for other Cnidaria (reviewed in Larson, 1986a), but is the same as that calculated from size frequencies reported in Thiel (1960) for *C. capillata* (0.06). The size of individual medusae on two different dates are given in Fish (1925), and in van der Maaden (1942) and Verwey (1942) for *C. capillata,* which give approximate instantaneous growth rates of 0.16, and 0.09–0.13, respectively. Average growth for *C. capillata* and *C. lamarcki,* combined (Dittrich, 1988), show that for them, $k = 0.02$–0.06, and for *C. lamarcki,* data in Russell (1931) give rates between 0.02 to 0.10 (average = 0.05). These instantaneous growth rates are generally within the range found in this study (0.02–0.13). Such values indicate that the mass of these medusae can double in 5 to 34 days (average = 12 days) and thus they are capable of exploiting fast-growing prey populations (*e.g.,* winter-spring zooplankton blooms) whenever they occur (Hernroth and Gröndahl, 1983; Larson, 1986a).

Initial maturation of *Cyanea* in the Niantic River, and the early movement of blastulae to their oral folds, is correlated with surface temperature. The effect of temperature may be indirect, affecting food source, or direct, affecting the metabolic activity of the medusae (*e.g.*, Heeger and Möller, 1987), but probably these and many other factors are involved with temperature serving as a surrogate for a complex of physical and biological interactions. However, this relationship is true only for larger medusae. Hamner and Jenssen (1974) indicate that maturation is size dependent in *Aurelia*, but they speculate that appropriate manipulation of the food supply might lead to precocious maturation of small individuals. If such a stimulus governs maturation in *Cyanea*, and is sufficient for large medusae, it seems reasonable that it is sufficient for all but the smallest individuals present at the same time. The physical or biological stimuli for maturation may be quantitatively or qualitatively different for large and for small medusae. If maturation were determined by a suite of conditions for which temperature is an index, all sizes of medusae should mature more or less simultaneously.

Maturation in *Cyanea* might also be decoupled from age of the medusa. The unimodal size frequency distributions exhibited by *Cyanea* in the Niantic River suggest that the small medusae which reproduce are more than a month older than larger specimens. These small individuals are unlikely to be large ones which have degrown, for the gonads rapidly and entirely regress in such medusae, so much so that they are difficult to biopsy (Hamner and Jenssen, 1974); even the smallest of these *Cyanea* (26 mm) are as easily sexed as are large individuals. It appears that all female medusae (which survive) in a given generation produce offspring. Plasticity in the size (and possible flexibility in the age) of reproducing individuals insures maximal reproductive output by the population regardless of ambient conditions, but how this is effected is not clear.

Planulae first appear on the oral folds of *Cyanea* at the time when the maximum average size of individuals is attained as is also true for *Aurelia* (Rasmussen, 1973; Dittrich, 1988), and after the maximum size is reached, the average size of *Aurelia* declines as it does in *Cyanea* (Rasmussen, 1973; Hamner and Jenssen, 1974; Kakinuma, 1975; Dittrich, 1988). Hamner and Jenssen (1974) and Dittrich (1988) indicate that decline in average size is associated with deterioration of medusae. Cargo (1974) mentions that *Chrysaora quinquecirrha* are found in a moribund state lacking tentacles or oral folds in nature for no apparent reason and thinks that the cause of deterioration merits study.

Deterioration may be induced by completion of embryogenesis to the blastula-planula stage as noted by de Lafontaine and Leggett (1988); the gonads of medusae in late stages of deterioration are devoid of germinal epithelium (pers. obs.), and there is no advantage for prolongation of life beyond this time. The temperature at which deterioration occurs ranges between 17° to 23°C, considerably less than that considered lethal to *Cyanea* (26.8°C) by Mayer (1914), and deterioration is neither size (nor age?) dependent as is also sexual maturation.

A functional relationship between deterioration of *Cyanea* and their reproduction has not been made in previous studies. That is, "spawning" (not defined, but probably meaning the appearance of blastulae or planulae on the oral folds) is followed by loss of tentacles and other body parts (Hoese *et al.*, 1964), or is followed by degeneration of feeding structures and death (Fancett, 1986); Berrill and Berrill (1981) simply say that medusae die after "spawning". Death might reasonably seem imminent when tentacles are lost, for the medusae can no longer feed. In *Cyanea*, the tentacles are lost early in the process of deterioration, while the planula-laden oral folds are still intact. Release of planulae and deterioration seem not to be sequential and separate events for *Cyanea*. Indeed, it appears that deterioration of *Cyanea*, and the loss of oral folds in particular, can be interpreted as a mechanism for deposition of most of its planulae (*e.g.*, Fig. 8) and in consequence is a normal extension of the reproductive process analogous to the post-reproductive parental role served by the death, detachment, and wind transport of tumbleweed (*Salsola pestifer*) in the disperal of seeds (Allee *et al.*, 1949).

Cyanea may provide transport for planulae to the benthos on its oral folds, though other medusae do so differently. For example, *Chrysaora* liberates gametes, with fertilization and development of planulae occurring in the plankton (Cargo, 1979); Cargo and Schultz (1967) found more-or-less continuous settling on suspended oyster shells from before August to the second week of September, as would be expected for planulae free in the water column. Also, *Aurelia* exhibits a pattern of planula settlement on plates suspended in the field similar to that for *Chrysaora* (Gröndahl, 1988) suggesting that the planulae are liberated as a free-swimming stage at intervals over an extended period (*e.g.*, Russell, 1970). These observations are consistent with finding mass occurrences of *Aurelia* planulae, and sporadic presence of *Chrysaora* planulae, in surface plankton (Widersten, 1968). In contrast, Widersten (1968) does not clearly indicate that planulae of *C. capillata* or *C. palmstruchi* (= *lamarcki*) are also found in plankton. If they are not, this might explain the observations of Gröndahl and Hernroth (1987) who report that no *Cyanea* settled on suspended plates from June to November, though their females with planulae were abundant; only once, late in the season (mid-November), did their planulae settle on such plates, and the medusae disappeared shortly thereafter (Gröndahl, 1988). This is expected if the planulae of *Cyanea* are not dispersed in the plankton as appears to be the case for other semaestomes, but rather are released, *en masse,* attached to oral folds lost from deteriorating medusa.

A problem with this interpretation is that healthy, intact medusae in a collecting bucket or in an aquarium "shed" planulae (and blastulae). To obtain polyps of *Cyanea* for observation in the field, Gröndahl and Hernroth (1987) and Gröndahl (1988) established aquaria containing female *Cyanea* along with settling plates which became colonized and could then be transported to field sites. In the confinement of an aquarium [or in a collecting bucket (pers. obs.)], the oral folds contact the surfaces of the container and the objects placed therein, and planulae are released under these conditions. However, that such contact is the stimulus freeing the planulae from the oral folds is difficult to test directly; while the null hypothesis potentially can be rejected, the alternative outcome is more likely (see above) but is ambiguous because to capture and transport medusae without their oral folds being disturbed or making surface contact is impossible. This interpretation that the oral folds of deteriorating medusae are a substrate for transport of planulae to the benthos relies on the field observations, above, and on the apparent absence of planulae in the water column. [It is unlikely that the appearance of planulocysts on shells are from planulae freely deposited some days, or weeks, earlier because the planula is short-lived (Lohman, 1908; Kaestner, 1969; Schneider and Weisse, 1985), and attach within a few hours (Brewer, 1984).]

The oral folds of *Cyanea* are sufficiently large, [33 ± 4% of total wet weight (unpubl.)] to accommodate the planulae it produces. It is a much-folded structure (Agassiz, 1862) with both an extensive surface area and a long margin. Measurements of the length of this margin on a small medusa (38 mm diameter) indicate that for each 10 mm of bell diameter the oral folds are 207 mm in length. Thus, if the same allometry holds, a 100-mm medusae has oral folds with a margin of about 2 m in length. This is more than sufficient to accommodate, in a band about 2 mm to 5 mm wide, the approximately 500,000 blastulae developing into planulae (200 mm × 100 mm), which a medusa of this size is conservatively estimated to produce (unpubl.). The accumulation of planulae along the margin of the oral folds is readily visible in reproducing specimens, and is of about these dimensions. The accumulated planulae also can be retained by the oral folds; von Lendenfeld (1884) reported that planulae develop almost to the polyp stage on the oral folds of *C. annaskala* (= *capillata*). The oral folds of other Scyphozoa may be proportionately as voluminous as those of *Cyanea.* For example, they are 18–38% of wet weight in *Chrysaora fuscescens* (Shenker, 1984), but their use for macrophagy in *Chrysaora* (Larson, 1986c) may be incompatible with the brooding of planulae, hence they release their gametes into the plankton. *Aurelia* does brood planulae (*e.g.,* Hargitt and Hargitt, 1910; Russell, 1970; Cargo, 1974), but their retention on the oral folds may be precluded by their small relative size [13 ± 4% of wet weight (unpubl.)].

The selective advantage accruing by deposition of planulae while still on the oral folds is not obvious. It would accelerate their descent to the benthos. The sinking rate of cnidarian planulae does not exceed 0.38 cm s^{-1}, and the swimming capacity of *Aurelia* planulae is even less, 0.042 cm s^{-1} (in Chia *et al.,* 1984). The sinking rate of developing embryos of *Chrysaora* is 0.01 cm s^{-1} (unpubl.). It is unlikely that the planulae of *Cyanea* would sink faster than these. In contrast, the sinking rate of oral folds is 1.4 ± 0.3 cm s^{-1} (unpubl.), one or two orders of magnitude more rapid than for isolated planulae. This, and the areal extent of the oral folds, undoubtedly alters the trajectory of descent and the extent of horizontal movement (in currents) in a way that perhaps is advantageous. In addition, transport to the benthos on the oral folds may facilitate the settlement of planulae by bringing them into more intimate contact with suitable substrate making it easier to penetrate the barrier of the boundary layer (*e.g.,* Vogel, 1981). Also, such transport could increase the likelihood of the successful development of earlier embryonic stages still in the confines of the oral folds which otherwise might not form normal planulae (Kakinuma, 1975).

The unexpected constancy of pattern and of numerical stability of *Cyanea* medusae in the Niantic River estuary [only 5.3×10^6 m^3 at MLW (Marshall, 1960)] suggests that the open water, neritic and oceanic, populations of *Cyanea* might be similar. In these even more stable environments, the wide swings in observed abundance may reflect more the vast volume in which they occur, and the currents to which they are exposed (Verwey, 1942; Shenker, 1984; Gröndahl, 1988), rather than representing inexplicable fluctuations in population size. Such regularity results from their rapid growth and efficient exploitation of a changing food supply, reproduction that is tied neither to size nor age, and on the consistent success in the transition to the benthic phase of its life history which could be effected by deposition of planulae while they remain on the oral folds of their nonfeeding, moribund parent.

Note: I have referred throughout this paper to *Cyanea* in the Niantic River estuary without giving a specific designation. There is a possibility that it is not *C. capillata* (*s.s.*) to which it unambiguosly keys (Larson, 1976; Shih, 1977). Its differences from typical *C. capillata* are comparable to those which distinguish *C. lamarcki* from *C. capillata* in British (Russell, 1970) and European (Gröndahl, 1988) waters. However, the general conclusions of this paper should apply at the generic level.

Acknowledgments

I appreciate the benthic samples provided by the staff of the Northeast Utilities Environmental Laboratory, Waterford, Connecticut; the retrieval of those samples and other help provided by Martha Smith Fassano; the courtesy afforded by the personnel of Bayreuther's Boat Yard; and the award of a Trinity College Faculty Research Grant for equipment funds and travel expenses. Finally, I thank Ronald J. Larson and an anonymous reviewer for their helpful comments.

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