ECOLOGY, BEHAVIOR AND PRODUCTIVITY OF MARINE FISH

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Summary

Fish are very diverse with many adaptations to the different habitats provided by the sea and the continental waters. They can be found from freezing temperatures to the tropics, and have a wide range of life histories. The maximum diversity is found in tropical littoral areas, probably related both to the stability of the oceanographic conditions and the complexity of the habitat. Diversity is maintained trough predation and competition. Most fishes have a pelagic phase as eggs and larvae that ensure dispersal and

colonization of new territories. The fish range from typical k-strategists with low fecundity, parental care and late maturity to r-strategists with fast growth and high fecundity with pelagic millions of eggs. The eco-biological adaptations of these ancient vertebrates to their habitat are striking and have enabled them to colonize the more extended habitat of the planet.

1. Introduction

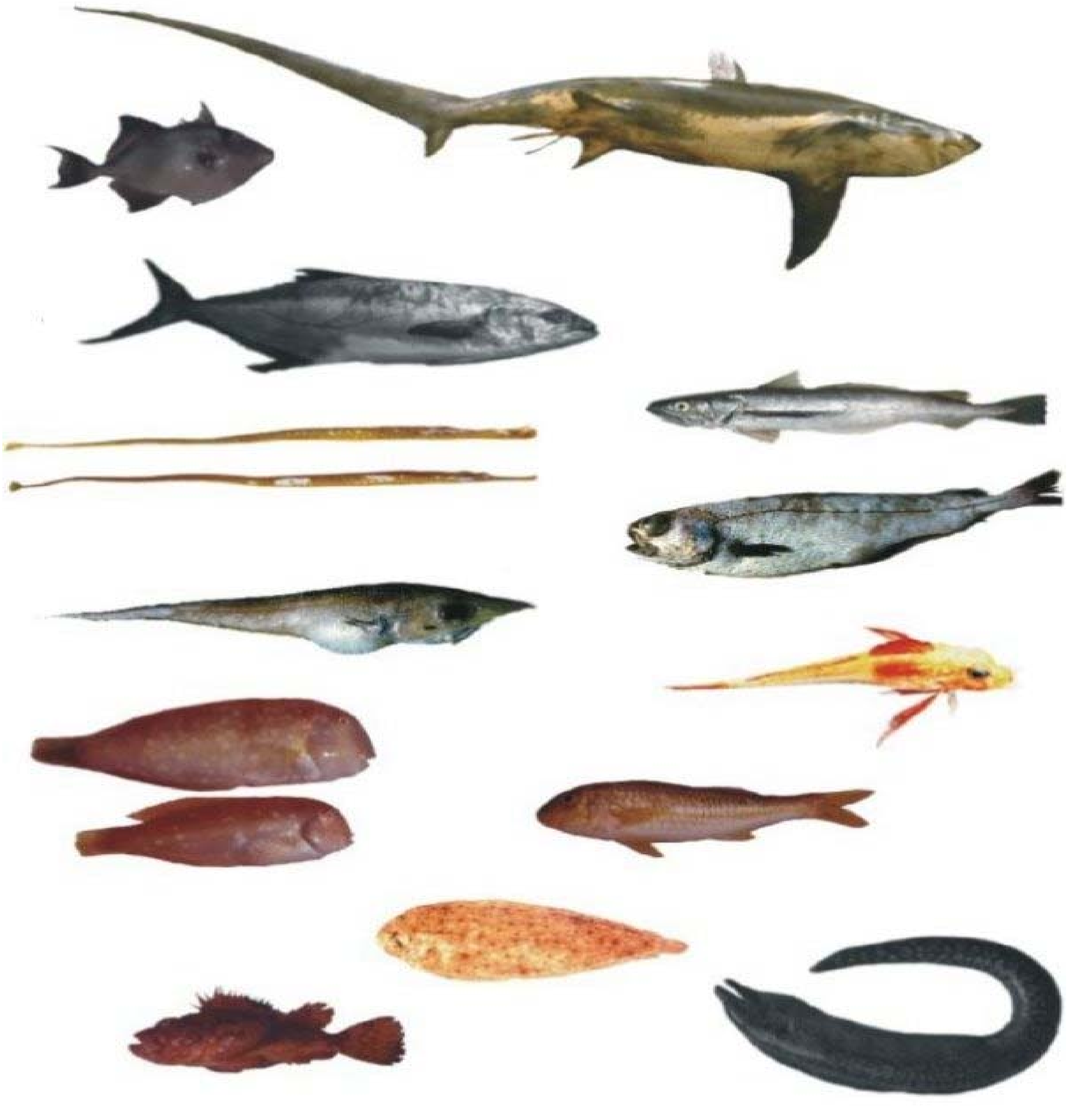

Figure 1: Differences in shape between fish from different habitats

Fish are the most ancient and numerous of vertebrates, exhibiting great diversity in ecology, life history patterns and morphology (Figure 1). Adult fish range in size by three orders of magnitude from gobies (*Aphia minuta*) which mature at less than 10 mm to whale sharks (*Rhiniodon typus*) of 10 m or more. Fish live in waters with average temperatures ranging from below 0ºC to above 30ºC. Over half of the recognized vertebrate species are fish and more and more are being described every year. Currently, there are around 25,000 valid species, classified into 482 families; about 60 % of which live permanently in the sea. There are also a small number of species dwelling both in fresh and marine waters: the catadromus species, such as eels, live in fresh water but enter the sea to breed; and the anadromus species, such as salmon and sturgeons, live in the sea but enter fresh water to breed.

There are five main classes of extant fishes, one of them the Chondrichthys, excluding Chimaeriformes, are collectively known as the elasmobranchs and have cartilaginous skeletons lacking a swim bladder. 96% of extant fishes are Teleostei and have bony skeletons, many of them have a swim bladder which enables them to sustain buoyancy. Studies in temperate coastal areas have found that abundance patterns of fish are influenced by the proportional representation of different habitat types. Changes in the composition of fish assemblages can, therefore, represent changes in the representation of habitats.

The diversity of marine fish is higher in coastal and littoral waters to depths of 200 m where approximately 11,300 species are found. The diversity is highest in the Indo-West Pacific, particularly in the areas between Papua-New Guinea and Queensland, Australia. Coral reefs have the highest fish diversity on an area-specific basis and 4,500 species are known from coral reefs and associated habitats. Approximately 130 marine species like tunas have circumglobal distributions in tropical oceans. From paleontological records and fish catabolism, it has been deduced that fish (finfish and elasmobranchs) are secondary sea dwellers, having had an evolutive period in freshwater.

Fish abundance and diversity arises not only from the evolution caused by competition between predator and prey but also between species needing the same resources. Living space may be more limiting than food supply in littoral rock and marine reef communities, whereas food supply may be more limiting in the pelagic system, both in prey species and possibly in their predators too. Food may be limiting at a particular stage of the life cycle, for instance during early larval development. On marine reefs all stages are found, from fine resource-partitioning - indicating competition has occurred in the past - to overlaps with several species sharing foods - indicating little or no competition (although the foods may be used differently) - to the presence of alternative species utilizing the resources, resulting from stochastic recruitment to the living space on a patch reef. Living space concerns protection from enemies and facilities for spawning as well as for food collection. Even for pelagic fish, space may be more structured than is comprehended at present; fish may be kept in certain water strata by chemical and physical preferences and by social interaction.

Fish are part of the ecosystem entering the flux of energy at different levels of the food chain. They can be phytoplankton feeders at the second link of the chain, or they can be apical predators like big tunas or sharks. Moreover, they can be fish predators or even cannibals that in turn are also eaten by fish. Marine mammals and birds also consume fish. Their remains reaching the marine floor sustain an important population of scavengers, such as small crustaceans. Fish can have an important influence on the dynamics of other organisms through herbivory and predation. Their feeding and excretion, as well as their role as prey, can make an important contribution to the trophodynamics of the ecosystem.

Besides the ecological importance of fish as components of the ecosystem and as part of the energy transfer in the food chain, man in fisheries ranging from a small- to an industrial- scale heavily exploits fish. This chapter is centered on marine fish, their behavior, biology and life histories, the population dynamics and exploitation are briefly presented, due to the limitation of space. The population dynamics, fishery, fishery management and socio-economic aspects of fish exploitation are not included although the references include further reading on these subjects.

2. Fish life history

Fish have adaptations to the fluid medium in which they inhabit, such as the hydrodynamic shape of all active swimming species. Any submerged organism experiences upthrust, given by the weight of the displaced fluid medium. Thus, in order to stay at the bottom of a water column, the density of the organism has to be greater than that of water; in fact most animal tissues are denser than water. Staying in open water is thus a problem that requires adaptations to allow an equilibrium between body weight and buoyancy plus hydrodynamic lift. For instance, many fish have special lipid tissues that aid buoyancy since they are less dense than water. Another adaptation is to have a swim bladder filled with gas. Some fish have reduced the density of their bones to reach a density closer to that of water. The location of the buoyancy system (the swim bladder or the fat tissue) has to be in balanced positions around the body center of gravity, otherwise it will hamper the trim of the fish, resulting in a head-up or head-down position. All these adaptations are costly, requiring energy particularly to maintain the synthesis and resorbtion of the gas. Fish larvae maintain buoyancy by their small size and density, although they may have extended fins or other adaptations to increase water lift.

Life history strategies result from natural selection for species to produce the maximum number of young surviving to maturity under the conditions imposed by their biotopes (i.e. to maximize their fitness). Natural selection would be expected to favor non-reproductive activities at the expense of reproduction only when they advance reproduction at a later stage in the life history and thereby maximize overall fitness. The result of this is that organisms under different selection pressures will have characteristic life histories.

2.1 Life histories

Fish display a remarkable range of life histories, from small pelagic gobies like *Aphia minuta,* which mature at a few months of age and die after spawning; to rockfish *Sebastes* spp., which attain maturity after 10 or more years and continue to spawn every year for three decades or more. Natural selection favors the individuals that make the greatest contribution to future generations. Ideally, a fish would mature early at a large size and produce numerous and large offspring over a long reproductive life span. However, in reality, resources are limited and when individuals allocate resources to improve one’s aspect of fitness, there will be a cost elsewhere. The evolution of these diverse life histories result from the different ways of combining growth, maturity, fecundity and egg size to maximize fitness, depending on physical and ancestral constrains and costs and benefits set by the environment.

Most teleosts have a bipartite life cycle, where early life is spent in the plankton, generally as a larval form (Figure 2) which bears little resemblance to juveniles or adults. The newly hatched larvae generally have positive phototropism moving towards the shallow waters. Fish larvae are lecitotrophic, starting to feed when the yolk-sac is absorbed. The duration of the larval phase is variable, from days to months, depending on the species and the water temperature. In Antarctic fish, reproduction frequently occurs in winter with long embryonic and larvae periods, the pelagic phase reaching up to two years. Some Pacific reef-fish can postpone settlement at the bottom until a suitable place is found. The duration of the planktonic phase and the possibility of moving from one water mass to another allows the colonization of new territories or the replenishment of depleted stocks.

Figure 2: Channichtyidae larvae

2.2 Reproduction

Fish do not reproduce at a fixed age or size, but along a trajectory of age and size that depends on demographic conditions and is determined both by genes and by the environment. The reproductive ratio is a function of body size in short-lived species, but depends on the supply of energy surplus to maintain requirements (except when feeding is very poor) in long-lived species. Many fish species, however, are very flexible in their behavior and can change allocations of resources to growth or reproduction according to environmental or social conditions.

Sexual reproduction can provide an advantage because it creates and perpetuates genetic diversity and allows the formation of novel genetic combinations that provide adaptations to ever-changing environments. Fish have separate sexes, but some can be sequential hermaphrodites. All elasmobranchs have separate sexes throughout their lives and population sex ratios are usually close to 1:1. Most temperate fishes are dioccious, but almost 50% fish families in the tropics contain hermaphroditic species. Sequential hermaphrodites may be either protogynous - in which adult females change to adult males - or protandrous - in which adult males change to adult females. The Lethrinidae, Scaridae, Labridae, Sparidae and Serranidae contain protogynous species. Protandrous hermaphroditism has been observed in Sparidae, Centropomidae and Platycephalidae. Selection should favor sex change with increasing size or age when one sex gains a relatively greater reproductive advantage with size or age. For instance, in species such as the protogynus razor fish (*Xirichthys novacula*) in which males defend a territory and attract females to mate, larger males have an advantage in sustaining a territory and in guarding the egg nests. In hermaphroditic species the sex ratio is biased depending on the length, hence the fishery might affect the sex ratio due to the removal of larger sizes. In the case of *X. novacula*, the fishery removes larger fish that are males, resulting in females turning to males at lower lengths. However, the smaller resulting males are less successful in guarding the nests and attracting females, thus producing a lower recruitment.

Sexual dimorphism in size, shape and behavior is frequent. The extreme case is the minute parasitic males of *Photocorynus* and *Ceratias* which live attached to the female body. In others there is only a difference in growth rates and longevity, like in the case of *Merluccius* females which get bigger and older. In elasmobranchs there is sexual dimorphism with males having claspers. The age at reproduction depends on the species and gender: most species do not mature in their first year of life and need to reach a determinate size in order to start maturing. The reduced resources available at midwater and depth have necessitated the evolution of many reproductive adaptations, such as hermaphroditism, extremes in sexual dimorphism and sex ratio adjustment.

2.4. **Fecundity, maturation and spawning**

Fecundity, defined as the number of eggs in the female prior to the next spawning period, varies very much in individuals of one species, but in general it increases as a function of the weight of the fish, hence with the cube of the length. When the number of eggs is a premium, the female is larger than the male, although in nest guarding species, the guarding sex is the larger one.

Few fish spawn only once in a lifetime; the majority spawn at repeated intervals (Table 1). Reproduction is generally external, with males and females liberating the sexual products in dense clouds in the water. In elasmobranches, reproduction is internal. In some littoral fish, there is nest construction and guarding, either by the male or the female or both, depending on the species. Some species collect the eggs in pouches, like the male seahorse (*Hippocampus*), or in the mouth (*Tilapia*) and guard them until hatching. Sexual reproduction might be continuous through the year or be limited to a short period. Some species lay all their eggs at the same time, while others are serial spawners, laying several batches of eggs during the reproductive season. Maturation and spawning are synchronized through environmental parameters such as temperature or light cycles. Some are synchronized with the lunar phases: the atherinind from California *Leuresthes tenuis* spawns at high tide on the beach and the eggs hatch at the next tide. Lunar rhythms are also shown by *Clupea harengus* and *Gadus capelanus*.

Type and fecundity	Seasonality of reproduction	Examples	Type of eggs and parental care
Big bang	Once in a lifetime	**Anguilla** *Aphia minuta*	Pelagic Buried in sandy bottoms No parental care
Total spawners	Very seasonal, annual or biannual	**Lates niloticus**	No parental care
	Seasonal for 5-10 years	**Gadus morhua**	10,000 to 10,000,000 pelagic eggs/year
Batch spawners	Broad spawning season, producing several batches of eggs	*Coryphaena hippurus*	100,000 eggs/batch, at least 3 reproductive periods/year for 2-3 years starting at age 0
Small-brood spawners	Short annual spawning season starting at 5-9 years of age, for 5-10 years	*Harpagifer antarcticus*	200-300 benthic eggs/season, parental care
	Every 1-2 years for 10-15 years	**Lamna nasus**	1-5 living offspring

Table 1: Summary of fish reproductive strategies.The r-strategists are at the top of the table, while the k-strategists are at the bottom.

Fecundity is also highly variable depending on the species: external reproduction is associated with lower success due to the dispersion of the gametes and the high mortality of the eggs. Some sort of egg care or incubation results in higher embryonic survival. So, depending on the reproductive behavior, the females might produce millions of eggs or only a few having typically K or R strategies. The number of eggs, their size and quality depend directly on the size of the female. It has also been found that the experience of the female increases the reproductive success. One of the effects of fishery exploitation is that females get mature at smaller sizes. Since the fishery removes the larger fish, the females can only reproduce once or twice. The combined effect of smaller, inexperienced females results in reduced stock reproductive potential, thus increasing the risk of stock collapse.

A number of fish groups produce living young. Viviparity has evolved repeatedly and independently from oviparity in many fish groups. From the 54 families of extant fishes bearing living young, there are 40 families of chondrichthyans, *Latimeria* and 13 teleost families with around 500 species.

There is no evidence of a phylogenetic trend that suggests a tendency to evolve towards the production of larger eggs. The partitioning of reproductive output between the size and number of offspring varies independently of body size. The general rule seems to be that pelagic spawning marine fish produce many small eggs and demersal spawners produce fewer, larger eggs. The colonization of the oceanic environment involved the production of pelagic eggs, a trend that is also found in deep-water fish which inhabit the more extended marine habitat.

3. Population dynamics

Fish have a spatial distribution which is not constant in time; populations might change depending on environmental and biotic parameters, denso-dependent relationships and behavior. The density distribution of the fish in space is studied by population dynamics. Fertility (number of eggs produced), birth and death rates, life span and especially the reproductive period, are relevant parameters to determine the population abundance and composition by age groups. The environmental variability determine, in part, the population dynamics through mortality effects.

The biotic population potential is expressed by:

$$dN/dt = rN \qquad (1)$$

where *dN* is the derivative of the population density increase function with respect to time *t* and *r* is the growth rate of population *N*. At the beginning, the population growth is exponential, becoming sigmoid with time. Due to limiting factors, the population growth decreases until an equilibrium is reached:

$$dN/dt = rN\ ((K-N)/K) \qquad (2)$$

where *K* is the asymptote of the sigmoid curve, there is the maximum number of individuals the environment can support. The denso-dependent limiting factors are space, food availability, natural mortality, and the independent ones are environmental parameters. The limiting factors express the ambient resistance against population growth and they regulate the numerical coexistence of the species constituting the community. They act on all the life phases (eggs, larvae, juvenile and adult) so that only a certain number reach the adult stage. There are K and R strategies, the former favoring the adult (growth, low fecundity, parent care and low mortality), while the R strategy tries to produce a very numerous brood, like in *Gadus aeglefinus* which produces 4 million eggs by spawning.

The population biomass will depend on a numerical factor, the recruitment of new fish through emigration or additions of juveniles; and a weight factor, depending on the growth of the individuals; and will decrease depending on the loss of individuals either by mortality or by emigration.

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Bibliography

Beverton R.J.H. & Holt S.J. (1957) On the dynamics of exploited fish populations. Ministry of Agriculture, Fisheries and Food, London (republished by Chapman& Hall, 1993). [The basis of population dynamics].

FAO (1995). Code of conduct for sustainable Fisheries. FAO, Rome. [A code of conduct to sustainable fisheries].

Gulland J.A. (ed.) (1988). Fish population dynamics. John Wiley, London.[The basis].

Harden-Jones F.R.(1981). Fish migration: strategy and tactics. In: Animal Migration (ed.D.J.Aidley), pp.139-165.Cambridge University Press, Cambridge. [The introduction to fish migration].

Jennings S. Kaiser M.J. Reynolds J.D. (2001). Marine Fisheries Ecology. Blackwell Science Ltd, U.K., 417 pp.[This is a comprehensive approach to the fish biology and ecology from the point of view of exploited species]

Murawski S.A. (1984). Mixed-species yield-per-recruitment analysis accounting for technological interactions. Canadian Journal Fisheries Aquatic Sciences 41, 897-916. [The problems of multispecies multigear fisheries].

Randall D.J. Farrell A.P. (eds.) (1997). Deep-sea fishes. Fish Physiology 16, Academic Press, San Diego, 387 pp. [This is the current state of the art on deep-sea fish biology and ecology].

Ricker W.E. (1975). Computation and interpretation of biological statistics of fish populations. Bulletin Fisheries Research Board Canada 191.[The basic work for fisheries statistics].

Panfili J., H. Troadec, H. de Pontual & P.J. Wright (eds.) (2001). Manual of fish sclerochronology Ed. IFREMER-IRD, 416 p.[this manual comprises the age determination basis, methods and applications in a comprehensive way].

Pauly D. Christensen V.Walters C. (2000). Ecopath, ecossim and ecospace as tools for evaluating ecosystem impact of fisheries. ICES Journal Marine Science 57, 697-706.[A new approach based on energy transfer in the trophic chain].