

Cnidarian "Parasites" on *Solmissus incisa*, a Narcomedusa*

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SUMMARY: A narcomedusa, *Solmissus incisa*, was collected off central California in the Monterey Submarine Canyon at 230 m in October 1996. The medusa was viewed and collected from the RV *Point Lobos* using the remotely operated vehicle (ROV) *Ventana*. Advantages of such *in situ* observation include the ability to recognize parasites (which appear as small, opaque circles) on the bell of the specimen. In the laboratory, the circular objects were found to be "parasitic," cnidarian-like juveniles developing within the epidermis, stages that moved freely, extending and retracting their tentacles. It is not known whether these juveniles are true parasites – *i.e.* juveniles of another species drawing nutrition from the host medusa, or whether they are offspring being brooded. *Solmissus* is one of the most numerous genera of medusae in Monterey Bay, and this is the first report of parasites on members of that genus in the California Current system.

Key words: Hydromedusae, Narcomedusae, *Solmissus*, parasites, brooding, midwater medusa, California Current, submersible collection

INTRODUCTION

Narcomedusae are a major group of open ocean cnidarians that are found in deep water. *Solmissus incisa* is a mesopelagic or bathypelagic narcomedusa living below 400 m (Larson, *et al.*, 1991). Narcomedusae have separated their tie from the benthos with no well-known associated stage other than parasitic juveniles. Parasitic associations can be very complex in the Phylum Cnidaria and some taxa brood their young in specialized pouches within the adult epidermis. Narcomedusae are dioecious and some larvae develop directly while others go through planula-actinula-medusa stages, but the ecology of some stages is complicated by parasitism by the actinula (Hyman, 1940). The egg may devel-

op in the mesoglea or gastric pouches of the parent, sometimes with the aid of a nurse cell. Development may then proceed directly in the parent from egg to actinula; actinulae bud off other actinulae that later transform into medusae. Or planulae may leave the parent entirely and associate with other hydromedusae as a parasite, attaching to the manubrium or the subumbrella (Hyman, 1940). Very little is known about the complicated parasitic and/or brooding characteristics of deep-sea medusae. *In situ* observations of live organisms are recent and information about swimming behavior and associations of narcomedusae with other pelagic organisms has been very difficult to obtain from preserved specimens.

Narcomedusae generally are difficult to sample, both because they are delicate and they live in deep water. Sampling with submersibles and by SCUBA is imperative to successfully collect these gelatinous

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organisms without significant damage to their fragile bodies (Mackie and Mackie, 1963; Mills and Goy, 1988; Larson, *et al.*, 1989, 1991). Narcomedusae are called 'holoplanktonic', *i.e.* always floating freely; however, the developmental cycle may include parasitism of early life history stages on adult medusae, in stomach pouches or in the coelomic cavity (Bouillon, 1987). When parasitizing adult medusae, larvae remain associated with planktonic organisms so, in a wide sense, they are holoplanktonic. Our knowledge of narcomedusae life histories is limited, as fewer than ten species have a known life cycle. Development in narcomedusae is poorly understood because the parasite and host body forms are complex and most are still not identified (Bouillon, 1987).

Not only are narcomedusae parasitic on other hydromedusae but also, many pelagic cnidarians commonly have associations with juvenile organisms in separate, non-related taxa. For example, arthropod crustacean, *Cancer gracilis*, juveniles and megalopas are adapted to associate with or 'hitch-hike' on the large scyphomedusa *Chrysaora fuscescens* in Monterey Bay and drop off the bell when they are transported close to shore (Graham, 1994). Observations of parasitic hyperiid amphipods living a benthic-like existence on medusae are also numerous. Hyperiid amphipods are hypothesized to be the descendents of benthic crustaceans which have developed an association with a pelagic substratum, gelatinous zooplankton (Laval, 1980). Hyperiid can be difficult to study because they leave their host when they are collected with nets (Laval, 1980). Fortunately, such associations can be documented using ROV collection, which usually does not cause hyperiids to flee. The complex associations of internal and external parasitic larvae, from the same or separate taxa, must be studied *in situ* and with gently collected, fresh specimens because with brooding and parasitism, the association can be fragile and require delicate handling of specimens.

MATERIALS AND METHODS

The collection was made from the 33.5 m Research Vessel *Point Lobos* based in Moss Landing, California and its remotely operated vehicle (ROV) *Ventana*, both owned and operated by the Monterey Bay Aquarium Research Institute (MBARI). MBARI has been collecting and surveying Monterey Bay with

this submersible since 1989. The *Ventana* is an ISE Hysub 40-1850 powered by a 40hp electro/hydraulic power pack and equipped with low-impact collection devices, including detritus and suction samplers (Robison, 1993). ROV pilots on the ship maneuver the *Ventana* while video images and oceanographic data are relayed in real time to the scientists on the ship through optical fibers in the umbilical cable. A Sony BetaCam BVM30 is used on the ship to videotape each dive in its entirety, allowing subsequent viewing and analysis onshore. The study site was located over the axis of the Monterey Submarine Canyon at 36° 42' N, 122° 02' W where the water column depth is 1600 m. The submarine canyon begins not far from the Moss Landing Harbor mouth and cuts through the continental shelf, allowing the study of mesopelagic species within 5 km of shore in central Monterey Bay.

RESULTS

A single specimen (specimen 1) of *Solmissus incisa* was collected on 23 October 1996 at 230 m depth in Monterey Bay, California. As the vehicle approached the swimming medusa, the velum and the oral surface were directed upward. The tentacles were rigidly outstretched below the bell with distal ends curved outwards (Fig. 1a). The velum pulsed

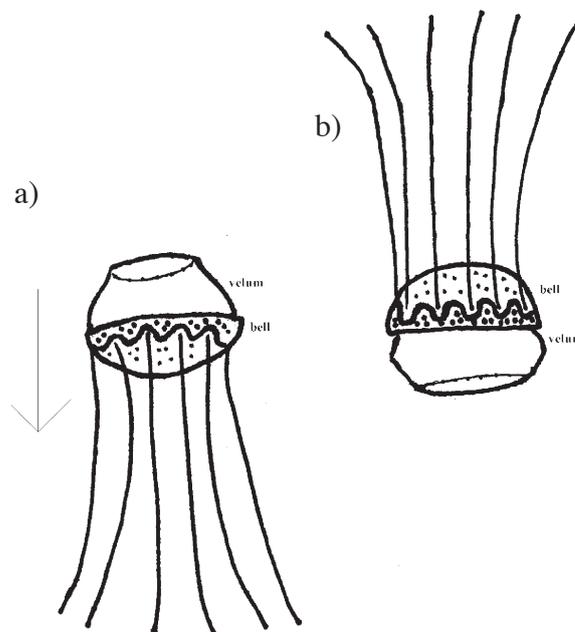


FIG. 1. – a) *S. incisa* swimming. The arrow shows the downward direction of movement. The velum is pulsing above the bell; b) Position when *S. incisa* stops pulsing and rotates in the water column so the velum is below the bell.

consistently, propelling the medusa down, yet when the vehicle paused to videotape, the medusa stopped pulsing, rotated slowly around until its oral surface was downward, essentially suspended 'upside down' from the original position in which it was viewed (Fig. 1b). The medusa remained in this position for one minute and then turned over and began pulsing again. Video images were recorded of this specimen *in situ* for three minutes.

With the ROV video camera, it was possible to see a hyperiid amphipod associated with the surface of the bell. At first, a number of similarly sized, circular objects were seen concentrated on the bell. On closer observation, I saw two distinct types of objects, both appeared to be inside the organism, though their exact location was difficult to discern. Randomly dispersed, clear bubbles were spread along the entire surface of the bell, later found to be oil droplets. Distributed across three lappets were separate, concentrated opaque spheres, later found to be "parasites." This medusa was collected gently by the ROV in the suction sampler for closer examination at the onshore laboratory.

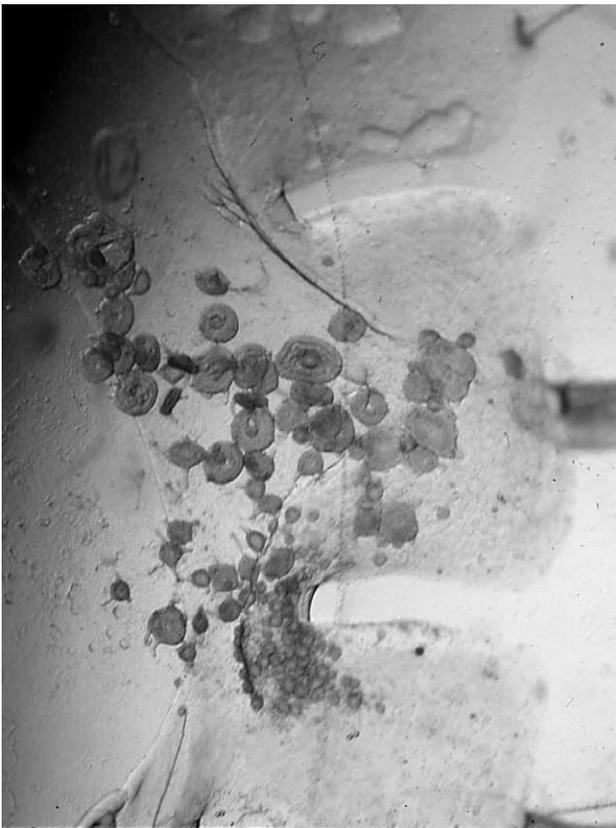


FIG. 2. — Cluster of parasites in different developmental stages on the rectangular lappets of *S. incisa* collected in Monterey Bay. Tentacles and a mouth are visible on more developed individuals. Oil droplets are visible as clear bubbles on the upper lappet.

The specimen (1) of *Solmissus incisa* with opaque, spherical bodies was collected in close proximity to three other specimens of *Solmissus incisa*. The first of these was seen at 223 m pulsing regularly with rectangular lappets and an amphipod on its surface, the second and the third were smaller specimens at 228 m and 264 m with no obvious amphipods. As the vehicle descended, at least six more *Solmissus incisa* were observed. I did not see any of the clear bubbles or opaque spheres on the bells so none of these medusae were collected. From the video transmission, I did not see eggs or reproductive products on any of these medusae, even though eggs can normally be seen with the ROV camera.

In the laboratory, the specimen (1) of *S. incisa* was found to have a 50 mm bell diameter and twenty tentacles with purplish hue. It appeared to be full-grown and possibly of reproductive size. The tentacles were approximately 60-70 mm long and 8 mm apart. There were twenty stomach pouches with an oval outline, longer than wide. The marginal lappets were rectangular in shape, each with an average of three statocysts. The mouth was a small, simple opening in the center of the bell. The specimen and associated parasites were photographed in the laboratory with a Nikon camera attached to a Zeiss dissecting scope at 1x power.

The opaque spheres or "parasites" were concentrated on one side of the bell (Fig. 2) and the epidermal, hyperiid amphipod was on the oral side of the medusa. There were approximately 45 individual parasites in different development stages and they ranged in size from 0.2-1.0 mm in diameter, not including small tentacles that were extended away from the body (Fig. 3). They each had 2-6 tentacles and smaller protrusions around the circumference that looked like developing tentacles and each had a small mouth opening in the center. No statocysts were visible. No food particles were seen in the developing parasites but some pigment gave them a distinguishable visual texture. The parasites did not look like food items for the adult medusa, as they were not being digested nor were they encapsulated in mucus. The parasites resembled juvenile cnidarians in body form, having tentacles, a small mouth and a rounded bell (Fig. 4).

With a dissecting scope, it was possible to see that the opaque spheres were constantly moving. The bodies could extend and contract tentacles, moving past one another to a different position. They reached out with a tentacle, touched another

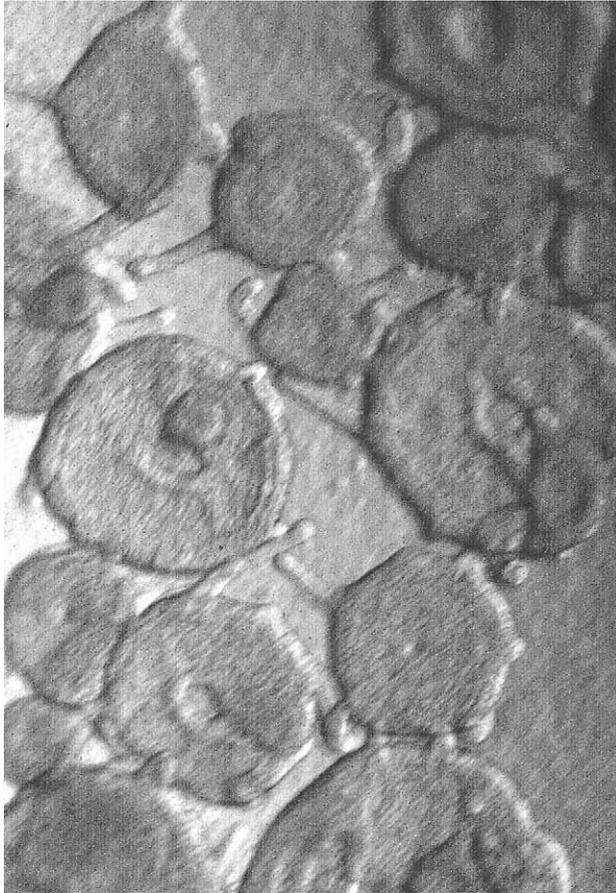


FIG. 3. – Numerous parasites (0.5-1.0 mm diameter) on *S. incisa* showing different developmental stages.



FIG. 4. – A single parasite (1.0 mm diameter) with tentacles of different lengths. The mouth opening is visible in the center of the body.

individual and contracted the tentacle. They seemed to move freely inside the medusa and were not attached to each other or the medusa. They glided using their tentacles to pull them along inside the medusa. Using forceps to peel back the thin, transparent, epidermal tissue layer on the oral side of the medusa, I removed one fairly well developed specimen from the outer edge of the bell near the stomach cavity. It was comparatively large and had six tentacles. This individual maintained its form for several days off the host body and developed further but not into an identifiable species.

DISCUSSION

Life histories and development

Narcomedusae have lost their connection to inorganic, benthic substrates and, unlike most of their benthic-dependent hydrozoan relatives, the entire narcomedusan life cycle occurs in the pelag-

ic realm. However, there is another way to maintain an association with a substrate: utilize another living organism during a larval stage of the life cycle. The life cycles of several parasitic narcomedusae were described by Bouillon (1987), including revisions of previous accounts of their embryonic and larval development. He noted that narcomedusae consistently maintain close associations with other organisms, *e.g.*, other narcomedusae, anthomedusae, leptomedusae, trachymedusae and scyphomedusae in the mesopelagic zone. The life cycle of narcomedusae is complicated and the most remarkable parasitism is shown by some of the developing stages, which can be parasitic on other planktonic medusae (Russell, 1953). Two genera of narcomedusae produce an amoeboid cell stage that can be either self-parasitizing or which can inhabit the mesoglea of a trachymedusa. The amoeboid cells are associated with a nurse cell and develop into tentacled larvae, which may develop directly into free-swimming medusae or bud off similar larvae which

develop into medusae (Russell, 1953). The parasitic stage may also be a pelagic hydroid that can bud new medusae or form an asexually produced piece of tissue, the stolon (Mills, 1991).

Another example of complex life histories in narcomedusa is polyembryony, or embryonic budding when one sexually produced embryo buds into many genetically identical buds that are then brooded by the adult (Craig *et al.*, 1997). It is difficult to identify the diverse stages of narcomedusa parasites or brooded young, even after they are liberated from host medusae. Although they are no longer tied to the benthos, narcomedusae may still alternate between substrate-adapted morphologies, associated with other organisms, and pelagic stages, which are free living.

Brooding/parasitism

It is difficult to recognize the diverse stages of narcomedusae parasites, as they are small, not well developed and enclosed in tissue and therefore, are undoubtedly significantly underreported. Standard observation and collection techniques for deep-sea medusae can damage adult specimens and parasites beyond recognition (Larson, *et al.*, 1991). In the Mediterranean, the behavior of *Solmissus albescens* and *Solmissus marshalli* (Mills and Goy, 1988) was examined *in situ* and no parasites on the bell were reported. Parasites were not observed in studies of representatives of eight narcomedusan genera in the NW Atlantic, Arctic and Antarctic (Larson, *et al.*, 1989) or on medusae in northwestern Atlantic mid-water (Larson *et al.*, 1991), when examined *in situ*. However, many small parasitic narcomedusae were reported developing in the stomach pouches of two *S. albescens* specimens in a manned submersible study (Mills, *et al.*, 1996) but these specimens were not examined further.

Medusae parasitic on narcomedusae have been reported in the literature, but little is known about their development. Hyman (1940) briefly noted larval and juvenile medusae in the stomach cavity of *Solmissus* found in Puget Sound but reported nothing more about them. Bouillon's (1987) list of narcomedusae parasites and hosts does not include *S. incisa* as a host. Larval and juvenile *Cunina*, a narcomedusa, have been found in the stomach cavities of other narcomedusae hosts, including *Solmundella*, *Pegantha* and *Cunina* (Bouillon, 1987). Perfectly formed young medusae were found in a bowl that adult *S. marshalli* had been kept in for three days.

The young medusae were 3 mm wide but their taxonomic identity was not determined (Mackie and Mackie, 1963). Developing larvae have been reported in an adult specimen of *S. marshalli* collected in Puget Sound (Mackie and Mackie, 1963). In most studies, juveniles on medusae were more commonly considered parasites than brooded young, but more medusae must be collected *in situ* and reared in the laboratory to determine the nature of these associations and to exclude the possibility that the "parasites" are brooded offspring of the host or parent.

Advantages to brooding and "parasitism" include protecting and enhancing the survival of young by providing a safe, internal habitat for development. In other cnidarian taxa, brooding is the major function around which specialized reproductive structures have arisen (Campbell, 1974). For example, some scyphozoan embryos are brooded in special pouches in the folds of the mouth lobes, where they develop into ciliated planula larvae (Pearse *et al.*, 1987). Individual hydromedusae are dioecious and eggs may be freely spawned or brooded, retained for fertilization and development to larval stages (Mills and Strathman, 1987). In some jellyfish, brooding may occur internally within the gastric cavity or externally, following a free-swimming stage, with planulae brooded on a parent of a different species (Campbell, 1974). In many species, brooding consists of no more than harboring free-floating larvae. Internal brood chambers exist in platyctenid ctenophores yet there is no evidence that they receive nourishment from the parent. The brooding embryos may be in the same stage of development or several different stages simultaneously and have been observed "escaping" through the adults' epidermis (Pianka, 1974).

S. incisa specimen collected in Monterey Bay

Brooding in cnidarians is commonly reported (Hyman, 1940; Campbell, 1974; Pearse *et al.*, 1987), especially for scyphozoans and anthozoans; however, for narcomedusae, an association with young life history stages is commonly reported as "parasitism" (Bouillon, 1987). From the diversity of sizes and shapes I saw on this specimen, I believe these "parasites" were successfully developing on their host. In the specimen from Monterey Bay, each parasite was independent, moving separately, not attached to the medusa. I cannot exclude the possibility that the "parasitic" juveniles developing in *S. incisa* were possibly juveniles brooding within the

adult/parent tissue. They were protected under a thin epidermis and could possibly have drawn nutrition from the adult through gastric secretions or by intercepting digesting amoeboid cells. Some were primary larvae, actinula-like with a mouth and at least two tentacles and when developed, the young medusa should leave the host, possibly through the mouth as they are developing within the gastric cavity.

I was able to view the living, healthy specimen with an ROV, which allowed me to examine behavior and physical characteristics not obvious unless specimens are viewed directly underwater. Close ROV observation gave me the opportunity to observe the size and distribution of parasites on the bell and collect the medusa without damaging its tissue. The parasites looked very similar to the oil droplets when viewed *in situ* and therefore could be easily misidentified. In the laboratory, I was able to distinguish these parasites from prey-derived oil droplets that indicate the medusa had fed recently (Larson *et al.*, 1991). The parasites resembled very early stages (54 hour embryos) of a hydrozoan with direct development (Freeman, 1983). Furthermore, the internal, cnidarian-like parasites are so small, that after a specimen is preserved and the color and/or texture is lost, the parasites may even then be too difficult to see or distinguish from oil droplets or pigment spots in the laboratory. Thus, making many observations of live, undamaged specimens aids in recognizing the parasitic association. It is much more effective to see such delicate associations with *in situ* viewing because not all medusae have parasites. Specimens with suspected parasites require gentle collection and further lab examination to verify the presence of juvenile cnidarian-stages versus oil droplets or external hyperiid parasites.

The swimming behavior of the *Solmissus incisa* reported here might favor contact with parasites and increase the encounter rate. The swimming speed and direction of *S. incisa* was affected only slightly by the presence of the ROV. *Solmissus marshalli* has been reported to be a weak swimmer with only the outer part of the umbrella and the velum contracting (Mackie and Mackie, 1963). *Solmissus albescens* was observed in the western Mediterranean with a submersible and was almost always actively swimming, regardless of the time of day. The tentacle positions during locomotion in *S. albescens* (Mills and Goy, 1988) differs slightly from those in the *S. incisa* specimen in Monterey Bay, although these two species are very nearly related (Russell, 1953).

Postures for *S. albescens* include holding the tentacles up above the bell with tentacle ends slightly recurved or tentacles held straight down below the bell (Mills and Goy, 1988). The swimming behavior of *S. incisa* is unique and similar behavior has not been reported for other narcomedusae or *Solmissus* species: *S. incisa* holds its tentacles rigidly outstretched, arching below the bell while the velum is opening and closing above, propelling the medusa down in the water column. Continuous pulsing of the velum brings a backwash of water against the underside of the bell, allowing a greater volume of water to flush the oral side of the medusa thus possibly increasing contact with free floating "parasitic" organisms. This posture may make it easier for parasites to be pushed or sucked onto the surface of the bell and then into the stomach cavity, where they may remain during development.

This sighting of cnidarian-like parasites in association with *S. incisa* is rare. In Monterey Bay, where *S. incisa* is common, numerous specimens have been collected over the years and yet none have been reported to have parasites. If these parasites are developing narcomedusae, this modification of the holoplanktonic life cycle facilitates larval development in a protected environment, in an adult medusa of the same or different genus. Larvae able to parasitize adult medusae and develop in a semi-protected environment within the epidermis should continue to develop until being liberated as medusae. Other hydrozoans, including hydroids and siphonophores, accomplish this substrate association within self-colonies; in narcomedusae, brooding or parasitism provides an association with a safe, organic substrate and ensures release in a suitable habitat.

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