Chapter II

BIOLOGY AND ECOLOGY OF AQUA-SPHERE

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Irrespective of the nature of the environment, whether it is the sea, river, lake or pond, organisms make even the hot spring and ground water as their habitat. Organisms living in the earth's aquasphere are called aquatic organisms. Primeval forms of life were born and a major part of history of evolution has progressed in the sea. Therefore, biodiversity in the aquasphere, which has several endemic species, is higher than that in aerosphere and terrasphere. We can find all phyla of prokaryotes, protists, fungi, plants and animals in the aquatic environment. Animals that have strong connection with aquatic environment in their life such as the seabirds and seals are also members of aquatic organisms, and constitute a part of the ecosystem through interrelationships among them. The aquatic environments can be differentiated into riverine, coastal, and deep sea ecosystem. However, as most water bodies on earth including the seas and inland water bodies have some connections to other water bodies, the boundary of the ecosystems is obscure. Ecosystems are connected through migration of organisms and material transportation. In order to live in water, aquatic organisms have developed specialized adaptive functions and organs. The endemic and common organs, tissues and cells such as gills, lateral line, swim-bladder and chloride cells are some examples. These functions characterize not only the behavior of aquatic organisms but also their life history, population structure, reproduction, feeding, migration etc. For example, being denser than air, water offers higher buoyancy to organisms thereby helping large scale dispersion at larval stage, which is a common characteristic trait in aquatic species. In this chapter the authors will discuss about the biodiversity, and the physiological and ecological peculiarities and commonalities of organisms in the aquatic ecosystem.

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1. LIVING ORGANISMS IN AQUA-SPHERE

1.1 Advent and evolution of aquatic organisms

Although the theory of panspermia implies that spores of the earliest life on

the Earth came from space, it is commonly believed that earliest life was born in Primordial Ocean on the Earth 4 billion years ago. Living organisms are defined as the ones with a cell membrane, metabolic system and function of self reproduction. It still remains a issue as to how these necessary conditions were met with in the process of evolution. However the chemical evolution theory which states that, organic substances were produced from inorganic substances in the primordial ocean and life was born by the reactions among organic substances, is widely accepted.

The first primeval form of life originated as a chemosynthetic autotrophic organism in a reductive environment such as the hydrothermal vents in deep sea. The common ancestors which led to macroevolution later branched to eubacterium and archaebacterium. They are classified in prokaryote in the 5 kingdoms theory. Eubacterium-like fossils were discovered in a 3.8 billion year old sedimentary rock in Greenland. About 2.7 billion years ago, a cyanobacterium that produced oxygen through photosynthesis appeared and the Earth changed to an oxygen-rich planet as we see today. About 2 billion years ago, eukaryotes were born as the result of incorporation of other cells and symbiosis. With the progress of intercellular symbiosis, cyanobacterium and aerobic bacterium were imported to other cells and formed the chloroplasts and mitochondria, respectively. Plants and animals originated from those eukaryotes.

About a billion years ago, unicellular organisms conjugated with each other to form a living organism. This was the appearance of multicellular organisms. Early forms of multicellular organisms were small fungi. Towards the end of Precambrian period (800–600 million years ago), strong global cooling occurred and the whole earth was covered with ice. This is the snow ball earth age. The mega scale climate change and global freezing caused mass extinction of protists. When snow ball earth ended 600–500 million years ago, large multicellular organisms called Ediacaran biota suddenly appeared and most of them became extinct before the Cambrian period (570–510 million years ago). After that, evolution was accelerated. Most of the modern day animal phyla appeared in the ocean. The sudden increase of biodiversity known as Cambrian explosion is represented by the Burgess shale fauna that were discovered as fossils from the Burgess shale in British Colombia, Canada. Fishes appeared in the Ordovician period (510–440 million years ago), and flourished extensively in the Devonian period (410–370 million years ago). Since then, fishes have flourished in the aquatic environments up to the present. On the other hand, in late Devonian (360 million years ago), amphibians and tetrapod animals that developed from Sarcopterygii like lung fish or coelacanth, found their way on to the terrestrial environment.

After Ordovician, living organisms on the Earth experienced five mass extinctions. Every time after extinction, survivors implemented rapid adaptive divergence in open niches. Various causes are considered to be responsible for mass extinction, such as the impact of huge meteor, strong volcanic activity and supernova explosion. Undoubtedly, the driving force of the evolution was due to these abiotic environmental changes. However, it is well known that the changes

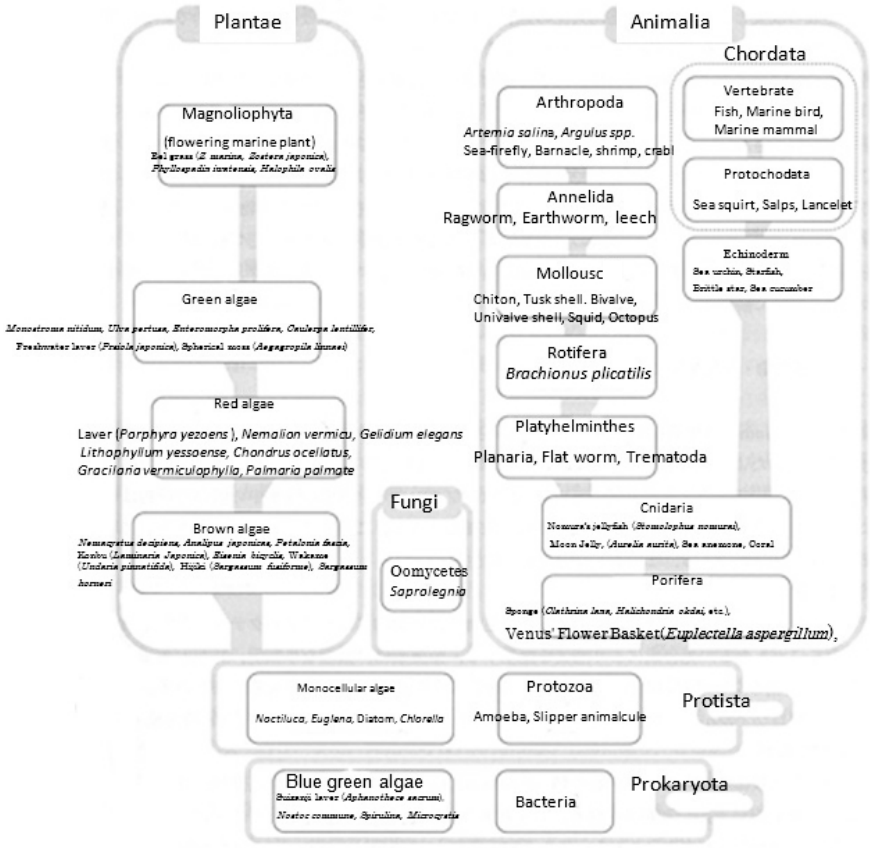

Fig. 2.1. Phylogenic systematic of aquatic organisms in five kingdoms theory.

in the composition of air due to the appearance of photosynthetic cyanobacteria and progress of intercellular symbiosis following it, led to the occurrence of eukaryotes. It should be noted that organisms can change the environment and promote evolution through environmental changes.

The classic theory of biological classification was based on the two kingdom system, in which organisms were divided into two groups (plants and animals). With the identification of species relationships in the evolutionary processes and the origin of life by means of contemporary molecular genetic studies, the framework of biological classification has been rearranged. Different classification systems have been put forth so far: the three kingdom system in which unicellular organisms were given independence as protista; the four kingdom system in which fungi was separated from plants because they do not have a photosynthetic function; and the five kingdom system in which prokaryotes without nuclear membrane were separated from protista. Recently the eight kingdom system

dividing protista to smaller groups is also suggested, although the theory is still arguable. In this text book, major aquatic species are put in a dendrogram based on the five kingdom system at corresponding positions (Fig. 2.1). Typical species in each taxon will be introduced in the following paragraphs.

1.2 Procaryote and Protoctista

1) Bacterium

Bacterium as well as cyanobacterium is classified as Procaryote. Density of bacteria in aquatic environments is far higher than that estimated in classical science. Sea water contains around 10^6 bacteria/ml. Bacteria in the ocean have important functions in oceanic food chain. Dissolved organic substances derived from phytoplankton are absorbed, metabolized and finally mineralized by bacteria. After mineralization, the nutrient salts are absorbed again by phytoplankton.

2) Blue green algae

Blue green algae lack the nuclear membrane and are classified into Procaryote. They are sometimes included into Bacteria as Cyanobacterium. They produce oxygen through photosynthesis. Blue green algae exhibit various forms such as a fine single cell, colonies (clusters of cells), catenoid colony (filaments of cells without a capsule), and trichomes (filaments of cells with a capsule), have chlorophyll *a* and are without flagellum. Their assimilation products are cyanophycin starch and cyanophycin granules.

3) Monocellular algae

Dinophyta, diatoms, euglenophyta and monocellular chlorophyta are classified into monocellular algae that have nuclear membrane (Eukaryote). Chlorophyll *a* is common in all the monocellular algae. In addition to Chl *a*, euglenophyta and monocellular chlorophyta have chlorophyll *b*, and Dinophyta and diatoms have chlorophyll *c*.

1.3 Plants

Major plants in the aquatic environment are macro algae. Most are marine, divided into brown, red and green algae. In addition to macro algae, monocotyledons, which are called sea grasses or flowering marine plants occur in coastal areas.

1) Brown algae

Most brown algae are marine species, composed of multiple cells. Migratory cells such as gametes and zoospores have a pair of flagella of unequal length on the lateral side of the cell. As pigments they have chlorophyll *a*, *c* and β carotene. The presence of large amount of fucoxanthin gives these algae a brown color.

Assimilation products are laminarin and mannitol. Some species contain slimy polysaccharides (alginic acid or fucoidan). Brown algae exist in various forms, such as filaceous, foliaceous and arborized forms, and have well developed body with size of the fronds sometimes reaching several meters.

2) Red algae

More than 5,000 species of red algae are known in the world. Most of these

are marine species. Their germ cells have no flagellum and lack mobility. As pigments, they have chlorophyll *a* and *d*, and a large amount of phycoerythrin as red chromoprotein, as well as phycocyanin, a blue chromoprotein. Their assimilation product is red algae starch. They have a cell wall composed of cellulose and thick gelatinous polysaccharide.

3) Green algae

About 10,000 green algae are known in the world, with 80% being freshwater species. They have a number of flagella at the top of migratory cells, and the lengths of flagella are uniform irrespective of the number. As pigments, they have chlorophyll *a* and *b*, carotenoids and xanthophylls. The assimilation product of photosynthesis is starch. There are various forms in green algae: *Ulva* is foliaceous; and Spirogyra is filamentous. Charophyta are usually given an independent taxon, because of its unique structure, they are sometimes included in green algae in some classification system.

4) Flowering marine plants

Flowering marine plants is a name for marine plants that produce flowers and seeds. Typical species is *Zostera*. *Zostera* has thin columnar nodes on the stem from where grow the hairy roots. Long thin leaves grow into the water from the upper part of the stem forming the sea grass bed, which provides living space for various organisms.

1.4 Animals

1) Marine sponge

Marine sponges are the lowest form of sessile animals. They do not develop the germ layers such as ectoderm and endoderm during the process of embryonic development. Despite being multicellular, distinct organ differentiation is not observed. Marine sponges occur in various shapes: pot like, fan like and cup like. The body surface is covered by many small pores called ostium, through which water and food is drawn in. A large exhalant aperture exists on the top, and water is thrown out from here after the food particles are filtered and retained inside. Sponges have a well developed water exchange system between the small pores and the large aperture. On the inner wall of the cavity called the gastral cavity, many colored cells with flagella exist and water current is caused by the action of these flagella. Calcarea, Domospongiae, Hexactinellid and Sclerospongiae constitute the marine sponges.

2) Cnidarian

Cnidarians are diploblastic animals. The cells making their body are composed of two layers, ectoderm cells (mainly outside), and endoderm cells (inside). Between two layers exist the gelatinous tissue called mesogloea. The form is basically actinomorphic. Siphons radiating from the gastral cavity form the gastro vascular system. The life cycle is divided into two types: planktonic jelly fish stage and sessile polyp stage. Cniadarian is composed of Hydrozoa, Cubozoa, Scyphozoa and Anthozoa. Anthozoa can be divided into Octocorallia and Hexacorallia. Scleractinia in Hexacorallia form coral reef.

3) Flat worm

Shape of these worms is generally flat and hence the name flat worm. They have no specialized organ for circulation and respiration. These are divided into Cestida, Trematoda and Turbellaria. Most of the Turbellarians are free living in aquatic environment, feeding on micro benthic organisms. Some flat worms are parasitic, and have extremely simplified body structures.

4) Trochelminth

Trochelminth is a group composed of aquatic micro organisms called rotifer, mainly distributed in freshwater regions. However, some are oceanic and some terrestrial. Most are less than 1 mm in size, and grow to a maximum size of 100 to 500 μm. These are mainly planktonic, though sometimes they are groveling on surfaces of algae and sediments. Parthenogenesis is common. Species in which males appear continuously are rare. Some species completely lack males. *Brachionus plicatilis* is euryhaline species propagating by parathenogenesis and bisexual reproduction. After the establishment of mass culture technique by parathenogenesis, this species is used as food organism for the early stages of aquatic animal in aquaculture.

5) Mollusc

Mollusc is a large phylum next to arthropod. In addition to shells, squids and octopus, sea slugs, clione, and nautilus are also classified into this taxon. Mollusc are mostly oceanic, although some Gastropoda (Viviparidae, Pleuroceridae etc.) and Bivalvia (freshwater mussel, Corbiculidae etc.) are distributed in the freshwater. Several gastropods (snails and slugs) live in terrestrial environments. Mollusc commonly have lamellas called mantle and produce shell secreting calcium bicarbonate from the mantle. Several species such as octopus, slugs, and sea slugs do not produce external shell.

6) Annelids

Generally, the structure of Annelids is a tandem line of circular segments (mesodermal somite). They have ladder-like nervous system composed of a cerebral ganglion and ventral nerve tracts, and lack skeleton. Respiration is through the gills or skin. Annelids are divided into Polychaeta, Oligochaeta and Hirudinae. Polychaeta have many chaetae on parapodium, Oligochaeta have small chaetae and Hirudinae have no chaetae. These are distributed in a wide range of environments from lands, freshwater to ocean. Most are benthic and have important roles in material circulation near the bottom.

7) Arthropod

Arthropods are distributed in various habitats such as oceanic, terrestrial, underground, aerial and parasitic, and have the largest number of species. The surfaces of their body are covered with external skeleton made from chitin. The old external skeleton is shed during ecdysis when the body size increases with growth, and new external skeleton is produced on the surface. The frame of the body is a repeated structure of somites.

Aquatic species are common. Among these, Crustacea includes many important species for fisheries such as shrimps and crabs, and also for food organisms in aquaculture such as brine shrimp and water flea. Copepods, the

major component of zooplankton, and Cirripedia, a taxon including barnacles, are also included in Crustacea.

8) Echinoderm

Sea urchin, sea star, brittle star and sea cucumber belong to echinoderm. These are bilaterally symmetrical during the larval stages, though most develop pentagonal radial symmetry through metamorphoses. They have fine tubules called siphonosome on the surface. The siphonosome is a unique organ system of echinoderm called water vascular system, and the tubules are filled with liquid, the composition of which is similar to seawater. Siphonosomes stretch and shrink by the pressure of liquid from the water vascular system and are used for movement and feeding. The siphonosomes also function as respiratory and sensory organs. The echinoderms are distributed in every oceanic environment, from coastal zones to deep sea and from tropical to polar regions, though there are no freshwater and terrestrial species.

9) Protochordates

Protochordates are represented by sea squirt and amphioxus. They are considered to be the nearest relation of vertebrate, because they have axis called notochord and tubular nerve. They are divided into urochordate and cephalochordate. Protochordata and vertebrate are combined as Chordate.

Urochordates, a group of sea squirt, are tadpole like and planktonic in larval stage. Amphioxus, a species in protochordata, is considered to keep the morphology of the ancestor of vertebrates and have a cartilaginous notochord from head to tail. Many vertebrata lose the notochord when the vertebrae are formed during development. Amphioxus retains the notochord throughout its life. Different from vertebrates, they have no cranial and vertebral bones. This taxon is very important in the discussion on evolution of vertebrates.

10) Vertebrates

Vertebrata is the most advanced taxon in animal, with the vertebra (back bone) composed of tandem line of vertebral bones. The brain and spinal cord are well developed to form the central nervous system, and are protected by the skull and vertebra, respectively. Vertebrata are commonly divided into fish, amphibian, reptile, bird, and mammal. Among these, fish, marine birds and marine mammals are distributed in aquatic environments.

Fish

Osteichthyes are called fish in a narrow sense, though Agnatha and Chondrichthyes are also commonly called fish in comprehensive term. Agnatha is a taxon of jawless vertebrate and are considered to be the earliest originated vertebrate because the first ancestor of vertebrates lacked jaws. The vertebra is rudimentary and the cylindrical notochord is retained throughout its entire life. Because of lacking jaws, their predatory ability is low. Extant species of agnathonae are myxiniformes (hagfish) and petromyzontiformes (lamprey). Eyes of myxiniformes are degenerated and lack lenses. Large mucosal glands lining along both sides of the body secrete a large amount of mucus. All agnathonae are oceanic species and ion composition and osmolarity of the body fluid are approximately the same as seawater especially among vertebrates. The mouth of

petromyzontiformes is round, forming a sucker. They parasitize other animals such as fish using the sucker. They develop to adult through ammocoetes stage. *Lethenteron japonicum* goes downstream to the sea after metamorphosis and lives as a parasite in the sea and comes back to the river for spawning after maturation. *L. reissneri* spends its entire life in freshwater.

Internal bones of Chondrichthyes are cartilages. These are oviparous or viviparous, and regulate blood osmolarity by accumulating urea. The rectal gland that opens to the rectum excretes excess NaCl and regulates NaCl concentration to nearly half the seawater level. Many Lorenzini's organs, electroreceptors are distributed on the skin of the head. Condrichthyes are divided into Holocephali, which includes chimaeriformes, and Elasmobranchii such as sharks and rays. The gill cavity of Holocephali is covered with the operculum, and open to external environments through a pair of gill slits, whereas Elasmobranchii have 5–7 gill slits on each side. The difference between sharks and rays is that gill slits are located laterally in sharks and ventrally in rays.

A characteristic of Osteichthyes is that they have the internal skeleton made from hard bones. The gill cavity is covered with the operculum that is connected with the outside through a pair of external gill slits. Osteichthyes are divided into Dipnoi, Crossopterygii, and Actinopterygii. In some classification system, Dipnoi that is represented by lungfish and Crossopterygii that includes coelacanth are categorized into Sarcopterygii, because they have many similarities.

Dipnoi has a well developed lung and is able to breathe air. They have many characteristics similar to Chondrichthyes. Crossopterygii has rectal glands and retains urea in their body. Osteichthyes are divided to Chondrostei, Holostean and Teleostei. Ossification of the internal skeleton in Chondrostei is incomplete. Sturgeon belongs to Chondrostei. The body of Holostean is covered with hard scales, and has ability of aerial respiration. Amiidae (bowfin) and Lepisosteiformes (gar) are included in Holostean. Teleostei is a large taxon and is differentiated into many species occupying more than 90% of the existing fish species. Generally, ossification of the internal skeleton is complete. When they have scales, the scale is cycloid or ctenoid scales. The air bladder has no ability of aerial respiration. Teleosts have evolved varyingly and various characters was specialized with the differentiation to each taxon. Therefore, systematic classification of teleosts is rather difficult, and their detailed phylogenic system is still uncertain.

Seabirds

"Seabirds" is a collective term used here for the avian species, the food of which depends on oceanic organisms, and is not based on phylogenetic systematics. There are 9000 species of birds, among which, about 300 species are seabirds. Avian species are genealogically divided into 26 orders. Seabirds belong to only 4 orders, namely Sphenisciformes (penguin), Procellariiformes (albatross, shearwater, etc.), Pelecaniformes (pelican, cormorant, booby, etc.), and Charadriiformes (seagull, sea swallow, plover etc.). Living on the sea, the seabirds take in seawater. Therefore, salt gland is developed above eyes of

seabirds for excretion of excess salt. Reproduction of seabirds is performed on lands.

Marine mammals

Marine mammals are those that live in the sea. When we include mammals in freshwater, the term aquatic mammals is used. They are mainly composed of Cetacea, Pinnipedia, and Sirenia. Cetacea are considered to have developed adaptations to diverse aquatic environments on the earth. Existing species are divided into Mysticeti and Odontoceti. Mysticeti are whales that have food filtration boards in their mouth called baleen through which small crustaceans and fish are filtered and eaten. Odontoceti have teeth in their mouth. The teeth are used to catch food and have no ability of masticatory function. Dolphin are small Odontoceti.

Pinnipedia are the mammals that have fin like four limbs. The whole body is covered with fur. Their lives are mainly dependent on aquatic environments, although their reproduction is performed on rocky reef, sand beach or ice. Otariidae (sea lions), Phocidae (sea dogs) and Odobenidae (walrus) belong to Pinnipedia.

Sirenia are composed of Trichechidae (manatee) and Dugongidae (dugong). They can be distinguished by the shape of tails. Trichecus have a paddle-like tail fin and Dugongidae have a crescent-shaped tail fin.

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2. AQUATIC ECOSYSTEMS

2.1 Plankton and benthos

Ecosystems are systems circulating energy and materials, and include all of the physical, chemical and biological processes. The oceanic environment is divided into pelagic ecosystem and benthic ecosystem. Pelagic ecosystems exist without direct contact with the sea bottom. Benthic ecosystems constitute the sea bottom or coastline. Their biological components are divided into plankton, nekton and benthos. Plankton have limited swimming ability and are passively carried away by water flow. They are generally small but large jelly fish are also included in plankton. Nekton have high swimming ability and can actively move around in water. Many fish species, a portion of mollusks and marine mammals are included in nekton. Benthos live on or in the substrate of sea bottom, rocky shore and sandy beach, are composed of various species and include representatives of all animal phyla on the Earth. By definition, there are intermediate groups in the classification. Krill, larval and young fish, and low swimming ability fish such as lantern fish are called micro-nekton having intermediate properties between plankton and nekton. Many benthic organisms are known to have the ability to extend their living sphere and move in water at night. A group called demersal plankton such as mysids use bottom and adjacent upper water as living space. In addition, many benthic species have planktonic larval stages in their

early life history. Species which spend a part of their life as plankton are called meroplankton, while those that are planktonic throughout their life are called holoplankton. Many plankton species living in coastal area temporally live in bottom sediment as resting eggs or spores attaching on substrate to overcome degradation of environment.

2.2 Typical ecosystems

Phytoplankton are the primary producers in pelagic ecosystems that produce organic substances through photosynthesis. Zooplankton such as copepods are the secondary or higher producers. Differences in biological components among coastal, offshore and upwelling ecosystems originate from the difference in the size of primary producers derived from variations in nutrient supply and transfer efficiency of energy to higher trophic levels. There is no primary producer in the mesopelagic ecosystem, and production is dependent on the supply of organic substances from upper euphotic zone. Although marginal light reaches the disphotic zone, there is no photosynthetic activity. However, in spite of lower biomass compared to the euphotic zone, biodiversity is high and various species exist in this zone. Specialized forms, functions and life history strategies such as bioluminescence and sex reversal are developed for existence and propagation.

Rocky reef ecosystem mainly composed of attached organisms such as algae, shells and barnacles is produced in the intertidal zone of rocky shores. The prominent nature of this ecosystem is the vertical zonation observed in distribution of species. These ecosystems are influenced by wide fluctuations of physical conditions (temperature, salinity, humidity etc.) and differences in tolerance to these fluctuations. Interspecies competition for space and predation are the major factor determining the structure of such regions.

Sandy beach includes intertidal zone, though its looks like desert without living organisms. Biomass and species diversity is generally lower in sandy beach ecosystem compared to rocky reef ecosystem. One additional reason why we feel rare existence of organisms in sandy beach is that the sizes of organisms are small and most of them are living in the space among sands burying their body in sands to prevent the impact of wave and strong sunlight. Main primary producer in the environment is benthic algae, though organic substances, the driving force of the ecosystem, are supplied externally from pelagic and terrestrial ecosystem. Vertical zonation can be observed in sandy beach ecosystem in intertidal zone, though the zones are not prominent as in rocky reef ecosystem. Coasts with substrate composed of fine particles called silt (<0.02–0.002 mm) are called tidal flat or muddy tidal flat, spreading at river mouth. Physical disturbance by currents and waves is small in tidal flat. Commonly tidal flat ecosystem receive large amount of organic substances and nutrients from land ecosystem and the production of the ecosystem is very high. Primary production is mainly performed by benthic microalgae (diatoms, dinoflagellates, blue green alga etc.). Filter feeders and sediment feeders that consume organic substance produced by the benthic microalgae or supplied from outside are dominant in the system. Shells, crustaceans

and polychaeta, the typical biological groups of tidal flat, are valuable food resource for fishes living in tidal flat and migratory birds such as plover and snipe. Organic matter decomposition by bacteria is active and water purifying capacity is high. Pollution load from land to coastal zone is reduced in tidal flat.

Areas where macroalgae or sea grasses flourish are seaweed bed or seaweed forests. In Japan, these are classified based on the dominant species. Kelp beds (Laminariales in cold water area), sargassum beds (Sargassacea), and sea oak and sea trumpet beds (Laminariales in warm water) are developed on rocky reefs, while sea grass beds (Magnoliophyta) are developed on sandy shores on the coast of Japan. In many cases, algal beds are formed in the subtidal zone shallower than 40 m. The growth of macro algae is usually very rapid. It is known that Laminariales grow more than 30 cm per day in optimum condition. Algal bed is one of the most productive aquatic ecosystems. The macro algae provide habitat to periphyton communities and attaching animals on the algae and shelters from higher predators to larval fish. However, minor portion of organic substances primarily produced in algal beds is directly consumed in their system. Major portion is supplied to sea bottom and other ecosystems as detritus. Some macro algae having air chambers like sargassum, which are transported to open ocean as floating seaweed after removal from the substrate, provide spawning ground and nursery to certain fishes such as saury and yellowtail. In a phenomenon called "iso yake" (Shore fire), macroalgae disappear from wide area of original algal beds due to high grazing pressure of animal such as sea urchin and high temperature leading to a decrease in coastal resources supported by algal beds.

Coral reefs composed of hermatypic corals occupy 0.2% of ocean area. Growth temperature of the hermatypic coral is 23–29°C and the distribution of coral reef is limited to tropical and a part of subtropical area. Most prominent characteristics of the coral reef ecosystem are richness of biomass and biodiversity, comparable to tropical rainforest. At least, more than 500 species of hermatypic corals exist in coral reefs in the Indian and Pacific Ocean, while 25% of all fish species are reported in the coral reef areas. One of the possible major factors leading to a higher diversity of species is the complexity of spatial structure of the coral reefs. Corals are mixotrophic animals belonging to Cnidaria. Coral reef is a colony composed of many individual corals. The reefs are aggregation of external structure made with calcium bicarbonate excreted from individual corals. In addition to feeding on zooplankton, they possess a symbiotic dinoflagellate called zooxanthella in their body and utilize the photosynthetic products of the symbiont. Bleaching of corals caused by the departure of zooxanthella from corals because of environmental stress such as warm temperature, is an issue recently. In coral reef ecosystem, zooxanthella, attached algae and pelagic phytoplankton are the primary producer. Little nutrients is supplied from outside to coral reef ecosystem, and it is thought that regenerating production (detailed explanation is provided in the latter part of this book) is dominant in this ecosystem. In addition to richness of species compared to other oceanic ecosystems, various complex interspecific relations such as symbiosis and peculiar food habits can bee seen in coral reef ecosystem. The deep sea

bottom ecosystems are supported by the supply of organic settling particles produced in the surface layer. Settling particles are decomposed in water column in the process of precipitation. Organic content of settling particles decrease exponentially with depth and biomass that can reach the deep sea bottom is limited. However, completely new ecosystem was discovered by deep ocean surveys in the later 1970s. This was the biological community around hydrothermal vent discovered in the middle ocean ridge. After that, similar communities were discovered around cold seepages observed in subduction zone. The largest characteristic of hot and cold seepage ecosystem is that the primary production in these systems depends on bacteria which obtain energy for synthesis of organic substance by oxidation of reductive substances such as hydrosulfite and methane. These systems are called chemosynthetic ecosystem. The biomass around the seepages is quite high reaching 10^3 to 10^4 times higher the surrounding deep sea bottom. The community of hot and cold seepage ecosystems is almost exclusively occupied by endemic species such as tube worms and deep-sea cold-seep clams. Many species live in a symbiotic relationship with chemosynthetic bacteria. However, biodiversity of the community is low at species and phylum levels. The community is composed of polychaetes including tube worms, mollusks and crustaceans.

2.3 Food chain and food web

The functions and nature of ecosystems discussed in the following paragraph will focus on the pelagic ecosystem because of its relative simplicity. For example, the tuna living in open ocean feeds on middle size swimming organisms such as flying fish and squids, which feed on small fish like sardine, that eat zooplankton such as krill and copepods, copepod eat micro zooplankton such as ciliate, which feed on flagellate whose body size is 2–20 μm in length, and flagellate eats phytoplankton smaller than 20 μm. This means that tuna is located six steps higher in the trophic level. The process in which materials and energy is transported from primary producers such as phytoplankton to higher trophic level is called food chain. Actual predator-prey relationship in ocean is more complicated. However, concept of food chain and trophic level is convenient for us, because we mainly utilize higher trophic level organisms in fisheries. In this concept, production of trophic level (n) is expressed as follow.

$$P_n = \text{primary production} \times E^n. \tag{1}$$

Here E is ecological efficiency obtained by division of production at n (P_n) by production of the food organisms (P_{n-1}: one step lower production).

$$E = \frac{P_n}{P_{n-1}}. \tag{2}$$

Ecological efficiencies in ocean are 10–20%. The values are low in open

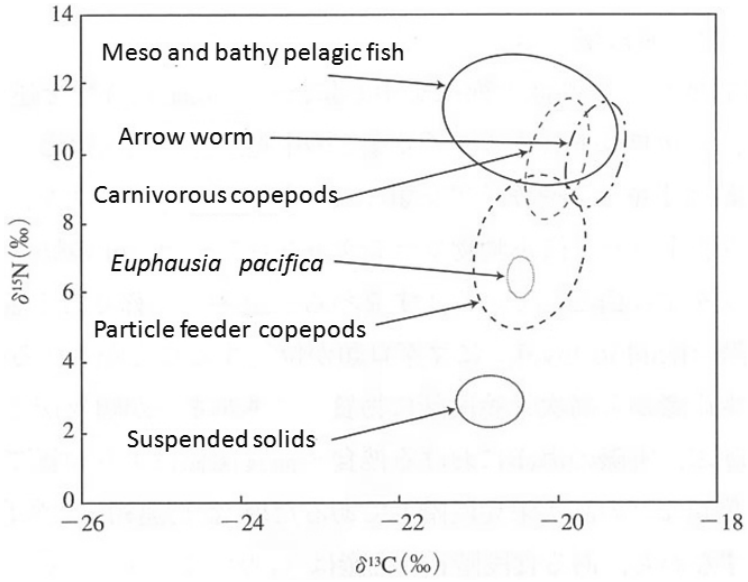

Fig. 2.2. Carbon and nitrogen stable isotope ratio in major plankton and micro nekton in west subarctic Pacific Ocean (modified from Sugisaki and Tsuda, 1995).

ocean and higher where biomasses are high and structures of biological community in the ecosystem are simple. The theoretical maximum value of ecological efficiency is total growth efficiency of the target biological group (amount of production/amount of food).

The results of tentative calculation of production of pelagic ecosystem in several typical food chains using Eq. (1) is shown in Table 1.4 (Chapter I). It can be observed that the production in upwelling area account for more than 50% of total fish production in the world. Continuous supply of nutrients from bottom layer, large size of phytoplankton at starting point of food chain such as diatom and existence of fish that directly eat phytoplankton, thus shortening the food chain, contribute to high fish production.

Pelagic fish resources which contribute to high biological production such as sardine and anchovy are globally supported by large scale upwelling ecosystem. However, resource of sardines along the coast of Japan exceptionally does not depend on upwelling ecosystem. The questions why the sardines can maintain relatively large resource and why its fluctuation is synchronized with other resources in upwelling ecosystem is still an issues along with the big question concerning the mechanism of species exchange of pelagic fish in this area.

Measurement of stable isotope ratio of nitrogen in components of living organisms is a useful method for estimation of trophic level. Stable isotope ratio is generally expressed as per thousand ratio of deflection from standard substance.

$$\delta^{15}\mathrm{N}(‰) = \left(\frac{\left(\frac{^{15}\mathrm{N}}{^{14}\mathrm{N}}\right)_{\mathrm{sample}}}{\left(\frac{^{15}\mathrm{N}}{^{14}\mathrm{N}}\right)_{\mathrm{reference}}} - 1 \right) \times 1000. \quad (3)$$

In nitrogen metabolism, isotope fractionation occurs mainly in ornithine cycle and the nitrogen isotopic ratio of an organism becomes 3–4‰ higher than their food organisms. Conclusively, higher trophic level organisms have higher isotopic nitrogen ratio. Isotope fractionation of carbon rarely occurs in living organisms compared to nitrogen. Therefore, carbon isotope ratio in body component is used for estimation of origin of the food chain on which the organisms depend, and nitrogen isotopic ratio is used as indicator of food level. Take a case when food habit and trophic level of an organisms are unknown, for example. When the nitrogen isotopic ratio of primary producer is 2‰ and that of target species is 9‰, then the difference is 7‰. From this value we can estimate the trophic level of the target organisms approximately 2 step higher than the primary producer.

In the discussion above, we consider the food chain as a straight single flow of materials and energy, although the actual predator-prey relationship is more complex. Organisms that eat multiple food species, or eat organisms without differentiation of plant and animal are not rare. Different from terrestrial plants, phytoplankton needs little organic matter for body cellulose. The differences in chemical composition between plants and animals, and herbivores and carnivores in aquatic environment are not always distinguishable. When we correlate the predator-prey relationship in an ecosystem based on the stomach contents, extensive meshed pattern is obtained. Figure 2.3(a) is the food web off Hokkaido coast based on the Walleye Pollack. It can be seen that copepods were important foods in spring particularly for small fish and the relative importance decreased with seasons (Fig. 2.3(b)). As shown in this example, food web is not stable. It fluctuates with time and changes with growth even in the same species. It is important to survey food webs for understanding of structure of ecosystem. However, we still do not know the mechanism that compose and support structure and complexity of food web. We arithmetically calculate the materials and energy flow from food web and analyses are performed by ecological numerical models putting factors of major components in the web.

2.4 Microbial loop in food chain

The above paragraph explains the flow of materials and energy transport from primary production to higher levels. This food chain is the grazing food chain. However all products by phytoplankton are not transported to upper level. Bacteria are a largest biomass group in pelagic ecosystem which depends on the dissolved organic substances for nutrient sources (Fig. 2.4). Dissolved organic

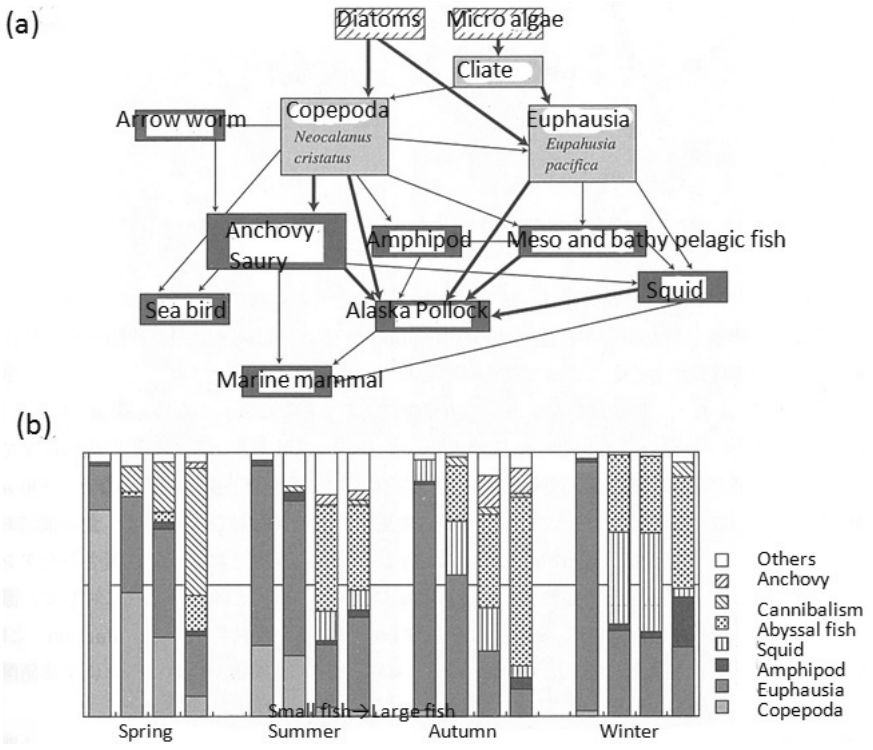

Fig. 2.3. Food web in Oyashio region drawn by centering Alaska Pollock (*Theragra chalcogramma*) (a) and weight composition of stomach contents in Alaska Pollock (b).

substances are derived from direct discharge from phytoplankton, exudates from physical crushing while phytoplankton is being eaten (sloppy feeding) and discharge from higher trophic levels. Bacteria obtain energy by mineralization of the organic substances. Nutrients like ammonium are produced by mineralization from nitrogen containing substances, and support phytoplankton production. Summing up the process, the circular structure (loop) of phytoplankton–dissolved organic substances–bacteria–nutrient salts–phytoplankton is produced. Dissolved organic substances are discharged from all trophic levels, though greatest discharge is from microorganisms smaller than 200 μm such as phytoplankton, small flagellates, and ciliate and do not directly contribute to production of large size organisms. The cyclic structure in food web is called microbial loop. Production using ammonium from microbial loop is called regenerated production. On the other hand, primary production depending on the supply of nitrate from deeper layer is called new production. The ratio of new production in primary production is called the f-ratio, and is calculated from the ratio of nitrate and ammonium taken by phytoplankton in the system.

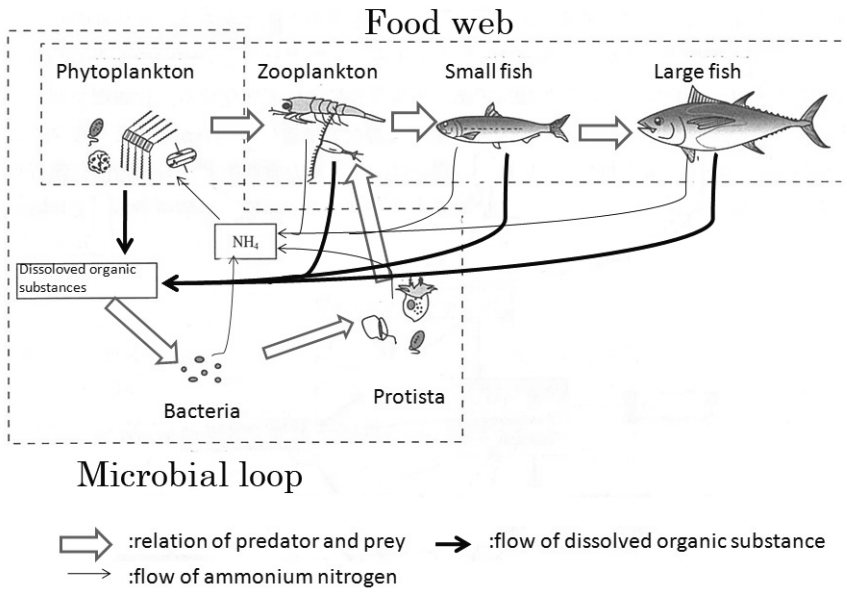

Fig. 2.4. Conceptual drawing of the relation between food chain and microbial loop.

Generally, f-ratio is low in open oceans, high in upwelling regions and low in production period of high latitudes. In other words, it is high when the supply of nitrate from lower layer and light intensity are high and is low in the season and area of low supply of nitrate. A comparison of the Japan Current region and the Oyashio region, for instance, shows that annual primary production per 1 m^2 is 100 g and 160 g carbon. There is only 1.5 times difference between them. However, when we compare the new production, values for Japan Current and the Oyashio region are around 10 g and 100 g respectively. The production in Oyashio region is ten times higher than in the Japan current region. Regeneration production does not contribute higher production even at its highest level. On the contrary, new production contributes to production of higher predator and supply of settling organic to distrophic layer and bottom.

2.5 Secondary and higher producers

Important secondary producers (primary consumer) in upwelling region and coastal area are small crustacean ranging from 0.5 mm to 50 mm such as copepoda and euphauiacea (krill), and those in the open ocean are micro zooplankton such as heterotrophic flagellate and ciliate (Fig. 2.5). Copepods are the most dominant animal group in the ocean which account for about 70% of total biomass sampled by common mesh size (0.1–0.5 mm) plankton net. Copepods function as food for many higher predators and their early stage larva (nauplius) is important food organisms for early stage fish. Their life span is from several weeks to 3 years.

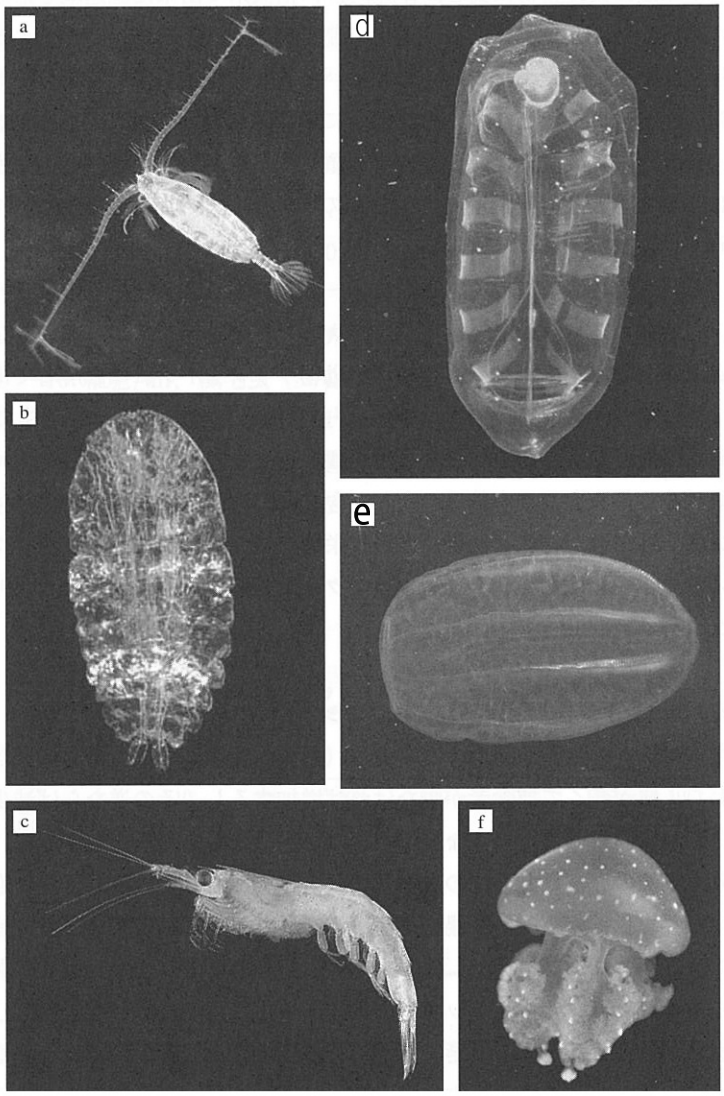

Fig. 2.5. Typical zooplankton. Copepod, Family Calanus (a), Copepod, Family Sapphilna (b), Euphausia (c), Salp (d), Comb jelly (e) and Jelly fish (f) (photos were provided by Dr. Jun Nishikawa and Dr. Ryuji Machida).

It is short in small species in high temperature regions and is long in large species living in low temperature regions. Many species shift their habitat depth diurnally and seasonally and play a role in vertical transportation of materials. Euphausiacea are crustaceans larger than copepods. They occupy around 10% of total animal

biomass in many seas, and are important food organisms for middle and large sized fish and whales. Fishing of Pacific Krill (*Euphausia pacifica*) and Antarctic Krill (*Euphausia superba*) are implemented in the adjacent sea off Japan and Southern Pacific Ocean, respectively. The life span of Euphausiacea is estimated to be several months to several years. This is a major species that form sound scattering layer (DSL: deep sea scattering layer) in the sea. Chaetognatha (arrow-worm) have comparable biomass to Euphausiasea. Totally about 120 species exist in the ocean. They have transparent arrow shaped body and are considered to be so-called "sit-and-wait" predators. They are estimated to be a major predator of crustaceans in the pelagic ecosystem.

The other important macro zooplankters are Salps, Larvaceans, Cnidarians and Ctenophores. These are called gelatinous plankton, because they have no hard outer shell like Crustaceans and are characterized by their fragile body tissues. Salps and Larvaceans are Urochodate, also called Tunicates because their body is covered by tunic (a gelatinous fragile tissue). They produce filtering net made with mucoid filaments which filters particles. Therefore, they can eat smaller particles and can utilize more abundant particles than crustacean. Their growth rates are higher than crustacean. Larvaceans secrete a structural object called house. The discarded houses are utilized as habitat or food by several other organisms and thought to have important roles in the ocean especially in mesopelagic and bathypelagic zones. Cnidaria and Ctenophora are also carnivores and their bodies are particularly fragile. Hence the sampling and fixation of Cnidaria and Ctenophora are difficult and their classification and ecology is still not sufficiently understood. However, increase of their biomass has been reported in various seas attracting global attentions.

Generally zooplankton such as copepods have body size larger than 0.2 mm and are called meso zooplankton. Group of organisms smaller than 0.2 mm that cannot be sampled by plankton net are called micro zooplankton. In a broader sense of the term, bacteria, the decomposer, is included in this group. When this term is used only for secondary producers in a narrower sense, Ciliate and flagellate are major component of micro zooplankton. Flagellates is a generic name of micro particle feeders with a flagella, and include many taxa such as heterotrophic Prasinophytes and Dinophyta. Ciliates are divided into shelled groups such as tinitinids and the others without a shell such as Oligotrichida, which are dominant in the ocean. Micro zooplankton are the major consumers of phytoplankton, in oligotrophic open ocean particularly in subtropical region. Flagellates mainly consume bacteria and pico plankton and ciliates consume nano size particles. These two groups are the major components of the microbial loop.

2.6 Top down control and bottom up control

Increase and decrease of biological group can be expressed as a function of amount of resource (food or nutrient salts) used by the group and quantity of predator, because mass of the group increases in rich food and less predator

condition and decreases in inverse condition. Ecosystems are chains or webs of sequence of the inter-relationships. Therefore, biomass of a biological group at a trophic level is regulated by biomass at both upper and lower trophic levels. In case the regulation of lower biomass is dominant, the biomass is controlled by supply of nutrient salts in the ultimate sense and the relation is called bottom up control. Inversely when biomass in the upper level is dominant, the relation is called top down control. In pelagic ecosystems in upwelling regions and oligotrophic oceans, nutrient supply determines the outline of the ecosystem and we can consider that the ecosystem is bottom up control. In certain oceanic regions, the structure of the ecosystem is influenced by the existence of highest predator and we can identify the ecosystem as top down. For example, stock of pink salmon fluctuates in two years cycle in adjacent Bering Sea in Pacific subarctic region. Biomass of food organisms such as copepod decreases and biomass of phytoplankton increases in the sea, when the stock of pink salmon increases. Such an influence by higher predator transmited to lowest trophic level is called trophic cascade. Top down controls are rare in pelagic ecosystem, and are prominent in rocky reef ecosystem and algal bed ecosystem.

Although bottom up control is dominant in pelagic ecosystem in ocean, it is obvious that increase of nutrient salts not always simply provide the increase of fish production, when we imagine the phenomenon of red tide. For the explanation of the phenomena in which lower production and higher production are not directly connected, miss match hypothesis, bottle neck hypothesis, optimal window hypothesis etc. are presented. All these hypotheses are paying attention to the sensitive period in life span of higher predator for their survival. Whether optimal environmental factors such as enough food are provided during the period is key issue in the hypotheses.

2.7 Size dependant food chain and size distribution

Dissolved substances and particulate substances are separated by 0.2–0.6 μm mesh filters. There are various particles that vary in 9 digit in size from colloid particle, virus (10^{-8} m) to blue whale (30 m). For plankton, less than 0.2 μm, 0.2–2 μm, 2–20 μm, 20–200 μm, 0.2–20 mm and larger than 20 mm are called ultra plankton, pico plankton, nano plankton, micro plankton, meso plankton and mega plankton respectively.

Generally, number of smaller particle is larger than number of larger particle in aquatic environment. In the case of common coastal area, the density of bacteria (0.5 μm) is 10^5–10^6 cells/ml, and that of diatom (20 μm), and ciliate (50 μm), is 10^2–10^3 cells/ml and 0.1–1 cells/ml, respectively. As shown in this example, individual densities decrease with increase of body size. Electrical measurement of particle size in seawater became common in 1980s. When we plot the data in those reports taking logarithmic body size in horizontal axis and abundance volume in vertical axis, the slope of the relation is 0 or slightly negative (Fig. 2.6). This means that density of biomass in unit volume water is similar among different particle size, or that, in another word, expected value of

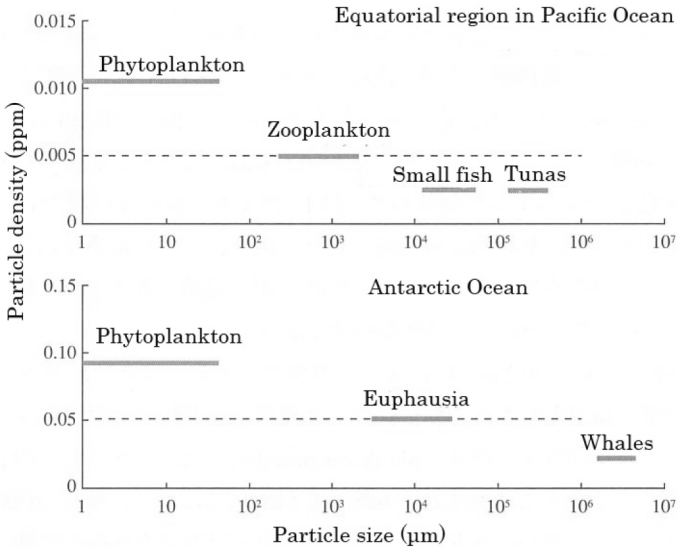

Fig. 2.6. Biomass and body size of dominant organisms in equatorial Pacific Ocean and Antarctic Ocean (modified from Sheldon *et al*., 1974). Dotted lines express total average biomass estimated by author.

biomass of virtual fish or whale size in cup or bucket is similar to the measured biomass of phytoplankton in seawater in the cup or bucket. The mechanism on which the relation is sustained among different body sizes is still not clarified, though it is considered that the size dependant predator-prey relationship has strong relationship to the mechanism. Prey-predator relation in pelagic ecosystem is "large eats small" relation. This relation means that body size of the organisms increase with elevation of trophic hierarchy from phytoplankton (primary producer) to higher trophic level. Oceanic organisms eat organisms of which body size are 1/3 to 1/30 of themselves. It is considered that even between two species having similar body shape, their food requirements do not overlap, if their body sizes differ more than 1.5 times.

As mentioned above, body size is an important factor in ocean pelagic ecosystem. Diurnal vertical migration, in which organisms living in deep layer during day swim up to shallower layer at night, are observed in many species such as krills and copepods. This is a behavior to prevent predation by visual search predator. Organisms less than 1 mm do not need such behavior because they are hardly discovered by visual search predator. Prominent diurnal vertical migration is often observed in relatively large zooplankton. Many species live in surface layer during the small sized larval stage and start diurnal vertical migration with their growth. Largeness of body size means susceptibility of predation by visual search predator. However, on the other hand, large organisms are capable of escaping from the predators. It is reported that large size or stinger species

dominate in food organisms and species that have thick shell dominate in diatom and ciliate in oceans where predation pressure by particle feeding copepods is high.

2.8 Biodiversity

Number of phytoplankton species in the ocean is estimated to be about 3500–4500. This number is far less compared to the 25000 in terrestrial plants. Number of crustaceans in aquasphere is about 3000. On the other hand, 1,500,000 species are reported in terrestrial insects and it is estimated that there may be a total of 30,000,000 species when we include the number of unreported species. Recently, many unreported species have been discovered in deep sea by observation from submarine and sampling by fine mesh nets. However, these new findings will scarcely change the ratio of oceanic species in total number of species in the Earth. It is thought that species ratio of oceanic organisms including benthic organisms is about 15% of the total number of species. If we consider the number of higher taxa, 28 animal phyla exist in ocean among 33 total number of animal phyla. Among them 13 phyla are endemic. Most of them are benthic, and only 11 phyla are completely pelagic throughout their life. From these facts, we can recognize that pelagic environment in open ocean is not easy to enter for many species. Diversity of plankton community is not so high in species level and in higher taxa level.

Prominent characteristic of pelagic ecosystem is higher local diversity. Sometime more than 100 species of crustaceans are sampled by one tow of plankton net or several tens of phytoplankton are sampled from 10 ml of sample water. “Plankton paradox” is responsible for the high local diversity. In other words, why so many species coexist in such a homogeneous environment? Gause’s axiom (elimination of competition) “in equilibrium condition, species of survivor in a trophic level is less than the number of resource species” is proven at least in laboratory and adaptive phenomena are observed in fields. Therefore, the species that predominate in growth rate will remain in competition in the community of phytoplankton, that depends on limited nutrient such as nitrogen and phosphorous, theoretically. For this reason, the fact that a few dozens of phytoplankton exist in limited environment is paradoxical.

Generally, pelagic ecosystem is composed of a few dominant species and a lot of minority species. It is enough to pay attention to the dominant species in the analysis and discussion of material and energy flow. However, actual ecosystem is somewhat different from simplified mathematical models. Mechanism of survival and functions of the minority species are important outstanding issues.

Existing species are few in high-latitude region where the biomass is large and many in low-latitudes where biomass is small. In the comparison between South Pole and North Pole, biodiversity is slightly higher in South Pole. It is considered that large environmental fluctuation in winter makes worse living condition of North Pole. In vertical pattern of biodiversity of phytoplankton, biodiversity is low in surface layer where biomass is large and is high in mid layer where biomass is small (Fig. 2.7). As above, richness in species where physical

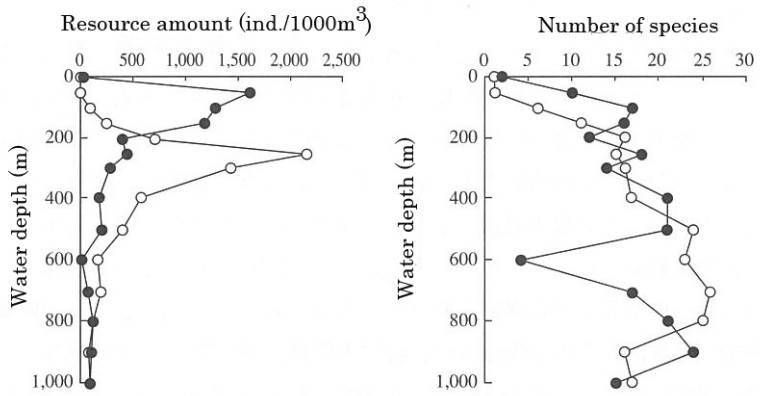

Fig. 2.7. Vertical distribution of biomass and number of species of copepods in Family Scolecitrichella in central region of Sagami Bay.

environment is stable, supply of nutrient is insufficient and biomass is small like deep sea and low latitudes is the nature of pelagic ecosystem. The mechanism which supports the coexistence of many species in such stable and poor nutrient environments is still unsolved question and several hypotheses are proposed as main mechanism such as partition of niche, nonequilibrium (disturbance before reaching equilibrium), patchiness (deflection of distribution), existence of micro habitat such as house of Larvaceans, predation and density dependent mortality (selective predation or infection of dominant species) etc.

2.9 Spatial distribution and its uniformity

In biological oceanography, the place where an organism is densely distributed than surrounding space is called patch. The wording of "patch" sometimes makes confusion, because open space is also called patch in the sciences concerning intertidal zone and forest. The contrasting wording of "patch" symbolically expresses the difference between terrestrial ecosystem where spatial competition is severe and pelagic ecosystem where biomass is tenuous and spatial competition is not so severe or not observed. Patchiness is a mechanism which supports biodiversity and is a result of nonequilibrium, existence of microhabitat and predation.

Vertical fluctuation in biomass is large in pelagic ecosystem. Generally biomass is high in surface layer and decreases with depth. Oceanic species can be divided into neuston (in the surface microlayer), surface layer species (shallower than 200 m), mid layer species (200–1000 m) and deep layer species (deeper than 1000 m). Each existing species have their species specific vertical distribution pattern. Many species exist in a water column and each species has its own vertical distribution pattern, as a result, all parts of the water column are occupied by organisms (Fig. 2.8). In addition to this, many species diurnally migrate in the

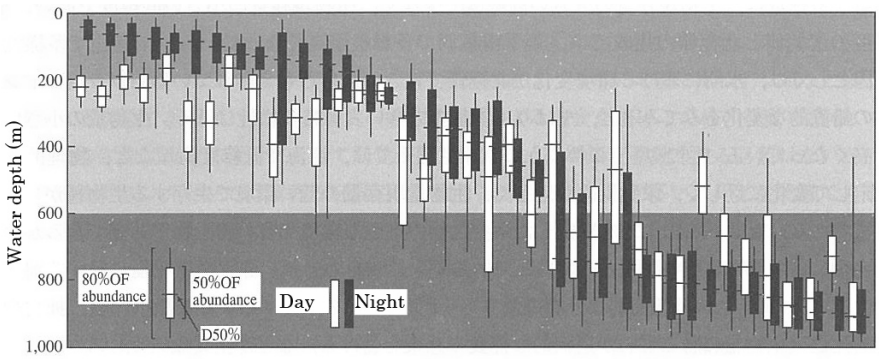

Fig. 2.8. Vertical distribution in day and night of 38 species in Scolecitrichella Family copepods in Sagami Bay (modified from Kuriyama and Nishida, 2006).

water column and accelerate material fluxes from surface layer to deeper layers.

There are different scientific approaches for horizontal distribution pattern depending on the space scale. In global scale, horizontal distributions of plankton and micronekton are corresponding to the distribution of water body and have been studied in biogeography. Knowledge of smaller scale horizontal distribution is not sufficiently accumulated. Recently, densely aggregated thin layer of plankton was discovered by observation from submersible vessel, species specific aggregation was observed by SCUBA diving observation, and micro scale patches were observed by towable video picture system. Through these observations, roles of plankton patches smaller than 10 km will be revised. Zooplankton can make patches actively by themselves as fish. Averagely, density of food organisms in ocean is low. Existence of many organisms, especially that of upper food level strongly depends on patch of food organisms. For example, Mysticeti will not be able to exist, if krill distribute evenly without patch.

Patch of phytoplankton is controlled by diffusion by turbulance of water and population growth, whereas patches of upper predator higher than copepods have more complicated structure and it is obvious that the structure is influenced by their own behavior. It could generally be estimated for animals that the purposes for formation of patch are escape from predation, increase of mating chance and increasing of food searching capacity. For plankton, of which distances among individuals are wide comparing to their body size, the merits of patch formation is presumed to be escape from predation and increase of mating chance.

(Atsushi Tsuda)

3. PHYSIOLOGY OF AQUATIC ANIMALS

3.1 Cells, tissues and organs

Physiology is a natural science to understand the control mechanism of

biological objects by analysis of various biological functions in reductionism. How are living bodies composed? What function does each element have? How do the elemental function connect with each other to perform function at individual level? Mechanism to keep adaptable relation with environment and other individuals is also a part of physiology. For accurate understanding of physiology, basic knowledge of cells, tissues and organs is required. However, it is beyond the scope of this text book to provide details of fundamental knowledge of cytology and histology. Many books are available on this topic, and the authors recommend to refer these books. See chapter I general theory, in "*Fundamentals of Fish Physiology*" for an overview.

Structure and functions of cells and tissues are fundamentally similar among fish and mammals and also among many invertebrates. However, we have to pay attention to positions of several aspects of fish in evolutionary processes and of other living organisms and prominent characters for adaptation to aquatic life. Surface epithelial tissue (epidermis) of fish is multiseriate like terrestrial vertebrates. However the tissue is soft and not keratinized in outermost layer. Alternatively, the surface is covered with mucus secreted from mucilage cells. It is said that the mucus has a function to reduce resistance from water while swimming in addition to the function of protection of epidermis. Epidermis of invertebrates is simple epithelium and covered with mucus like fish or covered with cuticle as crustaceans for protection.

3.2 Ontogeny and growth of fish

According to their external morphology, developmental stage of fish is divided into the embryonic, larval, alevin (juvenile), adolescent, immature, adult and senescent stages. The embryonic stage extends from fertilization to hatching, followed by the larval stage after hatching. Larvae just after hatching have the yolk sac on the abdomen. The early larval stage is from hatching to the completion of yolk absorption. From complete absorption of yolk to completion in number of the fin ray in each fin is the late larval stage. In alevin stage, although the shape of fish is incompletely developed, fish of this stage have the same elements as adult fish. In the young stage, the morphological characters resemble the adult fish. The external morphology of immature-stage fish is the same as mature-stage fish, although reproductive capacity is not functional. When the reproductive capacity becomes functional, fishes are called adult fish. Then, the reproductive capacity decreases with age, and fish enter old age.

1) Fertilization and embryonic development

External fertilization is common in most fishes, whereas eggs are fertilized internally in some elasmobranches, coelacanths and teleosts. In species that perform internal fertilization, males have well developed copulatory organs. Ontogensis starts at the moment of fertilization (fusion of male and female pronuclei). In the case of external fertilization, motility of sperms is initiated by dilution of the semen with environmental medium after ejaculation. In teleosts, a micropyle opens at the animal pole of the egg shell. A spermatozoon enters the

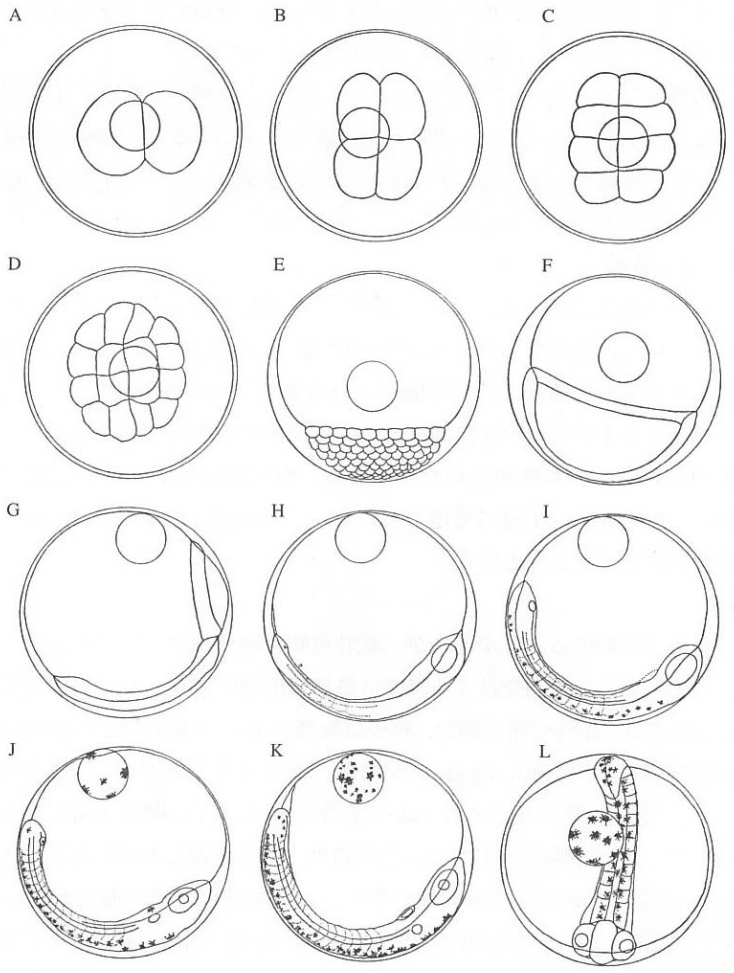

Fig. 2.9. Embryonic development of black sea bream. A, 2-cell stage; B, 4-cell stage; C, 8-cell stage; D, 16-cell stage; E, Morulatage; F, Blastula stage; G, Formation of embryonic body; H, 4-somite stage (appearance of optic vesicle and Kupffer's vesicle); I, 10-somite stage (appearance of pigment); J, 16-somite stage; K, L, 20-somite stage (from Iwai, 1991).

egg through the micropyle. At the time of entry of spermatozoon, eggs are still in the process of oogenesis at the middle phase of the second maturation division. Just after the entry of spermatozoon, the second maturation division is completed and female pronucleous is formed with discharge of second polar body. Simultaneously with the entry, the micropyle is closed and other spermatozoa can not enter the egg after that. Then, cortical alveoli on the surface of the egg breaks down and the contents are dischareged to the space between the egg shell and egg. As a result, the egg shell is pushed up and the perivitelline space is formed. The

spermatozoon discards its tail, and forms male pronucleous and then fuse with female pronucleous.

Fertilized eggs of elasmobranches and most teleosts have large amounts of yolk. Their cleavage type is discoidal cleavage, a type of cleavage in which cleavage occurs only in the animal pole in earlier stages (Fig. 2.9). After fertilization, the cytoplasm aggregates in the animal pole to form a blastodisc. The first cleavage is a vertical one that happens in the center of the blastodisc and blastcoel is formed in a vertical direction. As a result, two blastomeres are formed. The second cleavage occurs in a cross direction of the first cleavage to form four blastomeres. Two third cleavages occur in a direction parallel to the first cleavage to form eight blastomeres. With the progression of cleavage, the number of blastomeres increases and the size of each blastomere decreases. Blastomeres form a blastoderm on the animal pole, and gradually expand to cover the yolk. At the marginal region of the blastoderm, a thickened layer forms a germ ring. Then, an embryonic shield appears. Differentiation of the ectoderm and endoderm is caused by the gastrulation. Differentiation of germ layers proceeds and an embryonic body is formed. The embryo develops somites, optic vesicles and ear vesicles. Embryo grows with the increase of somites, and eventually the heart start beating and the blood circulation is activated.

2) Hatching

When embryos develop to a certain stage, embryos break the egg shell. This is hatching, aided by hatching enzymes secreted from hatching gland cells, and movement of embryos. Hatching gland is located on the surface of embryos and the yolk-sac, though the distribution pattern of this gland is different among fish species. During the late embryonic stage, hatching gland cells develop and accumulate granules of hatching enzyme in the cytoplasm. Prior to hatching, the enzyme is secreted from the embryonic body. Hatching enzyme is a protease that functions to soften and decompose the egg shell. The hatching gland cells disappear after hatching is completed.

3) Metamorphosis

Metamorphosis is the morphological change that occurs when the fish develops from a larval stage to an alevin stage. Larvae of Heterosomata, a group of flat fish and flounder, are bilaterally symmetrical. By the time of settling to the bottom at an alevin stage, an eye on one side moves to the opposite side and two eyes get located on one side. The metamorphosis is induced by thyroid hormones. Larvae of Anguilliformes (eels) and Elopiformes are called leptocephalus. The body of leptocephali is transparent with willow leaf-like shape. These characters are adaptive to planktonic life. Leptocephali metamorphose to elver (glass eel). During metamorphosis, the body of the fish is shrunk and the length is shortened. After completion of metamorphosis when the body shape becomes similar to adult, they start growing again. Metamorphosis is not only changes in body shape but also involves changes in physiology and behavior.

4) Growth

Physical growth of Osteichthyes, as well as many other vertebrates, is accelerated by the growth hormone (GH), which induces production and secretion

of insulin-like growth factor-1 (IGF-1) mainly in the liver. IGF-1 is secreted into blood circulation and transported to target organs such as cartilages, bone and muscle. IGF-1 combines with IGF-1 receptor in target organs and induces protein synthesis and cell division. A small amount of IGF-1 is also produced in other organs, and functions locally in specified organs in a paracrine or autocrine manner. Major part of IGF-1 in blood is combined with IGF-1 binding proteins. These proteins control the amount of free IGF-1 which can combine with IGF-1 receptor. On the other hand, secretion of GH is controlled by hypothalamic hormones. Growth hormone-releasing hormone (GH-RH) stimulates GH secretion, and somatostatin suppresses GH secretion.

3.3 Maturation and reproduction

The reproductive mode of fish is classified into sexual reproduction by fertilization of heterogametes (large eggs and small spermatozoa) as other many vertebrates. Most fish are diecious, though hermaphroditism, in which an individual fish has both ovary and testis, is not rare. Black sea bream (*Acanthopagrus schlegeli*) differentiate into males at first, and then undergo sex reversal to females (protandry). Inversely, in multicolorfin rainbowfish (*Halichoeres poecilopterus*), the ovary appears at first and then the testis develops in turn (protogyny). Social factors induce sex reversing in bluestreak cleaner wrasse (*Labroides dimidiatus*) and anemone fish (*Amphiprion clarkiionnsome*). It is also known that ambient temperature that the fish larvae experience affects sex determination in many fish species.

1) Differentiation of gonads

Differentiation of the gonad starts by the formation of the genital ridges on the base of both sides of the dorsal mesenterium along the body axis. The genital ridges originate from the coelomic epithelium and are dorsally projected in the body cavity. Primordial germ cells are scattered on the coelomic epithelium at first, gradually migrate toward the genital ridges, and are finally incorporated in the genital ridges. The genital ridges are then suspended from the dorsal side of the body cavity with the mesenteriolum to form gonads. With the differentiation of undifferentiated gonads into the ovary and testis, primordial germ cells in the ovary are called as oogonia and those in the testis are called as spermatogonia.

2) Oogenesis

The process of oogenesis is largely divided into the proliferation, growth and maturation phases. In the proliferation phase, oogonia proliferate by repeated mitosis. When oogonia start the meiotic division (reduction division), the cells become oocytes. In prophase I (the early stage of the first reduction division), oocytes suspend the division and enter the growth phase. The growth phase is divided into the primary growth phase, before the onset of yolk accumulation, and the secondary growth phase, in which the size of oocytes increase with accumulation of yolk materials. Primary growth phase is composed of the chromatin nucleolus stage and the following perinucleolus stage. In the chromatin nucleolus stage, each pair of homologous chromosomes makes a bivalent chromosome. When oocytes reach the perinucleolus stage, their size increases

slightly and nucleoli line along the nuclear membrane in a large nuclear that is called a germinal vesicle in the case of oocytes. In the secondary growth phase, yolk vesicles, oil globules and yolk globules are accumulated in oocytes. Yolk vesicles appear in the peripheral region of cytoplasm. Later, yolk vesicles change to cortical alveolus, and make perivitelline space by discharging the content at the time of fertilization. Following accumulation of yolk vesicles and oil globules, oocytes accumulate yolk globules and grow rapidly. With the development of oocytes, follicular tissues develop around the oocytes. Those follicular tissues are responsible for the production of sex steroid hormones. In the yolk globule stage, granulosa and theca cell layers can be clearly recognized on inner and outer sides, respectively, of the basal membrane. Zona radiata appears between the oocyte plasma membrane and granulosa cell layer, which corresponds to the future egg shell.

After accumulation of yolk materials (vitelline), oocytes enter the maturation phase. The germinal vesicle (nuclear), which is located in the central region of oocytes in the growth phase, moves to the animal pole and locates just beneath the micropyle. Then, the nuclear membrane disappears, and oocytes restart meiosis. However, after the discharge of the first polar body, meiosis is suspended again at the mid phase of the second meiotic division. Oocytes in this phase are matured eggs ready to be spawned. The fully matured eggs depart from the follicular tissues covering the eggs, and are ovulated to the ovarian cavity or body cavity dependent on fish species. During this process, yolk globules fuse together to be transparent, and eggs increase their size by absorption of water. Ovulated eggs are discharged into the surrounding environment from the genital pore (spawning). After spawning, the second meiotic division restarts by the entry of spermatozoon into the egg, and the second polar body is discharged.

The process of oogenesis is controlled by an endocrine system called the hypothalamic-pituitary-gonadal axis (Fig. 2.10). When proper environmental and physiological condition is available, neurosecretory cells in the hypothalamus secrete gonadotropin-releasing-hormone (GnRH) to the pituitary. GnRH acts on gonadotropin (GTH)-secreting cells in the proximal pars distalis of the pituitary, and induces the release of follicle-stimulating hormone (FSH) in the growth phase and luteinizing hormone (LH) in the maturation phase.

In growth phase, FSH released in the blood reaches the ovary and induces the production of estradiol-17β (E_2), a female steroid hormone, or estrogen, in the follicular tissue. As the first step, testosterone (T) is produced from cholesterol by a series of biochemical functions of enzymes in theca cells in the follicular tissue. Then, T is transformed to E_2 by aromatizing enzyme in granulosa cells. E_2 released to blood acts on the liver for synthesis of vitellogenin (VTG), which is a precursor of yolk protein. VTG is transported to the ovary through the blood circulation and incorporated into oocytes. When the accumulation of yolk is completed and the oocytes enter the maturation phase, a large amount of LH is secreted from the pituitary within a short period (LH surge). In response to the LH surge, the follicular tissue produces maturation-inducing steroid (MIS), instead of E_2. 17,20β-dihydroxy-4-pregnen-3-on (17,20β-P), a representative MIS of

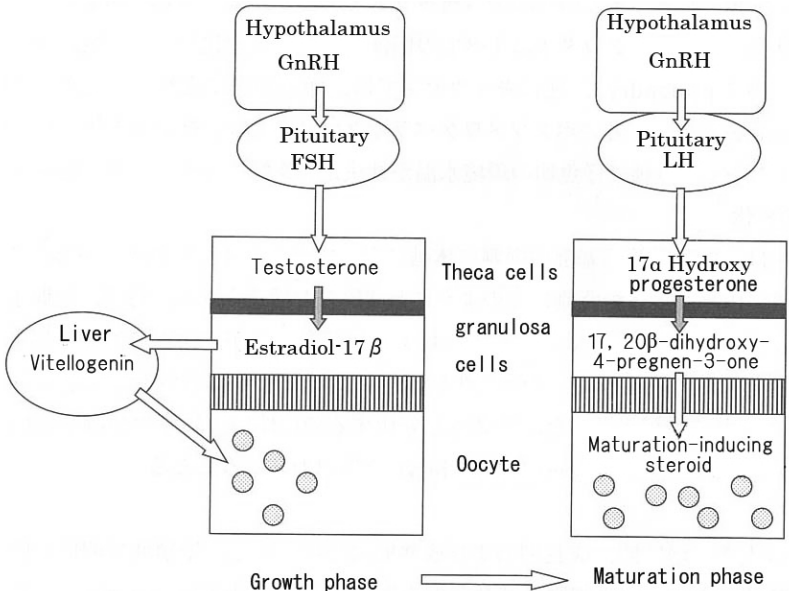

Fig. 2.10. Endcrine regulation in oogenesis of fish.

fish, is made in granulosa cells by transformation from 17β-hydroxyprogesteron that is produced in theca cells. MIS induces the final maturation of oocytes.

3) Spermatogenesis

The testis is composed of many seminal lobules. Elongated tube-like lobules are called seminiferous tubules. In the seminal lobules, cysts enfolded by Sertoli cells make a single layer along the internal wall, and germ cells exist in the bosom of Sertoli cells. Leydig cells, steroid hormone-producing cells scatter among lobules.

The process of spermatogenesis is divided into the proliferation, meiosis, spermiogenesis and maturation phases. In the proliferation phase, type A spermatogonia proliferate gradually by mitosis. When spermatogenesis starts, spermatogonia actively divide and proliferate to become slightly smaller type B spermatogonia. At the beginning of meiosis, type B spermatogonia shift to primary spermatocytes, which produce slightly smaller secondary spermatocyte by meiosis I. Furthermore smaller spermatids are produced from secondary spermatocytes by meiosis II. In the spermiogenesis phase, spermatids metamorphose to spermatozoa through condensation of the chromatin, transformation of the nucleus, differentiation of the flagellum and omission of the cytoplasm. Spermatogensis until spermiogenesis stage is implemented in seminal lobules. Metamorphosed spermatozoa are discharged from lobules to testicular ducts (vas deferens). This process is called spermiation. However, spermatozoa just after spermiation is immature without the capacity of movement. The

maturation phase is the process, in which immature spermatozoa develop motility to become mature spermatozoa. Spermiated spermatozoa are exposed to a high pH environment in the testicular ducts. This condition gives capacity of motility to spermatozoa. This process is sperm maturation, and mature spermatozoa are discharged to an external environment through ejaculation that occurs in sexual behavior with female.

Spermatogenesis is also controlled by the hypothalamic-pituitary-gonadal axis. There also exist two types of GTH (FSH and LH) secreting cells in the pituitary gland of males. However, according to the report using eel, all processes of spermatogenesis can be induced by LH alone, and thus the function of FSH in males is not clear. GTH acts on Leydig cells to induce production of 11-ketotestosteron (11-KT), a major androgen in fish. 11-KT induces in turn production of activin B, which accelerates proliferation of type B spermatogonia. Meanwhile, the process of sperm maturation is induced by 17,20β- P.

4) Reproductive cycle

Fish inhabiting temperate regions, where seasonal changes are clear, mature and spawn in a particular period during the year, showing an annual reproductive cycle. This is caused mainly by seasonal changes in temperature and day length. The responses to environmental changes vary among fish species. For example, in bitterling (*Rhodeus ocellatus ocellatus*) which spawn from spring to summer, rise in water temperature during early spring triggers yolk accumulation and spawning. The spawning season extends to summer; however, the gonad degenerates in early autumn, when the fish detect shortening of day length. On the contrary, in landlocked salmonids and ayu (*Plecoglossus altivelis*) that spawn in autumn, shortening of daytime in autumn induces gonadal maturation. Some fish living in tropical areas, where seasonality is poor, mature and spawn in accordance with the cyclic environmental fluctuations such as lunar phase and dry and wet season.

3.4 Respiration and circulation

Respiration is divided into external respiration in which oxygen is taken from outside to inside of body and carbon dioxide is discharged from the body and internal respiration (cellular respiration) in which oxygen is utilized and carbon dioxide is discharged from the cell. In cells, mitochondria synthesize ATP in the process of oxidization of carbohydrate using oxygen (O_2) from outside producing water and carbon dioxide as final products. The reaction can be expressed as following formula.

$$C_6H_{12}O_6 + 6H_2O + 6O_2 + 39ADP + 38Pi \rightarrow 6CO_2 + 12H_2O + 38ATP.$$

In the process of evolution, respiratory organs for intake of oxygen from outside the body and circulatory system for transportation of oxygen to parts of body are differentiated. Tetrapod animals expanded their habitat on lands where oxygen is sufficient. On the other hand, fish developed mechanisms for effective

intake of oxygen from water, which contained marginal oxygen in heavier unit space compared to air.

1) Circulatory system in fish

Circulatory system of animals after Reptilia is dual circulation system, in which blood from heart is transported to lung, returned to the heart after absorbing sufficient oxygen and is then sent to various parts of body from the heart. Circulation system of fish is single circulation system, in which blood from heart is transported to the gill, the respiratory organ where it becomes oxygenated blood, then distributed to other parts of the body through arteries, and is brought back to the heart through capillaries and veins. The heart of mammals is composed of two auricles and two ventricles, while the fish has more simple heart structure composed of one auricle and one ventricle.

Heart

Fish heart is composed of sinus, atrium, ventricle and bulbus arteriosus in teleosts or conus arteriosus in selachians. All these components are contained inside a pericardial cavity. Sinus is thin membranous space mainly composed of connective tissue. Venous blood from whole body comes back to sinus. A valve exist between sinus and atrium to prevent back current of blood and the region is the pace maker of rhythm of the heart. Cardiac muscles in atrium are well developed and the function of atrium is to pump blood to ventricle. Blood from atrium is transported to ventricle through valve between atrium and ventricle. Ventricle is made with thick muscle layer and pumps the blood transported from atrium after little pause to whole body by strong contraction force. Bulbus arteriosus and conus arteriosus have elasticity. They keep a portion of blood by expanding. Their function is rectifying the blood current to prevent transportation of excess amount of blood to gills.

Cardiac muscle is striated similar to skeletal muscle. Muscle filaments of skeletal muscle are bundled in parallel and the edge of the bundle forms tendon that attaches to the connective tissue. Cardiac muscle is crooked and the filaments connect to other filaments at the edge and forms complicated webbing structure. Skeletal muscle filaments contract with the signal from end plate of nerve system, impulse of excitation happened in a part of cardiac muscle transmits to other filaments through the connection and the contracts happen sequentially in cardiac muscle. Each filament has its unique rhythm of contraction, though, as a whole heart, the rhythm is conducted by pace maker that contracts in most quick rhythm. The pace maker is inhibitory controlled by cholinergic nerve.

Blood circulation

Blood from heart enters the systemic circulation through gills. Blood flows from the heart through ventral aorta and afferent branchial artery and reaches the gills, from where it enters the capillary network in ordinary filaments of gill. After completion of gas exchange, the blood in both efferent branchial arteries joins into dorsal aorta. From this junction, a portion of the blood flows in anterior direction to head through carotid artery. Dorsal aorta runs immediately beneath vertebrae. After branching arteries such as celiac artery to various splanchinic organs, dorsal aorta connects to caudal artery. Arteries repeat branching and form

capillaries and connect to veins. The veins join to form larger veins carrying the blood back to the heart. On the way, caudal vein branches into capillaries in the kidneys, while the vein from visceral organs branches in the liver and forms the renal portal vein and hepatic portal vein, respectively.

2) Respiratory system in fish

Including the rare species that can breathe air, fish have gills as respiratory organ and obtain oxygen from water. Water, the medium of oxygen, can contain only 1/30 of oxygen which contained in air, and diffusion speed of oxygen in water is 1/8000 of that in air. In addition, water is about 8000 times denser and about 60 times more viscous compared to air. Thus far higher amount of energy is required for exchanging water than for exchanging air. However, there is no risk of evaporation of moisture from surface of respiratory organ and fine structure of gill is well developed in fish. Fish can intake oxygen effectively to a maximum level. Respiration system is divided to following three process, namely, gas exchanges at gill, gas transportation in blood and oxygen consumption.

Gas exchange at gill

Osteichthyes generally have four pairs of gills. Each gill is lined with gill filaments (Fig. 2.11). Venous blood from afferent branchial artery enters the gill filament through afferent filamental artery. Through capillary in ordinary filament of gill, blood is transported to efferent filamental artery vessel, efferent branchial artery and the dorsal aorta. Network of capillaries cover the thin respiratory epithelial cell layer in ordinary filament. Gas exchange takes place during the blood's transit in the capillary. Gill filaments separated alternately to both sides to form double lines. The blood flow in ordinary filament is from inside to outside of the double lines. In contrast to terrestrial animals which take air to lung by reciprocal motion, fish take water from mouth and drain from the branchial pore. The movement of water on the gill is a one way flow from outside to inside between ordinary filaments. Current of blood and water form opposed flow in each other. The opposed flow makes gas exchange in fish effective, and is a prominent nature of respiration of fish.

Gas transportation in blood

Oxygen diffused in the gill filaments combines with hemoglobin in red blood cells. The binding of O_2 and hemoglobin is reversible reaction. In higher O_2 environment, binding O_2 increases, and inversely in lower O_2 environment, binding O_2 decreases. Affinity of O_2 is also influenced by CO_2 concentration. In same O_2 concentration, binding O_2 decreases with increase of CO_2 concentration. Because of these natures, hemoglobin bind effectively with O_2 in gill where O_2 concentration is high, and discharge O_2 in peripheral tissues where CO_2 concentration is high.

CO_2 is soluble in water. CO_2 is dissociated in red blood cell by carbonate dehydrase to hydrogen ion (H^+) and bicarbonate ion (HCO_3^-). H^+ binds with protein unit in hemoglobin and HCO_3^- is exchanged with Cl^- in blood plasma and discharged to blood plasma. In gill, HCO_3^- in blood plasma exchanged with Cl^- in red blood cell and transformed to CO_2 by carbon anhydrase, and discharged to outside through gill.

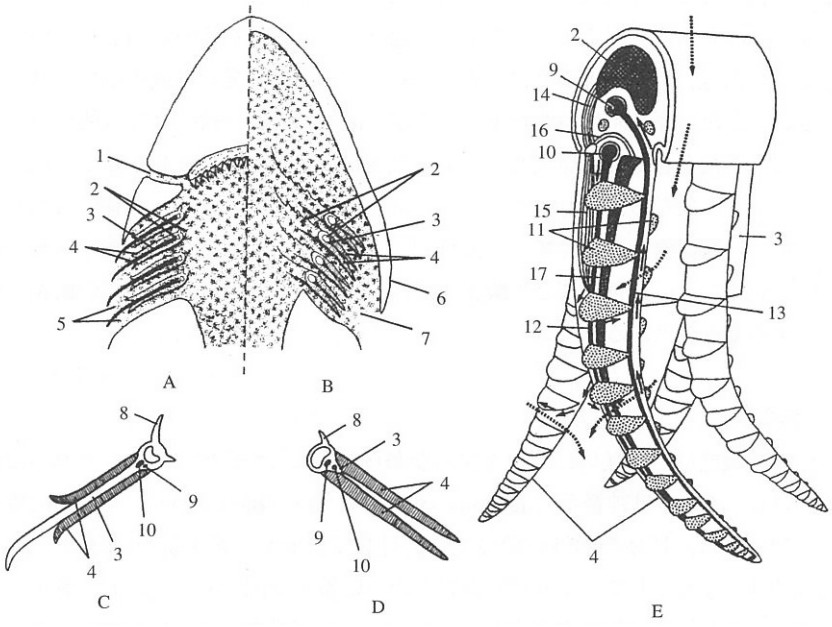

Fig. 2.11. Pattern diagram of cross section of fish gill. A, Elasmobranchii; B, Osteichthyes; C, Gill of Elasmobranchii; D, Gill of Osteichthyes (modified from Bond, 1996); E, Structure of Osteichthys gill and water and blood flow (Iwai, 1985). 1, Respiration pore; 2, Gill arches; 3, Gill septum; 4, Gill filament; 5, Pharyngeal slit; 6, Opercle; 7, Gill slit; 8, Branchial sieve; 9, Efferent branchial arteries; 10, Afferent branchial arteries; 11, Ordinary filament; 12, Afferent filamental artery; 13, Efferent filamental artery; 14, Abductor muscle; 15, Adductor muscle; 16, Ligament; 17, Midrib. Solid lines represent blood flow. Dotted lines represent water flow.

Oxygen consumption

Oxygen consumption is the amount of oxygen taken by fish from water for respiration, and varies widely among fish species. Generally oxygen consumption in active fish species is high, and low in inactive species. Vigorous exercise change metabolism in muscle from aerobic metabolism to anaerobic metabolism because of insufficient oxygen supply and lactic acid is accumulated in muscle. Dissolved oxygen in environmental water fluctuates widely and sometimes oxygen deficiency happens. Resistance of fish to oxygen deficiency differs among fish species. This is related to oxygen affinity of hemoglobin. Oxygen deficiency resistant fish such as eel can saturate oxygen in low oxygen concentration environment, though fish that actively swim without rest cannot saturate oxygen without enough amount of oxygen. It is thus very important to understand species nature in oxygen consumption for assessment of the upper limit of rearing density and feed amount, because dissolved oxygen concentration in rearing water is fluctuate depending on the rearing density and feeding level through respiration of fish.

3.5 Nervous system and sensory organ

Various functions of living organisms should work together in good harmony. Nervous system and endocrine system are the major system in living organisms that control the various functions. In addition to these systems, immune system can be counted to the controlling systems of functions in some aspect. Nervous system is effective for quick response to changes in the external and internal environment. Endocrine system controls relatively slow and long term response. Information accepted at a specific organ such as light, sound, and smell is transmitted to the central nervous system through nerves and processed. Information from central nerve system is again through nervous system transmitted to the effecter organs such as muscle and quick responses such as feeding and escape are induced.

There are several types of neurons (nerve cell) that make up the nervous system. Basically, dendritic outgrowth attached on cell body receives and transmits the signals to other cells or effector organs such as muscle through axial fiber. The signals are transmitted as electric excitations, named impulse, which are electric alterations depending on entrance and exit of ions at cell membrane to next cells through intermediation of synapse. For further details on the mechanisms of electric excitation and function of synapse, the author recommends to refer "*Fundamentals of Fish Physiology*" and other text books.

1) Nervous system of fish

Central nervous system

Central nervous system originates from hollow tubular structure made by constriction of ectoderm in early development called neural tube. Anterior part of the neural tube swell up in the process of development and forms brain, while the posterior part forms the spinal cord. Finally, the brain differentiates into olfactory bulb, telencephalon, diencephalon, mesencephalon, metencephalon and myelencephaon. Each part of the brain has a specific function. Parts of primary center in brain have been identified in various senses. In mammals, major center for controlling of total nervous system is cerebrum (telencephalon in narrow sense), though the center is optic tectum, which is located in dorsal part of mesencephalon, in lower vertebrates. In posterior part of the brain are the column-shaped bundles of neurons (nucleus) called sensory column for dorsal column and locomotion column for ventral column. Based on the information organized in optic tectum, signals transmitted to muscles through locomotion column decides the fish behavior.

Peripheral nervous system

Peripheral nervous system interfaces the brain and spinal cord (central system) and peripheral tissues such as sensory and effector organs. There are two pathways in peripheral nerves. One is cranial nerves, stretching from the brain, and the other is spinal nerves, which stretch from the spinal cord. Both have somatic nerves which are related with the sense and movement of skeletal muscle and autonomic nerves controlling involuntary movement. The cranial nervous system has 12 pairs of nerves, each with a specialized function. Spinal nerves are

classified in the dorsal region as sensory nervous system, and in ventral region as locomotory nervous system. Sensory signals from peripheral organ enter spinal cord from dorsal root and are transmitted to the center. Information for locomotion originated in the brain is send to peripheral muscles through ventral root.

2) Sensory function in fish

Sense is a phenomenon in which internal or external changes are recognized by the organisms as follows. Firstly, the body's internal or external change is detected by sensory organs such as eyes, ears, skin, and nose. The information is transformed to nervous signals in the organs and is sent to the central nervous system. Finally, the change is recognized by the organisms. Sensory organs are composed of sense receptor cells and supporting organs. The excitation energy causes change in membrane protein and changes membrane potential by switching flow of ions in ion channels. Finally change of potential generates impulse and transmits signal to the central nervous system. Receptor cells are classified into four groups, namely photoreceptor, mechanoreceptor, thermoreceptor and chemoreceptor cell. In this book the author will elaborate on the sense of vision, sense of hearing, sense of lateral line, sense of smell and sense of taste, because these are highly related with physiology and ecology of fish.

Sense of vision

Major photoreceptor organ of fish is eye, though it is known that pineal body can accept photo stimulus. Figure 2.12 shows the structure of eye. Light entering through the iris is reflected by the lens creating an image on the retina. In addition to photoreceptor cells, horizontal cell, bipolar cell, amacrine cell, ganglion cell and Mullar cell exist in the retina. Among these, horizontal cell, bipolar cell, amacrine cell, ganglion cell are intermediate nerve cells, and Mullar cell is a neuroglia cell. These cells form well organized multilayer structure in the retina. Energy of photon induces transformation of visual substance in outer segment of receptor cell, causing electrical change in the receptor cell. The signal is transmitted to bipolar cell and ganglion cell, and impulse is generated. The impulse is transmitted to the center through optic nerve. Horizontal cell and amacrine cell transmit the impulse horizontally in each layer and is related to the regulation of sensitivity.

There are two types of photoreceptor cells, the rods and cones. Rods have rhodopsin and porphyropsin as visual substances and are highly sensitive. Cones have four opsins as visual substances, namely the red, blue, green, and ultraviolet sensitive opsins. Sensitivity of cones is low but is related to color vision. Rods and cones move vertically in retina. In light environment, rods elongate downwards. In this condition, rod is covered by pigment epithelia and little light can reach visual substances. Conversely in dark condition, rod extend upwards without shade of pigment epithelia and can catch the scant light. Sensitivity of cone is related to light environment of fish. It is a trend that fish living in blue sea have blue light sensitive cones, while fishes living in green lake and turbid waters respectively have the green and red light sensitive cones as major cones.

Sense of hearing

Fish do not have external ears, but have internal ears and can recognize

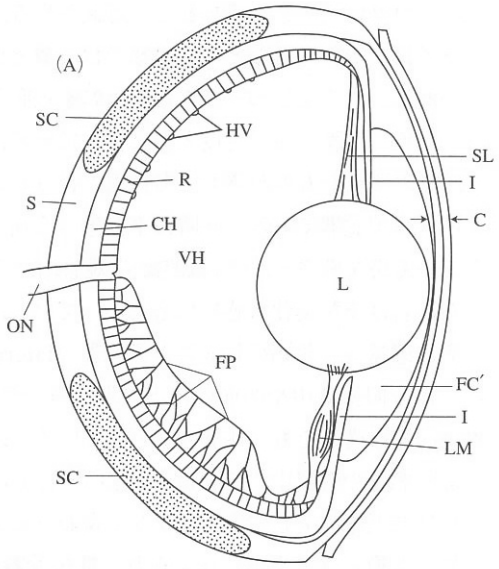

Fig. 2.12. Pattern diagram of cross section of osteichthyes eye. C: Cornea. CH: Choroid. FC: Anterior chamber. FP: Prossesus falciformis. HV: Glass body vessel. I: Iris. L: Lens. LM: Lens muscle. ON: Optic nerve. R: Retina. S: Sclera. SC: Cartilage. SL: Suspension ligament. VH: Glass body (from Tamura, 1991).

sound. Internal ear is composed of three semicircular canals and three otolithic organs. Otolithic organs are utriculus, sacculus and lagena and contain otoliths named lapillus, sagitta and asteriscus, respectively. Otoliths are placed on a patch of hair cells called macula. Hair cell is a sensory cell with cilia. When pressure waves reach to the body of fish, the wave causes vibration of fish body. At that moment, movement of otolith gets behind the movement of the hair of cell (stereocilla) in macula, because the otolith is heavier than the hair. As a result stereocilla is leaned by otolith. This mechanical change causes electrical change in the cell and the signal is transmitted to the central nervous system and is recognized as sound by brain.

Ostariophys is a taxon in which fish have four pairs of bone connecting the bladder and internal ear called Weberian apparatus. Sound passing through the water vibrates the bladder. These vibrations are efficiently transmitted to internal ear by the bones. Cypriniformes (carp), Siluriformes (catfish), and Characiformes (tilapia) are ostariophys. They have high quality audible spectrum and sensitivity. Generally, it is said that fish living on soft bottom such as the pond, generally have good sense of sound, while carnivorous fish have weak sense of sound.

Internal ear controls the balance as well as functions as sound receptor. Each semicircular canal has ampullary part on the edge and macular with hair cell exits

in the ampullary. The hairs respond to the movement of lymph in the semicircular canal and works for the recognition of angular velocity vector.

Sense of lateral line

Lateral line organs are distributed on body surface of fish and form lateral line system. There are canal neuromasts, which are located in the canal organ embeded in scales on lateral line or skin of head, and free neuromasts on the surface of skin. There is basically no difference in the structure and functions of two neuromasts.

Neuromast is composed of sensory cells that have sensory hair and supporting cells. Whole neuromast is covered with gelatinous processes called cupula. Lateral line as well as auditory organ is mechanoreceptor in which the movement of the sensory hair is transformed to electric signal and sent to the central nervous system. Auditory organ receives sound as a pressure wave. In case of lateral line, movement of water is received as action of water particles. Pressure wave has long distance effect. Distance effect means that attenuation rate of the wave decreases with distance. As a result the wave can reach far place. Action of water particle has short distance effect. The power of movement varies inversely proportional to 2 power of distance. This means that there is a steep gradient in stimulations from source of water action on whole body. This is considered to be the reason why fish can recognize position of food organisms and existence of motionless obstacles. Free neuromast shows high sensitivity to vibration under 20 Hz and canal neuromast shows high sensitivity to 20–40 Hz. Canal organ is considered to have important roles in rheotaxis, group formation and detection of obstacles in water.

Sense of smell

Sense of smell and taste are chemical senses which detect chemical substances dissolved in water. A pair of nostrils on the right and left side of the snout works as the organ for sense of smell. Each nostril has a pair of opening back and forth and nasal cavity is formed between the openings. In the cavity, olfactory rosette composed of gathers of olfactory lamella is formed. Many olfactory cells distribute on the lamella. When olfactory cell receives smell, impulse is created in the axial fiber which is elongated from edge of the cell. A bundle of the fiber is a olfactory nerve. The impulse is transmitted through the fiber to mitral cell in olfactory bulb. Mitral cell is the primary center of smell. Then the impulse is sent to telencephalon through olfactory tract and smell is recognized. Positions of the olfactory bulb differ among fish species. In case when olfactory bulb directly connects with olfactory rosette, the olfactory tract is long. Inversely, when olfactory bulb is close to the telencephalon, the tract is short.

Fish have high sensitivity to various amino acids. The relation between sensitivity to amino acids and searching and feeding behavior is well studied. Interestingly, sensitivity to smell have higher similarity among fish species, regardless of fresh water or sea water, migratory or benthic, carnivorous or herbivorous and so on, though the sensitivity to taste varies among fish species and is related to food habit.

Sense of smell is related with the recognition of pheromone. A prostaglandin

from ovulated female of gold fish induces male tracking behavior. It was thought that in striped catfish (*Plotosus lineatus*), which makes a close swarm, smell of the group works as aggregation pheromone.

The famous behavior related with sense of smell is homing habit in salmon that migrates between the river and sea. Smell of the river after hatching till the migration to sea is imprinted in the salmon, which detects the smell and finds the mother river for spawning. The smelling substances have not been identified, although amino acids and bile acids from plants and animals have relation to this phenomenon.

Sense of taste

Taste as well as smell is the sense for detection of chemicals in water. However, taste is different from smell, because taste bud is specialized receptor for taste and its projection part in central nervous system is medullary. Olfactory organ is a long distance receptor though taste bud is contact receptor, which located mainly in mouth. However, many other taste buds distribute body surface centering around head and have various function.

In mammals, sense of taste is to distinguish the sweet, salty, sour and bitter taste. Some fish respond to sweetness, though sensitivity to bitterness is low except the sensitivity to bitterness of quinine. On the other hand, fish show good respond to extractive components of food organisms such as amino acids, low molecular peptides and nucleic acids. These substances are supposed to stimulate appetite. It is known by comparison of response to various amino acids that there are differences among fish species in variety and number of amino acids which stimulate fish. Relative stimulation effects of each amino acid also differ among fish species.

3.6 Endocrine system

Substances secreted by the endocrine glands (hormone) are transported by blood, and induce physiological changes by binding with receptors in target organs. Autocrine means phenomena in which substances secreted from a cell act on the same cell. Paracrine is the phenomena in which substances act on adjacent cell. The substances secreted for autocrine and paracrine are included in hormones. Some nerve cells, or neurons, secrete peptides or biogenic amines. This phenomenon is called neurosecretion, and the secreted substances are referred to as hormones. Major hormones and their physiological functions are listed in Table 2.1.

1) Pituitary gland

The pituitary gland, located below the base of the diencephalon, secretes various peptide and protein hormones. It is embryologically separated into two parts. One is the neurohypophysis, which originates from the diencephalon, and the other is the adenohypophysis, which originates from epithelial cells on the roof of the mouth. Adenohypophsis is further divided into the rostral pars distalis, proximal pars distalis and pars intermedia. The main part of the rostral pars distalis is occupied by prolactin (PRL)-producing cells, and adrenocorticotropic

Table 2.1. Major hormones and their functions in fish.

Organ	Hormone	Function
Pituitary gland	Prolactin	Freshwater adaptation
	Adrenocorticotrophic hormone	Acceleration of cortisol secretion
	Thyroid-stimulating hormone	Acceleration of thyroid hormone secretion
	Gonadotropic hormone	Production of sex steroids, Development of gonad
	Growth hormone	Promotion of growth, Seawater adaptation
	Melanophore- stimulating hormone	Dispersion of melanin granules
	Soinatolactin	Acid-base regulation, Body color regulation, Stress response
Nottrobypophysis	Arginine vasotosin	Blood pressure increase, Contraction of gonoduct, Increase of glomerular filtration
	Isotocin	Contraction of gill vein
	Melanin-concentrating hormone	Concentration of melanin granules
Pineal gland	Melatonin	Light and dark rhythm
Thyroid gland	Thyroxine	Tissue differentiation
	Triiodothyronine	Growth acceleration, Acceleration of metamorphosis, Smoltifcation
Stannius corpuscle	Stanniocalcin	Repression of calcium intake
Ultiniobranchial gland	Calcitonin	Calcium regulation
Interrenal gland	Cortisol	Glyconeogenesis, Seawater adaptation
Cliroinaffin cell	Adrenaline	Increase of heart beat, blood pressure, blood sugar
	Noradrenaline	Contraction of vein, Concentration of melanin granules in melanophores
Kidney	Angiotensin	Increase of blood pressure, Inducement of water drinking, Antidiuretic reaction
Islet of Langerhans	Insulin	Decrease of blood glucose, Acceleration of glucose and lipid accumulation
	Glucagon	Increase of blood sugar, Acceleration ofdecomposition of glycogen and triglycerides
Caudal hypotliephysis	Urotensin	Metabolism of water and electrolytes

hormone (ACTH)-producing cells make palisaded layers in the nearest part to the neurohypophysis. Gonadotropic hormone (GTH)-, thyroid-stimulating hormone (TSH)-, and growth hormone (GH)-producing cells are mainly located in the proximal pars distalis. Secretory cells in the pars intermedia are melanophore-stimulating hormone (MSH)- and somatolactin (SL)-producing cells. The neurohypophysis is an aggregation of nerve axes and endings of neurosecretory cells, whose cell bodies are located in the hypothalamus. Anterior part of the eurohypophysis corresponds to the median eminence of mammals and controls hormone release from adenohypophysial cells by secretion of various hypothalamic hormones. Posterior part (neural lobe) deeply intrudes into the pars intermedia to form the neuro-pars intermedia. From here, neurohypophysis hormones such as arginine vasotosin (AVT), isotocin (IT) and melanin-concentrating hormone (MCH) are secreted.

Adenohypophysial hormones can be divided into (1) GH-PRL family, (2) GTH-TSH family and (3) POMC family according to their molecular structures. GH, PRL, SL are considered to be derived from a common ancestor gene because of their structural similarity. PRL is an important hormone in freshwater adaptation, being involved in retention of Na^+ and depression of permeability in the gills. In addition to its growth-promoting action, GH functions as a seawater-adapting hormone. SL is related to acid-base regulation, body color change, and stress responses. GTH (LH and FSH) and TSH are both glycoproteins composed of α and β chains. Since the α chain is common among these hormones, the functional difference is attributed to β chains. TSH accelerates production and secretion of thyroid hormones. GTH induces production of sex steroid hormones and gonadal development. ACTH and MSH are produced by processing of proopiomelanocortin (POMC), their common precursor molecule. ACTH acts on the interrenal gland (corresponding to the adrenal cortex in mammals) and induces production and secretion of cortisol. MSH disperses melanin granules in melanophores to make the body color darker. Among the neurohypophysis hormones, AVT leads to increase in blood pressure by contracting smooth muscles around the blood vessels. AVT is also involved in contraction of gonoducts and increase in the filtration rate of glomeruli. IT is known to contract blood vessels in the gills. MCH lightens the body color by aggregating melanin granules in melanophores.

2) Pineal gland

The pineal gland is a vesicular-shaped photoreceptor projecting from the dorsal side of the diencephalon. Photoreceptor cells in the pineal gland send information of light condition to afferent nerve fibers and transform the information to humoral signals by secretion of melatonin. Secretion of melatonin is high in the dark and is suppressed by light. The circulation level of melatonin shows prominent diurnal rhythm. Although physiological function is not clear in fish, melatonin is considered to send light and dark rhythm to various organs in the body. In particular, melatonin is suggested to be related to reproductive cycles.

3) Thyroid gland

Thyroid glands in fish are distributed in connective tissues along the ventral aorta and afferent branchial arteries. Thyroid glands produce and secrete thyroxine

(T_4) and triiodothyronine (T_3) which are thyrosine derivatives containing iodine. Thyroid hormone secretion is induced by TSH secreted from the pituitary. Thyroid hormones are involved in tissue differentiation and growth promotion, and induce metamorphosis in flounder larvae. In smoltification of salmonid fish prior to downstream migration to the sea, guanine is deposited in the skin and the body color changes to silver due to thyroid hormones.

4) Stannius corpuscle and ultimobranchial gland

Stannius corpuscle is an endocrine organ specific to teleosts and holosteans, found scattered in and around the kidney and secretes stanniocalcin, a glycoprotein hormone. Stanniocalcin controls the increase in calcium ion concentration in blood by suppressing the intake of calcium ion by the chloride cells in the gills.

Calcitonin is secreted from parafollicular cells in the thyroid gland in mammals, it is produced in the ultimobranchial gland in fish, which is an isolated endocrine organ. Calcitonin is a peptide hormone composed of 32 amino acids. In mammals, it decreases calcium ion concentration in blood by stimulating calcium intake by bone tissues. In fish, calcitonin is involved in regulation of calcium concentration, although its function is not very clear.

5) Interrenal gland and chromaffin cells

Interrenal glands and chromaffin cells are homologous of adrenal cortex and adrenal medulla, respectively, in mammals. Both exist in the head kidney as cell masses in Osteichthyes. Cortisol, produced in interregnal glands, induces gluconeogenesis, and increases blood glucose levels. Although salmon fasts during upstream migration for spawning, it can obtain energy from proteins in the body, as it produces sugars from amino acids by gluconeogenesis. Cortisol also helps in the adaptation to seawater. It induces differentiation of seawater-type chloride cells in the gills and secretion of ions from cells.

Adrenaline and noradrenaline secreted from chromaffin cells have similar functions to sympathetic nerves, such as increase of heart beats, elevation of blood pressure, increase of blood glucose level, contraction of blood vessels, and aggregation of melanin granules in melanophores.

6) Islets of Langerhans

Islets of Langerhans are endocrine glands mainly scattered in the exocrine gland of the pancreas as cell masses, though they also exist as isolated corpuscles called Brockman corpuscles near the gall bladder. Islets of Langerhans secrete insulin and glucagon. These hormones regulate blood sugar levels, acting in an opposing manner. Insulin depresses the blood glucose level with accumulation of sugars and lipids. Inversely, glucagon elevates the level by accelerating decomposition of glycogen and triglycerides.

3.7 Osmotic regulation

Cells of multicellular organisms are usually not in direct contact with outer environments but are soaked in body fluid (blood and intercellular fluid) as an internal environment. Though there are several exceptional species, body fluids of vertebrates are similar in ion composition and concentration, and the osmolality is about 300 mOsm/kg H_2O. Fish are not exceptional vertebrates. In particular,

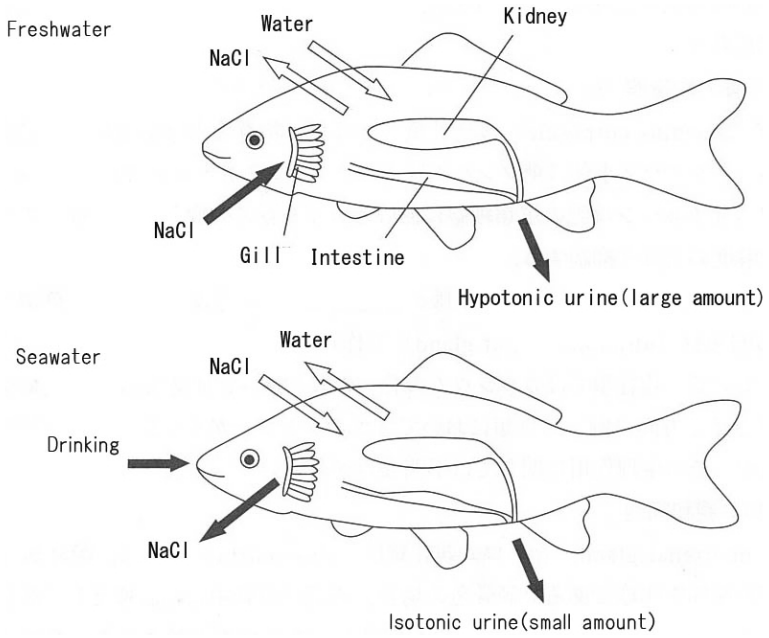

Fig. 2.13. Osmoregulation system in fish. Black arrows indicate active movements of water and NaCl. White arrows indicate passive movements of water and NaCl.

teleosts, the major group of fish, maintain their body fluid osmolarity at about one third of seawater osmolality, Even stenohaline fish, which can live either in freshwater or in seawater, or euryhaline fish, which can be adapted to both freshwater and seawater have body fluid in similar osmorality On the other hand, hagfish, an Agnathan living in the sea has body fluid similar to seawater in osmolality. Body fluid of marine Elasmobranchii contains one half of inorganic ions of seawater and a large amount of urea, and the osmolality is thus slightly higher than seawater.

In general, the gills, kidney and intestine play important roles in osmoregulation in teleosts (Fig. 2.13). Marine teleosts face salt load and water loss; ions enter the body through body surface such as the gills, and water leak out from their body. To solve this osmotic problem, excess monovalent ions are actively excreted from chloride cells. Fish compensate for water deficiency by drinking large amount of seawater and absorbing water in the intestine. The kidney produces urine isotonic to the body fluid, and discharge divalent ions with urine. In freshwater teleosts, on the other hand, water enters into the body and ions flow out of the body. To deal with the water load and salt loss, freshwater fish produce a large amount of dilute urine and discharge excess water with ions retained in the body. For the supply of deficient ions, fish absorbs ions dissolved in minute quantities in the surrounding water through the gills.

1) Chloride cells

Chloride cells are ion-transporting cells distributed mainly on the gill epithelium. The cells contain numerous mitochondria in the cytoplasm. The plasma membrane of the inner side (basolateral membrane) intrudes intricately into the cytoplasma to form tubular structures that enlarge the area of the basolateral membrane. On the membrane of the tubular structures various ion-transporting proteins exist, and transportation and exchanges of ions occur between the inside and outside of the cells. The apical membrane in contact with outer environments provides the site of ion transportation between the cell and surrounding water. In fish adapted to seawater, chloride cells discharge excess salts in the body to prevent excessive increase of blood osmolality in high salinity condition. In fish adapted to freshwater, on the other hand, chloride cells actively absorb ions such as Na^+, Cl^- and Ca^{2+}, which are lost by diffusion, to maintain the ion balance. Ion transport by chloride cells is active transport, which consumes ATP. The driving force of the ion transport is provided by Na^+, K^+-ATPase located on the basolateral membrane. The enzyme is known as sodium-potassium pump.

2) Kidney

The kidney of Osteichthyes is divided into the head kidney and body kidney. The head kidney is a hematopoietic organ (blood-producing organ) and the body kidney produces urine. The body kidney is composed of numerous nephrons. A nephron is composed of a renal corpuscle and a renal tubule connecting to the corpuscle. The renal corpuscle is composed of glomerulus, an aggregate of blood capillary from the renal artery, and a Bowman's capsule covering the glomerulus. Blood transported from the renal artery to the glomerulus is filtered to produce urine. The renal tubule connects with the renal corpuscle at the neck segment, followed by the proximal convoluted segment, distal convoluted segment and collecting duct. The duct leads to an excretory pore through the ureter.

Freshwater fish rarely drink water and produce a large amount of hypotonic urine in the kidney to discharge the excess water in the body. Dissolved glucose and ions such as Na+ and Cl^- filtered in the glomerulus with water are reabsorbed along the renal tubule. In marine fish, the major function of the kidney is excretion of divalent ions with water retained in the body. For the excretion of monovalent ions, the gill is more important than the kidney. Divalent ions such as Mg^{2+}, SO_4^{2-} and Ca^{2+} are discharged from the proximal convoluted segment in the renal tube. The kidney produces isotonic urine to the body fluid, although the amount is small to minimize loss of water. The size and number of glomeruli in marine fish is generally smaller than that in freshwater fish. In a prominent case, some fish completely lost glomeruli. Such fish are called aglomerular teleosts. Monkfish (Lopphiidae) and pipefish (Syngnathoidei) belong to aglomerular teleosts.

3) Intestine

Whereas freshwater fish rarely drinks water, marine fish drink a large amount of surrounding water to compensate for the osmotic water loss. Absorption of water in the intestine is dependent on the difference in osmolality between the body fluid and ingested water. Ingested seawater is desalted during the passage

along the gastrointestinal tract, and consequently the osmolality is reduced to a near isotonic level in the rectum, where water absorption mainly occurs. Salts absorbed in the gastrointestinal tract are excreted from the gill.

3.8 Biological defense

Mechanisms for normalization of various abnormal conditions within body produced by apotosis, canceration, attack of pathogens such as bacteria, virus and parasites, etc. are self defense mechanism. Self defense mechanism works for controlling of internal environment of living organisms coordinating with nervous system and endocrine system. We can consider self defense mechanism systematically by dividing it into innate immunity and acquired immunity. In innate immunity, the system responds quickly and nonspecifically regardless of cause of the disease. It includes phagocytosis of bacteria, bacteriolysis by complements, agglutination of bacteria by lectin (inclusive term of proteins which bind with sugars) etc. On the other hand, basic function of acquired immunity system is production of antibody by lymph cell (B cell and T cell). The response is not swift to the first attack of pathogen though the defense system is quickly established to the second attack by specialization and memory of pathogen. The phenomenon of acquired immunity is observed only in vertebrates. However, the system functions incompletely in low temperature condition and is still insufficiently developed in fish. In this context, it is important to understand the innate immunity.

Biological defense can also be divided into defense at the exterior wall and defense within the body. Exterior wall of fish including the intestine is covered with mucus, which works for elimination of bacteria. In addition to this function, liquid defense factors contained in mucus such as lectin and antibodies keep off the entrance of aliens. Internal defense system such as phagocytosis by leukocytes and production of antibodies by B cells eradicates the pathogens entering through the exterior wall.

1) Leukocyte

Blood cells are the free cells floating in blood vessel and lymph duct, and are divided into red blood cells and white blood cells (leukocyte). Granulocytes, lymphocytes and monocytes are the major leukocytes. Each have specialized mechanism to eliminate foreign objects. Among them, lymphocyte works mainly in acquired immunity and the others are blood cell for inate immunity.

Granulocytes are blood cells which contain many granules in the cell and are divided into eosinophil, basophil and neutrophil based on their dye-affinity. Eosinophil is observed in few species such as yellowtail (*Seriola quinqueradiata*) and the function is still not clarified. Many basophils are observed in carp and puffer. Rapid infiltration of basophils to inflammatory lesion is known, although detailed function is still unclear. Many neutrophils are observed in all fishes and respond quickly to invasion of exogenous substances such as bacteria. These are known to have ability of phagocytosis to exogenous substances, and sterilization capacity.

Monocyte is a large blood cell with basophilic cytoplasm. It migrates from blood vessel to tissues and differentiates into macrophage. However, in case of fish, it is difficult to morphologically differentiate monocyte from macrophage. It follows the neutorphil responding to invasion of exogenous substances, and represents active phagocytosis. This blood cell has high capacity to distinguish self and non-self, recognizes the apoptotic cells as an intruder and engulfs the cells. Furthermore, monocyte fragments the exogenous substances and expresses the fragments on its cell membrane. This blood cell also works as an antigen presenting cell to transmit information of antigen to T cell.

T cell and B cell are the lymphocytes. B cell redifferentiates into plasma cell receiving antigen stimulation and secretes antibodies. In case of fish, the antibody is IgM. There are several types of T cell. Among them, helper T cell (Th cell) induces immune reaction by stimulation of B cell. Cytotoxic T cell (Tc cell) breaks down denatured cells such as virus infected cells.

2) Acquired immunity

When invasion of alien happens, neurophil migrates at first, and endocytoses and sterilizes the exogenous substances. Then macrophage appears and decomposes it by intracellular digestion. After that, the segment is bound with major histocompatibility complex (MHC) class II and is expressed on the cell membrane to present antigen to other cell. The antigen is recognized by antigen receptor of Th cell, (T cell receptor; TCR). Binding of antigen induce secretion of cytokine, and cyotokine activate B cell. "Cytokine" is a collective term for proteins relating to intercellular information. By the stimulation of cytokine, B cell proliferate and differentiate to plasma cell to attack the exogenous substance by secretion of specific antibody to antigen. Antibody has various functions in addition to the function of neutralization of toxicity by binding toxic substances. Opsonic effect is an effect to make toxic substance easy to be phagocytized by macrophage and other phagocytes by binding the surface of toxin. Complement activation is a function of antibody, known as "classic path way", in which complement is activated to induce complement fixation reaction with antigen-antibody complex. By complement fixation reaction, molecular size of antigen-antibody complex decreases and gradually the complex is solublized. A portion of B cell and T cell become memory cell. When same substance invades the body, the memory cells can respond quickly and strongly to prevent being affected by the same disease.

IgM and TCR can respond to various antigens, because of the variety in amino acid sequence at N-terminal exodomain. The variation is produced in the process of maturation of B cell and T cell by recombination of genes. Each cell has its own unique amino acid sequence of IgM and TCR. When an antigen invade in the body, B cells and T cells of which IgM or TCR can bind the antigen are selected and respond to antigen.

If the invader is virus, antibody cannot bind with the virus in the cell. In that case, the cell express the segment of protein which produced from gene of virus on MHC class I molecle informing that the cell is infected. Tc cell recognizes the cell and the cell is destroyed by cytotoxicity of Tc cell. By this process, propagation of virus can be inhibited.

Compared to advanced clinical trials in immunology in mammals, immunological research in fish is still at a primitive stage. However, information is dramatically increased by recent development of molecular biological analyzing methods. As an example, markers for Th and Tc cells are clarified and functional analyses are progressing. Many cytokines, related to intercellular information transmission, are discovered. The author believes that the day will arrive when we can draw a whole picture of fish immune system without supposition from the knowledge of mammals.

3) Innate immunity

Acquired immunity is characterized by specificity and memory. On the contrary, innate immune system works nonspecifically to invaders without memories. Cellular factors as well as humoral factors are included in innate immunity system. As cellular factor, endocytosis and sterilization by neutorphil and macrophage are innate immunity function. Moreover, inate immune system includes humoral factors, such as complement and lectin in mucus on the cell surface are humoral factors working in inate immune system. In addition to complement are lectin, antibacterial proteins, lysozymes that resolves cell membrane, and transferrin, which take up iron from bacteria by chelating reaction.

Complement

Complements are composed of 30 proteins. Complement system is a cascade of sequential reactions called complement-fixation reaction. The system represents various functions in cascade reactions. There are three pathways in activation of complement, namely classical pathway, alternative pathway and lectin pathway. Classical pathway starts by activation of C1 protein with binding of antibody to antigen. Alternative pathway starts by activation of C3 protein independently with reaction of antigen. Lectin pathway starts by binding of manose binding lectin in blood plasma with sugar chain on the surface of microorganisms. In later process, complement membrane attack complex is produced and bacteriolysis is induced. Activity of alternative pathway is high in fish blood plasma. From this, alternative pathway is older pathway in evolution of complement system. Not only bacteriolysis by complement membrane attack complex, intermediate product in complement reactions induces migration of leukocyte to exogenous substance invasion site, and opsonic activities induces phagosytosis of leukocyte by binding the surface of microorganisms to make it easy to be recognized.

Lectin

Mucus of many fish species shows coagulation activity of red blood cells of rabbit. The reaction is an effect of lectin. Many lectins are known in animals and plants. Among these, lectins in the body surface mucus of fish are rich in variety. Eel and conger eel have galectin that bind with galactose. In addition to this, eel has C type lectin. C type lectin usually needs Ca ion for expression of its activity, but the C type lectin of eel requires no Ca ion for its activation. This may have relation to the nature of eel that they can inhabit fresh water which is low in Ca content. Rhamnose binding lectin was discovered from the mucus of pony fish. Until then, it had been found only in fish and sea urchin eggs. From torafugu

(*Takifugu rubripes*), was discovered the lily type lectin that have homology to lectin of Liliales plant and no homology to any lectin from animals. Many lectin in body surface are supposed to have activity for coagulation of bacteria to prevent the attachment of bacteria on body surface. The reason and mechanism why fish lectins have undergone variation in evolutionaly history is puzzling and interesting.

4. ECOLOGY OF AQUATIC ANIMALS

4.1 Life history

1) What is life history?

Life history of an organism is its lifetime pattern of growth and reproduction. Body size, growth rate, reproduction, and life span etc. are the major parameters involved in life history. Life history patterns vary among species and each species or populations have its own specific parameters. These are called life history traits. For examples, Medaka (*Oryzias latipes*), whose life span is 1–2 years, hatch out from a 1.5 mm diameter egg, reaches 3–4 cm in body length in the next year and spawns from spring to summer. Whale shark (*Rhincodon typus*) is viviparous. It grows inside the mother's body, and is released when it grows to about 50 cm. It needs 30 years for maturation, breeds every year for several years and has long life span. Generally small species have a short life span and early maturation, while large species have a long life span, late maturation and multiple reproduction.

Life cycle is sometimes used with a similar meaning as life span. However, this word means a cycle composed of growth and reproduction, and is used particularly when we focus on reproductive pattern such as nuclear phase and alteration of generation. Life history is also used similarly in some situation, though, in that case, it includes more wider ecological phenomena in the life of organisms. In life history study, life table, which is often used in demography, is important. Life table summarizes predicted mortality rate by the next birth day and average life expectancy and so on of each age and sex. This is a useful method to recognize life history quantitatively from various view points.

2) Life history of aquatic organisms

Many marine animals spend the planktonic larval stage in sea-surface layer prior to their benthic life or nektonic adult life. The larvae have different morphology from that of an adult, which is modified to prevent from sinking or for maintaining the position in a water column. Therefore, we can collect various larvae by towing plankton net in sea. Only a few can be identified to the species level, and there are many species in which relation between their adult and larvae was not identified. As an example, fish in Anguilliformes commonly pass through the leptocephalus stage in their larval development. Leptocephalus is transparent and flat. Their shapes are far different from those of adults, which are elongated like a snake. Therefore, we had believed that they belong to completely different taxon and gave the larvae a specialized genus name as "*Leptocephalus*". When a living leptocephalus caught in coastal water was kept in an aquarium, it was

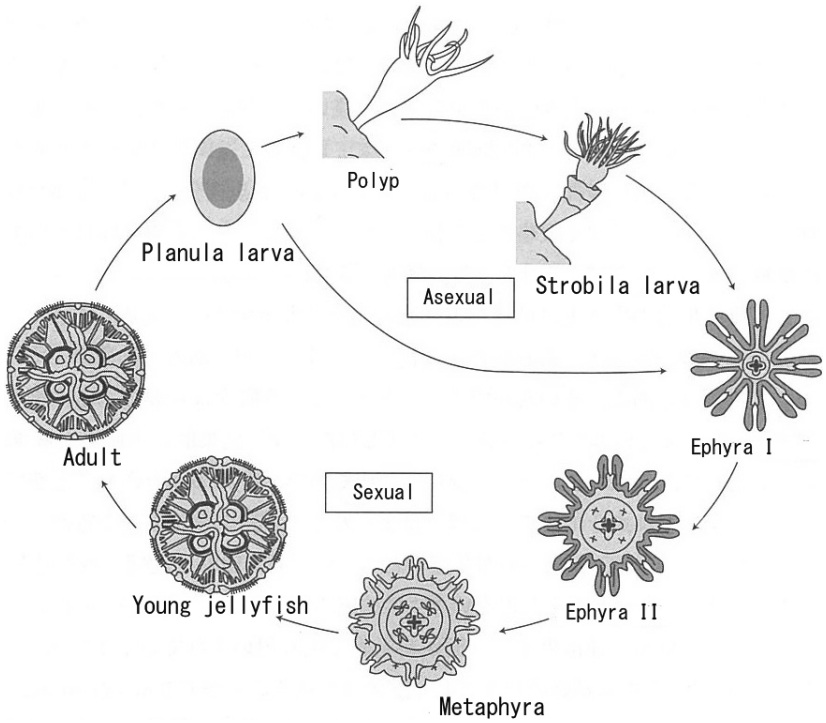

Fig. 2.14. Life history of moon jelly. Moon jelly has both sexual reproductive generation (jellyfish) and asexual reproductive generation (polyp).

discovered that the leptocephalus changed to a juvenile eel. By this, it was confirmed that leptocephalus is the larva of anguilliformes fishes.

In life history of jellyfish, which sometime cause big damage to fisheries by their mass propagation, there are two generations and their life history is complicated (Fig. 2.14). One is jellyfish generation which breeds by bisexual reproduction in planktonic life. The other is polyp generation which breeds by unisexual reproduction in sessile life. Female jellyfish receives the spermatozoa discharged by male jellyfish in the surrounding water, and fertilizes the eggs inside the body. When the egg hatches, the larva develops to planula larva and swims out from the mother's body. Several days after, planula attaches on the substrate and metamorphoses to polyp larva. Polyp breeds asexually and makes colonies. Then horizontal segment appears in the polyp. Larvae at this stage are called segmenting polyp or strobila. Each segment grows to ephyra larva and begins to swim in the surrounding water. Ephyra is larvae of individual jellyfish and it grows up to adult jellyfish through metaphyla stage and young jelly fish stage. However, some planula larvae directly metamorphose to ephyra. This flexibility in life history as well as high fecundity and regenerating power is the

key to understand why jellyfish could continue to exit on the earth for more than 1 billion years.

3) Life history strategies

Needless to say, basic studies for description of life history from the view point of natural history are important in aquatic biology in which even species identification of larval stages is still impossible in many species. However, theoretical approaches to understand life history from the view point of evolution and adaptation have been adopted recently. Many concepts to explain why and how such varied life histories are developed are proposed.

The concept of *r* selection and *K* selection by MacArthur and Wilson is a pioneer work in this field. They explained the reason of success and failure in settlement of newly migratory organisms on the island by two ways namely *r* selection and *K* selection. Eventually, it was recognized that the directions of these two selection are incompatible with each other and the concept of *r* selection-*K* selection lead to the studies of life history strategy. In evolution of organisms, one of the two strategies is selected depending on the nature of species and environment. In *r* selection, organisms adapt to the environment by increasing reproduction rate to increase the number of the population. In *K* selection, organisms adapt by increasing competitive power. Here, *r* represents intrinsic rate of natural increase of a population. Species which has higher *r* value can increase individual numbers in a population more rapidly within a period. *K* means carrying capacity that is the upper limit of population density in an environment where resources such as food and space are restricted. In case when only a few individuals exist in a large space with abundant food, the best reproductive strategy is to make as many offspring as possible (*r* strategy). However, when that population density is near the upper limit, large amount of energy is needed in order to survive severe competition among individuals. In that case, to make offspring that have high competitive power (*K* strategy) is the best strategy. From these mechanisms, organisms that select *r* strategy generally have rapid growth rate, small adult size, large number of small offspring and short life span. Inversely, *K* strategy species have slow growth rate, large adult body size, small number of large offspring, and long life span. Generally, aquatic animals spawn larger number of smaller eggs compared to terrestrial animal. That means many aquatic animals select *r* strategy. When we compare between sea and river, there are many organisms which select *r* strategy in sea because of richness of food resources and space and wide distribution of their larvae. On the contrary, many river species select *K* strategy. However, there are many exceptional organisms where we cannot explain all phenomena only by *r* selection and *K* selection.

Life histories of living organisms have evolved in order to maximize their adaptive value to the best possible level. When a character of organism changes in the optimizing theory of adaptability, the change will not continue endlessly in one direction. There are some constraints. Among the constraint, concept of tradeoff is important. When organism tries to spawn large eggs, the organisms need large energy to make large egg. The organism should accept decrease in

number of eggs as a result because of the constraint in energy allocation. Inversely, when it spawns small eggs, it needs small energy for production of one egg and can spawn large number of eggs. From large egg, large offspring will hatch and adaptability increases. However, the number of eggs produced must be reduced, and the organism should accept the disadvantage of reduced number of offspring. Organisms should select either large size-small number of egg strategy or small size-large number of egg strategy. Competitive relationships of two incompatible characters such as egg size and egg, as in this example, is named "trade off".

Rotifers (*Brachionus plicatilis*) are small zooplankton about 0.2 mm in length and are important food for the early stage of marine fish. Typical tradeoff can be observed in reproduction strategy of rotifer (Yoshinaga *et al*., 2000). In good condition in which rotifers are given sufficient amount of food, they start spawning at an young age, spawn many offspring and finish their life within short period (*r* strategy). On the other hand, rotifers in starved condition spawn one third of the offsprings but live twice of the life span compared to rotifer in good condition (*K* strategy). This means that starvation makes life span longer in exchange for decrease of number of offspring. This is a tradeoff in energy allocation between body cells of mother and reproductive cells, which will be the offsprings. In poor nutritional condition, survival of offspring is uncertain. Rotifers are considered to adopt the strategy to survive long period by suppression of reproduction in order to maintain absolute adaptability waiting for a chance to reproduce. Strategy to control reproduction and spawning chance depending on condition is called temporally dynamic reproductive strategy.

4.2 Population structure

1) Population and population genetics

It has been recognized by development of modern genetics that species that was considered to be a unit of biological classification is not necessarily a genetically uniform group. In a species, there exist multiple groups which have different gene pool. A group which has same gene pool in a same species is a population. Population is produced, when exchange of genes is disturbed by separation of distribution area of a species due to some obstacle, or due to difference in spawning season in the same area. In ecology, term of population is used in the meaning of genetically uniform group. Tight relationships among individuals such as copulation, competition and co-operation are maintained in a population. Based on these tight relationships, not only gene composition but also fertility rate, mortality rate, population density, distribution pattern, age structure, sex ratio etc. are homogenously shared in a population and its population specific nature is developed. As a result, the difference among population becomes prominent. On the contrary, homogeneity of species is maintained, huge uniform population is formed, when separation of species does not exist and free mating is possible in species.

Studying genetic composition of population to estimate historical process of

the change is population genetics. Changes in genetic composition of population precedes evolution. Therefore, population genetics is a study to clarify elementary step in evolution. Interpretation of same phenomenon is widely different depending on the resources, whether the ecological information is obtained from a single reproductive group that share same gene pool or from multiple groups. Therefore, to know population structure of a species is fundamental in ecology. Moreover, extinction of species and collapse of biological resource starts from extinction of each local group. We have to make proper counter measures for maintenance of a local group instead of considering a counter measure for the whole species to prevent extinction of species.

2) Populations in aquatic organisms

Aquatic organisms living in marine and fresh water have their specific nature in population genetics (Palumbi, 1994; Waples, 1998). Generally, ocean has no prominent obstacle for migration. Organisms living in the ocean have wide distribution area, high fertility, and specific morphology of egg and larvae suitable for their planktonic life in the ocean. However, habitats of fresh water organisms are separated by land and most of them complete their life in a limited area. Most of the fresh water organisms have strategy to certainly nourish a small number of offspring. In addition, fresh water organisms have limited freedom of distribution because of constraint of flow from upstream to downstream. From these differences in environment of habitat and nature of ecology, each aquatic organism forms specific genetic structure of population adapted to the environmental condition. Marine organisms, in which genes are mixed widely, large scale genetic variation in a species are small and population structure is rarely recognized. Inversely, fresh water organisms living in limited habitat tend to make small genetic groups.

Sardine (*Sardinops melanostictus*) is a globally distributed cosmopolitan species. There are only five populations in the world, namely South Africa, Oceania, Chili, California and Japan populations (Okazaki *et al*., 1996). Inversely, Stumpy bullhead (Nekogigi *Pseudobagrus ichikawai*) is a natural monument species in Japan. This species is distributed only around Ise Bay, which lives in still stream and pools in river making small patch. Genetic difference was observed among populations of this species even though the distance among habitats of each population is several ten meters.

Giant mottled eel (*Anguilla marmorata*) distributed from the western Indian Ocean to the eastern Pacific Ocean have the widest distribution area among all anguillid eels ranging over two oceans. From this wide distribution, it is unimaginable that giant mottled eel form one large reproductive group by whole species and it was anticipated that several genetic groups existed in giant mottled eel (Fig. 2.15). Samples from various distribution areas were analyzed using mitochondrial DNA and microsatellite genes. As a result, the species was found to be composed of four distinct genetic populations, namely the North Pacific, South Pacific, Indian Ocean and Mariana population (Minegishi *et al*., 2008). Environmental characters of habitat and ecological nature of population influence not only visible morphological characters but also invisible genetic structures.

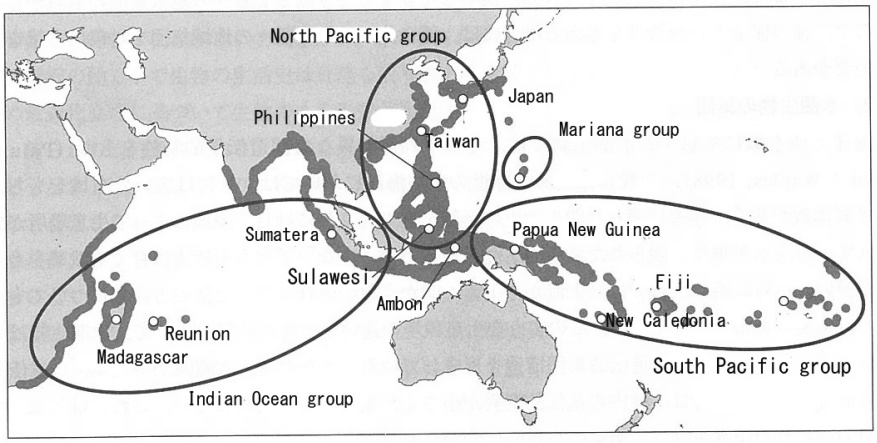

Fig. 2.15. Geographical distribution (shadow) and population structure (circle) of giant mottled eel. This species was composed of four populations in Indian and Pacific Ocean.

3) Speciation

When gene exchanges among populations in a species become rare, reproductive isolation is established and new species is born. This phenomenon is called speciation. In this context, term of species is based on currently recognized biological species concept. A species is group of individuals that can mate with each other and isolated from other groups in reproduction. Typical speciation processes are allopatric and sympatric speciation. In former process, reproductive isolation is caused in each locality by geographical separation. In latter process, reproductive isolation is caused in the same locality by some mechanisms such as sexual selection, food preference etc. that makes the mating between two populations impossible. Most speciations are considered to be allopatric. Richness of endemic species in isolated lake and island is produced by allopatric speciation. Famous example of sympatric speciation is Cichlids in African lakes. It was discovered that explosive speciation occurred in the lake after formation of the lake and the mechanisms of the sympatric speciation are studied.

Prior to speciation, establishment of population structure occurs as shown in the example of giant mottled eel. Speciation occurs when genetically different populations are formed in a species and eventually complete reproductive isolation is established between the groups. Current status of giant mottled eel is considered to be in the process of differentiation for future multiple new species. Recently, genes relating to the process of speciation are explored and molecular mechanisms of speciation are gradually being elucidated. When actual molecular mechanism keeping reproductive isolation will be clarified in the nearest future, theoretical models for process of speciation will be more realistic and predictive accuracy of biological response to environment change will progress.

4.3 Reproduction

1) Reproductive variations

Success in reproduction in order to make large number of offsprings is the biggest concern for animals. All organisms have been selected to maximize their lifetime reproductive success, though the reproductive patterns differ widely among species. Some species produce large number of eggs or infants. Other species make a few offspring. There are species which bring up offspring by utilizing large amount of energy and time for caring of eggs or infants after delivery, and some species which leave their offspring without any care after birth. When we compare lifetime spawning times, some such as chum salmon (*Oncorhynchus keta*) spawn eggs once in its lifetime (semelparity), though most of vertebrates spawn several times in their lifetimes (iterparity). Some large mammals and seabirds participate in reproduction for more than ten years.

2) Reproductive pattern of fish

Typical reproduction pattern of fish, as representative aquatic animal, may be summarized as follows. A female releases large number of small eggs (about 1 mm in diameter) in water, males discharge sperm, and the eggs are fertilized in water. Larval fish hatch out from the fertilized eggs floating in water for a while. The larvae grow up to alevin by absorbing the yolk, and the juveniles later obtain food on their own. However, some fish fertilize eggs in their body, and some bear alevin from the body after hatching out and larval development. As shown in this example, actually, fish employ various reproductive strategies. As spawning behavior, not all fish scatter the eggs in surrounding water. Some spawn adhesive eggs on water grass. Salmonids make hole for spawning. Three-spined sticklebacks (Itoyo, *Gasterosteus aculeatus*) make nest using aquatic plants for their fertilized eggs. Some guard fertilized eggs until hatching or take care by sending oxygen rich water. Further, mouthbreeder fish care for their offspring by carrying the offsprings in their mouth for several days during and after the hatching period.

The relation between egg size and number of ovarian eggs is also very diverse in fish. Ikura and Mentaiko, important fisheries food for Japanese, are the eggs of chum salmon (*Onchorhynchus keta*) and Alaskan pollock (Suketoudara, *Theragra chalocogramma*), respectively. There is no large difference in body size of the adults of the two species (about 1 m in standard length). However, the diameter of Ikura is about 7 mm and chum salmon spawn about 3000 eggs. On the contrary, Mentaiko is composed of small eggs about 1.2 mm in diameter and Alaskan pollock spawns 2 million eggs. As the theoretical explanation of the relation between egg size and number of ovarian eggs, theory by Smith and Fretwell is well known (Smith and Fretwell, 1974). Number of eggs produced is determined depending on the allocation of required amount of resource to individual egg. For the egg spawned, the larger egg can expect higher survival. Parents want to spawn maximum number of eggs in the size in which they can expect sufficient survival. Resultingly, number and size are determined to maximize sum of the adaptability of offsprings from one spawning of a female. The approach to compare the estimated relationship from this theory and data sets

obtained from actual fish species gives an important insight into their life histories.

Theoretical studies and its verification of reproductive performance are actively investigated, although fundamental information of reproductive performance have not been obtained in many oceanic fish. Spawning area of the Japanese eel (*Anguilla japonica*), commonly inhabiting the rivers and lakes in East Asia, has been enigmatic in fisheries science. After more than 70 years of patient field survey, newly hatched larvae of the Japanese eel were collected and the spawning area was pinpointed near the Suruga Seamount located in the southern West Mariana Ridge (Tsukamoto, 2006). However, spawning of Japanese eel is still not observed and their reproductive ecology is still not clear.

3) Reproductive pattern of reptiles and birds

Aquatic reptiles (sea turtle, sea snake, crocodile), some seabirds (penguin) and marine mammals are aquatic animals that spend most of their life in water. Except cetaceans (whale, dolphin) and sirenia (dugong, manatee) in marine mammals, others have to go ashore for reproduction. Reptiles protect their eggs from desiccation during the period of incubation by covering egg by egg shell and membrane. Nursing by parents is evolved in crocodile, though most of reptilians do not take care of eggs during and after incubation.

In birds, nursing by either one or both parents is common. Spheniscidae (penguins), the most adapted species for aquatic environment in avians, spend most of their life in sea, though they come ashore for breeding. They incubate eggs and nourish their juveniles going alternatively to the sea to get food after copulation and spawning. Burden for the parental care of offsprings is fairly high. As an example, in case of emperor penguin, that implement nursing on landfast sea ice in Antarctic sea in winter, their nursery ground is far from opening of ice to sea. The interspace of their alternation of care by couple is long. Paticularly, male penguins come to nursery ground early in breeding season and incubate eggs and take care of hatched chicks for 15 weeks in starved condition after spawning of female until female returns from foraging trip to sea. Body mass of male decrease from 40 kg to 2/3 of initial weight. Cost for parental care is very high, though life span of sea bird including penguin is long. Therefore, in the season when food or climatic condition is not suitable for reproduction, they commonly give up nursing for keeping their body conditions and try breeding next year.

4) Reproductive pattern of mammals

Females take care of her infants after parturition in mammals. This is a characteristic of mammals in which females have mammary glands. Even in platypus (*Ornithorhynchus anatinus*) which lay eggs, female lactates her infants. Generally female invest more energy for reproduction than that of male because of lactation. Phocidae (true seal) and Otariidae (eared seal such as sea lion and fur seal) implement parturition and lactate on land or on ice (Fig. 2.16). Duration of lactation in Otariidae is from several months to more than 1 year. Females of sea lion ocasionally go to sea for foraging and come back to nursery ground for lactation. They repeat their trips during the period of lactation (foraging cycle strategy). Duration of lactation of Phocidae vary from as short as 4 days (hooded

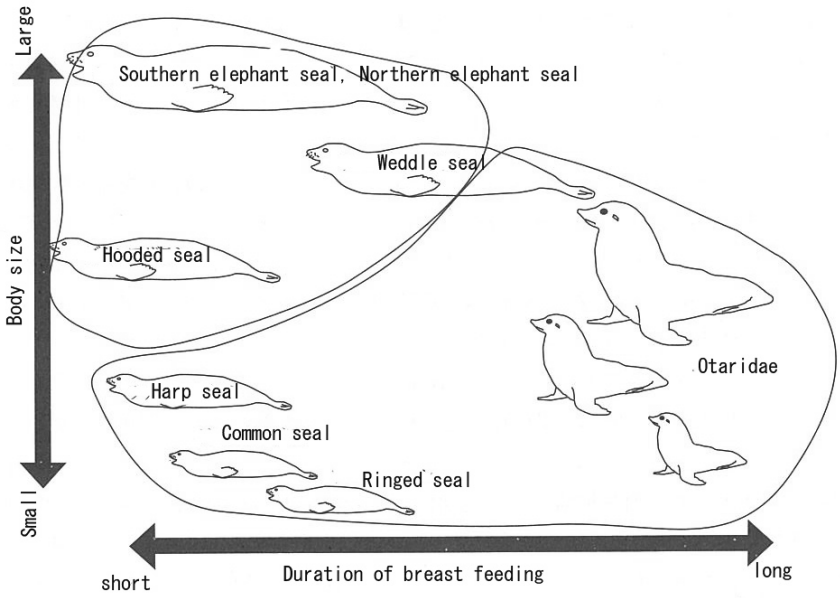

Fig. 2.16. Reproductive strategies of pinnipedia.

seal, *Cystophora cristata*) to as long as 8 weeks (Weddell seal, *Leptonychotes weddlellii*). Phocidae often do not feed during lactation and spend the period in fasting condition (fasting strategy). During this period they use their stored fat as energy source. The body mass of females decrease nearly to half of the original mass. Small seals and Weddell seal tend to have the characteristics of both the fasting and the foraging cycle strategies. They go to sea for foraging in later half of the period of lactation. In whales and sirenia, they give birth and lactate in sea without going ashore, some have long duration of lactation up to 2 years.

4.4 Feeding

1) Optimal foraging theory

In contrast to the plants which can produce energy by photosynthesis, animal should obtain energy by feeding for maintenance of the life, growth and reproduction. Feeding behavior includes all activities for obtaining, processing and digesting food. Foraging is a term used in wider meaning relating to the behavior that includes searching, hunting, catching and eating. For the survival and reproduction of their offsprings, animals living under natural condition must obtain quality food by spending minimum time and energy. Optimal foraging strategy is fundamentally to maximize the fitness i.e. survival rate and reproductive success. However, in empirical research, the strategy is evaluated by more direct indicators such as energy or time used, food amount obtained, or accumulation of

fat. In researches for optimal foraging strategy, various mathematical models have been proposed applying the fundamental dogma that animal decides its behavior to make benefit expressed as evaluation functions maximum in the constrained condition. The adequacy of the theory is usually confirmed by comparing theoretical prediction with result of observation.

It is difficult to verify the prediction by theoretical model in aquatic animals because of difficulty of direct observation. In some fresh water fish, aquatic insects and fish living in shallow sea, several empirical studies based on detailed observations exist. However, in large aquatic animals that live in the ocean and travel horizontally and vertically wide areas, we often cannot answer the most fundamental question "what do they eat". As a direct method to know the food habits of aquatic animals, stomach contents are surveyed by catching the animal. We can figure out the process of food shift depending on growth stage, season and habitat by detailed observation of stomach contents from the dissected fish. However, we have to know that data obtained by this method is only a time cross section data and it is not information of each individual but an average of the population.

2) Stable isotope analysis

Stable isotope analysis is a method to determine the diet of individuals and trophic relationships. We can investigate what an individual animal feeds during its life. Isotopes are different types of atoms (nuclides) of the same chemical element, each having a different number of neutrons. Stable isotopes are not radioactive. Because of the difference in number of neutrons, isotopes differ in mass number. Carbon has three isotopes, ^{12}C, ^{13}C and ^{14}C. Among these ^{12}C and ^{13}C are stable istopes. Nitrogen has ^{14}N and ^{15}N as stable isotope. Abundance ratio of heavier stable isotopes are small in natural condition. Usually the absolute abundance ratio of stable isotope is inconvenient for comparison. In general, the ratio (R_{sample}) of ^{13}C (or ^{15}N) to ^{12}C (or ^{14}N) in the sample is compared to the ratio of the international standard ratio ($R_{standard}$) using the equation:

$$\delta^{13}C,\ \delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 1000(‰).$$

When abundance ratio of heavier stable isotope in sample is larger than that of the standard, δ indicates positive value.

Using this method in studies of feeding ecology of aquatic animals, we compare the ratio of stable isotopes in tissue of the consumer and various potential prey items. In past knowledges, $\delta^{13}C$ shows little difference at each successive step up the trophic scale in a food web. Using this character of carbon stable isotope, we can identify the source of carbon by finding primary producer which has similar $\delta^{13}C$ value. $\delta^{15}N$ increases 3.4‰ at each successive step up the trophic scale in a food web. We can estimate trophic level of the animal in the food web by dividing the difference of $\delta^{15}N$ between primary producer and that animal by 3.4‰.

In the studies of feeding ecology, stable isotope analysis is used for not only invertebrate and fish but also for higher trophic level predators such as reptiles,

seabirds and marine mammals. Immature loggerhead turtles were considered to feed on planktonic organisms such as jelly fish and salps during migration in open ocean, while the adults fed on benthic organisms such as shrimps, crabs, and shellfishes in shallow coastal area of Japan. However, a study using stable isotope analysis of turtle eggs clarified that some adult females are estimated to feed on planktons in open ocean, and the others showed values indicating that they feed on benthos in shallow water. Since female loggerheads return to the same nesting area at about 2 years intervals, nesting females include both newly recruited individuals and remigrants. The above results were common in the recruits and remigrants, which indicates that they do not change their feeding habitats during the reproductive stage (Hatase *et al*., 2002).

3) Animal-borne recorder

Use of animal-borne recorders is now making it possible to record foraging behavior of animals under natural condition. The instruments are being miniaturized, though, pioneer studies were conducted in seabirds and marine mammals using relatively large units. Three-dimensional pattern of sperm whales (*Physeter macrocephalus*) diving deeper than 1000 m for foraging can be calculated from the time series data of depth, speed and direction. Odontocetes such as dolphins and most toothed whales have the ability to locate objects or preys by producing a directional beam of intense high frequency sound pulses and then listening for echoes from the targets. The sounds are named clicks and the range of the wavelength is about 15 kH–160 kH. This capacity is called echolocation. Some animal-borne recorders can record the sound produced by animals. When sperm whales are in a search mode, they produced a slow series of clicks, listening for echoes. Once they detected an echo from a target, they produced an accelerating series of clicks and quick turns and bursts were recorded at deepest part of their dives (Miller *et al*., 2004). Unfortunately, we do not have any information of preys that they captured at deep depths (1000 m). However, the prey capturing behavior of predators was recorded in more details than those of terrestrial animals.

Miniaturized animal-borne cameras are used for animals which forage in waters shallower than 40 m. A 70 g camera was deployed on the seabird weighing about 2 kg, for recording the foraging behavior and surrounding habitats used by European shag (*Phalacrocorax aristotelis*). These birds were observed to search for preys at the seafloor and probed into the sand with their bill, presumably to catch lesser sandeels. In contrast, birds travelled along the rocky bottom while searching for bottom-living fish such as butterfish (Watanuki *et al*., 2008). European shag flies out to foraging area and brings back the prey caught for feeding it to chicks in their nests. This feeding pattern is named central place foraging. Amount of food caught was estimated to be larger in longer foraging trips than those in shorter foraging trips (Sato *et al*., 2008). This means that they shortened staying time in foraging area when distance of the trip was short and they stayed longer period there in the case of long trip.

It will be possible in the nearest future to verify theoretical predictions about optimal foraging behavior of aquatic animals if development of instruments

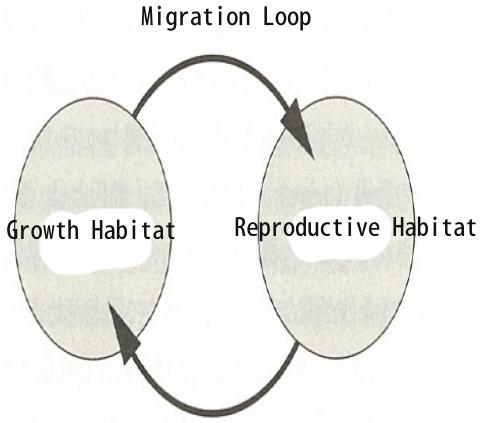

Fig. 2.17. Migration loop model by connecting the typical reproductive habitat and growth habitat of migratory animal.

provide information on contents and amount of preys and time and energy for foraging.

4.5 Migration

1) Migration loop

Many aquatic animals shift their habitat with growth stage or changes in environment. This is called migration. In short, migration is habitat transition among multiple habitats. In many cases, migration means the behavior of animals shifting their habitats from one place to another at a particular period of their life or particular season, and returning back to the original place at a later stage in life (Fig. 2.17). Essence of life is reproduction and growth. The places for reproduction and growth have important meaning in the life history. When the places for reproduction and growth for a species is separated into different places, the species starts migration. Therefore we can define most migrations as transitions between reproductive place and nursery area. We call some migration as feeding migration, optimum temperature migration or spawning migration depending on the purpose of migration. However the purpose is different between outward and homeward migration. These terms express only a part of the whole migration.

A circle connecting the reproductive place and nursery area is called migration loop showing typical migratory pathway of species or population. Commonly, reproductive place or spawning area is narrow enough to increase the encounter rate for mating partner, while nursery area is wide to ease the competition for food and home range. Migration loop is unique for a species or a population. When deviation of the migration loop occurs in a species or population, reproductive isolation is induced and speciation or population differentiation starts. Migration loop is thus an expression of the life history of

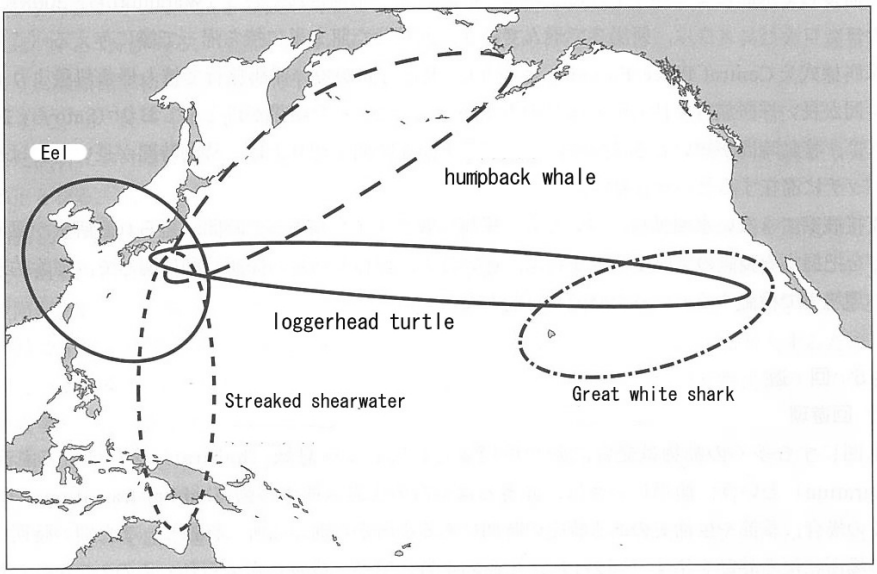

Fig. 2.18. Migration loops of various aquatic animal in North Pacific Ocean. Examples of mammal (hampback whale), sea bird (streakes shearwater), sea turtle (loggerhead turtle), and fish (eel and great white shark).

organisms and we can superimpose the life history on the migration loop. Outward route from reproductive place to nursery area generally is the way for larvae and juveniles with low physical capacity. Their travels are dispersion with passive transportation by current and winds. Therefore, destination is not previously decided and the nursery area produced as the result of dispersion is wide. On the other hand, homeward routes are for adults with well developed capacity for locomotion and orientation, who can accurately reach their reproductive destinations. Figure 2.18 shows several typical migration loops of aquatic animals.

2) Requirement of migration

There are three requirements to complete the migration with safe arrival to destination. First of all, enough capacity of locomotion to travel the distance to the destination is required. In case of fish and whales, they need enough swimming capacity and birds need enough flying capacity. Secondly, they need navigation capacity that includes capacity of orientation and recognition of destination. It is not just sufficient to have both of the two capacities, but also an internal drive to induce the migration is essential. In ethology, this drive is defined as an internal factor that induces the animal to start a behavior. However, drive is produced in the brain and it has not been physiologically clarified yet. Migration starts and is completed when three requirements namely capacity of locomotion, ability of navigation and drive are satisfied.

Table 2.2. Migration types of fish.

Migration type	Spawning ground	Species
Oceanodromy	Sea	Tuna, Saury, Yellowtail
Potamodromy	Fresh water	Pale chub, Isaza (*Gymnogobius isaza*)
Diadromy		
Anadromy	Fresh water	Chum salmon, Wakasagi smelt, Ice goby
Catadromy	Sea	Eel, Ayukake (*Cottus kazika*), Roughskin sculpin
Amphidromy		
Freshwater type	Fresh water	Ayu, Yoshinobori (*Rhinogobius* spp.), Small egg type sculpin
Marine type	Sea	Mullet, Sea bass

Capacity of locomotion can be evaluated by measurement of the body fat, endurance of swimming and oxygen consumption in circulation aquarium. For capacity of navigation, solar compass, magnetic compass, esthesiophysiology of sense of smell and other behavioral characteristics are studied. Navigation system of chum salmon (*Oncorhynchus keta*) when they return to Japan is summarized as follows. Salmon recognizes direction to return to Japan approximately by solar compass, then they travel using magnetic compass to find their way correctly. Finally, they use sense of smell to find the native river where they were born. It was observed that the drive in migratory birds is prolactin, while thyroid hormone was suggested as the possible drive in fish in the research paper reporting that blood thyroxin content is higher in migrant juvenile ayu (*Plecoglossus altivelis*) that swim upstream than those swimming downstream. However, it is still doubtful whether or not thyroxin has a principal function in migration as the drive. Future studies integrating the behavior science and physiology are needed.

3) Migration type

Migrations of fish are classified into various types (Table 2.2). The migration performed only in ocean is termed oceanodromy. What is completed in freshwater area such as river and lake is potamodromy. On the other hand, diadromy is migration between sea and rivers and include migration of several important species such as salmon, eel and ayu. Diadromy is further classified into three sub types. Anadromy is migration in which fish go upstream, while catadromy is migration in which fish go downstream for spawning. Migration without relation to spawning is amphidromy. Amphidromy is further divided into fresh water type amphidromy and marine type amphidromy depending on whether fish spawn egg in fresh water or sea water, respectively. Anadromy includes migration of masu salmon (Sakuramasu *Oncorhynchus masou*), ice goby (Shirouo *Leucopsarion petersii*) and sturgeon. Eel, fourspine sculpin (Kamakiri, *Cottus kazika*) and roughskin sculpin (Yamanokami, *Trachidermus fasciatus*) are catadromous fish.

Ayu and lake goby (Yoshinobori, *Rhinogobius brunneus*) are amphidromous fish. Anadromous fish species are mainly distributed in high latitudes, while many catadromous fish species are distributed in lower latitudes. Amphidromous fishes are intermediate types between anadromy and catadromy, and distributed from tropical to temperate areas at middle latitudes in both hemispheres. About 150 species are known as diadromous fishes. Their ratio in total fish (over 25000 species) is less than 1%.

Sometimes landlocked type appears in anadromy and fresh water type amphidromy species by the blockage of their path to sea. Small ayu (Koayu) in Lake Biwa and Miyabe dolly varden in Shikaribetsu Lake are examples of landlocked type. In these cases, fish migrate to river and lake as an alternative for sea. It should be interpreted as variation of diadromy not as potamodromy. In several diadromy fish, some individuals do not migrate to sea. As shown in these examples, migration type is flexible. Variation of migration type in a species results in polymorphism of life history. As an example, masu salmon is an anadromous fish, but the juvenile of masu salmon go downstream to the sea in season of melting snow during the next spring after their birth. Males which grow rapidly do not show downstream migration to the sea in the season and remain in the river as resident type (Yamame). They participate in reproduction as early matured male in next autumn. Eel is a catadromous fish species. Most of them migrate upstream at juvenile stage and grow in freshwater habitat. However it is known that some eels do not migrate upstream throughout their life and continue to grow in coastal waters and estuary (Tsukamoto *et al*., 1998). These are termed as sea eels. These are example of derivation of multiple migration types and polymorphism in life history. Clarification of the mechanism of occurrence of resident type may give us a clue for the question why fishes migrate.

4) Evolution of migration

It is a fundamental question, how the large scale migrations such as in salmon and eels, which migrate distances extending over several thousands of kilometers was established. Probably, their migrations initially began as a small scale migration and have evolved into larger scale with time (Fig. 2.19). Salmon originated in fresh water in higher latitudes. They started small scale migration within fresh water areas and extended their tours for foraging from river (reproductive habitat) where food and predators were poor. Eventually, they found marine habitat as nursery areas. Expanding their migration loop from fresh water to estuary, and then to ocean, they evolved the present migratory path which covers a distance of several thousand kilometers. On the contrary, eel originated in low latitudes, tropical regions as marine fish. They invaded fresh water area where food organisms were rich by chance and their growth rate increased. As a result, their productive success increased and their catadromous behavior was established. Driving force for establishment of migration loop in both the species was the difference of productivity between river and ocean. It is considered that existence of resident types of salmons and sea eels are presenting their ancestral behaviors.

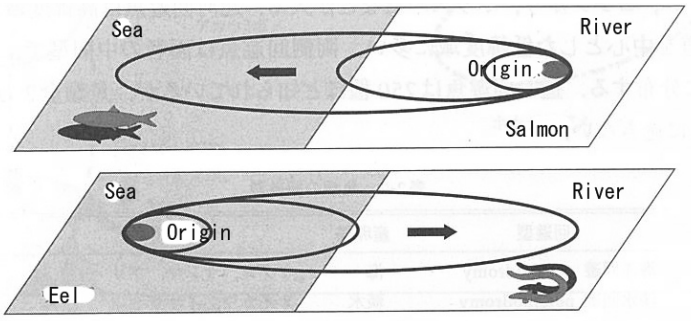

Fig. 2.19. Evolution in migration of eel and salmon. Salmon expanded their migration loops from fresh water to sea. Eels expanded their migration loops from sea to fresh water.

4.6 Buoyancy and behavior

1) Buoyancy

One of the important characteristics of aquatic animals is that they have buoyancy for balancing the body weight. All animals living on the earth experience the force of gravity acting vertically downward. Amplitude of the gravitational force is weight (kg m/s^2) that is equal to product of mass (kg) and acceleration of gravity (m/s^2). When animals move horizontally, they have to support their weight by lifting force produced by wings in the case of flying animals or by two or four limb in the case of terrestrial animals. However, in case of aquatic animals which mainly live in water, they receive buoyancy vertically upward that is equal to the weight of liquid pushed away by body (Fig. 2.20).

$$\text{Buoyancy} = (m/\rho_t + V_{air})\rho_w g.$$

Where m is mass of the animal (kg), ρ_t is density of animal body tissues (kg/m^3), V_{air} is volume of air in the body of animal, ρ_w is the density of liquid surrounding the body of animal (kg/m^3), g is gravitational acceleration of the earth (m/s^2). Average of gravitational acceleration on the surface of the earth is 9.806. The value in polar region is higher than that at equator. Density of liquid varies with salinity, temperature, pressure and so on. For the animals living in sea, ρ_w = 1,026 (kg/m^3), for the animals living in freshwater, ρ_w =1,000. When the density of body tissues, ρ_t is equal to density of surrounding water, ρ_w, buoyancy that works upward equilibrates to force of gravity that works downward without air in the body (V_{air} = 0). This condition is neutral buoyancy. Animals which attain neutral buoyancy do not need energy for maintenance of the depth. They can allocate their energy efficiently to horizontal movement. Actually, in comparison of energy cost (J/kg/m) for transportation of unit material (1 kg) for unit horizontal distance (1 m), swimming is most cost effective and the second is flying. Walking is the last.

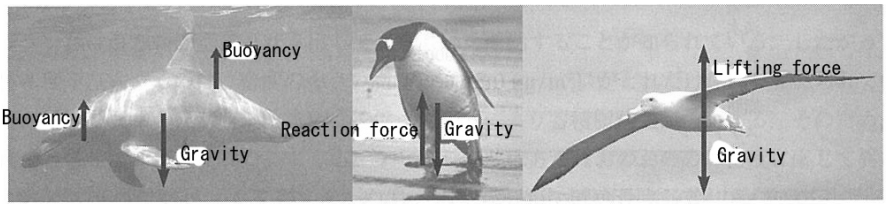

Fig. 2.20. Forces acting to animal during their horizontal movement. Swimming Indian Ocean bottlenose dolphin, walking gentoo penguin and flying wandering albatross (provided from Mai Sakai).

2) Way of fish

Densities of body tissues such as bone (ca. 2,000 kg/m^3) and muscle (ca. 1,060 kg/m^3) are larger than fresh water and seawater (Table 2.3). Therefore, bodies of animals sink in water. Animals need several ways to attain neutral buoyancy in water. A method commonly observed in teleost, the representative of aquatic animals, is storing air in bladder. Shapes of bladders differ among species, though the volume ratio of bladder to whole body is about 4% in marine fish and 7% in fresh water fish. The reason for the ratios is that the density of body tissue of fish which has a swim bladder is 1,070 (kg/m^3) whether it is fresh water fish or marine fish. That means required volume of air to get neutral buoyancy to support body weight which is 4% heavier than seawater or 7% heavier than fresh water is 4% or 7% of body volume, respectively.

There are disadvantages in obtaining neutral buoyancy using swim bladder. One big disadvantage is that the method is not fit for vertical movement. Volume of gases inversely relates to pressure. Ten meters change in depth makes a difference of 1 barometric pressure. Fish that have swim bladder cannot regulate density promptly in response to the changes of depth. Some aquatic animals solve this problem by storing the air in containers with hard wall. Cuttlefish have a calcified internal structure called cuttle bone and store air in it. Shell of nautilus is separated by the dividing walls, and each chamber is filled with gas. Buoyancy organs of cuttlefish and nautilus are not affected by changes of pressure caused by change in depth. They can thus easily repeat vertical movement.

The other disadvantage of having air in the body is detection by predators. Swim bladder reflects the sound because of large difference in density between the water and body tissues. The fish therefore cannot escape from the “eyes” of odontocetes with a capacity of echolocation.

Some fish do not rely on gas to obtain buoyancy. Elasmobranchii have no bladder. Some of them have large volume of the liver instead of the bladder. The liver often contains large amount of squalene (a fat belonging in terpenoids). The density of squalene is very low (860 kg/m^3), and the large liver thus contributes to make total body density close to surrounding water.

Some fish has heavier density than seawater. Skipjack tuna (Katsuo, *Katsuwonus pelamis*) do not have swim bladder. The density (1,090–1,097

Table 2.3. Body density or body tissue density of various aquatic animals.

Category	Species	Density (kg/m^3)	Remarks
Seawater fish	Flounder	1.073	Without bladder
	Skipjack tuna	1.090–1.097	Without bladder
	Ocean sunfish	1.027	Without bladder
	Brown hakeling	1.070	Measured after depression of bladder
Freshwater fish	Japanese dace	1.075	Measured after depression of bladder
	Seema	1.063	Measured after depression of bladder
	Chinese sturgeon	1.060	Measured after depression of bladder
Cephalopoda	Squids	1.055–1.075	Without bladder, after removal of shell
Birds	Penguins	1.026	
	Phalacrocoracidae	1.030	
Seawater		1.026	
Freshwater		1.000	
Bone		ca. 2,000	
Muscle		ca. 1,060	
Lipids		ca. 930	
Saualene		860	

kg/m^3) is much heavier than seawater. Therefore they swim continuously all the time expanding both side of pectral fins horizontally to get lift force and keep their depth. Density of benthic fish (1,060–1,070 kg/m^3) like flounder and flat fish is heavier than seawater. This is related to their life style of staying on the sea bottom.

3) Way of turtle

Similar body density to fresh water or seawater contributes for the efficiency of horizontal swimming. However, various ways are needed for air breathing animals to maintain neutral buoyancy in water because they are keeping air inside of the body. Sea turtles are air-breathing animals and dive under the water keeping air in their lung. Adult females of loggerhead turtle spend time in the sea near their nesting grounds. They do not drift at the sea surface but dive to more than 10 meters depth and stay there for 20–40 minutes and swim up to the surface for breath. They repeat dives and subsequent surfacing. When they stay at the mid layer without swimming, they are gradually ascending with slow vertical speed (<1 cm/s). From this the turtles achieve neutral buoyancy during the gradual ascent phase. In a field experiment turtles were equipped with weights and the weights were released at a depth to decrease their body density artificially. The turtle changed the residence depth deeper after release of weight. This indicates that the turtle does not control their body density by keeping a volume of air equivalent to the weight in lung to attain neutral buoyancy. They presumably remain at a particular depth where the total body density including air in the lung balances the density of seawater (Minamikawa *et al.*, 2000).

4) Way of penguin

Seabirds such as penguins and cormorants have similar body density to seawater (Table 2.3). However, the buoyancy exceeds the weight when they are near surface layer because they have air in their feather and body. Moreover, it is known that penguin start their dive inhaling air in their respiratory system. They move wings with high frequency at the beginning of dive to descend against buoyancy. The wing stroking frequency decreases while descending. They can get neutral buoyancy in deeper layer because of high water pressure. They can search and capture preys at several hundred meter depth. In surfacing, they stop wing beat at several tens meter depth. After that, penguin swim in surface by gliding in the balance of force of buoyancy upward and "lift" force downward on flippers like flying birds gliding in air using gravity and lift force produced by their wings (Sato *et al*., 2002).

5) Way of seal

It is known that seals start diving after exhaling the air. Consequently, their total body density is determined by accumulated volume of fat with low density (ca. 930 kg/m^3). Accumulated body fat in a female seal decreases rapidly during lactation by energy loss for her pup. As a result, total body density differs between early and late lactations. Swimming gaits of seals differ depending on the total body density. Fat individual accumulating much fat use the flippers more frequently for descending than for ascending because its buoyancy exceeds the gravity. Inversely, thin individual, with total body density higher than seawater, descend to several hundred meter depth without stroking flippers and ascend to the surface using its flippers (Sato *et al*., 2003).

(Katsumi Tsukamoto and Katsufumi Satoh)

CONCLUSION

As mentioned in the initial part of this chapter, primeval form of life was born in the sea and lives have evolved progressively and explosively in aquatic environments. Whether it is terrestrial or aquatic, most of the variations in organisms today have been nurtured in the sea. The sea was a maternal environment for primitive organisms and seawater is sometimes considered to be similar to the amniotic fluid. It is not an accidental coincidence that the body fluid of marine invertebrates that evolved in the sea is similar to seawater. When we take vertebrates as examples, it can be supposed that they expanded their habitat from aquasphere to land, developing their physiological mechanisms for adaptation to new environments. Ancient fish lived in the sea and invaded the brackish and freshwater areas to evolve to Osteichthyes, and a portion of them (Sarcopterygii) succeeded in moving from freshwater area to land. However, the evolution of vertebrates is not only a simple way from sea to river and river to land. There exist many marine fish that went back to the sea from river, and marine mammals that made their way back to the sea from land. These differentiations have occurred repeatedly in the process of evolution, leading to the biodiversity observed today.

Those vertebrates that went back to the sea had developed their body, and the sea could not be amniotic fluid for them. They had to get some new mechanisms to adapt to seawater. The diversity was produced in the complicated relationship between changes in environments and development of physiological mechanisms. Ecology and physiology tend to be thought as completely separated biological phenomena. However, when we think back of the history of evolution, ecology and physiology of all living organisms are closely related in the temporal axis of evolution and enables the diversity and coexistence of species of organisms.

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