Manabu Yoshida
Juan F. Asturiano *Editors*

Reproduction in Aquatic Animals

From Basic Biology to Aquaculture Technology

Springer

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Preface

Even though there are many animals in terrestrial habitats, there is great biodiversity to be found in aquatic ecosystems. Furthermore, aquatic animals show various reproductive systems: many animals perform external fertilization, others show internal fertilization without mating, some are viviparous, etc. This means that the reproduction systems of aquatic animals are highly diverse, and they are excellent models for studying adaptive evolution and species-specificity of fertilization. In addition, many aquatic animals such as fish, crustaceans, and mollusks are important as fishery and aquaculture resources. Nevertheless, their reproductive systems are also diverse, resulting in difficulties in cultivation, especially in the production of juveniles. Thus, comprehensive knowledge of the reproductive systems of various aquatic animals will help us understand the systems of each animal, resulting in breakthroughs in the research areas and aquaculture technologies. However, only a few books overviewed the reproductive systems of aquatic animals from invertebrates to fishes since many researchers focused their animals of interest. Therefore, our aim with this book was to overview the various reproductive systems of aquatic animals.

The idea for this book was initially conceived in the International Symposium on "AQUAGAMETE: Reproduction of Aquatic Animals" held in the Joint Meeting of the 22nd International Congress of Zoology and the 87th meeting of the Zoological Society of Japan, which was held from 14th to 19th November 2016 in Okinawa, Japan. Three years have passed since the initial planning, and we have developed the book ideation. In order to introduce up-to-date knowledge on the reproduction systems of various aquatic animals from basic biology to aquaculture technology, we invited up-and-coming researchers to contribute. This book consists of 17 chapters and a foreword that details the history of spermatology to be read before the main chapters. Finally, the book covers the reproductive systems of both sperm and egg in cnidarians, annelids, arthropods, mollusks, echinoderms, ascidians, elasmobranchs, teleosts, and amphibians. Four chapters focus on the technological and aquaculture aspects, in particular relating to fishes.

This book is designed for people who are neither experts/well-read/knowledgeable in the field of reproductive biology nor aquaculture. The assumed readers are graduate students and postgraduates in biology and agricultural sciences and also non-academics who are interested in the field.

We hope that this book will be useful to many readers, particularly scientists and technicians in the field of reproductive biology and fishery science area.

Finally, we would like to thank all the authors and contributors who made this book a reality.

Miura, Japan
Valencia, Spain
September 2019

Manabu Yoshida
Juan F. Asturiano

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Foreword: A Brief History of Spermatology

Jacky Cosson

This foreword mostly aims to introduce, from a historical stand point, how the notions of gametes emerged, and to describe the tortuous approach by the pioneer scientists who first discovered and explored the functions and structure of aquatic animal gametes and their interactions. Sperm cells most likely became of interest to scientists due to the fact that they hold the key to life and have an incredible ability to move, in spite of their small dimensions.

It is commonly acknowledged that *spermatology* is a scientific domain dealing with the structure and function of spermatozoa. For this reason, it can be supposed that the history of spermatology began in 1677 with Leeuwenhoek's description of the spermatozoon, the male entity, responsible for animal procreation and rendered visible for the first time through his microscope. Therefore, it is considered that spermatology starts at this date as biologists enjoy to attribute a structure to a function. For obvious reasons, this foreword mostly covers the last three-and-a-half centuries, if we accept Leeuwenhoek to be the "inventor" of spermatozoa.

It is out of the present topic to discuss the history of human reproduction, in its medical aspects. Instead, in this book, we will concentrate more specifically on the gametes of aquatic animals with our main aim being to trace how the study of aquatic animals can be so important in the understanding of the mechanisms of gamete interaction.

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Let Us Go Back to/Return to the Seventeenth Century

Long before the identification of the individual elements later called “spermatozoa,” Leonardo da Vinci, by reference to Hippocrates, wrote: “The origin of our semen is located in the brain and in the lungs and it is in the testis of ancestors that the final mixing occurred.” This premonitory statement contains quite a lot of veracity that modern science would finally establish as true: the **brain** definitely contributes “psychologically” to the delivery of sperm to the female for reproduction; the **lungs** constitute an organ making a large use of cilia which are homologue to flagella in their constitution and the **testis** contributes to the efficient mixing of the ancestor’s genomes during the meiotic process of spermatogenesis.

Already in 1623, L. Gardinius (L. du Gardin) assumed that there were fertilizing particles in male semen, but it wasn’t until 1677 that they were in fact observed by the human eye and described. However, the priority comes to Antonie van Leeuwenhoek, who in that year found spermatozoa in the semen of fish, frogs, and mammals, thanks to one of his rudimentary microscopes made of a single spheroidal lens. His publication to the Royal Society *De Natis E Semine Genitali Animalculis* (1678) remains famous and frequently cited.

In his letter (1677), he described that there are “living animalcules” in human semen: “The size of animalcules is ten thousand times less than a water louse. They move like a snake or like an eel swimming in water, have globule at the end, and are very flexible.” He supported his letter with a drawn picture of what had been seen under the microscope (see Fig. 1). He continued to observe many other animals in his later works and showed that the animalcules were produced by the testes. Leeuwenhoek knew his discovery was important to the understanding of reproduction and insisted that “a sperm cell was the only thing that made an embryo, and that the egg and uterus merely nourished it as it grew.” At that time, the prevailing view on reproduction was that the embryo grew from the egg alone, after the semen added a “volatile spirit” to spark its development.

In the context of his epoch, he called them animalcula and interpreted them in Aristotelean terms that could be considered nowadays as quite male chauvinist. “Life comes from the male whereas the female produces nutrition for it in the egg.” Two sentences from Leeuwenhoek’s letter read as follows: “What I investigate is

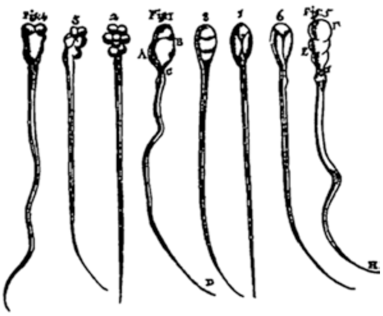

Fig. 1 Drawn picture of spermatozoa by Leeuwenhoek. (From Leeuwenhoek, *Phil. Transact. Roy. Soc.,* 12: 1040–1046). This figure is Public Domain

only what, without sinfully defiling myself, remains as a residue after conjugal coitus. And, if your Lordship should consider that these observations may disgust or scandalize the learned, I earnestly beg your Lordship to regard them as private and to publish or destroy them, as your Lordship thinks best." Evidently, the Royal Society did not regard the topic to be indecent as they published the letter. One hundred years later, scientists were perhaps more prudish, as exemplified by this statement by Herman Schützercranz, physician of the Swedish king: "You cannot and ought not know whatever happens at fertilization," which denotes a lack of openness for a medical doctor. Whereas Leeuwenhoek's famous letter undoubtedly is the first description of spermatozoa, the events around his discovery are more complex.

According to Cole (1930), Leeuwenhoek's letter to the Royal Society in November 1677 wasn't published until 1679 and was preceded by a communication to the Académie Française (French Academy) by Christiaan Huygens, dated July 30th 1678. Huygens describes in this communication small animals similar to tadpoles in the semen of a dog. His comments, after translation into English read as this premonitory sentence: "This discovery seems very important and should give employment to those interested in the generation of animals," predicting the advent of *artificial propagation of animals*. Nevertheless, in a letter dated March 26th 1678, Huygens admits to having seen and read Leeuwenhoek's letter of 1677. In August 1678, Nicolas Hartsoeker published a letter in the Journal des Savants (drafted by Huygens because of Hartsoeker's inability to write in French), in which he describes animals similar to little eels in the semen of the cock; the latter differed thus in shape from the tadpole-like animalcula of the dog. It is amazing to note that this is the first example of comparative spermatology! In conclusion, two investigators published data on spermatozoa in the year 1678; both did so during the time span needed for Leeuwenhoek's letter to be translated from Dutch to Latin (in three different versions) and printed by the Royal Society. Such huge delay in the transmission of information seems incredible in today's internet era!

Furthermore, Leeuwenhoek himself attributed the discovery of the animalcula to a certain "Dominus Ham," that is Mr. Ham, a person who never published anything on semen nor its content. This man is commonly believed to be Ludwig van Hammen of Danzig, but according to Cole (1930) it is more likely to be Johan Ham, a Dutchman from Arnhem, born in 1650 or 1651, a student at the time of his discovery, and who later became a Doctor in Arnhem. Apparently, Johan Ham was the first person to see mammalian spermatozoa and Leeuwenhoek was informed by him; thus, Huygens became the first to publish data on mammalian spermatozoa and Hartsoeker the first to publish data on avian spermatozoa.

Leeuwenhoek later studied and described spermatozoa from other classes of animals.

All observations on animalcula were met with great interest. Robert Hooke (the first man to use the word "cell") thus had to demonstrate the existence of spermatozoa to King Charles II, who expressed his delight to see the animalcula. Yet, the significance of the animalcula remained obscure. To some philosophers, the huge number of animalcula made no sense for any idea of conception. According to

Leeuwenhoek: "Eventually, thousands of those animacules were agitating in a tiny space of a sand grain size." And after all, Leeuwenhoek had found a multitude of small creatures when he examined scrapings from the teeth (probably bacteria). To others, the existence of small swarming creatures validated the idea that offspring comes from the male. The man-like homunculi depicted by Hartsoeker and Dalenpatius are famous and classically used as illustrations in Fig. 2.

Some investigators went so far as to claim that they could see horse animalcula in horse semen and donkey animalcula in donkey semen and that the donkey animalcula had longer ears. Still others claimed that they could see male and female animalcula and even mating and childbirth among these!

The humunculus also seemed to confirm the preformation concept, that is, the belief that everything is present in the seed although in a miniaturized form and that development merely consists of an increase in size. The preformationists could either be animalculist or ovist; the latter believed that the animal is already formed in the egg. An ovist would thus claim that he could see the chick in the unfertilized egg. The preformationist theory has the merit that it explains original small men were contained already in the organs of Adam and Eve. It also has the consequence that the human race will become extinct when the stock of seed is exhausted.

The ovist school can be said to have begun with the publication by Harvey in 1651 of his influential book *De Generatione* with its prophetic quote on the frontispiece "Ex ovo omnia," "all (animals) from eggs." Harvey thus believed that the male (semen) played no part in the formation of the fetus.

During an experimental dissection of a mated roe deer, he could find no spermatozoa in the uterus. The debate between believers in epigenesis (i.e., the embryo and its parts undergo differentiation of initially undifferentiated entities) and believers in preformation went on for several centuries. If a vote had been taken in the seventeenth century, the preformationists would have won by a wide margin although some thinkers, such as Descartes, were supporters of epigenesis.

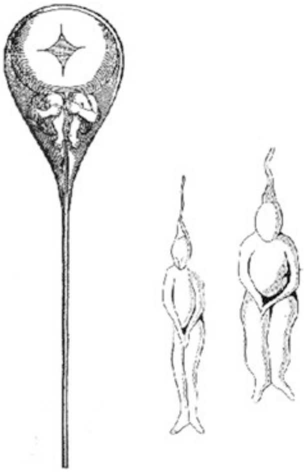

Fig. 2 Drawing of homunculi in sperm by Hartsoeker. (Left: from Essai de dioptrique 1694) and by Dalenpatius (right: from *Nouvelles de la République des Lettres*, 1699). This figure is Public Domain

The structure and meaning of the animalcula was also debated at the end of that century. P. Dionis (1698) asked for further inquiries as he believed that they are formed by minute fibers in semen exposed to air. M. Lister (1698) also inquiring about the origin of the seminal animalcula concluded (free translation from Latin): "Homunculi in great numbers: when I reflect upon it, I leave it to be cared for by others, to me it is a fairy tale."

Leeuwenhoek's importance as a microscopist is widely recognized. Less known is the fact that he also tried to investigate inheritance by an experiment. He mated a gray rabbit buck with a white rabbit doe and noted that all the young were gray—another "proof" of the validity of the "seed-dominant" concept. Evidently, he did not perform—or at least did not report—a control, that is a cross between a white male and a gray female.

Continued in the Eighteenth Century

The uncertainty continued into the eighteenth century. E. F. Geoffroy and C. du Cerf (1704) observed numerous, but non "fully mature" animalcula in boys, well developed and active ones in adults, few and feeble ones in old men, and no animalcula in sterile individuals. They would conclude that animalcula are needed for reproduction and can hence be considered the founders of *andrological spermatology*. Other opinions also prevailed; M. Schurig (1720) in his *Spermatologia Historico Medica* considered the animalcula to be only an "active portion of the semen agitated in a viscid mass." A. Vallisnieri (1721) and P. L. M. de Maupertuis (1744) admit that animalcula exist but claim that they have no direct relation to reproduction: they are *entozoa* (tapeworms) and keep the semen fluid. The philosopher J. M. Gestner (1737) accepts seminal animalcula as a fact but claims that their discovery is to be credited to Hippocrates who, according to Gesner, was able to see them by his "enormous force of reason" rather than by using a microscope!

During this eighteenth century, the great naturalists were against the idea of animalcula playing a role in reproduction. Carl Linnaeus (1746) believed them to be inert "corpuscules," P. Lyonet (1751) to be "entozoic" parasites, G. L. L. Buffon (1752) and J. T. Needham (1749) to be aggregates of living organic molecules derived from the mucilaginous part of the semen. The entozoa hypothesis seems to have been very popular, and several attempts were made to include them in the classification of animals: according to Hill (1752), the animalcula are *infusoria* (protists) and deserve a genus name, *Macrocercus*, related to Vorticella and Euglena. Spallanzani (1776) ranks them among the animals and Blumenbach (1779) again among the "infusorial" animals, with the genus and species name *Chaos spermaticum*. Cuvier (1817) classifies them in the genus *Cercaria*. Bory de Saint-Vincent (1827) similarly regards them as belonging to the family *Cercariae* and invents a new genus name, *Zoospermos*. Carl Ernst von Baer (1827) modified that name to *Spermatozoon*, a word that caught on and is still in use today.

It was inevitable that artificial insemination would sooner or later be performed and that the outcome of such studies would influence the thinking on the role of spermatozoa. The first such experiment in Europe was performed by M. Jacobi in 1763, when he discovered how to fertilize fish eggs with milt. It must be noted that the artificial propagation of fish had been developed in China many years before by Fan Li (born in 517 B.C.), with no understanding of the fact that sperm cells were the fertilizing elements present in milt. Not long after Jacobi, Lazzaro Spallanzani succeeded in performing artificial fertilization not only in fish and frogs but also in a bitch (Gabriel and Vogel 1955; Castellani 1973; Sandler 1973). He also filtered the semen in 1784 or 1785 and noted that frog eggs were fertilized by the seminal fraction that could be squeezed out of the filter paper, but that no fertilization occurred when the filtrate was added to the eggs.

Experiments of this kind would eventually become decisive to our understanding of the role of spermatozoa. Yet, Spallanzani himself did not draw the correct conclusion. He had previously performed some experiments where he had added frog semen, which he supposed was devoid of spermatozoa, to eggs and these had then developed. He concluded from his various experiments that it is the "seminal aura" outside the animalcula that is capable of fertilization. It was only much later that this type of experiment was repeated and that the correct conclusion was drawn. The priority thus goes to Povost and Dumas, who in 1824 published their data and interpretations. The technique of artificial insemination may have a much older history however. There is a rumor that an Arabic person, named Hegira, in 1332 had a stallion ejaculate on a cloth that he then inseminated in his mare's vagina and that a foal was born after the expected period (Adlam 1980). The funny part of the story is that the stallion was not his own and the semen was a theft from a competitor and was performed in the darkness of the night by exposing the stallion to the smell of a mare's vaginal secretion. There may even be records of artificial insemination in the Talmudic books. These records may, however, refer to legends rather than to actual experiments.

Then in the Nineteenth Century

Not long after Spallanzani's experiments, artificial insemination had even been practiced in humans (reviewed in Adlam 1980). The first records are from the end of the eighteenth century. More important from a scientific point of view were the observations performed by Koelliker in 1844. He examined semen from many species of marine animals and also performed some insemination experiments. He could, among others, draw three fundamental conclusions: (1) semen of all animals contain spermatozoa, (2) these are formed from cells in the testes, and (3) spermatozoa have to come into contact with eggs for a fertile union to occur.

Fifteen years later, Koelliker could also conclude from more insemination experiments that it is the sperm head that is essential for fertilization to occur and after yet another 20 years, Hertwig (1892) made a statement in his doctoral thesis that made him famous: "Fertilization is the union of sexually differentiated nuclei." (Die Befruchtung beruht auf die Verschmelzung van geschlechtlich differenzierten Zellkernen.) By this definition of "fertilization," the important events in reproduction are those which involve the nuclei and their contents, a concept which has been fully verified by cytogenetics, the branch of biology that developed at the beginning of the last century as a result of the fusion of genetics and cytology.

It is interesting however to note that Hertwig advanced his thesis on the fertilization events without having been able to see fertilization occur. The first person to watch sperm entry into an egg (that of a sea urchin) actually was Hermann Fol during experiments conducted in the *Zoological Station in Villefranche-sur-Mer* (France). Two of the publications of Fol (1878, 1879) contain the very first description of the ability of a spermatozoon to fertilize and penetrate the egg of an echinoderm. The first person to see a mammalian egg was C. E. von Baer (1827) and the priority of transferring fertilized mammalian eggs and embryos from the biological mother to a surrogate mother (a rabbit doe) belongs to an Englishman, Walter Heap.

Finally, it was only in 1870 that the observations of Schweiger-Scidel and La Valette allowed the spermatozoon to acquire the status of fertilizing cell and these notions are confirmed etymologically, as the appellation of "spermatozoon" literally means "semen looking like an animal."

And Now Reaching the Twentieth Century

Improved microscopes and improved microscopical techniques were of decisive importance for further investigation of the spermatozoa. In an effort to approach "comparative spermatology," initiated by Leeuwenhoek and further developed by Koelliker, there were prominent investigators, such as La Valette St. George and Emil Ballowitz, who published some of their observations in the last decades of the nineteenth century. Somewhat later, Gustaf Retzius became a leading spermatologist.

He described the detailed structure of several hundred animal species, including many rare animals from all six continents. This is a unique investigation that could never be repeated. He noted (as others had done before him) that related species tend to have spermatozoa of similar structure and that it is possible to draw phylogenetic conclusions from sperm data. The fact that pangolin, echidna, and platypus have spermatozoa of the reptilian (sauropsid) type, whereas marsupials and other mammals have not, is thus an indication that the eutherian mammals branched off the mammalian stem before the appearance of the marsupials, and that the pangolins are the most primitive extant eutherians. He also noted that coelenterates, polychete worms, and mussels have small spermatozoa of a characteristic shape, which he referred to as "primitive" spermatozoa. Half a century later, Franzn showed that "primitive spermatozoa characterize animals that broadcast their spermatozoa into the ambient water," usually for external fertilization. The shape of the spermatozoa is thus dependent both on the reproductive biology and on the phylogenetic position.

The contribution of B. Baccetti and coll. in Sienna (Italy) and D. W. Fawcet (1970) illustrates the continuity of the investigation field of “evolutive spermatology.”

By the turn of the nineteenth century, Frank Lillie in the famous *Woods Hole Lab* observed that during fertilization sperm are controlled by a substance released from the sea-urchin egg and was thus establishing the basis of chemotaxis as a sperm guidance mechanism. Using sea water with a high potassium content, he also observed parthenogenesis.

The only organelle that is sperm specific and quite widely distributed in the animal kingdom is the acrosome. It was first described by Valentine, given its present name “acrosome” by Lenhossck and shown to contain the lytic enzymes acrosin, initially termed lysin by Hibbard and Tyler, and hyaluronidase by Leuchtenberger and Schrader.

The rather dramatic transformation of the acrosome upon contact with the egg or with egg-water was first described by Jean Dan (1952) and termed the acrosome reaction. Localized under the acrosome is the sub-acrosomal material, termed the *perforatorium* by its discoverer, Waldeyer. He also undergoes experiments on the acrosome reaction as was described by Arthur L. Colwin and Laura H. Colwin (1955).

Other sperm organelles are those that are also found in somatic cells. This is true, for instance, of mitochondria, flagellar axonemes, microtubular arrays, etc. In some cases, our knowledge of these organelles has come from the study of the somatic cells, in other cases spermatozoa have been shown to be the ideal study object. It would take too much space to explore extensively here all the various sperm organelles with morphological and biochemical tools. The book that is dealing with several aspects of aquatic animals spermatology provides large information on these topics.

Obviously, because of the global topic of the book devoted to *Reproduction in Aquatic Animals: From Basic Biology to Aquaculture Technology* published by Springer Nature and edited by Manabu Yoshida and Juan F. Asturiano, readers of this book will also be able to access important information that deals with the sperm/egg interaction that involves the egg partner of various aquatic species.

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Part I
Overview

Chapter 1
Overview: Reproductive Systems in Aquatic Animals

Manabu Yoshida

Abstract Many animals live in aquatic habitats. Regarding reproduction, all terrestrial animals perform internal fertilization, whereas aquatic animals show various reproductive systems: internal fertilization without mating, external fertilization, viviparous, oviparous, and parthenogenesis. In this chapter, I would like to provide an overview of the reproductive systems of aquatic animals and introduce each chapter in this book.

Keywords Fertilization · Reproductive systems · Internal fertilization · External fertilization · Viviparous · Oviparous · Hermaphrodite · Oocyte maturation · Sperm function · Assisted reproductive technology

1.1 Introduction

In the animal kingdom, there are about 30 phyla. Major animal groups (phyla and classes in Vertebrata) are shown in Fig. 1.1. Many animals belonging to the two highly evolved phyla—Vertebrata and Arthropoda—and some invertebrates, e.g., earthworms (Annelida) and snails (Mollusca), live in terrestrial habitats, and some parasitic animals, e.g., Ascaris (Nematoda) and tapeworms (Platyhelminthes) live in the body of other animals. Almost all other animals live in the aquatic habitat. Although they belong to Vertebrata or Arthropoda, many fishes and crustaceans live in water. In fact, only one group of animals does not live in the aquatic environment—phylum Onychophora, a small group related to Arthropoda. Corresponding to the diversity in aquatic animals, their reproductive system is also highly diverse. All terrestrial animals perform internal fertilization, whereas aquatic animals show

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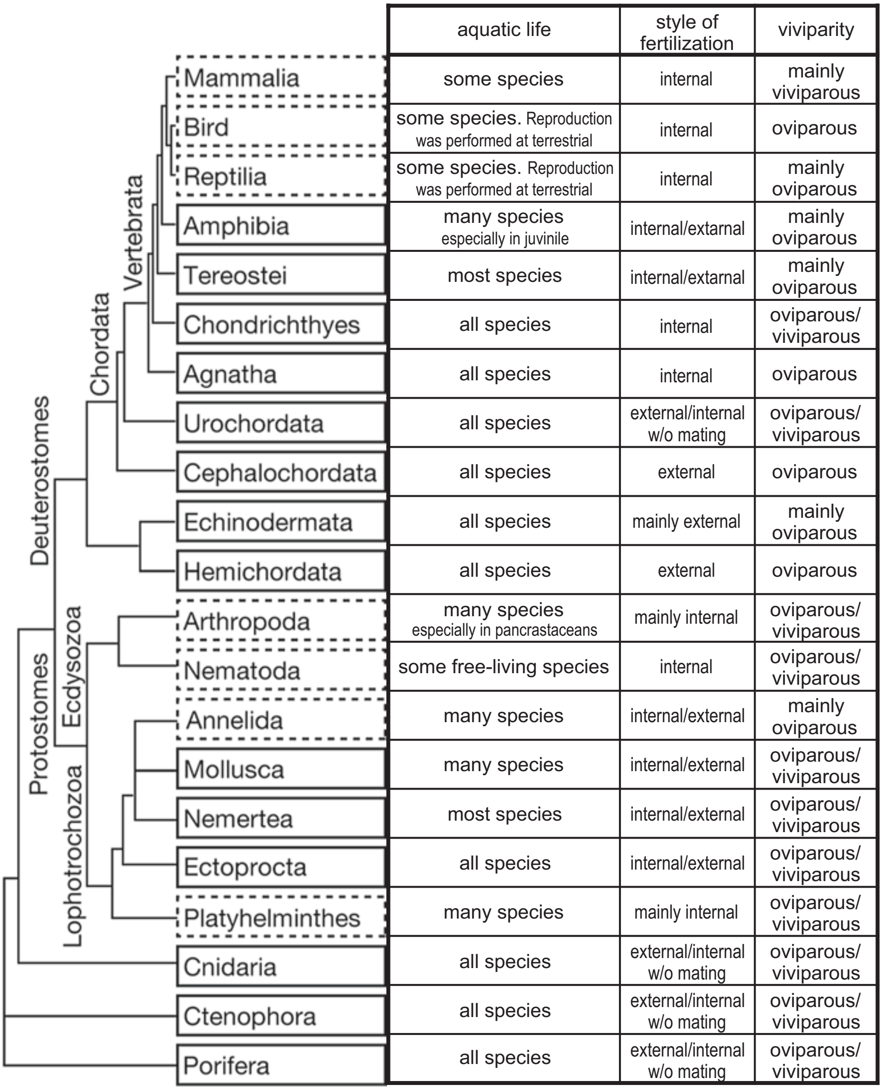

	aquatic life	style of fertilization	viviparity
Mammalia	some species	internal	mainly viviparous
Bird	some species. Reproduction was performed at terrestrial	internal	oviparous
Reptilia	some species. Reproduction was performed at terrestrial	internal	mainly oviparous
Amphibia	many species especially in juvinile	internal/extarnal	mainly oviparous
Tereostei	most species	internal/extarnal	mainly oviparous
Chondrichthyes	all species	internal	oviparous/ viviparous
Agnatha	all species	internal	oviparous
Urochordata	all species	external/internal w/o mating	oviparous/ viviparous
Cephalochordata	all species	external	oviparous
Echinodermata	all species	mainly external	mainly oviparous
Hemichordata	all species	external	oviparous
Arthropoda	many species especially in pancrastaceans	mainly internal	oviparous/ viviparous
Nematoda	some free-living species	internal	oviparous/ viviparous
Annelida	many species	internal/external	mainly oviparous
Mollusca	many species	internal/external	oviparous/ viviparous
Nemertea	most species	internal/external	oviparous/ viviparous
Ectoprocta	all species	internal/external	oviparous/ viviparous
Platyhelminthes	many species	mainly internal	oviparous/ viviparous
Cnidaria	all species	external/internal w/o mating	oviparous/ viviparous
Ctenophora	all species	external/internal w/o mating	oviparous/ viviparous
Porifera	all species	external/internal w/o mating	oviparous/ viviparous

Fig. 1.1 Major animal groups (phyla and classes in Vertebrata), habitat, and style of fertilization

various reproductive systems; some are internal fertilizers with or without mating and many aquatic animals perform external fertilization (see Fig. 1.1).

In this chapter, I would like to provide an overview of the reproductive systems of aquatic animals and to help the readers understand the focus on specific animals in each chapter.

1.2 Taxa and Living Habitats

The salinity of water is the most important factor affecting life of all animals and plants. There are three habitats in the aquatic environment: seawater (saline water), freshwater, and brackish water.

1.2.1 Seawater

Seawater, or saline water, is water whose salinity is approximately 3.5% (35 g/L) and mainly located in the oceans which cover about 70% of the surface of the earth. As the major diversifications of modern Metazoa, e.g., the Cambrian explosion, occurred in the ocean, most animal phyla are still seen in the seawater habitat. Despite several difficulties in evaluation, the total number of seawater animal species is estimated at approximately 200,000–250,000 species (Bouchet 2006). The major animals are the mollusks (approximately 52,000–75,000 species), arthropods (approximately 40,000–50,000 species), fish (approximately 15,000 species), flatworms (approximately 15,000 species), annelids (approximately 12,000 species), and nematodes (approximately 12,000 species) (Bouchet 2006). Interestingly, even though insects are the major group on the earth, and in terrestrial and freshwater habitats, there are only a few insect species in the seawater habitat.

1.2.2 Freshwater

Freshwater is water containing <0.5 g salts per 1 kg water. Freshwater is located on land, and it covers only 0.8% of the surface of the earth (Dudgeon et al. 2006). Because low osmolality induces an influx of water and delivers a fatal blow to an animal cell, which has no cell wall, the freshwater habitat is a more severe environment than the seawater habitat. The total number of described freshwater animal species is approximately 126,000 species. Many of the animals are hexapods (insects and collembolans) (approximately 76,000 species) and other arthropods (approximately 18,000 species), and another major group is the vertebrates (approximately 18,000 species) (Balian et al. 2008), which have well-developed systems for osmotic regulation and water-resistant skins.

In contrast, 43% of all fish species (approximately 14,000 species) predominantly live in the freshwater habitat (Nelson et al. 2016); one reason being that teleost fish seem to be derived from a freshwater ancestor (Carrete Vega and Wiens 2012).

Amphibians also live mainly in the freshwater habitat. Amphibians comprise approximately 6000 species, and about 80% of these are aquatic living or water dependent (Vences and Kohler 2008). Among them, only 144 species are salt-tolerant (Hopkins and Brodie 2015). See Chap. 11 for details.

1.2.3 Brackish Water

Brackish water is water whose salinity is between that of fresh water and seawater. It exists in areas where fresh water and seawater are mixed, such as estuaries. As salinity of the area changes irregularly, animals living in brackish water should have a tolerance for changing osmolarity. In addition to euryhaline species, locally adapted stenohaline species, which are typically found in seawater habitats, are also found in these habitats (Cognetti and Maltagliati 2000). Some teleost fishes such as mullet, seabass, flatfish, and eel are highly adapted to brackish water, and some bivalves, annelids, and crustaceans also live in these areas.

1.3 Reproduction Systems

As described in Sect. 1.1, the reproduction systems of aquatic animals are diverse, and they are excellent models for studying the adaptive evolution and species specificity of fertilization. In this section, I would like to introduce the types of the reproduction systems in aquatic animals (also see Fig. 1.1).

1.3.1 Asexual Reproduction

Although I do not want to focus on asexual reproduction because the main theme of the book is "sexual reproduction," asexual reproduction is a popular system in animals, and I should discuss this system first. Asexual reproduction is a type of reproduction producing offspring from a single parent without meiosis; that is, the offspring does not arise from gametes but from a part of the parent's body. Budding and fragmentation are types of asexual reproduction in metazoans. Many aquatic invertebrates including starfishes (Echinodermata), ascidians (Urochordata), planarians (Platyhelminthes), and medusae, and corals (Cnidaria) reproduce in this manner. For example, many hydromedusae have two life stages: one is the asexual stage of the polyp that produces polyps and medusae by budding and fragmentation, and the other is the sexual stage of the medusa that produce their gametes by meiosis. Some planarians switch their reproduction systems between the sexual and asexual stages (Kobayashi et al. 2012). As costs of reproduction are lower and producing offspring is faster than that by sexual reproduction, many asexually reproducing animals build a colony of clone individuals, for example, corals, bryozoans, colonial ascidians, and sponges.

1.3.2 Parthenogenesis

Parthenogenesis is also a type of reproduction producing offspring from a single parent, and it is usually considered as one type of asexual reproduction. However, in this system, the offspring arises from a gamete (usually the egg) without fertilization. Therefore, I consider that parthenogenesis is not an "asexual" (non-sexual) but a "unisexual" reproduction system. Parthenogenesis is also observed in several aquatic animals including vertebrates such as some amphibians, sharks, and teleosts (Neaves and Baumann 2011).

1.3.3 Internal or External Fertilization

As cells in all animals, including gametes, must live in some aquatic conditions, all terrestrial animals perform fertilization internally. Quite a few aquatic animals also perform internal fertilization, such as many crustaceans, snails, elasmobranches, and amphibians. In contrast, many aquatic animals perform external fertilization (see Fig. 1.1). Interestingly, some animals, such as jelly fishes and bryozoans, perform internal fertilization without mating; they spawn their sperm into the surrounding aquatic environments, their sperm swim and go into the female body, and finally they find the egg, and fertilization occurs.

1.3.4 Viviparity or Oviparity

All animals showing external fertilization lay their eggs in the external environment, and their embryos develop outside the body of the parent. Some animals showing internal fertilization also release their fertilized eggs and the embryos develop in the external circumstances. This developmental style is called "oviparity." In contrast, some animals showing internal fertilization keep their fertilized egg in the body, and the embryos develop inside the mother's body until larvae or juveniles. This developmental style is called "viviparity." Embryos of viviparous animals are usually supplied with additional nutrition from the mother (matrotrophy), but that of some viviparous animals use only the yolk of the eggs and are not supplied with additional nutrition. The latter style is sometimes distinguished from viviparity and called "ovoviviparity." The most famous viviparous animals are mammalians, but interestingly, there are viviparous animals in almost all taxa. Viviparous animals are considered to have evolved from oviparous animals (Blackburn 1999; Lode 2012), and the evolutionary transition from oviparity to viviparity occurred many times; for example, viviparity has evolved between 98 and

129 times considering only the squamate reptiles (Bystroff 2018). Among aquatic animals, many elasmobranches are viviparous and ovoviviparous, and many researchers have studied the variation in developmental styles. In Chap. 10, we focus on the developmental styles observed in elasmobranches.

1.3.5 Hermaphrodite or Dioecious

One of the important features is hermaphroditism; many fishes can change their sexes and many invertebrates are hermaphrodites. Although some hermaphrodite animals, like the nematode *Caenorhabditis elegans*, perform self-fertilization, that is, fertilize an egg and a spermatozoon from the same animal (one type of parthenogenesis); many hermaphrodite animals prevent self-fertilization as seen in many plants (Sawada et al. 2014). In the internal fertilizers like the sea hare, spermatozoa, and eggs are separated and only non-self-sperm received by mating can access the egg. However, in the case of external fertilizers, gametes themselves should recognize self and non-self-partners. The ascidians (Urochordata) are well-known hermaphrodite animals, and the system of self/non-self-recognition between gametes has been investigated (Sawada et al. 2014). In Chap. 9, the system of ascidians is reviewed thoroughly.

1.4 Sexual Behaviors

Sexual behavior is one of the interesting subjects in reproductive biology and depends on the reproductive system.

Fishes are one of the major, developed animal group in aquatic animals. Irrespective of internal fertilization or external fertilization, many fishes show mating behavior, and fertilization occurs just after spawning. Usually, the fish sperm, especially freshwater fish sperm, have very short lives; the lifetime of these sperm is around 30 s to a few minutes (Cosson et al. 2008). Thus, mating behavior is adapted and optimized to perform fertilization. Furthermore, motility of the sperm is regulated precisely by environmental elements: osmolarity, ions, and egg-derived factors among others (Cosson et al. 2008). Regulation of motility in the fish sperm is reviewed in Chap. 4.

Another interesting mating behavior has been observed in squids (Mollusca), which is one among alternative reproductive strategies. Usually, the female squid receives spermatophores from the male partner (called a “consort”) by mating and stores them in the storage organ in her body (Iwata et al. 2011). The spermatozoa await ovulation in the storage organ, and after ovulation/spawning of the egg, the spermatozoa reach the egg on/near the oviduct in the mantle cavity. However, the male “sneaker” comes and releases his sperm near the mouth of the female, and some sperm succeed in fertilizing the egg. Interestingly, the sneaker spermatozoa behave differently from the consort spermatozoa; the sneaker spermatozoa form a cluster even though they can swim freely (Hirohashi et al. 2013). The alternative reproduction tactics of the squids and sperm behaviors are reviewed in Chap. 13.

The benthic invertebrates showing external fertilization, e.g., sea urchins, ascidians, and corals, usually spawn their gametes directly into the external water. In these cases, it is a hard mission for the sperm to find its partner egg. Thus, the egg often releases sperm activation substances and attractants to ensure fertilization. This topic is reviewed in Chaps. 3 (general introduction and ascidians), 8 (corals), and 12 (sea urchins).

1.5 Behavior of Gametes

1.5.1 Behavior of the Egg

In general, mature oocytes are arrested at the prophase I of meiosis with the large nucleus (germinal vesicle) in the ovary of the female body. After stimulation for ovulation, the oocytes re-enter meiosis, induce germinal vesicle breakdown, and become “fertilization-eligible” eggs. Progression of meiosis after stimulation of ovulation is varied and species-dependent; e.g., the unfertilized eggs of many vertebrates, including amphibians and fish, are arrested at metaphase II, whereas sea urchin eggs finish meiosis completely before fertilization. Maturation of oocytes is described in detail in Chaps. 6 (fish) and 7 (invertebrates).

The ovulated “fertilization-eligible” eggs usually have vitelline coats (often called “chorion”), and they often impede the entry of the sperm into the egg. Especially in the fish, the chorion is too thick and too hard for the sperm to penetrate it. Instead, there is a tiny passage on the chorion, named “micropyle,” to enable the sperm to access the egg (Yanagimachi et al. 2013). Moreover, some guides and/or guidance molecules are located on the chorion around the micropyle (Yanagimachi et al. 2013; Yanagimachi et al. 2017). Chapter 5 reviews the mechanism of sperm guidance toward the micropyle in the fish egg.

1.5.2 Behavior of the Sperm

Considering the sperm, the spermatozoa are usually immotile while stored in the male body and initiate their motility when they are ejaculated or spawned from the body (Yoshida et al. 2008). As described in Sect. 1.4, the sperm of many external fertilizers show chemotactic behavior toward the egg to find the conspecific egg. The initiation of sperm motility and sperm chemotaxis are reviewed in Chaps. 2 (overview), 3 (invertebrates), and 4 (fish). When the spermatozoa approach the egg, spermatozoa of many animals show acrosome reaction. Interestingly, the teleost spermatozoa have no acrosome, and they can enter the egg without acrosome reaction. In this context, the fish sperm cannot penetrate the chorion of the egg, so it looks for the micropyle to access the egg (see Sect. 1.5.1).

1.5.3 Polyspermy Block

The egg should receive only one spermatozoon for fertilization that is the fusion between female and male pronuclei, to maintain the genome in the embryo. Thus, almost all eggs prevent multiple sperm entry. The system is called "polyspermy block," which is one of the interesting aspects of research on fertilization (Dale 2014). It is reviewed in Chaps. 6 (fish), 7 (invertebrates), and 11 (amphibians).

Interestingly, the egg of some amphibian species like newts, receive multiple sperms during fertilization, but for fusion of the pronuclei, only one male pronucleus is selected from the spermatozoa that enter (see Chap. 11 for details).

1.6 Issues of Reproductive Biology for Aquaculture

In aquatic animals, fish, mollusks, and crustaceans are useful as food and are a target for farming (aquaculture). In this book, we also focus on the topics of reproductive biology in aquaculture. Especially, the establishment of the complete culture technology of some high-value fish, like tuna, eel, and sturgeon, is demanded as these fish have become endangered because of overfishing. However, as described above, reproduction systems of aquatic animals are varied and species-dependent. Reproducing juveniles is one of the difficulties in establishing aquaculture methods. In Chap. 14, the practical case of the European eel is reviewed.

Furthermore, an assisted reproductive technology is also demanded in aquaculture for the conservation and propagation of the animals. One of the technologies is cryopreservation of gametes; the technique provides flexibility in the production of embryos/juveniles and stocking of elite broodstock and/or endangered animals. Chapter 15 reviews the cryopreservation of sperm in aquatic animals. Another important technique in assisted reproductive technology is germ cell transplantation, which enables surrogate production. In Chaps. 16 and 17, there are reviews of studies on the technology used in the sturgeon and teleosts, respectively.

1.7 Conclusion

As overviewed in this chapter, reproduction systems in aquatic animals are highly diverse, and it is difficult to grasp the whole picture of reproduction. We hope this book helps readers understand features of the reproductive systems in each aquatic animal.

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Part II

Basic Knowledge of Male Gametes in Aquatic Animals

Chapter 2
Introduction to Sperm Motility of Aquatic Animals

Jacky Cosson

Abstract The purpose of this chapter is to present a historical point of view on sperm motility, showing how pioneer investigations using sea urchins as a model species gradually radiated to other aquatic species because of their ability to approach more specific questions.

Keywords Flagellum · Axoneme · Fish · Shellfish · Echinoderms · Jellyfish

2.1 Introduction

During evolution, aquatic animals have preceded terrestrial ones, mostly because life appeared initially in water and, the latter remains absolutely necessary for the maintenance of living creatures. If one tries to trace the evolution of scientific knowledge in the field of sperm, eggs, and their association with fertilization, it also appears that basic notions have been acquired through observations of aquatic species.

In this regard, this book flies over a great diversity of species that will be briefly explored in the present paragraphs: it is conceived as an overview so as to avoid overlap with the detailed and more specific chapters coming afterward.

2.2 Interest to the Reproduction of Aquatic Animals

The first human interest to aquatic animals has probably been associated with the possibility of rising some species, using aquaculture as a substitute to fishing, a more hazardous activity. An overview of the main aquatic species considered as

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important in aquaculture partly overlaps the panel of species that have been used to establish important steps in reproductive biology.

A non-exhaustive list includes: (1) fish species, either marine species (e.g., sea bream, sea bass) as alternative to fishing or traditional freshwater species such as those of central Europe (e.g., carp, trout); (2) shellfish such as oysters, commercially important in Europe or Japan; (3) other species of interest for sport-fishing or fishkeeping, both popular hobbies, for high-value products such as caviar from sturgeons or jewels from black pearl oysters; and (4) research and conservation of species as detailed afterward in the present book.

2.3 Importance of Marine Stations

These marine stations are places of predilection, mostly because they offer a source of great diversity of biological material from the sea and are enjoyable spots of scientific melting pot where to organize meetings or summer schools. As examples, let us mention *Woods Hole* in Cape Cod (USA), the *Zoological Station* in Napoli (Italy), the *Misaki Marine Biological Station* in Misaki (Japan), etc.

2.4 Various Aquatic Species Used Historically in Reproductive Biology

2.4.1 Sea Urchin

First of all is *sea urchin*, a historically very important species: sea urchins allow basic observations on sperm motility. Mostly the advantages of sea urchins are that they provide a huge amount of milt per individual, a crucial property for early biochemical studies, and they are gravid most of the year with mature sperm cells able to swim for very long periods. As examples early studies on sea urchins were developed by F. Lillie in the *Marine Biological Laboratory* (MBL) in *Woods Hole* (USA) then later by Barbara and Ian Gibbons (1981) in the *Kewalo Marine Lab* (Hawaii) and by Charles Brokaw (Brokaw and Gibbons 1975) in the *Caltech's Kerckhoff Marine Lab* (USA) while very long ago, fertilization of sea urchin eggs was observed for the first time by H. Fol (1879) in the Marine Station of *Villefranche sur mer* (France).

The studies of Sir Gray (1955) on the description of sea urchin sperm movement remain a fundamental pillar that underpins the resistance force theory (RFT) and furnishes the physical basis of flagellar movement. Mostly, flagella develop waves that initiate close to the head/tail junction and propagate backwardly towards the distal tip. The viscosity of the swimming solution offers a resistance to the wave propagation which, by reaction, provokes the forward translation of the whole sperm