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Ecology, Anatomy, Reproduction, and Diet of the Atlantic Horse Mackerel, *Trachurus trachurus*: A Comprehensive Review

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ABSTRACT

The Atlantic horse mackerel, *Trachurus trachurus*, is a semi-pelagic fish species with a broad distribution in the temperate, tropical, and subtropical coastal waters of the Atlantic, Mediterranean and Indian Oceans. As a significant species for both commercial and recreational fisheries, it plays a pivotal role in the marine food web. This review synthesized current knowledge of the ecology, reproduction, and growth patterns of *T. trachurus*, emphasizing its critical biological attributes. Furthermore, it examined the main threats and conservation challenges this species faces, alongside the implications for fishery management. The review culminated with strategic recommendations for future research and monitoring initiatives aimed at filling the existing knowledge gaps and enhancing fishery's sustainability.

INTRODUCTION

Pelagic fish make up the majority of the fish biomass found in pelagic ecosystems **(Fanelli *et al*., 2023)**. These species such as small fatty pelagic fish, also called blue fish, (i.e. horse mackerel, sardines and mackerel) are abundant but hardly exploited **(Eymard, 2003)**. These types of pelagic species live between the surface and the bottom of the ocean. Small pelagic fish can also be considered continental shelf fish **(Sutton, 2013)**. They include several hundred species with common characteristics: a dark blue color on the back and a silver color on the belly, which are supposed to protect them from predators, an elongated shape, and an often-gregarious lifestyle. Atlantic horse mackerel (*Trachurus trachurus*), anchovy (*Engraulis encrasicolus*), herring (*Clupea harengus*), round sardinella (*Sardinella aurita*), Sardine (*Sardina pilchardus*), and flat sardinella (*Sardinella maderensis*) play important ecological roles in the Mediterranean Sea marine ecosystem **(Ouled-Cheikh *et al.,* 2022)**. They also represent significant quantities of fish catches in the globe **(Alheit & Peck, 2019; Hunnam, 2021)**, and are also the most coveted species by the feed milling industry for the manufacture of fish oil and fishmeal. Pelagic fish species account for 25% of all landings worldwide, mostly through anchovies, sardinellas, sardines, mackerels and herrings **(FAO, 2018)**. Nevertheless, these small pelagic fish stocks are particularly susceptible to variations in oceanic climate, leading to significant variations in their abundance and distribution over decades **(Asiedu *et al*., 2021)**.

Small pelagic fish are essential species in the marine food web, whose continued existence is vital to keep the ecosystem in balance. They can control the abundance of zooplankton they consume **(Peck *et al*., 2021)**. In fact, the strong fluctuations in their massive biomasses linked to overexploitation by fishing or environmental variations can affect ecosystem components both upstream and downstream. Downstream, this group can exert a top-down control over zooplankton. Conversely, small pelagic fish can exert upstream control over predators. It is through these ecosystem control roles that small pelagic fish are crucial to the trophic dynamics of upwelling ecosystems **(Chouvelon *et al*., 2015)**.

In addition to key ecological characteristics, small pelagic fish are characterized by: (i) a wide distribution and dynamics along the coast, in search of optimal conditions of temperature and food availability; with a typical life cycle of three to four years **(Raybaud *et al*., 2017; Schickele *et al*., 2020)**; (ii) a distribution spreading further offshore for round sardinella and horse mackerel and closer to the coast in shallow waters (a depth of less than 50m) in the case of *Bonga shade* and flat sardinella **(Deme *et al*., 2019)**; (iii) a structure organizing juveniles, young fingerlings and adults along a depth gradient. For example, horse mackerels concentrate their adults at greater depths, moving away from the coast. Thus, the smallest individuals are generally the most accessible to fisheries due to their proximity to the coast **(Sutton, 2013)**; and (iv) a gregarious behavior facilitating their detection and catches contributing to the variability of their abundance **(Kasumyan & Pavlov, 2018)**.

Among the small pelagic fish, *T. trachurus*, commonly called the common scad or the European horse mackerel, is an economically important species that is heavily consumed around the world **(Abaunza *et al*., 2003; Costa *et al*., 2021)**. It is primarily destined for exploitation and has an extensive presence in the Central East Atlantic and Mediterranean fisheries. This species is caught for processing into oil and meal and has been used for human consumption since the 1970s. In Europe, the fish individual is eaten fresh in such countries as Spain and Portugal. However, nearly 90% of the horse mackerel fished is exported, primarily frozen, to countries such as Japan and West Africa

(Eymard, 2003). Small pelagic fish are key species in the marine food chain, and their presence is essential for maintaining ecosystem balance. They can regulate the abundance of the zooplankton they consume **(Peck *et al*., 2021)**. In Morocco, with a coastline that stretches over 3,500km long (500km on the Mediterranean and 3,000 km on the Atlantic coast), the maritime fishing sector plays an important economic and social role in the Moroccan economy. Horse mackerel is very common throughout the Mediterranean Sea **(El Achi *et al*., 2021)**. In Morocco, the latest report from the Department of Maritime Fisheries indicates that the 2022 pelagic fish catches reached 1,347,813 tons. Of this, 44,320 tons were horse mackerel, which generated a turnover of 185,316,000 Dh in the Atlantic Zone. In the Mediterranean Zone, horse mackerel catches were reported at 3,245 tons **(DPM, 2022)**.

This work aimed to study the Atlantic horse mackerel based on its biology, its dynamics, and its feeding behavior, with the objective of adopting a good fishing management policy for this carangid. This review is the result of an in-depth bibliographic analysis, which would allow us to establish a solid base of research and knowledge of *T. trachurus*.

1. PRESENTATION OF THE CARANGIDAE FAMILY

The Carangidae family consists of a group of seawater bony fish belonging to the order Perciformes, which includes the perch-like fishes. The Carangidae family is one of the most diverse and abundant families in tropical and subtropical seas, comprising about 33 genera and 146 species, with a wide variety of shapes and colors. They are poikilothermic animals, meaning that their body temperature varies with the ambient temperature **(Mukherjee *et al*., 2018)**. The first fossils of this family date back to the early Tertiary era **(Berg, 1958)**.

The body of the carangids is usually slightly compressed laterally, either naked or covered with small and smooth scales that are often detached and scattered in fish traps. The head is large and flattened, with a prominent ridge on the back of the skull. The mouth is protractile, meaning that it can be extended forward. The eyes and the gills are located on the sides of the head. The lateral line is a sensory organ that runs along the body, usually straight and only curved at the front. Some species have bony plates or scutes along the lateral line **(Letaconnoux, 1951; Gherram, 2019)**.

Fins are the appendages that help a fish swim and balance. Carangids have two dorsal fins, with the first one being short and tall, with spiny rays. On the other hand, the second is longer and lower, with soft rays. The anal fin is like the second dorsal fin but located on the opposite side of the body. The pectoral fins are positioned on the body sides, near the gills. The pelvic fins are on the lower side of the body, near the anus. The caudal fin is located at the end of the tail and can have different shapes depending on the species. The fins can have different colors and patterns, which can help identify the species.

2. CHARACTERISTICS OF *TRACHURUS* GENUS

The genus *Trachurus* comprises 15 recognized species of fish **(Karaiskou *et al*., 2003)**. These species are distinguished from other carangids by having two lateral lines, which are sensory organs that run along the body. In the Mediterranean Sea, three species of *Trachurus* are found: *T. trachurus*, the Mediterranean scad or the Mediterranean horse mackerel, *T. mediterraneus* **(Steindachner, 1868)**, and the blue jack mackerel or the painted comber, *T. picturatus* **(Bowodich, 1825)** (Fig. 1).

The most evident feature distinguishing all three species from one another comes from the length of the accessory lateral line, which is a branch of the main lateral line running along the dorsal side of the body. In *T. trachurus*, the accessory lateral line almost reaches the end of the second dorsal fin; in *T. mediterraneus*, it terminates just beneath the first dorsal fin, and in *T. picturatus*, it has an intermediate length **(Zohra, 2011)**.

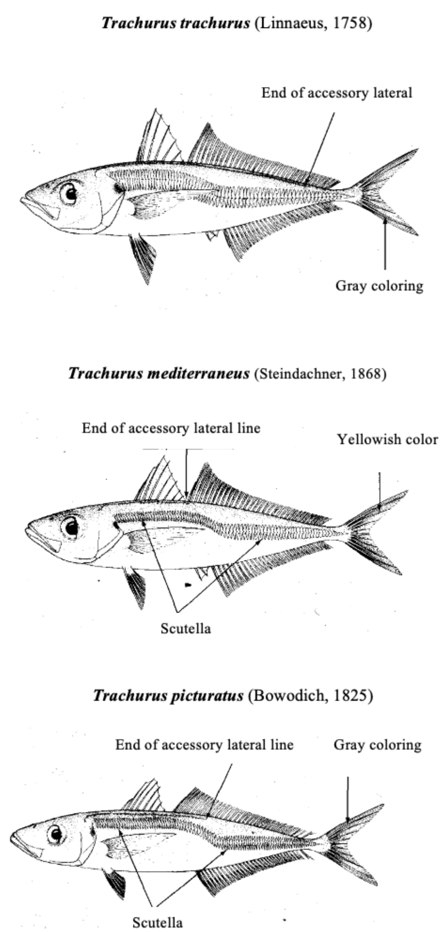

Fig. 1. Morphological characteristics of *Trachurus* genus **(Lloris & Rucabado, 1998)**

3. MORPHOLOGICAL DESCRIPTION OF *T. TRACHURUS*

Trachurus trachurus is a fish species that has a fusiform body shape, meaning that it is tapered at both ends. The body is pearly on the sides and darker on the back. The eyes are large and have fatty eyelids that cover most of the eye. The nostrils are small and narrow and located on either side of the head (Fig. 2). A small black spot is usually visible at the tip of the operculum. The first branchial arch features gill rakers on the upper and lower parts. Gill rakers are bony projections that help filter food from the water. The mouth is tubular, long, oblique, and can be extended forward. The upper jaw is broad and has a large bone called the maxilla. The lower jaw is prominent and protrudes beyond the upper jaw. Teeth are tiny and arranged in a row on both jaws. These features make this fish species a predator. It is mainly a saltwater fish, but it can also tolerate brackish water. Moreover, it lives in warm waters **(Quéro, 2003)**.

The Atlantic horse mackerel has 23 vertebrae, which are the bones that make up the backbone. The vertebrae are adapted to aquatic life and support the fins and the lateral line. The fins are the appendages that help the fish swim and balance. *T. trachurus* has two dorsal fins, which are on top of the body. The first dorsal fin is short and tall, with eight spiny rays. The second dorsal fin is longer and lower, with one spiny ray and numerous soft rays. The soft rays are flexible and support the fin membrane. The second dorsal fin extends from the middle of the back to almost the tail **(Meunier & Ramzu, 2006)**. The pectoral fins are located on the sides of the body, close to the gills. They reach and cover the lateral line, which is a sensory organ that runs along the body. Pelvic fins are found on the lower side of the body, close to the anus. They are also called the ventral fins. The anal fin is almost symmetrical to the second dorsal fin but is positioned on the opposite side of the body. It has two small spines at the front, which are separated from the rest of the fin. The caudal fin is at the end of the tail and is very forked. The caudal peduncle is the slender, thin part of the body that connects the tail to the trunk. The maximum weight of the fish is 2kg, and its size can reach 60 and 70cm in fork length, i.e. the length between the tip of the snout and the end of the middle rays of the caudal fin. Fork length is generally between 15 and 30cm **(Eymard, 2003; Charef-Belifa, 2009)**.

The color of the fish varies depending on the age and the environment. The upper part of the body and the top of the head are dark, almost black or grayish to greenish blue. The lower part of the body and the belly are paler, whitish to silvery. The young fish, unlike the adults, are silvery gray with green reflections **(Rahmani, 2020)**.

4. INTERNAL ANATOMY

The internal structure of fish consists of a skeleton, a circulatory system, and a digestive system. The skeleton is made up of cartilage or bone, and includes the skull, the vertebrae, and the fins. The circulatory system is simple and consists of a heart, blood vessels, and blood. The digestive system comprises the mouth, pharynx, esophagus, stomach, intestine, liver, spleen, and pancreas.

The mouth of *T. trachurus* is tubular, long, oblique, and can be extended forward. The upper jaw is broad and has a large bone called the maxilla. The lower jaw is prominent and protrudes above the upper jaw. The teeth are short and arranged in a single row on both jaws. These features make this fish species a predator. The eyes are large and have fatty eyelids that cover most of the eye. The nostrils are small and narrow, and located on either side of the head. A small black spot is usually visible at the tip of the gill cover. The gills are located on the sides of the head and help the fish breathe in water. The first gill arch has gill rakers on both the upper and lower parts. The gill rakers are bony projections that help filter food from the water.

The esophagus is a tubular structure that connects the mouth to the stomach. The stomach is internally wrinkled in the longitudinal direction and can expand or contract depending on the season and the reproductive state of the fish. During sexual maturity, the stomach is almost empty and very small. During sexual rest, on the other hand, it is capable of a great expansion. At the lower and anterior part of the stomach, there is a pocket that contains a variable number of pyloric caeca. These caeca are long, thin-walled, and joined together by a thin membrane called the mesentery. They help digest and absorb food **(Letaconnoux, 1951)**.

The intestine is a tube that connects the stomach to the anus. It is folded back on itself twice forming a loop. The intestine absorbs nutrients and water from the food. The liver is a small organ that is pressed against the stomach and the pyloric caeca. It produces bile, which helps digest fats. The spleen is a dark red organ that is located between the folds of the intestine and the pyloric caeca behind the liver. It helps filter blood and fight infections. The pancreas is a diffuse organ that is hidden by fat tissue. It covers the entire gastrointestinal system. Moreover, it produces enzymes and hormones that help digest and regulate blood sugar (**Letaconnoux, 1951)**.

Fish have two rather specific organs: the gills and the swim bladder. The gills are used for respiration and exchange gases with the water. The swim bladder is a large organ that occupies the entire abdominal cavity. It is filled with gas and helps the fish adjust its buoyancy and depth. In general, the swim bladder is terminated by two horns that are separated by the first haemal processes of the caudal trunk. The haemal processes are bony projections that protect the blood vessels of the tail **(Dorson *et al*., 2018)**.

The reproductive system consists of a pair of glands that are in the abdominal cavity under the swim bladder in its posterior region **(Dorson *et al*., 2018)** (Fig. 2). They are richly supplied with blood vessels and have the shape of two cords. Their size and color vary with the age of the fish and its sexual maturity. The glands produce gametes, which are the reproductive cells. The male and female reproductive glands, testes and ovaries, produce sperm and eggs, respectively. The testes are milky white, and the ovaries are orange yellow. Usually, the testes and ovaries are symmetrical and elongated organs that span the length of the general cavity from the spot behind the anus to the height of the liver. They compress all the other organs, and the stomach is almost always completely empty. When fish reach three years old, they can reproduce sexually. The males and females have different reproductive seasons. The females are sexually active year-round, while the males have a shorter reproductive season. The fish are gonochoristic, meaning that they have separate sexes and oviparous, meaning that they lay eggs. The eggs are fertilized externally in the water **(Prolonge-Chevalier, 2007; Zohra, 2011)**.

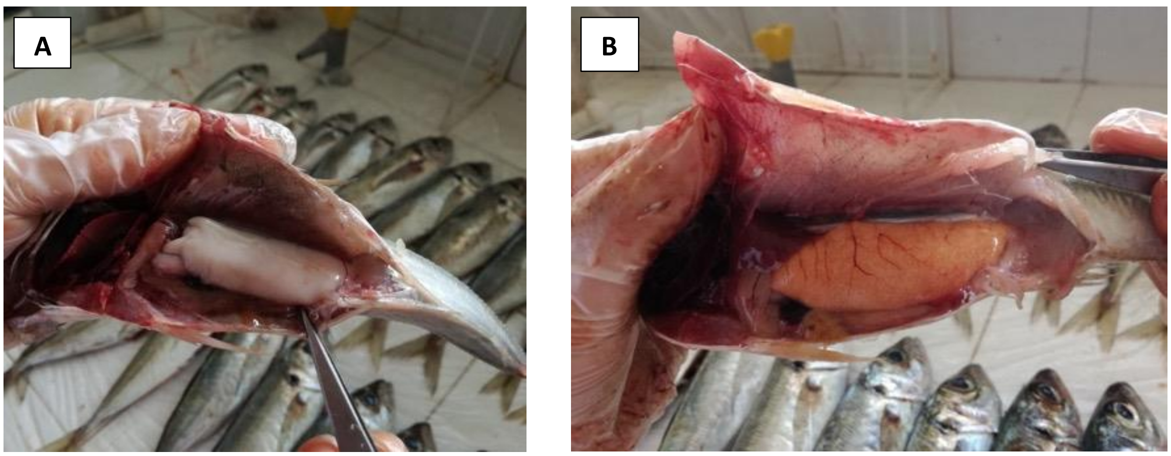

Fig. 2. Reproductive system of *Trachus trachurus* showing: **A.** Male reproductive glands (testes), and **B.** Female reproductive glands (ovaries)

5. GEOGRAPHIC DISTRIBUTION

All oceanic waters in temperate, moderate subtropical and tropical zones are home to *Trachurus* species along their coasts **(Leitão *et al*., 2018)**. *T. trachurus* is an adaptable species that can live in different oceans and seas. In the Atlantic Ocean, this species ranges from Iceland to Senegal in the eastern part and from Argentina to Canada in the western part **(Abaunza *et al*., 2008)**. It is also found in the Norwegian Sea, the English Channel, and the North Sea **(Bektas & Belduz, 2009)**. It inhabits the continental shelf and the continental slope from 10 to 500m depth **(Giacomo *et al*., 2018)**. In contrast, in the Mediterranean Sea, this species is very popular and widespread and can be present in the Sea of Marmara, and occasionally in the Black Sea **(Gherram *et al*., 2018)**. It is also present along the Algerian and Moroccan coasts of the Mediterranean Sea **(Eymard, 2003; Abattouy *et al*., 2014)** (Fig. 3). *T. trachurus* is found in the eastern and western parts from Japan to Australia and from California to Chile **(Froese & Pauly, 2020)**. Moreover, in the Indian Ocean, *T. trachurus* is found in the western and southern parts from South Africa to India and from Madagascar to Australia **(Froese & Pauly, 2020)**.

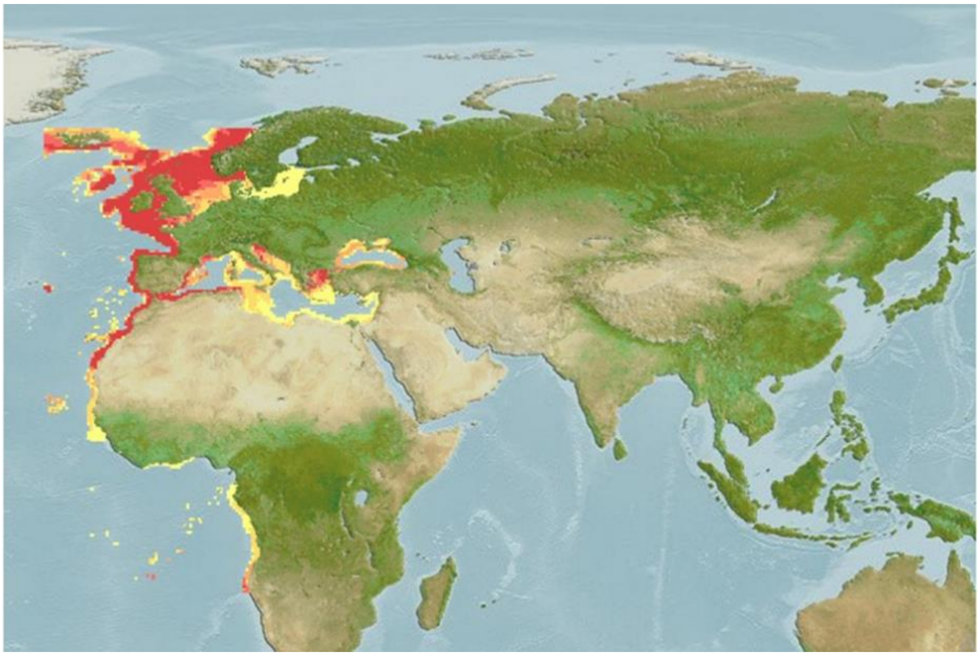

Fig. **3.** Geographic distribution of *Trachurus trachurus* **(Fishbase, 2019)**

6. SPECIES HABITATS

Trachurus trachurus hunts in large schools in the water column **(D'Elia *et al*., 2014)**. It is generally present on sandy seabeds at depths of 100 to 200m but can sometimes reach depths of 600m or more. It also lives in the pelagic zone and sometimes near the surface, depending on environmental conditions **(Sutton, 2013)**. Therefore, it can be considered a semi-pelagic species, because it moves between the surface and the bottom, or between different water layers **(Quéro, 2003; Jardas *et al*., 2004)**. Its habitat preferences are poorly understood, but they may be influenced by a variety of hydrographic features such as temperature. In addition, it can adapt to brackish water **(Santic *et al*., 2002)**. Its activity is relatively reduced outside the warm season. Moreover, it is a migratory fish species and an excellent swimmer. It migrates and approaches the coasts in summer, which makes it more abundant and easier to catch. It returns to the open sea in winter at depths of around 400m, where it is less accessible to fisheries. Its fishing also decreases as the spawning period ends, as the schools become more dispersed **(Abaunza *et al*., 2003; Rumolo *et al*., 2017)**. Furthermore, it is a species with pelagic behavior, whose larvae and juveniles often congregate under any floating object, which may provide them with protection from predators. The larvae live at an average depth of 20m between March and September **(Michael, 2002)**. When they reach 4mm long, they have four to five spines on the outer row, and approximately five on the inner row of the gill cover. This number increases as they grow. These larvae have many dark pigment cells on the jaw, head, and throughout the abdomen **(Russel, 1976)**.

7. MIGRATION AND BATHYMETRY

The Atlantic horse mackerel is a highly migratory fish. It can travel long distances depending on its needs, such as feeding, spawning, and predator avoidance. The distribution of fishing catches and data obtained from surveys provide indications of the migration routes of different groups **(Gherram *et al*., 2018)**. Three types of migration are known for this species:

- **Nychthemeral migration (Motility)**

This type of migration is part of the species' daily behavior, influenced by a day-night cycle. Large schools of horse mackerel are found close to the bottom and in the middle of the water during the day; while at night, they scatter and form a layer just above the seabed **(Macer, 1977)**. The migration of this fish species can be mainly affected by the water temperature. This species generally occupies continental seas to a depth of 200m. However, some specimens have been recorded at depths of 500m **(Rumolo *et al*., 2017)**.

- **Seasonal migration**

This type of migration is related to the reproductive cycle of the species, which varies according to the geographic location and the water temperature. After spawning, horse mackerels migrate north along the slope of the continental margin during June and July. From July to September, they remain off the Norwegian coast and migrate to the central North Sea in October and November. Subsequently, they begin a return migration to the western area, passing through Scotland and the Shetlands **(Gherram *et al*., 2018)**. During the month of June, the North Sea horse mackerel migrate northeast from the English Channel along the Dutch coast where they spawn in July, heading to the west coast of Denmark in August. In the third and fourth quarters, horse mackerels are abundant in the southern and southeastern parts of the North Sea; however in October, they have been observed to cross the channel in western and southern directions **(Mahe *et al*., 2007)**. It is possible that the western and North Sea spawning groups mix in the central North Sea during the third and fourth quarters, and in the Western Channel mainly in the fourth quarter. Little information is available on the migratory behavior of horse mackerel in the Bay of Biscay. The presence of *T. trachurus* was also observed throughout the year along the Algerian coast as well as the Atlantic coasts of Portugal and Spain **(Gherram *et al*., 2018)**.

- **Trophic migration**

This type of migration is related to the species' feeding behavior that depends on the availability and distribution of prey. *T. trachurus* lives near the bottom and also throughout the water column. In spring, the fish disperses much more widely, migrating northward from the southern Black Sea to feed and reproduce as water temperature rises

(Polonsky, 1965). This species heads south in autumn at temperatures below 10°C. It withdraws from feeding areas in the southern Norwegian and North Seas and migrates to wintering grounds further south **(Zohra, 2011)**. Moreover, it migrates to the English Channel and along the continental margin in the Bay of Biscay and the Celtic Sea **(Macer, 1977)**. *T. trachurus* from the Romanian Black Sea coast overwinters in the Sea of Marmara **(Smith-Vaniz *et al*., 2015)**. The North Sea stock appears in April in the southern North Sea, reaching the west coast in July and southern Norway in August. Parts of the western stock can reach Trondheim Fjord in July- August **(Iversen *et al*., 2002)**. *T. trachurus* has been observed in the company of the lion's mane jellyfish, *Cyanea capillata* L., and various other jellyfish. This recent discovery marks a new association for this species.

8. ECOLOGICAL CHARACTERISTICS

- **Nutrition**

Figuring out how fish feed in their natural habitats is an essential step toward understanding their biology and ecology. Their feeding habits reflect not only predatory activities but also explain variations in their growth, foraging, and feeding behavior, migrations, and even certain aspects of reproduction. In addition, data on food composition is utilized to predict trophic levels, which is vital for managing fisheries and quantifying the effect of fishing on ecosystems. Information on the place of fish in food webs is also helpful in understanding how marine ecosystems function and how they are influenced by natural or human interventions. *T. trachurus* is a voracious carnivorous fish (benthopelagic). Its diet is based on pelagic prey (copepods and teleosts) and benthic prey (primally crustaceans). It is a very active predator, moving from the bottom to the surface, where it rises to hunt, particularly during the first part of the night, which is its principal activity period. This was confirmed by several studies **(Jardas *et al*., 2004; Šantić *et al*., 2005; Bayhan & Sever, 2009; Villegas-Ríos, 2009; Bayhan *et al*., 2013; Shawket *et al*., 2015; Koç & Erdoğan, 2019)**.

The food of *T. trachurus* is varied and includes four or five major groups or taxonomic units of prey (crustaceans, mollusks, echinoderms and fish, teleosts, etc.). Its diet includes a wide variety of fish, such as juvenile mugilid species, blue whiting (*Micromesistius poutassou*), and *S. pilchardus*. The species also feeds on small crustaceans, which constitute the most diverse group, such as euphausiids, mysidaceans, amphipods, copepods, decapods, isopods, cumaceans, small swimming crustaceans, brachyurans and macrourids. Additionally, it consumes molluscs (bivalves, scaphopods, gastropods and cephalopods, squids), vertebrates (teleosts and teleost eggs), and echinoderms. However, the food of *T. trachurus* is based primally on small swimming crustaceans, and euphausiids constitute the dominant fraction of its diet. Several authors have highlighted the diversity of its diet **(Bayhan & Sever, 2009)**.

On the other hand, the feeding strategy developed by this species varies depending on its stage of growth. In fact, the size of the predator influences its food composition. The species would tend to adapt its feeding habits according to its size and therefore according to its age. Juveniles prefer euphausiids, while adults tend to be piscivorous. Therefore, the food differs according to the individual's size, and they tend to eat larger and larger prey as they grow **(Koç & Erdoğan, 2019)**.

- **Diet by length classes**

The study of the diet shows that the principal preys of *T. trachurus* are crustaceans **(Koç & Erdoğan, 2019)**. In the first two classes (1 and 2), for a fish length lower than 20cm, teleosts (anchovies, sardines) are the most favored prey group. The diet does not change much with the seasons, and small animals with shells are the main food for the smallest two classes of sizes. When they grow bigger (class 3), they prefer and mostly eat young fish (with bones).

To sum up, the smallest group of sizes likes to eat small animals with shells; the next group chooses small shrimp-like animals, and the largest group mainly hunts young fish (with bones). This means that the food they eat depends on how big they are. We can say that this fish has a very adaptable diet, and it can find food in any environment. This is consistent with literature data showing that the frequency of feeding is higher in smaller individuals, and that this is thought to be associated with prey size, as smaller prey are digested faster than larger fish prey **(Bayhan & Sever, 2009)**.

Research into the feeding biology of horse mackerel in Morocco reveals that stomach content analysis indicates a diversified diet for *T. trachurus*. This species feeds primarily on crustaceans, with Teleostei classified as complementary prey. A total of 21 prey categories were identified in the stomach contents. Furthermore, diet fluctuations were found to be associated with environmental factors, including upwelling, temperature variations, chlorophyll concentration levels, and dissolved oxygen levels **(El Achi *et al.*, 2021; Maroua *et al*., 2023)**.

- **Eating habits**

After the spawning in summer, the fat content of *T. trachurus* becomes very low. However, in August and September, its energy content increases rapidly due to intensive feeding. The formation of opaque zones in the otoliths is therefore to be expected during periods of intensive feeding, allowing rapid growth and increased calcification **(Zohra, 2011)**. This fish stops feeding in part once water temperature goes under 10°C. When the water temperature reaches 8- 9°C, it stops feeding and migrates for the winter. After overwintering, the energy consumed by gonad development (in winter and spring) and spawning will result in the formation of a transparent zone in the otoliths **(Abaunza *et al*., 2008)**. In the North Sea (except in July), *T. trachurus* feeds mostly on fish, whiting being the most significant prey, followed by other gadids and herring. Further south, invertebrates make up the bulk of the fish's diet, including crabs, decapods, and other crustaceans **(Dahl & Kirkegaard, 1986)**.

However, **Dahl and Kirkegaard (1986)** reported a clear diurnal feeding pattern in the eastern North Sea, but with more intense feeding in the morning than at night. A change in food preferences with age has been demonstrated; small individuals (less than 20- 24cm) feed mainly on crustaceans, gobiids, and haddock, while larger specimens prefer herring. In the English Channel, adult horse mackerels apparently feed 70% of the time on crustaceans and only 17% of the time on fish; these proportions vary monthly **(Macer, 1977)**. However, *T. trachurus* is a planktivorous fish for which crustaceans (euphausiids and copepods) are the main prey. **Porumb (1979)** reports a different diet between the two sexes: females feed mainly on the Mediterranean sand eel, *Gymnammodytes cicerellus* (Rafinesque) (benthic fish), while males feed on the sand smelt, *Atherina mochon pontica* (Eichwald), and wandering polychaetes **(Koç & Erdoğan, 2019)**. Regarding samples from northwestern Spain, **Cabo (1950)** suggested that juveniles are planktivorous, while adults are mainly piscivorous. In the southern Bay of Biscay, *T. trachurus* shows seasonal differences: it feeds on crustaceans in spring, while in autumn, fish over 30cm start to eat other fish (blue whiting, gobiids, anchovies), which accounts for 45% of the food volume in this length range. A diurnal feeding pattern has also been described, with feeding peaking around midday in spring (for fish over 30cm) and at sunrise in autumn. In Portuguese waters, *T. trachurus* feeds mostly on zooplankton, especially euphausiids and copepods. It is not until they are 20cm long that fish become their main prey **(Abaunza *et al*., 2003)**.

9. REPRODUCTION

- **Reproductive cycle of teleosts**

Fish reproduction is a complex process. It is regulated by hormones and depends heavily on environmental conditions, in particular temperature and photoperiod that affect the timing of gonad maturation, the development of secondary sexual features, and reproductive behavior. These changes lead to a reproductive period during the year, when environmental conditions are favorable for an optimal juvenile development **(Waldron & Kerstan, 2001)**.

The extreme diversity of fish is manifested in their modes of reproduction and development. Most fish are single-sex, but about 10% of species are hermaphrodites, meaning that they have both male and female reproductive organs **(Prolonge-Chevalier, 2007)**.

Fish reproduce according to two methods of fertilization **(Gaillard, 2006)**:

- External fertilization: Oviparous females release the eggs into the external environment. They are then fertilized by males by the release of sperm. In this type of fertilization, there is no mating. It is the specific recognition that exists between sperm and eggs that enables fertilization.

- Internal fertilization: Male sperm are deposited inside (or near) the female reproductive system, and their union takes place within the female. Three main modes of reproduction have been identified **(Buslé & Quignard, 2004)**:
    - Oviparity: A few species of teleosts perform intra-ovarian self-fertilization and lay eggs.
    - Ovoviviparity: The embryo is only housed in a female genital cavity, without any trophic relationship with the mother. This simple bond implies an exclusive use of its own yolk reserves.
    - Viviparity: The embryo receives, in the female genital tract, maternal nourishment other than that supplied by its yolk sac.

The reproductive cycle entails a series of physiological and behavioral processes influenced by a range of abiotic and biotic environmental factors. Understanding the timing and duration of egg-laying is crucial for comprehending population dynamics. Various indices have been employed to determine the breeding period. **Rahmani (2020)** used the gonadosomatic ratio, histological analysis of female ovaries, monitoring of sexual maturity phases, and egg quantity.

- **Breeding, spawning period and sexual maturity**

Seasonal gonadal changes (gametogenesis) in teleosts follow successive stages. However, the rates of these changes vary greatly between species. Gametogenesis involves both oogenesis (oocyte growth) and spermatogenesis (growth of male germ cells) **(Abaunza *et al*., 2003)**. Spermatogenesis is divided into three stages: spermatocytogenesis, meiosis, and spermiogenesis. Three types of reproduction are defined **(Abaunza *et al*., 2003)**:

- Synchronous reproduction: a rare type in which all germ cells are at the same stage. This type of reproduction is found in fish that spawn once in their lifetime and then die (semelparous species).
- Group-synchronous reproduction: in this type of reproduction, there are two populations of germ cells that develop at the same time; the first is at an early stage, and the second is at a late stage.
- Asynchronous reproduction: this type of reproduction is the most common. All stages occur in the gonads. *T. trachurus* has this type of reproduction.

Trachurus trachurus spawning period varies from one region to another; this phenomenon is affected by certain climatic factors like temperature and physicochemical parameters (e.g., salinity). Indeed, a slight temperature rise can induce spawning **(Lévêque, 2006)**. This species has a reproductive strategy characterized by a gonochoric and oviparous state, with an extended spawning season **(Gordo *et al*., 2008)**. *T. trachurus* spawning period involves a migration to the coast in spring and to the open sea in autumn. Atlantic horse mackerel has a high reproduction rate **(Murua & Saborido-**

Rey, 2003). Spherical and smooth eggs are released in water. When hatched, larvae barely measure 5mm. Females spawn their eggs at temperatures ranging from 18 to 21°C. Eggs are spawned in batches and they are pelagic, their diameter varies between 0.9 and 1.1mm **(Artüz, 2000)**. Sexual maturity is attained at two years for females and around three years for males. The sexes are separated, and fecundation takes place outside the body. Males reach maturity at a shorter length compared with females and seem to be sexually active almost all the time, whereas females are only sexually active in spring and summer, with a peak in June- July **(Mahe *et al*., 2007)**. Oviposition is preceded by a fasting period that accompanies sexual maturity (swelling of the ovaries and testes) **(Mouneimne, 1978)**.

The eggs are pelagic, spherical in shape, with a fat droplet. The diameter of the egg varies from 0.92 to 1.02mm, while that of the fat droplet varies from 0.22 to 0.26mm. The envelope is very thin, transparent, and cohesive; the yolk is vascular-lobular. The body length of newly hatched pre-larvae averages 2mm. The large ovoid yolk sac protrudes from the head, and the fat droplet is located near its anterior border **(Key, 2015)**. The larvae, soon after hatching, have a much reduced yolk, with the droplet being carried forward, and the intestine extending far back, while the fins are large and pigmented **(Letaconnoux, 1951; Artüz, 2000)**.

Trachurus trachurus grows rapidly during its first year, and then progressively slows down with age **(Letaconnoux, 1951; Nasri *et al*., 2021)**. Its lifespan is very long (around 30 years), with a maximum length reaching 70cm **(Overko & Mylnikov, 1979)**. Determining the age of fish is essential for the use of several fishery models to study growth. This is generally done using bone pieces, vertebrae, head bones, or more classically, scales, and sagittate otoliths **(Wright *et al*., 2002)**.

Research on *T. trachurus* reproduction in Morocco is limited. A thesis by **Nasri (2022)** revealed two distinct Mediterranean spawning seasons: late winter to early spring (February- April) and summer (July- September). Concurrent macroscopic and histological studies have delineated varied reproductive timelines across the Mediterranean:

- Bay of Béni Saf: February to July, with a peak in June **(Rahmani *et al*., 2020).**
- Bay of Oran: January to May **(Gherram *et al*., 2018)**.
- Aegean Sea: April to August **(Aydin & Erdoğan, 2018)**.
- Gulf of Skikda: December to April **(Azzouz *et al*., 2019)**.

CONCLUSION

This review provides a deeper insight into the reproductive biology of *T. trachurus*. It is a semi-pelagic migratory species that is widespread along the coasts, with three migration modes, diel, seasonal, and trophic. The feeding strategy developed by this species varies depending on its stage of growth; it is a very active predator with a very flexible diet. This fish demonstrates considerable plasticity in its diet and can feed in any environment. Its diet comprises small crustaceans, mollusks, vertebrates, and echinoderms. *T. trachurus* has an asynchronous reproduction. The spawning period differs from region to region; this phenomenon is influenced by climatic conditions like temperature and physicochemical parameters. Its reproduction rate is high. Sexual maturity is attained at the age of two years for females, and around three years for males, who have permanent sexual activity, while females are active in spring and summer.

However, this species faces several threats and challenges for its conservation and management, such as overfishing, climate change, habitat degradation, and pollution. Overfishing is one of the main causes of the decline of *T. trachurus* stocks, especially in the Atlantic and the Mediterranean, where the fishing effort and catch have exceeded the sustainable levels **(El Mghazli *et al*., 2022)**. In turn, climate change can affect the distribution, abundance, growth, reproduction, and survival of this species by modifying water temperature, salinity, oxygen, currents, and food availability **(Albo-Puigserver *et al*., 2022)**. Moreover, habitat degradation can result from the destruction or alteration of the coastal and marine ecosystems that provide shelter, food, and nursery grounds for this species, such as seagrass beds, coral reefs, and mangroves **(Rogers *et al*., 2019)**. Pollution can also harm the health and quality of this species, by exposing it to contaminants, such as heavy metals, pesticides, plastics, and oil spills, which can accumulate in its tissues and affect its growth, reproduction, and survival **(Köker *et al*., 2021; Maaghloud *et al*., 2021)**.

It is therefore essential to implement effective conservation and management actions for *T. trachurus*, on the basis of the latest scientific information and the precautionary approach, to guarantee its long-term sustainability and resilience. These measures include setting catch limits and quotas, regulating fishing gear and methods, monitoring and enforcing compliance, creating marine protected areas, reducing greenhouse gas emissions, restoring and conserving habitats, as well as preventing and reducing pollution.

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