The reproduction and development of sharks, skates, rays and ratfishes: introduction, history, overview, and future prospects

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This volume had its origin in a Symposium on the Reproduction and Development of Cartilaginous Fishes that was held at the annual meetings of the American Elasmobranch Society and the American Society of Ichthyologists and Herpetologists in Charleston, South Carolina in June 1990. The aim of this symposium was to bring together many of those scientists interested in chondrichthyan reproduction and development in order to assess the current state of knowledge in these fields.

The chondrichthyan fishes occupy a pivotal position in comparative and evolutionary studies of vertebrate reproduction and development. They are the oldest surviving group of jawed vertebrates and they possess both the adult vertebrate Bauplan and the vertebrate program of embryonic development. The major features of the female reproductive system, including its embryonic origin, structure, physiological function, and biochemistry, apparently were established early in vertebrate evolution and are fully developed in chondrichthyan fishes. These features of the female reproductive system have been retained during the evolution of the other classes of vertebrates. Much the same can be said for the male reproductive system. Moreover, viviparity, placental nourishment of developing embryos, and the hormonal regulation of these events made an initial appearance in this group.

The twenty-two articles contained in this volume bring together a wide variety of complementary research by investigators from seven countries. It is hoped that presentation of this disparate body of research and thought in one place will provide perspective on current research activity, call attention to those areas in which the research endeavour is deficient, and identify opportunities for future study. The appearance at this time of a volume on the reproduction and development of cartilaginous fishes is quite opportune. The continued existence of these fishes, which survived the great extinction events of Earth’s history, is now threatened by over-exploitation unless immediate steps for their conservation are undertaken. Knowledge of their reproduction and development not only is an end in itself, but is of critical importance in devising successful conservation and resource management strategies.

Chondrichthyan fishes

The cartilaginous fishes, class Chondrichthyes, are the oldest surviving group of jawed vertebrates. They are a large and diverse group that includes approximately 900 to 1100 living species of sharks, skates, rays and ratfishes. Throughout their history, which dates back at least 400 million years, they have been a successful major component of the marine ecosystem. The Chondrichthyes appeared as recognizable shark-like fishes in the late Silurian-early Devonian. At a relatively early time, i.e. the Devonian-Carboniferous boundary, they diverged into two groups, the Holocephali and the Elasmobranchii. The minor subclass Holocephali is a small group, primarily inhabiting deep water, that contains 31 to 50 species of chimaeras, ratfishes, and elephantfishes. The dominant subclass, Elasmobranchii, not only includes the living sharks, but also includes the batoid fishes, i.e., skates and rays,
which diverged from the sharks in the early Jurassic. The cartilaginous fishes survived the major extinctions during the Permian-Triassic transition and at the end of the Cretaceous, and they appear to be as diverse as they ever were (Carroll 1986, Compagno 1990). (See Compagno 1988, 1990 for a definitive treatment of sharks and a modern synthesis of chondrichthyan diversity and life history patterns; Springer & Gold 1989 is a useful introduction to the group.)

The Elasmobranchii includes the living sharks, rays, and skates. There are about 375 to 500 species of sharks that are assigned to eight orders. The ground sharks (Carcharhiniformes) with 56% of the shark species are the dominant order. There are three other major groups, the dogfish sharks (Squaliformes), carpet sharks (Orectolobiformes) and mackerel sharks (Lamniformes) that respectively comprise 23%, 8% and 4% of the living sharks. The remaining 8% of the species are found among four minor orders, the frilled and cow sharks (Hexanchiformes), saw sharks (Pristiophoriformes), angel sharks (Squatinoformes), and bullhead sharks (Heterodontiformes) (Compagno 1990). The rays or batoid fishes are derived from neoselachian sharks and consist of five orders that include about 494 to 572 species. The skates (Rajiformes) contain 44% of the batoid species and are most diverse in deep water and at the higher latitudes. Guitar fishes (Rhinobatiformes) with 11%, electric rays with 9%, and sawfishes (Pristiformes) with 1% account for the remaining batoid species (Compagno 1990).

The overwhelming majority of chondrichthans are marine and most of these species (55%) are found on the continental shelves where they range from the intertidal zone to a depth of 200 m. Cartilaginous fishes display an extraordinary diversity in their morphology, size, ecology, and behavior. In an attempt to systematically analyze this diversity, Compagno has categorized these fishes on the basis of a number of alternative life-history styles. He has divided the living and fossil chondrichthans into at least eighteen ecomorphotypes. An ecomorphotype or ecomorphological type is defined as, 'a particular grouping of taxa that may or may not be phylogenetically related by similar morphology, habitat, and behavior' (Compagno 1990). The littoral ecomorphotype is regarded as the most primitive type and would seem to be the evolutionary origin for radiation into a number of specialized ecomorphotypes, such as the tachypelagic, archipelagic, and macrooceanic.

Even though this volume is devoted to reproduction and development, we thought that it would be appropriate to provide an introduction to the two topics, which could serve as a guide for the non-specialist. In addition to the contributions in this volume, more information can be found in Wourms (1977), Dodd (1983), Callard et al. (1988), and Wourms et al. (1988). Cartilaginous fishes display a diversity of reproductive modes. All recent chondrichthyan fishes employ internal fertilization via paired intromittent organs. Fecundity is low. With few exceptions, they produce a relatively small number of large, heavily yolked eggs. They are either oviparous or viviparous. In both instances, young are large, well-developed and relatively precocial. The style of producing precocial offspring appears to have been adopted early in the evolution of the chondrichthans. It may, in part, account for the long continued success of the group. Oviparity is the primitive mode of reproduction. The Holocephali (ratfishes and chimaeras) are oviparous with the possible exception of a single fossil species. All of the skates (Rajiformes) and a minority of the sharks are oviparous. Viviparity is the dominant mode of reproduction. About 515 species (55%) of the chondrichthyan fishes give birth to living young. In contrast, only about 2–3% (510 species) of the bony fishes (Osteichthyes) are viviparous. With the exception of the skates which are egglayers, the other four orders of batoid fishes, i.e. stingrays, guitar fishes, electric rays, and sawfishes (about 270 species), are viviparous. The majority of sharks, i.e. 70% (245–270 species) are viviparous. Among the chondrichthians, viviparity is estimated to have evolved from oviparity on as many as 18 occasions (Wourms & Lombardi 1992). In addition to the oviparity vs. viviparity dichotomy, other factors such as trophic relationships can be used to categorize reproduction. At least five reproductive