GELATINOUS ZOOPLANKTON

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Introduction

Gelatinous zooplankton comprise a diverse group of organisms with jellylike tissues that contain a high percentage of water. 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 reflect the nature of the open ocean environment better than any other group. Whether as predators or grazing herbivores, they 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 are sparse or unpredictable. Gelatinous zooplankton exhibit many common adaptations to this habitat.

- Transparent tissues provide concealment in the upper layers of the ocean, an environment without physical cover. Transparency is less common below the photic zone.
- The high water content of gelatinous tissues gives the organisms a density very close to that of sea water. The resulting neutral buoyancy decreases the energy required to maintain depth, but may actually require more energy overall, because of drag.
- The environment lacks physical barriers, strong turbulence, and current shears, so that gelatinous bodies do not need great structural strength. However, fragility makes many species difficult to sample or handle, and excludes most from more energetic coastal environments.
- High water content and noncellular jelly permit rapid growth and large body sizes, which can act as, or produce, large surfaces for the collection of food.
- Relatively large size makes gelatinous animals too big to be attacked by some predators, while their high water content reduces the food value of their tissues, which may also deter predation. Large size also permits commensal crustaceans to live on or in the body.

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 some of the major groups will be highlighted.

Taxonomic Groups

Radiolaria

Species of polycystine radiolarians form large gelatinous colonies up to several meters in length. Thousands of individual protists are embedded in a common gelatinous matrix from which their pseudopodia extend into the water. The combined efforts 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 grow on the metabolites of the radiolarians. In turn, the radiolarians digest the zooxanthellae, so that these colonies are planktonic homologues 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, the Scyphozoa, and the Cubozoa. Since the morphology and life history of all three groups is broadly similar, it is practical to treat them together here. There are perhaps 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. A wide variety of prey is eaten by different medusae, ranging from larval forms and small crustaceans to other gelatinous animals and large fish. Many 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 have lost the polyp stage and evolved instead a variety of sexual and asexual reproductive mechanisms that do not require a benthic habitat. There are several classification schemes for Cnidarians; the group names given here are common usage, but these vary in different taxonomies.

Anthomedusae This order of hydromedusae includes small species ranging in size from less than 1 mm to several centimeters. 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, but some also bud medusae directly (**Figure 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 hydroids, but some species produce new medusae by budding or fission (**Figure 1B**).

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 on 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 (**Figure 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 (**Figure 1C**).

Coronatae This order of scyphomedusae includes mainly deep-water 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 (**Figure 1G**).

Semaeostomae The familiar large jellyfish 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 (**Figure 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 virulently toxic nematocysts of any Cnidarians. Some species are responsible for human fatalities. Cubomedusae are also unusual in possessing complex, image-forming eyes, which are not as well developed in other medusae (**Figure 1F**).

Siphonophores

The Order Siphonophora comprises a large and diverse group of predatory Cnidarians in the Class Hydrozoa. Their complex life cycles 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

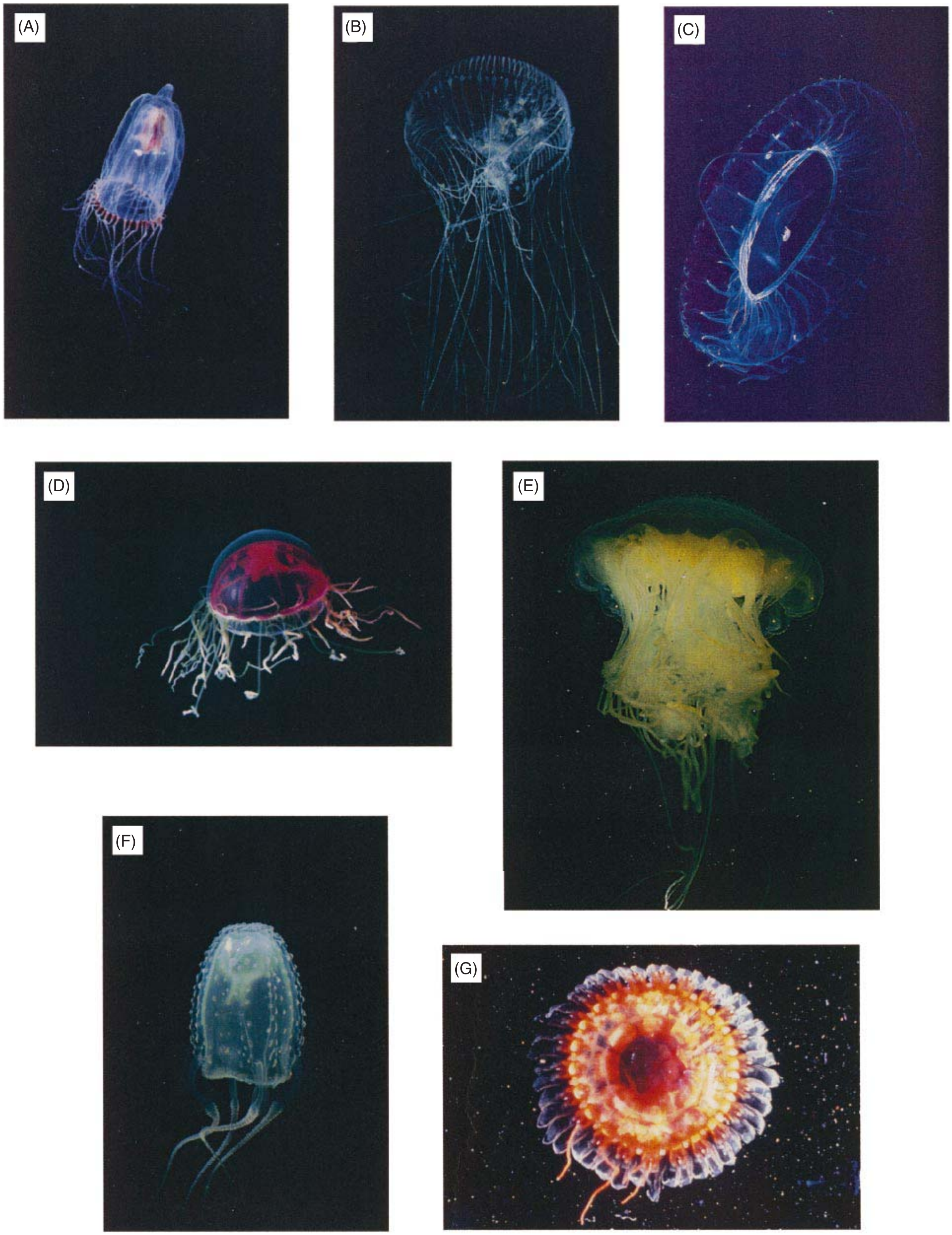

Figure 1 Medusae. (A) *Pandea conica*, an anthomedusa about 2 cm high. (B) *Aequorea macrodactyla*, a leptomedusa about 10 cm in diameter. (C) *Cunina globosa*, a narcomedusa about 5 cm in diameter. (D) *Benthocodon hyalinus*, a trachymedusa about 3 cm in diameter. (E) *Cyanea capillata*, a semaeostome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

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 millimeters 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 three 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-of-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 (**Figure 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. (**Figure 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 (**Figure 2B**).

Ctenophores

Ctenophores are exclusively marine gelatinous animals all but a few of which are holoplanktonic. Although they superficially resemble the Cnidaria, morphological and molecular studies indicate that Cnidarians and ctenophores are not closely related. 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. The members of one species of cydippid, *Haeckelia rubra*, eat medusae, and retain the nematocysts of their prey ('kleptocnidae') for defensive use in their own tentacles. Before this behavior was known, these nematocysts were considered strong evidence for a close relationship between Cnidarians and ctenophores (**Figure 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

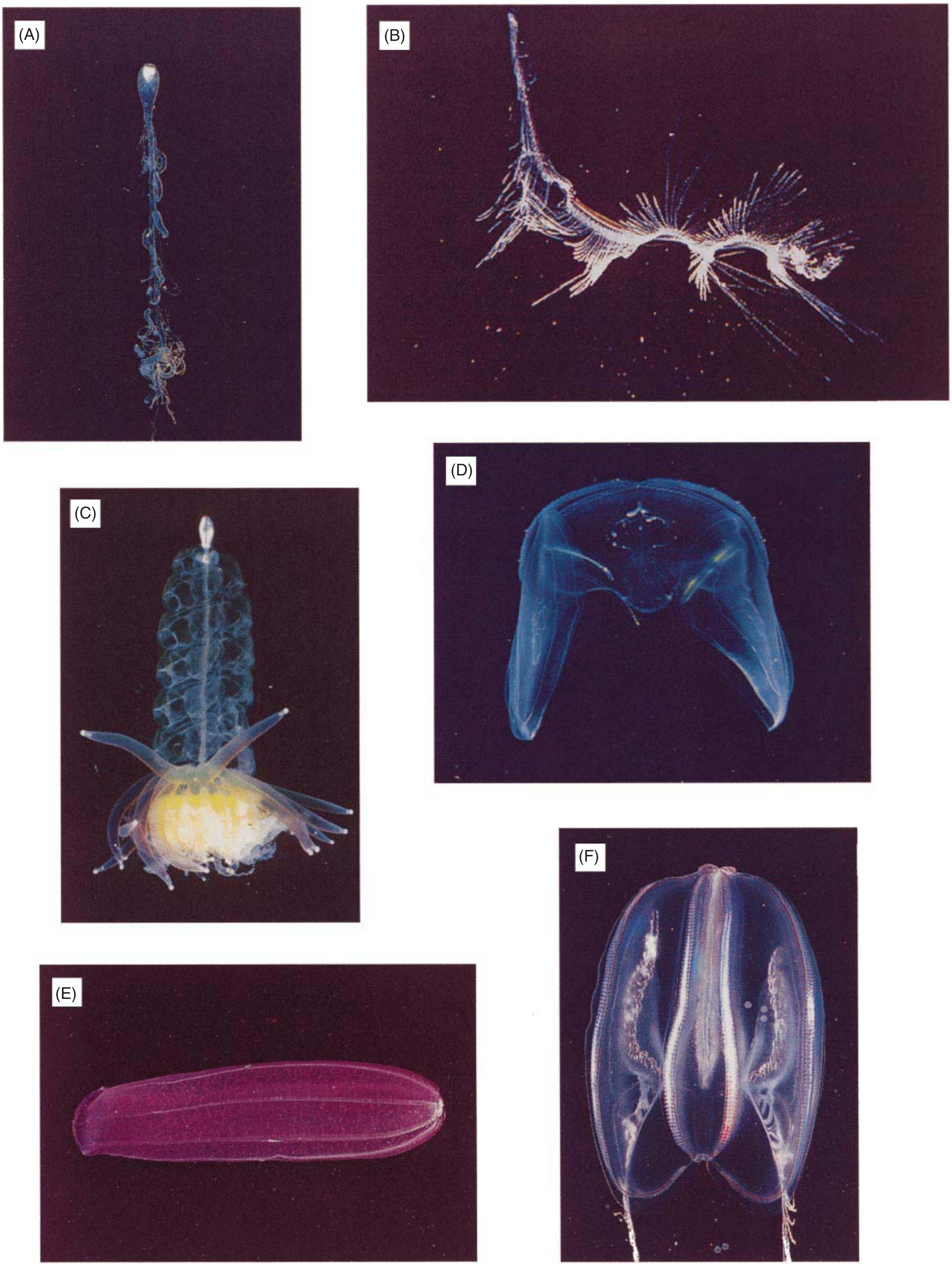

Figure 2 Siphonophores and Ctenophores. (A) *Rhizophysa filiformis*, a cystonect siphonophore up to 2 m long. (B) *Sulculeolaria* sp. a calycophoran siphonophore up to 1 m long. (C) *Physophora hydrostatica*, a physonect siphonophore about 10 cm high. (D) *Ocyropsis maculata*, a lobate ctenophore about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

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 (**Figure 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 ribbonlike 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 (**Figure 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 mollusks. 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 (**Figure 3D**).

Pteropods

This molluskan group comprises two orders in the gastropod subclass Opisthobranchia. The foot in pteropods is modified into two wingshaped 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 of which (Pseudothecosomata) 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 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 (**Figure 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* (**Figure 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 (seven genera and 22 species) with sucker-bearing arms similar to cephalopod tentacles; the Notobranchaeidae (one genus and eight species), with suckerless feeding arms called buccal cones; the Clionidae (eight genera and 16 species); and the Cliopsidae (two genera and three species) (**Figure 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

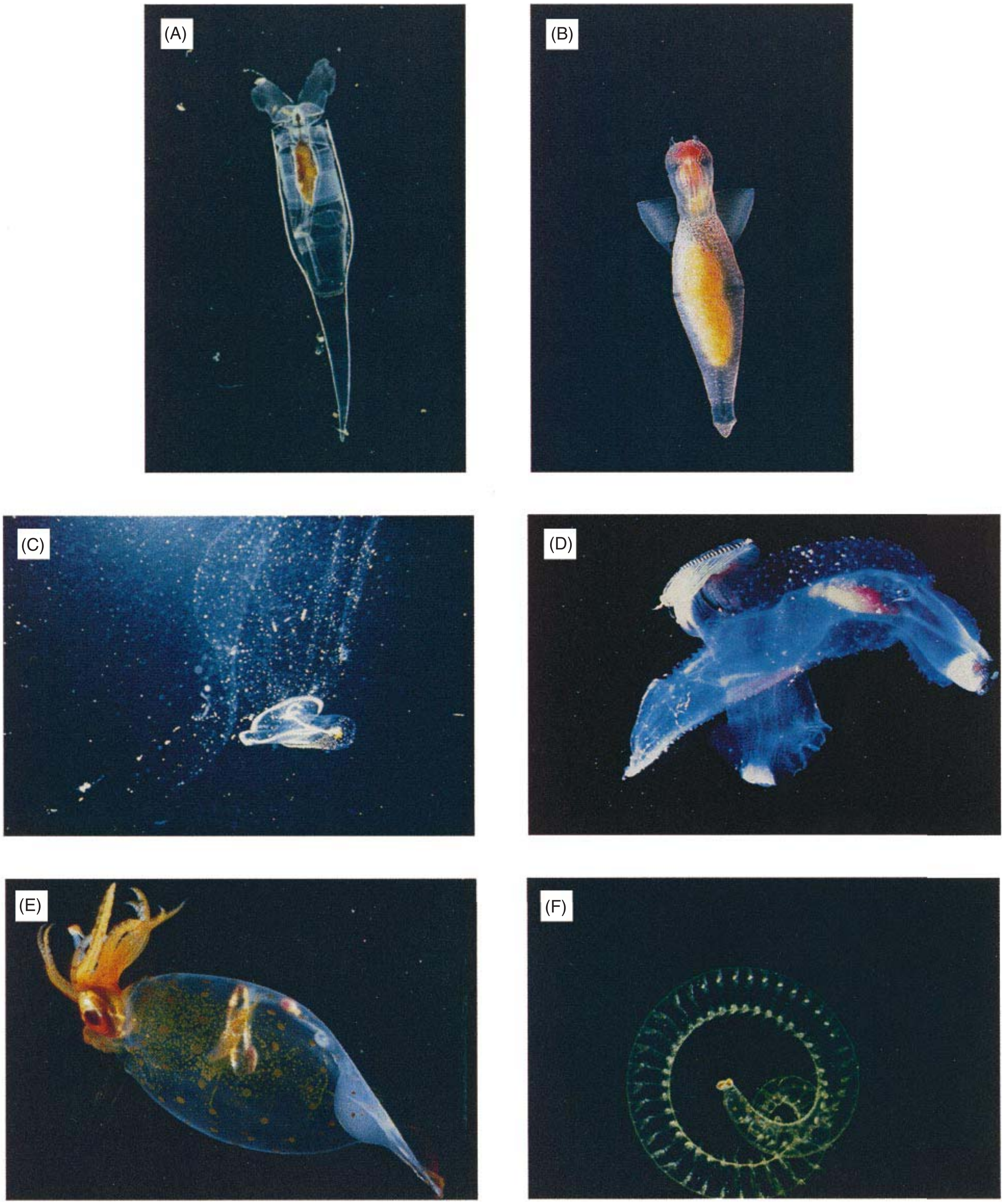

Figure 3 Mollusks and Polychaete. (A) *Cuvierina columnella*, a euthecosome pteropod about 1 cm high. (B) *Clione limacina*, a gymnosome pteropod about 2 cm high. (C) *Corolla spectabilis*, a pseudothecosome pteropod about 10 cm in diameter, with mucous web in background. (D) *Carinaria* sp. a heteropod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

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 (**Figure 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, which 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. (**Figure 3F**).

Crustaceans

Although arthropods cannot really be considered gelatinous because of their exoskeletons, there are some examples of 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. It is likely that the transparency of these species is a form of protective coloration, since they live on transparent gelatinous hosts.

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 Larvacea or Appendicularia. 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 Larvacea comprises a single order of small organisms that filter food particles using an external mucous structure called a house. Both Thaliaceans and Larvaceans are widely distributed in the oceans, and are 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 centimeters to a meter in length, but colonies of at least one species can attain lengths of 20 m.

Doliolida This order of the Thaliacea comprises six genera and 23 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 five asexual stages and one sexual stage, several of which occur together as parts of large colonies of thousands of zooids. These colonies may attain lengths over 1 m, but are fragile and are 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 (hermaphrodites?) that produce the larvae and begin the whole cycle again (**Figure 4B**).

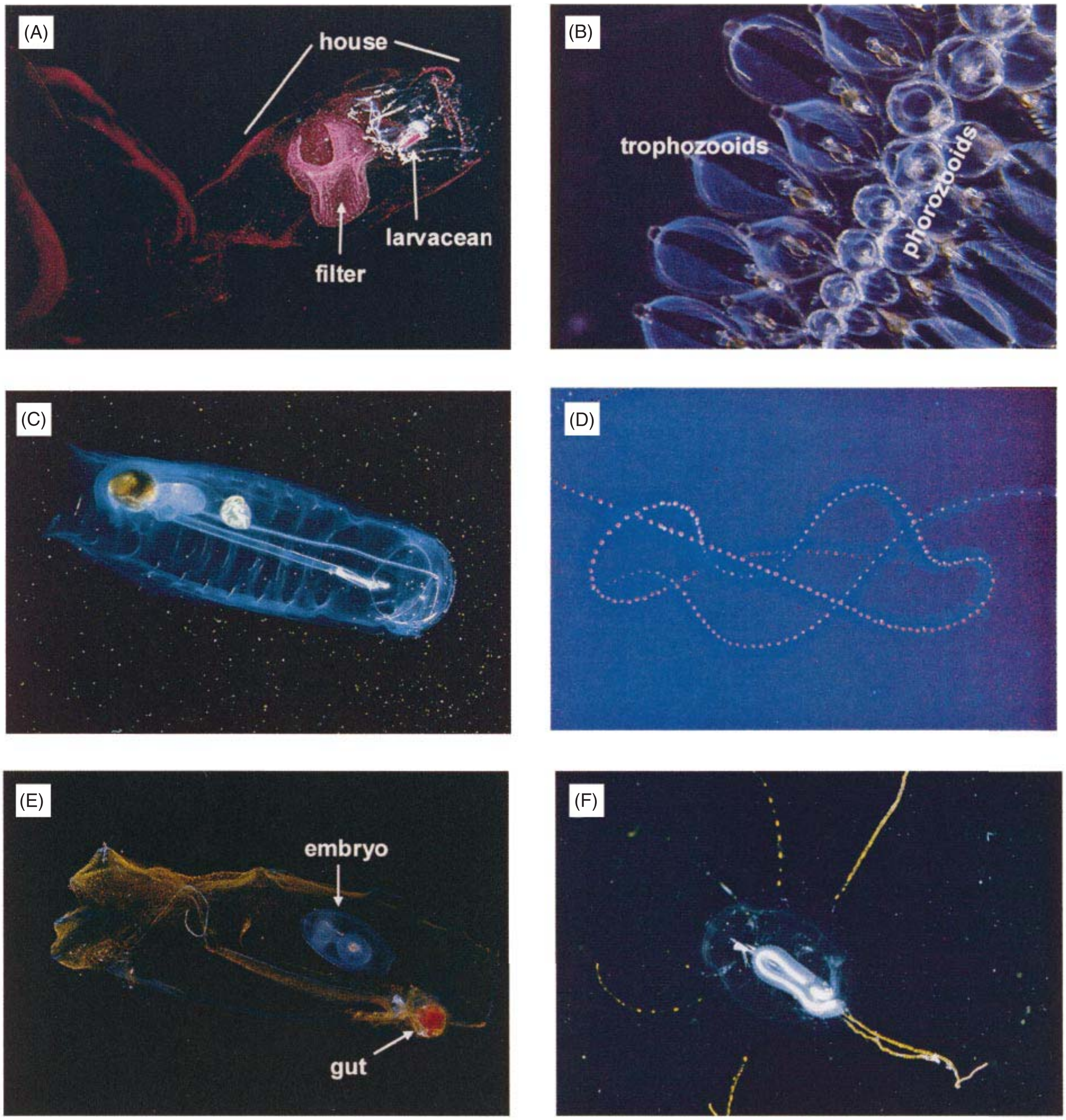

Figure 4 Pelagic Tunicates. (A) *Megalocercus huxleyi*, a larvacean of about 5 mm body length, house length about 4 cm. (B) *Dolioletta gegenbauri*, portion of a colony showing gastrozooids and phorozooids, individuals 2–5 mm long, colonies up to 1 m. (C) *Salpa maxima*, solitary generation salp, up to 25 cm long. (D) *Salpa maxima*, chain of aggregate generation salps; orange dots are guts of salps; individuals are 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. (All photographs by L. P. Madin.)

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 meters long (**Figures 4C–F**).

Larvacea This class (also called Appendicularia) is divided into three families (with 15 genera and 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 larvacean'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 larvacean via a mucous tube. The complex house is formed as a mucous secretion on the body of the larvacean, produced by specialized secretory cells. It is inflated with sea water, 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 larvacean expands a new house (there may be several house rudiments on its body, awaiting expansion) and resumes filter feeding. The abandoned houses can be an important source of marine snow and serve as food for various planktonic scavengers (**Figure 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 parts 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. Much 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, but 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 size and low metabolic costs. In addition to attaining large sizes with relatively little food input, gelatinous organisms such as medusa and ctenophores are able to 'degrow' when deprived of food. Metabolic rates remain unchanged, and the animal simply shrinks until higher food levels allow it to 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 outcompete other types of zooplankton and form dense populations over large areas, which can have considerable impact on ecosystems. A dramatic recent example was the accidental introduction of the ctenophore *Mnemiopsis leidyi* into the Black Sea from the eastern seaboard of the Americas. In the late 1980s, this ctenophore reproduced in prodigious quantities, and the resulting predation on zooplankton and larval fishes led to the collapse of pelagic fisheries in the Black Sea. These fisheries have to some extent recovered, but seasonal blooms of this ctenophore continue to occur in the Black Sea, just as they do on the eastern shores of the Americas. Reports of *Mnemiopsis* in the Caspian Sea suggest that the pattern may be repeated.

Many other gelatinous species form dramatic seasonal blooms, such as the medusa *Chrysaora quinquecirrha* in the Chesapeake Bay, the salp *Thalia democratica* off Florida, Georgia, and Australia, and the medusa *Pelagia noctiluca* in the Mediterranean. In the Southern Ocean, immense populations of the salp *Salpa thompsoni* alternate with those of the

Antarctic krill *Euphausia superba*. The formation of large aggregations through rapid reproduction appears to be a common strategy for taking advantage of favorable conditions. Dense populations are sometimes further concentrated by wind or current action, or are transported close to the coast from their normal habitats farther offshore. The combination of rapid growth and advection can cause the sudden appearance of swarms of medusae, ctenophores, or salps in coastal waters. Although these blooms may sometimes have serious or even catastrophic effects on other organisms, including fisheries or human activities, they are a natural part of the life histories of the species, and not events for which remedial action is needed, or even possible. Gelatinous zooplankton are normal components of virtually all planktonic ecosystems. They are among the most common and typical animals in the oceans, whose biology and ecological roles are now becoming better understood.

See also

Plankton. Zooplankton Sampling with Nets and Trawls.

Further Reading

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GENERAL CIRCULATION MODELS

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Introduction

A general circulation model (GCM) of the ocean is nothing more than that – a numerical model that represents the movement of water in the ocean. Models, and more particularly, numerical models, play an ever-increasing role in all areas of science; in geophysics broadly, and in oceanography specifically. It was perhaps less the early advent of supercomputers than the later appearance of powerful personal workstations (tens of megaflops and megabytes) that effected not only a visible revolution in the range of possible computations but also a more subtle, less often appreciated, revolution in the very nature of the questions that scientists ask, and the answers that result.

The range of length scales and timescales in oceanography is considerable. Important dynamics, such as that which creates 'salt fingers' and hence influences the dynamically significant profile of density versus depth, takes place on centimeter scales, while the dominant features in the average circulation cascade all the way to basin scales of several thousand kilometers. Timescales for turbulent events, like waves breaking on shore, are small fractions of seconds, while at the opposite end, scientists have reliably identified patterns in the ocean with characteristic evolution times of order several decades.[1]

Most simply, a 'model' is no more than a mathematical description of a physical system. In the case of physical oceanography, that description includes the following elements:

- The momentum equation ($F = m\dot{v}$, but expressed in terms appropriate to a continuous medium), or often in its place a derivative form, the 'vorticity equation'.
- An equation to express the principle of mass conservation.
- A heat equation, which describes the advection (carrying by the fluid) and diffusion of temperature.
- A similar 'advection–diffusion' equation for salinity.
- An equation of state, which relates the pressure to the density.

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[1] It is useful to distinguish extrinsic evolution times, which span geologic time, from intrinsic variation, which characterizes an isolated ocean and atmosphere, thus neglecting such secular influences as orbital variation, change in the earth's rotation rate, variation in the solar constant, etc. Although not all causes of variability have been identified, it is possible that even documented evolution over thousands of years may reflect the latter, intrinsic, variability.