Crossota millsae (Cnidaria: Trachymedusae: Rhopalonematidae), a new species of viviparous hydromedusa from the deep sea off California and Hawaii

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Abstract

A new species of deep-sea jellyfish, *Crossota millsae* (Cnidaria: Hydrozoa: Trachymedusae: Rhopalonematidae), is described from the North Pacific Ocean off California and Hawaii. Discrete depth sampling showed this species lives at depths below 1000 meters in both geographic locations. The species is more abundant off California than off Hawaii. The greatest population densities were found at ~2500 m off California and at ~1250 m off Hawaii. The burnt-tangerine color of the inner bell and bright pink to lavender color of the ring and radial canals, manubrium and gonads make living specimens of this species difficult to confuse with any other known species of hydromedusa. Sexually dimorphic differences in gonad morphology are evident. The pendant testes contained spermatids at various stages of spermatogenesis as observed using scanning electron microscopy. Ova develop directly into small medusae that reside subumbrellarly between the radial canals of the mother. Various developmental stages of *C. millsae* are shown in photographs and terminology of brooding and viviparity is discussed relative to other Cnidaria.

Key words: Cnidaria, Hydrozoa, Coelenterata, *Crossota,* gelatinous zooplankton, reproductive biology, vertical distribution, bathypelagic jellyfish

Introduction

Brooding and viviparity by deep-sea animals are considered to be adaptations to the scarce resources of the deep sea, and these strategies have evolved in many different types of animals, including bivalves, crustaceans, chaetognaths, polychaete worms and cnidarians (*cf.*, Gage & Tyler 1991; Young 2003). For medusae, it is difficult to view extended parental care of young strictly as a "deep-sea adaptation", because many kinds of cnidarians, including tropical corals and intertidal anemones, are known to harbour their young after fertilization or brood asexually produced juveniles. The well-known plasticity of cnidarian

reproductive strategies has resulted in viviparity and brooding as adaptive responses to several different ecological pressures. This has been reviewed by Fautin *et al.* (1989).

Quite a few species of pelagic Cnidaria are known to maintain their young as developing juveniles. These include Scyphozoa, such as epipelagic species of the genera *Cyanea, Aurelia* and *Chrysaora* which brood planulae in their genital pouches or on their oral arms (Berrill 1949) and the deep-sea species *Stygiomedusa fabulosa* (Russell & Rees 1960) which has four specialized brood chambers in the bell projecting into the stomach that house asexually produced juveniles. Some hydrozoan jellyfish, *e.g.*, *Sarsia* spp. (Hyman 1940) and *Rathkea* spp. (Kramp 1968), asexually bud off small medusae from the manubrium.

While conducting research on the ecology and physiology of gelatinous organisms off California and Hawaii (Thuesen & Childress 1994), we discovered a uniquely pigmented species of trachyline hydromedusa new to science at depths below 1 kilometer. This bathypelagic species was brooding young medusae in subumbrellar space between the ovaries. In this report, I describe this new species of Hydrozoa, make observations on its reproductive biology and provide information on its depth distribution off California and Hawaii.

Materials and methods

Sample collection. Specimens were captured off California and Hawaii during research cruises of the research vessels *New Horizon*, *Point Sur*, and *Western Flyer*. Cruises of the RV *New Horizon* took place during September, 1995, 160 km off Point Conception, California (123° E, 34°50' N), and during June and July, 1996, off Oahu, Hawaii (158°20' E, 21°20' N). This species was also found in the San Clemente basin during a research cruise of the RV *Point Sur* during September of 1988 and during other cruises of the RV *New Horizon* during 1990 and 1991 (Thuesen & Childress 1994). Specimens were collected from these ships using a Mother Tucker Trawl (MTT) with a 10-m^2 mouth and a 30-liter insulated cod end (Childress *et al*. 1978). Ship speed was maintained below 1 knot. For the depth distribution observations, the MTT was fitted with a MOCNESS type opening-closing mechanism controlled from the deck of the ship via a conducting cable. The MTT has a very large length to mouth ratio that minimizes turbulence in the net, and the insulated cod end further protects fragile specimens from heat shock and physical damage. Only oblique tows were conducted off California, but most tows conducted off Hawaii were horizontal. Average depths for horizontal tows were computed based on the time spent at each depth. In October, 2001, during a cruise of the RV *Western Flyer* off Monterey, California (bottom depth to 3500 m), specimens were collected using the suction pump cassette sampling device and detritus samplers of the Monterey Bay Aquarium Research Institute's ROV *Tiburon* (Robison 1993; http://www.mbari.org/dmo/vessels/tiburon.html).

Microscopy. Photographs of this new species were taken with a hand-held Nikon camera fitted with a macroscopic lens aboard ship immediately after collection with the MTT. *In situ* digital video was taken by the Monterey Bay Aquarium Research Institute's ROV *Tiburon* off California. A Nikon Coolpix 990 digital camera attached to a Nikon SMZ-U dissecting microscope was used to take images of specimens collected with the ROV *Tiburon*. Formalin-preserved testes were prepared for scanning electron microscopy with 1 hour post fixation in 1% OsO_4, rinsed in 0.1 M phosphate buffer, dehydrated through an ethanol/phosphate buffer series, transferred to 100% acetone, critically point dried, and then sputter-coated with gold-palladium. Observations were carried out using an Amray 1810 scanning electron microscope, and images were captured to a personal computer. Brightness and contrast of SEM images were adjusted using Adobe Photoshop.

Results

Order Trachymedusae

Family Rhopalonematidae Russell, 1953

Genus *Crossota* Vanhöffen, 1902

***Crossota millsae*, new species**

(Figs. 1-3)

Synonymy. *Crossota* sp. A in Thuesen (1992) and Thuesen & Childress (1994).

Type material. All specimens are deposited in the Santa Barbara Museum of Natural History (SBMNH). Holotype: a female specimen of 17 mm height with developing juveniles captured at 2540 m off Monterey, California, on dive 366 of the ROV *Tiburon* on October 4, 2001 (SBMNH No. 349314). Paratype A: a male specimen of 12.5 mm height captured at 3244 m off Monterey, California, on dive 364 of the ROV *Tiburon* on October 2, 2001 (SBMNH No. 349315). Paratype B: six juveniles captured in San Clemente Basin off Southern California using the Mother Tucker Trawl in March, 1995 (SBMNH No. 349316).

Description. Bell reaching 28 mm diameter and 18 mm height. Inner bell pigment is burnt-tangerine; ring canal, 8 radial canals, manubrium and gonads are bright pink to lavender; mesoglea is colorless; peduncle is absent. Outer bell almost hemispherical to slightly cone-shaped with numerous exumbrellar furrows. Statocysts on short stalks (n =16, 2 per octant); velum thin reaching 35–55% of bell radius. Body more fragile than other species of *Crossota*. Up to 220 tentacles all in one row with rings of nematocysts; abscission zone (Fig. 3c) near base of each tentacle; remaining tentacle stubs usually display characteristic undulating fringe around bell; 11–13 stubs per undulation and two undulations per octant. Sexually dimorphic gonads attached ~4 mm from the manubrium.

Testes are pendant sausages (Fig. 1b) (can shrink to cones in preserved specimens); ovaries globular with eggs developing into juveniles while attached to the mother (Figs. 1c, d, 2). Juveniles (5 mm diameter) pink with orange tentacles, clear radial canals (Fig 3b). Juveniles (5 mm) with tentacles in groups (3–4 each), groups alternately per- and interradial (Fig 3b).
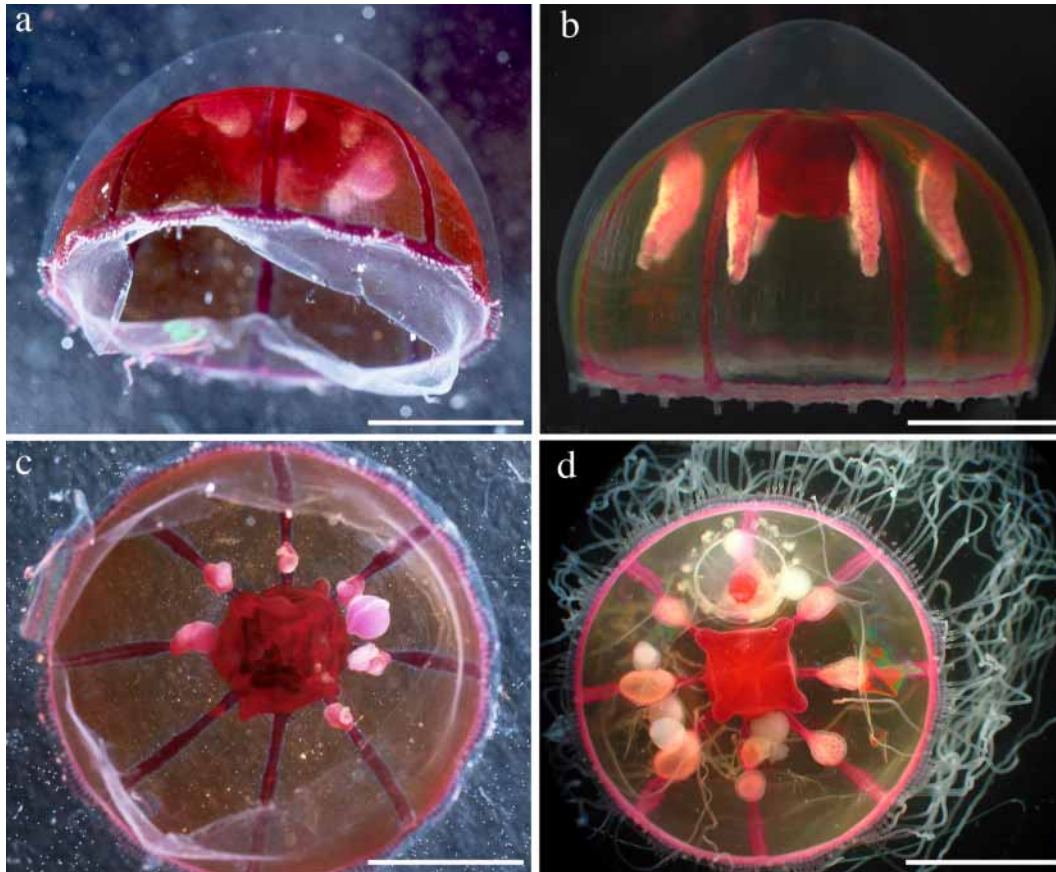

FIGURE 1. *Crossota millsae*, sp. nov. a) Lateral view of female specimen. Scale bar = 9 mm. b) Lateral view of male paratype specimen. Note the exumbrellar furrows. Scale bar = 5 mm. c) Oral view of female shown in Fig 1a with developing juveniles. Scale bar = 9 mm. d) Aboral view of female with developing juveniles. Scale bar = 10 mm.

Taxonomy. This species belongs to the genus *Crossota* due to its pendant gonads, exumbrellar furrows, lack of a peduncle, and absence of centripetal expansions into the ring canal (Kramp 1968). These characteristics distinguish it from the closely related genera *Vampyrocrossota* Thuesen, 1993, *Benthocodon* Larson & Harbison, 1990 and *Voragonema* Naumov, 1971. This species is distinguished from other species of *Crossota* by its pigmentation, location of gonads and arrangement of the tentacle abscission zone that

leaves a characteristic undulating fringe of tentacular bases following abscission. In previous keys to the genus *Crossota* (Kramp 1959; 1968), *Crossota millsae* fails at the second couplet and falls intermediate between the two lugs. The gonads of *C. alba* are located slightly nearer to the ring canal than to the base of the manubrium. *Crossota brunnea*, *C. rufobrunnea* and *C. norvegica* all have gonads that cluster near the base of the manubrium. Below is a key to the four species of *Crossota* found in the Pacific Ocean based on Kramp (1968).
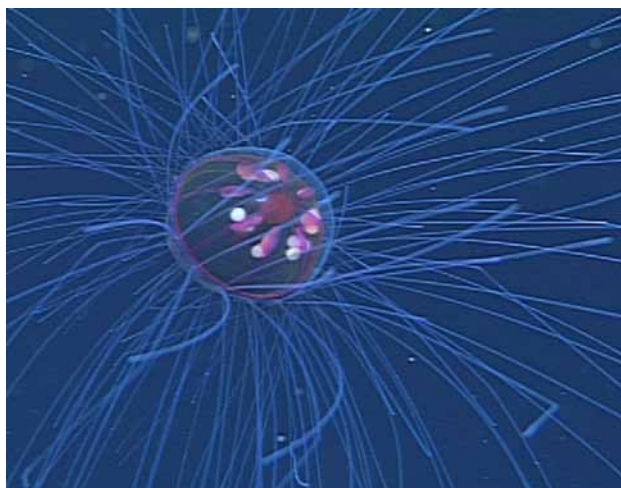

FIGURE 2. *In situ* video frame of *Crossota millsae* sp. nov. taken off California from the Monterey Bay Aquarium Research Institute's ROV *Tiburon*. This is a female specimen with developing juveniles.

Key to the species of *Crossota* in the Pacific Ocean

1   Gonads nearer ring canal than manubrium; umbrella colourless .... *C. alba*
-    Gonads located nearer manubrium than ring canal, umbrella pigmented 2
2   Gonads located approximately halfway between base of manubrium and mid-point of radial canal, umbrella with burnt-tangerine pigment .... *C. millsae*
-    Gonads near base of manubrium 3
3   With 200-250 tentacles in one row; umbrella deep reddish brown ...... *C. rufobrunnea*
-    With 600 or more tentacles, apparently in several rows; umbrella pale brown .... *C. brunnea*

Etymology. It is my pleasure to name this beautiful animal in honor of my friend and colleague Dr. Claudia E. Mills of Friday Harbor Laboratories to acknowledge her many substantial contributions to the study of gelatinous zooplankton and her willingness to share her knowledge with others.
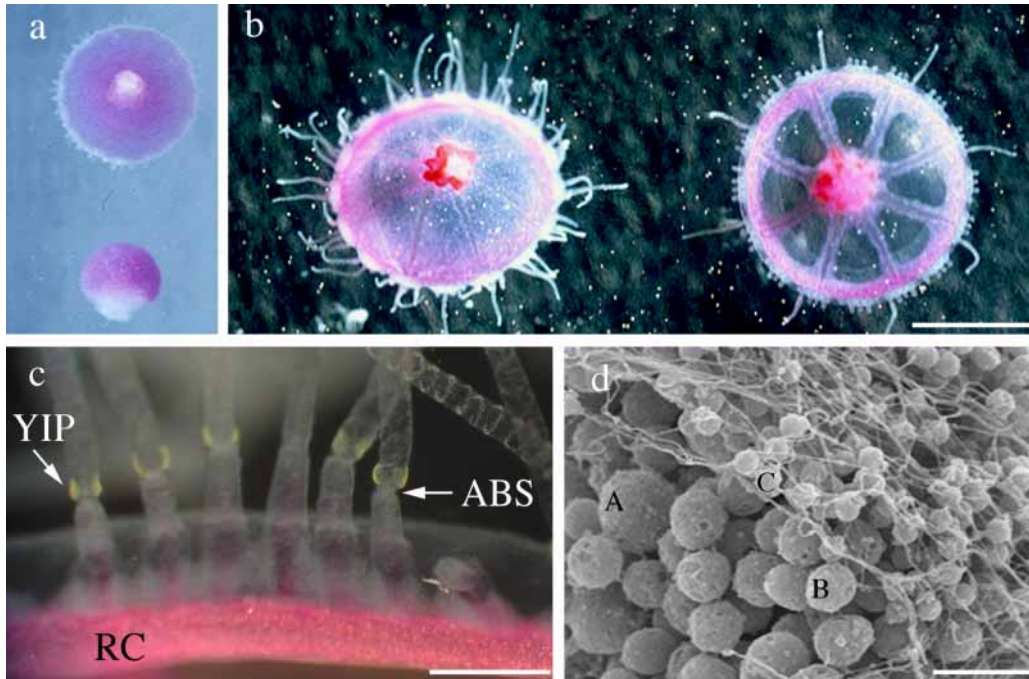
FIGURE 3. *Crossota millsae*, sp. nov. a) Two of the juvenile paratype specimens representing different stages of early development, scale bar = 2.5 mm. b) Two of the juvenile paratype specimens representing later stages of development, same scale bar as in Fig 3a. c) Abscission zone at base of tentacles. ABS = abscission point, RC = ring canal, YIP = yellow iridescent pigment. d) Scanning electron micrograph of spermatids from testes of the male specimen shown in Fig. 1b. Three size classes of spermatids are noted, A ~10 µm, B ~5 µm and C ~2 µm. The smallest spermatids have developing flagella. Scale bar = 10 µm.

Distribution. This medusa is a common species in the bathypelagos off California and Hawaii. Depth distributions for this species in these two regions are shown in Table 1. Due to precarious sea floor topography, tows were not conducted at greater depths at our study site off Hawaii, which makes conclusive comparisons of depth distributions between the two sites a bit weak. Off California, the greatest population densities were found at tow depths from 2144–3254 meters. Off Hawaii, the greatest densities are at average tow depths from 1200-1300 meters. Small individuals recently released from the mother were collected at great depths, e.g. station 87. A single small individual was collected at station 76 (average depth = 947 m), suggesting that ontogenic vertical migration may take place after the young are released from the mother. This species has recently been observed in the Sea of Cortez (Steven Haddock, Monterey Bay Aquarium Research Institute, pers. comm.).

TABLE 1. Capture records for *Crossota millsae* sp. nov. collected from the North Pacific Ocean off Point Conception, California in September, 1995 and off the leeward shore of Oahu, Hawaii in June and July of 1996. Oblique tows were made off California, and horizontal tows were made off Hawaii. All trawls with an average depth over 1000 m are shown. n.d. = no data.

Location	Depth (m)			Volume	Number of	Density
Station	Minimum	Maximum	Average	$(1000\ m^{-3})$	Individuals	$(Ind.10^{-6}\ m^3)$
California						
5	1000	1250	1125	59.4	4	67.3
40	993	1253	1123	38.4	0	0
14	1250	1755	1503	29.5	3	101.7
18	1724	2319	2022	87.4	9	103.0
39	2144	2763	2454	111.1	15	135.0
30	2248	2754	2501	104.5	11	105.3
10	2755	3254	3005	136.9	17	124.2
6	2797	3250	3024	159.4	0	0
15	3250	3797	3524	190.0	4	21.1
Hawaii						
2	1165	1291	1225	164.0	2	12.2
8	1024	1232	1084	195.9	6	30.1
14	943	1268	1107	256.5	0	0
26	977	1291	1120	195.0	6	30.8
33	1198	1536	1337	162.3	8	49.3
39	1076	1505	1270	199.6	14	70.14
45	1187	1466	1309	186.9	15	80.25
51	886	1406	1115	182.6	4	21.9
53	1028	1102	1075	37.4	2	53.5
56	1111	1383	1283	157.5	0	0
62	1058	1300	1223	187.9	19	101.1
68	1228	1377	1292	200.3	16	79.9
74	1574	1689	1616	26.9	0	0
75	1419	1574	1463	153.6	0	0
76	894	1042	947	70.0	1	14.3
80	1282	1662	1506	177.1	9	50.8
86	1088	1206	1123	119.1	0	0
87	745	983	915	51.1	1	19.6
91	987	1152	1051	141.5	6	42.4
97	911	1336	1129	n.d.	10	n.d.
98	1035	1130	1090	n.d.	3	n.d.
102	1010	1421	1159	n.d.	12	n.d.

Testes. Scanning electron microscopy of male gonads revealed spherical structures interpreted as spermatids (Fig. 3d). Three size classes of spherical spermatids were observed, ~10 µm, ~5 µm and ~2 µm. The smallest size class was associated with flagella. Although the mating and fertilization processes are unknown, the obvious sexual dimorphism and common co-occurrence of males and females lead to the assumption that fertilization has taken place and that the juvenile development described herein is not parthenogenic.

Development. Eggs begin to develop within the ovary and burst out as small white spheres as they develop into juvenile medusae. More than one egg will develop at a time, and development can be sequential (Figs. 1 & 2). A series of developing juveniles are shown in Figures 3a & b. The developing eggs change shape and color from white globular embryos to pink mushroom-shaped larvae (Fig. 3a) as they mature. Small pink lipid droplets identical in size and color to those of the ovary and adult radial canals are apparent in the bell of the juveniles. The ring canal develops first followed by formation of radial canals. Juveniles reach almost 6 mm in length before separation from the mother. Juveniles begin to develop tentacles while still attached, and keep them curled up as seen in Figure 1d. They are probably able to start capturing prey as soon as they break away from the mother or perhaps even beforehand within the subumbrellar space. The manubrium maintains its stout appearance after separation. The pigmentation of juvenile individuals is composed of lavender droplets similar to the composition of the adult ovaries and radial canals. Once free-living, the apex of the juvenile bell develops a faint tangerine color that spreads downward during maturation (not shown). The presence of the lipid-like droplets in both the adult and juvenile suggests that nutrients are being transferred from the mother to juveniles.

Tentacles. All adult specimens lost their tentacles in the net during capture; living specimens with tentacles extended were video taped *in situ* from the Monterey Bay Aquarium Research Institute's ROV *Tiburon* (Figure 2). Aboard ship, one specimen captured with the ROV was observed to autotomize its tentacles as it hung motionless in the water. The tentacles were negatively buoyant and sank slowly to the bottom of the chamber. At the base of each tentacle above the abscission zone, the tentacles have a yellow pigmented region that is slightly iridescent (Fig. 3c). Tentacles of some specimens are colorless, but they are magenta in other specimens. The cnidae of this species are clustered in rows around the tentacles (Fig. 3c), but the annulations are not as prominent as those seen in *Voragonema pedunculata* (Matsumoto et al. 1997).

Discussion

Distribution. The overall abundance of *Crossota millsae* is greater off California than Hawaii, reflecting the generally higher productivity of the California Current system compared to the central North Pacific Ocean. However, the population density at one station

off Hawaii was of a similar magnitude, i.e., over 100 individuals per 10^6 m³, with the stations off California, demonstrating the overall abundance of this species at great depths in both these regions of the North Pacific Ocean. Although many of the same species of bathypelagic hydromedusae have been observed off both Hawaii and California, including *Crossota alba* and *Crossota rufobrunnea*, not all species are found in both regions. For example, we have not collected *Vampyrocrossota childressi* off Hawaii, although *V. childressi* is now known from one station off British Columbia (53°N, 145°W, Charles B. Miller, Oregon State University, pers. comm.).

Off California, some other bathypelagic hydromedusae have been reported to have depth distributions restricted below one kilometer. Alvariño (1967) reported that *Haliscera bigelowi* (as *Homoeonema alba*) and *Aegina citrea* were found only below 1000 meters. The narcomedusa *Solmissus incisa* was reported by Thuesen & Childress (1994) and Childress *et al.* (1989, as *Solmaris* sp.) as another deep living species. All three of these species are now known to also inhabit shallower waters (Thuesen, personal observations; Kevin Raskoff, Monterey Bay Aquarium Research Institute, pers. comm.). The benthopelagic species *Voragonema pedunculata* (cf. Bouillon *et al.* 2001) although found at great depths just above the sea floor, is also known to inhabit waters as shallow as 100 m off central California (Matsumoto *et al.* 1997). Other deep-living hydromedusae off California are known to have distributions extending to shallower depths (Alvariño 1967; Thuesen 1993; Thuesen & Childress 1994; Purcell *et al.* 2001). *Crossota millsae* is therefore the only species of hydromedusae in this region reported to be restricted to great depths.

One parameter that has been used to describe the depth distributions of pelagic organisms is minimum depth of occurrence (MDO), the depth below which 95% of the population can be found (reviewed by Childress 1995). Thuesen & Childress (1994) assigned *C. millsae* (as *Crossota* sp. A) a MDO of 1100 m based on a smaller data set. The data presented in this paper suggest that a MDO closer to 1250 m is a better descriptor of the depth characteristics of the *C. millsae* population off California. Its MDO off Hawaii is difficult to calculate because of the limited data at greater depths, however the MDO may be somewhat shallower off Hawaii than California. The greatest population densities were found at ~1250 m off Hawaii and ~2500 m off California. Upper-midwater island-associated communities of macrozooplankton and micronekton are known to occur off Hawaii (Reid *et al.* 1991), and it is possible that the distribution of *C. millsae* off Hawaii shifts shallower due to effects of the islands on these communities.

Testes and spermatogenesis. Tardent (1978) reported the size range of cnidarian spermatozoa to be 1-5 µm, and the smallest spermatids observed in our study fall within that range. Development of spermatocytes to spermatids to spermatozoa in cnidarians can follow several division strategies, even within the same species (Tardent 1978). Without knowledge of the internal subcellular anatomy, it remains unknown if the largest spheres observed in the testes of *C. millsae* are spermatocytes or spermatids. It appears from the three size classes of spheres observed with SEM that the smallest spermatids of *C. millsae*

are the result of two divisions, spermatocyte to spermatid I to spermatid II. However, it is possible that the largest spheres could be spermatids that directly divide into either 2 or 4 spermatids. Since the testes of hydromedusae are basically epithelial sacks tightly packed with developing germ cells (Miller 1981), the number of sperm in one individual can be estimated from morphological measurements. Assuming the volume (V) equation for a testis is that of a sausage, with $V = \pi r^2 h - 4/3 \pi r^3$, with length (h) = 4.0 mm, and width (2r) = 0.6 mm, and a radius of 1.25 µm for the final spermatid stage, the total testicular volume of 8 testes is 8.14 mm^3 which corresponds to a maximum of ~10^9 sperm. The spermatogenic cycle can range from several days to more than a week in epipelagic hydromedusae, and spermatogenesis can persist for over a month (Miller 1981). It is unknown how many sperm are produced over the lifespan of *C. millsae*, but 10^9 is the baseline estimate. More study is necessary to determine if the pathways, timing and persistence of spermatogenesis in this and other deep-sea hydromedusae are markedly distinct from epipelagic species.

Development. The reproductive biology of Cnidaria has been reviewed by several authors (cited in Fautin 2002). Very little is known about the developmental biology of deep-sea hydrozoans. Rhopalonematid hydromedusae are characterized by the absence of an asexual polyp stage (cf. Hyman 1940) and reproduction that proceeds strictly sexually. *Crossota millsae* appears to be investing a significant degree of energy as it cares for its young. Lecithotrophic juveniles also appear to gain nutrients from the mother as they grow larger. The presence of tentacles on juveniles still attached to the mother suggests that these young may be able to catch prey swept into the subumbrellar cavity. Development evidently occurs year round since brooding individuals have been captured over the entire year off California.

Chia (1976) defined clearly the terminology regarding sexual reproduction in sea anemones. He defines viviparous reproduction as internal fertilization followed by the release of juveniles sufficiently developed that they may live an independent life when set free from the mother. Although fertilization has not yet been observed, I have used the term viviparity, *sensu* Chia, to define the development and parental care observed in *C. millsae*. The obvious sexual dimorphism and common co-occurrence of males and females seems to warrant this assumption. Viviparous reproduction was contrasted with brooding species, as the latter are released as larvae then provided with parental care as they develop into juveniles. Chia categorized many sea anenome species as following an oviparous-brooding-lecithotrophic strategy, *e.g.*, anemones of the genus *Epiactis*. *Epiactis* spp. release non-ciliated larvae which attach to the column of the parent anenome and develop into juveniles while attached to the adult (Edmands 1995). The brooding of asexually pro-duced juveniles by *Stygiomedusa fabulosa* (Russell & Rees 1960) would not meet Chia's definition of the term viviparity, if the young are produced asexually as believed. In corals, the term brooding has been widely used to apply to embryos resulting from both sexual and asexual reproductive processes (*e.g.*, Goffredo & Telò 1998), and it seems sensible to follow that broader definition of brooding with pelagic cnidarians also. Viviparity is a

more specific term that refers to juveniles produced through sexual reproduction. Further studies on *C. millsae* will help elucidate the intricacies of the reproductive biology of bathypelagic cnidarians.

Acknowledgements

References

Alvariño, A. (1967) Bathymetric distribution of Chaetognatha, Siphonophorae, Medusae, and Ctenophorae off San Diego, California. *Pacific Science*, 21, 474–485.

Berrill, N.J. (1949) Developmental analysis of scyphomedusae. *Biological Review,* 24, 393–410.

Chia, F.-S. (1976) Sea anemone reproduction: patterns and adaptive radiation. In: Mackie G.O. (Ed.) *Coelenterate Ecology and Behavior*, Plenum Press, New York, pp. 261–270.

Bouillon, J., Pagès, F. & Gili, J.-P. (2001) New species of benthopelagic hydromedusae from the Weddell Sea. *Polar Biology*, 24, 839–845.

Childress, J.J. (1995) Are there physiological and biochemical adaptations of metabolism in deep-sea animals? *Trends in Ecology & Evolution*, 10, 30–36.

Childress, J.J., Barnes, A.T., Quetin, L.B. & Robison, B.H. (1978) Thermally protecting cod ends for recovery of living deep-sea animals. *Deep-Sea Research*, 25, 419–422.

Childress, J.J., Gluck, D.L., Carney, R.S. & Gowing, M.M. (1989) Biomass distribution and oxygen consumption in a deep-sea benthic boundary layer dominated by gelatinous organisms. *Limnology and Oceanography*, 34, 915–932.

Edmands, S. (1995) Mating systems in the sea anemone genus *Epiactis*. *Marine Biology*, 123, 723–733.

Fautin, D.G. (2002) Reproduction of Cnidaria. *Canadian Journal of Zoology*, 80, 1735–1754.

Fautin, D.G., Spaulding, J.G. & Chia, F.-S. (1989) Cnidaria. In: Adiyodi, K.G. & Adiyodi, R.G. (Eds.) *Reproductive biology of invertebrates. Volume IV, Part A Fertilization, Development, and Parental Care.*, John Wiley & Sons, Chichester, pp. 43–62.

Gage, J.D. & Tyler, P.A. (1991) *Deep-sea biology: A natural history of organisms at the deep-sea floor*, Cambridge University Press, Cambridge, 504 pp.

Goffredo, S. & Telò, T. (1998) Hermaphroditism and brooding in the solitary coral *Balanophyllia europaea* (Cnidaria, Anthozoa, Scleractinia). *Italian Journal of Zoology*, 65, 159–165.

Hyman, L.H. (1940) *The Invertebrates: Protozoa through Ctenophora*, McGraw-Hill, New York, 726 pp.

Kramp, P.L. (1959) The hydromedusae of the Atlantic Ocean and adjacent waters. *"Dana"-Report*, 46, 1–283.

Kramp, P.L. (1968) The hydromedusae of the Pacific and Indian Oceans. *"Dana"-Report*, 72, 1–200.

Larson, R.J., & Harbison, G.R. (1990) Medusae from McMurdo Sound, Ross Sea, including the descriptions of two new species, *Leuckartiara brownei* and *Benthocodon hyalinus*. *Polar Biology*, 11, 19–25.

Matsumoto, G.I., Baxter, C. & Chen, E.H. (1997) Observations of the deep-sea trachymedusa *Benthocodon pedunculata*. *Invertebrate Biology*, 116, 17–25.

Miller, R.L. (1989) Cnidaria. In: Adiyodi, K.G. & Adiyodi, R.G. (Ed.) *Reproductive biology of invertebrates. Volume II, Spermatogenesis and sperm function.*, John Wiley & Sons, Chichester, pp. 23–73.

Naumov, D. V. (1971) Gydroidnye i stsifoidnye medusy iz Kurilo-Kamchatskogo zhelova. (Hydromedusae and Scyphomedusae from the Kurile-Kamchatka trench). *Trudy Inst. Okeanol.*, 92, 9–17.

Purcell, J.E., Breitburg, D.L., Decker, M.B., Graham, W.M., Youngbluth, M.J. & Raskoff, K.A. (2001) Pelagic cnidarians and ctenophores in low dissolved oxygen environments. In: Rabalais, N.N. & Turner, R.E. (Ed.) *Coastal hypoxia: consequences for living resources and ecosystems*, American Geophysical Union, Washington, D. C., pp. 77–100.

Reid, S.B., Hirota, J., Young, R.E. & Hallacher, L.E. (1991) Mesopelagic-boundary community in Hawaii: micronekton at the interface between neritic and oceanic ecosystems. *Marine Biology*, 109, 427–440.

Robison, B.H. (1993) Midwater research methods with MBARI's ROV. *Marine Technology Society Journal*, 28, 32–39.

Russell, F.S. & Rees, W.J. (1960) The viviparous scyphomedusa *Stygiomedusa fabulosa* Russell. *Journal of the Marine Biological Association of the United Kingdom*, 39, 303–317.

Tardent, P. (1978) Coelenterata, Cnidaria. In: Seidel, F. (Ed.) *Einleitung zum Gesamtwerk Morphogenetische Arbeitsmethoden und Begriffssysteme, Reihe 1, Lieferung 1: A-1*, Gustav Fisher, Jena, pp. 69–415.

Thuesen, E.V. (1992) *Enzymatic activities, metabolic rates and chemical compositions of midwater chaetognaths, medusae, and certain nemertean and polychaete worms in relation to habitat depth*, University of California, Santa Barbara, 136 pp.

Thuesen, E.V. (1993) *Vampyrocrossota childressi,* a new genus and species of black medusa from the bathypelagic zone off California (Cnidaria: Trachymedusae: Rhopalonematidae). *Proceedings of the Biological Society of Washington*, 106, 190–194.

Thuesen, E.V. & Childress, J.J. (1994) Oxygen consumption rates and metabolic enzyme activities of oceanic California medusae in relation to body size and habitat depth. *Biological Bulletin*, 187, 84–98.

Vanhöffen, E. (1902) Die Craspedoten Medusen der deutschen Tiefsee Expedition 1898-1899. I. Trachymedusen. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee Expedition "Valdivia"*, 3, 55–86.

Young, C.M. (2003) Reproduction, development and life-history traits. In: Tyler, P.A. (Ed.) *Ecosystems of the Deep Ocean*. Elsevier, Amsterdam, pp. 381–426.