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Stealthy slugs and communicating corals: polyp withdrawal by an aggregating soft coral in response to injured neighbors

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Abstract: The polyps of *Discophyton rudyi* (Verseveldt and van Ofwegen, 1992), a small, aggregating, alcyonacean soft coral found on rocky shores in the northeast Pacific Ocean, are selectively preyed on by the nudibranch *Tritonia festiva* (Stearns, 1873). In the laboratory, *D. rudyi* retracted their polyps when exposed to water-borne cues from a conspecific colony that was successfully attacked by *T. festiva*. This same inter-colony response was elicited by attacks simulated with fine scissors, but not by (*i*) the presence of *T. festiva* attempting to feed but prevented from damaging its prey, (*ii*) the simple withdrawal of the soft coral polyps, or (*iii*) seawater controls. The cue(s) eliciting polyp retraction therefore emanate from the soft coral and not its nudibranch predator. *Tritonia festiva* often attacks neighboring colonies, which are usually separated by only a few millimetres, in rapid succession but will not attack colonies with retracted polyps. It also cannot move rapidly to reach more distant colonies. Therefore, polyp retraction by one colony in response to predation on a neighboring colony effectively serves as an anti-predatory alarm response. Although aggregations of *D. rudyi* are largely clonal, the response to water-borne cues from injured conspecifics does not appear to be clone-specific. Few examples of intra-specific alarm responses are known from sessile marine invertebrates, but the similarities between them suggest that other examples may be found in suspension or deposit-feeding taxa that form dense aggregations and are preyed on by stealthy partial-predators likely to attack adjacent individuals or colonies in rapid succession.

Résumé : Les polypes de *Discophyton rudyi* (Verseveldt et van Ofwegen, 1992), un petit corail mou alcyonacé qui forme des agrégats sur les plages rocheuses du nord-est du Pacifique, subissent la prédation sélective du nudibranche *Tritonia festiva* (Stearns, 1873). En laboratoire, *D. rudyi* rétracte ses polypes lorsqu'on l'expose à des signaux transmis dans l'eau provenant d'une autre colonie effectivement attaquée par *T. festiva*. Cette même réaction d'une colonie à l'autre peut être provoquée par une attaque simulée avec des ciseaux fins, mais non par (*i*) la présence de *T. festiva* qui cherche à se nourrir, mais qui est empêché d'endommager sa proie, ni par (*ii*) le simple retrait des polypes du corail mou, ni enfin (*iii*) dans un témoin d'eau de mer. Le ou les signaux qui déclenchent la rétraction des polypes émanent donc du corail mou et non de son prédateur nudibranche. *Tritonia festiva* attaque souvent des colonies adjacentes (qui sont ordinairement à quelques mm l'une de l'autre) en succession rapide, mais il n'attaque pas les colonies à polypes rétractés. Il ne peut non plus se déplacer rapidement pour atteindre les colonies plus éloignées. C'est pourquoi, la rétraction des polypes dans une colonie en réaction à la prédation dans une colonie adjacente sert effectivement de réaction d'alerte contre le prédateur. Bien que les agrégats de *D. rudyi* soient des clones, la réaction aux signaux transmis dans l'eau par les coraux blessés de la même espèce ne semble pas être spécifique au clone. On connaît peu d'exemples de réactions d'alerte intra-spécifiques chez les invertébrés marins sessiles, mais les similarités qui existent entre elles laissent croire que d'autres exemples pourraient exister chez les taxons qui se nourrissent de particules en suspension ou de dépôts de surface, qui forment des agrégats importants et qui sont exploités par des prédateurs partiels furtifs susceptibles d'attaquer des colonies ou des individus adjacents en succession rapide.

[Traduit par la Rédaction]

Introduction

Predation-induced, intra-specific alarm responses have been documented in mobile invertebrates from terrestrial, aquatic, and marine habitats (e.g., Synder and Synder 1970; Cimino et al. 1991; Hazlett 1994; Swenson and McClintock 1998; Ichinose et al. 2003; Vadas and Elner 2003; Wyatt 2003). Extensive evidence also exists for chemical communication and induced chemical defenses against predators in terrestrial plants (reviewed by Dicke and Bruin 2001). However, few examples of intra-specific alarm responses in sessile invertebrates have been reported. Howe and Sheikh (1975) and Howe (1976) described an alarm response between individuals of the clonal sea anemone *Anthopleura elegantissima* (Brandt, 1835) that is mediated by a pheromone, anthopleurine. Anemones attacked by the specialist nudibranch *Aeolidia papillosa* (L., 1761) release the pheromone, which induces a series of defensive behaviors in neighboring anemones. More

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Fig. 1. *Discophyton rudyi* and *Tritonia festiva* from Cape Arago, Oregon. (A) Aggregation of *D. rudyi* on rock fragment collected in May 1987; rule in centimetres. (B) Cluster of expanded colonies of *D. rudyi* on a rock fragment collected in February 1984. (C) Left lateral–dorsal view of *T. festiva*, 30 mm long. (D) Single colony of *D. rudyi* immediately following a successful attack by *T. festiva* in the laboratory. The holes in the colony mark the position of polyps that were severed and ingested by the nudibranch.
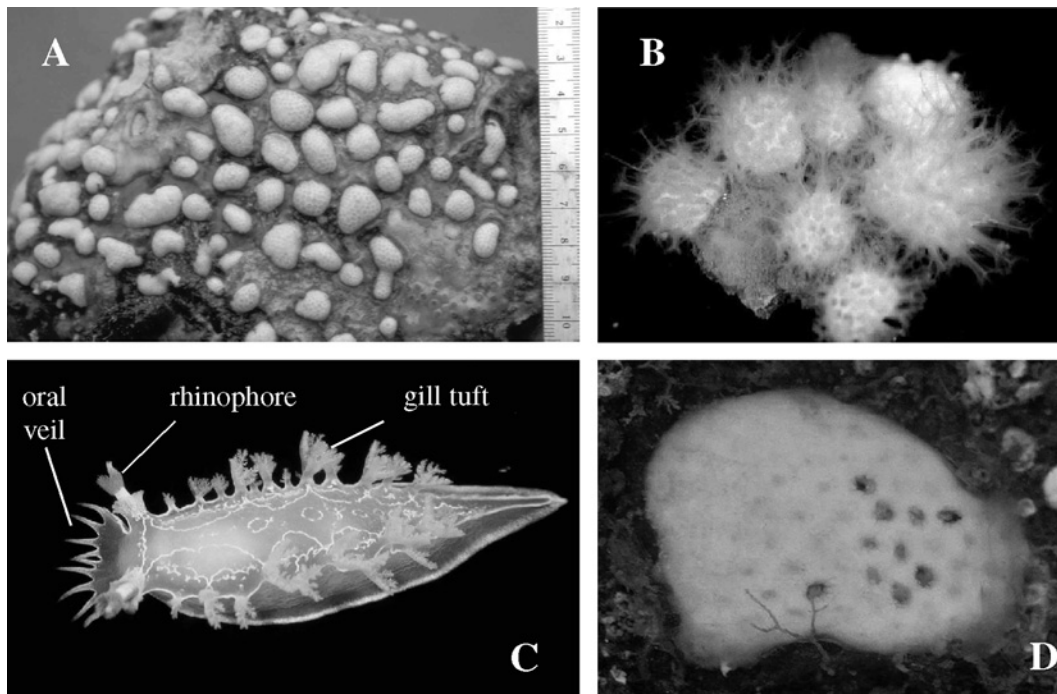
recently, Rosenberg and Selander (2000) found that the ophiuroid *Amphiura filiformis* (O.F. Müller, 1776), which can be considered functionally sessile while feeding, responded to partial predation by fish on upstream conspecifics by lowering and burying their arms in the surrounding sediment. While studying the feeding behavior of the nudibranch gastropod *Tritonia festiva* (Stearns, 1873) on the alcyonarian soft coral *Discophyton rudyi* (Verseveldt and van Ofwegen, 1992), colonies not touched by the nudibranch were observed in the laboratory to retract their polyps within seconds to minutes following a successful attack by the nudibranch on another colony, all of which were in still water disturbed only by the addition and removal of the nudibranch for feeding. The present study was conducted (*i*) to document further this inter-colony response and (*ii*) to determine if the cues eliciting polyp retraction emanate from the soft coral or the nudibranch. No attempt was made to determine the nature of the cue itself.

Study organisms

Discophyton rudyi is a small (5–15 mm in diameter and 2–5 mm thick) disc to bean-shaped soft coral common under low intertidal ledges and boulders on outer coast rocky shores in the northeast Pacific Ocean (McFadden 1991; McFadden and Hochberg 2003). It propagates asexually by fission to form aggregations of up to hundreds of colonies, each separated by only a few millimetres (McFadden 1997) (Figs. 1*a*, 1*b*).

Tritonia festiva (Fig. 1*c*) preys exclusively on octocorals, specializing on their polyps, and is common on shores in Oregon and Washington where octocorals are abundant (Goddard 1984, 1998, 2000; unpublished data). The nudibranch uses

its rhinophores and digitate frontal veil to locate expanded soft coral colonies, and experiments conducted in a two-armed flume revealed that *T. festiva* could detect *D. rudyi* from distances of at least 40 cm (unpublished data). Upon contact with the polyps of *D. rudyi*, *T. festiva* immediately stops crawling, lifts its frontal veil, and begins positioning itself for a surprise attack. The head is slowly lifted, and the expanding oral canal is aligned with polyps in the vicinity of the initial contact using the tactile sense of both the frontal veil and the oral canal (Fig. 2*a*). Contact by these two structures (which in addition to the initial contact is usually the only contact with a colony prior to an attack) can cause the polyps of *D. rudyi* to curl their tentacles, but does not cause them to retract into the colony mass. Once positioned (about a 20 s process), the nudibranch lunges repeatedly into the colony, using its jaws and radula to bite off polyps before they can retract into the spiculate colony mass (Fig. 1*d*). An average attack on *D. rudyi* lasts 24 s, consists of 2–4 separate lunges, and results in ingestion of 4 polyps (range = 1–12 polyps, *n* = 32 attacks by 6 *T. festiva*) (unpublished data).

Following an attack, *T. festiva* continues foraging and the nudibranch repeats the above sequence as soon as contact is made with polyps on a neighboring colony. When the polyps of another colony are contacted during an attack in progress, *T. festiva* often skips the positioning phase described above and attacks the neighboring colony as a continuation of the first attack. *Tritonia festiva* was never observed to initiate an attack on colonies with fully retracted polyps.

Methods

In winter and spring of 1984 and summer and fall of 1986, *D. rudyi* and *T. festiva* were collected intertidally from

Fig. 2. Sequence showing *T. festiva* attacking a colony of *D. rudyi* in a laboratory aquarium and the subsequent response of an adjacent colony that was not touched by the nudibranch. (A) *Tritonia festiva* preparing to attack colony 1. Note the fully extended polyps on colony 2. (B) Response of colony 2, 33 s after image A was taken and 21 s after initiation of the attack on colony 1. Note that all of the polyps on colony 2 have been completely withdrawn. As the nudibranch was attacking colony 1, an eyedropper pipette was squeezed three times to generate a small current over the nudibranch and colony 1 and toward colony 2. Images digitally captured from a DVD recording of an 8 mm movie filmed in March 1984.
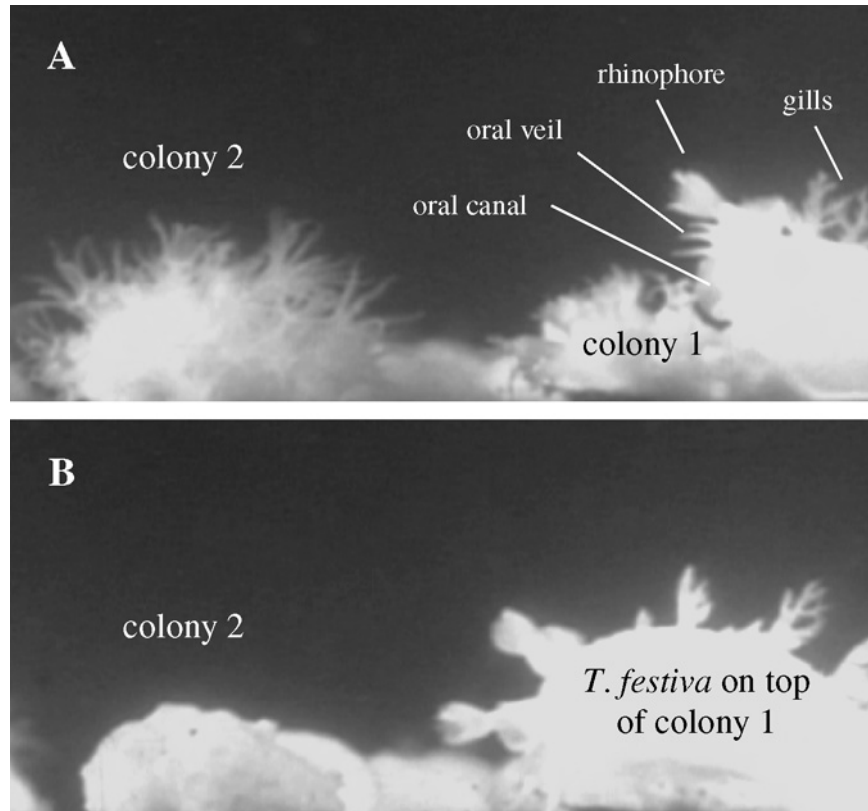
Cape Arago, Oregon (43°18′N, 124°24′W). Nudibranchs were held separately in 500 mL glass beakers on a flow-through seawater table at ambient temperature (10–13 °C) and periodically allowed to feed on soft corals. The soft corals were either scraped off rock surfaces or collected intact on pieces of sandstone using a hammer and chisel. Colonies removed from rocks were transplanted onto pieces of ceramic tile (4–9 cm^2) or onto glass microscope slides. Transplanted colonies were held in place by cotton thread until they had attached to the new substrate, after which the thread was removed. Colonies were not separated by specific site or aggregation and therefore were mixed with members of different clones. All coral colonies were held on a flow-through seawater table at ambient temperature with indirect natural lighting. The seawater was unfiltered, providing some planktonic food for the corals; they were also occasionally fed *Artemia* Leach, 1819 nauplii, but not within a day of the experimental trials.

A series of experiments were conducted in May and June 1984 and between August and December 1986 to determine if the coral or the nudibranch was the source of the alarm cues. Expanded test colonies of *D. rudyi* were exposed to seawater containing stimulus colonies treated as follows (each of these is followed in parentheses by the name given to that treatment, and treatments are numbered in the order in which they were conducted): (1) an expanded colony of *D. rudyi*

attacked by *T. festiva* ("attack by *Tritonia*"); (2) an expanded colony from which 3 to 9 polyps were severed using fine dissecting scissors ("simulated attack") (as soon as the polyps were severed on these colonies, the remaining polyps contracted as in an attack by *T. festiva*); (3) seawater not exposed to either the soft coral or the nudibranch ("seawater control, no polyps"); (4) a *T. festiva* induced into its attack behavior by contact with an expanded colony, but not allowed to damage that colony ("attack behavior by *Tritonia*, no damage to polyps"); (5) seawater surrounding undisturbed, expanded *D. rudyi* ("undisturbed polyps"); and (6) an expanded colony manually prodded with a glass rod into contracting its polyps ("polyps prodded into retraction"). Based on preliminary observations of *T. festiva* feeding on *D. rudyi* (see above), the first two treatments, but not the last four, were expected to stimulate retraction of the polyps on the test colonies.

The experimental procedure consisted of pipetting 1 mL of water drawn from within 1–2 cm of the stimulus colony or nudibranch and then pipetting that water from a distance of 1–2 cm and at a rate of about 1 mL/s toward the extended polyps of the test colonies, which were in glass finger bowls (9 or 19 cm diameter, holding 250 or 1500 mL of seawater, respectively; the larger finger bowls were needed to hold the test colonies on larger fragments of rock — see below). In each trial, pipetting was done three times in a continuous

Table 1. Response of expanded test colonies of *Discophyton rudyi* to seawater treated with injured or uninjured conspecific colonies.

Treatment	Response of polyps on test colonies			Number of trials
	Complete retraction	Partial retraction	No retraction	
1. Attack by *Tritonia*	74	11	0	18
2. Simulated attack	69	15	0	15
3. Seawater control, no polyps	0	5	75	22
4. Attack behavior by *Tritonia*, no damage to polyps	0	2	84	11
5. Undisturbed polyps	0	2	94	16
6. Polyps prodded into retraction	6	6	82	16
7. Simulated attack following trials in treatments 3–6	85	17	0	12

Note: Values are the number of colonies that responded by complete, partial, or no retraction of their polyps. Total number of colonies used per treatment exceeds the number of trials owing to the use of clumps of coral colonies on their original rock substrate (see Methods).

sequence, but from different angles, followed by gently pumping the pipette a few times to expose all test colonies to small currents containing the stimulus water. Pipettes were rinsed in freshwater three times between trials. The response of the polyps on each test colony within 30 s of pipetting was categorized as (*i*) no retraction, (*ii*) partial retraction, or (*iii*) complete retraction into the colony mass.

Test corals were either transplants or intact on fragments of their original rock substrate. Because the latter contained naturally occurring aggregations of colonies, multiple test colonies were used in many of the trials. Trials with at least three test colonies could therefore be scored in all three of the response categories. Colonies were not reused in treatments 1 and 2. However, in treatments 3–6 (the four expected not to stimulate polyp retraction), colonies were drawn at random from the same pool of colonies collected in November 1986.

To evaluate the responsiveness of the test colonies used in treatments 3–6, dissecting scissors were used periodically to simulate an attack on one of the test colonies and then the response of its neighbors tested to water pipetted from over the damaged colony. The results of these tests are presented as treatment 7 ("simulated attack following trials in treatments 3–6"). The colonies so tested were returned to the pool and may have been used again in the remaining treatments, but only if their polyps were fully re-extended.

The trials for treatment 4 (attack behavior by *Tritonia*, no damage to polyps) were conducted as follows. *Tritonia festiva* was allowed to contact and position itself normally for an attack on an expanded coral colony. Just as the nudibranch was about to strike, the coral was pulled away, and the nudibranch completed its feeding motion without damaging the colony. For each trial, this was done 5–10 times, and then the seawater surrounding the anterior end of the nudibranch was pipetted onto the test corals. Seven *T. festiva* were used in these trials.

The responses of the test corals to the different treatments were compared with contingency table analyses using the *G* statistic with the Williams correction (Sokal and Rohlf 1981). First, the proportion of colonies with each response was calculated for each trial. These proportions were then summed for each response category for each treatment. These sums, rather than the number of colonies responding, were used in the analyses. Results of the two attack treatments were compared with one another and with the seawater control. However, the results of treatments 4–6 were not compared statistically with one another or with the seawater control, because test corals may have been reused between these treatments (see above).

Results

Discophyton rudyi responded to water-borne cues from an attack by *T. festiva* on conspecific colonies (not necessarily from the same clone) by completely or partially retracting their polyps (Table 1, Fig. 2), and the responses to this treatment were statistically indistinguishable from the responses to the simulated attacks ($G_{adjusted} = 0.02$, $p = 0.90$; 2 × 2 cell frequencies of 15.3 and 2.7 vs. 13.0 and 2.0, respectively, using the two retraction response categories but not the negative response category, since there were no negative responses). Responses to an attack by the nudibranch and to a simulated attack were both obviously different from the responses to the seawater control (Table 1; $G_{adjusted} = 45.48$ and 40.70, respectively, $p < 0.001$ for both 2 × 2 tests; using cell frequencies of 18 and 0 vs. 1 and 21, and 15 and 0 vs. 1 and 21, respectively, lumping the two retraction response categories). There was little or no response by the test colonies to treatments 4–6 (Table 1). Moreover, the responses to all three of these treatments were virtually indistinguishable from the responses to the seawater control. Six test colonies in two trials did completely contract their polyps following the prodding of stimulus colonies in treatment 6, raising the possibility that some of the stimulus colony polyps were damaged by the prodding with the glass rod and released alarm cues.

In treatment 7 (the simulated attacks conducted immediately following some of the trials in treatments 3–6), the response of the test corals was similar to that observed in the simulated attack trials conducted separately in treatment 2 (Table 1).

Discussion

Discophyton rudyi consistently retracted their polyps in

response to water-borne cues from colonies attacked by *T. festiva*. Initial observations that contact by *T. festiva* searching for prey or preparing for an attack did not stimulate polyp retraction in *D. rudyi* suggested that the nudibranch was not the source of the cues stimulating polyp retraction in neighboring colonies. This was confirmed by (*i*) the lack of response of test colonies to water surrounding *T. festiva* induced into their attack behavior (which included full protraction of the buccal mass) but not allowed to damage stimulus colonies and (*ii*) the response of test colonies to stimulus colonies whose polyps had been artificially severed in the absence of the nudibranch.

The sensitivity of *D. rudyi* to water-borne cues from injured neighbors is evidenced by (*i*) their consistent response, usually within seconds, to water from the vicinity of an attack; (*ii*) early observations (see Introduction) that a single colony successfully attacked by the nudibranch elicited polyp retraction in numerous colonies present in 1.5 L of seawater disturbed only by the addition and removal of the nudibranch; and (*iii*) that the response is elicited by severing only a few polyps on stimulus colonies using fine dissection scissors. Colonies responding to injured neighbors remained mostly contracted for less than 1 day compared with 2–3 days for colonies actually attacked by *T. festiva* (personal observations).

With one exception, the coral colonies used in these experiments were not separated by precise collection locality or aggregation, and the clone specificity of the retraction response was not investigated. However, collection sites at Cape Arago spanned a distance of about 2 km. Given the limited dispersal capability of *D. rudyi* and McFadden's (1997) finding that clones rarely exceed 30 cm^2 in area, it is likely that the test and stimulus colonies used in many of the trials were from different clones, representing many genotypes. In the exception, three colonies collected from Cape Blanco, Oregon (50 km south of Cape Arago), were tested to a simulated attack on a colony from Cape Arago; all three responded with a rapid and complete retraction of their polyps. The alarm response in this species therefore does not appear to be clone-specific.

Because *T. festiva* often attacks adjacent colonies in rapid succession, but will not attack colonies whose polyps are withdrawn (personal observations), polyp retraction by *D. rudyi* in response to attacks on neighbors can effectively deter predation by the nudibranch and prevent the loss of feeding polyps. The costs of this response are reduced feeding time, the energy needed to simultaneously withdraw and later expand all polyps, and perhaps impaired aerobic respiratory ability. Colonies stimulated frequently to withdraw their polyps might also be more susceptible to settlement and overgrowth by competitors for space (e.g., sponges, bryozoans, and ascidians), some of which have been observed overgrowing small aggregations of *D. rudyi* in the field (Goddard 1984, p. 158; personal observations).

Although these experiments were conducted in mostly still water in the laboratory, the cues stimulating polyp withdrawal also seem likely to deter predation by *T. festiva* on wave-exposed rocky shores, despite the strong, turbulent flows, and potential for rapid attenuation of the signal away from injured colonies. Both *D. rudyi* and *T. festiva* are often found in less wave-exposed microhabitats, such as the undersides of cobbles and ledges, and in caves (personal observations). More importantly, however, the soft coral occurs in aggregations, with only a few millimetres separating neighboring colonies (Figs. 1*a*, 1*b*) (McFadden 1986; McFadden and Hochberg 2003). Because the nudibranch usually attacks neighboring colonies in rapid succession, but cannot move rapidly to reach more distant colonies, the signal does not have to travel far to be effective. In addition, the turbulent flow and reductions in colony-level flow speeds that result from the aggregated distribution of this species (McFadden 1986) may also promote short-term retention of the cues in the vicinity of an injured colony and its neighbors.

The apparent sensitivity of *D. rudyi* to injured conspecifics, as well as the consistency, benefits, and potential costs of its polyp-withdrawal response, suggest that this response may be an alarm response, mediated by a signal that has evolved as a specific defense mechanism against specialized predation by *T. festiva*. Biochemical studies to isolate and characterize the signal, and determine if a pheromone is involved, are therefore warranted.

Although few examples of anti-predatory alarm responses are known from sessile marine invertebrates, *D. rudyi* shares some biological and ecological features with *Anthopleura elegantissima* and the ophiuroid *Amphiura filiformis* (see Introduction) that might indicate other examples of this phenomenon in other sessile (or largely sessile) organisms. All three are suspension-feeding organisms that occur in dense aggregations. All are preyed on by stealthy, partial predators likely to attack the feeding structures of a number of individuals (or colonies) in rapid succession, and all can hide or withdraw their susceptible feeding structures out of reach of their specific predators. Other organisms with these characteristics that might reveal similar examples of alarm responses include infaunal bivalves preyed on by siphon-nipping fish (e.g., Peterson and Quammen 1982); sessile Cnidaria and Bryozoa forming aggregations of colonies, rather than single large colonies; and sedentary spionid, terebellid, and cirratulid polychaetes whose extended feeding tentacles might be susceptible to partial predators.

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