Biological characteristics of tuna

Tuna and tuna-like species are very important economically and a significant source of food, with the so-called principal market tuna species - skipjack, yellowfin, bigeye, albacore, Atlantic bluefin, Pacific bluefin (those two species previously considered belonging to the same species referred as northern bluefin) and southern bluefin tuna - being the most significant in terms of catch weight and trade. These pages are a collection of Fact Sheets providing detailed information on tuna and tuna-like species.

Related topics

Tuna resources

Tuna fisheries and utilization

Related information

FAO FishFinder Aquatic Species - fact sheets

Related activities

FAO activities on tuna

Table of Contents

Taxonomy and classification

[**Family:** Scombridae] : Scombrids

[**Family:** Istiophoridae **Family:** Xiphiidae] : Billfishes

Upper systematics of tunas and tuna-like species
Scombrids and billfishes belong to the suborder of the Scombroidei which position is shown below:

```
Phylum : Chordata
  └── Subphylum Vertebrata
        └── Superclass Gnathostomata
              └── Class Osteichthyes
                    └── Subclass Actinopterygii
                          └── Infraclass Teleostei
                                └── Superorder Acanthopterygii
                                      └── Order Perciformes
                                            ├── Suborder Scombroidei
                                            |      └── Family Scombridae
                                            └── Suborder Xiphioidei
```

├── Family Istiophoridae
└── Family Xiphiidae

Scombrids

The scombrids belong to the family of the ***Scombridae*** which is comprised of 15 genera and 51 species. These species are assigned to 2 sub-families:
the ***Gasterochismatinae*** with only 1 species and the ***Scombrinae*** divided into 4 tribes:

the mackerels (Scombrini)
the seerfishes or Spanish mackerels (Scomberomorini)
the bonitos (Sardini)
the tunas (Thunnini)

The tribe ***Thunnini*** (tunas for ichthylogists) contains 14 species in 4 genera:

Thunnus (8 species)
Katsuwonus (1 species)
Euthynnus (3 species)
Auxis (2 species)

However, in several languages, the word "tuna" is used for members of both the tribe ***Thunnini*** and the tribe ***Sardini*** (8 species).

Origin of the word "tuna"

The word "tuna" is applied to certain members of the family Scombridae, a group of marine fishes including tunas, bonitos, mackerels, seerfishes and the butterfly kingfish. However, for ichthyologists, tuna refers to any of the 14 species of the tribe Thunnini within the family Scombridae (Klawe, 1977). The word "tuna" seems to have come into use in the second half of the last century, but it is not clear why it replaced the older name "tunny". It may have been brought to southern California by fishermen originated from Europe, either from the Dalmatian coast of the former Yugoslavia or from the Iberian Peninsula (Klawe, 1976). The European names of tuna (thon in French, atún in Spanish, tonno in Italian, …) find their origin in the latin name *thunnus* itself issued from the Greek name θύννος, (*thýnnos*) derived from the verb "*thynno*" which means "*to rush*".

Principal market tuna species

Among the 14 species of tuna, skipjack, yellowfin, bigeye and albacore constitute more than 80% of the world catch since 1950. Three other species, Atlantic bluefin, Pacific bluefin and southern bluefin tuna, are also commercially important due to the high prices paid for them. These above-mentioned species are often referred as "principal market tuna species".

Billfishes

The billfishes include 2 families: the Xiphiidae with one species, the swordfish (*Xiphias gladius*) and the Istiophoridae with 12 species within 4 genera.

The systematics of billfishes was recently revised by Orell et al. (2006) and Collette et al. (2006) using molecular analyses of nuclear DNA and mitochondrial DNA cytochrome b, leading to the distinction of billfishes from scombroids in a separate suborder, Xiphioidei and to the revision of billfish genera. Moreover, the lack of justification for separating the Atlantic sailfish (*Istiophorus albicans*) from the Indo-Pacific sailfish (*I. platypterus*) leads the author to gather them both under the latter genus. Similarily, Atlantic blue marlin (*Makaira nigricans*) and Indo-Pacific blue marlin (*M. mazara*) are regrouped in the single genus *Makaira nigricans*.

Scientific and common names in English, French and Spanish of tunas and tuna-like species

Tunas and bonitos

Scientific name	Common names, acknowleged by FAO, in: English French Spanish; 3-alpha code			
Thunnini	**Tunas**	**Thons**	**Atún**	
Thunnus alalunga	Albacore	Germon	Atún blanco	ALB
Thunnus albacares	Yellowfin tuna	Albacore	Rabil	YFT
Thunnus atlanticus	Blackfin tuna	Thon à nageoires noires	Atún aleta negra	BLF
Thunnus maccoyii	Southern bluefin tuna	Thon rouge du Sud	Atún del Sur	SBF
Thunnus obesus	Bigeye tuna	Thon obèse	Patudo	BET
Thunnus thynnus	Atlantic bluefin tuna	Thon rouge de l'Atlantique	Atún rojo del Atlantico	BFT
Thunnus orientalis	Pacific bluefin tuna	Thon rouge du Pacifique	Atún aleta azul del Pacifico	PBF
Thunnus tonggol	Longtail tuna	Thon mignon	Atún tongol	LOT
Katsuwonus pelamis	Skipjack	Listao	Listado	SKJ
Euthynnus affinis	Kawakawa	Thonine orientale	Bacoreta oriental	KAW
Euthynnus alleteratus	Little tunny	Thonine commune	Bacoreta	LTA
Euthynnus lineatus	Black skipjack	Thonine noire	Barrilete negro	BKJ
Auxis rochei	Bullet tuna	Bonitou	Melvera	BLT
Auxis thazard	Frigate tuna	Auxide	Melva	FRI
Sardini	**Bonitos**	**Bonites**	**Bonitos**	
Allothunnus fallai	Slender tuna	Thon élégant	Atún lanzón	SLT
Cybiosarda elegans	Leaping bonito	Bonite à dos tacheté	Bonito saltador	LEB
Gymnosarda unicolor	Dogtooth tuna	Bonite à gros yeux	Tasarte ojón	DOT
Orcynopsis unicolor	Plain bonito	Palomette	Tasarte	BOP
Sarda australis	Australian bonito	Bonite bagnard	Bonito austral	BAU
Sarda chiliensis	Eastern Pacific	Bonite du Pac.	Bonito del Pac.	BEP

Sarda orientalis *Sarda sarda*	bonito Indo-Pacific bonito Atlantic bonito	oriental Bonite orientale Bonite à dos rayé	oriental Bonito mono Bonito atlántico	BIP BON

Seerfishes and mackerels

Scientific name	**Common names, acknowleged by FAO, in: English French Spanish; 3-alpha code**			
Grammatorcynus bicarinatus *Grammatorcynus bilineatus*	Shark mackerel Double-lined mackerel	Thazard requin Thazard-kusara	Carite cazón Carite cazón pintado	SHM DBM
Scomberomorini *Acanthocybium solandri* *Scomberomorus brasiliensis* *Scomberomorus cavalla* *Scomberomorus commerson* *Scomberomorus concolor* *Scomberomorus guttatus* *Scomberomorus koreanus* *Scomberomorus lineolatus* *Scomberomorus maculatus* *Scomberomorus multiradius* *Scomberomorus munroi* *Scomberomorus niphonius* *Scomberomorus plurilineatus* *Scomberomorus queenslandicus* *Scomberomorus regalis* *Scomberomorus semifasciatus* *Scomberomorus sierra* *Scomberomorus sinensis* *Scomberomorus tritor*	**Seerfishes** Wahoo Serra Spanish mackerel King mackerel Narrow-barred king mack. Monterey Spanish mackerel Indo-Pacific king mackerel Korean seerfish Streaked seerfish Atlantic Spanish mackerel Papuan seerfish Australian spotted mackerel Japanese Spanish mackerel Kanadi kingfish Queensland school mackerel Cero Broad-barred king mackerel Pacific sierra Chinese seerfish West African Spanish mackerel	**Thazards** Thazard-bâtard Thazard serra Thazard barre Thazard rayé Thazard Monterey Thazard ponctué Thazard coréen Thazard cirrus Thazard atlantique Thazard papou Thazard australien Thazard oriental Thazard Kanadi Thazard de Queensland Thazard franc Thazard tigre Thazard sierra Thazard nébuleux Thazard blanc	**Carites** Peto Serra Carite lucio Carite estriado Carite de Monterey Carite del Indo-Pacifico Carite coreano Carite rayado Carite atlántico Carite papuense Carite australiano Carite oriental Carite canadí Carite de Queensland Carite chinigua Carite tigre Carite sierra Carite indochino Carite lusitánico	WAH BRS KGM COM MOS GUT KOS STS SSM PAP ASM NPH KAK QUM CER BBM SIE CHY MAW
Scombrini *Rastrelliger brachysoma* *Rastrelliger faughni* *Rastrelliger kanagurta* *Scomber australasicus*	**Mackerel** Short mackerel Island mackerel Indian mackerel Spotted chub mackerel Atlantic chub	**Maquereaux** Maquereau trapu Maquereau des îles Maquereau des Indes Maquereau tacheté Maquereau espagnol de	**Caballa** Caballa rechoncha Caballa isleña Caballa de la India Caballa pintoja Estorino del Atlántico	RAB RAF RAG MAA

Scomber colias *Scomber japonicus* *Scomber scombrus*	Atlantic chub mackerel Indo-Pacific Chub mackerel Atlantic mackerel	l'Atlantico Maquereau espagnol indo-Pacífico Maquereau commun	Atlantico Estorino del Indo-Pacífico Caballa del Atlántico	MAS MAS MAC
Gasterochismatinae *Gasterochisma melampus*	Butterfly kingfish	Thon papillon	Atún chauchera	BUK

Billfishes

Scientific name	**Common names, acknowleged by FAO, in: English French Spanish; 3-alpha code**			
Xiphias gladius *Istiophorus albicans* *Istiophorus platypterus* *Istiompax indica* *Makaira mazara* *Makaira nigricans* *Kajikia albidaKajikia audax* *Tetrapterus angustirostris* *Tetrapterus audax* *Tetrapterus belone* *Tetrapterus georgei* *Tetrapterus pfluegeri*	Swordfish Sailfish Indo-Pacific sailfish Black marlin Indo-Pacific blue marlin Blue marlin Atlantic white marlin Striped marlin Shortbill spearfish Striped marlin Mediterranean spearfish Roundscale spearfish Longbill spearfish	Espadon Voilier de l'Atantique Voilier de l'Indo-Pacifique Makaire noir Makaire bleu de l'Indo-Pacifique Makaire bleu de l'Atlantique Makaire blanc de l'Atlantique Marlin rayé Makaire à rostre court Marlin rayé Marlin de la Méditerranée Makaire épée Makaire bécune	Pez espada Pez vela del Atlántico Pez vela del Indo-Pacífico Aguja negra Aguja azul del Indo-Pacífico Aguja azul del Atlántico Aguja blanca del Atlántico Marlín rayado Marlín trompa corta Marlín rayado Marlín del Mediterráneo Marlín peto Aguja picuda	SWO SAI SFA BLM BLZ BUM WHM SSP MLS MSP RSP SPF

Fossil records

The first fossil records of *Scombridae* are dated from the beginning of the lower Eocene epoch (60-40 million years ago) during the lower Tertiary period. As for the *Istiophoridae*, the oldest fossils are dated from the upper Cretaceous epoch (70-90 million years ago) during the Secondary period. For the *Xiphiidae*, the oldest fossil records are dated from the Paleocene epoch of the lower Tertiary period, i.e. 57-65 million years ago (Berg, 1958).

Morphological characteristics

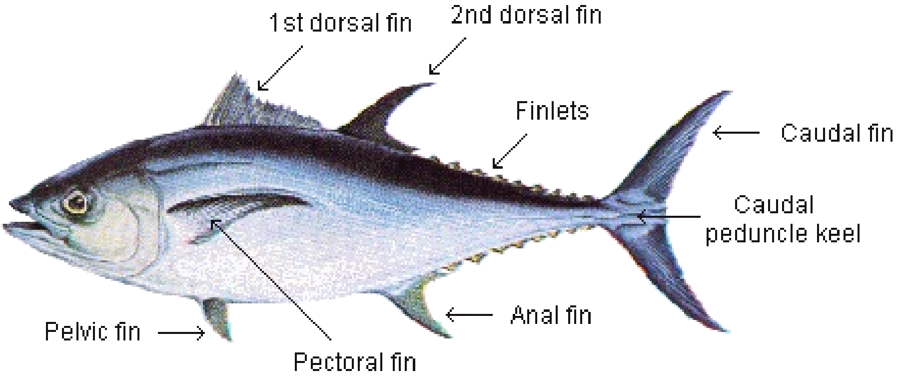
Morphology of larvae

It is often difficult or impossible to identify larvae and, in some cases, early juveniles by anatomical characteristics or colour patterns. Biochemical or genetic methods can be used to distinguished the larvae of the various species (Elliott and Ward, 1995, Chow *et al.*, 2003). Diagnostic keys are available for larvae between 3 and 12 mm standard length. Larvae smaller than 3 mm are virtually indistinguishable (Nishikawa and Rimmer, 1987).

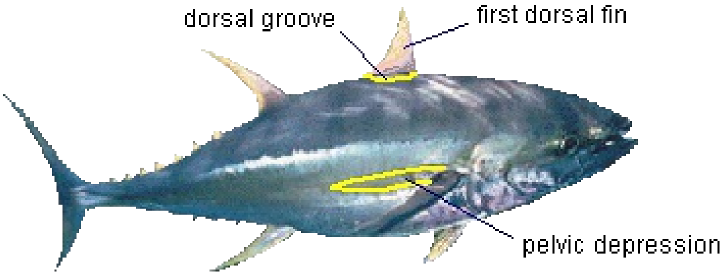
Morphology of juveniles and adults

Characteristics common to both scombrids and billfishes

Both scombrids and billfishes have two distinct dorsal fins, generally separated, the first one supported by spines and the second only by soft rays. The pelvic fins are inserted below the base of the pectoral fins. The caudal fin is deeply notched.



All scombrids and billfishes except swordfish have a pair of caudal keels on the middle of the caudal peduncle at the base of the caudal fin. The swordfish has only a large median caudal keel. The more advanced members of the Scombridae family also have a large median keel anterior to the pair of caudal keels. The bodies of all the Scombroidei are robust, elongate and streamlined. The first dorsal and first anal fins of all scombrids and billfishes, except swordfish, can fold down into grooves and the pectoral and pelvic fins into depressions when the fish is swimming rapidly.



The scombrids and billfishes, all have four gill arches on each side. The gill filaments are ossified as "Gill rays".

Scombrids

The scombrids are characterised by the presence of at least four finlets behind the dorsal and the anal fins. The pelvic fins are smaller than the pectoral fins or of equal size. Except for the primitive butterfly kingfish, which body is covered by large cycloid scales, the body of all the scombrids is naked or covered with small to moderate-sized scales. The bonitos (Sardini) are intermediate between the seerfishes and the tunas. As is the case for the tunas, they have a well-developed corselet of scales, but they lack the two longitudinal ridges on the upper surface of the tongue. The most primitive Scombrinae are the mackerels (Scombrini), the seerfishes (Scomberomorini) and the two-line mackerels (*Grammatorcynus* spp.). The mackerels have only two caudal keels, whereas the seerfishes and the two-line mackerels have a larger median keel in front of the pair of keels.

The tunas are the most highly evolved of the scombrids. They are unique among bony fish in having heat exchanger systems that allow them to regulate their body temperature, as can birds and mammals (see the thermoregulation).

Billfishes

The billfishes are characterised by their rostrum, an extension of the upper jaw, which extends much beyond the lower jaw.

Billfishes rostrum

The rostrum has a flat, sword-like cross section for the swordfish and a rounded, spear-like cross section for the Istiophoridae.
The swordfish is also characterised by the absence of pelvic fins and scales. Its dorsal fins are well separated, and has only one large median caudal keel. The Istiophoridae have long, rigid, tapering pelvic fins. Their bodies are covered with small, elongate, bony scales. Their first dorsal fin has a long base and terminates close to the origin of the second dorsal fin.

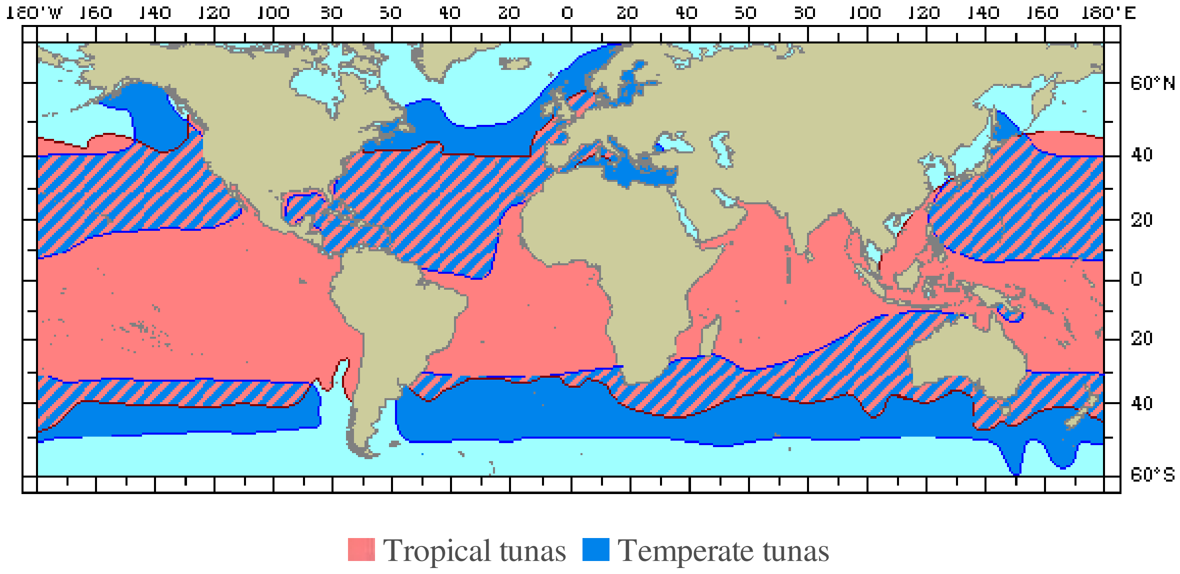
Geographical distribution

Tropical and temperate tunas

Because of different distributions due to their specific thermal tolerances and because of exploitation by different fisheries, a distinction is made between tropical and temperate tunas. Tropical tunas are found in waters with temperatures greater than 18° C (although they can dive in colder waters) whereas temperate tuna are found in waters as cold as 10°C, but can also be found in tropical waters (Brill, 1994).

Tropical tunas: skipjack and yellowfin
Intermediate tunas: bigeye
Temperate tunas: albacore, Pacific bluefin, Atlantic bluefin and southern bluefin

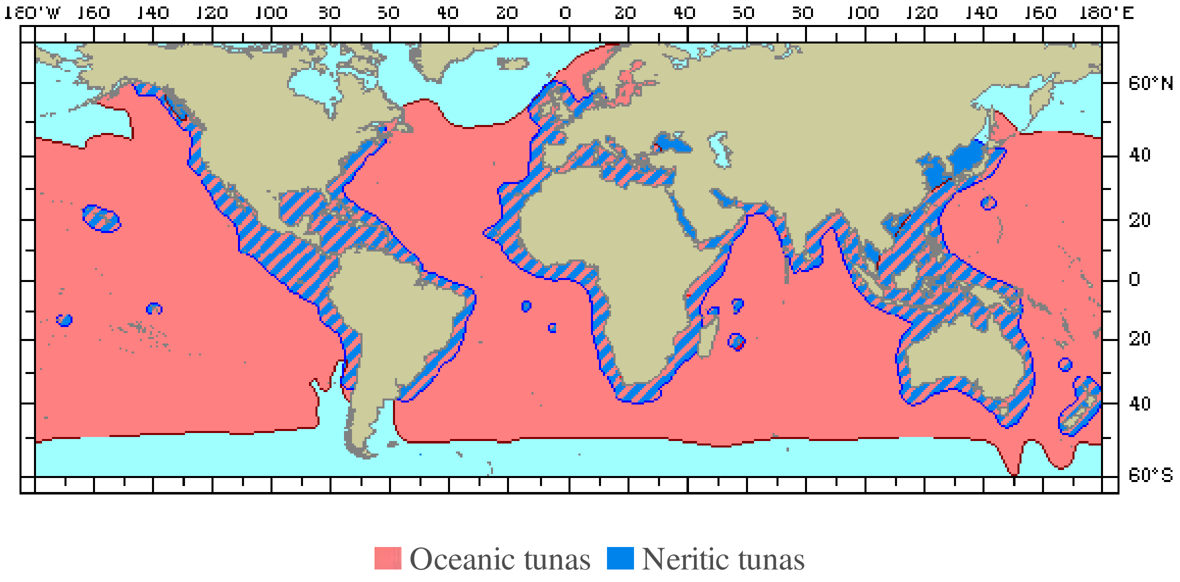
Tropical and temperate tunas



Scombrids

Tunas prefer oceanic waters, and 3 of the 8 species of ***Thunnus*** are found worldwide except in the Arctic Ocean. Most bonitos and little tunas (***Euthynnus*** spp.) are primarily neretic, *ie* coastal fishes, but the distribution of individual species is often widespread. The frigate and bullet tunas (***Auxis*** spp.) are probably both oceanic and coastal (Olson and Boggs, 1986). The slender tuna and the butterfly kingfish have circum-global distributions in the Southern Ocean. Most mackerels and seerfishes have restricted ranges of distribution. Exceptions are the Spanish mackerel and the wahoo which are found worldwide.

Oceanic and neritic tunas



Billfishes

Billfishes are widely distributed, at least, throughout the oceans in which they occur. The exception are the Mediterranean spearfish, which occurs only in the Mediterranean Sea, and perhaps the roundscale spearfish, which occur in the northeastern Atlantic Ocean around the Canary and Madeira Islands and in the western Mediterranean Sea. However, only the swordfish is cosmopolitan. All other *Istiophoridae* are being confined to the Atlantic Ocean or to the Indian and Pacific Oceans.

Occurrence of the tuna, bonito and billfish species in the different oceans

Common names	Scientific name	Areas of occurrence
Tunas and bonitos		
Skipjack	*Katsuwonus pelamis*	worldwide
Yellowfin tuna	*Thunnus albacares*	worldwide
Bigeye tuna	*Thunnus obesus*	worldwide
Albacore tuna	*Thunnus alalunga*	worldwide
Atlantic bluefin tuna	*Thunnus thynnus*	Atlantic Ocean
Pacific bluefin tuna	*Thunnus orientalis*	Pacific Ocean
Southern bluefin tuna	*Thunnus maccoyii*	southern parts of Atlantic, Indian and Pacific Ocean
Longtail tuna	*Thunnus tonggol*	Indian Ocean, western Pacific Ocean
Blackfin tuna	*Thunnus atlanticus*	western Atlantic Ocean
Kawakawa	*Euthynnus affinis*	Indian, western and central Pacific Oceans
Black skipjack	*Euthynnus lineatus*	eastern Pacific Ocean
Little tunny	*Euthynnus alleteratus*	Atlantic Ocean
Bullet tuna	*Auxis rochei*	worldwide
Frigate tuna	*Auxis thazard*	Indian and Pacific Oceans
Slender tuna	*Allothunnus fallai*	Southern Ocean
Billfishes		
Swordfish	*Xiphias gladius*	worldwide
Atlantic sailfish	*Istiophorus albicans*	Atlantic Ocean
Indo-Pacific sailfish	*Istiophorus platypterus*	Indian and Pacific Oceans
Black marlin	*Makaira indica*	Indian and Pacific Oceans
Indo-Pacific blue marlin	*Makaira mazara*	Indian and Pacific Oceans
Atlantic blue marlin	*Makaira nigricans*	Atlantic Ocean
Atlantic white marlin	*Tetrapterus albidus*	Indian and Pacific Oceans
Striped marlin	*Tetrapterus audax*	Indian and Pacific Oceans

Habitat and biology

Ecological niche

Tunas are pelagic marine fish, spending their entire lives relatively near the surface of tropical, subtropical and temperate oceans and seas. Scombrids and billfishes live primarily in the water layers above the thermocline, but are able to dive to depth of several hundred meters (see the Vertical distribution section). Tuna species attaining only small sizes and juveniles of those attaining large sizes are encountered in epipelagic waters (from the surface to the thermocline) whereas large tunas tend to be mesopelagic and are found also in deeper and cooler waters.

Epipelagic tunas: skipjack and bonitos, juveniles of large tunas, billfishes

Mesopelagic tunas (adults): albacore, bigeye and bluefin

Tunas that are found at both depth ranges: yellowfin, swordfish

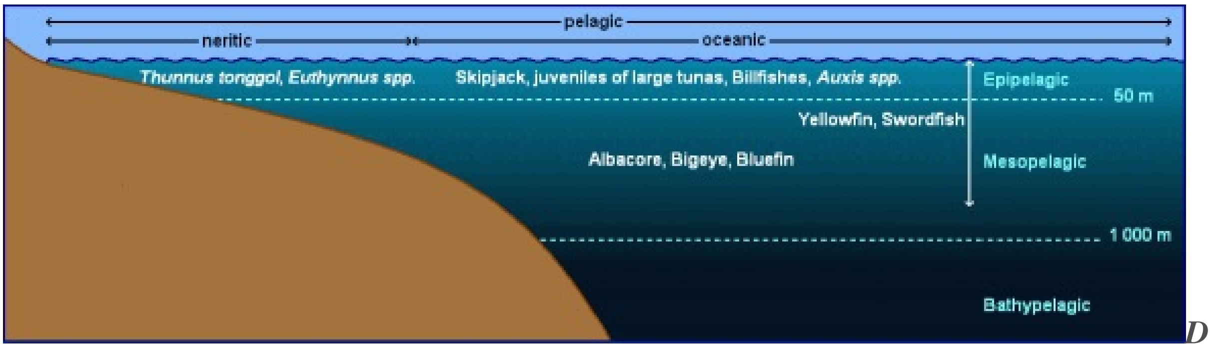
Some tunas are found in both offshore and coastal waters and others entirely, or almost entirely, in coastal waters.

Mid-ocean species: yellowfin and bigeye, swordfish

Coastal species: *Thunnus tonggol*, other bonitos than *Auxis spp.*, little tunas (*Euthynnus spp.*)

Species found in both waters: skipjack, albacore, Pacific bluefin, Atlantic bluefin and southern bluefin, *Auxis spp.*

Seerfishes are generally restricted to coastal waters and enter estuaries to feed. One species, the Chinese seerfish moves long distances in freshwater up the Mekong River in China.



Distribution of tunas and tuna-like in the water

Tuna and their environment

Important environmental parameters for tuna are the sea surface temperature, the quantity of dissolved oxygen in the water and the salinity. Lower thermal boundaries vary between 10°C for temperate tunas and 18°C for tropical tunas (see above; Brill, 1994). The minimum oxygen requirement is estimated between 2 to 2.7 ml/l for principal market tuna species except for bigeye tuna which can tolerate oxygen concentrations as low as 0.6 ml/l (Sharp, 1978 ; Lowe, 2000). Most tunas tend to concentrate along thermal discontinuities such as oceanic fronts (Sund, 1981).

Vertical distribution constraints and diving behavior

The vertical distribution of most species of tunas is influenced by the thermal and oxygen structure of the water column. Tuna species attaining only small sizes and juveniles of those attaining large sizes tend to live near the surface, whereas adults of large species are found in deeper waters. The use of deep longlines showed that bigeye can be found at depths as great as 300 m (Suzuki *et al.*, 1977). Albacore are also caught under FADs at depths to about 200 m (Bard *et al.*, 1998). Acoustic telemetry has shown that billfishes are found near to the surface during the day, descending more frequently to greater depths at night (Block *et al.*, 1992a). Yellowfin, Bigeye, Bluefin and Swordfish show deeper dives than other species of tuna and billfish (Fromentin & Fonteneau, 2001; Sund, Blackburn & Williams, 1981):

- Yellowfin tuna has been observed to dive at more than 1100 m (record of 1200 m, L. Dagorn *et al.*, 2006).
- Bigeye tuna are capable of diving to depths of more than 1200 m (record of 1800 m, Schaefer, *Comm. pers.*).
- Atlantic bluefin tuna are able to dive to depths in excess of 1000 m, encountering an exceptionally wide range of temperatures (Block *et al.*, 2005).
- Swordfish make large vertical excursions, coming close to the surface at night and diving as deep as 600 m during the day ((Carey and Robison, 1981); Sedberry and Loefer, 2001), even 900 m (Takahashi *et al.*, 2003).

Other tunas show lesser diving capabilities, as, for example, *Euthynnus affinis* which have been observed at 400 m depth (Lee, 1982).

Schooling behavior

Tunas use schooling to their advantage when they forage. Some tunas form parabolic-shaped schools to encircle their prey. Most tunas school according to size. Juveniles of tunas attaining large sizes are, therefore, often associated with tunas attaining only small sizes, such as skipjack or bonito. Schools of large adults consist of a few scattered individuals. Schooling offers protection for juvenile tunas by confusing predators and reducing the likelihood that any single fish will become a victim to a predator. Atlantic bluefin tuna can form giant schools spread over several nautical miles when migrating into the Mediterranean Sea to spawn during the summer. As is the case with the other fishes, the structure of tuna schools is maintained by the lateral line. Schools can gathered over 5000 individuals.

Migration and other movements

All tunas and tuna-like fishes move constantly to search for food and to keep water passing over their gills. Migrations are seasonal movements, often over long distances, for the purpose of feeding or reproduction. Temperate tunas, i.e. albacore, Atlantic bluefin and Pacific bluefin, migrate long distances between temperate waters, where they feed, and tropical waters, where they spawn without moving among different oceans. Southern bluefin tuna migrates among the southern parts of Atlantic, Indian and Pacific Oceans. Although, the distribution of the three species of bluefin is quite extended, their spawning is restricted to relative small areas of tropical waters. Tropical tunas, i.e. skipjack and yellowfin, are less migratory in terms of long-distance directional movements, although several tagged yellowfin released in the western Atlantic have been recaptured in the eastern Atlantic. Bigeye have some of the characteristics of both temperate and tropical tunas. They apparently do not make trans-oceanic migrations, but like the temperate tunas, they migrate back and forth between feeding grounds in temperate waters and their spawning grounds in tropical waters. When they are not making directional migration, tunas move nearly all the time in search of areas where the food is most abundant. Fishermen are sometimes able to predict on the basis of oceanic conditions where the fish are likely to appear and then, they can transfer their operations to those areas. Less is known of the movements of billfishes, but apparently, they make seasonal migrations between temperate waters, where they feed, and tropical waters, where they spawn. For instance, blue marlin display extensive trans-equatorial and inter-oceanic movements from the Atlantic into the Indian Ocean (Ortiz et al., 2003).

Swimming

Tunas are excellent swimmers, and their bodies are designed for high performance at both sustainable and burst swimming speeds (Dickson, 1995). Tunas must swim constantly to satisfy their oxygen requirements and consequently stay alive. The direction of movements of some species, such as skipjack, seem to be dictated solely by the availability of food. The movement of other species, such as the three species of bluefin, seem to be influenced by both the distribution of food and the need to return to their ancestral spawning grounds at the proper time. Tunas can move up to 15 km per night in order to forage on organisms that swim upward from deeper waters at that time.

Tunas have higher cruising speeds than do other active fishes, including other scombroids (Beamish, 1978; Block *et al.*, 1992b). The morphology of the body and caudal fin of tunas is optimal for prolonged, high-speed swimming. Similar body designs are found also in cetaceans, carangids, certain sharks and even the extinct reptilian ichthyosaurs. Webb (1984) lists the following morphological adaptations:

- a lunate tail of large span, but relatively small chord to maximize the thrust
- a narrow caudal peduncle to provide for locally-large amplitude displacements and to control the angle of attack
- a large anterior body depth and mass to reduce recoil energy losses
- a relatively-rigid streamlined body to both minimize the drag and maximize the thrust

Long-range swimming

The net distances travelled by tunas and billfishes (shortest distances between the locations of release and recapture) exceed those of any other fish, as shown by the following records obtained from tagging studies (from Joseph *et al.*, 1988 for tunas and Orbesen *et al.*, 2008 for billfishes):

- 10,790 km for a Pacific bluefin tuna (from southeast of Japan to off Baja California)
- 10,680 km for a black marlin (from off Baja California to Norfolk Island in the South Pacific Ocean)
- 9,500 km for a skipjack tuna (from off Baja California to the Marshall Islands)
- 8,500 km for an albacore tuna (from off California to off Japan)
- 7,700 km for an Atlantic bluefin tuna (accross the Atlantic Ocean)
- 15,744 km for a blue marlin (accross the Atlantic Ocean)
- 14,556 km for a black marlin (across the Pacific Ocean, comm.. pers.)
- 6,523 km for a white marlin (across the Atlantic Ocean)
- 3,845 km for a sailfish (across the Atlantic Ocean)

In addition, net movements of more than 5,000 km have been recorded for yellowfin tuna, bigeye tuna, blue marlin, striped marlin and sailfish.

Short-range, fast swimming

Scombrids and billfishes are adapted to fast swimming. The champions are, of course, the most highly evolved scombrids, the bonitos (Sardini) and the tuna (Thunnini) and the billfishes. They are able to exhibit startling bursts of speed, often exceeding one body length per second.The record (for all bony fishes) belongs to the black marlin (*Makaira indica*), which has been clocked at over 130 km/h.

Estimated maximun swimming speed of some tunas and billfishes

Species	Sustained in m/s	Burst in m/s
Scombrids		
Thunnus albacares(1)	0.64	20.46
Thunnus obesus (1)	0.6	-

Thunnus thynnus (1)	3.49	-
Katsuwonus pelamis (1)	0.84	9.41
Euthynnus affinis (1)	0.76	5
Auxis rochei (1)	0.68	-
Sarda chiliensis (1)	0.88	3.70
Sarda sarda (1)	0.35	1.2
Acanthocybium solandri (1)	0.4	21.23
Scomber japonicus (1)	0.92	2.25
Scomber scombrus (2)	0.98	5.4
Billfishes		
Tetrapterus audax (3)	1.8	-
Makaira indica (3)	-	36.1
Makaira nigricans (3)	1	2.25
Xiphias gladius (2)	-	24.86

References
(1): Magnuson (1978)
(2): Wardle and He (1988)
(3): Block *et al.* (1992b)

Physiological aspects of swimming

In order to swim at high speeds for long periods, tunas are capable of taking in and utilizing large amounts of oxygen.

In contrast to other fishes that contract their jaws and opercular muscles to pump water over their gills, tunas and billfishes (and some species of sharks) ram ventilate, that is they swim through the water with their mouths open, which forces water over their gills. This is an efficient way to get a large amount of water flowing through the gills at a low energetic cost, but it has an important drawback: tunas cannot stop swimming, or they will suffocate! They must swim at a speed of at least 0.65 m/s to provide sufficient flow of water over their gills.

The amount of gill surface of tunas is up to 30 times those of other fish, and for some tunas the absorptive surface approaches those of the lungs of mammals of comparable weight (Joseph *et al.*, 1988). This large surface enables the tunas to extract about half of the oxygen present in the water flowing over their gills.

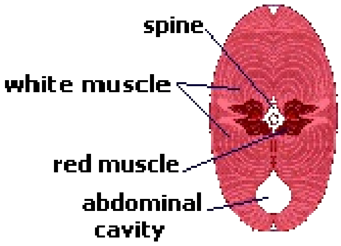
To transfer oxygen from the gills to the other tissues, tunas have hearts that are about 10 times the size, relative to the weight of the entire body, of those of other fish. The blood pressure of tunas is about three times those of other fishes, and their hearts pump blood at a rate about three times those of other fish. The blood of tuna has a hematocrit of 40%, a value usually associated with diving mammals.

Scombrids and billfishes, like most fish, have two types of muscle, white and red. The white muscles function during short bursts of activity, while the red muscles, which have a relatively large mass, allow the fish to swim at high speeds (up to 45 km/h) for long periods without fatigue, as demonstrated by tagging studies with conventional and sonic tags (Joseph *et al.*, 1988 ; Bushnell and Holland, 1997).

The proportion of red muscle is much greater for tunas than for other fish (Dickson, 1995) and their white muscles are capable of working in both aerobic and anaerobic conditions. Therefore, the increase in swimming speed can be portrayed as follows :

	sustained speed	high speed	burst speed
red muscle in action	yes		
white muscle in action			
aerobic condition	yes	yes	
anaerobic condition	yes	yes	yes

The red muscles are located deep within the body, and appear to be more important at the anterior part of the fish. They extend from the vertebral column to a lateral subcutaneous position. In contrast to other fishes, the proportion of red muscle does not seem to increase with the size of the tuna, probably because of greater muscle efficiency and labor sharing between red and white muscles, to which both endothermy and thermoregulation could contribute (Graham *et al.*, 1983).



Muscle

Heart and white muscle aerobic capacities are significantly greater in tunas than in billfishes and other scombrids.

Recovery from intense activities

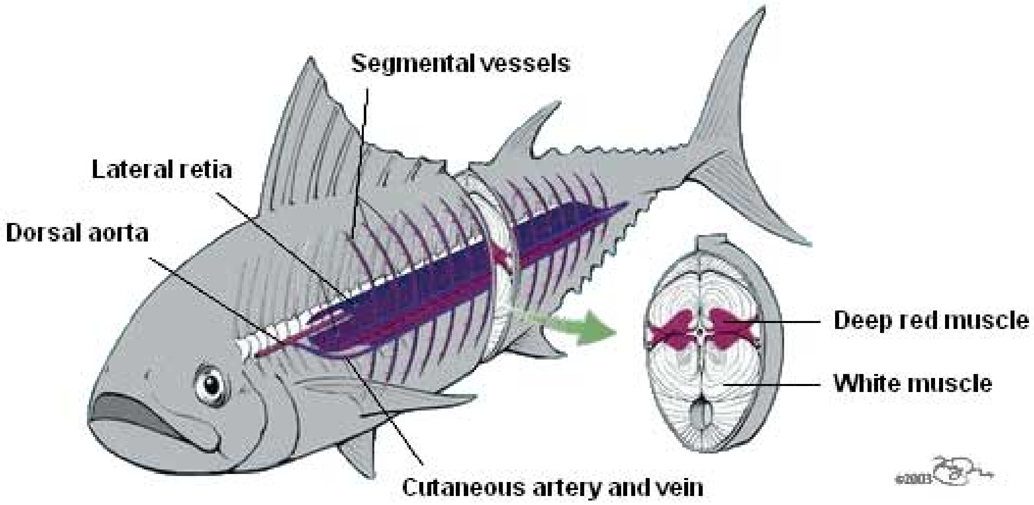
Furthermore, tunas and billfishes are capable of recovering more quickly than other fish after intense activities, such as that involved in capture of prey. For some tunas, the rates of removal of lactate from the blood and white muscle tissue approximate the rates measured in mammals, which allows the tuna to recover within two hours (Dickson, 1995).

Thermoregulation in tuna

As a consequence of swimming constantly to maintain hydrostatic equilibrium (Magnuson, 1973) and oxygenate the blood (Roberts, 1978), muscular metabolism continuously generates heat as a byproduct. Tunas get rid of this excess, but, on the other hand, the heat can be used by the tuna to enable them to forage in cold waters.

Metabolic mechanism for thermoregulation

Among all bony fish, the Thunnini are unique in their ability to regulate their body temperatures, due to a complex counter-current heat exhanger system, also called the *rete mirabile* (miraculous network) (Stevens and Neil, 1978). The only other fishes with this system are some sharks of the family *Lamnidae* (Collette, 1978).



Rete mirabile (from Weinheimer, 2003)

The tuna maintain their body temperatures above that of the ambient water by passing arterial blood through vascular countercurrent heat exchangers. All species of tuna have a lateral rete, consisting of small arteries branching from the lateral subcutaneous arteries and small veins emptying into the lateral veins (Graham *et al.*, 1983). In addition, many species of tuna also have a central rete within the vertebral haemal canal, consisting of arteries from the dorsal aorta and veins to the posterior cardinal veins (Stevens and Neil, 1978). The arterial blood is, then, warmed by the venous blood that flows through the red swimming muscles (Holland *et al.*, 1992).

The *rete mirabile* retains between 70 and 99 % of the heat produced by the red muscle fibers, and provide a barrier between the red muscle and the environment (Graham *et al.*, 1983). However, when excessive temperatures have been generated by heavy exercise, tunas appear to be able to control the efficiency of the heat exchangers by closing down some blood vessels of the *rete mirabile*, allowing heat to dissipate into the colder ambient water (Bushnell and Holland, 1997).

Measurements of body temperatures and ambient temperatures with histological analyses of the *rete mirabile* show that tunas as small as 207 mm in length can maintain their body temperatures more than 3°C above the ambient temperature, and thus can be considered to be endotherms (Graham *et al.*, 1983). Tuna body temperatures are often 10°C greater than those of ambient water. The maximum temperature difference was recorded for an Atlantic bluefin tuna, for which the body temperature was 21.5°C greater than the surrounding water (Graham *et al.*, 1983).

The thermoregulatory system cannot conserve heat indefinitely, and when a fish has been foraging in deep, cold water for an extended period, its body temperature decreases. When this happens, it can ascend to warmer water and disengage its thermoregulatory system to allow rapid warming of the tissues (Holland *et al.*, 1992).

Behavioural mechanisms for thermoregulation

Combined with the physiological mechanisms, movements into cooler water will facilitate heat dissipation (Bushnell and Holland, 1997).

Advantages of thermoregulation

Thermoregulation allows the tunas to sustain high swimming speeds for long periods and to recover quickly after prolonged exertion (Carey *et al.*, 1971), because most biochemical reactions proceed more rapidly at higher temperatures. Therefore, according to Bushnell and Holland, 1997, elevated body temperatures allow:

red muscle to contract more quickly, approaching the contraction rate of white muscle and consequently, contributing to high-speed swimming resulting from white muscle contractions
more rapid transfer of oxygen from blood to muscle cells
more rapid recovery, by enhancing the breakdown of lactic acid

In addition, being "warm bodied" allows the tunas to have a good vision at significant depths by maintaining their brains and eyes at greater than ambient temperatures (Bushnell and Holland, 1997). It also allows the tuna to be more sensitive to thermal gradients (Sharp and Dizon, 1978).
Also, because of that, the tuna can forage beneath the thermocline, in deep water, without suffering radical decreases in their core temperature. For example, a bigeye tuna was observed to dive 250 meters in one minute, going from 24°C to 9°C water (Holland *et al.*, 1992).

Trophic relations and growth

Growth stages

The following three stages can be distinguished:

larvae (recently hatched individuals which are considerably different in appearance from juveniles or adults)
juveniles (similar in appearance to adults, but sexually immature)
adults (sexually mature fish)

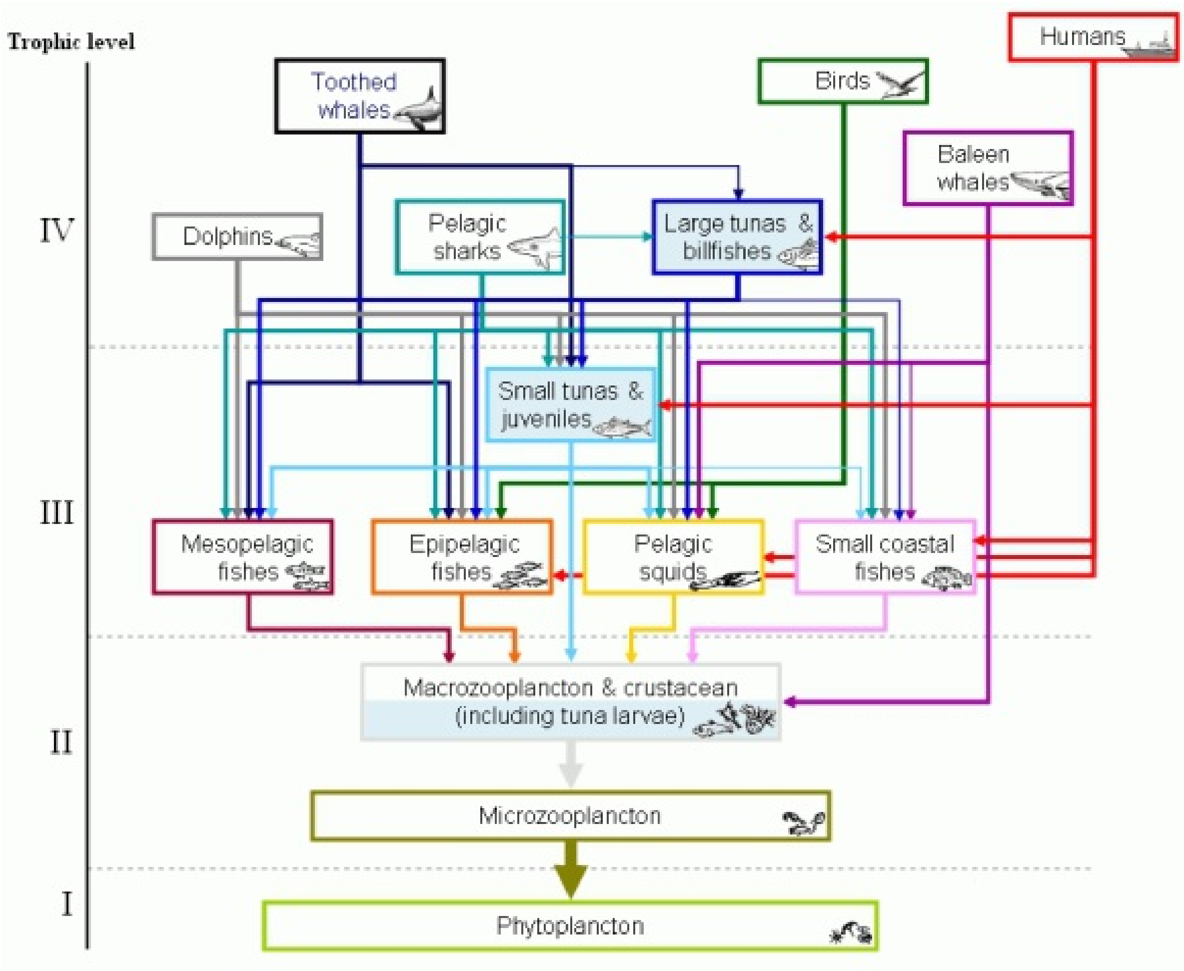
Trophic position of larvae

Larvae of tunas and tuna-like fishes live in warm surface waters and feed primarily on the zooplankton including small crustaceans and larvae of crustaceans, fishes, molluscs and jelly-fish. Larvae of tunas and tuna-like species are preyed upon by zooplankton foragers, such as larger larvae and early juveniles of pelagic fishes. Cannibalism is, therefore, an important cause of mortality for tuna larvae.

Trophic position of juveniles and adults

Tunas and tuna-like fishes in the oceanic food web

Tunas and billfishes prey on fish, squid and crustaceans. The larger individuals (wahoo, bonitos, tunas and billfishes), which feed on pelagic fishes, are positioned at the top of the trophic web. The smaller individuals (juvenile tunas and billfishes, mackerels and seerfishes) prey on zooplankton (mainly crustaceans) and constitute part of the ration of large scombroids, sharks, cetaceans and seabirds. Analyses of stomach contents of yellowfin and skipjack tuna indicate that they feed on small epipelagic fishes between 1 and 10 cm in length (Roger, 1994). Since these preys of yellowfin and skipjack feed directly on zooplankton (mainly copepods), it seems that the tunas are at the top of a short food web, which is probably very efficient from the point of view of energetics.



Position of tunas and tuna-like fishes in the oceanic food web

Food items

Tunas and billfishes are opportunistic feeders. At the species level, they do not have strong preferences for certain types of prey. However, on a regional scale and at a given time, a few species may represent almost all of the food of fish of a specific age group (Cayré *et al.*, 1988). Tunas and billfishes prey on pelagic or epipelagic fishes (including juveniles of tunas), crustaceans and cephalopods (squids). Yellowfin and bigeye tunas as well as swordfish feed on mesopelagic fishes (Ménard *et al.*, 2000, Allain, 2005). Coastal tunas feed on neritic and epipelagic prey (Olson and Boggs, 1986). Larger tunas feed on small pelagic fishes such as mackerels, small tunas, carangids or flying fishes.

Example of preys that are often found in the stomach of tunas

Foraging behavior of juveniles and adults

Tunas and billfishes are predators that locate their prey visually. To satisfy their food requirements tunas and billfishes have to swim long distances. Their type of locomotion is, therefore, particularly adapted to the search for prey in a large volume of water with the least expenditure of energy. However, they appear less effective than transient predators, such as esocids, in actually capturing the prey (Webb, 1984). To compensate for this, tunas tend to break up schools of prey, producing disorientation and straggling, and/or search for prey in schools (Webb, 1984; Partridge, 1982). Tunas can detect minute traces of scents of oils, proteins and amino-acids of the mucus layer produced by their prey. When prey is detected, some tunas show changes in their behavior consisting of a general increase of activity (also called frenzy): increase in swimming speed, change in swimming pattern, jaw snapping and display of dark stripes on the flanks. Tropical tunas and swordfish often dive down at significant depths below the thermocline (commonly at 500 m) to feed on mesopelagic fishes (Holland *et al.*, 1992). It is commonly believed that tunas feed during the day. However, sonic tracking experiments show that some tunas feed also at dusk, when mesopelagic micronecton migrate toward the surface (Bard *et al.*, 1998).

Growth of juveniles and adults

Growth rates

Most scombrids grow rapidly and reach their adult sizes in a few years. Average growth rates vary according to the species, the age and the location. In general, larger tunas grow to about 40 to 55 cm the first year, then the annual growth rate ranges between 20 to 30 cm per year decreasing with age. Tuna species attaining only small sizes grow to 20 to 35 cm in the first year and their annual length increments rapidly decrease to less than 10 cm. In the Atlantic and Indian Oceans, several studies have shown that yellowfin grow rapidly during the first year, slowing their growth during the next one or two years and then having again a fast growth before gradually slowing down as the maximum size is approached. Seerfishes and mackerels have also a fast growth during their first years of life. Sizes of 35 to 45 cm at age 1 year are common.

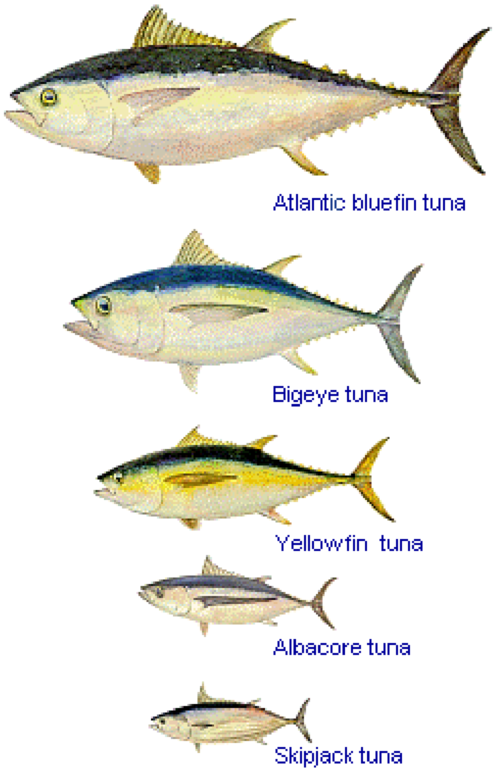
Billfishes can grow to more than 80 cm during their first year of life. After this very fast juvenile growth, adult growth rates are comparable to those of tunas.

Weights and lengths ranges

The maximum weights attained by tunas range from about 1 to 2 kg for bullet and frigate tunas to more than 600 kg for Atlantic bluefin tuna. The maximum lengths attained by tunas range from about 50 cm for bullet and frigate tunas to more than 300 cm for Atlantic bluefin tuna.

Seerfishes, mackerels and bonitos are relatively small (less than 1 meter in length), except for some species of seerfishes such as the king mackerel or the narrow-barred king mackerel which grow to more than 240 cm, for 70 kg.

The smallest billfish is the Mediterranean spearfish, which reaches a maximum length of a little more than 180 cm. The largest billfishes are the black marlin and the Indo-Pacific blue marlin, which reach lengths of more than 4 m and weights of more than 600 kg.



Relative sizes of tuna main market species

Size

Common and maximum sizes of tunas and billfishes

Tunas (1)

Scientific name	Common size (in cm)	Maximum size (in cm)	Maximum weight (in kg)
Auxis rochei	15-35	50	-
Auxis thazard	25-40	58	-
Euthynnus lineatus	30-65	70	9
Euthynnus alleteratus	30-80	100	12
Euthynnus affinis	30-60	100	13
Katsuwonus pelamis	40-80	108	33
Thunnus atlanticus	40-70	100	19
Thunnus alalunga	40-100	127	40
Thunnus tonggol	40-70	130	35
Thunnus albacares	60-150	200	175
Thunnus maccoyii	160-200	225	160
Thunnus obesus	70-180	230	200
Thunnus thynnus	80-200	300	650

Bonitos (1)

Scientific name	Common size (in cm)	Maximum size (in cm)	Maximum weight (in kg)
Cybiosarda elegans	35-45	50	5
Sarda sarda	30-50	85	7.5
other *Sarda* *	30-50	100	-
Allothunnus fallai	65-95	96	10
Orcynopsis unicolor	40-90	130	13
Gymnosarda unicolor	65-150	200	131

* *Sarda australis, S. chiliensis, S. orientalis, S. sarda*

Seerfishes and mackerels (1)

Scientific name	Common size (in cm)	Maximum size (in cm)	Maximum weight (in kg)
Rastrelliger faughni	-	20	0.75
Rastrelliger brachysoma	15-25	35	-
Rastrelliger kanagurta	15-25	35	-
Grammatorcynus spp.	-	60	3.5
Scomber spp.	15-30	40-50	1
Scomberomorus multiradius	-	35	0.5
Scomberomorus concolor	-	75-80	-
Scomberomorus guttatus	-	75-80	-
Scomberomorus niphonius	-	100	4.5
Scomberomorus cavalla	20-70	170	-
Scomberomorus commerson	30-90	220	45
Gasterochisma melampus	74-164	164	-
Acanthocybium solandri	100-170	210	80

Billfishes (2)

Scientific name	Common size (in cm)	Maximum size (in cm)	Maximum weight (in kg)
Tetrapterus georgei	-	160 BL	21
Tetrapterus pfluegeri	-	200 BL	45
Tetrapterus angustirostris	-	200 TL	52
Tetrapterus belone	-	240 BL	70
Tetrapterus albidus	130-210 BL	280 TL	82

Tetrapterus audax	140-280 BL	350 TL	200
Istiophorus albicans	125-210 BL	315 TL	58
Istiophorus platypterus	140-240 BL	340 TL	100
Xiphias gladius	115-190 BL	445 TL	540
Makaira nigricans	230-345 TL	375 TL	580
Makaira indica	170-210 BL	448 TL	700
Makaira mazara	200-300 BL	447 TL	900

Notes for billfishes: BL = Body Length, TL = Total Length

References:
(1): Collette and Nauen (1983)
(2): Nakamura (1985)

International Game Fish Association (IGFA) records

Tunas and bonitos

Common name	Record size (in cm)	Record weight (in kg)	Location and year of capture
Sarda chiliensis	-	6.3	off Baja California, 1980
Euthynnus lineatus	-	11.8	off Baja California, 1991
Euthynnus alleteratus	92.7	12.2	off Florida, 1976
Katsuwonus pelamis	99	18.9	off Mauritius island, 1982
Thunnus alalunga	123	40	off Canary Islands, 1972
Acanthocybium solandri	-	72	off Baja California, 1996
Thunnus albacares	208	176.4	west coast of Mexico, 1977
Thunnus obesus	236	197.3	off Peru, 1957
Thunnus thynnus	304	679	off Nova Scotia, 1979

Seerfishes and mackerels

Common name	Record size (in cm)	Record weight (in kg)	Location and year of capture
Scomber japonicus	-	1.9	off Baja California, 1986

Swordfish and billfishes

Common name	Record size (in cm)	Record weight (in kg)	Location and year of capture
Istiophorus albicans	-	61.4	off Nigeria, 1991
Tetrapterus albidus	-	82.5	off Brazil, 1979
Istiophorus			

Istiophorus platypterus	327.7	100.2	off Galapagos, 1947
Tetrapterus audax	-	224.0	off New Zealand, 1986
Xiphias gladius	445	536.1	off Chile, 1953
Makaira mazara	-	624.1	off Hawaii, 1982
Makaira nigricans	-	636.0	off Brazil, 1992
Makaira indica	442	707.6	off Peru, 1953

Source: IGFA (1995), note that IGFA records are not anymore on public domains and records might have changed since 1995.

Sexual dimorphism

Sexual dimorphism is observed with billfishes. For example, Atlantic Blue marlin exhibits sexually dimorphic growth patterns: somatic growth of male slows at about 100 kg round weight and males do not exceed 150 kg, while females can reach up to 910 kg (Wilson *et al.*, 1991). Similarly, swordfish exhibit a sexual dimorphism of growth: males grow more slowly and reach a lower asymptotic length than females.

Longevity

Longevities of tunas vary from a few years for the smaller tunas to 12 to 15 years for the larger tunas. The longevity record for tunas is about 20 years for the Atlantic bluefin tuna (Cort, 1990) or 25 years for the southern bluefin tuna (Gunn *et al.*, 2008). Longevities of 15 to 27 years (Pacific blue marlin) or 28 years (Indo-Pacific blue marlin) have been estimated for billfishes and for swordfish. Longevities of seerfishes and mackerels are moderate with some records at 16 years for the Spanish mackerel.

Natural mortality

For larger tunas and billfishes, adult natural mortalities range from 0.2 to 0.6. Juvenile natural mortalities are higher. Little is known on natural mortalities of seerfishes and mackerels.

Reproduction

Spawning

Spawning behavior

Tuna spawn in open water close to the surface. Eggs are released by females in several batches. For example, yellowfin tuna in the Pacific spawn nearly every day. However, for some species like the bluefin species, spawning is more seasonal.

Spawning areas and seasons

Tunas spawn in areas where the survival of their larvae is greatest. Most species of tunas spawn only in waters where the surface temperatures are greater than 24°C. Tropical tunas appear to spawn in equatorial areas all year around and at higher latitudes during the warm seasons. Albacore and bigeye appear to migrate annually from temperate feeding areas to tropical spawning areas. Bigeye larvae are less abundant than those of other tropical tunas, and are found mainly in equatorial waters in which the temperatures are greater than 28°C (Collette and Nauen, 1983). Atlantic bluefin, Pacific bluefin and southern bluefin tuna exhibit a homing behavior when they mature, and return to restricted areas in the Atlantic, Pacific and Indian Oceans to spawn. It is commonly accepted that there is a homing behavior, but to a lesser extent, in yellowfin in the Atlantic Ocean. Billfishes appear to spawn seasonally in warm tropical and subtropical waters.

Maturity and fecundity

Maturity

With the exception of bluefin tunas (*Thunnus thynnus*, *T. orientalis* and *T. maccoyii*), most tunas, seerfishes, mackerels and billfishes reach their age of maturity between 2 and 5 years of age. Due to their sexual dimorphism of growth, male billfishes are mature at a smaller size than female billfishes.

Maturity of tunas and billfishes

Tunas			
Scientific name	**Age**	**Size**	**Weight**
Auxis rochei		35 cm	
Auxis thazard		~30 cm	
Euthynnus alleteratus		40-50 cm	
Euthynnus affinis		45-50 cm	
Katsuwonus pelamis	2 years	Female: 42-50 cm Male: 45-52 cm	
Thunnus alalunga	5 years	90 cm	15 kg
Thunnus albacares	2.5-3 years	100-110 cm	20-30 kg

Thunnus maccoyii	11 years		
Thunnus obesus	3-3.5 years	100-110 cm	
Thunnus thynnus (East Atl.)	4 years	115 cm	30 kg
Thunnus thynnus (West Atl.)	8 years	190 cm	120 kg

Bonitos

Scientific name	Age	Size	Weight
Sarda sarda		~40 cm	

Seerfishes and mackerels

Scientific name	Age	Size	Weight
Scomberomorus guttatus	1-2 years	40-50 cm	
Scomberomorus maculatus	2 years	25-35 cm	
Scomberomorus cavalla	4 years	60-70 cm	
Scomberomorus commerson		70-90 cm	
Acanthocybium solandri	2 years	90 cm	

Billfishes			
Scientific name	**Age**	**Size (LJFL)**	**Weight**
Tetrapterus pfluegeri		150 cm	17-19 kg
Tetrapterus albidus		Female: ~150 cm Male: ~140 cm	
Istiophorus albicans		Female: 160-180 cm Male: ~140 cm	Female: 18-20 kg Male: 10 kg
Xiphias gladius	3.5 years	150-160 cm	
Makaira nigricans		Female: ~250 cm	120 kg
Makaira indica		Female: ~180 cm Male: 130-160 cm	Female: ~200 kg Male: 60-80 kg
Makaira mazara	2-4 years	130-140 cm	Female: 60-80 kg Male: 40-50 kg

Fecundity

The batch fecundities of most species of tunas range from 2 to 70 million eggs, the lowest fecundity being for albacore and the highest for skipjack tuna and other small-sized tunas. Known batch fecundities of mackerels range from 300 000 to 1 500 000 eggs. Little is known on fecundities of seerfishes. Fecundity of wahoo has been estimated to 6 million eggs. Less is known on the reproductive biology of billfishes, but batch fecundity is estimated to range between 1 and 7 millions of ovocytes. Swordfish batch fecundity was estimated to 3.9 millions eggs in the Atlantic.

Maturity and fecundity parameters of the principal market species of tunas		
Scientific name	**Size and age at maturity**	**Annual batch fecundity**
Katsuwonus pelamis	about 3 years and 42 to 45 cm	7 to 76 million eggs
Thunnus alalunga	about 5 years and 90 cm	2 to 3 million eggs
Thunnus albacares	about 3 years and 100 cm	4 to 60 million eggs

Thunnus obesus	about 3 years and 100 cm	4 to 60 million eggs
Thunnus thynnus	about 4 years and 105 to 120 cm	5 to 30 million eggs

Sex ratio

It has been shown that for yellowfin, bigeye and albacore, the sex-ratio changes with the age of the fish with a predominance of males for the larger sizes. A predominance of females has also been observed for medium-sized Atlantic bluefin tuna. For skipjack, differences in the numbers of males and females have been observed locally. Predominance of females at older ages is observed for several species of billfishes.

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