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Note

Observations on the behavior of *Atolla* (Scyphozoa: Coronatae) and *Nanomia* (Hydrozoa: Physonectae): use of the hypertrophied tentacle in prey capture

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Coronate scyphozoans of the genus *Atolla* are among the most prominent medusae in the mesopelagic community. They have been observed in every ocean of the world (Russell 1970; Larson 1986, 1990; Pagès et al. 1992) although their contribution to the trophic ecology of pelagic ecosystems has been largely overlooked (Larson 1986). When encountered using submersibles, *Atolla* is always observed trailing one long tentacle (Hunt & Lindsay, pers. obs.). Estimates from videotaped records suggest this tentacle trails anywhere from 3 to 6 times the diameter of the bell. Speculation that this tentacle is used for feeding or for defense lacks direct evidence. Using submersibles to observe midwater animals in situ has revealed the function of this hypertrophied tentacle. It is used to capture prey, amongst which is the physonect siphonophore *Nanomia*.

Atolla was observed using its hypertrophied tentacle to catch *Nanomia*. Figure 1A is a videograph and Fig. 1B is a tracing of a videograph taken from the submersible *Dolphin 3K* Dive #326 on 30 May 1997. The dive was conducted in Sagami Bay, Japan, at 35° 00.00'N, 139° 13.50'E where bottom depth was 1211 m. Figure 1A shows an *Atolla* swimming at a depth of 751 m with its trailing tentacle in close proximity to two shorter-stemmed *Nanomia*. Figure 1B shows an *Atolla* actively tugging on a captured *Nanomia* which is bent at the point of tentacle contact on the stem. This bend was the leading point of motion which followed the medusa as it swam downward.

At 10:05:20 AM local time (GMT+9 h), the medusa was first observed vigorously swimming at a depth of 769 m. At 10:05:38 AM the *Nanomia* was observed for the first time. It had been caught and was being tugged as the medusa swam downward at an oblique angle. The pulse rate was once per second (7 bell contractions over 7 s). These animals remained equidistant as the medusa moved in a linear direction. The *Nanomia* then swam back and forth in sweeping arcs, changing direction and pulsing hard in an obvious attempt at escape. The oral surface of the medusa changed attitude, rotating synchronously with the movements of the siphonophore. The two animals disappeared off-screen at 10:05:57 AM and reappeared at 10:06:25 AM, still equidistant 47 s after confirmation that they were joined by the tentacle. *Atolla* swam swiftly upwards, first obliquely to the right, then obliquely to the left. The two disappeared off-screen at 10:06:43 AM and reappeared for the last time at 10:07:13 AM. The *Atolla* had decreased its pulse rate to slightly less than once per second (7 bell contractions over 10 s). By this time, the *Nanomia* had stopped swimming in long sweeping arcs, and was vigorously spinning in place about the tentacle's axis. It rotated 1+1/4 turns (450°) counterclockwise, pivoted back 1/4 turn clockwise, then changed direction again spinning two

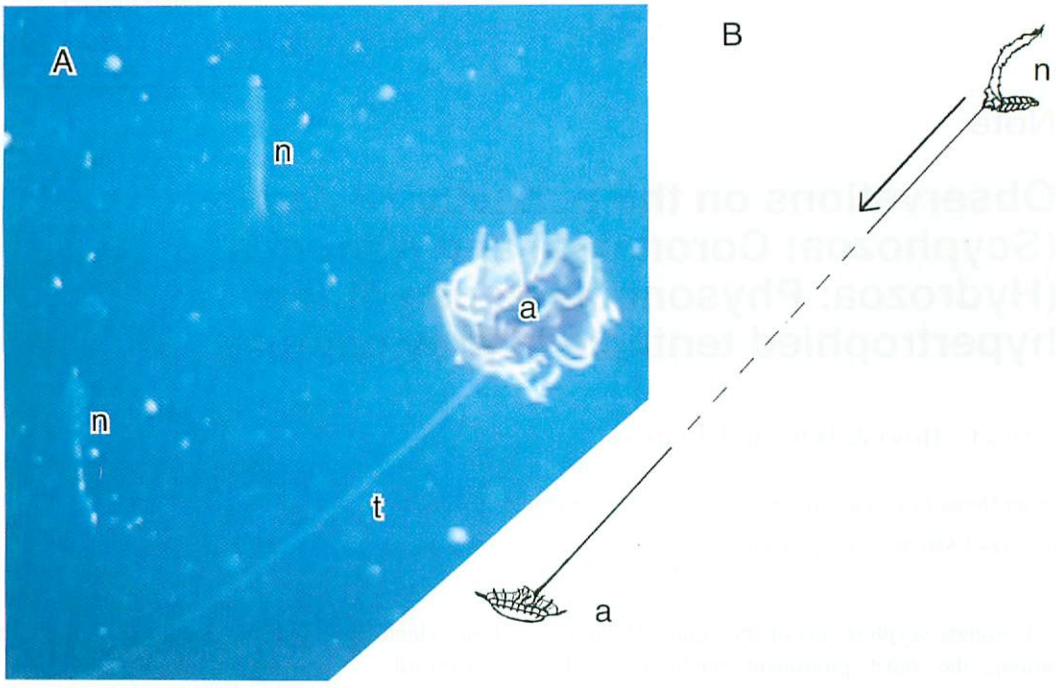

Fig. 1. **A.** Videograph showing an *Atolla* (*a*) with the tentacle (*t*) swimming in close proximity to two shorter-stemmed *Nanomia* (*n*). **B.** Tracing from a videograph showing an *Atolla* (*a*) tugging a *Nanomia* (*n*), bent where the *Atolla* tentacle is attached. The *dotted line* indicates a section of tentacle too faint to be seen in the videograph. The *arrow* indicates the direction of movement.

full rotations counterclockwise before disappearing off-screen. These turns occurred over a period of 10 s for a spinning rate of about 1 rotation per 3 s. The observation ended at 10:07:23 AM, 105 s after capture was observed. During this time, the *Nanomia* seemed to be reduced to spinning about the tentacle while the medusa was still actively swimming.

The feeding habits of scyphomedusae are not well known. Larson (1979) reported that *Nausithoe punctata* fed on zooplankton caught on its aborally arcing tentacles which quickly transported prey down to the mouth. He suggested that *Atolla* sp. and *Periphylla periphylla* may also feed this way based on in-situ photographs. He further cautiously suggested that the diets of these scyphomedusae may be similar to *N. punctata*, predominantly small crustaceans and fishes. We have always observed *Periphylla* and *Atolla* swimming with their tentacles curved aborally as has been described (notwithstanding the trailing tentacle of *Atolla* of course). However, in the case of *Atolla*, we suggest that the trailing tentacle may be used to capture *Nanomia* or other gelatinous prey, whereas the other tentacles are used to feed on copepods and other zooplankton. This may appear to be a rather complex feeding strategy, but scyphomedusae have been noted for their complex and remarkable behavior (see Hamner 1995).

Nanomia can be very common in the midwater realm (Widder et al. 1989; Mills et al. 1996), occasionally reaching abundances which disrupt commercial fishing by clogging the nets (Rogers et al. 1978). The distributions of *Atolla* sp. and *Nanomia* sp. (*N. ?bijuga*) in Sagami Bay, Japan, overlap considerably (Hunt & Lindsay, forthcoming). This overlapping distribution may be simply the result of both species avoiding surface waters. Specifically, increased light intensity in shallow waters may drive diel migration patterns as a measure to avoid predation (Zaret & Suffern 1976). Others have proposed selective metabolic advantages for some migrators (Enright 1977). Whatever the cause, *Nanomia* is a diel vertical migrator (Hunt, pers. obs.). *Atolla* may be avoiding the surface waters as well. It is probable that its dark red stomach would become easier for its predators to see as light increased. Hardy (1965) reported finding increased pigmentation in *Atolla* with depth. It has been suggested that dark stomachs in jellyfishes could mask bioluminescence emitted by prey within the stomach. Both *Nanomia cara* (Freeman 1987) and *Nanomia bijuga* (Widder et al. 1989) have been observed to bioluminesce from nectophores and bracts when disturbed. Thus the dark stomach of *Atolla* could be used to mask light emitted by *Nanomia* (or other prey) when engulfed.

Nanomia tend to change body shape by retracting the tentacles and contracting the stem when at depths within the distributional range of *Atolla* (Hunt & Lindsay, forthcoming). This behavior was only observed within the depth range where *Atolla* were present in Sagami Bay (n=65). Retracted tentacles and compact form might reduce the surface area that could contact the trailing tentacle of *Atolla*. Retraction of tentacles is a common response observed in many siphonophores when disturbed (Hamner et al. 1975; Hunt & Lindsay, pers. obs.) and likely facilitates more rapid escape by the colony. Not all *Nanomia* take this form at depth, but a significant percentage of them do (21% within the range of *Atolla* [n=304], 0% without [n=91]). Although we have observed *Nanomia* autotomizing bracts when disturbed by the submersible, the shortened stems discussed here do not appear to be the result of such behavior. The shorter-stemmed form contains closely spaced bracts and thicker stems due to the retraction of tentacles and the stem itself.

It is unclear whether or not the trailing tentacle captures only *Nanomia* or if it captures other prey as well. It is interesting to note, however, that in the Weddell Sea where *Nanomia* is not present, the range of *Atolla wyvillei* overlapped strongly with *Marrus antarcticus*, the most abundant physonect in the area (see Pugh et al. 1997).

In summary, several lines of evidence suggest a trophic relationship between the common coronate medusa *Atolla* and the common physonect siphonophore *Nanomia*. First, both genera are widely distributed in overlapping ranges in mesopelagic ecosystems around the world. Second, *Atolla* is always observed with one long tentacle trailing through the water as it swims. Third, *Nanomia* is often observed within the depth range of *Atolla* with its tentacles retracted and stem shortened which may help avoid the trailing tentacle. Fourth, *Nanomia* is bioluminescent and *Atolla* has a darkly pigmented gut. Such guts in medusae have been suggested to mask bioluminescence emitted by captured prey. Fifth, the trailing tentacle of *Atolla* was observed capturing a *Nanomia* which was endeavoring to escape. We submit here that *Atolla* uses its long tentacle to feed, and that *Nanomia* is among its prey.

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