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REPRODUCTION, GROWTH AND TROPHIC INTERACTIONS OF *DORIOPSILLA PHARPA* MARCUS IN SOUTH CAROLINA

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ABSTRACT

The dorid nudibranch *Doriopsilla pharpa* Marcus has been observed from Massachusetts to Florida. Specimens from creeks and tide pools were collected with their prey, the sulfur burrowing sponge, *Cliona celata,* in North Inlet Estuary, South Carolina. The nudibranch had an annual life cycle with oviposition from late March to early June. The smallest individuals observed copulating (≈10 mm in length) were 4–5 mm shorter than the smallest specimens observed ovipositing. The yellow eggs (203 ± 3 μm diameter) were deposited in masses of about 300 eggs. Type I shells were formed by the embryos and dropped at hatching. The capsular metamorphic development required 14–16 days at 23°C and the yolk supply sustained the juveniles about one week after hatching. *D. pharpa* from tide pools were significantly smaller than individuals from creeks, although summer and fall growth rates in the two populations were similar. The percentage of nudibranchs in obvious association with *C. celata* changed during the year, probably due to degradation of the sponge ventilation papillae caused by some factor other than changes in predatory behavior of *D. pharpa.*

Doriopsilla pharpa Marcus, a sub-tidal yellow-orange dorid, is a common nudibranch in North Inlet Estuary, South Carolina (Eyster, 1980). This nudibranch and its prey, the sulfur burrowing sponge *Cliona celata* Grant, inhabit shell rubble along the eastern coast of North America. *D. pharpa* has been observed in Massachusetts (M. P. Morse, pers. comm.), Maryland (Marcus, 1972), Virginia (R. Vogel, pers. comm.), North Carolina (Marcus, 1961), South Carolina (Shoemaker et al., 1978), Georgia (Marcus and Marcus, 1967), and Florida (pers. observ.). This paper reports on the reproduction, seasonal abundance, habitat, and food supply of *D. pharpa*. Growth of specimens from tide pools and creeks is compared and seasonal changes in association between the nudibranch predator and its sponge prey are also examined.

METHODS AND MATERIALS

During a study of the shell-less opisthobranchs of North Inlet Estuary, Georgetown County, South Carolina (33°20′N, 79°10′W), field observations of *D. pharpa* were made once or twice monthly from December 1975 through March 1977. North Inlet is a temperate, undeveloped, high salinity, high turbidity estuary with average salinity and temperature ranges of 20–35‰ and 15–30°C, respectively.

D. pharpa was collected from creeks and tide pools at low tide by hand, oyster tongs, or dredge. To examine seasonal and habitat variations in population density, specimens were collected from 1 m^2 quadrats along shallow creek banks in areas with various densities of *C. celata*. At low tide, water depth over these quadrats was less than 0.5 m. The quadrats were hand-sampled in triplicate in October and November 1976 and in January and February 1977.

Tide pools containing *C. celata* were selected for comparison with shell-rubble creek sites and for studying abundance and growth of *D. pharpa*. The tide pools were lined with oyster shell rubble (predominantly *Crassostrea virginica*) and occasional clam (*Mercenaria mercenaria*) valves. The tide pools (A, B, and C) were inundated during every high tide, with rising tidal waters entering tide pools B and C directly from a small tidal creek. Tide pool A was flooded by water flowing through tide pool B. Tide pool A measured 7 × 8 × 0.3 m at low tide; tide pools B and C were similar in size and shape.

Tide pool A, due to its more varied substrate, discrete borders and longer time between floodings, was selected for analysis of seasonal changes in the association between the nudibranch and shells with different sponge stages. Tide pool A was sampled from February 1976 through February 1977

for approximately 1 h each month. Tide pools B and C were examined irregularly. Shells or shell clusters were picked up and examined for nudibranchs and/or egg masses. Each *D. pharpa* was measured while it was actively crawling. It was then returned to its original shell and location in the pool. The time required for measuring the nudibranchs was not included in the timed sampling period. Movement of shell clusters in the tide pool caused sufficient turbidity to prevent biased selection of shells with abundant sponge or avoidance of shells without it. Care was taken to avoid unnecessary damage to shell clusters or exposure of sponges to the air for longer than a few seconds.

C. celata is classified as alpha, beta, or gamma stage depending on the extent of invasion of the sponge into the shell substratum (Vosmaer, 1933). An alpha stage sponge is one which is largely enclosed within the $CaCO_3$ material, while a beta sponge is one which has also encrusted the substratum. Gamma stage sponges have completely destroyed the calcareous substratum and are free-living. Since no beta or gamma stages of the sponges were observed in the study area, a new classification of pre-alpha, alpha, and alpha-plus stages was utilized. The shells examined were then classified according to the stage of their *C. celata* infestation; pre-alpha stage: shells in which *C. celata* was visually undetectable on the surface; alpha stage: shells exhibiting some *C. celata* papillae on and/or above the surface; alpha-plus stage: shells with abundant, protuberant *C. celata* papillae, half-way between classical alpha and beta stages.

At the conclusion of each timed sampling period, the number of *D. pharpa* observed per hour and the number observed per 150 shells examined were calculated. A shell was defined as any size cluster of oyster valves. The overall number of *D. pharpa* found with each shell type was then recorded and the percent association between predator (nudibranch) and prey (sponge) was calculated:

$$\% \text{ association} = \frac{\text{no. of } D. \textit{ pharpa} \text{ observed per shell type}}{\text{total no. of } D. \textit{ pharpa} \text{ observed}} \times 100$$

D. pharpa were collected from creeks each month from July through March and were measured for length, wet weight, and dry weight. To avoid altering the tide pool population, specimens were obtained only from creeks distant from the pools. To determine wet and dry weights, nudibranchs were rinsed briefly with distilled water, blotted dry, weighed to the nearest 0.001 mg, oven-dried overnight, and reweighed.

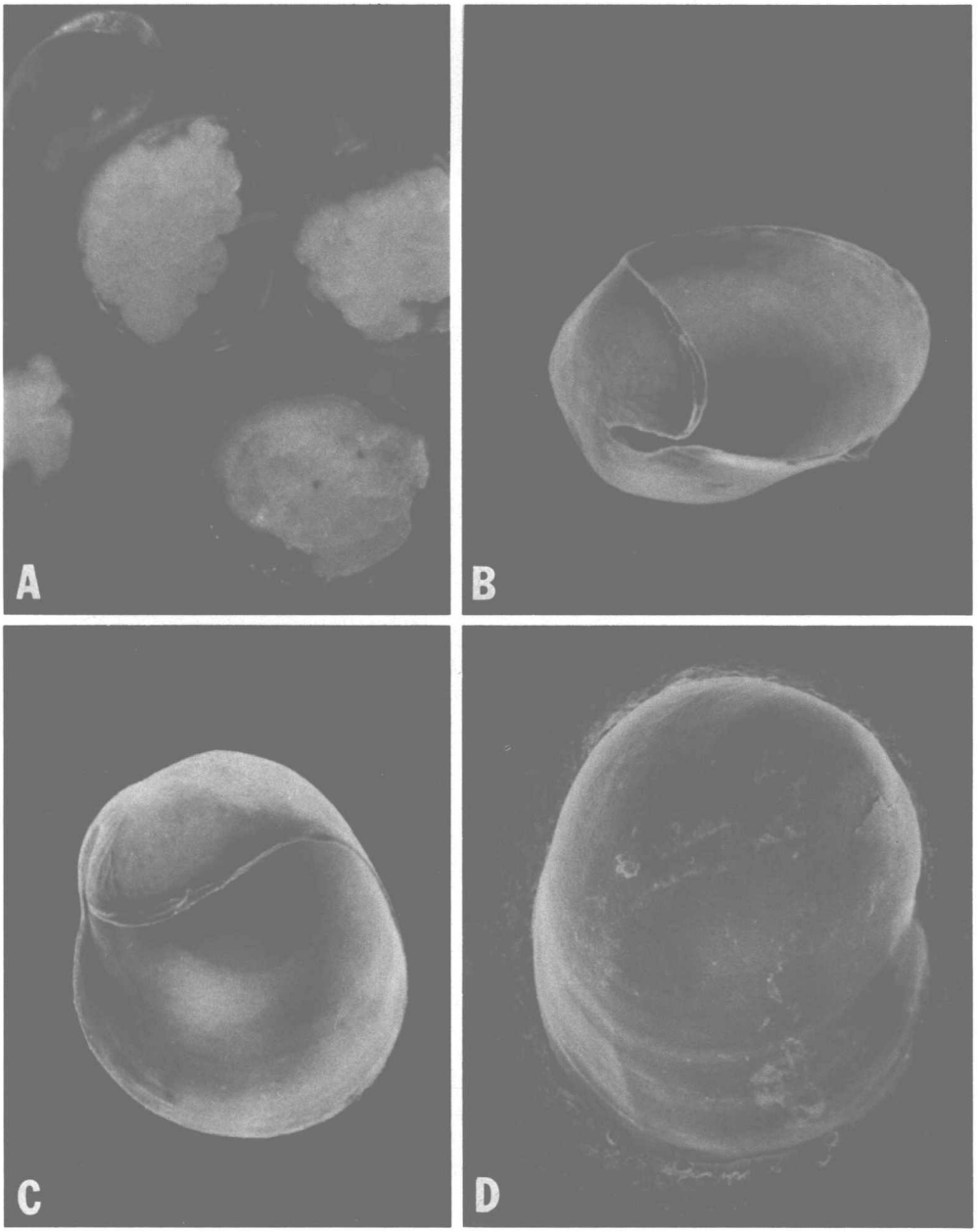
RESULTS

D. pharpa was present all year in areas with *Cliona*-infested shell rubble. Specimens resembled those described from the type locality (Beaufort, North Carolina; Marcus, 1961) except that five instead of four gill leaflets were present. The two largest specimens measured 20 × 16 mm and 25 × 15 mm. Most *D. pharpa* were found in shallow sub-tidal waters.

Reproduction and Development

D. pharpa had an annual life cycle, with oviposition restricted to late spring. The egg masses contained about 300 eggs and were laid flat against the substratum in a spiral pattern of 2–7 whorls. The eggs were well-spaced and usually in a single layer, though occasionally two deep in the center of the mass. The uncleaved eggs were yellow or orange and measured 203 ± 3 μm in diameter. The embryos developed into shelled veligers, which metamorphosed into juveniles within their individual egg capsules. Hatching occurred 14–16 days after oviposition (23°C). The egg capsules just prior to hatching measured 300 μm in maximum diameter. The Type I shells (Thompson, 1961) were left within the egg capsule or dropped nearby at hatching (Figures 1A–D). The shells averaged 216 × 188 × <188 μm and looked somewhat patelliform or cuplike (Type A of Thorson, 1946) when viewed laterally. They were colorless, transparent, and without surface sculpturing except for possible growth lines (Fig. 1D). The left side of each shell was sutured and the aperture bore a narrow, upturned lip.

In newly-hatched juveniles, the yellow yolk supply in the posterior two-thirds of the body was visible through the notum. The notum was bicordate and varied from round to elongate with increased activity. The postero-dorsal end of the



Figures 1A–D. A, portion of *Doriopsilla pharpa* egg mass showing discarded shell (upper left), aborted embryo (center), and unhatched juvenile (lower right). The juvenile hatched shortly after this picture was taken. B–D, SEM photographs of discarded shells (≈250×). B, ventro-lateral view showing open suture present in some shells; C, same shell, ventral view; D, dorsal view, showing possible growth lines.

notum was peaked and pointed in a posterior direction, but this peak was lost about 12 h after hatching as the visceral organs shifted. The foot was rounded anteriorly and pointed behind. The eyes were black and prominent.

Length of the juveniles at hatching was approximately 300 μm. After 4 days,

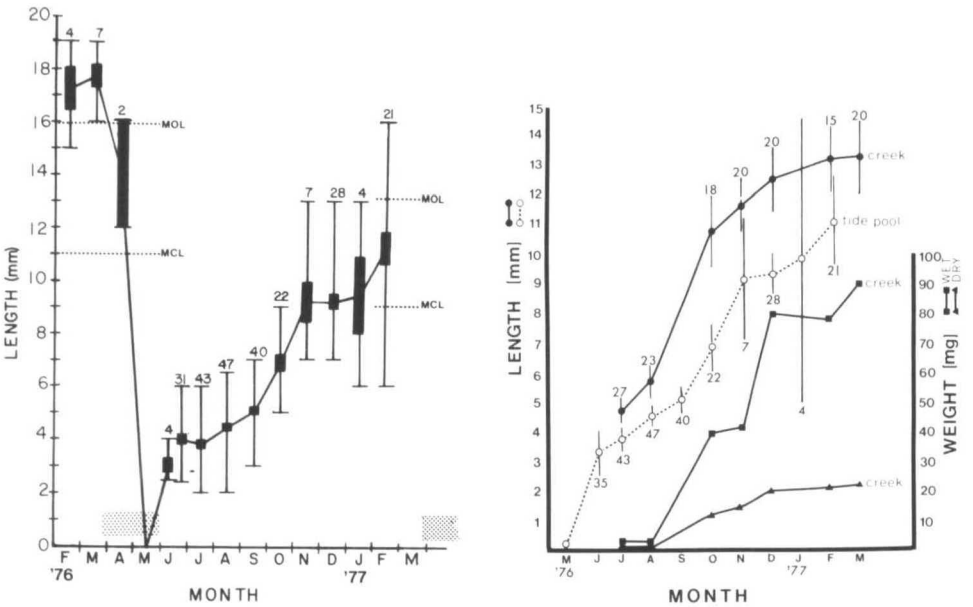


Figure 2. (Left) Mean body length of *Doriopsilla pharpa* from tide pools (narrow vertical bars = range; wide vertical bars = standard error; numbers above bars = sample sizes; MOL and MCL = minimum ovipositional length and minimum copulational length respectively, determined from freshly collected creek specimens; stippled horizontal bars indicate ovipositional periods).

Figure 3. (Right) Comparative field growth of *Doriopsilla pharpa* from creeks and tide pools. Growth of creek specimens is plotted in terms of mean length (circles), wet weight (squares), and dry weight (triangles). Growth of tide pool specimens is given only as mean length (open circles). Vertical bars indicate 95% confidence intervals. Numbers above and below the bars indicate sample sizes.

the rhinophoral and gill buds formed, the notum was no longer bicordate, the notal spicules were prominent, and small white glands appeared along the notal fringe. The spicules were arranged in horizontal layers, oriented radially in the notal fringe and diagonally in the notal center. The dorsal and ventral layers of these central spicules lay at right angles to each other. After 1 week, the yolk supply was almost depleted and the rhinophores were retractile, but unlamellated. Ten days after hatching, juveniles averaged 450 μm long. The smallest field specimens detected were 2.0 mm long and were probably about 6 weeks old.

Reproductively mature individuals were seen each year in spring. The age of first reproduction was about 10 months. The first egg masses were seen in the laboratory and were observed March 22 and March 31 at temperatures of 23°C (1976) and 21°C (1977), respectively. Minimum mating or minimum copulational length (MCL) and minimum ovipositional length (MOL) were determined from the smallest freshly-collected creek specimens observed copulating or ovipositing. The MCL was about 11 mm in 1976 and 9 mm in 1977; the MOL was 16 mm in 1976 and 13 mm in 1977 (Fig. 2). No tide pool specimens were collected for comparison but the onset of egg-laying in the pools occurred when individuals exceeded the observed creek MOL (Fig. 2). Although the MCL was 4–5 mm less than the MOL each year it is not known whether this species is typically protandrous. Both the MCL and MOL were lower in the second year. Although the 1976 MOL (16 mm) was reached in February, no eggs were laid until late March. A few days before oviposition first occurred eggs became visible through the ventral body surface.

Table 1. Reproductive characteristics of laboratory-maintained *Doriopsilla pharpa* from North Inlet Estuary, South Carolina, 1977 (n.a. = not applicable)

Observation Period (1977)	Date Collected	No. of Adults at Start of Observation Period	Total No. of Egg Masses	Eggs/Mass (range)	Eggs/Mass (x ± SE)	Reproductive Rate (Eggs/indiv/day)
29 Jan–15 Apr	29 Jan	10	1	335	335	n.a.
12–31 Mar	12 Mar	30	1	417	417	n.a.
1–30 Apr	12 Mar	8 (paired)	12	44–570	264 ± 52	12
		22 (as one group)	13	26–811	326 ± 66	6
		30 (total)	25	26–811	296 ± 42	8
1–17 May	30 Apr	5	12	21–834	291 ± 89	37
1–31 May	12 Mar	18	4	32–1,090	416 ± 233	5
1–13 June	12 Mar	5	4	67–170	117 ± 22	7
14–30 June	12 Mar	5	0	0	0	0

Table 1 summarizes reproductive characteristics of laboratory-maintained *D. pharpa*. Unlike individuals left in the field, specimens collected in late January and maintained with *C. celata* in the laboratory under a relatively constant temperature and light schedule (≈23°C; 14L:10D) did not increase in length. After 65 days in captivity, their average length was unchanged (9.8 mm at capture and 9.7 mm after 65 days), while field specimens had increased to a mean length of over 13 mm (the MOL) during the same period. Four out of 10 captive adults survived the 65 days. Of these four, three were 9 mm and one was 13 mm in length. At least one of the smaller specimens copulated but did not oviposit. The largest specimen copulated and produced a single, fertilized 335-egg mass in early April. In other words, field and laboratory reproductive seasons began at similar times (late March–early April) and field and laboratory MOL's and MCL's were comparable.

The reproductive rate of specimens kept in the laboratory was affected by such factors as length of captivity and numbers of individuals held together in aquaria. In May, freshly-collected specimens laid 37 eggs per individual per day, while specimens collected 7 weeks earlier produced only five eggs per individual per day. *D. pharpa* maintained in pairs had twice the reproductive rate of individuals in a large group (Table 1). It is not known whether the frequency of interruption of oviposition (to copulate) varied between these two groups and affected frequency of oviposition, as was observed in the nudibranch *Tenellia pallida* (Eyster, 1979). Throughout the reproductive season the mean number of eggs per egg mass was about 300 (range 21–1,090) although smaller egg masses were noted later in the season than in mid-season. The peak egg-laying period was April through May and no egg masses were seen before late March or after early June in either the laboratory (Table 1) or the field. Based on the reproductive rates in the laboratory (Table 1) and length of the reproductive season, the total fecundity of *D. pharpa* is estimated at 1–3 thousand eggs per individual (up to 37 eggs per individual per day for up to 78 days). Because no specimens were taken from the tide pools, reproductive rates in the two populations could not be compared.

Growth and Mortality

Length, wet weight, and dry weight of *D. pharpa* creek specimens were all highest in March, at termination of the 9-month study (Fig. 3). Mean length of adults did not change significantly in February and March (Figs. 2, 3) but it did

Table 2. Regression equations relating various size parameters of *Doriopsilla pharpa*, where y = mx + b; significance determined with Spearman's and Kendall's rank correlations (n = sample size)

	m	b	r^2	Significance	n
Length-width	0.620	−0.315	0.89	0.0001	163
Length-dry wt.	2.444	−12.413	0.88	0.0001	158
Length-wet wt.	9.710	−52.936	0.89	0.0001	158
Wet wt.-dry wt.	0.237	1.570	0.92	0.0001	158

decrease during oviposition (Fig. 2). Regression equations for the various growth parameters (length, width, wet weight, and dry weight) are given in Table 2. Both Spearman's and Kendall's rank correlation coefficients were calculated and all values were highly significant ($P \leq 0.0001$).

D. pharpa from tide pools were significantly smaller than creek individuals (see 95% confidence intervals, Fig. 3), although growth rates in the two populations were similar in summer and fall. In the winter, growth continued in the tide pools while growth in the creeks leveled off.

About 10% of the juveniles observed in tide pool A during 1976 survived to maturity, assuming low migration. Mortality continued throughout the year, and essentially all individuals died after reproducing. Post-reproductive mortality in the laboratory and in the field followed similar temporal trends. Of the adults collected in early March, 100% survived through March, 56% through April, and 17% through May. One very inactive specimen survived in captivity until mid-July. By comparison, if the number of adults observed per hour in the field in February was considered 100%, then the number observed in subsequent months was 100% in March, 25% in April, and <1% in May. In other words, among these adults the cumulative post-reproductive mortality was approximately 0% in March, 75% in April and 99% in May in the field and 0% in March, 44% in April and 83% in May in the laboratory. Only one adult (collected in mid-July) was seen in the field after mid-May. Thus, some *D. pharpa* may survive up to 17 months, but most live a year or less. Although parental and offspring generations of *D. pharpa* overlapped briefly during the reproductive season, no adults survived for two reproductive seasons.

D. pharpa placed directly from the field into holding tanks along with oyster shell rubble and associated fauna experienced high mortality. It was observed that the nudibranchs and *C. celata* ventilation papillae were both being consumed by the snapping shrimp *Alpheus heterochaelis*. The shrimp was able to detect, locate, and pick up a nudibranch dropped through the water column before it was able to right itself or attach to the substratum. It is not known whether *A. heterochaelis* contributes to *D. pharpa* mortality in the field.

Abundance and Association with Prey

The lowest detected abundance of *D. pharpa* occurred during the reproductive season (April–May) and highest abundance followed recruitment. Two estimates of seasonal abundance using tide pool data (the number of individuals observed per hour and the number observed per 150 shells) showed similar trends (Kendall's tau, $P < 0.002$) (Fig. 4). The number of individuals observed per hour ranged from 0 in May to 46 in August, while the number observed per 150 shells ranged from 0 in May to 41 in July. As many as nine juveniles or three adults were observed on a single shell. In contrast, abundance estimates based on quadrats in appropriate habitat failed to detect this annual cycle due to high inherent

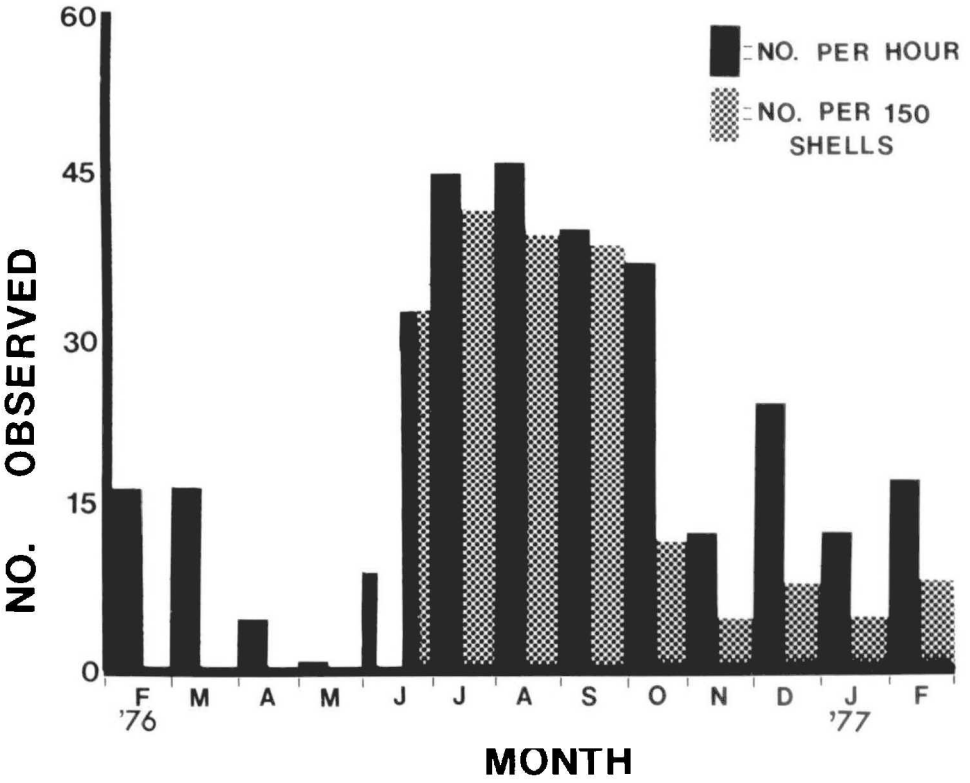


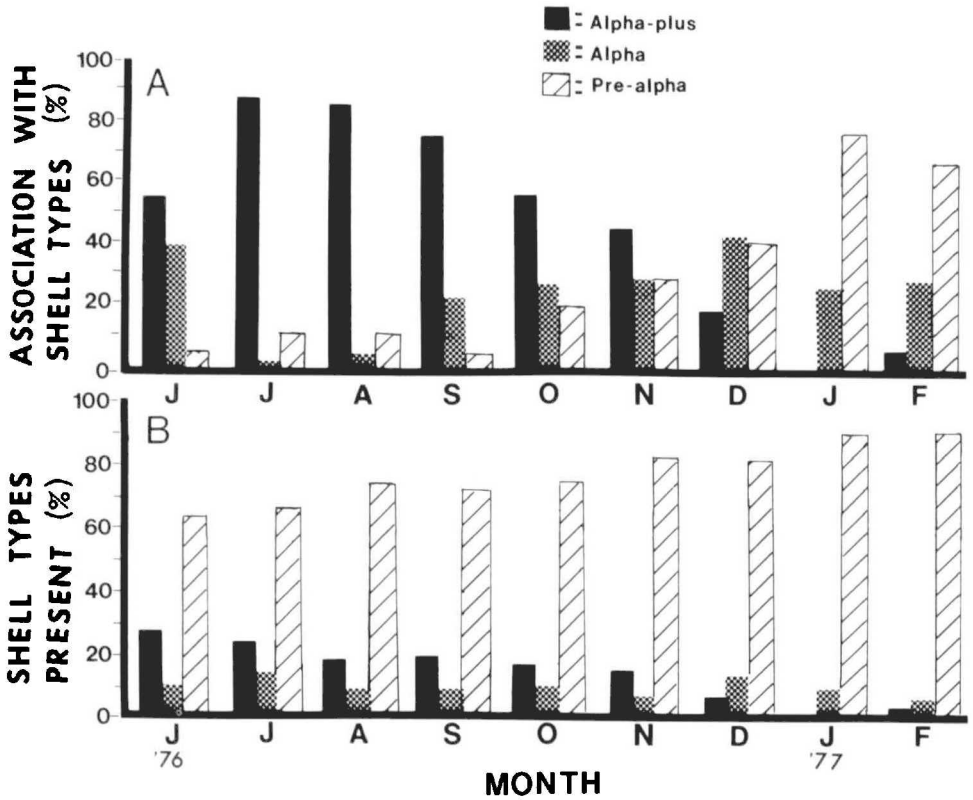
Figure 4. Abundance of *Doriopsilla pharpa* in tide pool A, estimated by two different methods (Solid bars = number observed per hour, February 1976–February 1977; checkered bars = number observed per 150 shells examined, May 1976–February 1977; two samples were taken in June).

sampling bias. For example, values on one sample date ranged from 2–12 specimens per m^2 in different locations and 1–7 per m^2 for replicates at a single station.

Fecal analyses of field-collected nudibranchs together with laboratory observations confirmed that *D. pharpa* feed on the sponge *C. celata*. Although *D. pharpa* occurred in close association with easily-detectable specimens of this sponge in the field, the percent association varied monthly, from 98% in September to 25% in January (Fig. 5A). Significant changes in this predator-prey association occurred from August to September, September to October, and December to January (Chi-square two-by-two contingency test, $P \leq 0.05$). Concurrently, changes were observed in the number of shells obviously infested with *C. celata*. The highest level of visible infestation (36%) was in summer and lowest (9%) in winter (Fig. 5B). Thus, as the number of shells with obvious *C. celata* decreased, the association between predator and prey decreased.

Discussion

Sampling techniques for determining seasonal abundance of nudibranchs include recording the number of individuals observed, either per unit time or per unit area. The former method, which allows an experienced observer to seek out appropriate microhabitats, is commonly used (Nybakken, 1974; Clark, 1975), and seems to provide more reliable results. Techniques involving unit shell and unit



Figures 5A–B. A, percentage of *Doriopsilla pharpa* found associated with the three shell types; B, percentage of shells of the three shell types. Percentages are based on total *D. pharpa* and shells examined monthly in tide pool A.

area (e.g. quadrat) observations are subject to bias due to spatial heterogeneity; the resultant sampling variability can easily mask existing seasonal variations. For instance, an erroneous winter peak rather than a summer peak in *D. pharpa* abundance could be interpreted from quadrat data in Guida (1976; note that Guida only intended to show the relative abundance of this nudibranch compared to other organisms). To determine general seasonal abundance trends of a particular species, time- and area-based methods are both appropriate only if the same station is sampled with replacement, as shown in Potts (1970) and in the present study.

As with many other nudibranchs (Miller, 1961; Clark, 1975) the distribution of *D. pharpa* in North Inlet Estuary, South Carolina, depended on the distribution of its prey. During most of the year, more than half of the *D. pharpa* examined were within a few centimeters of their food. The most probable cause of the winter decrease in nudibranch-sponge association (from 80% or greater in June–October to 25% in January) was the concomitant decline in abundance of *C. celata* ventilation papillae (Fig. 5), rather than a change in nudibranch behavior. As in North Carolina (Guida, 1976), only alpha stage *C. celata* were observed. Guida recorded a small (5%) decline in total volume of *C. celata* between October and February. Although such a decline may seem insignificant, the first parts of the sponge to disappear are the ventilation papillae. In the absence of beta and

gamma stages, these papillae are probably the only portion of the sponge available as food for *D. pharpa*.

As the sponge declined, the nudibranchs apparently did not move to shells with more abundant papillae. The nudibranchs may have been moving from shell to shell, but in January and February over 65% of the *D. pharpa* were found on pre-alpha shells. Some of these shells never had sponge but many others had been alpha or alpha-plus shells in which the papillae were reduced to below the outer layer of the shell or in which holes in the shell were left with no visible sponge remnants. It is not known whether these nudibranchs obtain food from within the sponge galleries (burrows), utilize some other food source on these shells, or decrease their food intake during winter, but virtual immobility of field specimens and inactivity of laboratory individuals in winter suggest a decreased metabolism.

Reduction of the sponge papillae could be caused by predation, physical stresses or both. It is unlikely that predation by *D. pharpa* alone caused the observed decline of papillae as *C. celata* is probably affected by temperature (de Laubenfels, 1952) or predation by other known spongivores. Sea urchins, snapping shrimp and xanthid crabs were frequently seen at creek stations, although only the crabs were noted in the tide pools. Guida (pers. comm.) found in North Carolina that beta stages of *C. celata* formed if these and other predators were excluded. Thus, *D. pharpa* is only part of this suite of predators which, along with physical factors, may be keeping the sponge in a pre-beta stage of development in North Inlet Estuary.

The life cycle of their prey also affects the nudibranch life cycles. Dorid nudibranchs, which rely on more stable food sources, generally exhibit slower growth and lower metabolic rates than aeolid nudibranchs, and have restricted egg-laying periods and synchronous growth cycles (Clark, 1975). Since rapid utilization of an ephemeral food supply is not necessary, growth to maturity can be slower in spongivorous nudibranchs such as *D. pharpa* than, for example, in hydroid-feeding aeolids or those dorids (such as *Doridella obscura*; Perron and Turner, 1977) which feed on opportunistic or short-lived prey. The sponge prey of *D. pharpa* varies in abundance but compared to hydroids is a stable source in that it is present year-round. As is typical of other dorids, oviposition in *D. pharpa* was restricted (to spring) and individuals followed a synchronous (one-year) life cycle. Even the type of veliger shell (Type I of Thompson, 1961) is typical of dorids (Soliman, 1977). Because its prey is reliably available and widely distributed, *D. pharpa* can survive without a planktonic dispersal stage or high post-hatch mobility. In fact, without a planktonic stage, its fecundity required to insure survival of the species is lowered, and its premetamorphic survivorship is increased (compare >90% in *D. pharpa* to 12% premetamorphic survival in the planktonic dorid *Adalaria proxima*; Thompson, 1958).

Fecundity is related to food availability and utilization (Lalli and Conover, 1973; Spight and Emlen, 1976). Because captive *D. pharpa* often failed to feed, fecundity in the laboratory may have been lower than in the field. Nudibranchs held in the laboratory for long periods laid fewer eggs than did newly-collected specimens (Table 1). On the other hand, newly-collected specimens may have laid more eggs initially than their field counterparts as a result of handling stress. Fecundity may also have differed between creek and tide pool specimens although this could not be tested since tide pool nudibranchs were not removed from the field. Several factors suggest that the larger creek specimens may have been more fecund. First, creek specimens had a more abundant food supply. Second, larger nudibranchs of a species tend to lay more eggs (Thompson, 1967). Third, if a minimum body size is required for reproduction in *D. pharpa*, then creek spec-

imens, which (apparently) reached their MOL several months earlier, could have then devoted energy to gonad growth while tide pool specimens were still contributing to somatic growth.

Size seems to be related to reproduction in *D. pharpa* since captive specimens failed to reproduce if their size decreased below the MCL or MOL values, but other factors such as age and environmental conditions are also important. Although the MOL was reached in late January or February no eggs were laid until 1–2 months later. Also, although the MCL-MOL values were both 2–3 mm lower in 1977 than in 1976, reproduction was initiated in late March of both years, presumably on cue from some environmental factor(s). The smaller size of specimens in 1977 than 1976 is attributed to more severe winter temperatures which probably had stressful effects on both the nudibranchs and their prey.

Continued smaller mean length of tide pool *D. pharpa* despite greater winter (Dec.–Feb. 1977) growth rates in the tide pool than in the creek specimens suggest that some factors, such as nutrition and temperature, may affect tide pool and creek individuals differently. Creek specimens were not collected in spring but in summer and fall creek and tide pool *D. pharpa* exhibited similar growth rates. In the tide pools, *C. celata* ventilation papillae were less abundant and shorter in winter, and year-round temperatures fluctuated more widely. Thus, tide pool nudibranchs and sponges may have been more stressed, accounting for the smaller size of these specimens (Fig. 3). Similarly, a comparison of three populations of *Onchidoris muricata* (Miller, 1962) showed that although all had the same annual life cycle, the growth rate was lower and the maximum size 50% smaller in the one population.

Differences in winter growth rate between the tide pool and creek populations are difficult to explain but there are several possibilities. First, creek specimens could reach their MOL in winter, then reduce growth, and save energy for spring reproduction. Meanwhile, the smaller tide pool specimens could continue to grow in order to achieve the MOL by spring. A second possibility is that while the tide pool environment is generally more stressful, the winter temperature fluctuations are greater than in the creeks. Therefore, at times temperatures may be high enough for winter growth in the tide pools but not in the creeks. Such periodic opportunities for growth could account for the difference in winter growth rates between the two populations. Thirdly, the lower abundance of sponge papillae in the tide pools in winter could be related to continued grazing pressure there, regardless of temperature. If the tide pool sponges are already more stressed than their creek counterparts, even minimal feeding pressure by *D. pharpa* or other spongivores could exceed the winter regenerative capacities of the sponge papillae. Determination of the forcing functions and their effect on the life history parameters of *D. pharpa* in these two populations require further study.

D. pharpa seems to have a life history typical of many dorid nudibranchs: its feeding is highly prey-specialized and its food supply is relatively stable; its growth cycle is synchronous and relatively long; its reproduction is synchronous, restricted to a certain time of year, and is followed by death. Variations in environmental factors between different habitats of *D. pharpa* may be exerting strong pressures on the life history of this nudibranch, pressures that can be especially important in a species of relatively low mobility.

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