J. mar. biol. Ass. U.K. (1988), 68, 689–699

Printed in Great Britain

IN SITU OBSERVATIONS OF DEEPWATER MEDUSAE IN THE GENUS *DEEPSTARIA*, WITH A DESCRIPTION OF *D. RETICULUM*, SP. NOV.

R. J. LARSON*, L. P. MADIN† AND G. R. HARBISON*

*Harbor Branch Oceanographic Institution, 9600 Old Dixie Highway, Fort Pierce, FL 34946
†Woods Hole Oceanographic Institution, Woods Hole, MA 02543

(Figs. 1–6)

Two medusae in the poorly known genus *Deepstaria* were observed during submersible dives in the Pacific and Atlantic oceans. The first specimen, identified here as *D. enigmatica* Russell 1967, was observed, photographed and videotaped at a depth of about 600 m in the Catalina Basin off California. The second specimen was observed and collected at a depth of 915 m near Bermuda, and is described here as a new species, *D. reticulum*. Both medusae have a voluminous, thin-walled umbrella, a gastrovascular system of anastomosing canals, elongate oral arms and no tentacles. Behavioural observations made from the submersibles suggest that the medusae trap prey by pursing their voluminous bells shut around organisms which swim into them.

INTRODUCTION

Medusae are common constituents of the meso-and bathypelagic fauna. Small, transparent trachyline hydromedusae are usually most abundant, but the larger (2–10 cm diameter) pigmented coronate scyphomedusae are often collected in trawl nets (Thurston, 1977; Roe, James & Thurston, 1984; Larson, 1986) or observed from submersibles (Mackie & Mills, 1983; Mackie, 1985; Larson, Madin & Harbison, unpublished observations). Larger (30–70 cm) deep-sea semaeostome scyphomedusae are only infrequently collected in nets (Harbison, Smith & Backus, 1973; Larson, 1986), and would appear to be the rarest forms. For example, Thurston (1977) collected over 16000 midwater medusae in trawls yet he did not report taking a single mesopelagic semaeostome. However, recent investigations using submersibles have shown that these medusae are much more common than net hauls alone would suggest (Smith, 1982).

Only three semaeostome genera, *Deepstaria*, *Poralia*, and *Stygiomedusa*, are known to be meso-bathypelagic. Each is monotypic and unusual in size and morphology. The rarest of them is probably *Deepstaria enigmatica* Russell 1967, which has a large and thin umbrella, a network of anastomosing canals and no tentacles. It was first described from a 50 cm diameter specimen collected off California by the manned submersible 'Deepstar' 4000 in 1966 (Russell, 1967; Barham, 1969). Additional notes on this specimen and on *Anuropus* sp., an isopod which was attached to the medusa, were published by Barham (1969) and Barham & Pickwell (1969). Since then a total of seven specimens, all fragmentary,

have been reported from the Atlantic, Pacific, and Southern oceans (Table 1). *Deepstaria* appears to be cosmopolitan in the deep water of all oceans. The systematic position of *Deepstaria* is unclear. Larson (1986) placed it in the semaeostome family Ulmaridae Haeckel, 1879 because of the presence of semaeostome-like oral arms and a gastrovascular system consisting of canals. *Deepstaria* also has some features in common with *Stygiomedusa* Russell, 1959, notably the absence of tentacles and anastomosing network of canals, but it is different in other important respects – the oral arms, gonads, and canal system. Larson (1986) concluded that it probably is not closely related to *Stygiomedusa*, and placed it in its own subfamily, the Deepstariinae.

Table 1. *Reported specimens of* Deepstaria *spp.*

Species	Location	Depth (m)	Reference
D. enigmatica	California	723	Russell (1967)
D. enigmatica	Caribbean	OT*	Phillips (1973)
D. enigmatica	Central Atlantic	510–1090	Winkler & van Soest (1981)
D. enigmatica	Oregon	1500–1750	Pearcy & Stuiver (1983)
D. enigmatica	Southern Ocean	OT*	Larson (1986)
D. enigmatica	California	600	Harbison (1987), this report
D. reticulum	Bermuda	915	This report

* Open trawl, depth not known

Nothing is known about the biology of this unique medusa, although Larson (1986) assumed that, lacking tentacles, it probably feeds in a novel manner. Here we report the behaviour of two specimens of *Deepstaria* seen from manned submersibles. One of these is the first intact specimen of *D. enigmatica* seen and photographed, the other medusa is so unlike *D. enigmatica* that we describe it here as a new species, *Deepstaria reticulum*.

METHODS

Observations, videotape recordings, and 35 mm photographs of *D. enigmatica* were made off the coast of southern California from the submersible 'Alvin' (Dive 966; November 1979; Madin and Harbison, observers), but the medusa could not be collected. The specimen of *D. reticulum* was photographed, videotaped and collected in a suction sampler from the submersible 'Johnson-Sea-Link II' (Dive 1427; 19 July 1987; Madin, observer) south-west of Bermuda. The specimen was preserved in 5% buffered formalin immediately after the dive.

RESULTS

Taxonomic account

Family Ulmaridae Haeckel, 1879
Subfamily Deepstariinae, Larson, 1986

Diagnosis. Umbrella large and uniformly thin. Tentacles absent. With a well developed coronal muscle at the umbrella margin. Rhopalia 8, or more (?). Gastrovascular system consists of a meshwork of thin canals, some are long and

straight (possibly primary) and run to the bell margin, most extend only a short distance before anastomosing with another canal. With or without (?) a ring canal. Stomach with 4–5 narrow, elongate, thickened oral arms with a longitudinal groove. Gonads of variable morphology. Cnidome: microbasic euryteles.

Genus *Deepstaria* Russell, 1967

Diagnosis. Same as for subfamily.

Deepstaria reticulum n.sp.

(Figs. 1–4, 6)

Diagnosis. *Deepstaria* with gastric cirri occurring on auriform plaques; gonads probably located in pits. Umbrellar epidermis and most of the gastrodermis pigmented reddish-brown.

Description. The medusa was not entire; it had sustained some damage prior to collection and was torn further during capture with the suction sampler (Fig. 1). The specimen has an umbrella approximately 60 cm in diameter (after fixation in formalin) which is uniformly thin (3–5 mm). The mesoglea is relatively firm. Both the ex- and subumbrellar surfaces are smooth, with scattered nematocyst clusters. Except for eight rhopaliar lappets, the umbrella margin is smooth, and tentacles are absent. The umbrella margin is folded under for a few millimetres towards the subumbrella (Fig. 2A).

Although part of the margin is missing in the preserved specimen, eight rhopalia can be distinctly seen in the videotape of the living medusa, due to the large size of the rhopaliar lappets. These lappets are thickened, blunt and rounded, and protrude about 5 mm from the margin (Figs. 2B, 3D, E). Each digitate rhopalium lies in a deep cleft between the paired rhopaliar lappets and bends upwards toward the exumbrella (Fig. 2B).

The subumbrella muscle is diffuse, and probably extends over the entire subumbrella, as evidenced by peristaltic motions seen *in situ* and recorded on videotape. The coronal muscle is well developed (12–14 mm wide) (Figs. 2A, 3D) and consists of a large number of circular, striated muscle bundles located deep in the mesoglea near the bell margin (Fig. 2A). The distal portion of the muscle bends over toward the subumbrella. Numerous fibres extend from the coronal muscle to the subumbrella (Fig. 2A). The coronal muscle is contracted and has pulled the margin into a small circle.

The stomach is relatively small (8 cm in diameter), circular in outline, and protrudes from the subumbrella as a short, thick-walled manubrium. Four elongate, tapered, oral arms extend from the stomach. The arms have a central longitudinal groove with thickened ridges on each side. The arms appeared to have been damaged before collection, and their length and exact shape could not be determined. At the base of each arm are paired auriform plaques, one on each side of the oral arm groove (Fig. 3A, C). These appear as four V-shaped

Fig. 1. *D. reticulum*, photograph of entire specimen after preservation (bar = 5 cm). The contracted umbrella margin is left and down from the centre.

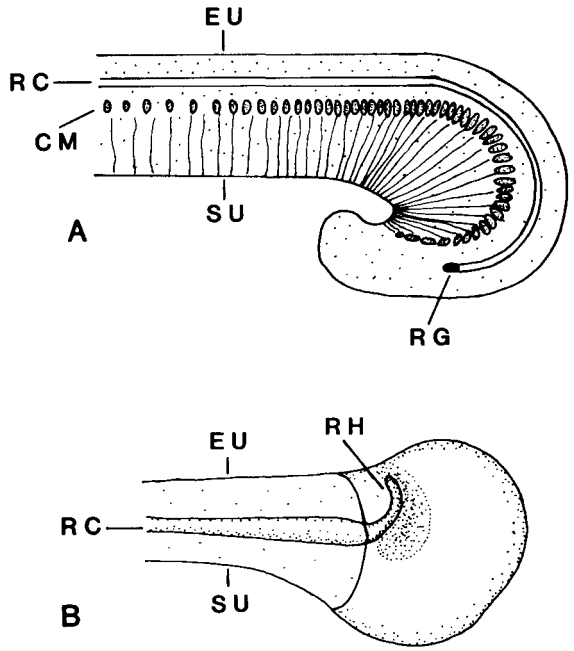

Fig. 2. *D. reticulum*, schematic cross-sectional diagrams. (A) Umbrella margin showing radial and ring canal, coronal muscle with fibres below. (B) Umbrella margin at rhopalium. EU, Exumbrella; CM, coronal muscle; RC, radial canal; RG, ring canal; RH, rhopalium; SU, subumbrella.

structures, with the point of the V directed toward the centre, as seen through the exumbrella (Fig. 4A). On the gastrodermal surface of the plaques are deep pits, from which the gastric cirri emerge, up to eight per pit (Figs. 3B,C,4B). The cirri are ribbon-like, 3–10 mm long and 0·5 mm wide.

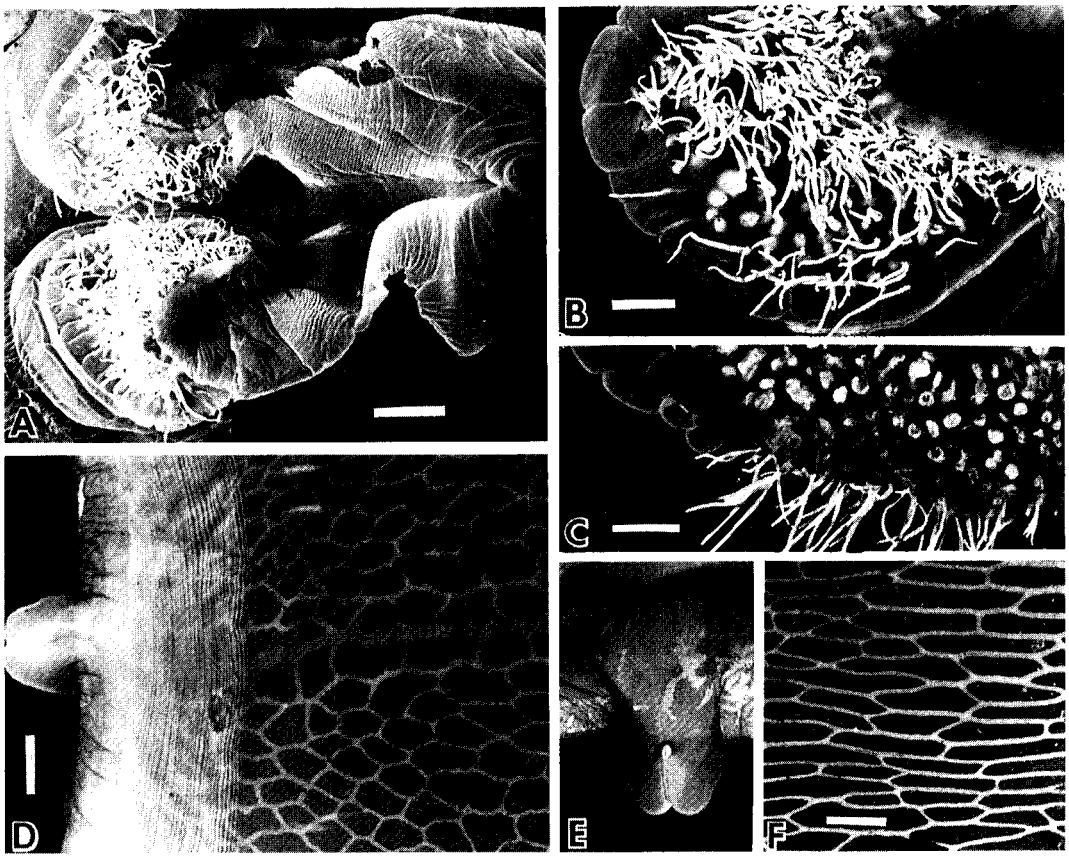

Fig. 3. *D. reticulum*, photographs of anatomy. (A) Portion of manubrium showing paired gastric plaques and longitudinal groove between them leading to oral arm (bar = 1 cm). (B) Portion of a gastric plaque seen from side facing the coelenteron. Gastric cirri can be seen emerging from pits (bar = 5 mm). (C) Portion of a gastric plaque viewed from side facing the subumbrella showing base of pits from which cirri emerge (bar = 5 mm). (D) Portion of subumbrella margin showing coronal muscle, rhopaliar lappets, major radial canal and smaller anastomosing canals (bar = 5 mm). (E) Rhopaliar lappets seen from exumbrellar side (bar = 2·5 mm). (F) Anastomosing canals from near mid-portion of umbrella (bar = 5 mm).

Surrounding the plaques is a thin membrane which attaches the plaques to the subumbrella. A fluid-filled sinus (subgastric sinus) occurs between the subumbrella and the plaques (Fig. 4B) and is probably analogous to the subgenital pouch of other semaeostomes e.g. *Aurelia*. Subgenital pits are absent. No gonadal tissue was recognized in the medusa.

The gastrovascular canals issue from the stomach near the distal portions of the gastric plaques. The canals are thin and form a narrow meshwork oriented radially (Fig. 3D, F). This meshwork becomes larger towards the mid-umbrella region and is less elongated near the margin. There are about 20 major straight (primary?) canals; some are rhopaliar, others interrhopaliar. These major canals are about twice the width of the other canals (Fig. 3D). A small ring canal is present in the turned-under portion of the bell margin.

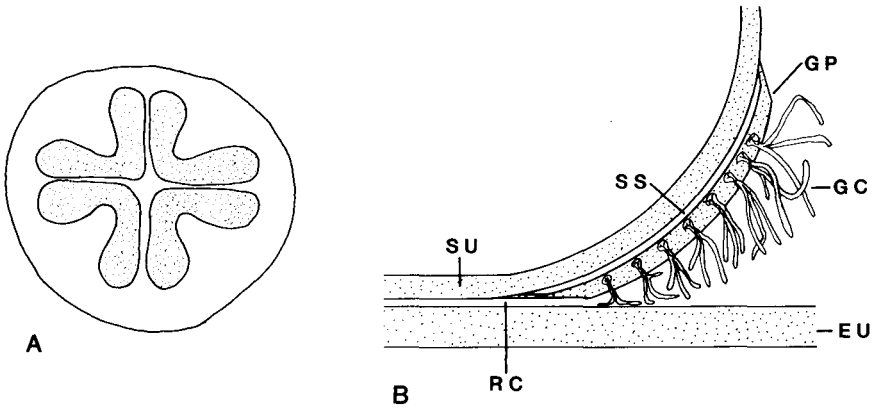

Fig. 4. *D. reticulum*. (A) View of stomach through exumbrella showing V-shaped pairs of gastric plaques (from videotape). (B) Diagrammatic cross-section through margin of stomach showing gastric plaque, cirri and subgastric sinus. EU, Exumbrella; GC, gastric cirri; GP, gastric plaque; RC, radial canal; SS, subgastric sinus; SU, subumbrella.

The cnidome consists only of microbasic euryteles (15–16 × 8 μm, undischarged capsule size) which are found in the gastric cirri and the epidermis.

The umbrella and the exumbrellar surface of the stomach are pigmented a deep reddish-brown. Most of the stomach and gastrodermis of the oral arms are a lighter brown, and the gastric plaques and gastric cirri are cream coloured.

The medusa had a single yellow isopod of the genus *Anuropus*, at the top of the subumbrella near the mouth. *Anuropus bathypelagicus* Menzies and Dow 1958 is known to be a symbiont of *D. enigmatica* (Barham & Pickwell, 1969; Phillips, 1973), and our specimen probably belongs to this species. The isopod was only 1·0 cm in total length, compared to a range of 1·8–6·0 cm for specimens collected in trawls, and 8·0 cm for the isopod reported by Barham & Pickwell (1969) from the original *D. enigmatica*.

Material examined. Holotype – USNM82982, 'Johnson-Sea-Link II' station 1427, 20 July 1987, 60 cm preserved diameter, sex undetermined.

Type locality. North Atlantic Ocean near Bermuda (32° 16′ N, 64° 44′ W) at a depth of 915 m.

Etymology. The species name is the Latin noun *reticulum*, meaning a small net, mesh-work bag, or purse, and used here in apposition to the generic name. It refers both to the anastomosing network of canals in the umbrella, and the habit of the medusa of pursing shut like a drawstring bag.

In situ *appearance and behaviour of* D. enigmatica *and* D. reticulum

During 'Alvin' dive 961, off Southern California, a large and intact specimen of *D. enigmatica* was seen by Madin & Harbison but not collected. Its size was estimated as at least 30 cm in height and slightly less in diameter. Black-and-white videotape and 35 mm colour photographs were taken (Fig. 5). The medusa

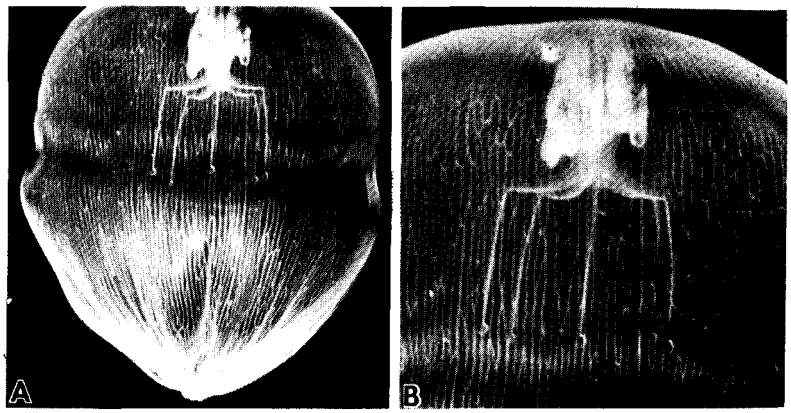

Fig. 5. *D. enigmatica, in situ* photographs from 'Alvin' dive 922. (A) Medusa with umbrella margin pursed shut. Peristaltic wave is moving upwards on umbrella. (B) Close-up showing the manubrium with sac-like folds around it and five oral arms with hook-like tips below. *Anuropus* isopod is attached to the subumbrella just to the left of the stomach.

was colourless except for the white gastrovascular canals and coronal muscle (as in the 'Deepstar' specimen, see colour photos in Barham (1969)). When first seen the medusa was drifting motionless with the umbrella margin down and open, giving the medusa a cylindrical shape. As the submersible came closer, the umbrella margin rapidly pursed shut, after which a peristaltic wave moved slowly up the bell from the margin. A complete sequence of photographs of this action was published by Harbison (1987, fig. 3). If the medusa is assumed to be about 30 cm high, then the wave of contraction moved at about 2 cm s^{-1}.

The photographs of *D. enigmatica* taken from 'Alvin' (Fig. 5) clearly show the tube-like manubrium and 5 narrow oral arms with recurved ends, like those figured by Russell (1967, pl. 1, fig. 4). Surrounding the manubrium are sac-like structures. This may be the thin walled manubrium as described by Winkler & van Soest (1981). No major straight radial canals are visible and no rhopalia can be seen owing to the orientation of the animal. Also visible in the photographs is a large crustacean, probably the isopod *Anuropus* sp., located on the subumbrella

near the stomach. This is approximately the same position occupied by the *Anuropus* on the 'Deepstar' specimen (Barham & Pickwell, 1969).

Colour videotapes and 35 mm colour photographs were also made of the *D. reticulum* specimen from Bermuda (Fig. 6). In the videotapes the four V-shaped pairs of gastric plaques are visible through the umbrella, and the large rhopaliar lappets are distinct. When first seen the medusa appeared damaged; a 5 cm hole and a flap of loose tissue could be seen in the umbrella. The ends of the attached tissue showed signs of regeneration, suggesting that this damage had occurred well before collection.

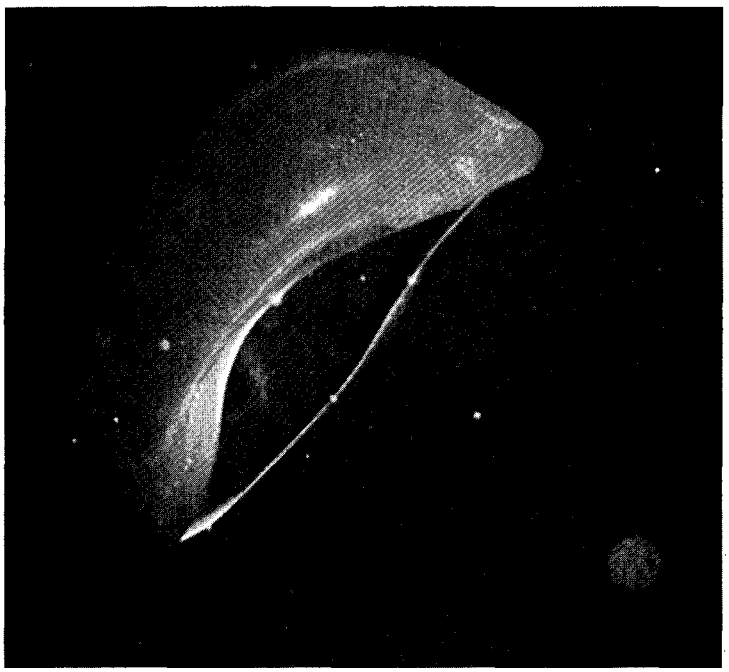

Fig. 6. *D. reticulum, in situ* photo from 'Johnson-Sea-Link' dive 1427. Diameter of medusa is about 60 cm. The reticulate canal pattern, the thinness of the bell, and four of the rhopalia are visible.

The medusa was first seen drifting about 0·5 m above a sloping bottom, with the bell expanded and open downwards. In this orientation, the animal was bowl-shaped, with a diameter about twice the height. Once near the submersible, the medusa was seen using peristalsis to swim slowly. Contraction waves passed down from the top of the umbrella to the margin, slowly propelling the medusa forward. When the submersible was manoeuvred to position the animal over the large collection canisters ('detritus samplers'), the margin of the medusa's bell contacted a protruding plastic knob and rapidly closed around it. Pursing of the umbrella margin over the knob took only a few seconds. The margin of the umbrella remained firmly clamped around the knob, while the rest of the medusa hung above like a balloon. Efforts to dislodge the animal with a stream of water

from the suction sampler were unsuccessful, and eventually the medusa was pulled off with the suction nozzle, resulting in some damage. The *Anuropus* isopod on the medusa remained attached to the subumbrella throughout these manoeuvres.

DISCUSSION

Morphological comparisons

Because none of the *Deepstaria* specimens collected so far have been complete it is difficult to determine which characters best distinguish these two species. The most obvious differences in the available material are the shape of the manubrium, the position of the gastric cirri, and the presence of absence of pigment.

In *D. enigmatica* the manubrium is a thin-walled tube and the gastric cirri are arranged in long paired zones at the base of each oral arm, one on each side of the oral arm groove (Russell, 1967, text-fig. 3; Winkler & van Soest, 1981, fig. 1a, 3). However, in *D. reticulum* the manubrium is apparently short and thick, and the gastric cirri are located near the umbrella. In the videotapes, the paired gastric plaques are visible through the exumbrella. The cirri, located on the plaque-like structures, are not evenly scattered, but clustered in small groups which emerge from pit-like pores in the plaques.

No gonads were apparent in the *D. reticulum* specimen, indicating that it was not sexually mature. In the *D. enigmatica* specimen described by Russell (1967, text-fig. 3) the gonads were found at the proximal ends of the fan-shaped mesenteries which continue distally into the oral arms. Gonads were apparently absent in the specimen described by Winkler & van Soest (1981) since they made no mention of them. Because the fan-like mesenteries of *D. enigmatica* were absent in *D. reticulum* the gonads may be located in the pits adjacent to the gastric cirri. In other scyphomedusae, the gonads are generally located adjacent to the gastric cirri.

The umbrella margin of these two *Deepstaria* spp. may be different but this cannot be ascertained until an intact *D. enigmatica* is described. It seems likely that if *D. enigmatica* had rhopaliar lappets as large and distinct as those of *D. reticulum*, they would have been noted on at least one specimen.

All *D. enigmatica* specimens seen so far have lacked pigmentation, while *D. reticulum* is deeply coloured both on the umbrellar epidermis and the gastrodermis of the stomach and oral arms. It is likely these two medusae differ in other ways, but this must await description of intact specimens.

Behaviour

These two species of *Deepstaria* display some unique behaviour; peristaltic locomotion and pursing of the bell margin are unknown in other medusae. Probably the peristaltic locomotion is necessary because the umbrella is too thin and the subumbrella musculature too diffuse to support more rapid pulsation. Our observations of both species of *Deepstaria* suggest that they usually hang

motionless with the umbrella open. Peristalsis was observed in both, but it was not possible to tell if it was spontaneous or stimulated by the presence of the submersible. The *D. enigmatica* pursed shut without obviously touching anything, while the *D. reticulum* only closed when it contacted the sampler.

It seems probable to us that medusae in this genus are large ambush predators in the meso- and bathypelagic environment. Based on their known behaviour and morphology, and analogy with other gelatinous ambush predators (Madin, 1988), we speculate that the feeding behaviour might be as follows. The medusae usually hang vertically and motionless with the bell open; occasional peristaltic contractions probably enable them to swim slowly, at least enough to retard sinking. Because the area of the subumbrella is so large, upward-swimming prey occasionally would swim into it. Once prey enter the large subumbrellar chamber, the contact stimulates rapid contraction of the coronal muscle, pursing the umbrella shut and trapping the prey. As the prey attempts to escape, it contacts nematocysts on the subumbrella, being repeatly stung until weakened. It may additionally become covered with mucus and further immobilized. Then peristalsis and ciliary movement could transport the prey towards the mouth where the oral arms could grasp and engulf it. It is also possible that peristaltic contractions could pump most of the water out through the constricted margin, bringing the prey into closer contact with the subumbrellar surface or the oral arms. 'Bagging' prey in this way is not known in other medusae, but does occur in some ctenophores (Harbison, Madin & Swanberg, 1978), anthozoans (Hamner & Dunn, 1980) and nudibranchs (Hurst, 1968).

Nothing is known about the diet of *Deepstaria*. Larson (1978) found evidence for a direct relationship between the size of the gastric cirri and prey size in scyphomedusae. If this is true for *Deepstaria*, in which the gastric cirri are mostly less than 1 cm in length, the prey may be small mesopelagic crustaceans like copepods, amphipods, and ostracods. Vertically migrating organisms might be particularly vulnerable to *Deepstaria* with its bell opened downwards. Gelatinous animals are unlikely prey because scyphomedusae that feed on gelatinous prey have pleated oral arms with a large surface area (Larson, 1978) and the oral arms of *Deepstaria* are very small. Larger organisms that are trapped may be strong enough to escape through the umbrella wall. This may have been how both the 'Deepstar' specimen and the medusa described here were damaged prior to collection.

We thank G. Ellis, pilot on 'Alvin' dive 961, and D. Liberatore, pilot on 'Johnson-Sea-Link II' dive 1427 for their expert help in observing, photographing and/or collecting these medusae. W. Hamner and B. H. Robison provided comments on the manuscript. This research was supported by the Harbor Branch Oceanographic Institution, NSF grant OCE-7722511 to G. R. Harbison and L. P. Madin, and a grant to L. P. Madin and B. H. Robison from the NOAA Office of Undersea Research. This is contribution No. 668 from the Harbor Branch Oceanographic Institution, No. 6746 from the Woods Hole Oceanographic Institution, No. 15 from the DSMC and No. 5 from the Beebe Project.

REFERENCES

BARHAM, E. G., 1969. A window in the sea. *Oceans*, **1**, 55–60.

BARHAM, E. G. & PICKWELL, G. V., 1969. The giant isopod *Anuropus*: a scyphozoan symbiont. *Deep-Sea Research*, **16**, 525–529.

HAMNER, W. M. & DUNN, D. F., 1980. Tropical Corallimorpharia (Coelenterata: Anthozoa): feeding by envelopment. *Micronesica*, **16**, 37–41.

HARBISON, G. R., 1987. Direct observation in plankton ecology. In *Science Applications of Current Diving Technology on the U.S. Continental Shelf* (ed. R. A. Cooper and A. N. Shepard), pp. 85–92. Washington, D.C.: National Oceanic and Atmospheric Administration. [Symposium Series in Undersea Research, vol. 2.]

HARBISON, G. R., MADIN, L. P. & SWANBERG, N. R., 1978. On the natural history and distribution of oceanic ctenophores. *Deep-Sea Research*, **25**, 233–256.

HARBISON, G. R., SMITH, K. L., JR & BACKUS, R. H., 1973. *Stygiomedusa fabulosa* from the North Atlantic: its taxonomy, with a note on its natural history. *Journal of the Marine Biological Association of the United Kingdom* **53**, 615–617.

HURST, A., 1968. The feeding mechanism and behaviour of the opisthobranch *Melibe leonina*. *Symposia of the Zoological Society of London*, no. 22, 151–166.

LARSON, R. J., 1978. *Aspects of Feeding and Functional Morphology of Scyphomedusae*. M.S. Thesis, University of Puerto Rico.

LARSON, R. J., 1986. Pelegic scyphomedusae (Scyphozoa: Coronatae and Semaeostomeae) of the Southern Ocean. Biology of the Antarctic Seas XVI. *Antarctic Research Series*, **41**, 58–165.

MACKIE, G. O., 1985. Midwater macroplankton of British Columbia studied by submersible Pisces IV. *Journal of Plankton Research*, 7, 753–777.

MACKIE, G. O. & MILLS, C. E., 1983. Use of the Pisces IV submersible for zooplankton studies in coastal water of British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*, **40**, 763–776.

MADIN, L. P., 1988. Feeding behavior of tentaculate predators: in situ observations and a conceptual model. *Bulletin of Marine Science*, in press.

PEARCY, W. G. & STUIVER, M., 1983. Vertical transport of carbon-14 into deep-sea food webs. *Deep-Sea Research*, **30**, 427–440.

PHILLIPS, P. J., 1973. The occurrence of a remarkable scyphozoan *Deepstaria enigmatica* in the Gulf of Mexico, and some observations on cnidarian symbionts. *Gulf Research Reports*, **4**, 166–168.

ROE, H. S. J., JAMES, P. T. & THURSTON, M. H., 1984. The diel migrations and distributions within a mesopelagic community in the north east Atlantic. 6. Medusae, ctenophores, amphipods and euphausiids. *Progress in Oceanography*, **13**, 425–460.

RUSSELL, F. S., 1967. On a remarkable new scyphomedusan. *Journal of the Marine Biological Association of the United Kingdom*, **47**, 469–473.

SMITH, K. L., 1982. Zooplankton of a bathyl benthic boundary layer: in situ rates of oxygen consumption and ammonium excretion. *Limnology and Oceanography*, **27**, 461–471.

THURSTON, M. H., 1977. Depth distributions of *Hyperia spinigera* Bovallius, 1889 (Crustacea: Amphipoda) and medusae in the North Atlantic Ocean, with notes on the associations between *Hyperia* and coelenterates. In *A Voyage of Discovery* [George Deacon 70th Anniversary Volume] (ed. M. Angel), pp. 499–563. Oxford: Pergamon Press.

WINKLER, J. T. & SOEST, R. W. M. VAN, 1981. First record of the scyphomedusa *Deepstaria enigmatica* Russell, 1967, from the mid North Atlantic Ocean (Coelenterata, Scyphozoa). *Bulletin. Zoologisch Museum, Universiteit van Amsterdam*, **8**(4), 33–38.