Plankton: Gelatinous Zooplankton☆

Laurence P Madin and G Richard Harbison, Woods Hole Oceanographic Institution, Woods Hole, MA, United States

Introduction

Gelatinous zooplankton comprise a diverse group of organisms with jelly-like tissues that contain a high percentage of seawater. They have representatives from practically all the major, and many of the minor phyla, ranging from protists to chordates. The fact that so many unrelated groups of animals have independently evolved similar body plans suggests that gelatinous organisms are well adapted to the nature of the water column environment. Whether as predators or grazing herbivores, they can be abundant in coastal environments, but also seem particularly well adapted to life in the oligotrophic regions of the world oceans, where their diversity and abundance relative to crustacean zooplankton is often greatest.

The gelatinous body plan has evolved in a world where physical parameters are relatively constant, but food resources sparse or unpredictable. Gelatinous zooplankton exhibit many common adaptations to this habitat.

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- Transparent tissues provide concealment in the upper layers of the ocean, an environment without physical cover. Transparency is less common below the photic zone, where gelatinous animals may be pigmented red or black.
- The high water content of gelatinous tissues gives the organisms a density very close to that of seawater. The resulting neutral buoyancy decreases the energy required for locomotion.
- The environment lacks physical barriers, strong turbulence and current shears, so that gelatinous bodies do not need great structural strength. However, their fragility makes many species difficult to sample or handle, and excludes many species from more energetic coastal environments.
- High water content and noncellular gelatinous tissue permit rapid growth and large body sizes, which can act as, or produce, large surfaces for the collection of food.
- Rapid growth and reproduction of some forms, together with relatively large size, can lead to development of dense population blooms, often in coastal waters where they affect fisheries, recreation or infrastructure.
- Relatively large size makes some gelatinous animals too big to be attacked by some predators, although they are often hosts to smaller symbionts and parasites.

Thus, as we look at the diversity of gelatinous zooplankton, we should keep in mind the forces that have led to their remarkable convergence. It is impossible to deal in a short article with the entire range of phyla that have gelatinous representatives, so we will highlight the major groups. Recent taxonomic studies of some groups have revised phylogenies and classifications based on genetic characters. The descriptions here are not intended as strict taxonomic classifications but rather operational definitions for readily distinguished groups based on morphology.

Taxonomic Groups

Radiolaria

Species of polycystine radiolarians form large gelatinous colonies ranging from a few millimeter in diameter to several meters in length. A few to thousands of individual protists are embedded in a common gelatinous matrix from which their pseudopodia extend into the water. The combined effects of individuals in the colony enable relatively large plankton (such as copepods) to be captured and ingested. In addition to the protistan members of the colony, the matrix also contains symbiotic dinoflagellates (zooxanthellae) that utilize the metabolites of the radiolarians. In turn, the radiolarians digest the zooxanthellae, so that these colonies are effectively planktonic analogues of coral reefs.

Medusae

The phylum Cnidaria has many gelatinous representatives, comprising various groups of medusae and the strictly oceanic siphonophores (see below). What are commonly called jellyfish are medusae belonging to three Classes of the Cnidaria—the Hydrozoa, Scyphozoa, and Cubozoa. Since the morphology and life history of all three groups are broadly similar, it is practical to treat them together here. There are at least 1000 species of hydro- and scyphomedusae, probably with more to be discovered, especially in deep or polar waters. All are carnivorous, capturing prey with specialized stinging cells, called nematocysts, typically borne on contractile tentacles. A wide variety of prey is eaten by different medusae, ranging from larval forms and small crustaceans to other gelatinous animals and large fish. Some epipelagic medusae also harbor zooxanthellae, and presumably they share their resources in the same way as the polycystine radiolarians. Many of these medusae are part of a life history that alternates between a sessile, benthic, asexually reproducing polyp and a sexually reproducing and dispersing planktonic medusa. However, many oceanic species lack the polyp stage and have instead a variety of sexual and asexual reproductive mechanisms that do not require a benthic habitat. Recent phylogenies and classifications for medusa and siphonophores are based on cladistic and molecular studies; the group names given here are traditional usage, but correspond in general to current taxonomic groups.

Anthomedusae

This order of hydromedusae includes small species ranging in size from less than 1 mm to several cm. The umbrella is usually shaped like a tall bell, and gonads are almost always found on the sides of the central stomach. There are four radial canals connecting the stomach to a marginal ring canal. Tentacles occur in varying numbers around the umbrella margin and sometimes around the mouth. Anthomedusae alternate with polyp forms called hydroids, but some also bud medusae directly (Fig. 1A).

Leptomedusae

These medusae are generally flatter than a hemisphere. They usually have four radial canals, but sometimes eight or more, or canals that are branched. Gonads are located on the radial canals, and there may be various sense organs on the margin. The stomach is sometimes flat, and sometimes mounted on a peduncle that can be quite long. There are tentacles around the margin but not the mouth. Leptomedusae also alternate with hydroid forms, but some species produce new medusae by budding or fission (Fig. 1B).

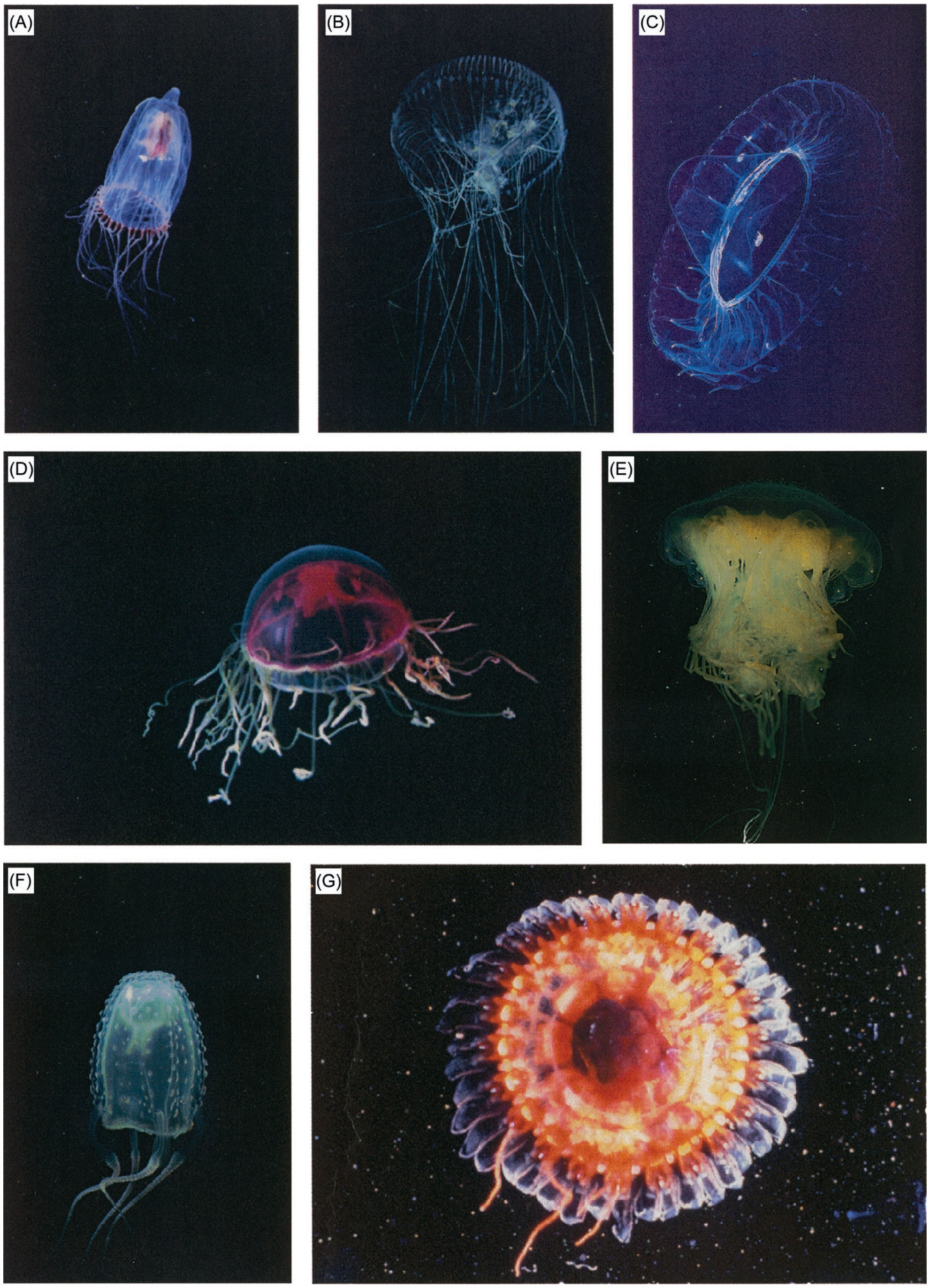

Fig. 1 Medusae. (A) *Pandea conica*, an anthomedusa about 2 cm high; (B) Aequorea *macrodactyla*, a leptomedusa about 10 cm diameter; (C) *Cunina globosa*, a narcomedusa about 5 cm diameter; (D) *Benthocodon hyalinus*, a trachymedusa about 3 cm diameter; (E) *Cyanea capillata*, a semaeostome scyphomedusa which can attain 1 m diameter; (F) *Carybdea alata*, a cubomedusa up to 15 cm high; (G) *Atolla wyvillei*, a coronate scyphomedusa up to 25 cm diameter. Source: All photos by L.P. Madin.

Limnomedusae

Both high and low umbrella shapes are found in this order. There are usually four radial canals, sometimes branched. Gonads are either on the stomach or the radial canals, and there is alternation of generations. Species of limnomedusae live in brackish, fresh (one species) or marine environments.

Trachymedusae

These medusae in the order Trachylina do not alternate generations, but develop young medusae directly from planula larvae, or by asexual budding. The umbrella is often high, with stiff mesoglea and well-developed muscle fibers. Most have eight unbranched radial canals and gonads located on them. Many trachymedusae live in deep water and are heavily pigmented (Fig. 1D).

Narcomedusae

Also in the Trachylina, narcomedusae have direct development from planulae, with a larval stage that is often parasitic on other medusae. There are no radial canals, but the flat central stomach is very wide and, in some genera, extends into radial stomach pouches. Tentacles are solid and stiff, and often extend aborally. Narcomedusae are common in epipelagic and mesopelagic environments; some are strong vertical migrators (Fig. 1C).

Coronatae

This order of scyphomedusae includes mainly deepwater species. The umbrella is divided into a high central part and a thinner marginal part by a coronal groove. The margin of the bell is divided into lappets; sense organs and solid tentacles arise from the cleft between lappets. The mouth has simple lips and the gastrovascular cavity is often deeply pigmented (Fig. 1G).

Semaeostomae

The large jellyfish familiar in coastal waters are mainly in this order of the Scyphozoa. The umbrella margin is divided into lappets, and bears sense organs and hollow tentacles. There is no coronal groove around the umbrella. The mouth opening is surrounded by four long oral arms, often frilled. Gonads are in folds of the subumbrella. Semaeostome medusa alternate with small benthic polyps called scyphistomae (Fig. 1E).

Rhizostomae

Medusae in this order of the Scyphozoa are mainly coastal species and can attain large size. They lack tentacles for prey capture, and instead ingest small particles carried into numerous small mouth openings by water currents. Some species in tropical waters host intracellular symbiotic algae.

Cubomedusae

Medusae in the class Cubozoa also alternate with a benthic polyp form, although details of their life cycles are poorly known. Cubomedusae can be quite large, and have the most virulent toxic nematocysts of any Cnidarians. Some species are responsible for human fatalities. Cubomedusae are also unusual in possessing complex, image-forming eyes, the functions of which remain uncertain (Fig. 1F).

Siphonophores

The Order Siphonophora comprises a large and diverse group of predatory cnidarians in the Class Hydrozoa. Their complex life cycle and colonial morphology are very different from the relatively simple hydromedusae and it is practical to consider the siphonophores as a separate group. The colonial, or polygastric, phase of the life cycle is the largest and most familiar. In this stage, siphonophores consist of an assemblage of medusoid and polypoid zooids, which are budded asexually from a founding larval polyp. The colony may include a gas float, nectophores or swimming bells, and a series of stem groups made up of feeding polyps and tentacles. In some siphonophores the stem groups break off as dispersal and sexually reproductive stages called eudoxids. The colony can be thought of as an overgrown, polymorphic juvenile stage that eventually bears the sexually reproductive adults. These are small medusoid zooids called gonophores, which produce gametes. Siphonophores range in size from a few millimeter to over 30 m in length, and occur throughout the water column. All are predators on other small zooplankton, and many genera are known to be luminescent.

The colonies are fragile, and usually break up into their various units when collected in plankton nets. For this reason, much of the taxonomy is based on the morphology of the pieces, principally nectophores, and the appearance of the intact colonial stage is not always known. The Order Siphonophora is divided into 3 suborders and 15 families.

Cystonectae

This suborder includes siphonophores that possess a float but no swimming bells, so they are at the mercy of ocean currents. The Portuguese man-o-war is the most familiar example. It has a float so large that the animal rests on the surface, but most cystonect species have smaller floats and are wholly submerged. Cystonects have virulent nematocysts and capture large, soft-bodied prey such as fish and squids (Fig. 2A).

Physonectae

These siphonophores have more complex colonies, comprising a small apical float, numerous swimming bells that form a nectosome, and a stem containing several groups of gastrozooids, tentacles, bracts, etc. The stem typically contracts when the animal is swimming, and then relaxes so that the stem and tentacles extend to maximum length for fishing. This group is a major contributor to the deep scattering layer in many regions of the ocean. The largest siphonophores (the Apolemiidae, over 30 m long) are found in this group. Physonects prey mainly on small zooplankton, and many species are strong swimmers and vertical migrators (Fig. 2C).

Calycophorae

In this group, which contains the largest number of species, the float is absent, and the nectophores are reduced, usually to two. A sequence of stem groups is budded, and breaks free as eudoxids. Calycophorans are the most diverse, widely distributed and abundant siphonophores. They catch small zooplankton, and when feeding, their tentacles form complex three-dimensional structures in the water, reminiscent of spider webs (Fig. 2B).

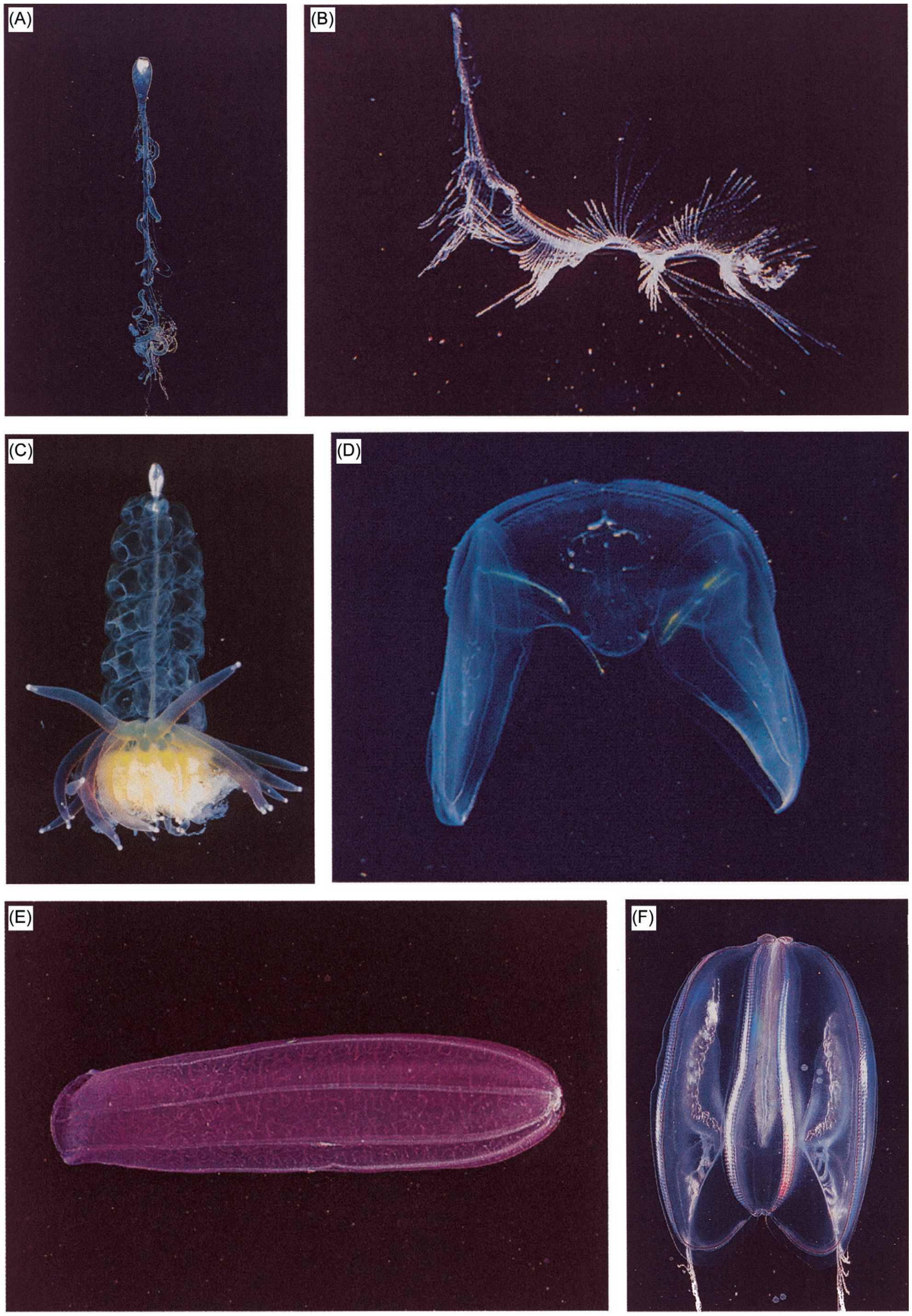

Fig. 2 Siphonophores and Ctenophores. (A) *Rhizophysa filiformis*, a cystonect siphonophore up to 2 m long; (B) *Sulculeolaria* sp. a calycophoran siphonophore up to 1 m long; (C) *Physophora hydrostatica*, a physonect siphonophore about 10 cm high; (D) *Ocyropsis maculata*, a lobate ctenophore about 8 cm diameter; (E) *Beroe cucumis*, a beroid ctenophore up to 25 cm long; (F) *Mertensia ovum*, a cydippid ctenophore about 4 cm high. Source: Photos A, C, D, F by G.R. Harbison, B, E by L.P. Madin.

Ctenophores

Ctenophores are exclusively marine gelatinous animals, all but a few of which are holoplanktonic. Although superficially resembling the Cnidaria, morphological and molecular studies indicate that cnidarians and ctenophores are not closely related, but diverged early in metazoan evolution. Ctenophores are predators that use tentacles equipped with “glue cells” or colloblasts to capture prey. The name “ctenophore” is Greek for “comb bearer,” referring to the comb-like plates of fused cilia that are used for propulsion. All ctenophores initially have eight meridional rows of comb plates, although in some groups these are lost or reduced during development. The vast majority of ctenophore species fall into six orders.

Cydippida

This group contains many species with paired tentacles that exit the body through tentacle sheaths. Species in the family Pleurobrachiidae catch prey ranging from small crustaceans to fish, while members of the Lampeidae feed mainly on large gelatinous animals like salps. One species of cydippid, *Haeckelia rubra*, eats medusae, and retains the nematocysts of their prey ("kleptocnidae") for defensive use in their own tentacles. Before this behavior was known, these nematocysts were considered evidence for a close relationship between cnidarians and ctenophores (Fig. 2F).

Platyctenida

This group is primarily benthic, and is distributed widely from the Arctic to the Antarctic. Members of the family Ctenoplanidae have comb rows as adults, and are found in the plankton in the Indo-Pacific; all other species in the order lose their comb rows as adults, and live primarily as creeping benthic organisms. Platyctenes have functional tentacles that capture prey.

Thalassocalycida

This order contains a single species, *Thalassocalyce inconstans*, which lives in the midwater zone. It superficially resembles a medusa in overall shape, but can easily be distinguished by its eight comb rows and paired tentacles.

Lobata

Members of this order all have oral lobes and auricles, specialized structures that are used in feeding. Most lobates move through the water with their oral lobes widely spread to form a sort of basket. Small prey, such as crustaceans, are trapped on the mucus-covered oral lobes and tentilla, which stream over the body or extend onto the oral lobes. Ctenophores in the family Ocyropsidae lack tentacles, and capture prey by enclosing them in their muscular oral lobes (Fig. 2D).

Cestida

These ctenophores are shaped like long flat belts. They appear to be related to the Lobata, but lack oral lobes and auricles. There are only two genera (*Cestum* and *Velamen*) in one family (Cestidae). The comb rows extend along the aboral edge of the ribbon-like body, propelling the animal with the oral edge forward. Small prey are captured by the fine branches of the tentacles that lie over the flat sides of the body. Cestids are characteristic of oceanic, epipelagic environments.

Beroida

Beroids lack tentacles altogether. Their large stomodaeum occupies most of the space in the body. All beroids are predators on other ctenophores, and occasionally salps. They capture prey by engulfing them, and can bite off pieces of the prey with specialized macrocilia located immediately behind the mouth (Fig. 2E).

Heteropods

The Phylum Mollusca contains many gelatinous representatives, and the gelatinous body plan has apparently arisen independently in several groups. The Heteropoda is a superfamily of prosobranch gastropods that includes the families Atlantidae, Carinariidae, and Pterotracheidae. Heteropods are visual predators with well-developed eyes, and a long proboscis containing a radula. Atlantid heteropods have thin, flattened shells into which they can completely withdraw their bodies. They feed on small crustaceans and other molluscs. The family Carinariidae includes eight species in three genera, *Carinaria*, *Pterosoma*, and *Cardiapoda*. These heteropods have a greatly reduced shell, enclosing only a small fraction of the body. Carinariids feed primarily on other gelatinous organisms, such as salps, doliolids, and chaetognaths. In the family Pterotracheidae, with two genera, *Pterotrachea* (four species) and *Firoloida* (one species), the shell is completely absent (Fig. 3D).

Pteropods

This molluscan group comprises two orders in the gastropod subclass Opisthobranchia. The molluscan foot in pteropods is modified into two wing shaped paddles responsible for swimming; their fluttering gives rise to the common name for pteropods, sea butterflies.

Thecosomata

This group contains the shelled pteropods, some of which (Euthocosomata) have calcareous shells and are not truly gelatinous, and others (Pseudothecosomata) which have gelatinous shells and tissues. There are over 30 species of euthecosome pteropods, in two families, the Limacinidae and the Cavoliniidae. Thecosome pteropods feed by collecting particulate food on the surface of a mucous web or bubble, produced by mucus glands on the wings, and held above the neutrally buoyant and motionless animal. The mucus is periodically retrieved and ingested along with adhering particles, then replaced by a newly secreted web. Some cavoliniids have

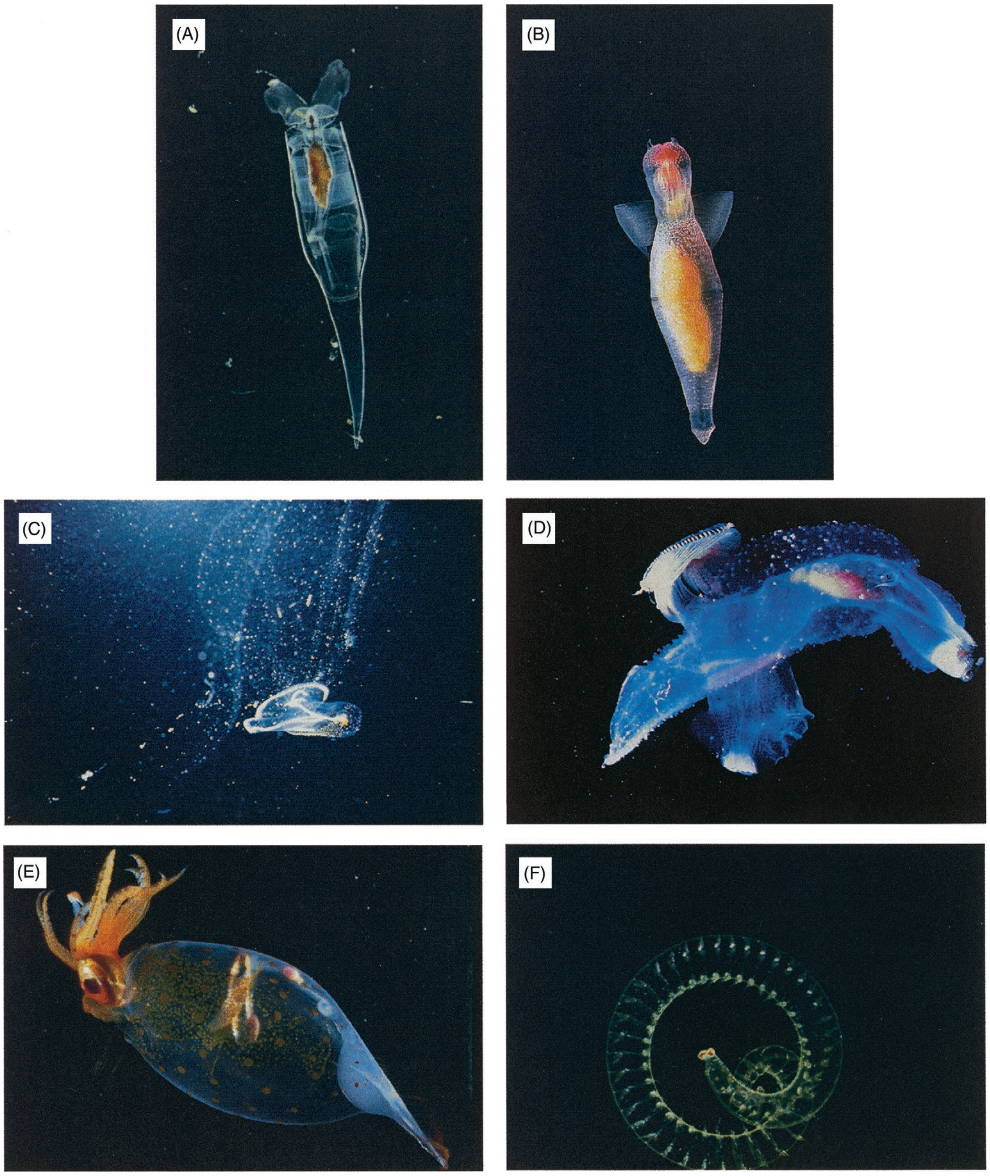

Fig. 3 Molluscs and Polychaete. (A) *Cuvierina columnella*, a euthecosome pteropod about 1 cm high; (B) *Clione limacina*, a gymnosome pteropod about 2 cm high; (C) *Corolla spectabilis*, a pseudothecosome pteropod about 10 cm diameter, with mucous web in background; (D) *Carinaria* sp. a heteropod about 10 cm long; (E) *Teuthowenia megalops*, a cranchiid cephalopod about 10 cm long; (F) Alciopid polychaete worm, up to 1 m long. Source: Photos A, B, C, E, F by G. R. Harbison, D by L.P. Madin.

brightly colored mantle appendages that may aid in maintaining neutral buoyancy or serve as warning devices to predators. When disturbed, animals lose their neutral buoyancy, and rapidly sink (Fig. 3A).

The Pseudothecosomata includes three families, the Peraclididae (one genus), the Cymbuliidae (three genera), and the Desmopteridae (one genus). Pseudothecosomes are larger than euthecosomes, and their mucous webs are correspondingly larger, reaching over a meter across in *Gleba cordata* (Fig. 3C).

Gymnosomata

Members of this order are poorly known, largely because they have no shells and contract into shapeless masses when preserved. Most species live in the deep sea, and only a few of the approximately 50 species have been observed alive. Gymnosomes appear to be highly specialized predators on particular species of thecosome pteropods. The order is divided into two suborders, the Gymnosomata and the Gymnoptera. The four families of the Gymnosomata include: the Pneumodermatidae (7 genera and 22 species) with sucker-bearing arms similar to cephalopod tentacles; the Notobranchaeidae (1 genus and 8 species), with suckerless feeding arms called buccal cones; the Clionidae (8 genera and 16 species); and the Cliopsidae (2 genera and 3 species) (Fig. 3B).

There are two families in the Gymnoptera, the Hydromylidae (one genus, one species) and the Laginiopsidae (one genus, one species). These groups are very different from each other and from other gymnosome pteropods, and some may not actually belong in the Order Gymnosomata.

Cephalopods

Although many cephalopods are active, muscular swimmers, there are several gelatinous and/or transparent genera. The family Cranchiidae is composed entirely of gelatinous species, including the genera *Taonius*, *Megalocranchia* and *Teuthowenia*. These relatively large, slow-moving squids probably capture prey through stealth rather than active pursuit. Vitreledonelliid octopods are also gelatinous (Fig. 3E).

Polychaete Worms

Two major groups of planktonic polychaetes are gelatinous, the Alciopidae and the Tomopteridae. Both are in the order Phyllodocida, although they are probably not closely related. Alciopids are characterized by well-developed eyes with lenses. Many have ink glands along the sides of their bodies, with may function analogously to the ink glands of cephalopods. Their habits are poorly known, but they may feed on gelatinous prey. Alciopids may attain lengths of nearly a meter. Tomopterids do not have well-developed eyes, but probably use chemoreception to locate prey. Some release luminous secretions from glands along their body when disturbed. Deep-sea tomopterids may be 25 cm long, but most shallow species are much smaller (Fig. 3F).

Crustaceans

Although crustaceans cannot really be considered gelatinous because of their exoskeletons, there are some forms with very transparent bodies, presumably also an adaptation for concealment. The most notable examples are species of the hyperiid amphipods *Cystisoma* and *Phronima*. Species of *Cystisoma* are large and transparent, and the enormous retinas of the compound eye are lightly tinted. Although the retinas of species of *Phronima* are darkly pigmented, the rest of the body is transparent.

Holothurians

Although the majority of holuthurian species are rather sedentary benthic deposit feeders, there are several deep-sea genera of swimming or drifting holothurians with gelatinous bodies. Species in the genera *Peniagone* and *Enypniastes* feed on bottom deposits, but can swim up into the water column. The genus *Pelagothuria* appears to be wholly pelagic, with a morphology that suggests it collects and feeds on sinking particulate matter. Few pelagic holuthurians have been observed alive and little is known of their life history or behavior.

Pelagic Tunicates

The subphylum Urochordata includes two classes of pelagic tunicates, the Thaliacea and the Appendicularia or Larvacea. Thaliaceans (including the orders Pyrosomida, Doliolida and Salpida) are relatively large animals with more or less barrel-shaped bodies. They pump a current of water through their bodies and strain phytoplankton and other small particulates from it with a filter made of mucous strands. The same current provides jet propulsion. Thaliaceans have complex life cycles with alternating generations and multiple zooid types. The class Appendicularia comprises a single order of small organisms that filter food particles using an external mucous structure called a house. Both Thaliaceans and Appendicularians are widely distributed in the oceans, and sometimes extremely abundant.

Pyrosomida

Pyrosomes form colonies made up of numerous small ascidian-like zooids embedded in a stiff gelatinous matrix or tunic. The colony is tubular, with a single terminal opening. Water is pumped by ciliary action through each zooid, and suspended food particles are retained on the branchial basket within the body. The excurrent water from each zooid passes into the lumen of the colony, forming a single exhalent current that provides jet propulsion. Most pyrosome colonies are a few cm to a meter in length, but colonies of at least one species can attain lengths of 20 m. Pyrosomes are bioluminescent and several species are vertical migrators.

Doliolida

This order of the Thaliacea comprises 6 genera and more than 20 species of small (2–10 mm), barrel shaped animals with circumferential muscle bands. The filter feeding mechanism is similar to that of pyrosomes, with currents generated by ciliary beating passing through a mucous net supported on the branchial basket. The life cycle involves up to five asexual and one sexual stage, several of which occur together as parts of large colonies comprising thousands of zooids. These colonies may attain lengths over 1 m, but are fragile and rarely collected intact. In most genera of doliolids, the life cycle begins with a sexually produced larva, which becomes the oozooid stage. This stage feeds initially, but then begins budding off the trophozooid and phorozooid stages, thus forming the colony. During this process the oozooid loses its branchial basket and gut, and transforms into the "old nurse" stage, whose function is to swim by jet propulsion and pull the attached colony along behind it. Contractions of the body muscles produce short exhalent pulses that move the colony rapidly. The trophozooids in the colony filter-feed to support themselves and the nurse. The phorozooids grow attached to the colony, but then break free to lead independent lives and produce asexually a small group of gonozooids. These eventually break free from the phorozooid, and become the sexually reproducing stages that produce the larva and begin the whole cycle again. Recently several unusual doliolid species with enigmatic life histories have been described from the mesopelagic zone (Fig. 4B).

Salpida. This order (with 12 genera and about 40 species) is of larger filter feeding animals, also with circumferential muscle bands. The salps alternate between two forms, an asexually budding solitary (oozooid) stage and a sexually reproducing aggregate (blastozooid) stage. The aggregate salps usually remain connected together in chains or whorls of various types. Swimming is by jet propulsion, produced by a pulsed water current generated by rhythmic contraction of body muscles. Food particles are strained from the water passing through the body cavity by a mucous filter, which is continuously secreted and ingested. The individual animals range in size from 5 to over 100 mm, and chains can be several m long. Some species of salps develop dense populations

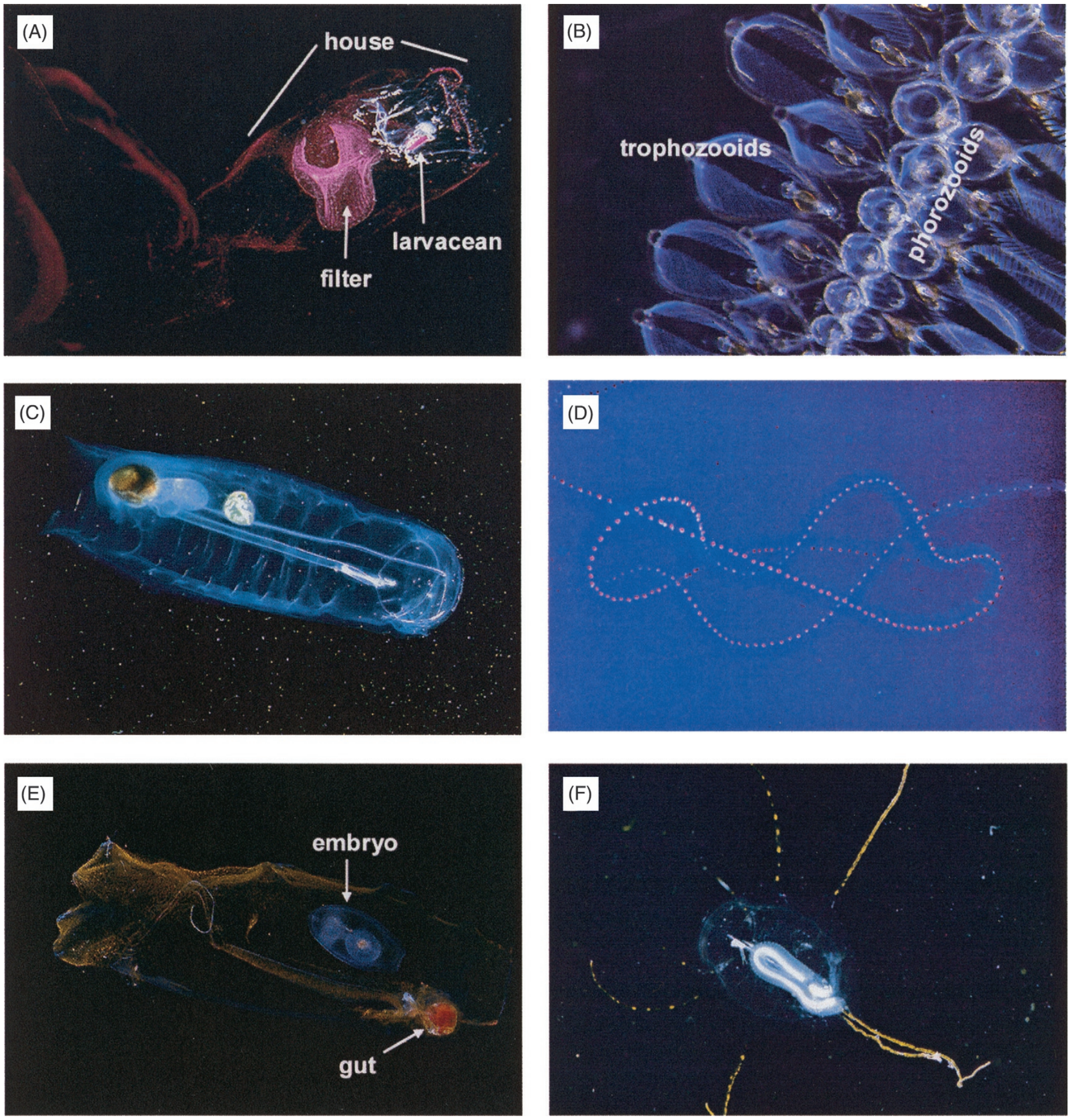

Fig. 4 Pelagic Tunicates. (A) *Megalocercus huxleyi*, a larvacean about 5 mm body length, house length about 4 cm; (B) *Dolioletta gegenbauri*, portion of a colony showing gastrozooids and phorozooids, individuals 2–5 mm long, colonies up to 1 m; (C) *Salpa maxima*, solitary generation salp, up to 25 cm long; (D) *S. maxima*, chain of aggregate generation salps, orange dots are guts of salps, individuals to 15 cm, chains up to 10 m long; (E) *Pegea socia*, aggregate generation salp with attached embryo of solitary generation, aggregate 7 cm, embryo about 1 cm; F. *Traustedtia multitentaculata*, solitary generation salp with appendages of uncertain function, about 3 cm long. Source: All photos by L.P. Madin.

and have a significant impact on ocean food chains by their grazing. Some are also strong vertical migrators, moving from the surface zone to midwater depths on a daily basis (Fig. 4C–F).

Appendicularia

This class (also called Larvacea) is divided into 3 families (with 15 genera and about 70 species) of small (1–10 mm) animals consisting of a trunk and long, flat tail. Larveaceans are also filter feeders on small particulates, but are unique among tunicates in the use of an external concentrating and filtering structure called the house. The house surrounds the animal, and contains a complex set of channels and filters made of mucous fibers and sheets. Water is pumped into the house by the oscillation of the appendicularian's tail; the exhalent stream provides slow jet propulsion in some species. Particles are sieved from the flow as it passes through the internal filter; they accumulate and are aspirated at intervals into the pharynx of the appendicularian via a mucous tube. The complex house is formed as a mucous secretion on the body of the animal, produced by specialized secretory cells. It is inflated with seawater, pumped into it by action of the tail, until it attains its full size, with all the internal structures expanding in proportion. Houses eventually become clogged with particulates and fecal pellets, and are then jettisoned. The appendicularian expands a new house (there may be several house rudiments on its body, awaiting expansion) and resumes filter feeding. The abandoned houses serve as food for various planktonic scavengers and can be an important source of marine snow, contributing to vertical flux of carbon (Fig. 4A).

Ecology of Gelatinous Zooplankton

Gelatinous zooplankton are found in all of the oceans of the world, from the tropics to Polar Regions. They also occur at all depths, and many of the largest and most delicate species have been collected in recent years from the mesopelagic and bathypelagic regions of the ocean. The absence of turbulence in the deep sea probably allows these species to attain such large sizes, but there are also robust species that thrive in surface and coastal environments. Examples include the Portuguese-Man-of-War (*Physalia physalis*), which lives at the air–water interface and can ride out hurricanes, and the ctenophore *Mnemiopsis leidyi*, which lives in estuaries with strong tidal currents and turbulence.

In general, gelatinous organisms have been rather neglected by zooplankton ecologists, primarily because their delicacy makes them difficult to sample and study. Most are damaged or destroyed in conventional plankton nets, and many deep-water siphonophores and ctenophores are too delicate to be captured intact even with the most gentle of techniques. More recent progress in understanding their biology has been based on in situ methods of study using SCUBA diving, submersibles or remote vehicles. These methods permit observation of undisturbed behavior and collection of intact living specimens. Advances in culture techniques and laboratory measurements have improved our understanding of energetics, reproduction and life history of some species, although most remain only partially understood.

Gelatinous animals occupy every trophic niche, ranging from primary producers (symbiotic colonial radiolaria) to grazers (pteropods and pelagic tunicates) and predators (medusae, siphonophores and ctenophores). In all these niches, the gelatinous body plan confers advantages of large size and low metabolic costs. In addition to attaining large sizes with relatively little food input, gelatinous organisms such as medusae and ctenophores are able to "de-grow" when deprived of food. Metabolic rates remain unchanged, and the animal simply shrinks until higher food levels allow it resume growth. This energetic flexibility is probably important to the success of gelatinous species in the oligotrophic open ocean and deep sea. Many species of medusae and siphonophores, for example, appear able to survive at low population densities spread over very large areas.

In other cases the efficiency of their feeding, growth and reproduction allows gelatinous species to out-compete other types of zooplankton and form dense populations over large areas, which can have considerable impact on ecosystems. In the last decade or two there have been significant increases in the population sizes and geographical ranges of several kinds of gelatinous animals, usually medusae, ctenophores or salps. Extensive and recurring blooms of these animals can affect fisheries by competing with fin fish or by clogging fishing nets. They can also be a serious nuisance to swimmers or beachgoers. In some cases coastal blooms of medusa or salps impair the operation of desalination plants or power plants that draw the animals into their seawater intakes.

These population increases may be due to several causes including climate-related changes in water temperature or circulation patterns, pollution impacts that disadvantage other species, reduction of predators or competitors by fishing pressure, and introductions of invasive species to places where they have no predators. Dense populations are sometimes further concentrated by wind or current action, or transported close to the coast from their normal habitats further offshore. There is also some evidence of a cyclical behavior of population growth for some medusae. These large blooms have been cited as evidence of degraded environmental quality in many parts of the world ocean, but are also evidence of the adaptability of many gelatinous species to changing conditions.

Further Reading

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