

## Seasonal cycles of activity and inactivity in some hydroids from Virginia and South Carolina, U.S.A.

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Hydroids investigated in estuaries of Virginia and South Carolina, USA, were characteristically seasonal in occurrence. Of 20 species studied in Virginia, 14 were active only during warmer months and 6 only during colder months of the year. Seven of the 18 species examined in South Carolina were active all year, whereas 9 were active only in warmer months and 2 only during colder months. Reflecting the differing temperature regimes of the two study areas, warm-water species were active for a longer period of time in South Carolina than in Virginia; cold-water species were active longer in Virginia than in South Carolina. Warm-water species commenced activity in late winter or spring at higher temperatures than those coinciding with hydranth regression in autumn or early winter. Activity in cold-water species began at lower temperatures than those observed at regression in spring. Correlations were apparent in the seasonality, water temperature tolerances, and latitudinal distribution of most species. Field observations and laboratory experiments demonstrated that a number of species survived unfavourable periods as dormant coenosarc in stems and stolons. With the return of favourable conditions, new growth began and hydranths were regenerated from dormant tissue. Water temperature is considered the prime factor influencing the seasonal activity–inactivity cycles of hydroids in the two study areas.

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La présence des hydroïdes récoltés en estuaire en Virginie et en Caroline du Sud, États-Unis, est essentiellement saisonnière. Des 20 espèces étudiées en Virginie, 14 se sont avérées actives seulement au cours des mois les plus chauds et 6, seulement au cours des mois les plus froids de l'année. Sept des 18 espèces trouvées en Caroline du Sud étaient actives durant toute l'année, alors que 9 ne l'étaient que durant les mois les plus chauds, et 2 seulement durant les mois les plus froids. Les espèces d'eau chaude étaient actives plus longtemps en Caroline du Sud qu'en Virginie, ce qui reflète bien les régimes de température différents aux deux endroits; les espèces d'eau froide étaient actives plus longtemps en Virginie qu'en Caroline du Sud. Les espèces d'eau chaude devenaient actives à la fin de l'hiver ou au printemps, à des températures plus élevées que celles qui sont reliées à la régression des hydrantes à l'automne ou au début de l'hiver. L'activité des espèces d'eau froide commençait à des températures plus faibles que les températures de régression au printemps. Il y a corrélation apparente entre l'activité saisonnière, la tolérance à la température de l'eau et la répartition latitudinale des espèces. Les observations en nature et les expériences en laboratoire ont démontré que plusieurs espèces survivent aux périodes de conditions trop rigoureuses sous forme de coenosarques en dormance dans les tiges et les stolons. Au retour des conditions favorables, la croissance reprend et les hydrantes renaissent des tissus en dormance. La température de l'eau est probablement le principal facteur déterminant des cycles saisonniers d'activité et d'inactivité des hydroïdes dans ces deux régions.

[Traduit par la revue]

### Introduction

Seasonal cycles of activity and dormancy are common in aquatic invertebrates. The phenomenon has been particularly well documented for certain freshwater species, in which resting stages of various kinds (e.g., gemmules, cysts, statoblasts, dormant eggs) are produced for the purpose of surviving unfavourable environmental conditions (Pennak 1978). Though marine environments are generally considered somewhat more stable in terms of physical factors, regular cycles of activity and dormancy appear more widespread among marine invertebrates than is generally recognized, especially in species living where periodic variations in environmental conditions are marked. For example, seasonal formation of gemmules was reported in three species of marine Porifera from North Carolina (Wells *et al.* 1964), and the sponge *Microciona prolifera* regresses to a dormant form during winter in southern New England (Hartman 1958; Simpson 1968; Knight and Fell 1987). Polyps of the scyphozoan *Chrysaora quinquecirrha* are scarce during the coldest part of winter in Chesapeake Bay, most surviving the period as podocysts (Cargo and Schultz 1967; Calder 1974). Nasonov (1926) observed regeneration of the calyx in the entoproct *Arthropodaria kovalevskii* following a winter absence in the Black Sea, evidently as a result of a seasonal freshwater

influx. A number of gymnolaemate bryozoans form resting stages during unfavourable periods, which later reestablish the colonies, and the phoronid *Phoronis hippocrepi* degenerates seasonally into fragments in the tubes, and these regenerate into worms with the return of favourable conditions (Hyman 1959). Seasonal patterns of activity and dormancy have even been documented among arthropods and invertebrate chordates. Summer encystment was observed in the marine harpacticoid copepod *Heteropsyllus nunni* by Coull and Grant (1981), and ascidians such as *Perophora viridis* overwinter in some areas as dormant tissue in the stolon (McDougall 1943).

Seasonal cycles of activity and dormancy have been reported in hydroids, but detailed research on the phenology of these animals is rather limited (for example, see Boero 1984). Publications on marine fouling often include information on hydroid seasonality, but most such studies involve recruitment of specimens on panels immersed for relatively brief intervals. As noted by Millard (1959), test panels are poor indicators of hydroid species composition in an area because few species settle and grow on such substrates.

The goals of this study were to determine the seasonality of the more common species of hydroids in estuaries of Virginia and South Carolina, particularly in relation to pronounced

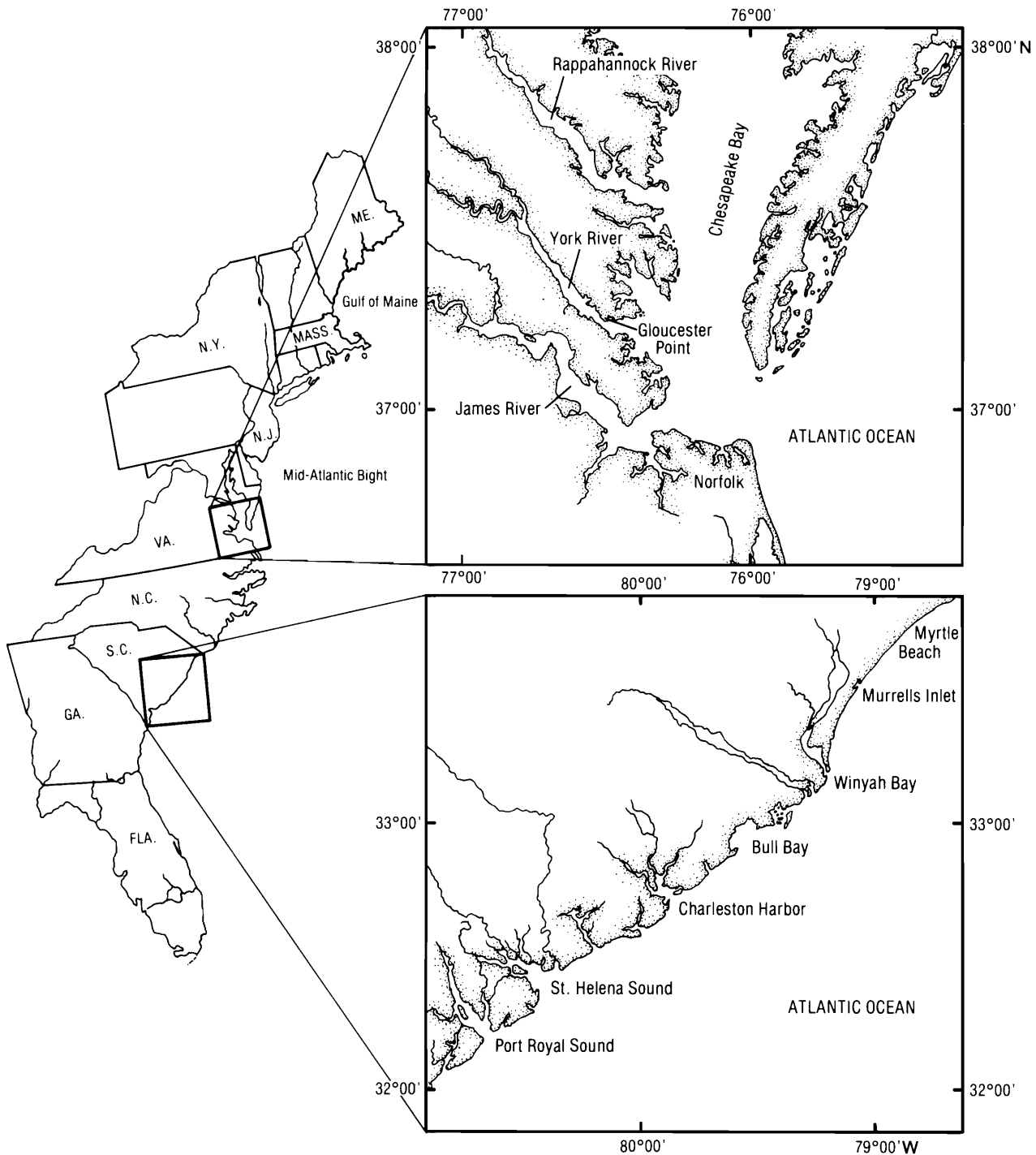


FIG. 1. The Atlantic coast of the United States, with details of the coastal zones of Virginia and South Carolina.

annual fluctuations of water temperature, and to assess the importance of dormant stages in their activity–inactivity cycles. The significance of dormant stages as a means of surviving periodically unfavourable environmental conditions is seldom addressed in accounts of the influence of physical factors on marine invertebrates.

#### Materials and methods

Investigations were undertaken to determine seasonal activity patterns and reproductive periodicities of hydroids in southern Chesapeake Bay, Virginia, between April 1966 and December 1967. Collections and observations were made, with few exceptions, at least once a week

at sites in the lower York River near Gloucester Point (Fig. 1). Methods of collection included diving (with and without SCUBA), dredging, manual intertidal collecting, and use of test panels. Supplementary information on hydroid seasonality in Virginia was obtained from records of specimens collected at more than 50 stations during the period from April 1965 to March 1968 (see Calder 1971). Collecting as part of that study was undertaken about once a month on the Rappahannock, York, and James rivers. Occasional collections were also obtained from the eastern shore of Chesapeake Bay.

In South Carolina, hydroids were collected along the entire coastline of the state (Fig. 1) during estuarine benthic surveys. Sampling gear utilized included dredges, grabs, trawls, and SCUBA. Most seasonality data presented in this paper were obtained between January 1974

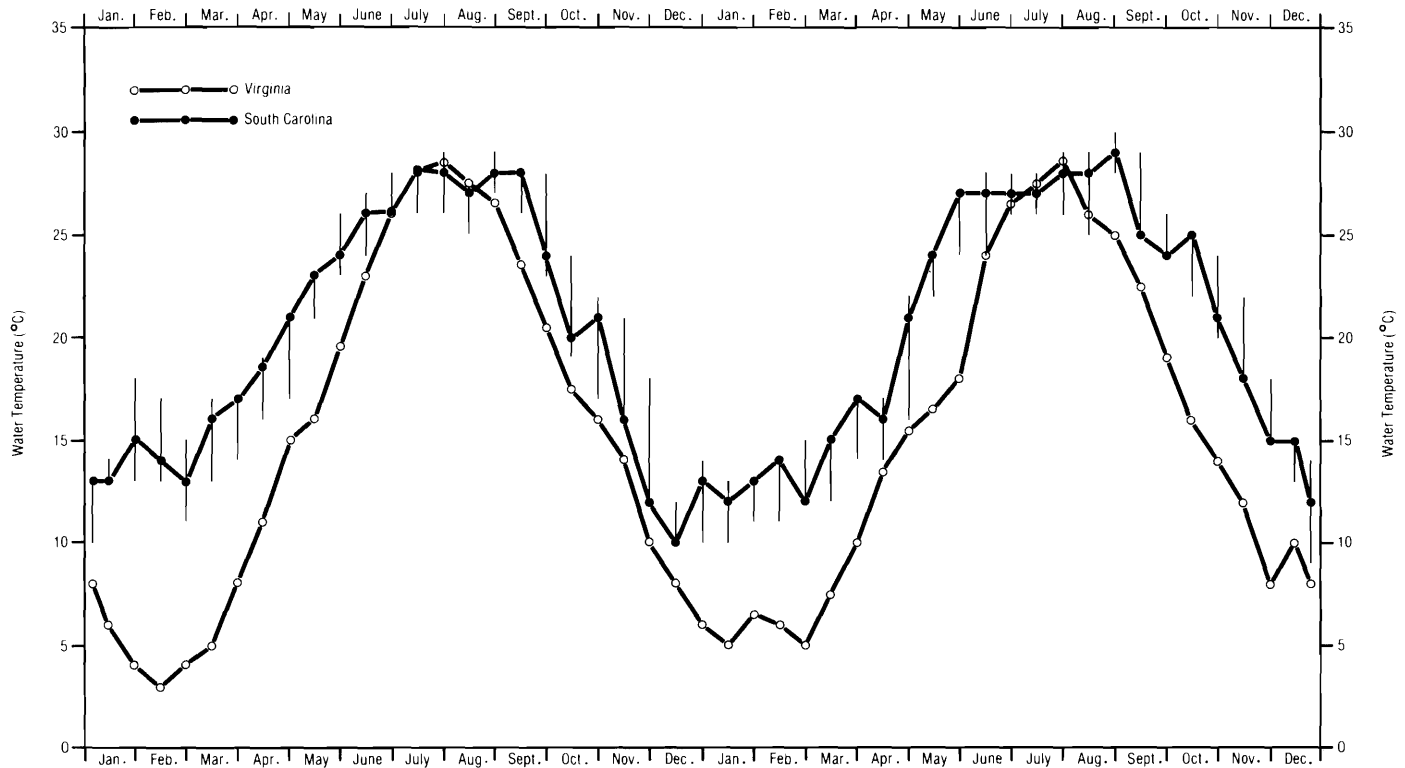


FIG. 2. Water temperatures at Gloucester Point, Virginia, during 1966–1967, and in Charleston Harbor, South Carolina, during 1974–1975. Vertical lines indicate ranges of temperature over 2-week intervals for South Carolina; comparable ranges are not available for Virginia.

and January 1976. Supplementary collections were made during September 1973–July 1981, December 1987, and February–March 1988. Schedules and sampling stations varied from one year to another (see Calder 1976, 1983; Van Dolah *et al.* 1984). No attempt was made to delineate reproductive periods of hydroid species in South Carolina.

The criterion used throughout the study to determine activity in hydroids was the presence of hydranths. Hydroids that were active all winter and inactive during part or all of the summer were categorized as cold-water species. Those active throughout the summer were grouped as warm-water species, irrespective of their activity or inactivity in winter; some of these species, with obvious warm-water affinities, remained active throughout the year in warm-temperate South Carolina.

Water temperatures, measured with stem thermometers, were taken with each collection of hydroids. The water in both study areas is relatively shallow and well mixed; differences in water temperature from surface to bottom were usually minor.

Laboratory experiments were conducted in Virginia to test the influence of water temperature on growth of dormant stems and stolons of *Bougainvillia rugosa*, *Eudendrium carneum*, and *Ectopleura dumortieri*. Experiments were undertaken in late February and early March 1967, when these species were locally inactive. Stems and stolons lacking hydranths, collected from the York and James rivers, were cultured in a constant-temperature bath at a temperature (25°C) characteristic of summer to determine whether hydranth formation would be initiated. Controls were held concurrently in a bath at 5°C, typical of winter temperatures in the area. Experimental and control groups both consisted of 10 dormant fragments each of the three species tested. Each hydroid fragment was placed in a separate glass bottle (65 mL capacity) filled with filtered seawater of 20‰ salinity, and all were cultured in the dark. The water was changed every 48 h, and specimens developing hydranths were fed *Artemia nauplii* once a day. After 192 h, presence or absence of hydranths was recorded. Culturing specimens for 192 h seemed to allow sufficient time for activity to commence because little difference was noted in the percentages showing regeneration between 192 and 384 h for any species. At the end of the first experiment, five bottles of each species were removed

from the 25°C bath and placed in the 5°C bath, and vice versa, to check the temperature effects observed initially. Five bottles of each species were kept at the original temperatures as controls. Procedures employed in the first experiment were repeated, and final observations were again recorded after 192 h. Results were tested statistically using the  $\chi^2$  test.

## Results

Seasonal water temperature fluctuations were pronounced in the estuaries of Virginia and South Carolina (Fig. 2). A range from about 3–5°C in winter to 28°C in summer was observed at Gloucester Point, Virginia, with temperatures rising from mid-March through June and falling from September through December. In South Carolina, observed water temperatures varied from highs of 29–30°C in summer to lows of 8–11°C in winter; during unusually cold winters (e.g., 1976–1977, 1977–1978, 1980–1981), temperatures dropped as low as 6°C (Mathews and Pashuk 1986). Water temperatures rose rapidly each year between March and June and declined rapidly between September and December.

Most species of hydroids studied in the two states were seasonal in occurrence, and observed activity patterns corresponded to annual cycles of water temperature. From their seasonality, hydroids in Virginia were divisible into warm-water and cold-water groups (Fig. 3). Of the 20 species for which adequate seasonal data were available, 14 were grouped as warm-water species and 6 as cold-water species. The species composition of the hydroid fauna changed completely from midwinter to midsummer, and vice versa. The greatest number of species occurred in May, when 19 of the 20 species studied were active. The fewest were active in February and March, when only six were found. Change in species composition was most pronounced during May and November, when overlap of warm- and cold-water species was greatest. Warm-water

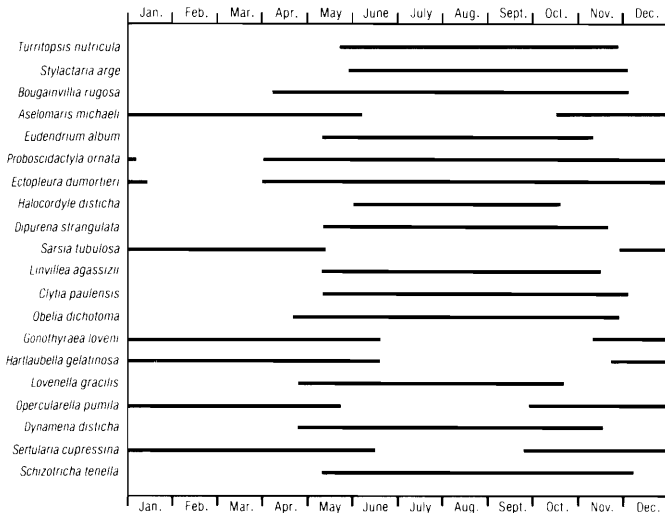


FIG. 3. Seasonal activity patterns of hydroids in Virginia.

species were active for an average of 30 weeks a year, compared with an average of 32 weeks a year for the cold-water species. The seasonal distribution of gonophore production in these species was even more restricted (Fig. 4), averaging 16 weeks a year for warm-water species and 23 weeks a year for cold-water species.

The hydroid fauna of South Carolina also included warm- and cold-water groups (Fig. 5), but the latter group was represented by only 2 of the 18 species studied. Among the 16 warm-water species, 9 were seasonal in occurrence and 7 were active throughout the year. Species numbers were low from mid-January to early March, and higher and remarkably uniform from one month to another the rest of the year. January and March were transitional months, when faunal change was greatest. Warm-water species were active for an average of 46 weeks a year, whereas cold-water species were active for an average of only 23 weeks a year.

Minimum observed water temperatures at the beginning and end of activity in warm-water species, and maximum observed water temperatures at the beginning and end of activity in cold-water species, are given in Tables 1 and 2. These data show that temperatures coinciding with the appearance of warm-water species in late winter or spring were usually higher than those at the cessation of activity in autumn or early winter. Conversely, cold-water species appeared in autumn or early winter at temperatures lower than at their disappearance in spring. The range of temperatures to which each species studied was exposed during activity is also given in Tables 1 and 2. These ranges represent the extremes over which species were found to be active during this study in Virginia and South Carolina, and are not absolute temperature tolerances.

The relation between numbers of warm- and cold-water hydroid species in an active state and water temperature is shown in Fig. 6. The number of warm-water species decreased with declining temperatures below 15°C in both states, although seven species in this group remained active all winter in the warmer waters of South Carolina. Above 20°C, numbers of warm-water species were constant with rising temperatures. Cold-water species declined in number above 15–20°C, and none remained active above 25°C in either state.

Implicit in the observation of regular seasonal activity cycles in hydroid species of the study areas is the probable existence of

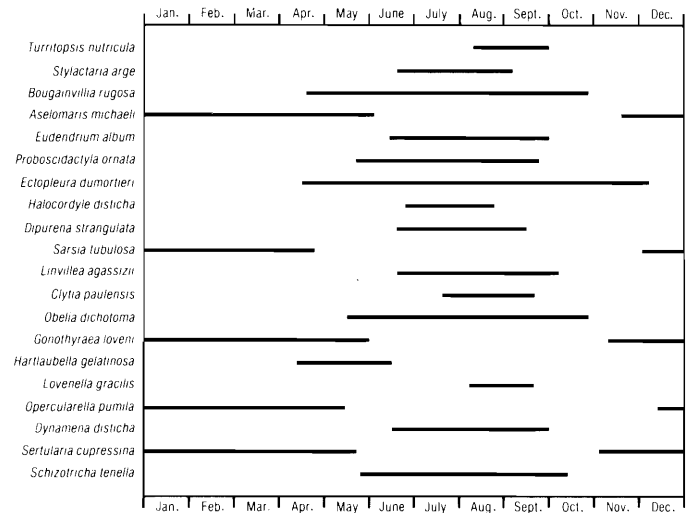


FIG. 4. Seasonal periods of gonophore production of hydroids in Virginia.

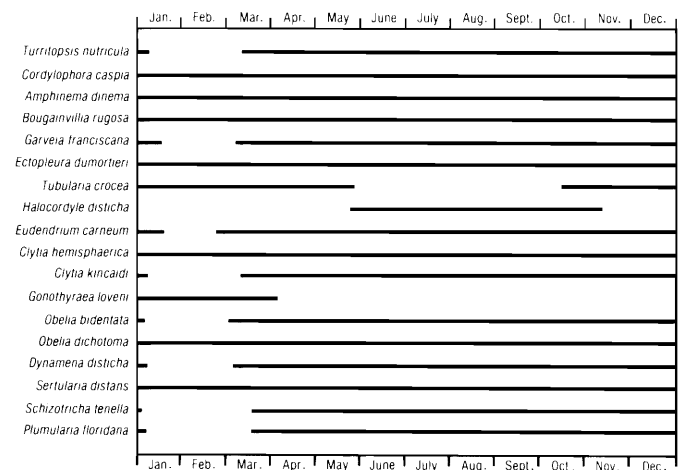


FIG. 5. Seasonal activity patterns of hydroids in South Carolina.

resistant stages in the life histories of these cnidarians. Toward the end of their activity cycle in Virginia, hydroids of the following species declined in abundance and vigour, underwent hydranth regression, and exhibited evidence of resorption of tissues into the stems: *Turritopsis nutricula*, *Bougainvillia rugosa*, *Aselomaris michaeli*, *Proboscidactyla ornata*, *Ectopleura dumortieri*, *Dipurena strangulata*, *Sarsia tubulosa*, *Clytia paulensis*, *Gonothyraea loveni*, *Dynamena disticha*, *Sertularia cupressina*, and *Schizotricha tenella*. With the return of favourable conditions, renewed growth and hydranth development from coenosarc in old stems, stolons, or both were observed in *Bougainvillia rugosa*, *Eudendrium album*, *Eudendrium carneum*, *Ectopleura dumortieri*, *Dynamena disticha*, *Sertularia cupressina*, and *Schizotricha tenella*. Similar observations were made in South Carolina for *Garveia franciscana*, *Eudendrium carneum*, and *Dynamena disticha*.

Experiments in Virginia with *Bougainvillia rugosa*, *Eudendrium carneum*, and *Ectopleura dumortieri* confirmed that winter-dormant coenosarc in stems and stolons is capable of regenerating the colony when subjected to warm temperatures in the laboratory. After 192 h of culture at 25°C, 80–100% of specimens showed new growth and hydranth development ( $p < 0.02$ ), whereas controls at 5°C remained dormant. Following

TABLE 1. Minimum observed water temperatures (°C) at beginning and end of activity for species of warm-water hydroids from Virginia and South Carolina, observed temperature ranges during activity periods of each seasonal species in the two study areas, and observed temperature ranges for species active all year

	Virginia			South Carolina		
	Beginning	End	Range	Beginning	End	Range
<i>Turritopsis nutricula</i>	18	9	9–27	15	9	9–29
<i>Cordylophora caspia</i>	—	—	—	A	A	9–30
<i>Stylactaria arge</i>	18	8	8–29	—	—	—
<i>Bougainvillia rugosa</i>	12	6	6–28	A	A	8–32
<i>Garveia franciscana</i>	—	—	—	14	9	9–30
<i>Amphinema dinema</i>	—	—	—	A	A	8–28
<i>Eudendrium album</i>	16	12	12–26	—	—	—
<i>Eudendrium carneum</i>	—	—	—	12	9	9–32
<i>Proboscoidactyla ornata</i>	10	5	5–26	—	—	—
<i>Ectopleura dumortieri</i>	10	4	4–27	A	A	9–30
<i>Halocordyle disticha</i>	18	20	18–29	20	15	15–29
<i>Dipurena strangulata</i>	18	10	10–26	—	—	—
<i>Linvillea agassizii</i>	16	14	14–27	—	—	—
<i>Clytia hemisphaerica</i>	—	—	—	A	A	6–30
<i>Clytia kincaidi</i>	—	—	—	15	10	10–32
<i>Clytia paulensis</i>	16	9	9–26	—	—	—
<i>Obelia bidentata</i>	—	—	—	16	10	10–32
<i>Obelia dichotoma</i>	20	11	11–27	A	A	8–30
<i>Lovenella gracilis</i>	15	20	15–27	—	—	—
<i>Dynamena disticha</i>	15	12	12–27	15	9	9–30
<i>Sertularia distans</i>	—	—	—	A	A	8–32
<i>Schizotricha tenella</i>	14	9	9–28	15	9	9–32
<i>Plumularia floridana</i>	—	—	—	15	10	10–32

NOTE: A, species active all year.

TABLE 2. Maximum observed water temperatures (°C) at the beginning and end of activity for species of cold-water hydroids from Virginia and South Carolina, and observed temperature ranges during activity periods of each species in the two study areas

	Virginia			South Carolina		
	Beginning	End	Range	Beginning	End	Range
<i>Aselomaris michaeli</i>	19	20	3–20	—	—	—
<i>Tubularia crocea</i>	—	—	—	20	25	6–25
<i>Sarsia tubulosa</i>	10	17	3–17	—	—	—
<i>Gonothyrea loveni</i>	13	24	3–24	10	19	9–19
<i>Hartlaubella gelatinosa</i>	10	25	3–25	—	—	—
<i>Opercularella pumila</i>	20	18	3–20	—	—	—
<i>Sertularia cupressina</i>	20	23	3–23	—	—	—

that experiment, transfer of half of the specimens of each species from one temperature to the other gave similar results after an additional 192 h. Growth was halted and regression of hydranths occurred in 100% of the specimens switched from 25 to 5°C, whereas controls maintained at 25°C showed no hydranth regression ( $p < 0.10$ ). Transfer of specimens from 5 to 25°C resulted in 20% (*E. carneum*,  $p < 0.50$ ) to 80% (*E. dumortieri*,  $p < 0.05$ ) regeneration, whereas controls at 5°C remained dormant.

### Discussion

Estuarine waters of Virginia and South Carolina were characterized by wide annual oscillations in temperature. Coinciding with these temperature fluctuations, most hydroid species

investigated were seasonal in occurrence, being generally divisible into warm- and cold-water groups, and the appearance and disappearance of active colonies was often abrupt.

Of hydroids common to the two study areas, warm-water species consistently had longer periods of activity in South Carolina than in the somewhat colder waters of Virginia. By contrast, duration of activity in cold-water species was longer in Virginia. Moreover, five cold-water species present in Virginia (*Aselomaris michaeli*, *Sarsia tubulosa*, *Hartlaubella gelatinosa*, *Opercularella pumila*, and *Sertularia cupressina*) do not range as far south as South Carolina in the western Atlantic. Conversely, the warm-water *Plumularia floridana* evidently does not occur northward to Virginia, except on *Sargassum* offshore (Calder 1983). *Ectopleura dumortieri*, *Bougainvillia*

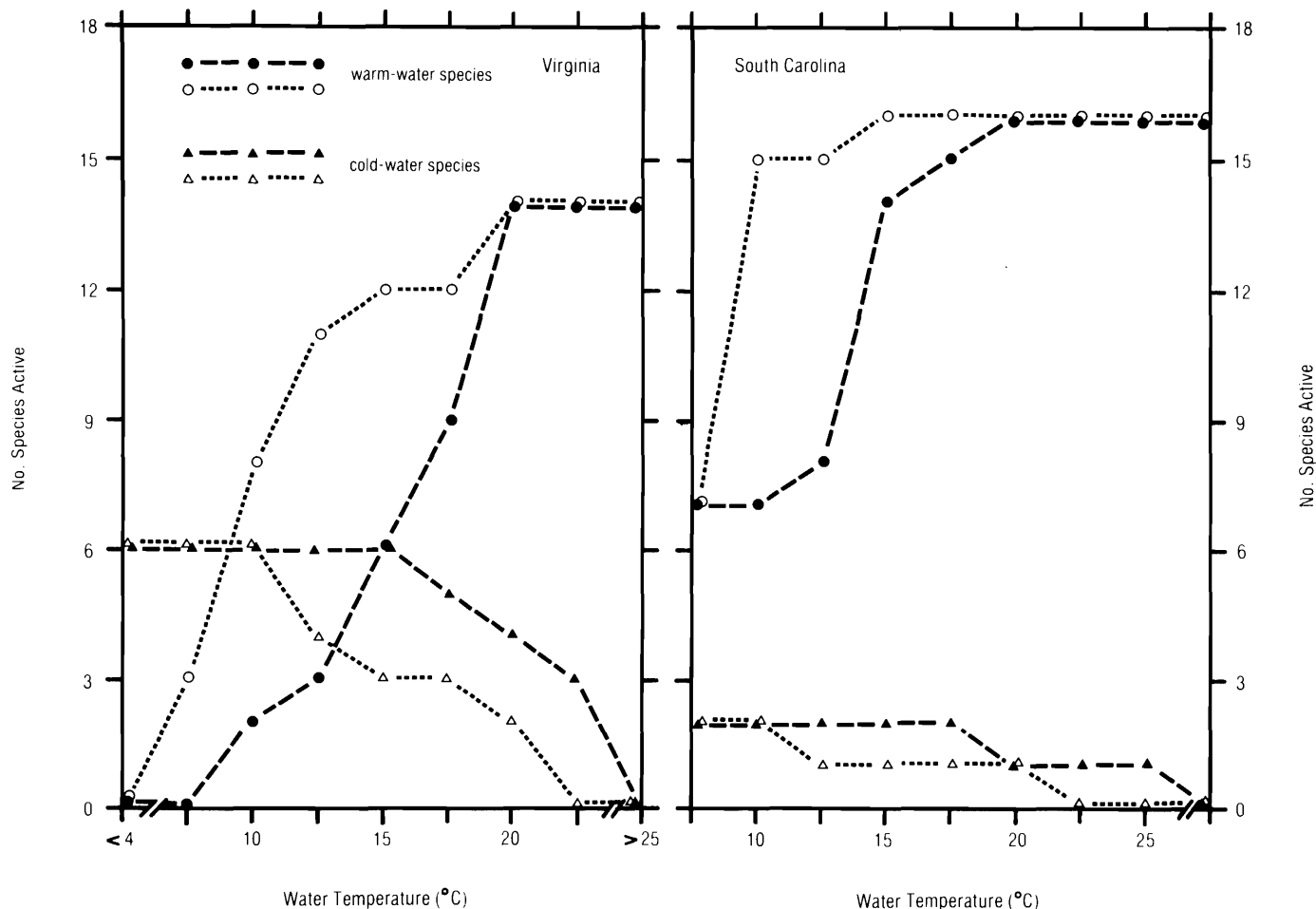


FIG. 6. Numbers of warm- and cold-water hydroid species active in Virginia and South Carolina, in relation to rising (broken lines) and falling water temperatures (dotted lines).

*rugosa*, and *Obelia dichotoma*, absent from the fauna during winter in Virginia, were active throughout the year in South Carolina.

With the exception of *Halocordyle disticha* and *Lovenella gracilis* in Virginia, warm-water species in this study commenced activity at temperatures several degrees above those coinciding with their disappearance in autumn or early winter. Cold-water species, except *Opercularella pumila* in Virginia, reappeared at temperatures below those noted at the end of their activity cycle in spring or early summer. The significance of this apparent pattern is uncertain, although it may increase the likelihood of a sustained period favourable for growth once regeneration has been triggered, even in the event that temperatures revert briefly toward critical levels.

Observed temperatures at the beginning of activity in species common to Virginia and South Carolina (Table 1, 2) were close or identical for some (e.g., *Dynamena disticha*, *Schizotricha tenella*), but less so for others (e.g., *Turritopsis nutricula*, *Gonothyrea loveni*). Likewise, the congruity of temperatures recorded at the end of activity in seasonal species from the two areas varied. Inconsistencies likely reflect the difficulty of establishing critical temperature parameters with precision from field studies, especially in areas subjected to wide and rapid temperature change.

Seasonal activity cycles of hydroid species were congruent

with their reported latitudinal distribution in the western North Atlantic. Typically boreal species, such as *Tubularia crocea* and *Gonothyrea loveni*, flourished and reproduced during winter in Virginia and South Carolina. Both were inactive during warm months. *Gonothyrea loveni* was observed only from January to April in South Carolina, at the southern limit of its range, between temperatures from the seasonal low of 9°C to a high of 19°C. Its seasonality in Virginia extended from November to June, at temperatures from 3 to 24°C. Farther north, in Cape Cod Bay, colonies of the species were active every season of the year, over a temperature range from 1 to 23°C (Calder 1975). At the northern end of its range, the species was present during summer in shelf waters of northern Canada (Calder 1970); accompanying temperature data were not given but the study area encompassed arctic and subarctic zones north of the 10°C isotherm. Collections from seasons other than late spring and summer from the Canadian north were unavailable, and it is not known whether *G. loveni* is active there at other times of year. Kinne (1956, 1970) suggested that temperatures above 19–20°C in midsummer and below 2–3°C during midwinter tended to induce dormancy in *G. loveni* in the Kiel Canal, Germany. All of the cold-water species in this study range well to the north of Cape Cod, Massachusetts, some even penetrating into arctic and subarctic waters (Table 3). At the other end of their range, over half of these species reach their

TABLE 3. Temperature-group designations of the hydroid species studied, and the northern and southern limits of their reported ranges in the western North Atlantic

	Temperature group	North	South
<i>Turritopsis nutricula</i>	Warm-water	Massachusetts	Caribbean Sea
<i>Cordylophora caspia</i>	Warm-water	Quebec	Caribbean Sea
<i>Stylactaria arge</i>	Warm-water	Massachusetts	Caribbean Sea
<i>Bougainvillia rugosa</i>	Warm-water	Chesapeake Bay	Caribbean Sea
<i>Garveia franciscana</i>	Warm-water	New Brunswick	Gulf of Mexico
<i>Aselomaris michaeli</i>	Cold-water	Maine	Chesapeake Bay
<i>Amphinema dinema</i>	Warm-water	Massachusetts	Florida
<i>Eudendrium album</i>	Warm-water	Atlantic Canada	Florida
<i>Eudendrium carneum</i>	Warm-water	Massachusetts	Caribbean Sea
<i>Proboscidactyla ornata</i>	Warm-water	Massachusetts	Caribbean Sea
<i>Tubularia crocea</i>	Cold-water	Atlantic Canada	Florida
<i>Ectopleura dumortieri</i>	Warm-water	Massachusetts	Caribbean Sea
<i>Halocordyle disticha</i>	Warm-water	Massachusetts	Caribbean Sea
<i>Dipurena strangulata</i>	Warm-water	Massachusetts	Florida
<i>Sarsia tubulosa</i>	Cold-water	Hudson Strait	Chesapeake Bay
<i>Linvillea agassizii</i>	Warm-water	Massachusetts	South Carolina
<i>Clytia hemisphaerica</i>	Warm-water	Atlantic Canada	Caribbean Sea
<i>Clytia kincaidi</i>	Warm-water	Chesapeake Bay	Caribbean Sea
<i>Clytia paulensis</i>	Warm-water	Chesapeake Bay	Caribbean Sea
<i>Obelia bidentata</i>	Warm-water	Maine	Caribbean Sea
<i>Obelia dichotoma</i>	Warm-water	Quebec	Caribbean Sea
<i>Gonothyrea loveni</i>	Cold-water	Arctic Ocean	South Carolina
<i>Hartlaubella gelatinosa</i>	Cold-water	Labrador	Chesapeake Bay
<i>Lovenella gracilis</i>	Warm-water	Massachusetts	Gulf of Mexico
<i>Opercularella pumila</i>	Cold-water	New Brunswick	Chesapeake Bay
<i>Dynamena disticha</i>	Warm-water	Massachusetts	Caribbean Sea
<i>Sertularia distans</i>	Warm-water	Massachusetts	Caribbean Sea
<i>Sertularia cupressina</i>	Cold-water	Baffin Island	North Carolina
<i>Schizotricha tenella</i>	Warm-water	Massachusetts	Caribbean Sea
<i>Plumularia floridana</i>	Warm-water	North Carolina	Caribbean Sea

southern limits at Chesapeake Bay, and only *Tubularia crocea* appears to occur as far south as Florida (Fraser 1944).

Of the 23 warm-water species investigated, only 4 occur north of Massachusetts, whereas over half range southward into the Caribbean Sea. Their phenology was the reverse of that for cold-water species. Species such as *Halocordyle disticha* and *Dynamena disticha*, frequent in the tropical and warm-temperature western Atlantic (Calder 1983, 1988), thrived and reproduced during summer in Virginia and South Carolina, but were inactive during colder months. *Dynamena disticha* ranges northward to Massachusetts (Fraser 1944, as *Sertularia cornicina*), but was absent in samples from boreal waters of Cape Cod Bay (Calder 1975). In Virginia the species was active from April to November, over a temperature range of 12–26°C. It was observed in South Carolina from March through early January, at temperatures between 8 and 30°C. In subtropical waters of Bermuda, *D. disticha* is apparently active all year, having been collected during each of the four seasons at temperatures ranging from seasonal lows of 18°C to highs of 30°C (unpublished data). These patterns of latitudinal distribution, water temperature tolerances, and seasonality in hydroids correspond generally to the observations of Hutchins (1947) concerning temperature as a factor in the geographic distribution of marine organisms.

Though observed seasonality patterns were correlated with water temperature, at least in part, other physical and biological factors are known to influence hydroid seasonality. For example, colonies of *Staurocladia portmanni* kept at constant temperature in the laboratory for a year by Brinckmann (1964)

exhibited a definite seasonality both in terms of activity and in production of medusa buds. Similarly, Brock (1975a, 1975b, 1975c) presented evidence that endogenous rhythms existed in laboratory-maintained cultures of *Laomedea flexuosa* which corresponded to the seasonal water temperature cycles of its natural environment. Brinckmann-Voss (1970) reported that the seasonality of smaller athecate species studied in the Mediterranean was apparently related to the seasonal growth of algae. She also observed that the commencement of spring activity in *Halocordyle disticha* occurred at the coldest time of year and did not coincide with rising water temperatures. Boero and Fresi (1986) observed seasonal patterns of activity in hydroids at intermediate and deep levels (0.5–20.0 m) at Portofino, Italy, whereas the fauna of shallow waters was remarkably stable throughout the year. Extremes of salinity have been implicated in periodic inactivity of the estuarine hydroids *Cordylophora caspia* and *Garveia franciscana* in some areas (Kinne 1956, 1971; Wedler 1973, 1975).

The regular seasonal activity cycles of hydroid species in the two study areas raises the question of how these organisms suddenly reappear as active colonies at a certain time of year. Although several hypotheses might be proposed, including annual repopulation from other regions, the abrupt and predictable appearance of hydroids at a given water temperature and season strongly suggests the existence of one or more stages tolerant of unfavourable seasonal extremes.

Dormant cysts and "resting eggs" are known in the life cycle of some species of hydroids (Werner 1954, 1955; Rees 1957; Bouillon 1975). However, dormant tissue in stems and stolons

provides another means for survival of unfavourable conditions, as shown in this and other studies. Cessation of growth, followed by dedifferentiation and resorption of hydranths, was observed with the onset of unfavourable environmental conditions in 13 of the species studied here. With the return of favourable conditions, new growth was detected arising from tissue in old stems and stolons in *Bougainvillia rugosa*, *Garveia franciscana*, *Eudendrium album*, *Eudendrium carneum*, *Ectopleura dumortieri*, *Dynamena disticha*, *Sertularia cupressina*, and *Schizotricha tenella*. Experiments with *Bougainvillia rugosa*, *Eudendrium carneum*, and *Ectopleura dumortieri* confirmed that new growth commenced and hydranths were regenerated when fragments containing dormant tissue were exposed to favourable temperatures in the laboratory.

Huxley and DeBeer (1923) noted that hydranths of certain Campanulariidae may not survive under conditions that do not appreciably affect the less specialized and more "plastic" tissue of the stem. Several studies suggest that hydranth regression, followed by dormancy in stems and stolons, is an important way in which hydroids survive unfavourable seasons. Hargitt (1900) observed that *Halocordyle disticha* thrived in summer at Woods Hole, Massachusetts, but declined in vigour during autumn. Hydranths eventually degenerated, the coenosarc receded into the perisarc of the hydrorhiza, and a more or less prolonged period of quiescence followed. A similar process was observed in *H. disticha* from Beaufort, North Carolina (McDougall 1943), and from the Mediterranean (Tardent 1963; Brinckmann-Voss 1970). Seasonal dormancy in stems or stolons has also been discussed in a number of other species, including *Tubularia indivisa* (Allman 1872; Elmhirst 1922), *Eudendrium* sp. (Bumpus 1898), *Tubularia crocea* (Hyman 1920; Moore 1939; McDougall 1943), *Clava multicornis* (Broch 1925), *Dynamena pumila* (Haddow 1937), *Cordylophora caspia*, *Garveia franciscana*, and *Gonothyrea loveni* (Kinne 1956, 1970), and *Lafoeina maxima* (Crowell 1982).

Regular cycles of hydranth regression and replacement have been reported in some species of hydroids (Crowell 1953). Some authors (e.g., Crowell 1953; Brock and Strehler 1963; and others) have considered this to be a rejuvenatory process, a hypothesis disputed by Hughes (1987). In any case, such hydranth regression–replacement cycles differ from the phenomenon of hydranth resorption or autotomy and dormancy in response to periodic environmental stresses, including unfavourable water temperatures (e.g., Morse 1909; Moore 1939; Berrill 1948; Tardent 1963).

As a corollary to allowing hydroids to survive periodically critical environmental conditions, dormant stages are important in their geographic distribution. For example, *Halocordyle disticha*, common in tropical regions of the Atlantic, Pacific, and Indian oceans (Calder 1988), survived winter temperatures as low as 3°C in Virginia while dormant. The boreal species *Tubularia crocea* and *Gonothyrea loveni* thrived in "warm-temperate" South Carolina during winter, withstanding temperatures of 30°C or more during summer in an inactive state. Dormant stages may also play a role in the long-range dispersal of hydrozoan species (Calder and Burrell 1969); the widespread distribution of the freshwater hydrozoan *Craspedacusta sowerbyi* is believed to have been facilitated by the formation of "resistant bodies," tolerant of desiccation and extreme temperatures (Acker 1976). Moreover, resistant stages have been implicated in the introduction and persistence of hydrozoan pests in self-contained aquaculture systems (Sandifer and Smith 1979). As noted by Broch (1925), detailed studies of the

formation and biology of resting stages may be necessary for the understanding of many biogeographical phenomena.

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