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Strobilation Of The Sea Nettle, Chrysaora Quinquecirrha, Under Field Conditions

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STROBILATION OF THE SEA NETTLE, *CHRYSAORA QUINQUECIRRHA*, UNDER FIELD CONDITIONS[1]

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The sea nettle, *Chrysaora quinquecirrha* (Desor, 1848), is locally abundant during summer along the east coast of the United States from southern New England to Florida. The venomous medusa stage of this species is a significant pest and a negative economic factor, particularly in the Chesapeake Bay region.

In common with many other cnidarians, *C. quinquecirrha* undergoes an alternation between polyp and medusa stages in its life history. While the medusa population dies off annually, the sessile polyp or scyphistoma stage may remain active all year and is potentially perennial (Truitt, 1939). The scyphistoma is capable of asexual reproduction, most commonly through podocyst formation. These cysts are also resistant to adverse environmental conditions. Given favorable conditions the scyphistomae undergo strobilation, a process leading to the production of free-swimming ephyrae. The proximal portion of the polyp remaining after strobilation undergoes renewed growth, returning the scyphistoma to normal size and morphology. It is then capable of continued asexual reproduction and perhaps repeated strobilation. The ephyrae develop rapidly into medusae, which are dioecious. Fertilization results in a free-swimming planula larva, which settles on a firm substrate and develops into the scyphistoma, thereby completing the life cycle.

While the morphological details of strobilation in *C. quinquecirrha* have been described (Littleford, 1939; Cones, 1969), little is known about the ecology and seasonal dynamics of the process. The only relevant field data available to date on strobilation in this species were based on collections of ephyrae by Cargo and Schultz (1966, 1967). The present study was undertaken to determine (1) when strobilation begins and ends in nature; (2) the percentage of polyps strobilating at a given time; (3) the number of ephyrae produced per strobila, as observed throughout the season; (4) whether a given polyp will strobilate more than once a season under field conditions.

Methods and Habitat Description

Studies on strobilation in *C. quinquecirrha* were conducted from March 1972 through February 1973 in Sarah Creek on the York River, Virginia. Shells of the oyster, *Crassostrea virginica,* were collected using hand tongs from an old, abandoned shell accumulation in the Northeast Branch of the creek and returned to the laboratory in water-filled buckets. Examination of the shells was completed and the number of adhering scyphistomae and strobilae present determined within

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eight hours after collection. Samples were taken biweekly during March and from November through February. Weekly samples were collected during the first half of April and from August through October. From mid-April through July, sampling was conducted two to three times weekly and the results pooled for the entire week. Enough substrate was collected so that most samples contained in excess of 100 scyphistomae. Greater quantities of shell were necessary for winter and mid-summer samples because scyphistomae were less abundant during these seasons than in spring, late summer and autumn.

In the laboratory, shells were immersed in a large preparation dish containing sea water and examined under low magnification (7–10 ×) using a dissecting microscope. As scyphistomae and strobilae were located and counted, they were dislodged from the shells and placed in Stender dishes for more detailed examination

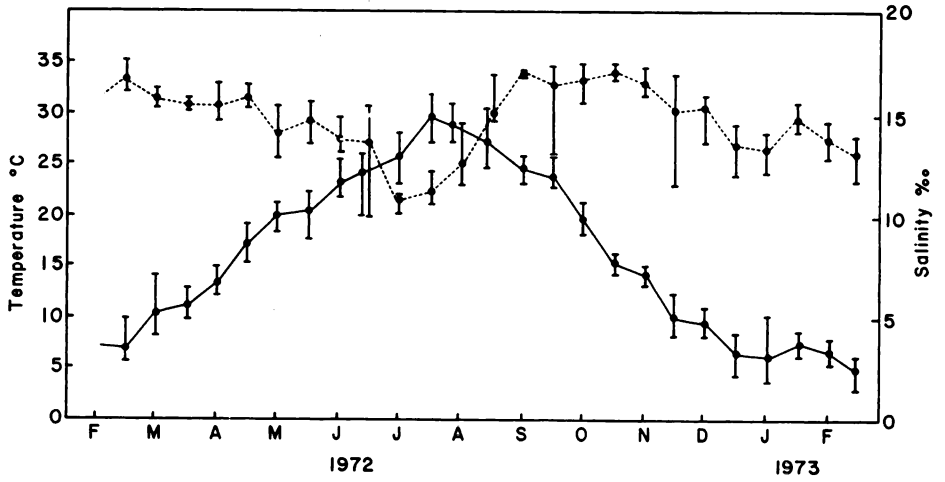

FIGURE 1. Salinity (dashed line) and water temperature (solid line) in Sarah Creek. Intersects indicate mean, vertical lines the range for the previous two-week interval.

at higher magnification. Small polyps, as well as large ones, were counted during the study. Three methods were used in identification of scyphistomae: (1) examination of the nematocyst complement (Calder, 1971); (2) determination of mouth shape (Morales-Alamo and Haven, 1974); (3) identification of the ephyrae liberated following strobilation (Calder, 1972).

All field-collected strobilae that had not liberated ephyrae prior to collection were placed individually in vials containing 4.5 ml of filtered sea water (17‰ salinity). These strobilae were held at 25° C (approximating ambient summer water temperatures) in an incubator until the total number of ephyrae produced could be determined. Identification was based on the morphology of the released ephyrae. After liberation of ephyrae, scyphistomae were removed to petri dishes and held in the laboratory until several had reattached. Upon reattachment, the exact location of each polyp was recorded and the petri dishes were secured to a retrievable rack and submerged, bottom up, in Sarah Creek. Scyphistomae were

checked for restrobilation in the field several times weekly with a 10 × hand lens. New polyps produced by asexual reproduction during the study were removed from the dishes.

Hydrographic data, including salinity, dissolved oxygen, water temperature, and water transparency, were collected several times weekly in Sarah Creek throughout the study.

TABLE I

Numbers of scyphistomae and strobilae in samples from Sarah Creek

Time interval	No. samples	No. scyphistomae	No. strobilae	Per cent of polyps strobilating
5 March–1 April	2	110	0	0.0
2–15 April	2	173	0	0.0
16–22 April	2	249	5	2.0
23–29 April	3	401	48	10.7
30 April–6 May	3	406	41	9.2
7–13 May	3	416	54	11.5
14–20 May	3	520	60	10.3
21–27 May	3	311	78	20.1
28 May–3 June	3	336	42	11.1
4–10 June	3	409	114	21.8
11–17 June	2	244	41	14.4
18–24 June	2	205	37	15.3
25 June–1 July	2	273	38	12.2
2–8 July	2	255	28	9.9
9–15 July	2	138	7	4.8
16–22 July	1	93	9	8.8
23 July–5 August	—	—	—	—
6–12 August	1	82	3	3.5
13–19 August	2	169	1	0.6
20–26 August	1	128	3	2.3
27 August–2 September	1	159	4	2.5
3–9 September	1	251	0	0.0
10–16 September	1	202	1	0.5
17–23 September	1	225	1	0.4
24–30 September	1	229	0	0.0
1–7 October	1	198	1	0.5
8–14 October	1	237	0	0.0
15–21 October	1	247	0	0.0
22–28 October	1	215	0	0.0
29 October–4 November	1	251	0	0.0
5 November 1972–3 March 1973	8	876	0	0.0

Sarah Creek is located on the north shore of the lower York River, 9 km from Chesapeake Bay. The creek divides into two branches, the Northwest and the Northeast, each having depths of 2 m for about 1.3 km (U. S. Coast Pilot, 1971). The shoreline is sandy at the entrance but elsewhere is predominantly muddy and bordered with saltwater cordgrass (*Spartina alterniflora*). The bottom consists of mud, except for accumulations of shell on private oyster grounds and near oyster houses. These shells provide substrate for a variety of epifaunal organisms, including scyphistomae of *Chrysaora quinquecirrha*.

Mean tidal range in the creek is about 0.9 m. Currents are weak except at the narrow entrance, where velocities reach about 0.5 m/sec. Hydrographic conditions fluctuate markedly in the creek (Fig. 1), both seasonally and in response to local weather conditions. Freshwater runoff from heavy rains rapidly decreases salinity and increases water turbidity. Salinities were below normal throughout the Chesapeake Bay system in 1972 due to heavy rains during the autumn of 1971. Unusually wet weather continued through the spring of 1972 and was followed by heavy rainfall during Tropical Storm AGNES in late June 1972 that further depressed salinities. In Sarah Creek salinities reached a minimum of 9.94‰ on 29 June. Waters of the creek are normally turbid, with maximum Secchi disc visibilities of about 2 m being attained in late autumn and early winter. In summer, visibilities are consistently below 1 m, and may drop as low as 0.3 m following heavy rainfall. Water temperatures increase or decrease rapidly depending upon air temperature.

TABLE II

Numbers of ephyrae liberated per strobila in samples from Sarah Creek. Strobilae having liberated ephyrae before collection were not included

Month	No. strobilae	No. ephyrae	Ephyrae/strobila
April	35	292	8.3
May	127	752	5.9
June	160	704	4.4
July	28	106	3.8
August	6	26	4.3
September	1	7	7.0
October	1	4	4.0
Totals	358	1891	5.3

Although the creek occasionally freezes over in cold winter periods, it did not do so in 1972–1973. Summer water temperatures reached a maximum of 32° C. There was no evidence of oxygen depletion in creek waters during the study. Dissolved oxygen values averaged 10.1, 7.8, 7.1, and 8.4 mg/liter for winter, spring, summer and autumn, respectively. The lowest value recorded was 4.4 mg/liter following a heavy rain on 4 May 1972. The creek is sheltered from wind, and maximum wave height observed in the creek during the study was about 0.3 m.

RESULTS

Scyphistomae of *C. quinquecirrha* were collected in Sarah Creek throughout the year, although most survived as podocysts during the coldest part of the winter. Strobilation extended over a period of 24 weeks during the study. Strobilae were first observed on 18 April, when three of 115 polyps collected were beginning to show segmentation. Water temperature on this date was 16.8° C, having risen from 14.9° C four days earlier. After 20 April, when two additional strobilae were collected, numbers of strobilating polyps in the samples rapidly increased (Table I). Strobilation peaked during May and June, with a maximum weekly percentage recorded during 4–10 June. Peak value for a single sample was obtained on 5 June

when 25.4% of the polyps collected were undergoing strobilation. Fresh water from Tropical Storm AGNES depressed salinities in Sarah Creek during late June (Fig. 1), but strobilation was already in decline and was not noticeably affected. Although strobilation continued throughout the summer, the percentage of polyps strobilating at a given time after June was relatively small. Only three strobilae were collected after August, the last on 2 October. These three were normal morphologically, and typical ephyrae were produced.

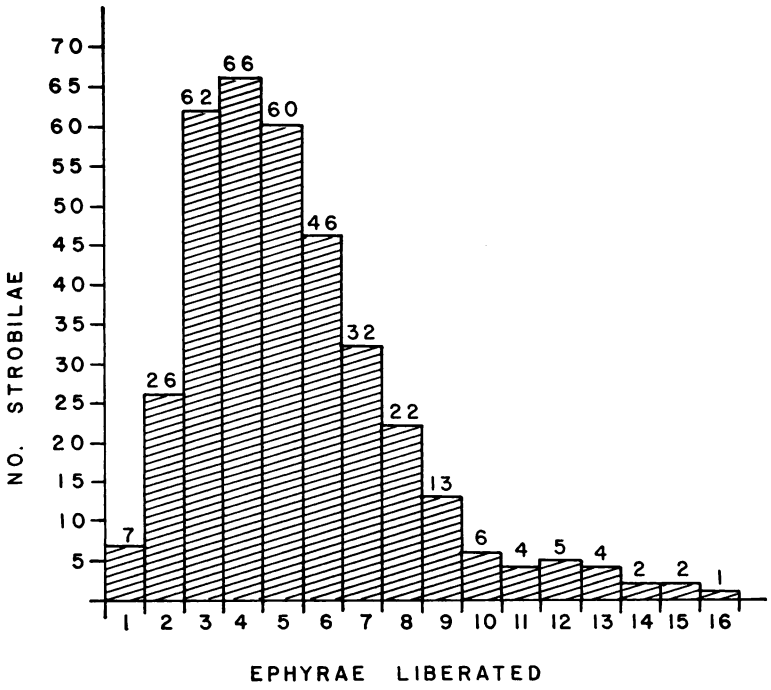

FIGURE 2. Frequency distribution of numbers of ephyrae produced per strobila.

Pulses of strobilation were evident from the samples. Peaks of strobilation for 23–29 April, 7–13 May, 21–27 May, 4–10 June, and 18–24 June were followed by lower levels on 30 April–6 May, 14–20 May, 28 May–3 June, 11–17 June, and 25 June–1 July respectively. These fluctuations did not correlate with any observed environmental factor except tidal rhythm. Strobilation peaks coincided with periods of increasing tidal amplitude as indicated in the 1972 tide tables (National Ocean Survey, 1971).

The number of ephyrae produced per strobila varied from one to 16 during the study (Fig. 2). The mean number of ephyrae per strobila was higher in spring than during the summer (Table II).

Studies conducted in late spring and early summer demonstrated that a scyphistoma can strobilate more than once in nature during a given season. Of 48 scyphistomae reimmersed in Sarah Creek following strobilation, 22 strobilated again

once, 11 strobilated twice, four strobilated three times and two strobilated four times. Most of the scyphistomae were observed for a relatively brief interval before being lost; the mean length of time a polyp remained on the dishes was 24 days. The two polyps that restrobilated four times were monitored over an interval of six weeks. Losses of scyphistomae were attributed largely to nudibranch predation, although some evidently became detached during strobilation.

Discussion

Waters of the Chesapeake Bay system are characterized by a wide annual range in temperature. Under these conditions strobilation in *C. quinquecirrha* undergoes a definite seasonal periodicity. During this study strobilation began abruptly in April as the water temperature approached 17° C. After reaching a peak during May and June, the process did not terminate as suddenly as it had begun but continued at a diminished rate throughout the rest of the summer and early autumn. No strobilation occurred from November through March, when cold water temperatures prevailed. The influence of water temperature on strobilation in *C. quinquecirrha* has been determined experimentally in laboratory studies by Cones (1969) and Loeb (1972). In these experiments strobilation was induced by elevating the water temperature in cultures of polyps maintained under cold conditions. Manipulation of water temperature has also been used to trigger strobilation in other species of scyphozoans under laboratory conditions (Russell, 1970).

Water temperature is not always as significant in the control of strobilation as it is for *C. quinquecirrha* in Chesapeake Bay. Thiel (1962) concluded that water temperature was not very important in regulating strobilation of *Aurelia aurita* in the Kieler Förde. He found that strobilation could occur throughout the year, and that there were two peaks, both coinciding with plankton blooms. His conclusion that food supply was the major factor controlling strobilation in the Kieler Förde was further confirmed through supplemental feeding experiments.

In addition to temperature and nutrition, a number of other factors are known to affect strobilation, including salinity, dissolved oxygen, light, chemicals, symbiotic zooxanthellae, and pH (Spangenberg, 1968; Russell, 1970). As with temperature, the relative significance of these factors varies from species to species and from location to location. Even within a given species, populations from different geographic areas may respond differently to the same factor. In *A. aurita*, strobilation occurs at much lower temperatures in European populations than in populations from Texas (Spangenberg, 1965; Russell, 1970). As Russell suggested, such differences are probably due to the existence of a number of races in this widespread species.

A series of pulses in the rate of strobilation was evident during this survey. An analogous series of peaks in the abundance of ephyrae in St. John Creek, Maryland, was noted by Cargo and Schultz (1967). They hypothesized that (1) the early peak was due to strobilation of polyps having survived through the winter, (2) a second and larger peak was due to the excystment of polyps from podocysts and their subsequent strobilation, and (3) later peaks were due to repeated strobilation in polyps. While not disagreeing with this hypothesis, the pulses of strobilation observed in Sarah Creek occurred in such a regular succession that another explanation is possible. In being about two weeks apart, the peaks coincided with periods

of increasing tidal amplitude, suggesting a semilunar periodicity in strobilation rate. It is also possible that chemical stimuli contribute to the pulses of strobilation. Loeb (1974) indicated that a neck-inducing factor (NIF) apparently plays a significant role in triggering strobilation in *C. quinquecirrha.*

Information regarding the number of ephyrae produced during strobilation in *C. quinquecirrha* varies considerably. According to Littleford and Truitt (1937), Littleford (1939), Truitt (1939) and Cones (1969), the number is relatively constant, varying only from five to six. Cargo and Schultz (1966) observed a range from three to nine, with a mode of five. Under laboratory conditions numbers from one to 16 (Crawford and Webb, 1972) and from five to 20 (Loeb, 1972) have been reported. The number produced by strobilae collected in nature during this study varied from one to 16, with a mean of five and a mode of four. Numbers of ephyrae per strobila were evidently highest early in the season. Monodisc strobilae were rare and typically smaller than those undergoing polydisc strobilation.

The phenomenon of strobilation in scyphozoans consists of two separate processes, namely segmentation and metamorphosis (Thiel, 1938; Spangenberg, 1968). This results in the derivation of several new organisms from the single original entity. In the segmentation process there remains after strobilation a small portion of the scyphistoma that is capable of totally regenerating itself and repeating the process. The occurrence of repeated strobilation in a given scyphistoma has been reported in several species. Gohar and Eisawy (1961) observed strobilation twice in succession within three weeks in polyps of *Cassiopea andromeda.* In *Mastigias papua* strobilation occurred three times in seven weeks (Sugiura, 1963), and *Cephea cephea* strobilated three times within a three week interval (Sugiura, 1966). Thiel (1962) demonstrated that a scyphistoma of *A. aurita* in the Kieler Förde could strobilate up to four times a year. In *C. quinquecirrha,* Littleford (1939) and Truitt (1939) noted that individual polyps underwent strobilation each summer for four successive years. Subsequent laboratory experiments by Cargo and Schultz (1967) and Loeb (1972) indicated that scyphistomae of *C. quinquecirrha* could strobilate repeatedly. Studies conducted in Sarah Creek during 1972 confirmed that repeated strobilation can also occur in nature.

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Summary

1. A 12-month study of strobilation in the sea nettle, *Chrysaora quinquecirrha,* was conducted under natural conditions in the field. Observations were made in a creek of the Chesapeake Bay system where scyphistomae of *C. quinquecirrha* were known to occur and where medusae are normally abundant each year.

2. Strobilation was seasonal in occurrence, beginning in April and lasting until early October.

3. Maximum rates of strobilation occurred during May and June. Instead of a single sustained peak during this period, strobilation was protracted into a series of pulses that coincided with periods of increasing tidal amplitude, suggesting a semilunar periodicity. Although strobilation continued into October, the percentage of polyps strobilating after June was relatively low.

4. The number of ephyrae produced per strobila varied from one to 16, with a mean of five and a mode of four. The mean number of ephyrae per strobila was higher in spring than during summer.

5. Observations on individual scyphistomae attached to petri dishes confirmed that repeated strobilation can occur in polyps of *C. quinquecirrha* in nature.

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