Dear Author:

Please find attached the final pdf file of your contribution, which can be viewed using the Acrobat Reader, version 3.0 or higher. We would kindly like to draw your attention to the fact that copyright law is also valid for electronic products. This means especially that:

- You may not alter the pdf file, as changes to the published contribution are prohibited by copyright law.

- You may print the file and distribute it amongst your colleagues in the scientific community for scientific and/or personal use.

- You may make your article published by Springer-Verlag available on your personal home page provided the source of the published article is cited and Springer-Verlag is mentioned as copyright holder. You are requested to create a link to the published article in Springer's internet service. The link must be accompanied by the following text: The original publication is available at http://link.springer.de or at http://link.springer-ny.com . Please use the appropriate URL and/or DOI for the article. Articles disseminated via SpringerLink are indexed, abstracted and referenced by many abstracting and information services, bibliographic networks, subscription agencies, library networks and consortia.

- Without having asked Springer-Verlag for a separate permission your institute/your company is not allowed to place this file on its homepage.

- Please address any queries to the production editor of the journal in question, giving your name, the journal title, volume and first page number.

Yours sincerely,

Springer-Verlag

K.A. Raskoff

Foraging, prey capture, and gut contents of the mesopelagic narcomedusa *Solmissus* spp. (Cnidaria: Hydrozoa)

Abstract Narcomedusae are the most common group of medusae in the mesopelagic depths of Monterey Bay, California. Numerous capture events of various prey taxa were recorded in situ and analyzed using the Monterey Bay Aquarium Research Institute's remotely operated vehicle "Ventana". In situ video analysis of the stomach contents of 82 *Solmissus incisa* and *S. marshalli* revealed 88 identifiable prey items. Most (88%) were gelatinous animals. Of these gelatinous prey, 60.3% were ctenophores, 20.5% were cnidarians, 12.8% were salps, 3.8% were chaetognaths, and 2.6% were polychaetes. Euphausiids accounted for 11.4% of the diet, but they were probably captured adventitiously, as the gut contents of ctenophore prey. The tentacle-first foraging behavior of the narcomedusae is an effective way to capture large, comparatively fast-moving prey, because the fluid disturbance caused by swimming is decoupled from the area of prey capture. This behavior contrasts with the prevailing models of feeding behavior in medusae. Stealth predation may be the dominant mode of capturing prey by medusae in the mesopelagic depths of the oceans.

Introduction

Solmissus is a cosmopolitan genus of narcomedusae with populations centered in the warm and temperate waters of most of the world's oceans (Mayer 1910; Kramp 1968). It is generally thought to be a eurybathic genus, spanning much of the water column, although capture

K.A. Raskoff
Monterey Bay Aquarium Research Institute,
7700 Sandholdt Rd, Moss Landing, CA 95039, USA

E-mail: kraskoff@mbari.org
Tel.: +1-831-7751895
Fax: +1-831-7751620

depths vary with geographic region and species. There are currently three commonly recognized species of *Solmissus*: *S. incisa* (Fewkes, 1886), *S. marshalli* Agassiz and Mayer, 1902 and *S. albescens* (Gegenbaur, 1857) (Kramp 1968). As with most of the narcomedusae, *Solmissus* spp. are thought to only have direct development, without a benthic polyp (Meyer 1910; Russell 1953; Kramp 1968; Bouillon 1987). Two species of *Solmissus* are currently recognized in Monterey Bay, California: the common *S. incisa* and the less abundant *S. marshalli*. *S. incisa* is often the most numerous medusa in the upper 700 m of the mesopelagic waters in Monterey Bay, with encounter rates over 50 medusae h^{-1} of ROV observation (Raskoff 2001a). As cnidarian predators, their numbers are surpassed only by *Nanomia bijuga*, a physonect siphonophore (Robison et al. 1998) and some calycophoran siphonophores (Silguero and Robison 2000).

Although there have been previous studies dealing with the swimming and foraging behaviors of this genus (Gladfelter 1970; Madin 1988; Mills and Goy 1988; Larson et al. 1989), there is little published information on prey capture and gut contents. Due to the fragile nature of most medusae, it is not possible to obtain reliable gut content data from towed net systems. The stomachs of narcomedusae typically break in the nets, spilling their contents, and medusae are also known to ingest prey items while in the net (Hamner et al. 1975; Youngbluth and Båmstedt 2001). The only reliable methodology available for assessing the gut contents of many planktonic predators is in situ observation combined with non-destructive sampling. Many of the most important contributions towards understanding the ecology of gelatinous organisms over the last 50 years have been accomplished through in situ observations, utilizing "blue water" SCUBA methods, remotely operated vehicles (ROVs), and submersibles (Pérès 1958; Hamner et al. 1975; Hamner 1985; Mackie 1985; Madin 1988; Mills and Goy 1988; Larson et al. 1989, 1991; Hamner and Robison 1992; Mills et al. 1996; Robison et al. 1998; Purcell et al. 2001; Raskoff 2001a,b).

S. incisa and *S. marshalli* from Monterey Bay are well suited for in situ video gut content analysis due to their relatively large size (up to 17 cm in diameter) and their transparent gut cavity. Prey can be easily seen and identified inside the gastrovascular cavity. Mills and Goy (1988) observed *S. albescens* from a submersible in the Mediterranean and recorded the first in situ observations on its swimming and feeding behavior. They were able to document the characteristic tentacle-first foraging behavior of *Solmissus* spp. and provided a first in situ report of gut contents (see Table 1). Larson et al. (1989) reported on the tentacle postures of several

Table 1 Known prey items of *Solmissus* species

Solmissus species	Prey taxon	*n*	Location	Reference
S. albescens	Ctenophora			
	Comb plate	1	Alboran Sea	Mills et al. (1996)
	Euplokamis stationis	1	Alboran Sea	Mills et al. (1996)
	Gastropoda			
	Cavolinia	Several	Ligurian Sea	Mills and Goy (1988)
	Thaliacea			
	Salpa fusiformis (chain)	1	Alboran Sea	Mills et al. (1996)
	Unidentified salps (eight)	1	Alboran Sea	Mills et al. (1996)
	Osteichthyes			
	Fish egg?	1	Alboran Sea	Mills et al. (1996)
S. marshalli	Ctenophora			
	Beroid	1	Monterey Bay	Present study
	Cydippid	2	Monterey Bay	Present study
	Unidentified ctenophore	3	Monterey Bay	Present study
	Hydromedusa			
	Euphysa sp.	1	Friday Harbor	Mills and Goy (1988)
	Siphonophora			
	Nanomia bijuga	1	Monterey Bay	Present study
	Thaliacea			
	Unidentified salp	1	Monterey Bay	Present study
S. incisa	Ctenophora			
	Beroe cucumis	2	Monterey Bay	Present study
	Cydippid	12	Monterey Bay	Present study
	Hormiphora californensis	4	Monterey Bay	Present study
	Pleurobrachia bachei	2	Monterey Bay	Present study
	Charistephane fugiens	1	Monterey Bay	Present study
	Unidentified ctenophore	19	Monterey Bay	Present study
	Unidentified ctenophore	1	Dry Torugas	Mills and Goy (1988)
	Unidentified ctenophore	1	Bahamas	Larson et al. (1989)
	Hydromedusa			
	Aegina citrea	1	Monterey Bay	Present study
	Haliscera conica	2	Monterey Bay	Present study
	Mitrocoma cellularia	3	Monterey Bay	Present study
	Unidentified medusa	3	Monterey Bay	Present study
	Siphonophora			
	Nanomia bijuga	4	Monterey Bay	Present study
	Unidentified siphonophore	2	Monterey Bay	Present study
	Unidentified calycophoran	1	Monterey Bay	Present study
	Annelida			
	Poeobius meseres	2	Monterey Bay	Present study
	Crustacea			
	Euphausia sp.	10	Monterey Bay	Present study
	Chaetognatha			
	Unidentified chaetognath	3	Monterey Bay	Present study
	Thaliacea			
	Unidentified salp	4	Monterey Bay	Present study
	Unidentified salp chain	6	Monterey Bay	Present study

narcomedusae, including *S. incisa*, using blue water diving and submersible observations. They found the same generalized tentacle positions described by Mills and Goy (1988).

Detailed microscopic studies of narcomedusae tentacles and nematocysts have shown that nearly all of the nematocysts are located on the outer side of the tentacles, which would be the area contacted by the prey in virtually all tentacle positions (Mills and Goy 1988). The shafts of narcomedusan nematocysts have an unusual pattern of five spine-rows, not found in any other cnidarian group (Purcell and Mills 1988; Carré et al. 1989). These long, heavily spined shafts appear to be well adapted for the capture of gelatinous organisms, surmised to be their primary prey (Mills and Goy 1988; Purcell and Mills 1988; Carré et al. 1989; Mills et al. 1996). All sizes of *S. marshalli* and small specimens of *S. incisa* also have small clusters of nematocysts on their exumbrellar surface.

Several recent studies have proposed models of prey capture by medusae based on their body type. Oblate medusae (flattened bell) or prolate medusae (tall bell) are hypothesized to have foraging modes that can be predicted from their general body shape (Costello 1992; Costello and Colin 1994, 1995; Colin and Costello 1996; Ford et al. 1997). According to these hydrodynamic models, medusae with flattened, oblate bells (like *Solmissus*) are thought to use swimming-generated flow to entrain slow-moving prey into fast-moving currents that pull the prey through the tentacles. These models have proved highly instructive in predicting prey selectivity for large, epipelagic scyphomedusae (Sullivan et al. 1994), but may not be applicable for the majority of meso- and bathypelagic medusae which forage in a manner not addressed in these studies. The present study addresses foraging by *Solmissus* spp. and relates their behavior to prior models of prey capture and fluid flow around feeding medusae. Observations were made of in situ feeding events and video gut content analyses of 82 individual *S. incisa* and *S. marshalli*.

Materials and methods

All observations were made at the MBARI midwater time-series site, located at 36°42.00′N; 122°02.00′W, over the axis of the Monterey Canyon in 1600 m of water (Fig. 1). The R.O.V. "Ventana" has completed over 400 mesopelagic dives at the MBARI midwater site; dives were typically made bimonthly. The "Ventana" is an ISE Hysub with a variety of sensors and modifications used for midwater research (Robison 1993). The video system employed a broadcast-quality, three-chip Sony DXC-3000 (1988–1999) and a Sony high-definition HDC-750A camera with an HDCA-750 back (1080i format) (1999–present). Video was recorded on high-quality BetaCam or HDTV tapes for subsequent analysis and annotation. Animals were captured for laboratory experimentation in 7.5 l "detritus samplers" (Youngbluth 1984; Robison 1993).

More than 2000 h of video tape from midwater dives in Monterey Bay were annotated by the MBARI video laboratory staff from 1988 to 1996. Possible feeding events were registered and entered into the MBARI annotation database. This database was then queried, and the original video was re-analyzed to confirm the feeding events and the organisms involved. From 1997 to the present, feeding events were recorded from the live video during midwater ROV dives by the author.

There are two macro-scale morphological differences between the two species of *Solmissus* studied: *S. incisa* has a larger maximum size and a greater number of tentacles than *S. marshalli* (summarized in Kramp 1968). Despite these differences, both species were found to consume the same prey items when medusae of similar size were compared. Thus, small *S. incisa* were found to eat the same prey as the largest *S. marshalli*. Therefore, in this study, both species of *Solmissus* were combined for gut content analysis.

Fluid flow around foraging medusae was examined in the laboratory ashore. Specimens of *Solmissus* spp. were collected with the ROV and brought back to the laboratory within 3 h. Medusae (*n* = 10) were placed into 26 cm (width)×100 cm (diameter) plank-

Fig. 1 Map of Monterey Bay showing the MBARI midwater time-series site (MWTS), in 1600 m of water over the axis of the canyon. Depth contours are in 500-m increments
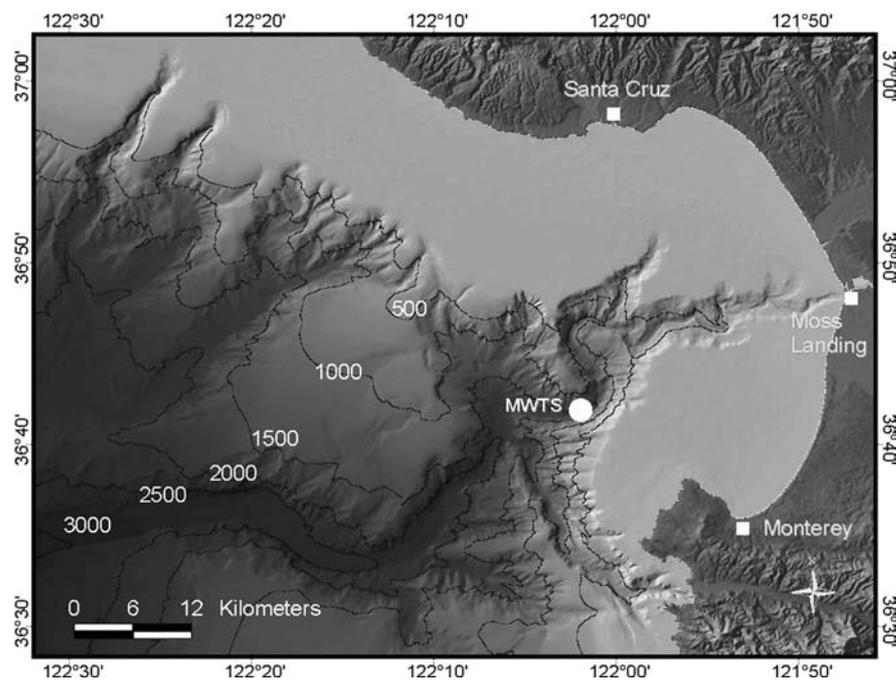
tonkreisels (Hamner 1990) in a dark, temperature-controlled room. Partially hydrated, neutrally buoyant *Artemia* cysts (ca. 300 μm in diameter) were used as particles for visualizing fluid flow around the swimming medusae. Side lighting with low-intensity white or red light was used to illuminate the particles. Swimming was videotaped with a Canon XL-1 digital video camera, both with and without an image intensifier (Astroscope 9350 VL, Electrophysics). Only video segments in which the medusae moved straight up or down were used for analysis. An extremely shallow depth of field was maintained so that only particles that were moving in the same plane as the swimming medusa were in focus and measured. Video segments of 1-s length (30 frames) were frame-grabbed and brought into Scion Image analysis software (version 4.0, Scion Corporation), and particle paths were recorded frame by frame.

Results

Foraging behavior

In situ video observation with the R.O.V. "Ventana" allowed for detailed study of several thousand individual *Solmissus*. Three basic foraging postures were observed, regardless of spatial orientation (Fig. 2). The first of these postures, "A", was with the tentacles foremost in "ramming" position. In this arrangement the tentacles were held up above (aboral to) the bell, parallel to the swimming axis of the medusa, ca. 45–90° off the plane of the umbrella (Fig. 2A). This was the most common position for *Solmissus* spp. of small to medium size (< 8 cm in diameter), the most numerous size class, with over 85% of this size class found in position "A". The second posture, "B", with tentacles perpendicular to the swimming axis, in plane with the umbrella, was most often seen in very large *S. incisa* (> 10 cm), with over 70% of this size class found in position "B" (Fig. 2B). In the third posture, "C", tentacles were held down below the bell, parallel to the swimming axis (Fig. 2C). While it was not uncommon to find large *S. incisa* in this latter posture (26%), it was very rare (< 2%) in the smaller *S.*
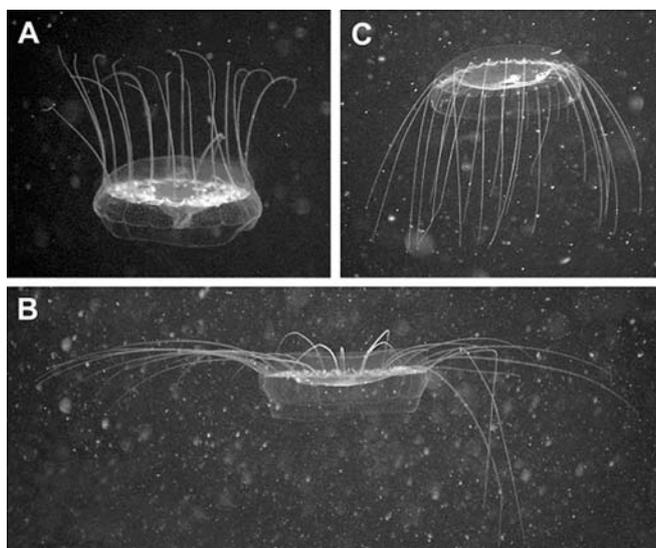
incisa and in *S. marshalli* of any size. In 24% of medusae in posture "A" the tentacles were modified into an amphicoronate pattern, where the tentacles would alternate between 90° off the plane of the bell (as seen in Fig. 2A) and 135° from the plane of the bell, pointing in towards the top of the umbrella, effectively creating a cone of tentacles within a cylinder of tentacles. Medusae were occasionally observed showing a combination of postures, with individual tentacles or groups of them oriented in different directions, but this was rare. It is worth noting that virtually all *Solmissus* were swimming when the ROV came upon them, with only the very large *S. incisa* sometimes encountered in an inactive state. In addition, medusae were found in all orientations, with individuals found swimming in all directions; however, swimming up or down were the two most common orientations. Video segments showing the common tentacle positions can be found on the internet at http://www.mbari.org/midwater/solmissus/solmissus. htm.

Prey capture

Nine prey capture events were observed in situ over the course of this study. Figure 3A–E shows a feeding

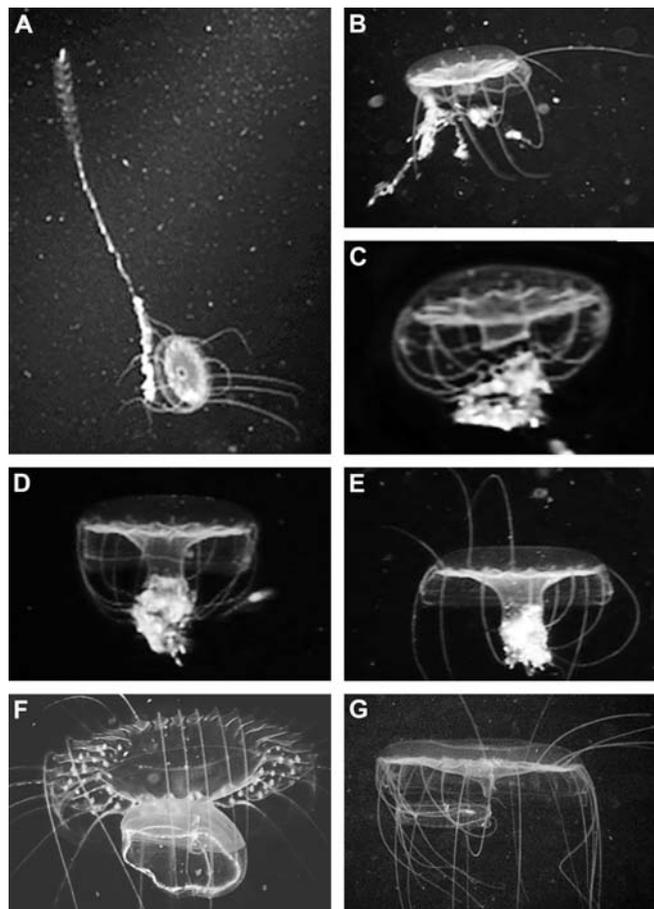**Fig. 2A–C** *Solmissus* spp. The three principal tentacle postures (**A–C**)

Fig. 3A–G *Solmissus* spp. Prey capture and consumption: *S. marshalli* catching and consuming *Nanomia bijuga* (**A–E**); *S. incisa* with *Mitrocoma cellularia* (**F**) and a large salp (**G**)

sequence which lasted ca. 40 min from capture to complete engulfment of the prey. Figure 3A shows a specimen of *S. marshalli* with its tentacles attached to the lower siphosome of a physonect siphonophore, *Nanomia bijuga*. In Fig. 3B the medusa holds the siphosome, while the nectosome of the siphonophore has separated from its siphosome and escaped. In Fig. 3C the medusa has compacted the siphonophore and moved it toward the mouth, which extends toward the prey. In Fig. 3D the prey is partially ingested, with the mouth of the medusa slowly moving over the prey, pulling the food into the stomach. In Fig. 3E the food is almost completely ingested, and the medusa has extended several tentacles above the bell. Soon thereafter, the medusa resumed swimming. Other feeding events observed with *S. incisa* feeding on the hydromedusa *Mitrocoma cellularia* and various salps followed this same general pattern (Fig. 3F, G). In general, swimming ceased during ingestion, although occasional pulsations of the bell appeared to help the mouth contact the prey. Once the prey was firmly grasped by the mouth the medusa resumed swimming and the tentacles resumed their position above the bell.

Prey items

Over the course of this study, over 4000 observations were made of *Solmissus* spp. Of these, 82 individual *S. incisa* and *S. marshalli* were found with prey in their gastric cavities. From these 82 individuals, a total of 88 prey items were identified. Figure 4 shows the contribution of each prey type to the total. Gelatinous taxa comprised 88.6%. Of these gelatinous items, 60.3% were ctenophores, 20.5% were cnidarians, 12.8% were

salps, 3.8% were chaetognaths, and 2.7% were polychaetes. Euphausiids accounted for 100% of the non-gelatinous prey items (11.4% of the total). Of the 82 medusae, only six were found with more than one item in their gastric cavities (counting salp colonies as a single item). The data show that roughly 2% of the *Solmissus* in the study area had prey in their gastric cavity.

Many of the prey items were identified to genus or species. In Table 1 the identities of the prey items found in this study, and in other investigations are listed. Of the identified ctenophores, cydippids were much more common than beroids (88% and 12%, respectively). Cydippid ctenophores identified to species included: *Hormiphora californensis* (Torrey, 1904), *Pleurobrachia bachei* A. Agassiz, 1860 and *Charistephane fugiens* Chun, 1879. Beroids identified to species were all *Beroe cucumis* Fabricius, 1780.

The cnidarians were represented by two main groups, medusae and siphonophores (60% and 40%, respectively). The medusae were typically large and distinct prey items, and these were often identified to species. *Mitrocoma cellularia* (Agassiz, 1865), *Haliscera conica* Vanhöffen, 1902 and *Aegina citrea* Eschscholtz, 1829 were identified in *Solmissus* spp. stomachs. Siphonophores are more easily deformed than are medusae and thus were more difficult to discern in the gut cavity. Nevertheless, on several occasions, captures of siphonophores were witnessed, allowing for positive identification to order, and, occasionally, to species. Four individuals of the physonect *Nanomia bijuga* and one calycophoran siphonophore were observed during capture and ingestion. Two additional physonect siphonophores were observed in the stomachs of *S. incisa*, but these could not be identified to genera.

Fig. 4 *Solmissus* spp. Percentage of prey items found in *S. incisa* and *S. marshalli* (*n* = 88)
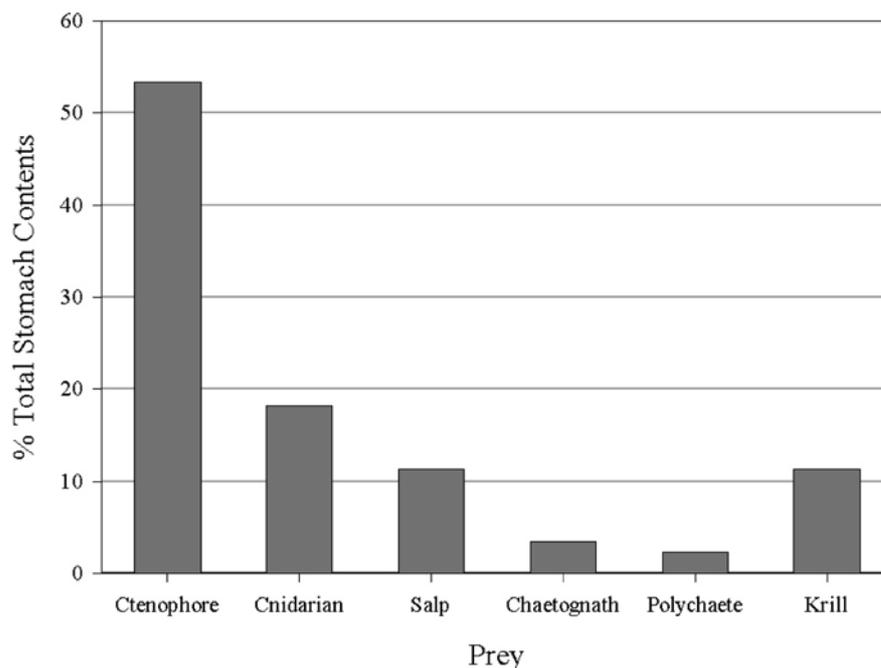
Salps were also observed at all stages of capture, ingestion and digestion. On six occasions, entire salp chains (4–20 individuals) were observed at various stages of consumption. Two chaetognaths were observed being captured and ingested, and another was observed in the gut cavity of *S. incisa*. The common midwater polychaete *Poeobius meseres* (Heath, 1930) occurred twice in stomachs of *S. incisa*. Video, which shows the capture and digestion of various prey by *Solmissus* spp., is available on the internet at http://www.mbari.org/midwater/solmissus/solmissus.htm.

Fluid flow

To investigate the flow of fluid around a swimming *Solmissus*, small freshly captured *S. incisa* were examined in the laboratory. There were no observed differences in swimming behavior under the white or red light. The particle traces from fifteen 1-s segments (30 video frames each), overlaid in proper scale and orientation, are shown in Fig. 5. Flow appeared to be laminar above the bell, showing only slight perturbation even when within 1 cm of the moving bell. These particles passed untouched through the tentacles. Particles flowed into an area of turbulence below the bell, and the particles were often entrained within toroidal vortices. These turbulent zones were caused by the swimming motion of the bell and the undulations of the velum. These flow patterns show that there was no appreciable turbulence above the exumbrellar surface of the bell or through the tentacles of the swimming medusa. This is true for both tentacle postures "A", with the tentacles held above the bell, and "B", with the tentacles held out in plane with the bell (Fig. 2A, B).
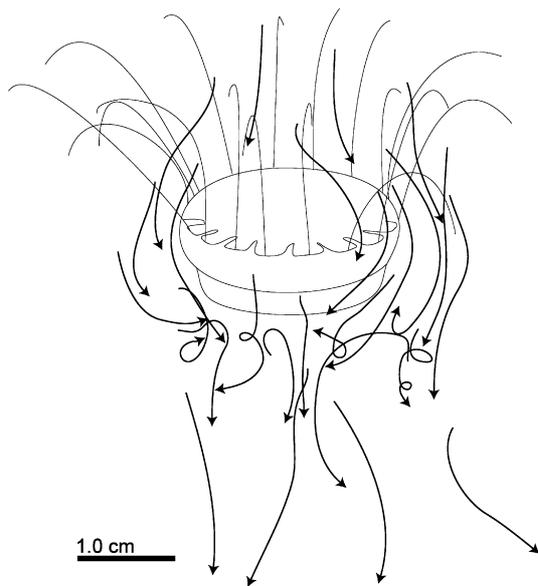

1.0 cm

Fig. 5 *Solmissus incisa*. Particle flow around a swimming *S. incisa*. Figure shows the paths of neutrally buoyant particles around a swimming medusa. Data from 1 s (30 frames) of video is shown. The medusa is shown in its starting position. *Scale bar*: 1.0 cm

Discussion

Foraging postures

Many narcomedusae show a characteristic feeding behavior, which is described herein as "ramming". Ramming behavior has been documented by other observers, but its functionality has not been resolved (Madin 1988; Mills and Goy 1988; Larson et al. 1989). In ramming behavior, the tentacles of the medusa are held out in front of the animal as it actively swims forward (Fig. 2A, B). This mode of foraging is not limited to *Solmissus* spp. Many other narcomedusae, coronate scyphomedusae (Larson 1979; Child and Harbison 1986; Larson et al. 1989; Youngbluth and Båmstedt 2001), and the freshwater limnomedusae *Limnocnida* spp. and *Craspedacustsa* spp. (J. Bouillon, personal communication; J. Costello, personal communication) exhibit ramming behavior. These medusae all have the ability to swim with raised tentacles in a posture similar to the *Solmissus* sp. shown in Fig. 2A.

In *Solmissus* spp., the tentacles are solid and non-contractile. They have, at their core, a single row of vacuolated cells, which provides the necessary stiffness to raise the tentacles above the bell while swimming (Mayer 1910). The tentacles are anchored into the umbrella with deep roots. This morphology is very much like what has been found for various coronate scyphomedusae (Larson 1979).

The majority (86%) of Monterey Bay *Solmissus* were found in postures "A" and "B" (Fig. 2A, B), with the tentacles held above the plane of the bell. Posture "A" was exclusive to *S. marshalli* and the small- to medium-sized *S. incisa* (<8 cm). A number of the smaller *Solmissus* were found with an amphicoronate tentacle posture (24%), with the tentacles alternating between two different angles, 90° and 135° from the plane of the bell. This pattern is a common posture for the tentacles of thecate hydroids (Cornelius 1995), but has not been reported previously for medusae. Nothing is known about the potential adaptive value of this sort of tentacle posturing, and it seems to be unique to *Solmissus*, as it has not been seen in other genera of narcomedusae (Raskoff, unpublished data).

The largest specimens of *S. incisa* were very rarely found in posture "A" (<4%), but swam almost exclusively in posture "B" (70%). This difference in tentacle posture was correlated with size. The large *S. incisa* may be unable to swim with their tentacles elevated to the extent reached by the smaller medusae, perhaps due to a considerable increase in drag on their longer tentacles. The larger medusae may shift toward a foraging strategy that maximizes capture area as opposed to stealth. Indeed many of the large *S. incisa* were found with quite large prey items in their guts, such as large salps and medusae, which smaller *S. incisa* or any-sized *S. marshalli* would be unable to ingest due to their gastrovascular cavity size. However, large *S. incisa* were

not limited to large prey. Small ctenophores and siphonophores were found regularly in the guts of large *S. incisa*.

Many of the largest *S. incisa* were found with their tentacles in posture "C" (Fig. 2C), with tentacles deployed below the bell margin. These individuals often swam in this position for extended periods of time. It is not known whether this shift between tentacle postures is specific to prey type, prey density, prey size, or whether it is simply a locomotory behavior, as suggested by Mills and Goy (1988). A swimming medusa would generate less drag in this position.

In addition to the three primary tentacle postures outlined above, there exist numerous variations on these postural themes. Medusae can have most of their tentacles up in an "A" posture, while a few reach down towards the mouth, as in posture "C". This tentacle pattern was often seen just after a medusa had ingested prey (Fig. 3E). It was not uncommon for a few tentacles to stay close to, or in the mouth after prey ingestion. This behavior may decrease the chance of a prey item escaping from the gut of the medusa. This is significant because the nematocysts of *Solmissus* spp. did not seem to kill or paralyze their prey. The medusae appear to merely harpoon their prey with nematocysts and hold on effectively until they are swallowed. Prey items were routinely seen moving actively while inside the stomach. Medusoid prey continued their rhythmic contractions, and ctenophore ctene rows continued to beat at normal swimming frequencies in the gut.

It has been noted previously that lateral or trailing tentacle postures (Fig. 2B, C) might increase the effective capture surface of a jellyfish (Madin 1988; Larson et al. 1989), yet the majority of *Solmissus* in our study were found in posture "A", which provides for little increase to the effective capture area of these medusae (Fig. 2A). It is proposed that the adaptive advantage of the tentacle-first foraging behavior in *Solmissus* spp. is for stealth predation on comparatively fast-moving prey. That is, the medusae are able to covertly move towards prey without being detected. Tentacle-first ramming behavior allows *Solmissus* spp. to approach prey with a minimum amount of water motion in advance of its position. Prey may first detect the predator only after the prey is within the cone of tentacles (Fig. 5). While not moving at all (such as a lie-in-wait predator) can be considered one type of stealth, *Solmissus* spp. have the advantages of being both a cruising predator, while retaining the stealth of a lie-in-wait ambush predator.

Prey items

Previous studies have shown that *Solmissus* spp. feed on a variety of species, including gelatinous prey, but adequate quantitative data on prey preference has been lacking (Mills and Goy 1988; Purcell and Mills 1988; Larson et al. 1989; Mills et al. 1996). Table 1 shows all of the prey items of *Solmissus* spp. reported in the literature, as well as those added by this investigation. Previous studies identified nine prey taxa. An additional 23 different prey types were observed for the two species of *Solmissus* found in Monterey Bay (Table 1).

Purcell and Mills (1988) and Carré et al. (1989) suggested that the cnida of narcomedusae were specially adapted for capture of soft-bodied prey items. Indeed, with the exception of the few krill found in the stomachs, all prey were gelatinous in composition. Furthermore, the ten krill found in this study may not have been caught directly, but were likely to have been inside the stomachs of cydippid ctenophores, known predators of krill and more readily digested (Matsumoto 1991; Raskoff, unpublished data). On one occasion, a cydippid ctenophore with a krill inside its gut was found in the stomach of *S. incisa*. On three other occasions, krill were seen intermixed with the remnants of freshly digested cydippids, suggesting that these krill also had been inside the ctenophores. It is not known how the other six krill were captured (none have ever been observed on the tentacles), but these observations suggest that krill are ingested primarily via capture of other gelatinous predators. Tentacle spacing of *Solmissus* spp. does not appear to be suited for capture of small prey items (Madin 1988; Purcell and Mills 1988). In order to check for small prey, 40 specimens of *Solmissus* spp., which had no observable prey in their guts when viewed with the video system, were carefully collected and brought to the surface. Their guts were immediately searched on the boat, yet no small prey (i.e. copepods, etc.) were ever observed.

Prey capture and flow

The tentacles of *Solmissus* and certain other species of medusae (noted above) are often held above the margin of the bell, away from its propulsive elements on the oral side. It is hypothesized that such a placement allows the medusa to ram into prey with a number of tentacles before fluid disturbance caused by the act of swimming can alert the prey.

Solmissus spp. prey on animals that are sensitive to water movement and which may exhibit predator-avoidance strategies linked to water disturbance. Siphonophores, medusae and ctenophore of the size range eaten by *Solmissus* spp. all have relatively fast swimming speeds and rapid escape responses, which would allow them to avoid large, moving predators such as *Solmissus* spp. if warned in time. In addition, many siphonophores and ctenophores have the ability to quickly reverse direction in an escape response (Mackie et al. 1987; Moss 1991; Matsumoto and Harbison 1993; Raskoff, unpublished data.). In particular, the siphonophore *Nanomia bijuga* has a very rapid escape behavior, produced by reversing its nectophore thrust (Mackie et al. 1987) when it is disturbed or touched. Nevertheless, *N. bijuga* was a common prey item of *Solmissus* spp. in this study (Fig. 4).

This mode of prey capture by *Solmissus* spp. is very different from that described in detail for other medusae in recent investigations (Costello 1992; Costello and Colin 1994, 1995; Colin and Costello 1996; Ford et al. 1997). Such models predict that "these morphologies are a specialization among the hydromedusae for the use of swimming-generated flow in feeding" (Colin and Costello 1996). According to these hydrodynamic models, medusae with flattened, oblate bells (like *Solmissus*) are thought to use swimming-generated flow to entrain slow-moving prey into fast-moving currents that pull the prey through the filtering tentacles, while prolate forms would be lie-in-wait ambush predators of fast-moving prey (Costello and Collin 1995). Similarities between the oblate hydromedusae and scyphomedusae were believed to represent convergence, based on swimming-generated, flow-feeding requirements (Colin and Costello 1996). These feeding models depend on high fluid disturbance to capture small, slow-moving prey. *Solmissus* spp. behave quite differently. The tentacle-ramming technique is adapted to capture large, comparatively fast-moving gelatinous prey, wherein fluid disturbance caused by the swimming is decoupled from the first contact with prey (Fig. 5).

It has recently been shown that oblate medusae have a more energetically efficient mode of swimming than do prolate forms (Ford and Costello 2000). The ramming, tentacle-first feeding strategy shown by *Solmissus* spp. may be an adaptation to both the scarcity of large prey in the deep sea and the importance of a physiologically efficient method of locomotion. The prey of *Solmissus* spp. are encountered in a hydrodynamically stealthy method, which enables the medusae to cover large amounts of water with kinematic efficiency, while still ambushing its prey.

Stealth predation may be a dominant mode of feeding in the mesopelagic depths of the ocean, where narcomedusae are among the most numerically abundant predators. In Monterey Bay, three of the six most common medusae are narcomedusae, all of which show tentacle-first ramming behavior (Raskoff 2001a). Future models of predation by medusae in the mesopelagic ecosystem must account for these poorly known, but numerically abundant predators.

References

Bouillon J (1987) Considérations sur le développement des Narcoméduses et sur leur position phylogénétique. Indo-Malayan J 4:189–278

Carré D, Carré C, Mills CE (1989) Novel cnidocysts of narcomedusae and a medusivorous ctenophore, and confirmation of kleptocnidism. Tissue Cell 21:723–734

Child CA, Harbison GR (1986) A parasitic association between a pycnogonid and a scyphomedusa in midwater. J Mar Biol Assoc UK 66:113–117

Colin SP, Costello JH (1996) Relationship between morphology and hydrodynamics during swimming by the hydromedusae *Aequorea victoria* and *Aglantha digitale*. Sci Mar 60:35–42

Cornelius PFS (1995) North-West European thecate hydroids and their medusae: keys and notes for identification of the species. Linnean Society of London, Shrewsbury

Costello J (1992) Foraging mode and energetics of hydrozoan medusae. Sci Mar 56:185–191

Costello JH, Colin SP (1994) Morphology, fluid motion and predation by the scyphomedusa *Aurelia aurita*. Mar Biol 121:327–334

Costello JH, Colin SP (1995) Flow and feeding by swimming scyphomedusae. Mar Biol 124:399–406

Ford MD, Costello JH (2000) Kinematic comparison of bell contraction by four species of hydromedusae. Sci Mar 64[Suppl 1]:47–53

Ford MD, Costello JH, Heidelberg KB, Purcell JE (1997) Swimming and feeding by the scyphomedusa *Chrysaora quinquecirrha*. Mar Biol 129:355–362

Gladfelter WB (1970) Swimming in medusae (Cnidaria: Hydrozoa and Scyphozoa) a study in functional morphology and behavior. PhD dissertation, Stanford University, Stanford

Hamner WM (1985) The importance of ethology for investigations of marine zooplankton. Bull Mar Sci 37:414–424

Hamner WM (1990) Design developments in the planktonkreisel, a plankton aquarium for ships at sea. J Plankton Res 12:397–402

Hamner WM, Robison BH (1992) In situ observations of giant appendicularians in Monterey Bay. Deep-Sea Res A 39:1299–1313

Hamner WM, Madin LP, Alldredge AL, Gilmer RW, Hamner PP (1975) Underwater observations of gelatinous zooplankton: sampling problems, feeding biology, and behavior. Limnol Oceanogr 20:907–917

Kramp PL (1968) The hydromedusae of the Pacific and Indian Oceans, sect. II and III. Dana-Rep Carlsberg Found 72:1–200

Larson RJ (1979) Feeding in coronate medusae (Class Scyphozoa, Order Coronatae). Mar Behav Physiol 6:123–129

Larson RJ, Mills CE, Harbison GR (1989) In situ foraging and feeding behavior of narcomedusae (Cnidaria: Hydrozoa). J Mar Biol Assoc UK 69:785–794

Larson RJ, Mills CE, Harbison GR (1991) Western Atlantic midwater hydrozoan and scyphozoan medusae: in situ studies using manned submersibles. Hydrobiologia 216/217:311–317

Mackie GO (1985) Midwater macroplankton of British Columbia studied by submersible Pisces IV. J Plankton Res 7:753–777

Mackie GO, Pugh PR, Purcell JE (1987) Siphonophore biology. Adv Mar Biol 24:97–262

Madin LP (1988) Feeding behavior of tentaculate predators: in situ observations and a conceptual model. Bull Mar Sci 43:413–429

Matsumoto GI (1991) Functional morphology and locomotion of the arctic ctenophore *Mertensia ovum* (Fabricius) (Tentaculata: Cydippida). Sarsia 76:177–185

Matsumoto GI, Harbison GR (1993) In situ observations of foraging, feeding, and escape behavior in three orders of oceanic ctenophores: Lobata, Cestida, and Beroida. Mar Biol 117:279–287

Mayer AG (1910) Medusae of the world, vol I. The hydromedusae. Carnegie Institution of Washington, Washington, D.C.

Mills CE, Goy J (1988) In situ observations of the behavior of mesopelagic *Solmissus* narcomedusae (Cnidaria, Hydrozoa). Bull Mar Sci 43:739–751

Mills CE, Pugh PR, Harbison GR, Haddock SHD (1996) Medusae, siphonophores and ctenophores of the Alboran Sea, southwestern Mediterranean. Sci Mar 60:145–163

Moss AG (1991) The physiology of feeding in the ctenophore *Pleurobrachia pileus*. Hydrobiologia 216/217:19–26

Pérès J-M (1958) Remarques générales sur un ensemble de quinze plongées effectuées avec le bathyscaphe F.N.R.S. III. Bull Inst Oceanogr (Monaco) 1134:28

Purcell JE, Mills CE (1988) The correlation between nematocyst types and diets in pelagic hydrozoa. In: Hessinger DA, Lenhoff HM (eds) The biology of nematocysts. Academic, New York, pp 463–485

Purcell JE, Breitburg DL, Decker MB, Graham WM, Youngbluth MJ, Raskoff KA (2001) Pelagic cnidarians and ctenophores in low dissolved oxygen environments. In: Rabalais NN, Turner RE (eds) Coastal hypoxia: consequences for living resources and ecosystems. American Geophysical Union, Washington, D.C., pp 77–100

Raskoff KA (2001a) The ecology of the mesopelagic hydromedusae in Monterey Bay, California. PhD dissertation, University of California, Los Angeles

Raskoff KA (2001b) The impact of El Niño events on populations of mesopelagic hydromedusae. Hydrobiologia 451:121–129

Robison BH (1993) Midwater research methods with MBARI's ROV. Mar Technol Soc J 26:32–39

Robison BH, Reisenbichler KR, Sherlock RE, Silguero JMB, Chavez FP (1998) Seasonal abundance of the siphonophore, *Nanomia bijuga*, in Monterey Bay. Deep-Sea Res II 45:1741–1751

Russell FS (1953) The medusae of the British Isles: anthomedusae, leptomedusae, limnomedusae, trachymedusae and narcomedusae. The University Press, Cambridge

Silguero JMB, Robison BH (2000) Seasonal abundance and vertical distribution of mesopelagic calycophoran siphonophores in Monterey Bay, CA. J Plankton Res 22:1139–1153

Sullivan BK, Garcia JR, Klein-MacPhee G (1994) Prey selection by the scyphomedusan predator *Aurelia aurita*. Mar Biol 121:335–341

Youngbluth MJ (1984) Manned submersibles and sophisticated instrumentation: tools for oceanographic research. In: Proceedings of SUBTECH 1983. Society of Underwater Technology, London, pp 335–344

Youngbluth MJ, Båmstedt U (2001) Distribution, abundance, behavior and metabolism of *Periphylla periphylla*, a mesopelagic coronate medusa in a Norwegian fjord. Hydrobiologia 451:321–333