

Feeding biology and ecological impact of an introduced nudibranch, *Tritonia plebeia*, New England, USA

R. A. Allmon and K. P. Sebens

Marine Science Center, Northeastern University, Nahant, Massachusetts 01908, USA

Abstract

The nudibranch *Tritonia plebeia* (Johnston) was first observed in New England in 1983, on vertical rock walls at 7 m depth off Nahant, Massachusetts. This northern European species preys exclusively on the soft coral *Alcyonium digitatum* (Linnaeus) in its natural habitat. At Nahant, it preyed primarily on the closely related *Alcyonium siderium* Verrill. Laboratory studies indicated that it could locate its prey by distance chemoreception and by visual orientation towards tall dark surfaces which could help it find the vertical walls, overhangs, and boulder sides where the soft corals occur. Field studies showed that *T. plebeia* fed primarily on colony bases, causing extensive damage and whole colony mortality. The most important endemic predator on *A. siderium*, *Coryphella verrucosa* (Sars), preyed preferentially on hydroids, but would graze polyps off the top portions of *A. siderium* colonies, causing little permanent damage to the colony, during the winter months when hydroids were scarce. Although *C. verrucosa* occasionally behaved agonistically toward *T. plebeia*, there was no indication in laboratory or field studies that either nudibranch had an effect on the other's foraging through interference competition. Extensive predation by *T. plebeia* caused the disappearance of *A. siderium* at two sites (Outer and Inner Shag Rocks) and a sharp reduction at a third site (Inner East Point). The higher mortalities at the Shag Rocks sites most likely occurred because of a simultaneous urchin (*Stroglyocentrotus droebachiensis*) population expansion. As space among aggregates of *A. siderium* opened up due to *T. plebeia* predation, urchins were able to forage on the vertical walls and scrape off remaining colonies. At a fourth site, Halfway Rock, where *T. plebeia* were seldom present, *A. siderium* colonies also suffered high mortalities. This increase in mortality began nearly a year before urchin populations increased, and during a summer of abnormally high water temperatures at Halfway Rock. The high temperatures, followed by urchin predation on remaining colonies could account for the disappearance of all *A. siderium* colonies at

this site. *T. plebeia* disappeared at all sites by summer 1986 and *A. siderium* populations have since stabilized, but community-level changes at all sites where *A. siderium* were removed have persisted.

Introduction

Tritonia plebeia (Johnston) has a broad distribution, occurring from Norway (Høisaeter 1986) to Portugal (Swennen 1961). It is particularly common in the British Isles (Miller 1961, Swennen 1961, Thompson 1967) where it is found subtidally among aggregations of the soft coral *Alcyonium digitatum* (Linnaeus) on which it preys (Alder and Hancock 1845–1855, Jeffreys 1869, Miller 1961, Swennen 1961, Thompson 1964, Salvini-Plawen 1972). Occurrences in the Mediterranean and Aegean Seas have also been reported (Swennen 1961). *T. plebeia* was unknown from New England waters until spring 1983 when specimens were identified from subtidal rock walls at East Point, Nahant, Massachusetts, USA (Kuzirian and Sebens, unpublished manuscript); there have been subsequent observations in summer 1985 from the coast of southern Maine, USA (L. Harris personal communication). By summer 1985, densities of *T. plebeia* at Nahant had exceeded those of all native nudibranchs, but this density peak was short-lived. Only one *T. plebeia* has been observed in the field since spring 1986. The egg masses, which were abundant since 1983, have also disappeared.

This study describes the feeding biology and ecological impact of this exotic nudibranch species on the existing subtidal rock wall community New England. It is unique in that extensive monitoring of this area was in progress five years prior to the appearance of *Tritonia plebeia* (Sebens 1985a, 1986) and therefore allowed quantitative comparisons of community structure before, during and after the arrival of this nudibranch. The results indicate that during its short presence, *T. plebeia* had a significant impact on the existing ecological balance.

Material and methods

Species identification and biology

Dr. A. Kuzirian (Marine Biological Laboratory, Woods Hole, Massachusetts) identified this nudibranch as *Tritonia plebeia* (Johnston). Identification was based on comparisons of all aspects of anatomy, radular morphology in particular, with museum specimens (Kuzirian and Sebens unpublished manuscript). Voucher specimens will be placed in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts. Preliminary observations on larval biology by Kuzirian confirm reports by Thompson (1961) that *T. plebeia* has a Type 1 larval shell with only $\frac{3}{4}$ to one whorl which is approximately 170 μm long at hatching. Although it is not known whether the larvae are planktotrophic, they are not direct developers (Kuzirian and Sebens unpublished manuscript). Egg masses were observed at the monitored sites off Nahant during all seasons, but were least common in the spring (Allmon unpublished data). Similarly, juvenile *T. plebeia* were observed in all seasons.

Study site

Field observations, photographs, and collections of *Tritonia plebeia* were made on subtidal vertical rock walls (7 to 12 m depth) at three sites near East Point, Nahant, Massachusetts, USA (42°25'N, 70°54'W) (Inner and Outer Shag Rocks and Inner East Point) and at one site 5 km offshore at Halfway Rock (42°30'N, 70°46'W). The Shag Rocks are south of East Point and are more exposed to wave activity than Inner East Point, on the northern side. Halfway Rock experiences the greatest wave energy (Sebens 1984). Water temperatures range from -1° to over 20°C annually (Smith and Sebens 1983).

Rock walls at these three sites support similar invertebrate communities, dominated by the anemone *Metridium senile* (Linnaeus), hydroids *Tubularia* spp., sponges *Haliclondria panicea* (Pallas), *Halisarca dujardini* Johnston, *Lewcosolenia cancellata* Verrill, and *Isodictya* spp., the colonial ascidians *Aplidium constellatum* Verrill and *Didemnum albidum* (Verrill), and the solitary ascidians *Molgula citrina* (DeKay) and *Dendrodia carnea* (Agassiz). Colonies of the octocoral *Alcyonium siderium* Verrill were also abundant until spring 1985 when they suffered a period of severe mortality. Rock walls frequented by herds of the sea urchin *Strongylocentrotus droebachiensis* are dominated by two crustose coralline algae, *Lithothamnion glaciale* Kjellman and *Phymatolithon rugulosum* Adey. Sebens (1983, 1985a, 1986) describes these communities in more detail.

Field monitoring

Eight permanently marked areas, each consisting of six 18×25 cm quadrats, were established at the study sites. Monthly photographic monitoring of these quadrats was

initiated as part of a long-term ecological study of New England subtidal rock wall communities (Smith and Sebens 1983, Sebens 1983, 1985a, b, 1986). Sites were photographed with a Nikonos III camera, Subsea MK 101 strobe and Hydrophoto 3 close-up lens with camera and strobe mounted on a rigid aluminum frame with a subject area of 18×25 cm.

Predation

Lengths of all *Tritonia plebeia* and *Coryphella verrucosa* (Sars) were measured from 35 mm slides (projected $1 \times$ magnification). All lengths reported here are of crawling nudibranchs. Since *T. plebeia* contracts its body while feeding, usually at the base of soft coral colonies, a geometric mean regression of contracted length to crawling length was performed in the laboratory on 25 individuals ranging in length from 13 to 38 mm. Each individual was first measured while feeding at a colony base (contracted), then removed and measured while crawling (extended). Lengths of contracted *T. plebeia* (Lc) from field photographs were then converted to extended lengths (Le) using a geometric mean regression ($\text{Le} = 1.617 \text{Lc} + 60.15$, $N = 25$, $r^2 = 0.56$).

Feeding by *Tritonia plebeia* on organisms other than *Alcyonium siderium* could not be accurately determined from photographs. Therefore, during SCUBA dives, individual nudibranchs were removed from vertical walls with forceps, and the substrata below their oral ends were examined. Only those organisms with visible somatic damage to the area directly beneath the nudibranch's mouth were considered prey items. In all cases where *T. plebeia* was removed from an *A. siderium* colony, there was obvious tissue damage beneath.

Predation on *Alcyonium siderium* by *Tritonia plebeia* and by *Coryphella verrucosa* was recognized in photographs by means of two criteria: (1) contact of the nudibranch's head with the colony and (2) retraction of all or most of the colony's polyps. Damage to the colony tissue also was visible in some cases. Diameters of colonies attacked (average diameter when contracted) were measured and the location of feeding on the colony (base, middle, top) was noted. Colony diameter correlates well with ash-free dry weight (Sebens 1984).

To test prey size preference by *Tritonia plebeia* and *Coryphella verrucosa*, comparisons were made between size distributions of the specific colonies attacked by nudibranchs and of all available *Alcyonium siderium* colonies at each site. Following the protocol used by Sebens (1984), slides from fall 1983 to spring 1986 were projected at life size and the mean diameters (contracted) of all *A. siderium* colonies attacked by *T. plebeia* and *C. verrucosa* were measured. Every *A. siderium* colony from January 1983, three months prior to the first appearance of *T. plebeia*, and later were measured similarly. Diameters of these colonies within 2 mm size classes were summed to represent the two-dimensional extent of those colonies available to the nudibranchs (probability of encounter), and thus the probability of predation by

such nudibranchs. These values were converted to expected numbers attacked, $E(d)$, after random encounter in each size class using the equation

$$E(d) = \frac{(\sum \text{diameters in size class}) \times N}{\sum \text{diameter all colonies}}$$

where N = number of all colonies. Mean diameters of colonies were compared statistically to means of colonies attacked by the two nudibranch species.

Densities

Population densities of *Coryphella verrucosa* and *Tritonia plebeia*, and of the urchin *Strongylocentrotus droebachiensis* (Müller) were calculated for each of the 3-mo intervals (seasons). Since there are large fluctuations in juvenile urchin abundances, only adult urchins (test diam. > 1.5 cm, Raymond and Scheibling 1987) were counted. Juvenile urchins have not been observed preying upon or grazing over *Alcyonium siderium* colonies and therefore, are unlikely to have a direct effect on the soft coral populations. Numbers of each species per photograph were converted to numbers per square meter and data were square-root transformed before calculation of means and standard deviations. Unlike mobile predators, long-lived soft coral colonies appear in photographs from one month to the next. To avoid counting the same colony more than once a season, photographs from only one month were used to calculate *A. siderium* densities for that season. Seasons, based on seawater temperature, are as follows: Winter (three lowest temperatures) = January, February, March; Spring = April, May, June; Summer (three highest temperatures) = July, August, September; Fall = October, November, December.

Laboratory experiments: Prey size preference

Size preference for large or small *Alcyonium siderium* colonies by *Tritonia plebeia* was tested in the laboratory. Healthy colonies attached to mussels (*Mytilus edulis* [Linnaeus]) or *Modiolus modiolus* [Linnaeus]) or rocks were collected from East Point, Nahant. "Small" colonies, having diameters (X) less than 13 mm, were clustered into three groups of 10 to 20 individuals each. Three "large" colonies ($X \geq 13$ mm) were chosen such that the sum of diameters of the "large" colonies approximated that of the "small" colonies. The sum of the diameters represents the total linear dimension available for random contact and subsequent predation by *T. plebeia* crawling across a two-dimensional surface. The colonies were arranged in a submerged plastic tray (36 × 28 × 5 cm) so that all bases were at the same height and the single large colonies were alternated with the groups of small colonies. Five nudibranchs (17 to 25 mm crawling length) were placed in the center of the tray. An opaque cover was placed over the tray to simulate low light conditions in the field without disrupting water flow. After 15 min, and then hourly for 4 h, individual nudibranch loca-

tions were mapped. Feeding individuals (oral veil lifted and mouth pressed against a colony) were noted. The experiment was repeated ten times, using fresh *A. siderium* colonies and nudibranchs. All nudibranchs were starved 24 h prior to use. Care was taken to remove mucus trails which could be chemotactic stimuli in subsequent trials (Allmon, personal observation, Todd 1979, 1981, Bretz and Dimock 1983). Before each trial, all *A. siderium* colonies were removed and the tray surfaces were wiped and rinsed with freshwater.

Substrate preference

Three tests were performed to investigate the ability of *Tritonia plebeia* to differentiate between vertical surfaces having different heights, contrasts, and quantities of food. In the first test, three dark grey rocks (75, 45, and 15 mm in height) were offered. In the second, a white and a grey rock having equal heights were offered. In the third, a dark rock and a similarly sized *Mytilus edulis* shell, with four attached *Alcyonium siderium* colonies, were available. These surfaces were placed in the corners of a 35 × 28 × 5 cm tray submerged 6 cm deep in a running seawater table. All tests were performed first in ambient light and then repeated in darkness to determine if selection was visual or chemotactic.

Five nudibranchs (19 to 28 mm in length) were placed in the center of the tray. Their location after 1 h was marked on a map. Each test was repeated ten times with new individuals. Between trials the tray was removed, cleaned, and reset. Objects were rotated 45° within the tray to avoid rheotactic response to currents in the seawater table or orientation to unrecognized gradients. All nudibranchs were starved 24 h prior to use.

Chemotaxis

Chemotactic response of *Tritonia plebeia* towards its primary prey, *Alcyonium siderium*, was tested using a Y-maze with arms 7.5 cm long, 1.5 cm wide, and 2.5 cm deep. Seawater flowed into two basins, one containing an *A. siderium* colony, which were connected to the Y-maze by aquarium tubing. A constant flow rate of 6 cm sec⁻¹ was maintained to simulate near-substrata flow rates in the field (Sebens 1984). A box was fitted over the maze to reduce light intensity, and a flap on the side allowed observation with minimal disturbance and light entry.

Individual *Tritonia plebeia* were placed 4 cm from the fork in the Y-maze. No nudibranch was used more than once each day and all individuals were starved for 24 h before use. The reaction of a nudibranch was considered "positive" if, within 15 min, it traveled at least 5 cm up the path leading to the basin containing the *Alcyonium siderium* colony. Its choice of the other path was considered a "negative" reaction. Individuals that entered neither path, or that were carried downstream by the current, were categorized as "other". Between trials, the Y-maze was rinsed with fresh-

water, wiped (to remove any mucus trails) and reset, with the soft coral colony alternated between basins for each trial.

Interspecific interactions

Interactions between *Tritonia plebeia* and *Coryphella verrucosa* were studied by placing one individual of each species with a colony of *Alcyonium siderium* in a large petri dish on the seawater table. All interactive behavior occurring within 15 min, on or off the soft coral, was recorded. The tank was cleaned between trials and another pair of nudibranchs used. Behavioral interactions were grouped into six categories: touch (contact of rhinophores with other nudibranch); taste (one or more contacts of mouth with body); climb (movement of one nudibranch onto the back of the other); aversion (retreat); no reaction (except retraction of rhinophores); bristle (the bristling of the cerata by *C. verrucosa* in a possibly antagonistic manner towards *T. plebeia*).

Results

Predation

Coryphella verrucosa feeds primarily on *Tubularia* spp. when this hydroid is abundant subtidally at Nahant during the summer and fall (Harris 1973, MacLeod and Valiela 1975, Kuzirian 1979, Sebens 1985 a). When this hydroid disappears in winter and spring, *C. verrucosa* becomes less prey-specific and has frequently been observed feeding on the soft coral *Alcyonium siderium* (Sebens 1983, 1985 a) and, at times, on the colonial tunicate *Botryllus schlosseri* (Morse 1969).

Of a total of 264 *Tritonia plebeia* observed in the field, 214 (81%) were preying on *Alcyonium siderium*. The remaining 50 (19%) were found nestled among the ascidians *Aplidium constellatum* and *Molgula citrina*. Observed damage to these ascidians seems to have been the result of tearing by *T. plebeia* rather than predation, since in laboratory aquaria this nudibranch did not eat either ascidian.

Sixty-three percent of all *Tritonia plebeia* observed in photographs or directly in the field fed at the bases of *Alcyonium siderium* colonies. *Coryphella verrucosa*, however, generally attacked the top or middle of a colony (Fig. 1A). Using the model of an idealized *A. siderium* (Fig. 1B), and average height and diameter measurements from field observations (Sebens unpublished data), percent surface areas for each of the three regions were calculated (base=20%, middle=47%, top=33%). Nudibranchs would be expected to be found feeding in numbers proportional to the available surface area if there was no active site selection. Chi-squared tests, however, showed that feeding distributions of both *C. verrucosa* and *T. plebeia* were significantly different ($P < 0.001$) from expected distributions. Fifty percent of observed *C. verrucosa* fed on the top, which consists of only 33% of the colony's surface area. *T. plebeia*, on the other

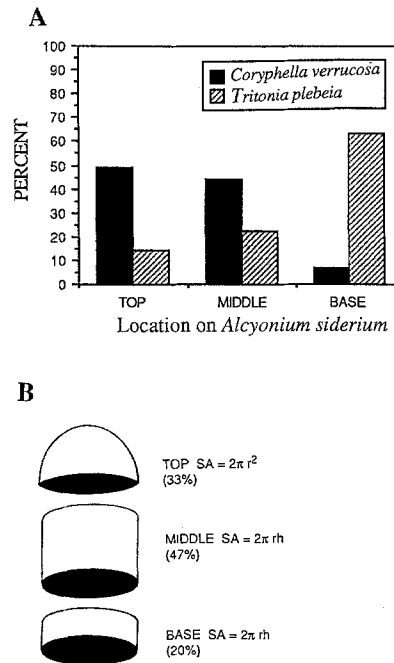


Fig. 1. *Tritonia plebeia* and *Coryphella verrucosa*. (A) Feeding distribution on top, middle and basal regions of *Alcyonium siderium* colonies in field. (B) Idealized *Alcyonium siderium* colony showing three regions. Percent surface area (SA) of each region was calculated using an average colony height of 29 mm and an average diameter of 19 mm (Sebens 1984). Base arbitrarily chosen to be lower 20% of colony height

hand, strongly favored the base; 60% of observed *T. plebeia* fed on the bottom 20% of the colony. Predation avoidance may explain this distribution: The dark brown *T. plebeia* is more cryptic among the bryozoans, hydroid bases, and amphipod tubes on the rock walls than on the light pink soft corals. *C. verrucosa*, however, is difficult to recognize on *A. siderium* because of the pink cerata and light colored body.

Analysis of variance (ANOVA) revealed no significant difference between the mean size of all *Alcyonium siderium* colonies at the field sites, weighted by encounter probability, and the mean size of those colonies attacked by *Tritonia plebeia* and *Coryphella verrucosa* (dark arrows in Fig. 2). This result suggests that *T. plebeia*, as a population, preyed on *A. siderium* colonies in proportion to their availability. However, as individuals, a linear regression of size *T. plebeia* (y) to size *A. siderium* consumed (x) showed that larger *T. plebeia* preyed on somewhat larger soft coral colonies (Fig. 3A; $y = .29x + 14.2$, $N = 119$, $r^2 = 0.77$; $P < 0.01$ for r^2). *C. verrucosa* did not show a significant trend (Fig. 3B; $N = 69$, $r^2 = 4.4 \times 10^{-4}$).

Densities

Densities of nudibranchs, urchins and soft corals on the vertical rock walls at Outer Shag Rocks, Inner Shag Rocks, Inner East Point and Halfway Rock are shown in Fig. 4. Both appearances and density peaks of *Tritonia plebeia* occurred first at Outer Shag Rocks, then at Inner Shag Rocks

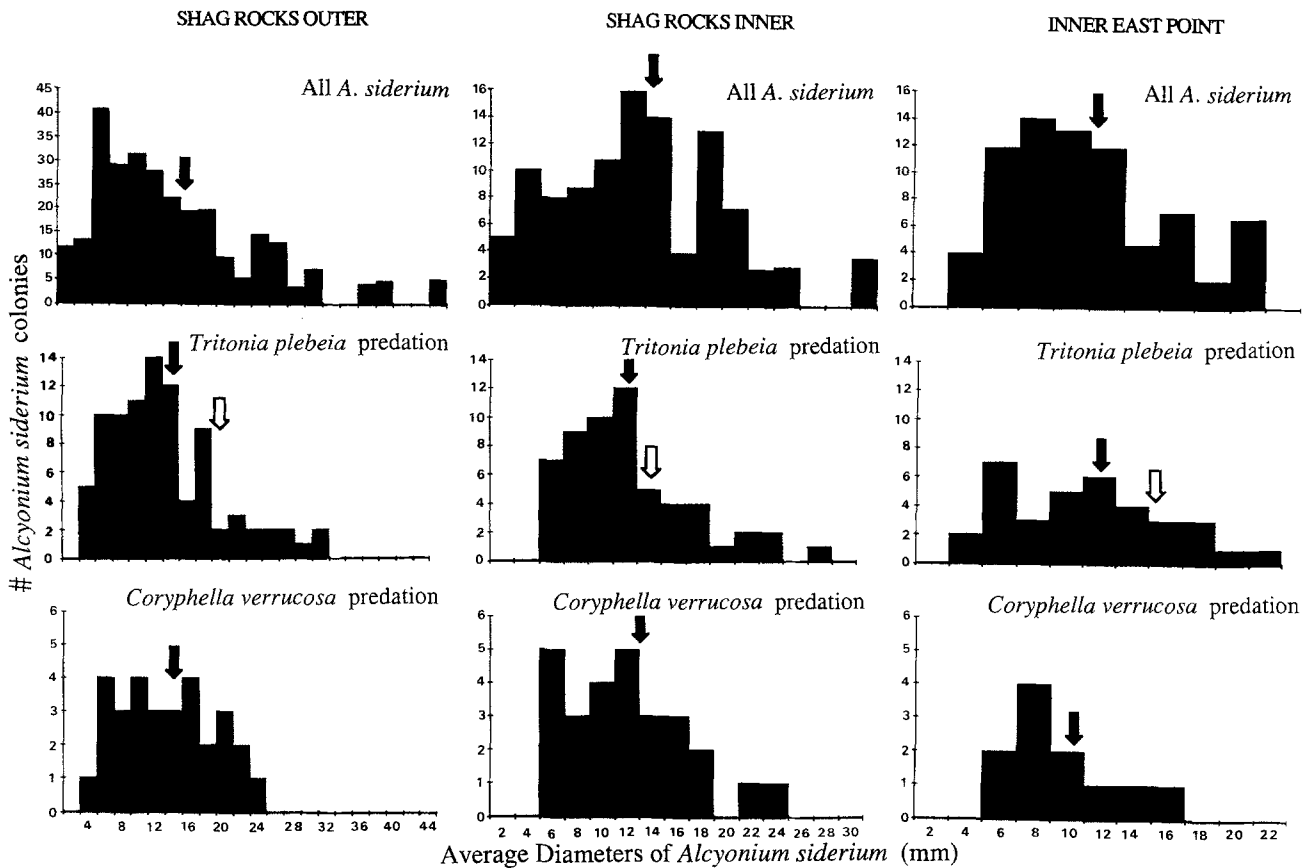


Fig. 2. *Alcyonium siderium*. Size-frequency distributions (diameters) of available colonies in the field in winter 1983 weighted by the probability of encounter, and colonies attacked by *Tritonia plebeia* and *Coryphella verrucosa* from spring 1983 to spring 1986 at all sites off Nahant. Dark arrows indicate mean colony diameter and mean diameter attacked by all nudibranchs. Light arrows indicate mean colony size attacked by only those *T. plebeia* of lengths (L) equal to individuals used in laboratory experiments (L > 20 mm). Mean colony diameters were compared by ANOVA and are not significantly different

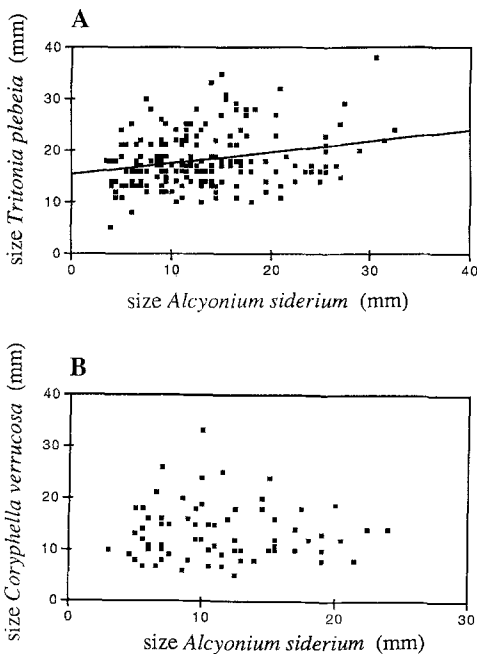


Fig. 3. *Tritonia plebeia*, *Coryphella verrucosa* and *Alcyonium siderium*. (A) Linear regression showing that larger *T. plebeia* feed on larger soft coral colonies. (B) No such positive trend for *C. verrucosa*

and lastly at Inner East Point (Fig. 5). *T. plebeia* became increasingly abundant at Outer Shag Rocks throughout 1984, reaching a peak density of 50 m⁻² in winter 1985. At Inner Shag Rocks, they appeared in summer 1983, but remained uncommon (< 3 m⁻²) until winter and spring 1985 when they reached densities of 53 m⁻² (Fig. 4 B). First sightings of *T. plebeia* at Inner East Point were in fall 1984. The population increased steadily to a peak density of 41 m⁻² in summer 1985 (Fig. 4 C). Only occasional *T. plebeia* were seen at Halfway Rock, always far less than 1 m⁻².

Sea urchins (*Strongylocentrotus droebachiensis*) consume a variety of invertebrates, including *Alcyonium siderium* in laboratory studies (Sebens unpublished data). In winter 1985, urchin densities on rock walls at Outer Shag Rocks increased from 5 to 75 m⁻², the highest level since monitoring began in 1980 (Fig. 4 A). Urchin densities at Inner Shag Rocks were high throughout 1985, with a peak of 61 m⁻² in summer 1985 (Fig. 4 B). During this same season the density of urchins at Halfway Rock jumped to 98 m⁻² (Fig. 4 D), nearly 50% greater than levels at the Shag Rocks sites. These population expansions onto vertical walls corresponded to increased numbers of urchins on horizontal surfaces as well. At Inner East Point, where urchins are rarely found on horizontal surfaces, there was no increase in the numbers of urchins on vertical walls (Fig. 4 C).

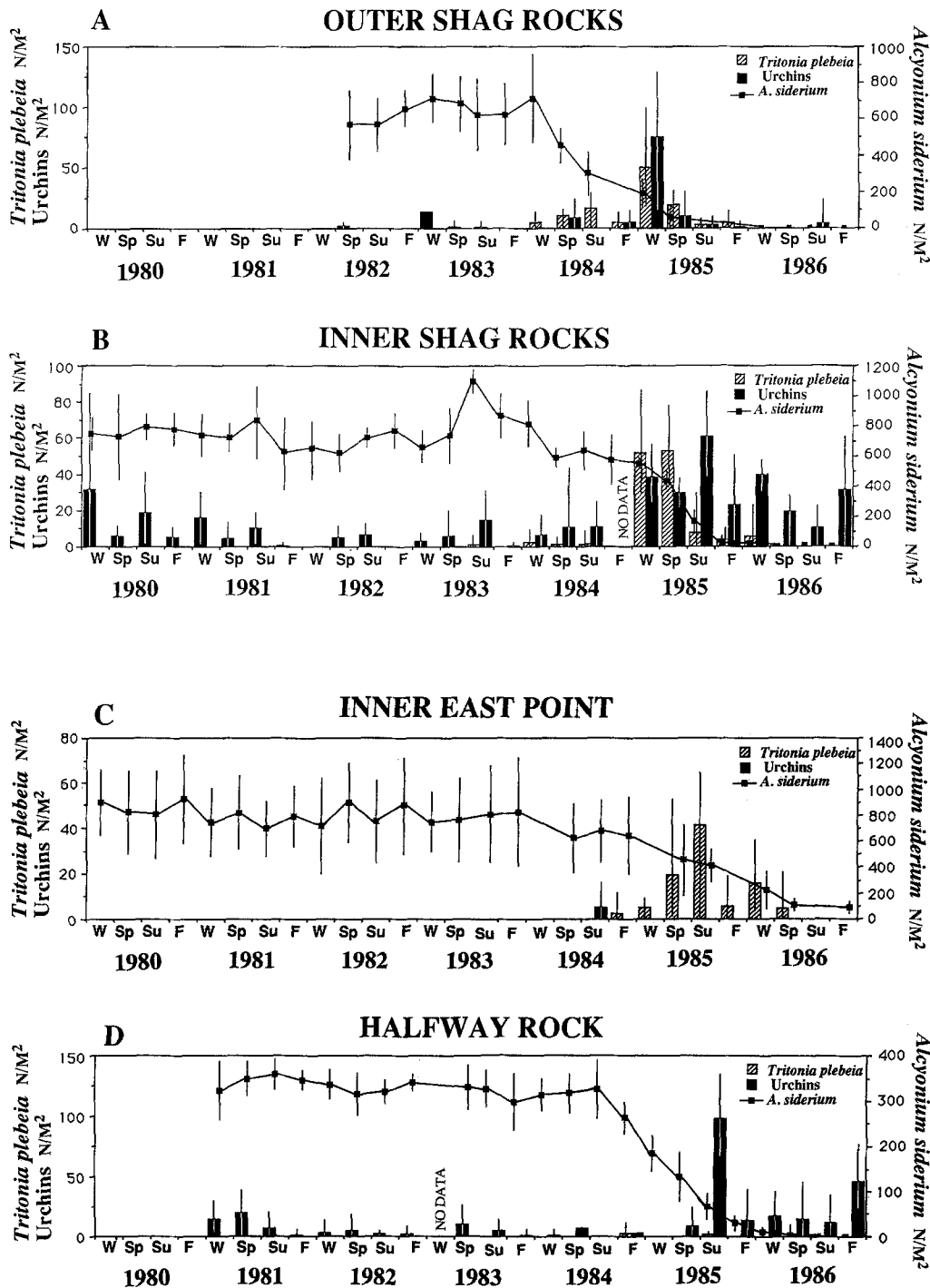


Fig. 4. *Tritonia plebeia*, *Strongylocentrotus droebachiensis* and *Alcyonium siderium*. Densities at four sites. At Inner East Point (C), where urchins were absent, *A. siderium* decreased gradually as densities of *T. plebeia* increased. At Outer and Inner Shag Rocks sites, (A) and (B), soft coral die-off was rapid and more severe, a result of combined predation of *T. plebeia* and urchins. Initial decline of *A. siderium* at Halfway Rock (D) began prior to an increase in urchin densities, and was probably caused by higher summer water temperatures in 1984 and 1985. Values are means \pm SD

The densities of *Alcyonium siderium* at all three sites fluctuated little prior to early 1984, except at Inner Shag Rocks where densities from spring to fall 1983 were unusually high (Fig. 4B). By 1986, few *A. siderium* remained on the vertical rock walls. Numbers of *A. siderium* at Outer Shag Rocks decreased from $713 \pm 244 \text{ m}^{-2}$ in winter 1984 to

$143 \pm 61 \text{ m}^{-2}$ in spring 1985. By spring 1986 there were no colonies left. Similarly, at Inner Shag Rocks, *A. siderium* numbers fell from $553 \pm 31 \text{ m}^{-2}$ in winter 1985 to $27 \pm 23 \text{ m}^{-2}$ in winter 1986, and none occurred by spring 1986. At Halfway Rock, *A. siderium* colonies were abundant in summer 1984 ($70 \pm 27 \text{ m}^{-2}$) but were gone two years later.

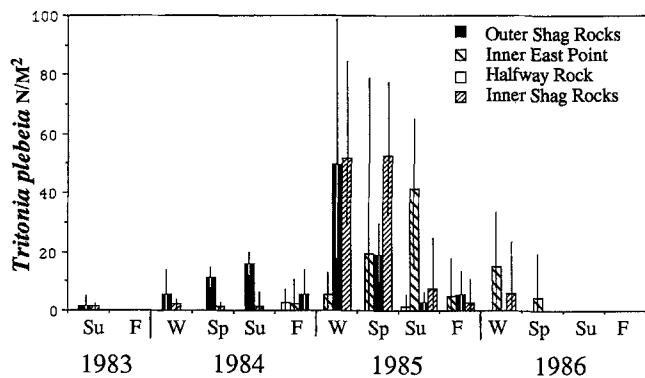


Fig. 5. *Tritonia plebeia*. Densities at Outer Shag Rocks, Inner Shag Rocks and Inner East Point. First appearances and subsequent density peaks were staggered, occurring at Outer Shag Rocks first, then at Inner Shag Rocks, and finally at Inner East Point. Values are means \pm SD. W: Winter (January, February, March); Sp: Spring (April, May, June); Su: Summer (July, August, September); F: Fall (October, November, December)

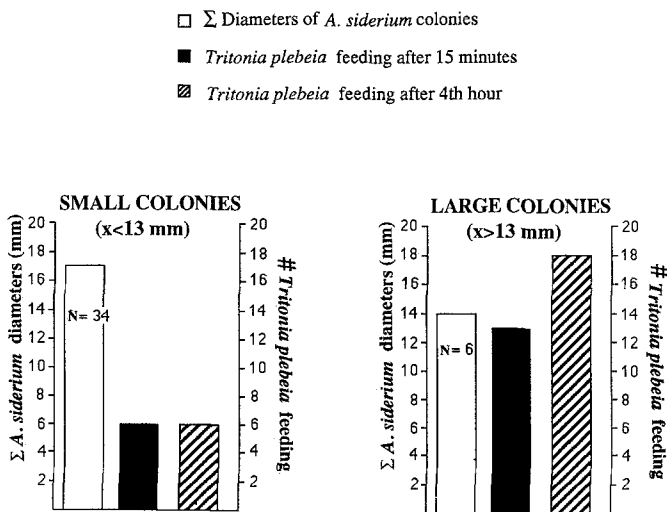


Fig. 6. *Tritonia plebeia*. Feeding distributions on “small” and “large” *Alcyonium siderium* colonies in laboratory. Mean diameter of small colonies = 5 mm \pm 2, $N=34$; of large colonies = 23 mm \pm 10, $N=6$. Chi-squared analysis revealed that more nudibranchs fed on large colonies both initially and after 4 h (initially: $\chi^2=4.58$, $P < 0.05$; after 4 h: $\chi^2=7.98$, $P < 0.005$), than would be predicted by random encounter

At Inner East Point, the drop in numbers of *A. siderium* was less severe, decreasing from 647 \pm 293 m⁻² in fall 1984 to 110 \pm 43 m⁻² in spring 1986.

Prey size preference

A Chi-squared analysis of data from lab experiments revealed that *Tritonia plebeia* fed preferentially on large colonies with a mean diameter greater than 13 mm (after 15 min: $X^2=4.58$, $N=12$, $P < 0.05$; after 4 h: $X^2=7.983$, $N=18$, $P < 0.005$) (Fig. 6). Movement from small colonies ($X < 13$ mm) to large colonies during the 4 h is suggested by

the increased level of significance over the test period. Only six nudibranchs attacked colonies of *Alcyonium siderium* with an average diameter less than 13 mm (“small” colonies), whereas 14 initially, and 18 finally, fed on “large” colonies ($X > 13$ mm). This is particularly significant considering the number of colonies available: there were 34 “small” and 6 “large” colonies. Of the 34 small colonies, only 5 were attacked at any one time, whereas all the larger colonies were attacked. *T. plebeia*, therefore, chose to aggregate (up to five individuals) on large colonies rather than locate an unattacked small colony.

This result seems to contradict the field observations that *Tritonia plebeia* did not select large colonies (see “Results:” Predation). However, the mean length of nudibranchs used in the laboratory tests ($X=23$ mm) was significantly greater than the mean size of those at Outer and Inner Shag Rocks and Inner East Point (16, 18, and 20 mm, respectively), and the larger nudibranchs might be expected to prefer large colonies. When the field data were analysed using only colonies attacked by nudibranchs of the same size as those used in the laboratory, the mean sizes of these colonies attacked (white arrows in Fig. 4) increased for all sites. At Outer Shag Rocks and Inner East Point these new means were significantly different from the mean size of all available *Alcyonium siderium* (ANOVA: $F=3.05$, $P < 0.05$; $F=8.92$, $P < 0.005$).

Substrate preference

Results of the laboratory experiments indicate that *Tritonia plebeia* differentiate between substrates using both visual and chemical cues. In ambient light, *T. plebeia* crawled immediately towards the tallest rock ($X^2=51.45$, $N=50$, $P < 0.005$). When the surfaces were of equal height, the darkest one was preferred ($X^2=12.1$, $N=50$, $P < 0.005$). The nudibranchs even avoided the mussel shell with pink *Alcyonium siderium* colonies in preference for the darker rock ($X^2=8.7$, $P < 0.005$). In darkness, the nudibranchs did not discern tall or dark from short or light rocks. They did, however, readily locate the soft coral colonies ($X^2=8.4$, $N=50$, $P < 0.005$). In the field, such behavior would help *T. plebeia* locate vertical walls where *A. siderium* colonies are located.

Chemotaxis

Tritonia plebeia exhibited chemosensory acuity in recognizing and locating prey. Y-maze results showed that *T. plebeia* could distinguish between water flowing from basins with and without an *Alcyonium siderium* colony. Of the 27 individuals 19 reacted “positively”; only three chose the alternative path. This difference is highly significant (X^2 , $P < 0.001$). Seven nudibranchs reached the fork in the maze and stopped, extending their heads and rhinophores into the current and waving them back and forth, without entering either path. Two of these lost contact with the wall and were

carried downstream by the current. The average time for the nudibranchs to reach the end of the Y-maze tube was 11 ± 3 (SD) min, whereas those that did not enter either path remained in the same general location for a minimum of 20 min.

Interspecific interactions

Tritonia plebeia and *Coryphella verrucosa* displayed very different behaviors (Fig. 7). In general, *T. plebeia* was relatively sedentary, while *C. verrucosa* was active. Encounters between the two species seldom resulted in defensive activity. When they did, *C. verrucosa* was the aggressor in all cases; *T. plebeia* usually retracted its rhinophores and remained motionless. Most encounters were brief, consisting of one or more 'tastes' (mouth contacting skin of the other animal) by *C. verrucosa*, followed by crawling up and over *T. plebeia*. The most aggressive interactions occurred while both nudibranchs were on *Alcyonium siderium*: *C. verrucosa* bristled its cerata, which contain nematocysts, at the head of the *T. plebeia*, causing the latter to retreat. A total of 76 interactions (24 on, and 52 off *A. siderium* colonies) were observed and recorded.

Discussion

In European waters, *Tritonia plebeia* is a specialist on the soft coral *Alcyonium digitatum* (Alder and Hancock 1845–1855, Jeffreys 1869, Miller 1961, Swennen 1961, Thompson 1964, Salvini-Plawen 1972). On subtidal rock walls off Nahant, *T. plebeia* fed almost exclusively on *Alcyonium siderium*, a close relative of *A. digitatum*. The native aeolid nudibranch *Coryphella verrucosa* also preys on *A.*

siderium during the winter when its hydroid prey is scarce (Sebens 1983, 1985b, 1986). Since both nudibranchs were feeding on a limited patchy resource, some interspecific competition was expected. However, evidence suggests that little direct interference competition existed between *C. verrucosa* and *T. plebeia*. First, *C. verrucosa* consumes a variety of invertebrates other than *A. siderium*, primarily the hydroids *Tubularia* spp. (Harris 1973). *T. plebeia* was more prey-specific, feeding almost exclusively on *A. siderium*. Second, *C. verrucosa* was an opportunistic predator, seldom remaining on one colony for more than a few minutes, whereas *T. plebeia* was sluggish, remaining in one location for up to several hours. Third, prolonged encounters between the two species were generally avoided. When contact was made, it was brief and rarely aggressive. Fourth, the population size of *C. verrucosa* had inexplicably declined well before *T. plebeia* reached its peak at Inner Shag Rocks (Fig. 8). By summer 1983, only an occasional *C. verrucosa* was seen on the monitored walls, reducing its influence on *A. siderium* populations after that time.

Prior to the introduction and subsequent population expansion of *Tritonia plebeia*, *Alcyonium siderium* populations suffered annual colony mortalities of 10 to 15% primarily from seasonal predation by *Coryphella verrucosa* and storm damage (Sebens 1984, 1985a). Predation by *T. plebeia*, however, had a significant effect on densities of the soft corals at Outer Shag Rocks, Inner Shag Rocks and Inner East Point sites. Declines in *A. siderium* populations were inversely correlated with the increase in *T. plebeia* numbers throughout 1984 and 1985. Although *T. plebeia* disappeared by early 1986, *A. siderium* continued to suffer high mortalities; the only colonies remaining by the end of 1986 were at Inner East Point.

The simultaneous population expansion of urchins on vertical surfaces at all sites, except Inner East Point where

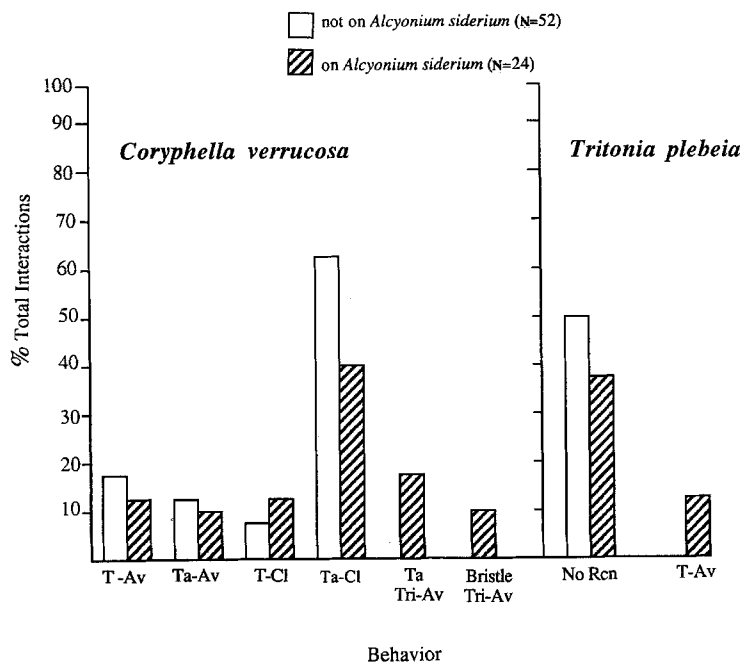


Fig. 7. *Tritonia plebeia* and *Coryphella verrucosa*. Ethogram of interactions on and off *Alcyonium siderium* colonies in laboratory. T: touch (rhinophore contact); Ta: taste (one or more contacts of mouth with body); Cl: Climb (movement onto body); AV: Aversion (nudibranch turned away); No Rcn: No reaction (only retraction of rhinophores); Bristle: bristling of cerata by *C. verrucosa* towards *T. plebeia*. Number of encounters on *A. siderium* = 24; number of encounters not on *A. siderium* = 52

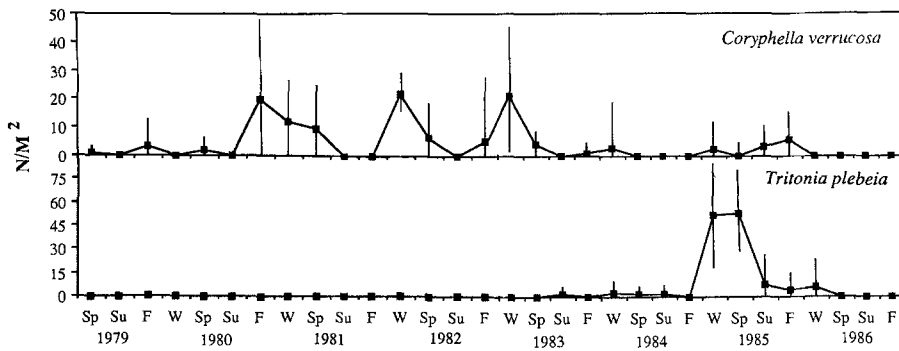


Fig. 8. *Tritonia plebeia* and *Coryphella verrucosa*. Densities from winter 1979 to fall 1986 at Inner Shag Rocks. Values are means \pm SD. Densities of *C. verrucosa* decreased the year *T. plebeia* was first observed but well before peak densities of *T. plebeia*

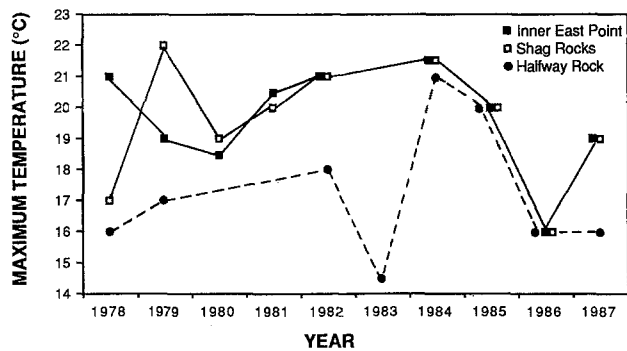


Fig. 9. Maximum annual temperatures at Shag Rocks Inner and Outer, Inner East Point and Halfway Rock from min-max thermometers at study sites. Coastal sites (50 to 100 m offshore) experience higher temperatures than Halfway Rock, 5 km offshore, except in 1984 and 1985 when Halfway Rock temperatures were abnormally high

urchins are rare, seems to have contributed to the decline in *Alcyonium siderium* numbers. *Tritonia plebeia* alone probably did not cause the complete decimation of *A. siderium* from Outer and Inner Shag Rocks in the few seasons that they were abundant. At Inner East Point, where urchins are rare, *T. plebeia* abundances reached densities comparable to those at the Shag Rocks localities, but the decline in the soft coral population was more gradual. By Fall 1986, 20% of the colonies mapped in spring 1985 were still alive on the wall and populations appeared to be recovering, while none remained at the Outer and Inner Shag Rocks study quadrats, although small aggregations persisted on nearby walls.

The decline in *Alcyonium siderium* densities at Halfway Rock began in summer 1984, close to a year before urchin densities increased and a year after the decline began at the Shag Rocks. Urchin predation, therefore, was probably not the initial cause of increased *A. siderium* mortalities at this site. Unusually high water temperatures are a more likely cause of the die-off. Whereas sites closer to land (Outer and Inner Shag Rocks, and Inner East Point) experience water temperatures of 20°C or more annually, no temperature higher than 17°C was recorded at Halfway Rock from 1979 to 1983. During the summer of 1984 and 1985, however, temperature peaks of 21° and 20°C respectively were recorded from 15 m depth at Halfway Rock (Fig. 9). Since temperatures over 17°C were rare, the *A. siderium* population at

Halfway Rock may have been either acclimated or better adapted to lower temperatures than the coastal populations. Hoffmann (1981 a, b, 1983) has shown that local genetic temperature adaptation occurs between populations of the anemone *Metridium senile* from this region. There have been several reports of similar increases in water temperatures causing mortality among coral colonies in Caribbean and Pacific waters (Glynn 1983, Goreau 1964, Roberts 1987).

Urchin densities on the rock walls at the Shag Rocks sites, where they have been abundant at least since 1978, increased dramatically during the periods when *Tritonia plebeia* was most abundant. At the same time, *Alcyonium siderium* densities dropped rapidly until all colonies were eventually gone. Urchins readily prey on encrusting invertebrates, including *A. siderium* (Larson et. al. 1980, Sebens 1983). However, abundances of this urchin on vertical rock walls with high concentrations of invertebrates are generally limited by the inability of the tube feet of the urchins to gain a firm hold on soft bodied invertebrates (Sebens 1983, 1985a, b). Urchins specifically avoid grazing within soft coral aggregations, due either to the stinging nematocyst cells of the octocoral, or to the presence of these large obstructions (Sebens 1983). In addition to predation, urchins may also inadvertently dislodge soft coral colonies from the walls as they graze (Sebens 1983).

Population expansions of urchins, to densities equivalent to those in 1985, did not affect *Alcyonium siderium* densities in previous years. Throughout seasons in 1980 urchin densities at Inner Shag Rocks were not significantly different from those in the same seasons in 1985, but there was no corresponding decline in the 1980 *A. siderium* population as a result of the high numbers of urchins. In summer 1985, however, these densities had decreased to a level significantly lower than those in summer 1980 (ANOVA: $F=110.2$, $P<0.001$), and continued to decrease.

Tritonia plebeia, absent in 1980, played a significant role in shifting the ecological balance that had persisted on the subtidal rock wall communities around East Point, Nahant. Although consumption of entire soft coral colonies by *T. plebeia* was not observed, damage to the bases from feeding often resulted in detachment of the colony from the substrate. This created spaces within the aggregates of *Alcyonium siderium* into which urchins could enter. Rather than move around the remaining colonies, urchins may have eventually "bulldozed" over some, scraping them from the

walls, or consumed them directly. As urchin densities increased, urchins may have been forced to take food that they would ordinarily avoid. Surfaces once encrusted with invertebrates were reduced to bare rock and coralline algae (Sebens unpublished data).

Since the disappearance of *Tritonia plebeia* in 1986, and the reduction of the numbers of urchins on the vertical walls, there is some evidence of recovery in the *Alcyonium siderium* populations. Densities on the monitored walls at Inner East Point have remained relatively constant since spring 1986. At Outer and Inner Shag Rocks, colonies are reappearing in cracks and under overhangs where urchin grazing is minimal.

The sudden appearance of *Tritonia plebeia* in the continuously monitored areas off Nahant could be either a range extension or, more likely, an accidental introduction. A range extension seems unlikely in this case because there have been no reports of *T. plebeia* in surveys off Iceland (Lemche 1938, 1941), Canada (Stimpson 1853) and northern Massachusetts (Gould 1870, Moore 1950). Similarly, no *T. plebeia* were observed during extensive quarter-annual surveys of *Alcyonium siderium* aggregates off East Port, Maine, by Kuzirian and colleagues from 1978 to 1979 (personal communication). Although there is no direct evidence of a human mediated introduction, the proximity of Nahant to Boston Harbor and the shipping channel suggests one. There are several reports of other molluscs surviving transport in the ballast waters of ships, and subsequently being accidentally introduced to new areas (Garrard 1972, Clarke 1979, Carlton 1985). Furthermore, the northward movement of this nudibranch away from Boston into southern Maine, against the predominantly southern current in this area, argues for a southern Gulf of Maine introduction and against a range extension from the north.

In summary, the appearance of the exotic species *Tritonia plebeia*, combined with an unusually high number of urchins, disrupted the invertebrate communities that had persisted at Outer and Inner Shag Rocks for more than 6 yrs. Where there were no urchins (Inner East Point), *Alcyonium siderium* densities also declined, albeit more slowly, and populations were not completely eliminated. In areas with abundant urchins, *A. siderium* suffered higher mortalities. If numbers of urchins on the walls at the Shag Rocks sites had remained at levels such as those prior to 1985, juvenile *Alcyonium siderium* may have been able to recolonize within the aggregations and to replace those larger colonies preyed on by *T. plebeia*. However, as the larger colonies were removed by predation, the juveniles that settled between these adult colonies lost their protection (Sebens 1983), and were "bulldozed" off the wall or consumed by urchins no longer constrained to the perimeters of the soft coral aggregations by the presence of large colonies.

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Note added in proof: *Tritonia plebeia* were observed in June 1988 at Monhegan Island, Maine at 25 m depth.