NOAA Technical Report NMFS Circular 397

Marine Flora and Fauna of the Northeastern United States. Cnidaria: Scyphozoa

Ronald J. Larson

August 1976

U.S. DEPARTMENT OF COMMERCE
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U.S. DEPARTMENT OF COMMERCE
Elliot L. Richardson, Secretary

National Oceanic and Atmospheric Administration
Robert M. White, Administrator

National Marine Fisheries Service
Robert W. Schoning, Director

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FOREWORD

This issue of the "Circulars" is part of a subseries entitled "Marine Flora and Fauna of the Northeastern United States." This subseries will consist of original, illustrated, modern manuals on the identification, classification, and general biology of the estuarine and coastal marine plants and animals of the Northeastern United States. Manuals will be published at irregular intervals on as many taxa of the region as there are specialists available to collaborate in their preparation.

The manuals are an outgrowth of the widely used "Keys to Marine Invertebrates of the Woods Hole Region," edited by R. I. Smith, published in 1964, and produced under the auspices of the Systematics-Ecology Program, Marine Biological Laboratory, Woods Hole, Mass. Instead of revising the "Woods Hole Keys," the staff of the Systematics-Ecology Program decided to expand the geographic coverage and bathymetric range and produce the keys in an entirely new set of expanded publications.

The "Marine Flora and Fauna of the Northeastern United States" is being prpared in collaboration with systematic specialists in the United States and abroad. Each manual will be based primarily on recent and ongoing revisionary systematic research and a fresh examination of the plants and animals. Each major taxon, treated in a separate manual, will include an introduction, illustrated glossary, uniform originally illustrated keys, annotated check list with information when available on distribution, habitat, life history, and related biology, references to the major literature of the group, and a systematic index.

These manuals are intended for use by biology students, biologists, biological oceanographers, informed laymen, and others wishing to identify coastal organisms for this region. In many instances the manuals will serve as a guide to additional information about the species or the group.

Geographic coverage of the "Marine Flora and Fauna of the Northeastern United States" is planned to include organisms from the headwaters of estuaries seaward to approximately the 200-m depth on the continental shelf from Maine to Virginia, but may vary somewhat with each major taxon and the interests of collaborators. Whenever possible representative specimens dealt with in the manuals will be deposited in the reference collections of major museums in the region.

After a sufficient number of manuals of related taxonomic groups have been published, the manuals will be revised, grouped, and issued as special volumes. These volumes will thus consist of compilations of individual manuals within phyla such as the Cnidaria, Arthropoda, and Mollusca, or of groups of phyla.

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Marine Flora and Fauna of the Northeastern United States. Cnidaria: Scyphozoa

RONALD J. LARSON[1]

ABSTRACT

This manual is an introduction to the scyphomedusae found in coastal waters from Maine to the Chesapeake Bay. It includes a discussion of their identification, collection, rearing, preservation, and nematocysts. Also included is an introduction to the natural history of the scyphopolyps and medusae, a discussion of stinging scyphomedusae, a glossary of terms, an illustrated synopsis of ephyrae, an illustrating key to the scyphomedusae (including the Stauromedusae), an annotated systematic list, a bibliography of major references, and finally an index.

INTRODUCTION

The class Scyphozoa of the phylum Cnidaria or Coelenterata as it once was called, are commonly known as "jellyfish," "sea nettles," and "sea wasps." Scyphomedusae, as these jellyfish are termed, are the most conspicuous of the jellylike animals. Some species reach 1 m or more in diameter and most are very colorful. All have stinging organs, hence the names "sea nettle" and "sea wasp." Scyphomedusae are seasonal; most species are seen during the warmer months. They represent the sexual stage of most scyphozoan species. The asexual stage is a small benthic (bottom-living) polyp (scyphopolyp) which is perennial. The scyphopolyp generally buds larval scyphomedusae (ephyrae) during the spring. The medusae are large by midsummer.

Scyphomedusae have a muscular saucer-shaped or hemispherical bell or umbrella which propels the medusae through the water by contracting and expelling water behind. Long threadlike tentacles often hang from the umbrella and are covered by stinging organs (nematocysts) which are used to capture prey. Surrounding the mouth are ribbonlike, curtainlike, or gelatinous arms which transport prey to the mouth.

Scyphopolyps are minute and rarely seen. They are saclike with a circle of tentacles around the oral end and are attached to the bottom by a stalklike peduncle.

Scyphozoans usually have a scyphomedusa and a scyphopolyp stage in their life history but one group remains as a polyp only. The Stauromedusae or stalked medusae lack a medusa stage. Some scyphomedusae lack a polyp stage; *Pelagia*, an oceanic medusa, has eggs which, when fertilized, transform directly into a juvenile medusa and bypass the normal polyp stage.

Scyphomedusae are generally regarded as pests because of their irritating stings, but many are ecologically important. *Chrysaora*, well known as the sea nettle, consumes large numbers of ctenophores which might otherwise be very detrimental to oyster and clam populations by feeding on their larvae. Other scyphomedusae prey on jellyfish which have few predators and feed on commercially important invertebrate and fish larvae.

Five orders of Scyphozoa are recognized. The Stauromedusae, or "stalked jellyfish," are not well known even though they may be abundant. They are inactive and cryptically pigmented and are difficult to see when attached to algae. The Cubomedusae, or sea wasps, are also infrequently seen but are infamous because of their potent sting. The Coronatae, or "crown medusae," are mostly deepwater (bathypelagic). The Semaeostomeae, commonly known as sea nettles, are the most familiar order, and most shallow-water scyphozoans belong to this group. The Rhizostomeae, which lack tentacles, are mostly tropical and are uncommon in New England waters.

DESCRIPTION OF ORDERS OF SCYPHOZOA

Order Stauromedusae—Small benthic scyphozoans which lack a free-swimming medusa stage. Stauromedusae are urn- or funnel-shaped and are attached to the substrate by a stalklike peduncle. In some forms, the margin is divided into eight arms, the knobbed tentacles project from the arm tips; in others the tentacles project from the margin. Modified tentacles, which may act as anchors or sense organs, occur on the margin between the groups of tentacles in some species. The gonads are paired, leaflike, or folded structures extending along the length of the calyx. A wormlike planula larva develops from the zygote and creeps over the substrate, eventually attaches itself and becomes a juvenile stauromedusa. Stauromedusae occur mainly in cold,

[1]Department of Marine Sciences, University of Puerto Rico, Mayaguez, Puerto Rico 00708; present address: Division of Echinoderms, U.S. National Museum, Washington, D.C. 20560.

shallow marine waters. Adult Stauromedusae usually occur only during the summer, and the wintering juveniles may be difficult to find because of their small size. Tropical and deepwater forms are rare.

Order Cubomedusae (Fig. 1)—Small- to medium-sized medusae with a somewhat cuboidal or rectangular-shaped transparent umbrella. A velarium, or shelflike projection, encircles the inner margin of the umbrella. Tentacles vary from four to many and are on bladelike projections of the bell, termed pedalia. Four rhopalia are located about midway between the corners of the umbrella near the margin. The mouth is at the end of a flask-shaped stomach which hangs within the umbrella. The life cycle of the Cubomedusae is unlike that of other scyphozoans. The cubopolyp has several features in common with hydrozoan polyps, e.g., solid tentacles, stenotele nematocysts. Cubopolyps metamorphose directly and totally into a single medusa, other scyphopolyps undergo transverse fission producing one to many ephyrae. Werner (1973) has placed the Cubomedusae in their own class, Cubozoa, because of this group's unique characteristics. Cubomedusae are tropical or subtropical me-

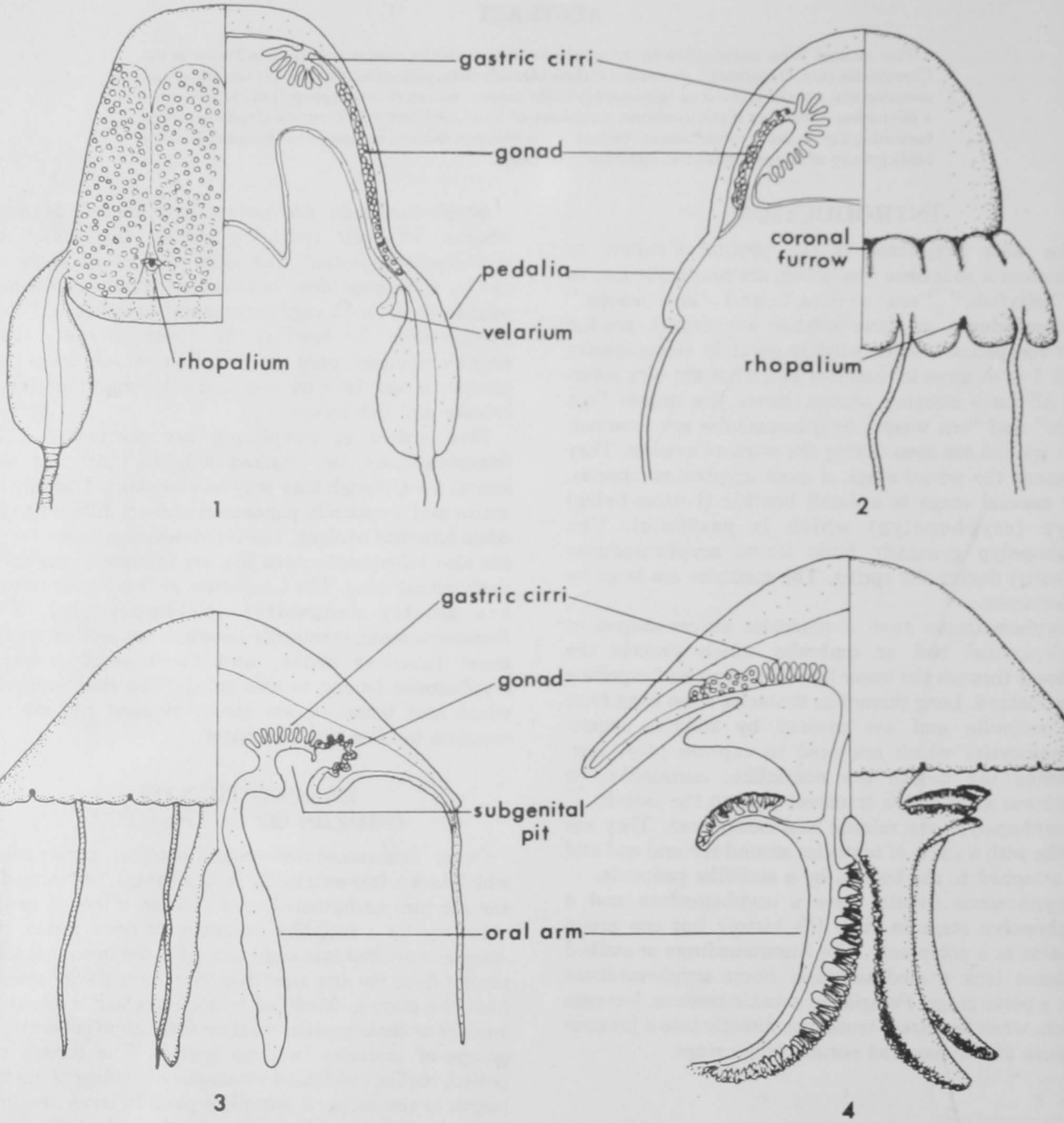


Figure 1.—Cubomedusa.

Figure 2.—Coronate medusa.

Figure 3.—Semaeostome medusa.

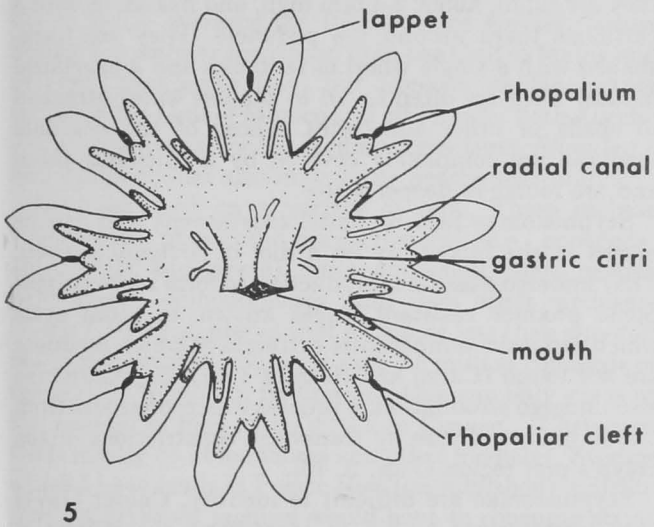
Figure 4.—Rhizostome medusa.

dusae but are occasionally transported into temperate regions by warm currents. Cubomedusae are known as sea wasps because of their virulent sting.

Order Coronatae (Fig. 2)—Small- or medium-sized medusae with flattened or dome-shaped umbrella which is divided into two regions by a circular (coronal) furrow. The tentacles occur between marginal lappets. Radial thickenings of the margin, termed pedalia, give rise to the tentacles, lappets, and rhopalia. The gonads are on four septa which project into the coelenteron. The Coronatae are mostly bathypelagic and darkly pigmented. The coronate polyp, all known species being placed in the genus *Stephanoscyphus*, is covered by a chitinous cuticle which has numerous circular annulations (Kramp 1959).

Order Semaeostomeae (Fig. 3)—Large medusae, usually saucer-shaped. The mouth has four long oral arms. These may be folded once as in *Pelagia*, or folded a number of times as in *Cyanea*. Tentacles occur between marginal lappets as in the Coronatae, or on the subumbrella. Gonads occur on folds of the gastrodermis. The polyp stage is small and naked or has a thin cuticle around its base and can encyst under certain conditions (Fig. 7). A typical ephyra (Fig. 5) is produced, usually by polydisc strobilation (Fig. 9). Semaeostomes are the most common scyphomedusae in temperate coastal waters.

Order Rhizostomeae (Fig. 4)—Large medusae, usually with a hemispherical umbrella. Marginal tentacles are absent, but eight oral arms serve both to capture and transport food to the gastric cavity by way of a canal system. A central mouth is usually absent; instead the mouth is formed by a large number of bifurcating grooves which lie on the ventral and lateral sides of the oral arms. The oral arms may have terminal appendages which have a high concentration of nematocysts at their tip. The gonads are folds of the gastrodermis as in the semaeostomes. The polyp stage has a long stalklike peduncle which is partially covered with a thin cuticle. Ephyrae are usually produced by monodisc strobilation (Fig. 10). Rhizostomes are mostly tropical, with only a few species extending into temperate waters.



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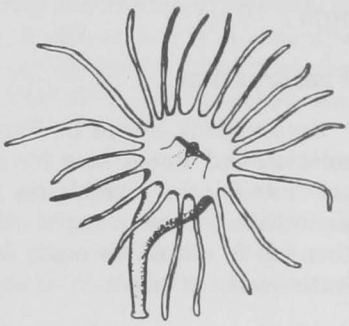
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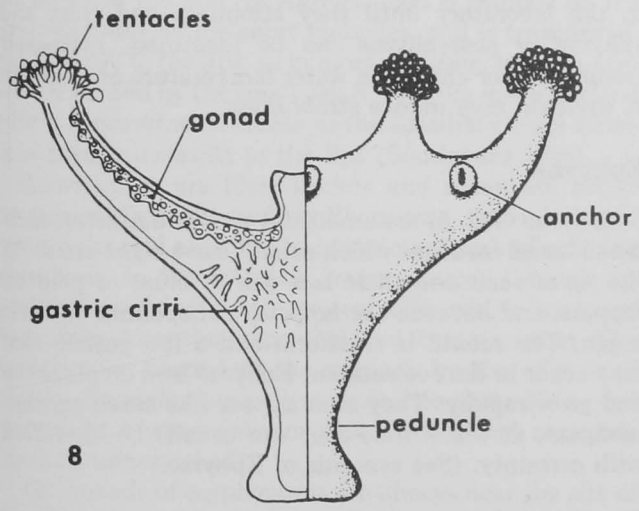

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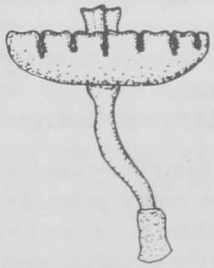
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Figure 5.—Ephyra, newly released.

Figure 6.—*Stephanoscyphus*.

Figure 7.—Semaeostome polyp.

Figure 8.—Stauromedusa.

Figure 9.—Semaeostome strobila.

Figure 10.—Rhizostome strobila.

METHODS

Collecting

To obtain medusae in the best possible condition they should be dipped from the water surface using a bucket or other large container. Deepwater species can be caught in plankton nets equipped with large sample buckets.

Scyphopolyps can be obtained by dredging, collecting at low tide, or diving. Polyps commonly attach to shells, oysters being a favorite substrate. Polyps will also settle on glass slides placed in areas where medusae spawn.

Rearing

Scyphozoans can be raised from embryos to maturity in the laboratory (Spangenberg 1965). Polyps can be reared in small dishes and fed newly hatched *Artemia*. Planktonic stages are more difficult to raise, requiring a large volume of circulating water and suspended food. Medusae should be fed daily, preferably more often. *Artemia* can be fed to such plankton-feeding forms as *Aurelia* and rhizostome medusae. *Chrysaora* can be fed ctenophores, *Artemia*, or other medusae. (See Russell 1970.)

Preservation

Scyphozoans should be fixed in a 20% formaldehyde solution and stored in a 5% neutralized formaldehyde solution. Alcohol dehydrates specimens, making them distorted. Ordinary paper disintegrates in Formalin, thus labels should be made from high-rag content and water-resistant paper.

NEMATOCYSTS

Nematocysts occur in all cnidarians. They are produced by specialized cells, cnidoblasts. A great amount of work has been done on the cnidoblast and how the nematocyst functions (Picken and Skaer 1966). Weill (1934) showed that the cnidome is taxonomically important; and recently Calder (1971) used nematocysts as a means of identifying polyps of *Chrysaora, Cyanea,* and *Aurelia.* (Also see Calder 1974.)

NATURAL HISTORY

Stauromedusae

Stauromedusae, contrary to what their name implies, are really polyplike. Some are permanently attached. Others can move in a somersaulting motion by adhering to the substrate with the oral end and releasing the pedal disc, then reattaching the disc at a new location; but none have been observed to swim.

They attach to algae, sea grass (*Zostera*), and other substrates in shallow areas which have adequate water circulation. They may be abundant, but because of their inconspicuous coloration and inactivity, they are rarely seen. Most of the diet consists of other benthic animals, with crustaceans being the major part of the food. Berrill (1962) noted that *Lucernaria* fed on the amphipod *Amphithoe* and the small gastropod *Lacuna.* At Woods Hole, Mass., I found mostly harpacticoid copepods and gammarid amphipods, and a few chironomid fly larvae in gastric cavities of *Craterolophus.* Prey, caught by the tentacles, cause one or all arms to fold over the mouth which then expands and engulfs the food.

Stauromedusae, like scyphistomae, occur year-round. Berrill (1962) found that Stauromedusae, along the coast of Maine, spawn during the summer and then die. Juveniles appear during the fall and become sexually mature by summer.

Apparently Stauromedusae are very sensitive to environmental conditions and have been difficult to raise in aquaria. Berrill (1962) remarked that they are becoming rare in Massachusetts Bay due to pollution.

Scyphistomae

Scyphistomae are the polyp stages of scyphomedusae; in the semaeostome (Fig. 7) and rhizostome medusae, they are small, about 2-4 mm high, and naked, or with a chitinous theca around the peduncle. They are flask-shaped with a single whorl of tentacles and a cruciform mouth. They are often found in shallow water attached to shells or other substrates. Those of the coronate medusae are completely covered by a chitinous theca and are found in deeper water.

Scyphistomae feed on small crustaceans and can be reared in the laboratory on a diet of *Artemia* nauplii. They undergo asexual reproduction to form more polyps. Some produce resistant stages known as pedal cysts which can resist temperature extremes at which medusae are not found (Cargo and Schultz 1967). Scyphistomae also undergo strobilation, a process which produces from one to many ephyrae by transverse constrictions of the polyp's oral region (Figs. 9, 10).

Scyphistomae are difficult to identify. Calder (1971) used nematocysts to aid in identifying the polyps of *Aurelia, Chrysaora,* and *Cyanea.* They can also be reared in the laboratory until they strobilate and then the ephyrae or postephyrae can be identified. Increased feeding and/or change in water temperature or addition of thyroxin may induce strobilation.

Ephyrae

Ephyrae (Fig. 5) are small, 1-4 mm in diameter, flattened larval medusae which usually have eight arms. At the tip of each arm there is a pair of blunt or pointed lappets, and between the lappets, a rhopalium or sense organ. The mouth is cruciform and a few gastric cirri may occur in the coelenteron. Ephyrae feed on plankton and grow rapidly. They soon appear like small scyphomedusae, at which time they can usually be identified with certainty. (See synopsis of Ephyrae.)

Scyphomedusae

By being planktonic, scyphomedusae may find food,

which is unavailable to the polyp, and can also distribute gametes over an extensive area thereby increasing the distribution of the species and also insuring that uninhabited substrates are utilized if conditions are favorable for the polyp.

Scyphomedusae are usually short-lived. They grow rapidly and later die due to changes in water temperature or other factors, which for the most part are not understood. *Chrysaora* ephyrae from the Chesapeake Bay are released in early June. By July these medusae are mature, and most have died by mid-September. *Aurelia* and *Cyanea* may live somewhat longer.

The occurrence of some scyphomedusae is related to water temperature. *Cyanea* in the Gulf of Maine are first seen in April or May and are mature by early summer (Bigelow 1926). *Cyanea* is found in the Chesapeake Bay early in the winter and matures by February or March. *Chrysaora* occurs only at higher temperatures (about 20°C) in the Chesapeake Bay in early May, and slightly later at Woods Hole, Mass. Because of this dependence on high temperatures, it apparently cannot strobilate in colder water and is not found north of Cape Cod. *Aurelia*, whose range overlaps the two previous species, occurs during the warmer months in both the Gulf of Maine and in the Chesapeake Bay, but appears earlier further south. In the Gulf of Mexico and off Florida, both *Aurelia* and *Chrysaora* can occur at almost any time. *Rhopilema* and *Stomolophus* also may occur nearly year-round.

Medusae feed on a variety of prey. These include ctenophores, planktonic microcrustacea (i.e., copepods, amphipods, and larvae), larval and small fishes, pelagic polychaetes, siphonophores, and even other medusae. Fraser (1969) calculated that a *Cyanea* less than one-half meter in diameter would eat over 1.5 million copepods of the genus *Calanus* in its lifetime. One can only guess at the amount of food eaten by a 2-m *Cyanea*. *Chrysaora* feeds mostly on ctenophores and other medusae. Studies which I have made in Puerto Rico (unpublished) indicate that a *Chrysaora* medusa would have to consume about 15 kg of ctenophore *Mnemiopsis* in order to attain a diameter of 150 mm. In *Aurelia*, food is trapped on the umbrella and by the short tentacles, and is transferred, not directly to the lips, as in most medusae, but to a food groove formed by the small velarium. Cilia move the food which is mixed with mucus to the adradial canals where it is then transferred to the lips (Southward 1955).

Rhizostomes are filter feeders and many are active swimmers. In forms such as *Rhopilema*, water is forced around the oral arms by the contracting umbrella during swimming. In *Stomolophus*, water is forced through the keellike appendages. Minute tentacles, which line these structures, filter the suspended food from the water. The food is then carried to the stomach by the cilia-lined canals. *Stomolophus* collected at Beaufort, N.C., fed mostly on bivalve veligers and harpacticoid copepods (author, unpublished).

The gonads of scyphozoans are always near the site of digestion. In semaeostomes and rhizostomes the gonads are infoldings of the subumbrella which also bear the gastric cirri. Some scyphomedusae spawn while still very small. *Chrysaora* reared by the author began spawning at the size of 55 mm and spawned almost nightly thereafter. Fertilization usually takes place within the gastric cavity or on the surface of the ovary. In *Cyanea* and *Aurelia* the embryos are retained on the oral arms. *Aurelia* has brood pockets on the oral arms of the female where embryos are retained until the planula is released.

The embryology is quite variable even within the same species. Segmentation is usually total but gastrulation depends upon egg size, with ingression in small eggs and invagination in large ones and by both methods in medium-sized ova. Usually a planula is produced, which settles and forms a polyp, but very large eggs may bypass both the planula and polyp and form a modified ephyra as they do in *Pelagia* (Berrill 1949).

Symbiosis is widespread in the Cnidaria and occurs frequently in the Scyphozoa. There are numerous reports of juvenile fishes associated with scyphomedusae; Mensueti (1963) discussed these associations. Associations between juvenile fish and medusae range from the fish seeking refuge under the umbrella, or between the tentacles, to predation with the larger fish eating bits of the tentacle or gonad. It is not fully understood how certain species of fishes, e.g., *Peprilus* and *Poronotus*, are able to feed on medusae without ill effects, but it is generally thought that antibodies may be involved and that the secretion of mucus by the fish may prevent the nematocysts from discharging.

Crustacea are also known to parasitize scyphomedusae; hyperiid amphipods may both steal food from medusae and feed on medusal tissue. Phillips et al. (1969) discussed the parasitic habits of the two species of brachyuran crabs on medusae in the Gulf of Mexico.

STINGING MEDUSAE

Chrysaora is popularly known as the sea nettle because its sting can be very painful. *Cyanea* also is a stinger; Russell (1970) noted that *Cyanea* was the cause of a mysterious death in Conan Doyle's story, "Adventure of the Lion's Mane." The majority of the Cubomedusae are stingers, as are coronate medusae, some producing a very severe sting. *Aurelia*, *Rhopilema*, *Stomolophus*, *Phacellophora*, and the Stauromedusae are not known to be severe stingers. Halstead (1965) gave an account of the nature of the wounds and medical aspects of stings. Cargo and Schultz (1967) found that when meat tenderizers containing proteolytic enzymes were mixed with water and applied to the affected area, the pain was quickly relieved.

GLOSSARY

anchors (Fig. 8) adhesive organs between arms of some Stauromedusae.
calyx funnel-shaped umbrella of Stauromedusae.
cnidoblast cell in which the nematocyst forms.
cnidome complement of nematocyst types present.
coelenteron gastric cavity or stomach.

coronal furrow (Fig. 2) circular groove which divides the exumbrella of the coronate medusae.

cruciform cross-shaped.

ephyra (Fig. 5) planktonic larva of Scyphozoa except Cubomedusae and Stauromedusae. Usually with 8 pairs of arms and 8 rhopalia.

exumbrella aboral or upper surface of umbrella.

gastric cirri or *phacellae* (Fig. 1) hollow fingerlike projections in the coelenteron which aid in digestion.

lappet flaplike structure making up the scalloped margin of the umbrella.

monodisc strobilation (Fig. 10) a single ephyra produced per strobila at one time.

oral arm armlike extensions of the corners of the mouth which hang from the subumbrella of the Scyphozoa, 4 in number in the semaeostomes (Fig. 3) and 8 in the rhizostomes (Fig. 4).

pedalia radial thickenings between lappets and coronal furrow of the coronate medusae (Fig. 2): bladelike projections of Cubomedusae to which the tentacles are attached (Fig. 1).

peduncle (Fig. 8) stalk of polyps, or Stauromedusae.

polydisc strobilation (Fig. 9) several ephyrae produced from a polyp at the same time.

rhopalium (Figs. 1, 2) hollow, club-shaped sense organ generally located near the umbrella margin, usually with a statocyst and, rarely, an ocellus or ocelli.

scyphistoma polyp of scyphozoan medusae excluding the Stauromedusae and Cubomedusae.

sensory niche open structure partially enclosing rhopalium in Cubomedusae.

strobila scyphistoma which is forming ephyrae.

strobilation process of producing ephyrae.

subumbrella oral or underside of umbrella.

velarium (Fig. 1) shelflike structure at margin of umbrella in Cubomedusae and *Aurelia*.

INTRODUCTION TO THE KEYS TO THE SCYPHOZOA

An attempt has been made in constructing the keys to include those features which are most obvious or which occur in both juvenile and adult specimens. As medusae grow, structures such as tentacles usually increase in number and oral arms become increasingly folded or complex, while other structures, e.g., rhopalia, usually remain unchanged. Because of the delicate nature of medusae they are often injured and parts may be missing or abnormal. Therefore, in using the key some discretion must be used for each specimen to determine which characters are usable.

Key to the Stauromedusae of the Northeast Coast of the United States

1 With anchors 2

1 Without obvious anchors 4

2 (*1*) Anchors large; no shieldlike covering; gonads extend into arms 3

2 (*1*) Anchors small with shieldlike covering at base; arms short; gonads do not extend into arms . . . . . *Thaumatoscyphus atlanticus*

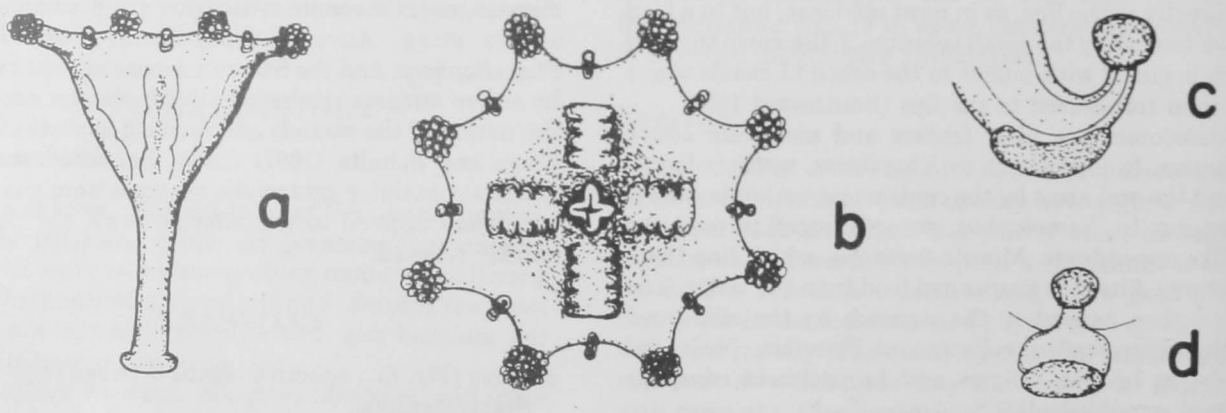

Figure 11.— *Thaumatoscyphus atlanticus*.
a. side view
b. oral view
c. anchor, side view
d. anchor, front view

3 (2) Arms short; anchors bean-shaped; calyx as high as broad . . . . . *Haliclystus auricula*

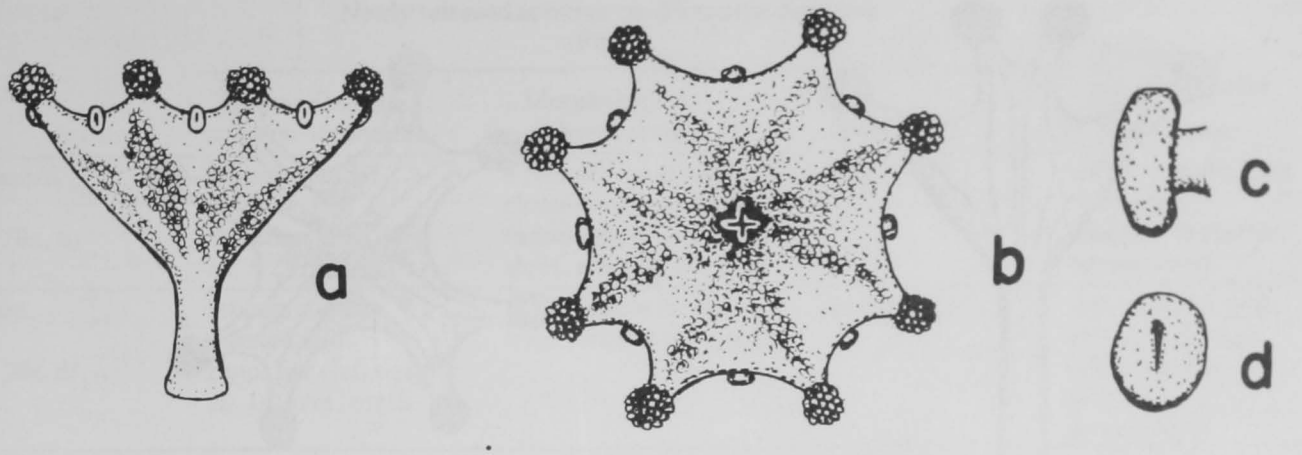

Figure 12.— *Haliclystus auricula*.
a. side view **b. oral view**
c. anchor, side view **d. anchor, front view**

3 (2) Arms long; anchors trumpet-shaped with short projection at center; calyx broader than high
. . . . . *Haliclystus salpinx*

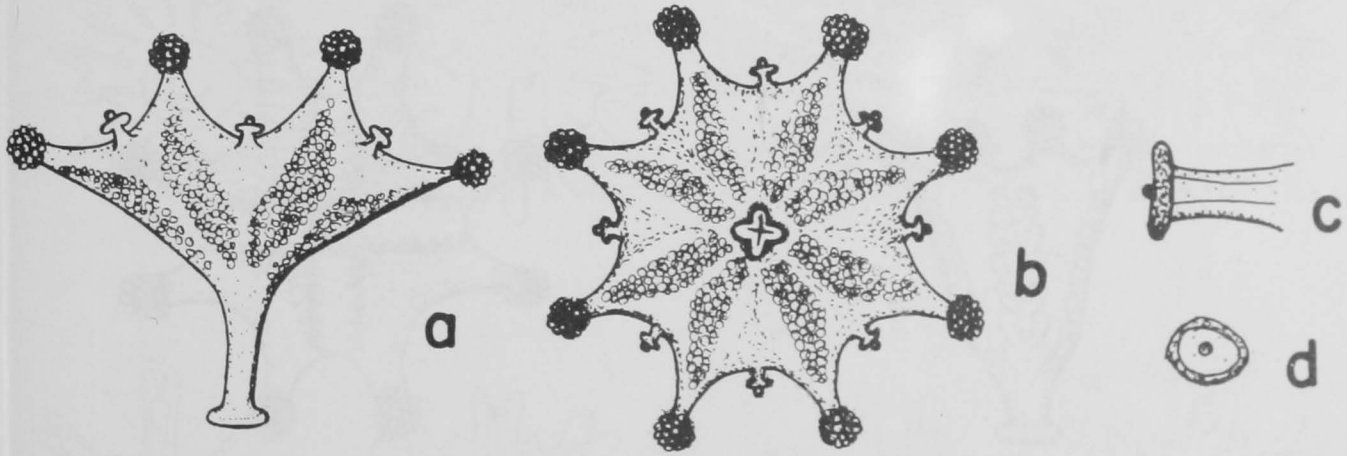

Figure 13.— *Haliclystus salpinx*.
a. side view **b. oral view**
c. anchor, side view **d. anchor, front view**

4 (1) Peduncle and arms long; arms paired; calyx broader than high; largest New England Stauromedusa . . . . . *Lucernaria quadricornis*

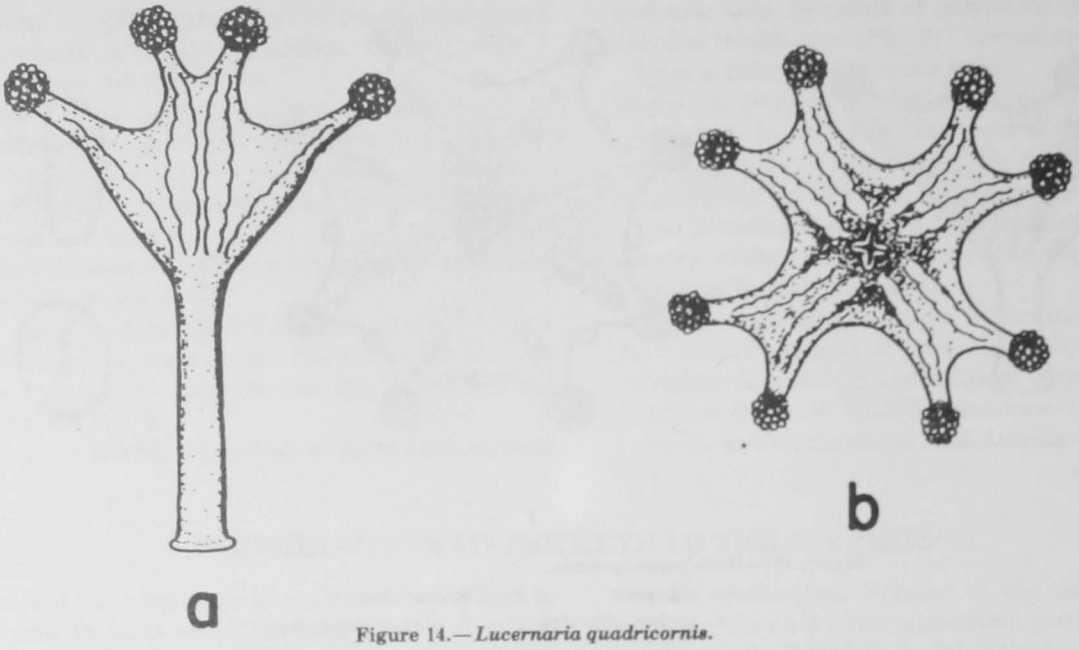

Figure 14.— *Lucernaria quadricornis.*
a. side view b. oral view

4 (1) Peduncle and arms short; arms not paired; calyx higher than broad . . . . . *Craterolophus convovulus*

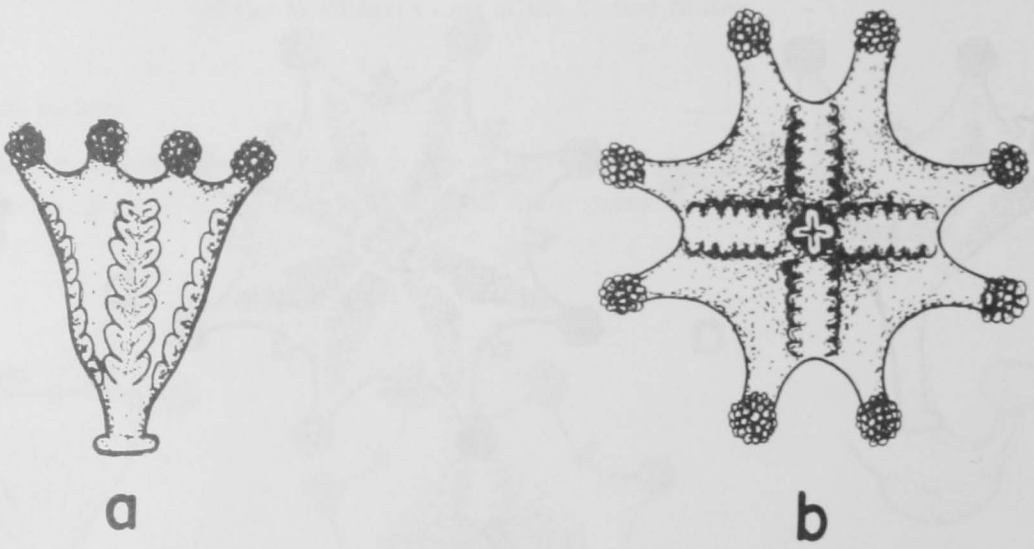

Figure 15.— *Craterolophus convovulus.*
a. side view b. oral view

Synopsis of Ephyrae of *Chrysaora, Cyanea, Aurelia*, and *Rhopilema*.
(See Russell 1970.)

	Newly released ephyrae ca. 2.5 mm in diameter (Fig. 5)			Postephyrae 5 mm in diameter
	Shape of lappets; position of rhopalia	Morphology of ephyral arms	Gastric cirri	Morphology
Chrysaora (Fig. 16a, b)	lappets slender pointed tips; rhopaliar cleft deep ca. 1/2 arm length	a pair of nematocyst clusters on each arm; radial canals in arms short, consists of 1 pair	lack	oral arms split; long ribbonlike; marginal tentacles; no ring canal
Cyanea (Fig. 16c, d)	lappets slender pointed tips; rhopaliar cleft deep ca. 1/2 arm length	radial canals in arms long, consists of 2 pairs	usually 4	oral arms not split, wide and flaring; subumbrellar tentacles; no ring canal
Aurelia (Fig. 16e, f)	lappets broad, tips blunt, rounded; rhopaliar cleft short 1/2 arm length	radial canal to rhopalium only	with 4 or more	oral arms split; short; marginal tentacles; ring canal present
Rhopilema (Fig. 16g, h)	lappets slender, tips pointed; rhopaliar cleft deep ca. 1/2 arm length	radial canals in arms long, consists of 1 pair	with 4 or more	oral arm split several times; no marginal or subumbrellar tentacles

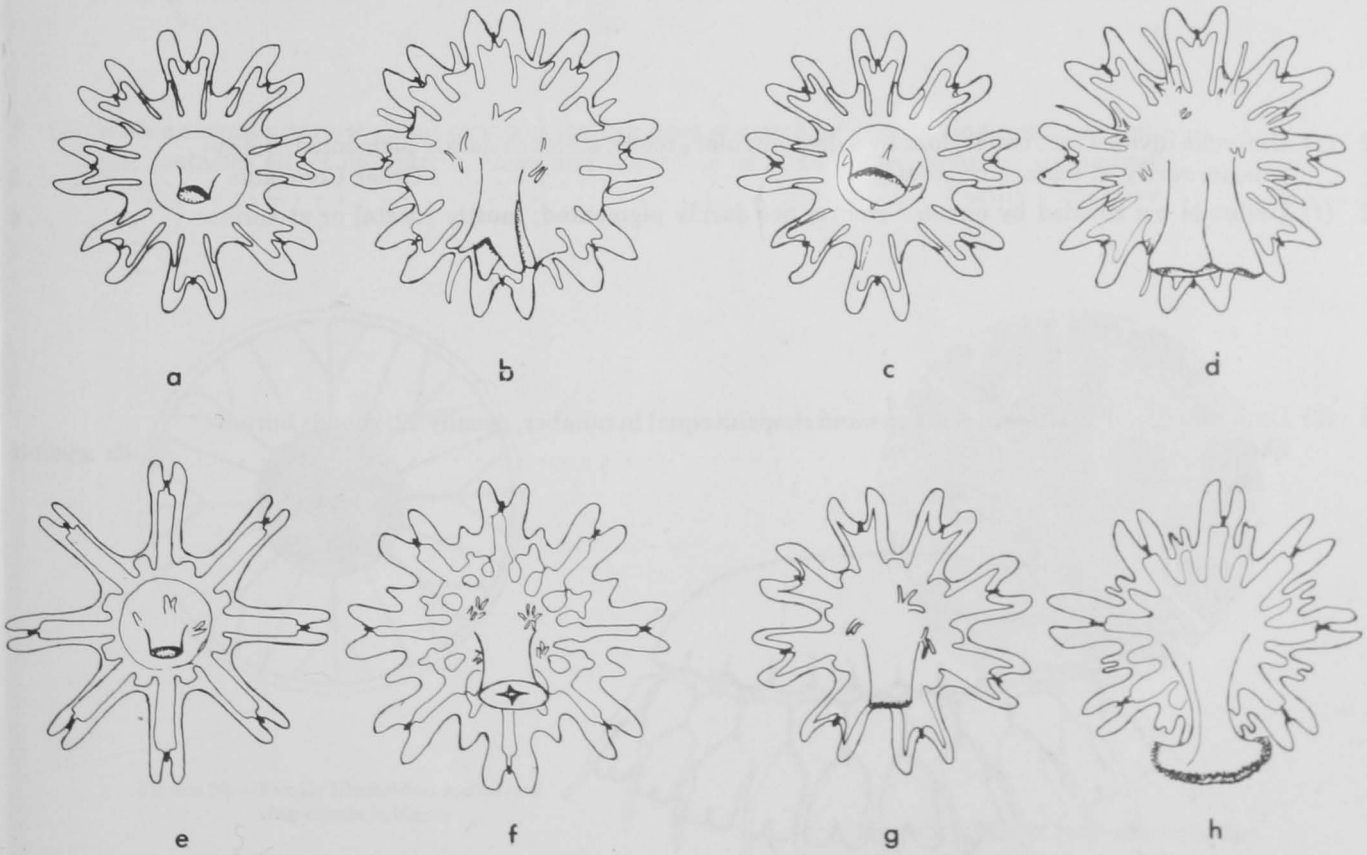

Figure 16.—Ephyrae (a, c, e, g); postephyrae (b, d, f, h).
a, b *Chrysaora quinquecirrha* c, d *Cyanea capillata* e, f *Aurelia aurita* g, h *Rhopilema verrilli*
(from D. Calder 1972, unpublished; and Calder 1973)

Key to the Pelagic Scyphomedusae of the Northeast Coast of the United States

1 Umbrella, saucer-shaped, dome-shaped, or hemispherical; with 8 or more tentacles, or no tentacles; with 8 or more rhopalia 2

1 Umbrella tall rectangular; 4 tentacles; 4 rhopalia; sensory niche with covering scale above and below; stomach supported by 4 mesenteries . . . . . .Order Cubomedusae . . . . . *Tamoya haplonema*

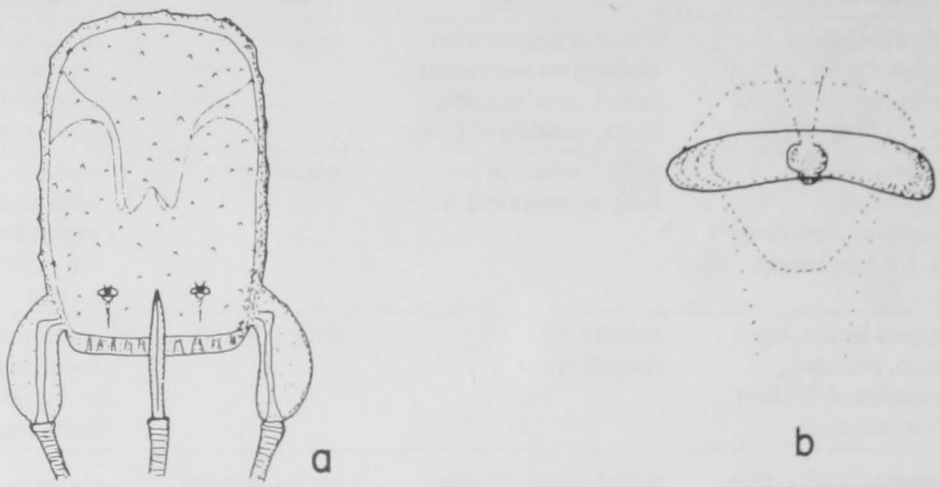

Figure 17.— *Tamoya haplonema.*
a. side view b. sensory niche, front view

2 (*1*) Umbrella divided into two regions by a deep circular groove; stomach darkly pigmented; bathypelagic, rarely at surface or coastal . . . . . Order Coronatae 3

2 (*1*) Umbrella not divided by circular groove, not darkly pigmented; mostly coastal or at surface 4

3 (*2*) Umbrella flat, disc-shaped; tentacles and rhopalia equal in number, usually 22; gonads button-like . . . . . .*Atolla wyvillei*

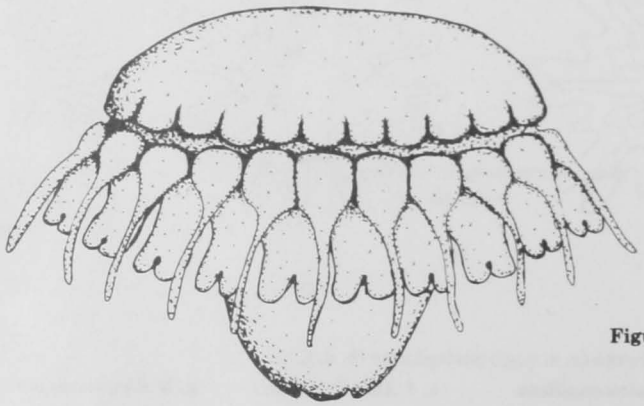

Figure 18.— *Atolla wyvillei*, side view.

3 (2) Umbrella conical or dome-shaped; usually 3 tentacles between rhopalia; 4 rhopalia; 12 tentacles; gonads horseshoe-shaped . . . . . *Periphylla periphylla*

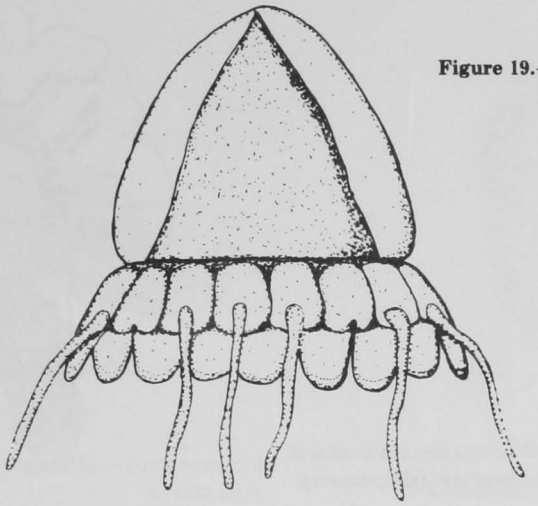

Figure 19.— *Periphylla periphylla*, side view.

4 (2) With marginal or subumbrella tentacles; 4 oral arms; distinct mouth; saucer-shaped umbrella . . . . . Order Semaeostomeae 5

4 (2) Without tentacles on umbrella; 8 tough gelatinous oral arms; mouth small or absent; umbrella usually hemispherical . . . . . Order Rhizostomeae 9

5 (4) With numerous narrow radial canals extending from stomach to margin; ring canal near margin; tentacles either on margin, short and numerous or in 16 linear groups on subumbrella . . . . . Family Ulmaridae 8

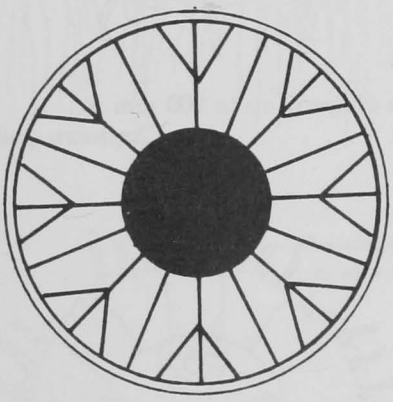

Figure 20.— Family Ulmaridae, radial and ring canals in black.

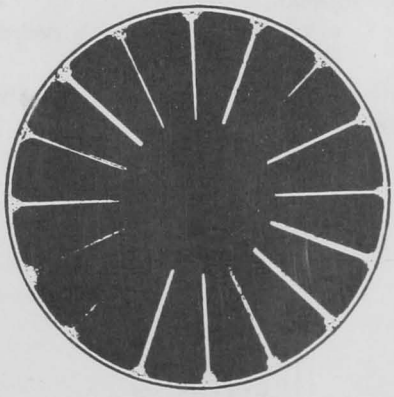

Figure 21.— *Cyanea* and family Pelagidae, stomach pouches in black.

5 (4) With broad stomach pouches extending to margin; without ring canal; tentacles long or 8 U-shaped subumbrellar groups 6

6 (5) Oral arms ribbonlike; tentacles on margin . . . . . Family Pelagidae 7

6 (5) Oral arms wide, curtainlike; tentacles in 8 U-shaped groups on subumbrella . . . . . *Cyanea capillata*

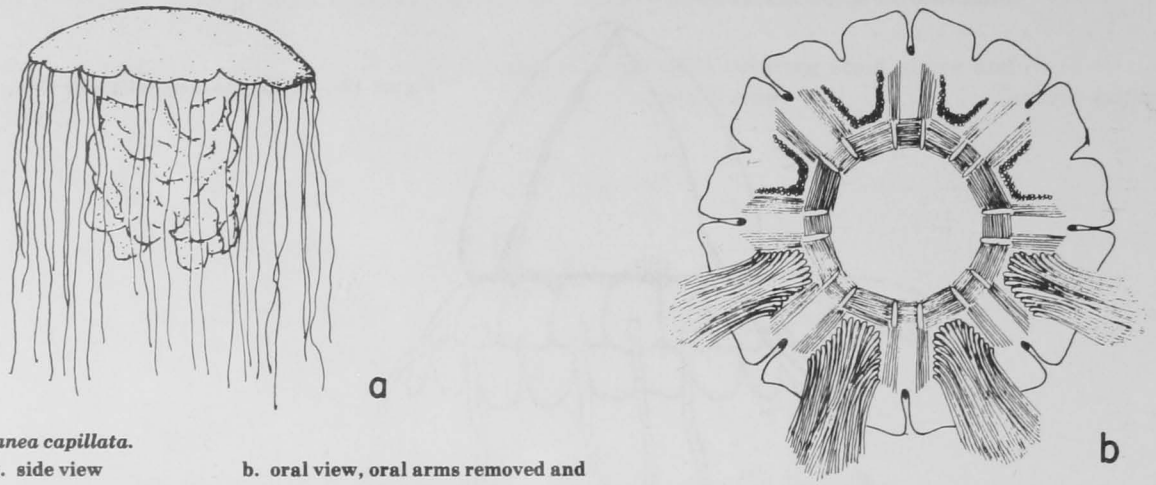

Figure 22.— *Cyanea capillata.*
a. side view **b. oral view, oral arms removed and four groups of tentacles removed**

7 (6) With 8 tentacles; exumbrella with prominent wartlike projections; umbrella nearly hemispherical in shape, usually less than 100 mm in diameter; oceanic . . . . . *Pelagia noctiluca*

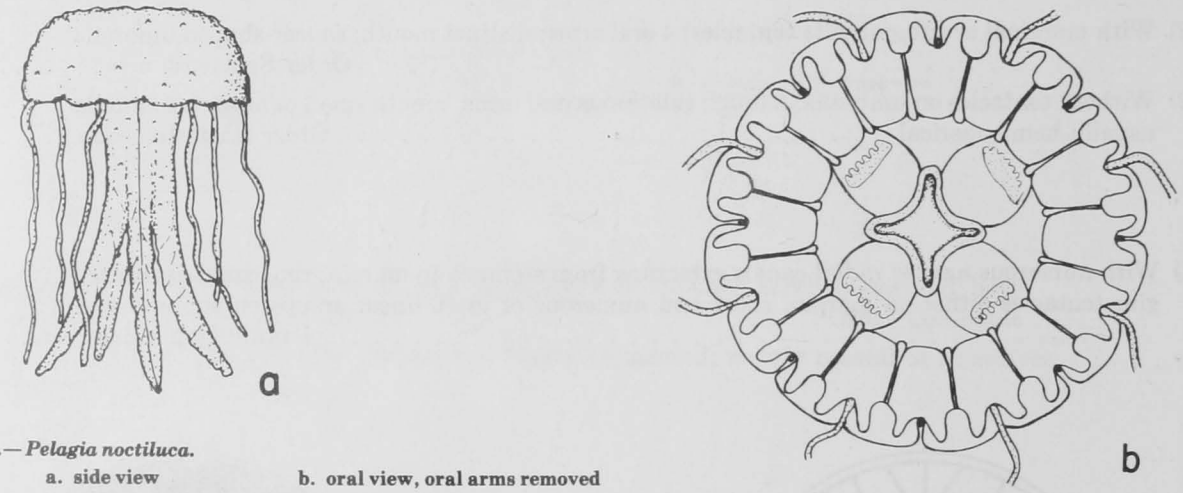

Figure 23.— *Pelagia noctiluca.*
a. side view **b. oral view, oral arms removed**

7 (6) With more than 8 tentacles; exumbrella smooth; umbrella saucer-shaped, up to 200 mm in diameter; estuarine or coastal . . . . . *Chrysaora quinquecirrha*

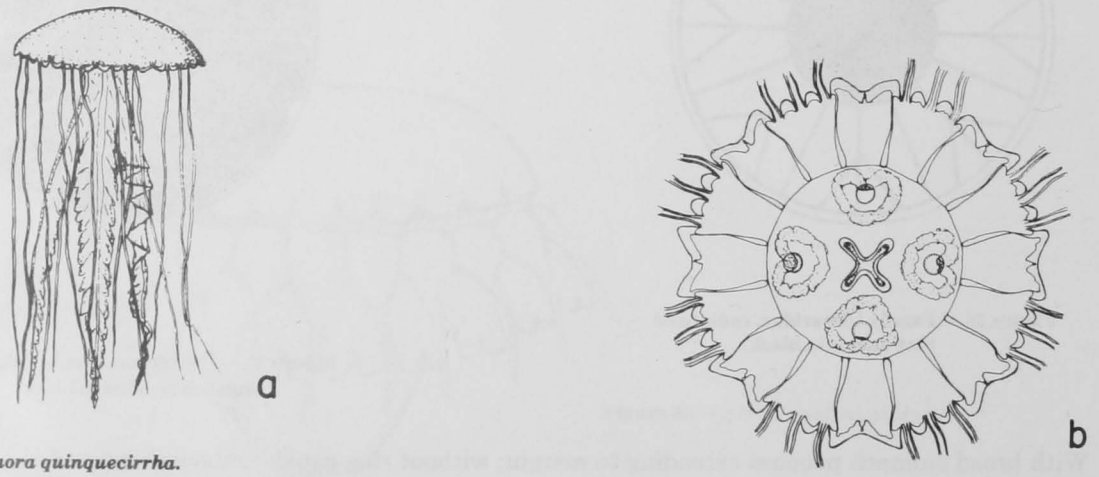

Figure 24.— *Chrysaora quinquecirrha.*
a. side view **b. oral view, oral arms removed**

8 (7) Marginal tentacles short and very numerous; oral arms folded, ribbonlike; gonads in 4 horseshoe-shaped groups; 8 rhopalia . . . . . *Aurelia aurita*

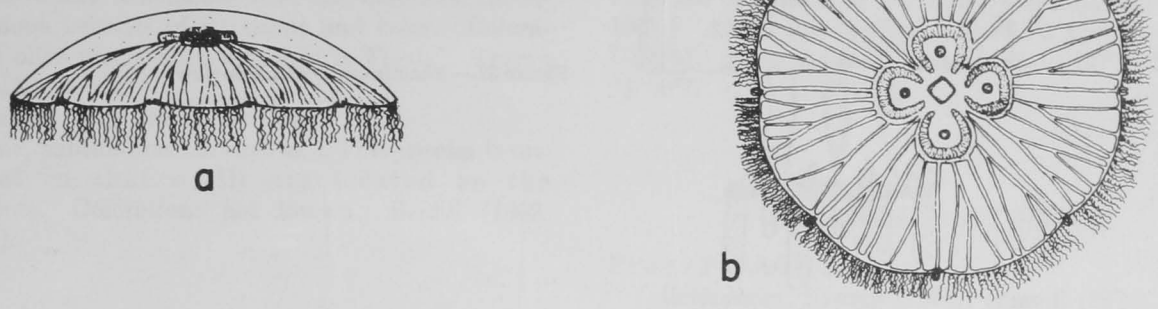

Figure 25.—*Aurelia aurita.*
a. side view **b. oral view, oral arms removed**

8 (7) Tentacles long, in 16 subumbrellar linear groups; oral arms broad, curtainlike; 16 rhopalia . . . . . *Phacellophora camtschatica*

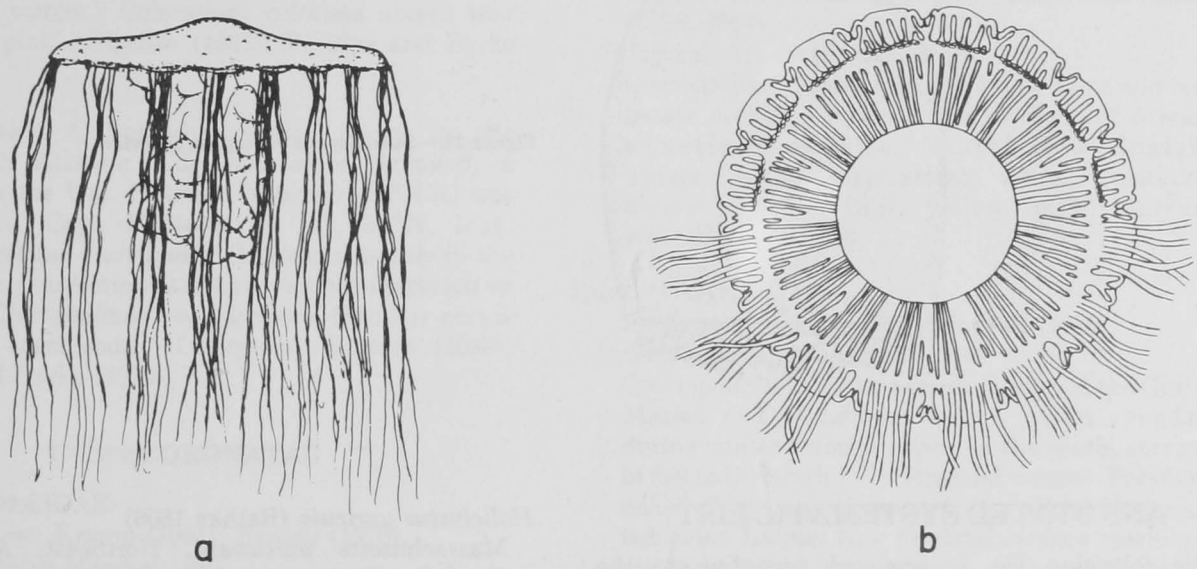

Figure 26.—*Phacellophora camtshatica.*
a. side view **b. oral view, oral arms and one-half of tentacles removed**

9 (4) Oral arms free along most of their length; spindlelike appendages hang from oral arms; umbrella hemispherical or flattened . . . . . *Rhopilema verrilli*

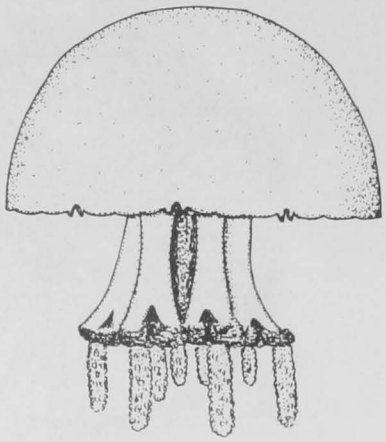

Figure 27.— *Rhopilema verrilli*, side view.

9 (4) Oral arms fused; no spindlelike appendages; umbrella higher than a hemisphere (globular) . . . . . *Stomolophus meleagris*

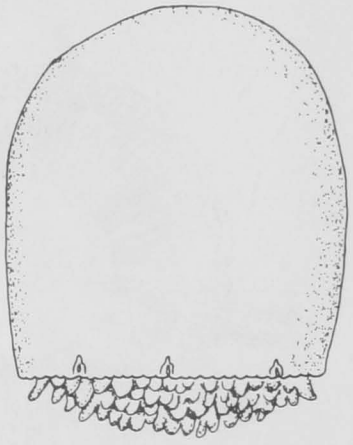

Figure 28.— *Stomolophus meleagris*, side view.

ANNOTATED SYSTEMATIC LIST

The following list is arranged according to the classification of Kramp (1961). Distribution notes are from published records and from museum specimens. Most of the species listed are represented by specimens in the U.S. National Museum, Washington, D.C., and the Gray Museum, Marine Biological Laboratory, Woods Hole, Mass. Notes on seasonal occurrence, habitat and life history, and coloration are included. References to important papers are cited for both the families and for each species.

CLASS SCYPHOZOA

ORDER STAUROMEDUSAE

FAMILY ELEUTHEROCARPIDAE

References: Berrill (1963); Kramp (1961).

Haliclystus auricula (Rathke 1806)

Massachusetts northward, Northeast, Atlantic, North Pacific, lower intertidal and subtidal on algae and *Zostera*, at Woods Hole most common on brown algae *Scytosiphon*. Juveniles easily confused with *H. salpinx*, but arms are very short. Coloration: highly variable, brown, green, red. Berrill (1962); Mayer (1910).

Haliclystus salpinx Clark 1863

Massachusetts northward, lower intertidal and subtidal on algae and *Zostera*. May be confused with juvenile *H. auricula* but with long arms. Coloration: variable, green, brown. Berrill (1962, 1963).

Lucernaria quadricornis O. F. Muller 1776

Massachusetts northward, Northeast Atlantic, Arctic, lower intertidal and subtidal mostly on *Laminaria*. Largest New England stauromedusa

reaching over 50 mm in length. Coloration: highly variable, brown, green, red. Berrill (1962, 1963).

FAMILY CLEISTOCARPIDAE

References: Berrill (1963); Kramp (1961).

Craterolophus convolvulus (Johnston 1835)

Massachusetts, Northeast Atlantic, intertidal on *Fucus* where it attaches near the bladders, inconspicuous because of its shape and color. Coloration: olive green when attached to *Fucus*. Kramp (1961).

Thaumatoscypus atlanticus Berrill 1962

Maine, subtidal on *Laminaria*. This species is unusual in that ocelli are located on the anchors. Coloration: not known. Berrill (1962, 1963).

ORDER CUBOMEDUSAE

FAMILY CARYBDEIDAE

References: Bigelow (1938); Kramp (1961).

Tamoya haplonema F. Muller 1859

Tropical Atlantic, Gulf of Mexico to Massachusetts. Probably carried north in the Gulf Steam. Mayer's (1910) report of this species in Long Island Sound is the only report of *T. haplonema* in the New England coastal waters. Coloration: colorless except tentacles, pink. Bigelow (1938); Phillips and Burke (1970).

Three other Cubomedusae also occur in the northwestern Atlantic. *Carybdea alata* Reynaud, a specimen in the U.S. National Museum (USNM) was collected off Cape Hatteras at lat. 35°N, long. 75°W. *Carybdea marsupialis* (Linneaus) occurs in the Gulf Stream near Bermuda but has not been reported on our coast. *Chiropsalmus quadrumanus* (Muller) occurs along U.S. coast south of Virginia. Bigelow (1938); Phillips and Burke (1970).

ORDER CORONATAE

FAMILY ATOLLIDAE

References: Kramp (1961); Russell (1970).

Atolla wyvillei Haeckel 1880

Cosmopolitan in deep oceans. A deep-sea species, bathypelagic, seldom occuring at the surface or on the continental shelf. Commonly taken in midwater samples in deep water usually below 500 m. Coloration: stomach dark red-brown. Russell (1970).

FAMILY PERIPHYLLIDAE

References: Kramp (1961); Russell (1970).

Periphylla periphylla (Peron and Lesueur 1809)

Cosmopolitan bathypelagic in deep oceans. Common in midwater trawl samples from deep water. It has been taken near the surface off New England. Coloration: stomach dark red-brown. Russell (1970).

At least four other coronate medusae may also occur in the northwestern Atlantic: *Linuche unguiculata* (Schwartz), a specimen at the U.S. National Museum, collected off Cape Hatteras, lat. 35°N, long. 75°W. *Nausithoe punctata* Kolliker, a specimen at the USNM collected off Georges Bank, lat. 40°N, long. 68°W. *Nauphantopsis diomedeae* Fewkes, not reported since the original description, off New England. (Kramp 1961.) *Atolla vanhoeffeni* Russell, a specimen at the USNM, collected off Virginia lat. 36°39'N. long. 74°39'W. (Russell 1970.)

ORDER SEMAEOSTOMEAE

FAMILY PELAGIDAE

References: Kramp (1961); Russell (1970).

Chrysaora quinquecirrha (Desor 1848)

Possibly cosmopolitan, western Atlantic distribution from Cape Cod to the Gulf of Mexico. Abundant during the summer months in estuaries, not common in the open ocean. Scyphistoma occurs on oyster shells in upper estuary. Popularly called "sea nettle" because of its stinging ability. Coloration: highly variable, pink, yellow, often with 16 yellow-ocher or red radiating stripes. Cargo and Schultz (1966, 1967).

Pelagia noctiluca (Forskal 1775)

Cosmopolitan open ocean species in warm and temperate oceans. Carried north in the Gulf Stream, sometimes seen in coastal New England waters. Lacks scyphistoma stage. Coloration: highly variable, blue, yellow, pink, tentacles red. Russell (1970).

FAMILY CYANEIDAE

References: Kramp (1961); Russell (1970).

Cyanea capillata (Linnaeus 1758)

Cosmopolitan in colder oceans. Occurs in the Gulf of Mexico and Florida northward. Most abundant during winter through spring in the south, summer to fall in the north (New England waters). Popularly called "lion's mane" because of the long red-yellow tentacles. Largest New England medusa reaching a meter or more in diameter. Coloration: highly variable, pink, red, yellow, brown. Russell (1970).

FAMILY ULMARIDAE

References: Kramp (1961); Russell (1970).

Aurelia aurita (Linnaeus 1758)

Cosmopolitan species in nearly all oceans except the Arctic. Popularly known as "moon jelly" because of the whitish umbrella. Coloration: bell clear; gonads, tentacles, pink, purple. Russell (1970).

Phacellophora camtschatica Brandt 1838

Occurs north of Cape Cod in the western Atlantic, probably the entire Pacific coast of the Americas and in the Mediterranean and off western Africa. Rarely taken in New England waters. Coloration: yellowish. Mayer (1910).

ORDER RHIZOSTOMEAE

FAMILY RHIZOSTOMATIDAE

References: Kramp (1961); Mayer (1910).

Rhopilema verrilli (Fewkes 1887)

Occurs in the northern Gulf of Mexico, North Carolina to Connecticut. An uncommon species, found along coast and in mouths of estuaries. Coloration: bell milky; oral arms brown. Mayer (1910); Calder (1973).

FAMILY STOMOLOPHIDAE

References: Kramp (1961).

Stomolophus meleagris L. Agassiz 1862

Occurs in the western Atlantic from Brazil to Cape Hatteras and from Panama to San Diego in the eastern Pacific. Specimens occasionally carried north to New England waters by the Gulf Stream. Popularly known as the "cabbage head jellyfish" because of its globular shape. Coloration: brown band at margin. Mayer (1910).

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SYSTEMATIC INDEX

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Coordinating Editor: Melbourne R. Carriker, Marine Studies Center, College of Marine Studies, University of Delaware, Lewes, DE 19958.

Editorial Advisers:

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Robert T. Wilce, Department of Botany, University of Massachusetts, Amherst, Mass.

The Board established the format for the "Marine Flora and Fauna of the Northeastern United States," invites systematists to collaborate in the preparation of manuals, reviews manuscripts, and advises the Scientific Editor of the National Marine Fisheries Service.

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COORDINATING EDITOR'S COMMENTS

Publication of the "Marine Flora and Fauna of the Northeastern United States" is most timely in view of the growing universal emphasis on environmental work and the urgent need for more precise and complete identification of coastal organisms than has been available. It is mandatory, wherever possible, that organisms be identified accurately to species. Accurate scientific names unlock the great quantities of biological information stored in libraries, obviate duplication of research already done, and often make possible prediction of attributes of organisms that have been inadequately studied.

Ronald J. Larson started his study of medusae during the summer of 1969 when he worked on the natural history and systematics of Hydromedusae from the Oregon coast. In 1972 he began working at the U.S. National Museum where use of the extensive collections and excellent library facilities furthered his education and initiated an interest in the systematics of the Scyphozoa. Currently he is involved with graduate studies at the University of Puerto Rico, Mayaguez, where he is investigating the functional morphology of scyphomedusae and aspects of growth and reproduction.

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