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Growth Cycle and Related Vertical Distribution of the Thecosomatous Pteropod *Spiratella ("Limacina") helicina* in the Central Arctic Ocean

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Abstract

The growth cycle and related vertical distribution of the thecosomatous pteropod *Spiratella ("Limacina") helicina* (Phipps) were studied. *S. helicina* has a life cycle of approximately 1.5 to 2 years in the central Arctic Ocean (Canada Basin). It spawns mainly during the spring to summer period, and on a small scale during the winter. The young double their sizes during the winter months of October to May, slow down in growth until late summer, and attain maximum size in early winter. The oldest disappear by late March. Gonadal tissue was first seen in young pteropods of 0.7 mm diameter, the predominant size from February to April. *S. helicina* 0.8 mm in diameter, the size predominant from May through July, are mature and hermaphroditic. Growth during the winter months suggests that particulate organic matter is available during this period to these obligate ciliary feeders. Vertical distribution is size and season-dependent. The youngest specimens collected (0.2 to 0.4 mm) were found concentrated in the first 50 m. The larger sizes dispersed during the summer months, and tended to concentrate in the top 150 m during the rest of the year. They aggregated in the top 50 m from late winter through early spring, and fall through early winter; then concentrated in the 100 to 50 m level until the end of winter. Numerous environmental factors seem to be involved in determining the vertical distribution of the species in the central Arctic Ocean.

Introduction

Spiratella ("Limacina") helicina (Phipps), a prominent member of marine zooplankton in polar and boreal waters, is the only thecosomatous pteropod recorded in the central Arctic Ocean (Leung, 1971). The role of *S. helicina* as a member of the Arctic fauna has become of particular interest as a result of Hansen and Dunbar's (1970) report of the species in the acoustical scattering layer associated with the 50 m pycnocline in the central Arctic Ocean (Canada Basin). It has been found concentrated at depths corresponding to locations of the scattering layers, and has been shown to be physically capable of causing accoustical reverberations. Earlier studies by Brodskii and Nikitin (1955), and Harding (1966) have established the distribution of *S. helicina* to be mainly within the Arctic layer of the water column (0 to 250 m). Aside from these observations, however, very little has been known of the biology of the species in the central Arctic Ocean.

This paper deals with the growth cycle, related vertical distribution and environmental factors which may be of influence in determining vertical distributional patterns of the species.

Materials and Methods

Samples used in this study were collected from the drifting ice stations: "Arlis I" at the periphery of the central Arctic Basin (74°-75°N; 143°-166°W), October, 1960-March, 1961, 29 stations; "Arlis II" in the central Arctic (83°-86°N; 169°-174°W), October, 1962-March, 1963, 16 stations; "T-3" in the central Arctic (84°-83°N; 112°-85°W), March, 1970-October, 1972, 85 stations.

The "T-3" series was collected by field workers from the University of Southern California (USC) and the University of Washington, in vertical tows made consistently at the following increments: 50 to 0 m, 100 to 50 m, 150 to 100 m, 200 to 150 m, 250 to 200 m, 300 to 250 m, 500 to 300 m, 700 to 500 m, 900 to 700 m, 1200 to 900 m. 1 m diameter, closing nets of 215 µm mesh were used. Samples from "Arlis I" and "Arlis II" were obtained by vertical and horizontal tows with 0.5 m nets varying in mesh from 73 to 215 µm. USC field workers did the collecting.

Shell diameters were determined by measuring across the shell from the end of the outer whorl with an ocular micrometer.

Vertical distribution was investigated among samples collected from "T-3" between March, 1970 and December, 1971, the period of most intensive sampling.

Gonadal maturation was determined from histological slides of *Spiratella helicina* of different sizes, at the period of their peak occurrence. Slides were prepared (method of Hsiao, 1939a) from specimens preserved in 7 to 10% buffered formalin, decalcified in 1% acetic acid, and whole-stained with methylene blue for ease in handling. 5 µm thick paraffin sections were prepared and stained with hematoxylin and eosin.

Results and Discussion

Growth-Cycle

Shell Diameters. Shell-diameter measurements of *Spiratella helicina* are presented in Table 1 as average monthly values. Two values are provided for months during which the array of sample diameters showed bimodal populations, one of large individuals (parent generation) and the other of smaller specimens (offspring generation). Individual measurements were pooled to derive the schematic growth cycle shown in Fig. 1.

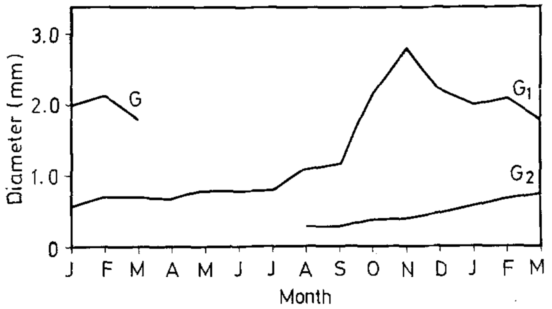

Fig. 1. *Spiratella helicina.* Schematic growth cycle based on pooled data from samples collected from the drifting ice stations "Arlis I", "Arlis II" and "T-3". G: parent generation of G_1; G_1: parent generation; G_2: offspring generation

During the growth cycle, young individuals of 0.3 mm diameter begin to appear in August and are prominent until November. The average diameter of the population of young specimens increases throughout the winter. The sizes double from 0.4 mm in October to 0.8 mm in May. External growth ceases between May and July, and continues again to an average maximum diameter of 2.8 mm. During the period of final growth, however, the population declines very noticeably in the proportion of individuals of 2 mm and larger found. Members of the adult population seem to disappear completely by the end of March; large individuals are not collected until the following winter (October).

Data in Table 1 show that veligers of 0.3 mm diameter appear again in March. The numbers, however, are so small that their presence is not reflected in Fig. 1, based upon average sizes for each month. This appearance of young suggests that spawning occurs during the winter months on a limited scale.

Gonadal Development. The adult *Spiratella* is hermaphroditic. Its gonad, or ovotestis, is a spiral structure posterior to the digestive gland, occupying the posterior whorl of the spiral shell. Detailed description of the structure and organization is available in the work of Meisenheimer (1905) and Hsiao (1939a), who worked on *S. helicina* and *S. retroversa*, respectively. Hsiao found that mature ova in *S. retroversa* ranged from 50 to 70 µm , had dark staining granules in their cytoplasm, and a poorly staining nucleus. Two prominent, mature accessory reproductive organs he described were the shell gland and the seminal vesicularis. The shell gland, according to the description, is histologically characterized by the presence of large secretory cells and tall, ciliated columnar cells. The seminal vesicularis is lined with cuboidal epithelial cells and is an elongated, pear-shaped organ connected to the hermaphroditic duct. These prominent characteristics of the mature hermaphroditic system were used to determine the maturity of the pteropods examined. Table 2 summarizes the observations on *S. helicina* of different sizes.

The data show that maturation of gonads does not occur on the average until the pteropods reach about 0.7 mm diameter, the size found predominantly from February to April. Accessory organs were difficult to identify until they reached about 0.8 mm diameter, the size predominant in May. Histologically, the hermaphroditic system of *Spiratella helicina* of 0.8 mm and larger were very similar.

Discussion

Derivation of Growth Cycle. The size of specimens taken at corresponding months from the different ice stations overlap within 1 standard deviation (Table 1). The periods in the growth cycle when the smallest and largest individuals occur, and when the largest forms disappear also overlap. The appearance of a small number of veligers, 0.3 mm diameter, in March is also consistent.

Growth and reproduction are influenced by fluctuations in a number of recognized environmental features. Among the most important seem to be light, temperature, and availability of food (Kinne, 1970). Throughout the central Arctic Ocean (Canada Basin) these features appear to be similar during any one period of the year. Because, hydrographically, the central Arctic water column is composed of 3 major water masses which vary very slightly in depth from one location to another (Coachman, 1963), temperatures experienced by animals at corresponding depths in different locations are very similar. Temperatures in the most fluctuating part of the column, the top 50 m, vary by a maximum of only 2C° throughout the year. Winter temperatures range between -1.65° and -1.85° C, and summer temperatures between -1.7° and 0°C. Light penetration, energy for primary production, is sharply controlled by the light cycle and the occurrence of snow cover during similar periods throughout the area. The availability of food is, thus, similarly limited until the spring-summer period occurring roughly from June-August (English, 1963, 1965).

On the basis of the shell-diameter measurements and the consistency of environmental features, I

Table 1. *Spiratella helicina*. Average shell diameters of individuals from the different stations. **standard deviations (SD) are provided for size groups based upon 9 or more measurements

Month	"Arlis I"			"Arlis II"			"T-3" (1970)			"T-3" (1971)			"T-3" (1972)		
	Diameter (mm)	Range (mm)	SD** (±)	Diameter (mm)	Range (mm)	SD (±)	Diameter (mm)	Range (mm)	SD (±)	Diameter (mm)	Range (mm)	SD (±)	Diameter (mm)	Range (mm)	SD (±)
January	0.6	0.4–0.9	0.10	0.5	0.5–0.6	0.02							0.5	0.4–0.6	0.09
	1.6	1.2–2.0	0.30	2.0	1.4–2.5	0.25									
February	0.7	0.5–0.8	0.09	0.5											
	2.2	1.0–3.0	0.57	2.8											
March	0.6	0.3–0.8	0.11	0.5			0.7	0.3–0.9	0.10						
	2.0	1.5–2.4					2.8	2.5–3.0		2.0	1.9–2.0				
April							0.7	0.5–0.9	0.08				0.7		
May							0.8	0.7–0.8	0.06				0.9	0.7–1.0	0.10
June							0.8	0.6–0.8	0.06						
July							0.8	0.7–1.0	0.10						
August										0.3	0.3–0.4	0.06			
							1.2	1.0–1.4	0.30	0.8					
September							0.3			0.3	0.3–0.5	0.02			
							1.2	1.0–1.4							
October	0.3	0.2–0.3	0.02	0.5	0.3–0.6	0.07				0.3	0.3–0.4	0.06			
	2.1	1.7–2.5		2.1	1.3–3.0	0.37							2.4	1.7–2.9	0.10
November	0.3	0.3–0.5	0.08	0.4	0.3–0.5	0.08				0.5	0.4–0.6	0.09			
	2.3	1.7–2.4	0.30	2.9	1.8–3.7	1.34									
December	0.5	0.3–0.7	0.10												
	1.9	1.8–2.2		2.3	1.3–2.9	0.36	2.1	1.6–2.4	0.22						

Table 2. *Spiratella helicina.* Shell size and gonadal development

Size (mm)	Gonadal state	Accessory organs	Comments	Month
0.4	No differentiation	Undeveloped	Primordial cells throughout body, in clumps	September
0.5	No differentiation	Undeveloped	Primordial cells throughout body, in clumps	November
0.6	No differentiation	Undeveloped	Primordial cells throughout body, in clumps	November
0.7	Some differentiation, but details indeterminate	Present, but not completely distinguishable	Differentiation throughout body	March, April
0.8	Mature ova, 37-46μ seen, male tissue present	Hermaphroditic organs present	Little histological difference from this size on	May, July
0.9	Mature ova, 43-71μ seen, male tissue present	Similar to that in 0.8 mm specimen		July
1.4	Mature ova, 43-57μ seen, male tissue present	Similar to that in 0.8 mm specimen		August

have interpreted the growth cycle of *Spiratella helicina* to be generally a uniform one within the central Arctic Ocean, and have therefore combined the data to derive the growth cycle shown in Fig. 1.

The life cycle of *Spiratella helicina* in the central Arctic Ocean appears to extend over 1.5 to 2 years. Supporting this estimate are the observations that the major spawning period starts in May when the population averages 0.8 mm, that veligers grow to 0.8 mm by May of the following year, and that an average of 2.8 mm (maximum 3.7 mm) is reached by November, after which the large specimens decline and disappear by March of the following year. If larger *S. helicina* such as the 8 mm individuals reported by van der Spoel (1967) in the sub-Arctic occur, then the life cycle of the species in the central Arctic Ocean may be longer. Our records of many years of sampling in the region, however, do not show such large specimens. Despite the obvious handicap of being unable to make fast tows routinely from the ice stations except when wind conditions cause fast movement of the islands, we have been able to collect adult specimens of such fast-swimming zooplankton as *Hymenodora glacialis* (decapod), *Clione limacina*, various medusae, an occasional octopus, and large amphipods; even fish have been caught. If such large *S. helicina* occur it is reasonable to assume that a few would have been collected over the long period of collections. It may be that larger *S. helicina* are unable to sustain themselves on the quality and quantity of food available to them during the long winter, and hence die out upon reaching a maximum sustainable size.

Spawning. Histological data show that *Spiratella helicina* has mature ova and fully developed accessory organs by about 0.8 mm diameter, the average size attained by the population in May (end of winter). This suggests that they can spawn from that size. Hansen and Dunbar (1970) have reported specimens of this size carrying egg masses. Since the major population of veligers appear in late summer and early winter (August-November) it appears that the major spawning period occurs during the spring and summer, starting in the late winter and ending before the following winter. The peak probably occurs during the May-July period, when cessation of external growth in the population was noted.

The cessation of growth in overall body size in *Spiratella helicina* during the reproductive period is common among animals. Energy demands require that only one of these processes predominate (Kinne, 1970). Growth after the major reproductive period is not as common; however, this feature does not appear to be an Arctic adaption since it is also displayed by the very closely related species found in the Gulf of Maine, *S. retroversa* (Hsiao, 1939b; Redfield, 1939).

Spawning does not seem to end entirely with the onset of winter. There appears to be some winter spawning on a small scale, for individuals of 0.3 mm diameter occasionally have been found in March (Table 1). Protracted reproduction has been found to exist among *Spiratella helicina* by Paranjape (1968).

The growth cycle of *Spiratella helicina* in the central Arctic is not unique to this region, but merely adapted to the occurrence of the spring-summer period of the area. It parallels that of *S. retroversa* (Redfield, 1939), which has its major spawning earlier in the year than *S. helicina*, during the spring period of the temperate region.

Major Growth Period and Food Supply. The fact that growth continues during the winter (October-May), with major size increase and gonadal development occurring during the dark months (October-March) suggests that food is available even during the winter months to these animals. *Spiratella* spp. are entirely ciliary feeders (Morton, 1954) dependent, therefore, upon the presence of particulate organic material (POM) of suitable size (phytoplankton, nannoplankton, detritus) for nutrition. Unlike a number of other Arctic and deep-water plankton from temperate areas which store reserves in the form of wax esters, pteropods do not appear to have this ability (Lee, personal communication), and hence are dependent throughout the year upon available food.

The presence of POM is dependent upon primary productivity, and the subsequent events in the food chain which lead to nannoplankton and detrital production. In the central Arctic, primary productivity occurs in an annual mono-cyclical manner in close association with local seasons (English, 1963, 1965), peaking during the biological summer (roughly mid-July through August), declining through September (autumn), pausing during the dark months (October-March) and resuming again from late winter as the sun appears. POM estimates, based upon amounts of particulate organic carbon for summer 1970 and 1971 (English, unpublished data for chlorophyll *a* X 75, where 75=C/Chl *a*: commonly used ratio for phytoplankton) and April 1971 (Holm-Hansen, unpublished data), shortly after the end of the dark period, at 25 m depth, were 32, 28, and 3 µg C/l, respectively. Because extensive annual surveys of organic particulates have not been conducted in the central Arctic Ocean, the major available data being limited to the end of winter (Kinney *et al.*, 1971; Holm-Hansen, unpublished), little can be said of the actual quantities of particulate material available to support POM-feeding zooplankton throughout the year. It can be said, however, that at a minimum, concentrations are as high as that of other deep ocean basins which support POM-feeding populations (Hobson and Menzel, 1969; Holm-Hansen, 1969). In the central Arctic, only a small proportion of the POM-feeding zooplankton is dependent throughout the year on external energy sources. Hopkins (1969) has shown that roughly 86% of the biomass is composed of copepods, and recent lipid studies (Lee *et al.*, 1972) have shown that the most prominent of these are capable of wax-ester production for energy reserves. Numerous other zooplankton are also capable of this activity, hence only a very small portion of the total biomass remains which requires POM throughout the year, *Spiratella* spp. being included.

Vertical Distribution

The data show seasonal vertical migration (Fig. 2). *Spiratella helicina* concentrated in the 50 to 100 m interval during the late winter months of March and April, migrated to the top 50 m during late winter to early spring (May-June), dispersed during the summer months, and reconcentrated at the end of summer. During September, the major concentration was in the top 50 m; however, in December there was a trend toward reconcentration at the 50 to 100 m depth interval.

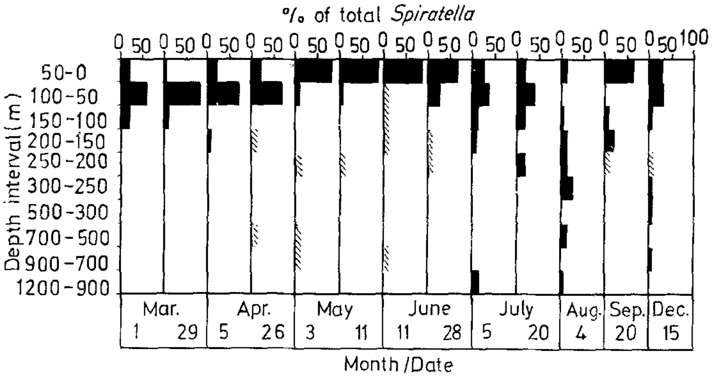

Fig. 2. *Spiratella helicina*. Vertical distribution of specimens collected from "T-3" during March-December, 1970. Values of 5% and less are indicated by lightly shaded, open bars

Vertical distribution limits varied with season. From late winter to the end of spring 90% of the population remained in the top 150 m of the water column, but dispersed down as far as 900 to 1200 m depth during the summer, continuing to be diffuse as late as December.

Vertical distribution as a function of size is shown in Fig. 3. *Spiratella helicina* larvae of 0.2 to 0.4 mm diameter (prominent from August to November) concentrated primarily in the top 50 m, while individuals of 0.5 to 0.7 mm (prominent from December to April) tended to concentrate at the 50 to 100 m interval. The persistence of small sizes less than 0.5 mm in the top 50 m accounts for the top-heavy distribution in September, and the shift to the 50 to 100 m interval by December as the pteropods on the average become 0.5 mm and larger. Sizes 0.8 to 0.9 mm (prominent from May to early July) were found mainly in the first 100 m. Specimens 1.0 to 1.4 mm, common during the summer, were dispersed - as would be expected

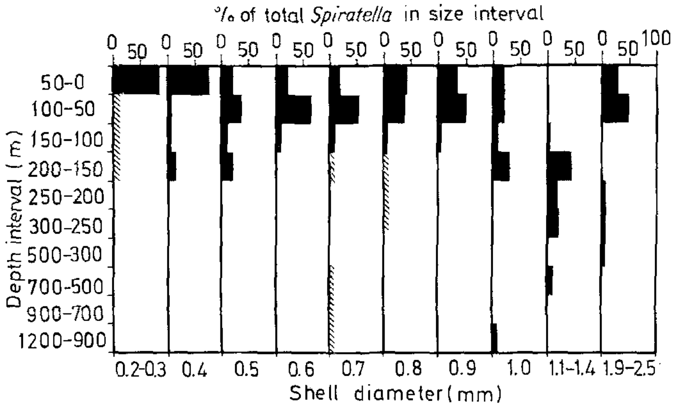

Fig. 3. *Spiratella helicina.* Vertical distribution, as a function of size, of specimens collected from "T-3" during March-December, 1970. Values of 5% and less are indicated by lightly shaded, open bars

from the general population trend in Fig. 2. *S. helicina* of 1.9 to 2.5 mm, found during fall and early winter, displayed the reconcentrating tendency described for the total population during this season.

Discussion

Seasonal migratory behavior as seen here is a phenomenon common to central Arctic zooplankton. Hughes (1968) reported the seasonal vertical migration of several copepods. Dawson (personal communication) has shown that the copepodites of *Calanus hyperboreus* concentrate in the top 50 m during the summer, and gradually migrate to deeper water by winter. Such migratory and aggregative behavior often is interpreted as response to a number of factors in the biological and physical environment. These include the availability of food, light, pressure, salinity, and avoidance of predators.

The availability of food in the water column throughout the year is of great importance to Arctic *Spiratella helicina* since, as mentioned earlier in the discussion of the growth cycle, these pteropods require a constant source of nutritive POM. Studies of POM in the Arctic water column made in April, shortly after the end of the completely dark period, have shown that it concentrates in the vicinity of 50 m (Holm-Hansen, unpublished data). At this time, *S. helicina* concentrates in the 50 to 100 m depth range (Fig. 2). Veligers of 0.2 to 0.3 mm are concentrated in the top 50 m (Fig. 3) - the euphotic zone of the Arctic water column (English, 1965) and hence the depth range of highest POM levels during productive months. Larvae of this size lack the adult swimming appendages, or "wings" (Paranjape, 1968), and therefore may find advantage in being present in the layers of highest food concentration.

Among other environmental factors influencing vertical migrations, light appears to be of some importance in the orientation and maintenance of the young in the top 50 m, since larvae are positively phototactic (Paranjape, 1968). The migration of adults to the top 50 m in May and June may also be influenced by light, as a trigger and in directional orientation.

The influence of temperature on the migration of central Arctic *Spiratella helicina* seems to be minimal, in view of the very small temperature change (about 0.5C°) that these pteropods normally experience in their vertical migration from the top 50 m to the 100 to 50 m interval. This species spawns, hatches, and spends its most formative period at temperatures ranging from -1.6° to -1.0°C. The maximum change it may experience would occur during summer dispersal, and may be roughly about 2C°.

Hydrostatic pressure does not appear to impose limits on the population, at least within 100 m depth. The downward movement is, on the whole, seasonal (Fig. 2). It is possible that tolerance varies with size, for only large, mature individuals have been found in depths below 200 m.

Salinity is often considered to pose physiological limits on vertical migration of zooplankton. It appears that in the Arctic this factor is influential in setting an upper distribution limit. *Spiratella helicina* concentrates at the 50 m level in preference to other parts of the top 50 m (Hansen and Dunbar, 1970). They thus concentrate in the salinity range of 29.8 to 32.0°/oo (data collected by the University of Washington at 50 m: Stations W1-W2, 1965; Stations 012-013, 1970), instead of spreading throughout the top 50 m of the water column which range in salinity from 28.5 to 33.5 °/oo (Coachman, 1963). In their dispersal down the water column during the summer, *S. helicina* live at salinities as high as 35°/oo, however this migration appears to be limited to adults.

Avoidance of predators by migration does not appear to be an advantage of the vertical movement of *Spiratella helicina*. *Clione limacina*, its well-defined predator (Lalli, 1970), has a parallel pattern of distribution (Mileikovsky, 1970).

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