DVD Marine Plankton

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Abstract

Marine plankton is made up of a large number of organisms that are small in size and represent a huge variety of animal and plant groups. A principal feature shared among these organisms is their inability to actively move against the influence of waves and currents. Besides species that spend their entire life cycle in the pelagic realm, larvae of many benthic animals also reside in the plankton for some time before settling to the bottom, this way also dispersing the species. The plankton provides the basis of marine food chains through the photosynthetic primary production of single-celled algae and zooplanktonic animals foraging on them. This DVD presents some examples of typical microbial, plant and animal members of the marine plankton and provides insights to their biology and ecology.

Chapter 1. Marine biocenoses

Marine organisms are diversified in various aspects, so in their biology. In the pelagic realm there are planktonic and nektonic life forms. Plankton (Greek: drifting) commonly comprises small organisms, which are dominated by the hydrodynamic forces of the ocean, such as currents and waves. Nekton can compensate those forces by own locomotory capabilities. Benthos comprises all organisms that either live on or within the sea bottom.

1.1 Plankton

Planktonic organisms are mentioned already by Plato (429 B.C.), who described medusae in his reports. Aristotle (389 B.C.) also mentioned planktonic life forms by implication when he described fish fry. The term plankton, however, was established only in 1887 by the marine physiologist Viktor Hensen from the Marine Science Institute in Kiel. Although most representatives of the plankton are microscopic, there are exceptions represented by larger organisms with poor locomotory abilities such as medusae. Due to their high content of water, they are almost neutrally buoyant and are passively moved by hydrodynamic forces.
▶**C 12700:** plankton sample

1.2 Nekton

Most representatives of the nekton (such as fish, seals, wales or squid) are usually streamlined as a hydrodynamic adaptation. This enables them to attain high swimming speeds and – contrary to plankton – emancipates them to some extent from the physical forces of the water.
▶**C 12701:** shoal of wrasses (*Diplodus* sp.)

1.3 Benthos

Seastars or crabs are typical life forms of the benthos. Some taxa with predominantly benthic animals have large representatives in the plankton,

such as the Ostracoda (*Gigantocypris* sp.) and the Amphipoda (*Thaumatops* sp.). Both associations, benthos and plankton, are linked by freeswimming larvae that are released into the water by benthic parental populations. The benthos also relies on the photosynthetic production of organic carbon by microscopic algae in the euphotic zone as a major carbon source.
▶**C 12702:** seastar (*Astropecten* sp.); undetermined crab

Chapter 2. Trophic relations

Marine food webs depend on the photosynthetic production of minute, mostly unicellular algae (phytoplankton) which are autotroph and represent the bulk of primary producers in the sea. Heterotrophic zooplankton feeds – as primary and secondary consumers – on the phytoplankton directly or indirectly. They themselves provide food for larger animals. The exudates, feces and carcasses of zooplankton together with other particulate organic matter form ‘marine snow’ that serves as food for other organisms. As in all coenoses parasitism also occurs among planktonic organisms.

2.1 Phytoplankton, primary producers

The bulk of phytoplankton taxa comprise diatoms, dinoflagellates and coccolithophorides. Under suitable environmental conditions they can multiply very fast by cell fission (phytoplankton bloom). Due to the fact that algae depend on sunlight for their photosynthethic production, they are limited to the upper water layers, i.e. the euphotic zone.
▶**C 12703**: phytoplankton sample

2.2 Zooplankton, primary and secondary consumers

Heterotrophic zooplankton comprises a much more diverse group than the phytoplankton. Often, single groups are dominant, such as the Crustacea and here the Copepoda that can constitute more than 70% of the zooplankton share of a sample. Animals from almost all phyla can be found in the plankton during some or all phases of their life cycle and are therefore called Mero- or Holoplankton, respectively.
▶**C 12704:** zooplankton sample; young fish feeding on copepods

Meroplanktonic larvae are often very different from their adult stages. The former develop through a metamorphosis (indirect development). In earlier times and even rarely now, larvae have been described under a separate name due to the fact that the life cycle of most species was unknown. An evolutionary advantage of indirect development with freeswimming larvae is certainly their contribution to the dispersal of a species. Development times of many months are reported in so-called teleplanic larvae. During these periods of time they can be drifted across oceans via currents (e.g. the Gulf and North Atlantic currents). Prominent examples are provided by prosobranch larvae (Gastropoda). A disadvantage of such an extended planktonic development is a high mortality rate due to abiotic and biotic factors.

2.3 Parasitism

The microoniscium larval stage of certain isopods (e.g. of the Bopyridae = Epicaridea) attaches as an ectoparasite to copepods and feeds on the hemolymph of its host.

▶**C 12705:** microoniscium (Isopoda: Bopyridae = Epicaridea)

2.4 Feces

Exudates, feces and carcasses of planktonic organisms provide other planktonic representatives with food, e.g. the nauplius larva of the benthic copepod *Paramphiascella* sp. that feeds on fecal pellets.
▶**C 12706:** feces; nauplius larva of the benthic copepod *Paramphiascella* sp. (Harpacticoida: Copepoda) crawling on a fecal pellet

2.5 Marine snow

Aggregates of particulate organic matter (POM) form so-called marine snow, that sinks comparatively fast to deeper strata and can reach the sea-bottom within a few days. Through this rain of particles organic substances descend to deeper zones and are eliminated from the euphotic zone for extended periods of time. This mechanism is also called ‘biological carbon pump’ or ‘carbon sink’. It plays a specific role in the regulation of the global CO_2-equilibrium.
▶**C 12707:** marine snow

Chapter 3. Locomotion

Planktonic organisms have by definition only limited capabilities for locomotion. Due to the vast diversity of planktonic taxa belonging to all biotic kingdoms, very diverse ways of locomotion have evolved as well as a variety of morphological, and physiological adaptations for buoyancy regulation.

3.1 Buoyancy regulation

To compensate for the fact that their specific weigth is higher than water, weight reduction, formation of floating appendages, and the incorporation of oil and gas are common adjustments to slow down sinking rates and thus save energy for swimming.
▶**C 12708:** floating appendages of copepods (Crustacea); chain-formation of *Chaetoceros* sp. (Bacillariophyta)

The bodies of many plankton organisms are equipped with floating devices in the form of setae in order to increase the resistance to sinking (e.g. in radioloaria, dinoflagellates, many Crustacea). Others have an elongate or disc-shaped body form and are thus summarized as rhabdoplankton (e.g. the dinoflagellate *Ceratium fusus)* or discoplankton (e.g. phyllosoma larvae of the rock-lobster *Palinurus* sp.), respectively.
▶**C 12708:** Rhabdoplankton, e.g. the dinoflagellate *Ceratium fusus.*

Buoyancy regulation is also provided by the reduction of weight, for instance by the reduction of shells and/or the reduction of calciumcarbonate (e.g. in the heteropods Carinariidae and Pterotracheidae). Instead, plankton organisms develop gelatinous masses, increase the proportion of water, or exchange heavy ions for lighter ones. Another way to enhance buoyancy, is the incorporation of oil and gas (e.g. by siphonophorans or fish-eggs). Some copepods use stored lipid droplets for buoyancy compensation as well as a food reserve for periods of starvation.
▶**C 12708:** lipid-droplets inside a copepod; gelatinous sheath of an invertebrate egg; oil-droplet of a fish-egg

3.2 Cilia

Many small plankton organisms, particularly invertebrate larvae, use cilia for their locomotion, which are often arranged in fields or bands. The body of the so-called Müller's larva of the turbellarians is completely covered by cilia. Besides locomotion, bands of cilia also serve other functions, as in the collection of food particles and the subsequent transport to the mouth.

Food particles are concentrated in a food groove and transported to the oral opening (downstream feeding in trochophore and veliger larvae). Another principle, called upstream feeding, involves a reversal of the ciliary beat upon contact with a food particle. Particles are collected here opposite to the direction of swimming (larvae of echinoderms and enteropneusts).

▶**C 12709:** phoronid actinotrocha larva; Müller's larva of polycladid turbellarians

3.3 Comb cilia

In Ctenophores the body is divided by cilia fused to combs arranged in 8 longitudinal rows. They beat synchronously from the mouth to the apical pole of the body, pushing ctenophores through the water with their mouth opening in front.

▶**C 12710:** the ctenophore *Pleurobrachia pileus*; comb cilia

3.4 Jet propulsion

An effective way of swimming is provided by jet propulsion, which is not only utilized by cephalopods, but also by medusae and other planktonic organisms. Medusae force water out of their subumbrellar cavity by rhythmically contracting the umbrella.

▶**C 12711**: the hydrozoan medusa *Obelia* sp.

3.5 Appendages

Many planktonic organisms swim with the aid of appendages, e.g. crustacean nauplii or copepods. For this purpose the appendages are often flattened or otherwise modified. Similarly, the foot of holoplanktonic molluscs (Gastropoda: Heteropoda and Thecosomata) is modified into fin-like structures.

▶**C 12712**: nauplius larva of the calanoid copepod *Temora* sp.

3.6 Migration and dispersal

Some planktonic organisms are able to migrate within restricted areas, often forming swarms. At the onset of dusk many zooplankton organisms migrate from deeper water layers, where they remain during the day, to the surface, moving back again to deeper layers before dawn (diurnal migration). Distances that are covered during these migration periods can be several hundred meters. Vertical patterns of distribution vary not only among species but also with season, sex, developmental stage or age.

▶**C 12713:** mysid swarm (Crustacea: Malacostraca)

Chapter 4. Unicellular planktonic organisms

Unicellular plankton organisms comprise bacteria, heterotrophic protists, and algae. Here, diatoms and dinoflagellates represent the bulk of photosynthetic primary producers. Protists are represented by radiolarians, foraminiferans and ciliates.

4.1 Bacteria (ultramicroplankton)

The smallest and most abundant organisms in the plankton are bacteria. Due to their minute size they belong to the ultramicroplankton (< 2 µm). They thrive in the pelagic but also on detrital particles or other plankton organisms. Bacteria are not characterized by a high diversity of forms but by their enormous metabolic potential. This enables them to make use of a broad spectrum of nutrients. They contribute enormously to the decomposition and recycling of organic material.
▶**C 12714:** Overview bacterial plankton; bacteria on decomposing alga; bacteria on the carcass of a copepod

4.2 Fungi

Besides, bacteria, animals, and plants, there are also fungi in the plankton. They develop tubiform hyphae and thrive on decaying organic material (detritus), or live as parasites on or inside the bodies of their hosts.
▶**C 12715:** overview fungi

4.3 Algae (Plants)

Photoautotrophic unicellular plankton is dominated by diatoms and dinoflagellates. They occur in all seas and provide the bulk of the photosynthetic primary production. In some groups there are photoautotrophic besides heterotrophic forms, as well as mixotrophic transient forms. Mass development of dinoflagellates can produce harmful algal blooms (HABs, also called red tides). Some diatom species produce toxins leading to severe intoxications by accumulation in the food web.

Green algae (Chlorophyta)

The green alga *Dunaliella* is a unicellular flagellate (Chlorophyceae: Volvocales) that can produce colonies under certain environmental conditions. The cells are naked, i.e. they do not have a shell or cell walls, as dinoflagellates do. They move through the water with the aid of their flagellae. They are extremely halotolerant and due to their small size they belong to the nanoplankton. A pigmented organ (eye spot) enables them to sense the direction of light and perform positive phototaxis.
▶**C 12716:** *Dunaliella* sp.; single individual

Among flagellates we find organisms with and without photosynthetic pigments, that can perform photosynthesis (i.e. they are photoautotroph) or can feed heterotrophically. Even transient, mixotroph forms between plants and animals are present in the plankton.

Diatoms (Bacillariophyta)

Diatoms are relatively large protists (0.1 – 0.5 mm), that can also form colonies. Their cell walls are made of silica and are rather rigid. Each cell is comprised of two shell valves: a smaller hypotheca and a larger epitheca fitting closely like a box. The structural diversity of shells is remarkably high.

▶**C 12716:** overview diatoms; diatom *Coscinodiscus* sp. in phase contrast

Unicellular diatoms are present in all seas in a large diversity of taxa and shape and are dominant primary producers. In temperate and cold zones they develop their maximum population densities in spring. There are estimates that 25% of the total primary production in marine waters is provided by diatoms.
In the radially symmetrical Centrales (e.g. *Coscinodiscus* sp.) the morphology of the cells can easily be observed. Their shells are very solid and build up a unique sediment in boreal waters.
▶**C 12716:** detail of *Coscinodiscus* sp.

Chloroplasts, i.e. cell organells carrying photosynthetic pigments, are located beneath the surface of the shells. In a time-lapse they can be seen moving. They appear to be brown in color since the green chlorophyll is masked by the pigment fucoxanthin.
▶**C 12716:** movement of chloroplasts in *Coscinodiscus* sp.

Other diatoms form colonies shaped like stars or chains, in which the cells remain together permanently after mitosis, e.g. in *Phaeodactylum tricornutum* and the genera *Thalassiosira* or *Bacillaria*. The pennate diatoms (Pennales) are characterized by elongate body forms contrary to taxa which have primarily centric body forms (Centrales).
▶**C 12716:** diatoms *Phaeodactylum tricornutum*; diatom star, overview, detail; *Thalassiosira sp*; *Bacillaria* sp.

Mass development of chain forming diatoms like *Chaetoceros* and *Thalassiosira* may result in the clogging of the gills of suspension feeders like mussels and fish. Other diatom species produce toxins, that accumulate in the food web and may result in harmful poisoning of animals and humans.

Prymnesiomonads (Haptophyta)

Representatives of the genus *Phaeocystis* (Prymnesiomonada) form an important component of the phytoplankton and are characterized by an enormous reproductive rate. They develop as single individuals, but also form gelatinous colonies of about 1 mm diameter. During mass development they produce a sticky mucus, providing them with the name ‘stinking water’. Some species of *Phaeocystis* produce dimethylsulfide (DMS), that is most probably an antagonist to the greenhouse-effect. *Phaeocystis antarctica* exudes a pigment into the slime-cover of the colonies that absorbs UV-radiation.
▶**C 12716:** *Phaeocystis* sp. gelatinous colony; single cells

Dinoflagellates (Dinoflagellata)

Dinoflagellates represent the secondmost important group of the phytoplankton besides the diatoms. Among them there are photoautotrophic as well as heterotrophic taxa. Also mixotrophic forms (e.g. *Peridinium* sp.) may occur, that are able to use

dissolved organic carbon from the sea water. Most of the genera show a peculiar cell-wall that consists of several cellulose plates (thecate forms) and show several long extensions. Dinoflagellates swim with two asymmetrical flagellae. During blooms of some species, seawater can be colored brown or red. Such ‘harmful algal blooms’ or ‘red tides’ are often connected with oxygen depletion and the exudation of toxins.
▶**C 12716:** dinoflagellate *Peridinium* sp.

Noctiluca spp. belong to the group of athecate dinoflagellates capable to produce bioluminescence. A blueish light is emitted when luciferin is split in an oxygen and energy dependent enzymatic reaction.
▶**C 12716:** accumulation of the dinoflagellate *Noctiluca* sp.

Noctiluca sp., with a diameter of about 1 mm, is a rather large dinoflagellate. Due to a lack of chloroplasts it is not able to perform photosynthesis, but it lives heterotrophically on small zooplankton caught with the tentacle. Food vesicles move within the cell by cytoplasmic currents.
▶**C 12716:** *Noctiluca* sp., single individual; *Noctiluca* sp. with food vacuole; movement of food vacuole

4.4 Radiolaria

Radiolaria are exclusively marine and planktonic protists. The majority of species occurs down to 350 m depth. The basic shape of the cell is spherical, with a central capsule, that is covered by ectoplasm which forms pseudopodia and needles or skeletal elements made of silica. Often there are symbiotic zooxanthellae and oil droplets incorporated. The latter also enhances buoyancy. Skeletons of radiolaria dominate sediments in several marine regions.
▶**C 12716b:** single radiolarian; accumulation of radiolaria

Chapter 5. Multicellular planktonic organisms

Heterotrophic zooplankton is commonly much more diverse than phytoplankton. Representatives of most animal phyla either belong to the plankton throughout their life or have certain developmental phases in the plankton – hence they are called holo- or meroplankton, respectively. Meroplanktonic larvae do not resemble their parents, but transform into the adult form by metamorphosis (indirect development).

5.1 Cnidaria

Cnidaria occur in the plankton as larvae but also as medusae or colonies of siphonophores. Scyphomedusae are among the largest planktonic forms of life. They are commonly called jellyfish due to their gelatinous umbrella. Their medusae develop from ephyrae that are detached from sessile polyps in a process called strobilation. All these forms move primarily by jet propulsion.

Hydrozoa

The life cycle of many Hydrozoa is characterized by an alteration of generations with a sessile asexual phase (polyp) and a free

swimming sexual phase (medusa) - a process called metagenesis. Some medusae are also able to propagate asexually by budding. These buds can be developed at the manubrium (as shown here for *Podocoryne* sp.), but also at the margin, the subumbrella, or the tentacles. Most of the hydromedusae are relatively small. The diameter of their umbrella varies between a few millimeters to centimeters. According to the form and position of the gonads, and other characters, Antho-, Lepto-, Trachy- and Narcomedusae are distinguished. Hydromedusae occur primarily in the epipelagic zone (0-200 m depth).
▶**C 12717:** hydrozoan medusa *Podocoryne* sp.

The siphonophores are a peculiar taxon among the Hydrozoa. Their colonies can become rather large and their individuals can be very specialized. The well known Portuguese man-of-war (*Physalia physalis*) occurs predominantly in the tropics and subtropics and sails before the wind at the sea surface by means of a gas-filled pneumatophor. Hence, this species belongs to the pleuston.
▶**C 12717:** siphonophore *Physalia physalis*

Scyphozoa

Scyphomedusae, such as the compass nettle (*Chrysaora hysoscella*) are called jelly fish due to the enormous development of the gallertous umbrella reaching a diameter of up to 1 m in some species. As in the hydrozoans their life cycle is characterized by a metagenetic alteration of generations. The medusae do not develop as single individuals on a polyp, but detach as disc-shaped ephyrae in a process called strobilation.
▶**C 12717:** compass nettle (*Chrysaora hysoscella*)

The disc-shaped *Ephyra* stage is often called a larva, despite the fact that it does not posses any true larval organs, i. e. organs, that are only developed in the larval phase and will be lost or transformed during metamorphosis to the juvenile adult. Four gastral filaments surround the manubrium of the ephyra. In the invaginations between the lobes, there are sensory organs that perceive gravity and light. In the course of the planktonic phase the ephyra grows into a juvenile medusa.
▶**C 12717:** ephyra of the moon jelly (*Aurelia aurita*); juvenile medusa (undetermined)

5.2 Ctenophora

Ctenophores resemble medusae in their gelatinous consistency and transparency. However, contrary to the cnidaria, they show a biradial body symmetry. On the surface there are eight rows of comb cilia running from the apical pole to the mouth providing locomotion. Ctenophores are predators and develop via a so-called cydippe stage.
The ctenophore *Pleurobrachia pileus* resembles gelatinous medusae of cnidarians. Collectively ctenophores and cnidarian medusae are called ‘gelatinous zooplankton’. The body of ctenophores is usually spherical to pear-shaped, but it can also be lobate (Lobata) or elongated and band-shaped, (*Cestus veneris*). Ctenophores have a biradial symmetry of the

body. Two perpendicular levels, the tentacle and the pharyngeal plane cross in the vertical main axis, which runs through the mouth opening and the aboral pole. At the apical pole the apical organ is situated, which assists in positioning using gravity force as an indicator.

Like the medusae ctenophores are predators. *Pleurobrachia* feeds primarily on planktonic crustaceans and larvae, which are caught by the aid of colloblasts on the tentacles. The tentacles are extendable and carry lateral branches with colloblasts. Despite their remarkable length, the tentacles can be completely retracted into pockets situated next to the aboral pole.

Ctenophores develop via a cydippe stage, that is a juvenile not a larval stage – similar to the Ephyra of the Scypozoa – due to the absence of larval organs. The body is pear-shaped and its organisation is similar to the adult. The cydippe is naturally smaller, and the longitudinal rows of the comb cilia are shorter than in the adult, though already developed in eight longitudinal rows. The apical organ is discernible.

▶C 12718: *Pleurobrachia pileus, Pleurobrachia pileus* catching prey, cydippe stage of an undetermined ctenophore; advanced cydippe stage

5.3 Turbellaria

Among the turbellarians only some representatives of the Polycladida develop a planktonic larva that is called Müller’s larva. It develops from a trochophore-like stage by the formation of 8 ciliated lobes. This larva can be caught using fine-meshed plankton nets. The larval phase lasts only a few days. The metamorphosis delivers a young turbellarian worm which can still be found in plankton samples before it settles to perform a benthic life.

▶C 12719: early larval stage of a turbellarian; Müller’s larva; juvenile turbellarian

5.4 Nemertea

The nemerteans represent a phylum with different developmental modes and therefore a diverse array of larvae. Best known is the pilidium larva of many heteronemerteans, that feeds on smaller planktonic organisms. The larva is helmet-shaped with laterally prolonged lobes and an apical tuft of cilia. Along the margin runs a band of cilia, whose beat provides the larva with a rotating forward propulsion.

Several deviations are common of this basic pattern. The mouth is situated ventrally in the middle of the larva and leads to a blind ending gut. During metamorphosis the juvenile worm develops in a cavity (amnion) formed around the intestine.

▶C 12720: nemertean pilidium larva

5.5 Rotatoria

Whereas rotifers are very abundant and diverse in freshwater plankton, there are only a few species in the marine plankton. Most of the rotifers are very small (<1 mm) and consist of about 1000 cells (eutely). The body is surrounded by a proteinaceous shell (lorica) made of keratin that shows spiniform emarginations. A charasteristic feature is the corona at the anterior part of the body. The beat of its cilia serves for locomotion and feeding.

The posterior part of the pharynx is transformed into a highly muscular part, the mastax, which carries complex hardened structures and serves in the break-up of food particles. The mobile foot is inserted at the posterior end and used for steering. It can be absent in pelagic species.
▶**C 12721:** corona, mastax of an undetermined rotifer

5.6 Gastropoda

Only a few of the about 70.000 marine gastropods known to date show a holoplanktonic life style. Typical representatives of the latter are heteropods and pteropods. Besides these holoplanktonic forms the veliger larvae of benthic adults are found in the plankton. The name of this larva is derived from its swimming organ, the velum, a paired, lateral emargination of the head.

Holoplanktonic snails

Among the prosobranchs, holoplanktonic heteropods are represented by only about 30 species worldwide. Only a few forms grow longer than a few centimeters (e.g. *Carinaria cristata* attaining a length of 50 cm). Heteropods develop the frontal part of the foot into an unpaired fin. Due to the fact that the balance point is determined by the shell, heteropods are swimming with the ventral side up.
▶**C 12722:** the heteropod *Atlanta* sp.

There are about 100 species of pteropods belonging to the opisthobranchs that are holoplanktonic and show adaptations to a pelagic existence. This includes a reduction of the shell or its transformation to an elongate form as well as the transformation of the foot into two lateral fin (or wing)-like parapodia. Locomotion is achieved by flapping movements of these parapodia. Among the pteropods two different evolutionary lines are hypothesized leading to the Thecosomata (shelled forms, e.g. *Creseis* sp.) and the Gymnosomata (naked forms, e.g. *Pneumodermopsis paucidens*). The Thecosomata are suspension feeders, assisted by fields of cilia, alternatively they produce mucous-nets to filter their food from the water.
▶**C 12722:** the thecosomate *Creseis* sp.; detail flapping wings; *Creseis acicula*

The empty shells of these animals are concentrated in some regions on the seafloor as so-called pteropod ooze.
▶**C 12722:** pteropod ooze

Due to the reduced shell, the insertion of the fins in mid-body and the streamlined shape, representatives of the Gymnosomata are good swimmers and primarily predatory. They grasp their prey using the suckers on their parapodia.
▶**C 12722:** undetermined gymnosome; *Pneumodermopsis paucidens*

Veliger larvae

Exclusively holoplanktonic as well as benthic proso- and opisthobranchs with a planktonic phase develop the same characteristic larva, the veliger. Its swimming organ from which its name is derived, is a paired lateral lobe of the cephalic region, the velum (from latin: sail). This lobe bears a ciliary band along its margin. As in most soft-bodied invertebrate larvae the ciliary beat not only provides a locomotory force but also collects small food particles in the food groove on the backside of the velar lobes. Taxa with extended planktonic larval phase show increased size and number of velar lobes. Due to enhanced swimming ability, these larvae can remain in the plankton for several months and disperse over long distances (long-distance veliger). The velar lobes can be retracted into the larval shell by retractor muscles. The hydraulic pressure of the hemolymph acts as an antagonist when the lobes are everted again. The less calcified, often transparent shell (protoconch) is transformed into the adult shell (teloconch) in most taxa.
▶C 12722: undetermined prosobranch veliger larva; veliger of *Mangelia* sp. (Prosobranchia); veliger of *Archidoris pseudoargus* (Opisthobranchia)

Among bivalves, a similar larval form can be found, the rotiger. It differs from gastropod veligers by its bivalved shell and simple, round velum.
Among benthic gastropods, the advanced veliger develops into a veliconcha larva. Although the velum is still present, the foot is already developed in this larva allowing crawling on the substrate in addition to swimming. This dual locomotory ability allows for an efficient search for a suitable settling site. The cephalic sensory organ and the tentacles are used to check for chemical clues. During the subsequent metamorphosis the velum will be resorbed or discarded.
▶C 12722: undetermined prosobranch veliconcha

5.7 Sipuncula

During the indirect ontogeny of sipunculans a secondary larva, the pelagosphaera, succeeds a trochophore larva. Its body consists of a frontal cephalic region, a middle region with a ciliary band and the trunk. The head and the middle region can be retracted into the trunk.
▶C 12723: pelagosphaera larva as seen in light- and electron microscope (SEM)

5.8 Polychaeta

Polychaetes are among the dominant invertebrate groups of the marine benthos. Some representatives of this group have adapted to a life in the pelagic realm – a minority representing roughly 140 of about 10.000 known species. Besides these holoplanktonic species, the larvae of many benthic polychaetes develop in the plankton. They show a trochophore as a primary larva and depending on the taxa involved, rather morphologically derived secondary larvae.

Adult forms

The alciopids and tomopterids are the most speciose families among holoplanktonic polychaetes. They are transparent and move predominantly by lateral undulation. Their parapodia are flattened and paddle-like and chaetae nearly completely reduced in the Tomopteridae. Only the long tentacular cirri bear internal chaetae (spirally rolled up due to fixation). The Alciopidae are characterized by large lenses to their eyes and an eversible pharynx. Both these morphological characters indicate a predatory mode of life.
▶**C 12724:** *Tomopteris* sp. (Tomopteridae); *Rhynchonerella* sp. (Alciopidae) (incomplete specimen)

Larvae

The trochophore larva is the primary larva of polychaetes. According to the Trochophore-theory this larval type is found in other invertebrate taxa as well (e.g. Mollusca, Sipuncula). Due to the orientation of the cleavage spindle during early embryogenesis, these taxa are called Spiralia. The initially spherical form of the trochophore is subdivided by two equatorial ciliary bands (proto- und metatroch) into a cephalic epi- and a caudal hyposphere. These ciliary bands provide locomotory power for a movement in spirals. At the apical pole there is an apical organ bearing a sensory tuft of cilia. Trochophore larvae have a gut with a ventral mouth (between proto- and metatroch) and a terminal anus that is surrounded by a ciliary band called telotroch.
▶**C 12724:** undetermined trochophore larva

The worm-like body of polychaetes develops by successive budding of similar segments from a preanal budding zone. The episphere provides the head region (prostomium) of later adults. According to the increasing number of segments, advanced larvae are called metatrochophore and later nectochaeta when parapodia and chaetae become functional. The distinction between these two stages, however, is sometimes difficult.
▶**C 12724:** undetermined metatrochophore larva; late metatrochophore larva

Developmentally advanced polychaete larvae show a diversified body architecture, as an adaptation to their pelagic life style. Aulophora larvae of the terebellid *Lanice* sp. produce a mucus tube, in order to regulate buoyancy. The larvae bearing 3-5 tentacles, can freely move inside, assisted by their chaetae, which find support at the inner wall of the tube.
▶**C 12724:** aulophora larva of *Lanice* sp. (Terebellidae)

The episphere of the mitraria larva of the Oweniidae grows during development also extending the ciliary band of the prototroch. This allows better swimming abilities following the increase of size and weigth. On the lower side of the epishere the mitraria larva is equipped with long, flattened, caudally directed chaetae. The segments of the developing worm (hyposphere) are inverted into the episphere forming a so-called endolarva. This adaptation helps

to keep up the positive hydrodynamic qualities of a sphere. With about four weeks mitraria and aulophora larvae spent a relatively long time in the plankton. They can be drifted away from the shore to the open sea, adding to a wide distribution of the species.
▶**C 12724:** mitraria larva of Oweniidae, Overview, detail

The larva of *Chaetopterus* is characterized by a large mouth and a variable number of cilia bands that provide efficient swimming locomotion. Advanced larvae develop tentacles and increasing number of segments.
▶**C 12724:** larva of *Chaetopterus* sp. (Chaetopteridae)

5.9 Crustacea

Crustacea are present in almost every plankton sample and represent the bulk of its biomass. Besides abundant holoplanktonic representatives of various systematic groups, namely from the Branchiopoda, Copepoda, Mysidacea, and Euphausiacea, crustaceans produce a vast variety of larval forms with many of them bearing specific names. The zoëa larva for example represents the typical hatching form of many marine decapod crustaceans.

Euphausids occur in large swarms and represent the staple food of baleen whales known as krill. While *Euphausia superba* represents the dominant species in the Antarctic, this place is taken over by *Meganyctiphanes norvegicus* in the Arctic (northern krill).

Adult forms

The Phyllopoda are represented by only about 10 species in the marine realm. These are primarily small forms living as suspension feeders or predators. Some species, as for example *Penilia* sp., bear a two-fold, non-calcareous carapace, that covers the body and its six pairs of legs. This species occurs seasonally in high abundance, so in the coastal plankton of the Mediterranean Sea.
▶**C 12725:** *Penilia* sp.; filtration of suspended food

Many Phyllopoda have a brood chamber in between the carapace and thorax in which the relatively small eggs develop. While the first antennae are small, the second antennae are well developed for locomotion.
▶**C 12725:** *Penilia* sp., brood chamber

Unlike *Penilia*, *Podon* and *Evadne* are predatory species. Their carapace is reduced and serves only as a brood chamber for the embryos. Like all water fleas they also use their second antennae for locomotion. Remarkable is their large, movable compound eye. Dorsal to the brood chamber the beating heart is discernible.
▶**C 12725:** *Evadne* sp.

Marine water fleas (Phyllopoda: Cladocera) are able to propagate rapidly by parthenogenesis. As in the limnetic environment (see *Daphnia* sp.), there is an alteration between parthenogenetic and bisexually produced generations (heterogeny). Contrary to partenogenetically developed eggs, bisexually produced resting

(dormant) eggs are able to withstand severe environmental conditions (e.g. freezing, anoxic conditions, salinity fluctuations). Parthenogenetic generations of limnetic species develop different body forms (cyclomorphosis) – a phenomenon that is modulated by environmental factors like temperature.
▶**C 12725:** *Podon* sp. with embryos

Copepods represent the dominant invertebrate group in most plankton samples. Due to their enormous abundance that according to some authors exceeds the number of all other metazoans on earth, they provide an important link of the food web. They feed primarily on unicellular algae of the phytoplankton and represent a remarkable protein source for many secondary consumers (fish, whales). Their feces, molts, and carcasses on the other hand form a very important part of marine snow, that plays a critical role in the delivery of organic material to deeper water layers. In most taxa the copepod body comprises 10 somites grouped into a wide cephalothorax, free thoracic somites, and a slender abdomen. The first pair of antennae is usually very long in planktonic taxa and provided with elongate or featherlike setae. The antennae are spread out to compensate for sinking. Locomotion is performed by gliding or jumping movements propelled by the thoracic appendages while the antennae are spontaneously aligned to the body.
▶**C 12725:** overview copepods

Most copepod females carry their eggs on the ventral side of their abdomen.
▶**C 12725:** the copepod *Pseudocalanus* sp. with egg sac

Copepods have a single median nauplius eye. Predatory planktonic species, like *Sapphirina*, *Corycaeus* or *Copilia*, have additional large, paired ocelli comprising of 2 lenses each connected by a cone-shaped membrane. They scan their environment by rhythmic lateral oscillations of the hind lense.
▶**C 12725:** the copepod *Corycaeus* sp.

Shrimp-like mysids live predominantly near the coast, as a component of the neritic plankton. They often form swarms that stay near the sea bottom during the day and ascend to the water column during the night. Typical for mysids is a pair of statocysts at the base of the uropods which form a caudal fan together with the unpaired median telson.

Larvae

The nauplius is the primary larva of the Crustacea. Different secondary larvae develop in various crustacean groups bearing taxon-specific characters. These larvae pass different stages (instars) separated by molts. In the Anostraca and the Cephalocarida, nauplii can develop in an anagenetic series of molts – during which segments and appendages are added without metamorphosis.

▶**C 12725:** cirriped nauplius larvae

Nauplius larva are characterized by 3 pairs of appendages (1st, 2nd antennae and mandibles), the latter two pairs forming biramous appendages. The limbs serve for locomotion as well as feeding. The unpaired nauplius eye is very conspicuous. Thoracic segments are only developed in the metanaupliar phase.
▶**C 12725:** nauplius of a cyclopoid copepod

Despite the fact that the nauplius represents a larva with rather underived characters, it has a body form that is well differentiated allowing systematic allocation. Cirriped nauplii for example are characterized by long spine-like extensions.
▶**C 12725:** nauplius of *Facetotecta* sp. (Thecostraca); nauplius of *Lepas* sp. (Cirripedia)

The nauplius larva of the northern krill (*Meganyctiphanes norvegicus*) bears long, setigerous appendages. On the abdomen the buds of additional appendages start to develop.
▶**C 12725:** nauplius of the euphausid *Meganyctiphanes norvegicus*

In several crustacean taxa the larvae hatch at a later stage. For example as zoëa larva in the Decapoda. In the course of such shortened development – often accompanied by parental care – all segments are developed inside the integument of the egg. Among the Malacostraca only a few groups show free-swimming nauplii, for instance the euphausids, the penaeids and some sergestids. Overall, the Crustacea exhibit a remarkable diversity of larval forms.
▶**C 12725:** zoëa II of the decapod *Solenocera membranacea*

The alima larva (or pseudozoëa larva) of the stomatopod *Squilla* is characterized by a transparent, strongly dorso-ventrally flattened cephalothorax that is armed with spines and allows efficient floating. Abdominal segments and pleopods are well developed and functional (for swimming) while the segments and appendages of the cephalothorax are still small and bud-like. However, the second maxilliped is already differentiated to the typical raptorial leg of stomatopods. The compound eyes of the alima larva have long stalks and can be moved in different directions.
▶**C 12725:** Pseudozoëa or alima larva of the stomatopod *Squilla* sp.; eye

In the antizoëa (erichthus larva) which precedes the pseudozoëa in the development of stomatopod crustaceans, the compound eyes are not yet stalked and the second pair of maxillipeds is not yet developed as a raptorial appendage.
▶**C 12725:** antizoëa or erichthus larva of a stomatopod

The zoëa larva is the hatching stage of most decapods. These larvae use their maxillipeds as swimming appendages while the

pereiopods are only present as anlagen. Therefore, metamorphosis involves also a change of function for the maxillipeds.
Typical for the zoëa of brachyuran decapods are strong dorsal and caudal spines on the carapace and the ventrally bent abdomen.
▶**C 12725:** zoëa larva of a brachyuran decapod

The megalopa of brachyurans can still be found in the plankton although it represents a transitional stage during the development to the juvenile. The megalopa has already developed chelate appendages and the maxillipeds are already functional oral appendages. This larva is able to swim with its pleopods but it can also crawl using its pereiopods. The transition to the juvenile crab correlates with a change from a planktonic to a benthic life style.
▶**C 12725:** megalopa larva of a brachyuran decapod

5.10 Chaetognatha

Chaetognaths feed primarily on planktonic copepods, that are captured with spines and teeth located laterally in the head region. Their elongated body is almost completely transparent and resembles an arrow with its lateral fins. Arrow-worms can accelerate very fast by dorsoventral oscillations of their musculature. Since they share many peculiar characters, their systematic position within the animal kingdom is still not clear.
▶**C 12727:** head of the chaetognath *Sagitta* sp. as seen in the electron microscope (SEM)

5.11 Tentaculata

The actinotrocha larva of the Phoronida represents one of the most peculiar invertebrate larva in the marine plankton. A cephalic epi- and a caudal hyposphere are distinguished by a horseshoe-shaped ring of ciliated tentacles. The metamorphosis is very fast and can be completed in about 15 minutes.
The episphere forms an umbrella-like hood above the mouth and carries an apical sense organ. Some species develop an additional secondary sense organ more anteriorly that is instrumental in identifying the substrate for a suitable habitat. The hind part of the larva is characterized by a circumanal band of cilia (telotroch), that is important for locomotion.
Metamorphosis to the juvenile worm is initiated by the eversion of the metasomal sac, that develops ventrally inside the hyposphere closely behind the circle of tentacles. The larval tentacles and the episphere are ingested during metamorphosis and serve as the first meal of the juvenile worms.
▶**C 12726:** actinotrocha larva of phoronids

5.12 Echinodermata

The pentaradiate and mostly benthic echinoderms develop very characteristic larvae that are bilaterally symmetrical and swim by the beat of cilia bands. A primary larva of all echinoderms is the dipleurula larva. Larvae of asteroids and ophiurans are characterized by long projections, that are stabilized by skeletal elements made of calcium carbonate.

Asteroidea (Sea stars)

The bipinnaria larva of seastars is characterized by the presence of two bands of cilia. A preoral ciliated band encircles the region in front of the mouth (preoral field) while a much longer postoral ciliated band limits the area of the mouth ventrally and follows the outline of the larva in wide loops. In the bipinnaria skeletal elements are absent. Due to the transparency of the larva the elongate pharynx, the spheric stomach and the hind gut are clearly discernible, as are the anlagen of the hydro- and somatocoel.
▶**C 12728:** advanced bipinnaria larva of an asteroid

Only in a few seastars the bipinnaria develops directly to the young adult. In most of the taxa it develops into another larval form, the brachiolaria with ciliated lobes drawn out to arm-like extensions. This larva may reach a size of 3 cm. Typically, there are three apical (brachiolar) arms, that play a role in the search of suitable substrata for metamorphosis.
▶**C 12728:** brachiolaria larva

Ophiuroidea (Brittle stars)

The ophiopluteus larva shows some similarities with the echinopluteus of echinoids. Although there are only 4 pairs of arms developed they are remarkably longer and laterally expanded. The arms are supported by skeletal rods of calcium carbonate. A closed ciliated band runs along the arms which is used for the accumulation of food particles as well as for a slow, gliding locomotion – with the mouth in anterior position.
▶**C 12728:** ophiopluteus larva of an ophiuran

Holothuroidea (Sea cucumbers)

The auricularia larva of the holothurians is similar to the bipinnaria of asteroids. But the cilia of the auricularia form a single coherent band, that follows the winding contour of the body. Its complexity develops with the growth of the larva. In contrast to the bipinnaria larva there are fragments of a larval skeleton in the form of small calcareous ossicles in the posterolateral lobes of advanced auricularia larvae.
▶**C 12728:** auricularia larva of a holothurian

5.13 Enteropneusta

The tornaria larva of enteropneusts resembles the bipinnaria or auricularia larva of echinoderms at first glance. Its ciliated bands, however, are even more elaborate and develop complicated folds and saddles, particularly in later stages. These bands function primarily in the capture of food particles while locomotion is primarily achieved by the characteristic circumanal band of cilia (Telotroch). The tornaria of some species can reach several millimeters in length and stay in the plankton for extended periods of time.
▶**C 12729:** tornaria larva; tornaria larva swimming

5.14 Chordata

The chordates are comprised of appendicularians, ascidians, thaliaceans and vertebrates. The last mentioned are only present in the plankton in the form of eggs and fish larvae. Appendicularians and salps are completely transparent as an adaptation to pelagic life. They feed on small plankton, that is accumulated by highly efficient mechanisms of suspension feeding.

Appendicularia

Appendicularia (or larvacea) are mostly small tunicates, only a few millimeter long. They bear a tail with a central chord clearly discerned from the body and bent at right angle. Appendicularians have developed a unique mechanism of food collection. Despite the fact that they do not have a pharyngeal basket such as the salps, they are able to accumulate smallest flagellates and heterotrophic protists (nanoplankton). Suspension feeding is provided by a gelatinous house that is exuded by the animal and covers it nearly entirely. By the propelling force of the tail, water is circulated through this structure and food particles are caught in a filter. The filtration rate is close to a few hundred milliliters per hour and nanoplankton is almost quantitatively retained. The gelatinous house can be very large in certain taxa (nearly 1 m in diameter). However, they are generally very fragile and are destroyed by the plankton net. They can be renewed, however, in a few minutes.
▶C 12730: appendicularian *Oikopleura* sp.

Under magnification the inner organs of the body as well as the base of the tail become visible in more detail. The weakly developed gonads (see eggs), the heart - beating rapidly, the stomach, the esophagus showing a dense coating of cilia and the dorsally (here ventrally) situated statocyst can also be observed.
▶C 12730: *Oikopleura* sp.; trunk

Feeding particles being trapped by the filtering apparatus are transported to the mouth and into the gut by cilia. The rapidly beating heart and the ovary situated at the upper caudal end of the trunk are conspicuous.
▶C 12730: *Oikopleura* sp.; suspension feeding of particles; detail

Ascidiacea

Ascidians develop via a tadpole-like larva which carries a tail with a central chorda and an outer transparent cuticle. At the anterior end they bear papillae that enable them to attach firmly when becoming benthic during metamorphosis.
▶C 12730: ascidian larva

Thaliacea

The comparatively small barrel-shaped body of salps belonging to the genus *Doliolum* is open at both ends and surrounded by a number of muscle bands like hoops of a barrel. Salps are typically transparent and feed on phytoplankton, which they filter out of the water by means of a pharyngeal basket. Rhythmic contractions of the muscle bands enable these animals to swim by jet propulsion. Their reproduction is characterized by a complicated life cycle.
▶C 12730: thaliacean *Doliolum* sp.

Vertebrata

Despite the fact that most adult fish belong to the nekton, their eggs and larvae are usually planktonic. Advanced embryos are generally well visible within the eggs. Several species include oil deposits in their eggs, to regulate their buoyancy (e.g. sardines and mackerel). Newly hatched larvae carry a yolk sac and show a distinct pattern of chromatophores. Flatfish develop larvae that are initially bilaterally symmetrical. The eyes then shift to the prospective upper side during metamorphosis.

Studies concerning the composition and geographic distribution of eggs and larvae of fish are important aspects in fisheries research. Contrary to planktonic fish larvae, juvenile fish are considered as nekton.

▶**C 12730:** undetermined fish eggs; juvenile fish

Chapter 6. Methods

The vertical and horizontal distribution of plankton in the sea depends on several parameters resulting in a certain degree of patchiness. The local composition also varies according to the time of the day. Some species emerge only during the day, others only at night. Most of the plankton organisms are very sensitive to changes of temperature and oxygen. Therefore, live organisms have to be studied immediately after sampling.

6.1 Plankton sampling

There is a non-homogeneous distribution of plankton (‘patchiness’) due to water movements, distribution of nutrients, oxygen, temperature gradients and the migration of plankton. Tropical seas are also called ‘blue deserts’ due to the low density of particulate organic matter and plankton organisms. With the aid of special nets made of fine-meshed gauze and towed at a speed of 1-2 knots, plankton is concentrated during sampling. The size class of organisms captured is determined by the mesh-size used. The use of a relatively wide-meshed net naturally excludes the capture of smaller organisms and vice versa, since the filtration rate of a fine-meshed net is too low to catch fast moving plankton organisms. Additionally animals are disturbed by a bow wave developing in front of the net. This develops, when the net is towed too fast or has not been properly cleaned before use. Caught organisms are accumulated at the end of the net in a beaker. According to objectives, vertical, diagonal or horizontal hauls are distinguished. The deployment of nets with a closing device allow for separate sampling in different water depths.

▶**C 12731:** plankton net sampling

6.2 Night sampling

The plankton composition at a certain water depth during day- and nighttime varies due to diurnal vertical migration. In the dark many plankton organisms are attracted by light and can easily be collected by a small net.

▶**C 12732:** night sampling

6.3 Laboratory studies

Studies of live plankton should take place immediately after sampling since changes in temperature, oxygen deficiency and increased light intensity cause a rapid mortality of sensitive plankton organisms.

▶**C 12733:** studying of plankton in the laboratory; plankton sample

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DVD Marine Plankton
Systematic position of the organisms displayed

Unicellular planktonic organisms

PROKARYOTA
- Bacteria

EUKARYOTA
- **Opisthokonta**
  - Fungi
- **Viridiplantae**
  - Chlorophyta (green algae)
    - Chlorophyceae
      - *Dunaliella* sp.
- **Chromista**
  - Heterokonta
    - Bacillariophyta (Diatomeae, diatoms)
      - *Coscinodiscus* sp.
      - *Phaeodactylum tricornutum*
      - *Thalassiosira* sp.
      - *Chaetoceros* sp.
      - *Bacillaria* sp.
  - Prymnesiomonada (Haptophyta)
    - *Phaeocystis* sp.
- **Alveolata**
  - Dinoflagellata
    - *Peridinium* sp.
    - *Noctiluca* sp.
- **Actinopoda**
  - Radiolaria
    - undetermined radiolarians

Multicellular planktonic organisms

- **Cnidaria**
  - Hydrozoa
    - Hydroida
      - Athecatae - Anthomedusae
        - *Podocoryne* sp.
    - Siphonophora
      - Cystonectida
        - *Physalia physalis*
  - Scyphozoa
    - *Chrysaora hysoscella* (compass nettle)
    - ephyra of a moon jellyfish (*Aurelia aurita*)
    - undetermined juvenile Scyphozoa
- **Ctenophora**
  - *Pleurobrachia pileus* (sea gooseberry)
  - undetermined cydippe
- **Turbellaria**
  - Müller’s larva
  - undetermined juvenile turbellarian
- **Nemertea**
  - pilidium larva

- **Aschelminthes**
  - Rotatoria
    - undetermined Rotatoria
- **Mollusca**
  - Gastropoda
    - Prosobranchia
        - undetermined veliger larva
        - veliger larva of *Mangelia* sp.
        - undetermined veliconcha
      - Heteropoda
        - *Atlanta* sp.
    - Opisthobranchia
        - veliger larva of *Archidoris pseudoargus*
      - Thecosomata (shelled pteropods)
        - *Creseis* sp.
        - *Creseis acicula*
      - Gymnosomata (naked pteropods)
        - undetermined Gymnosomata
        - *Pneumodermopsis paucidens*
- **Sipuncula**
  - pelagosphaera larva
- **Annelida**
  - Polychaeta
    - undertermined trochophore larva
    - undertermined metatrochophore larva
      - Tomopteridae
        - *Tomopteris* sp.
      - Alciopidae
        - *Rhynchonerella* sp.
      - Terebellidae
        - aulophora larva of *Lanice* sp.
      - Oweniidae
        - mitraria larva
      - Chaetopteridae
        - larva of *Chaetopterus* sp.
- **Arthropoda**
  - Crustacea
      - Branchiopoda
        - Phyllopoda
          - *Penilia* sp.
          - *Evadne* sp.
          - *Podon* sp.
      - Maxillopoda
        - Copepoda
            - *Pseudocalanus* sp.
            - *Corycaeus* sp.
          - Cyclopoida
            - undetermined nauplius larva
        - Cirripedia
          - undetermined nauplii
          - nauplius of *Lepas* sp.
          - facetotectan nauplius

- Malacostraca
  - Mysidacea
    - undetermined mysids
  - Euphausiacea
    - nauplius of *Meganyctiphanes norvegicus*
  - Stomatopoda
    - alima larva of *Squilla* sp.
    - erichthus larva
  - Decapoda
    - zoëa II of the penaeoid *Solenocera membranacea*
    - brachyuran zoëa
    - brachyuran megalopa

Chaetognatha
- *Sagitta* sp.

Tentaculata
- Phoronida
  - actinotrocha larva

Echinodermata
- Asteroidea
  - bipinnaria larva
  - brachiolaria larva
- Ophiuroidea
  - ophiopluteus larva
- Holothuroidea
  - auricularia larva

Hemichordata
- Enteropneusta
  - tornaria larva

Chordata
- Urochordata
  - Appendicularia
    - *Oikopleura* sp.
  - Ascidiacea
    - ascidian larva
  - Thaliacea
    - *Doliolum* sp.
- Vertebrata
  - Osteichthyes
    - fish eggs
    - fish fry