

Biology of *Trachurus mediterraneus* (Carangidae) off the Coast of Crimea (Black Sea)

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Abstract

This study examines the distribution, size-weight parameters, and feeding habits of Mediterranean horse mackerel *Trachurus mediterraneus* (Steindachner, 1868) during early development, along with growth, age structure, reproductive behavior, diet, and mortality rates of juveniles and adults in the northern Black Sea. Spawning peaks in July, as indicated by the gonadosomatic index dynamics. According to a logistic model, 50% of individuals reach sexual maturity at a total length of 11.09 cm at the age of one year. The highest abundance of eggs (69.9 ind./m²) and larvae (46.5 ind./m²) was recorded on July 28, 2019, in the Caucasus research area. Growth parameters estimated using the von Bertalanffy model were: asymptotic length (L_{∞}) 21.8 cm, asymptotic weight (W_{∞}) 77.2 g, and growth coefficient (k) 0.25 year⁻¹. Mortality estimates ($Z= 1.03$, $M= 0.49$, $F= 0.54$ year⁻¹) indicate an exploitation rate (E) of 0.53, indicating a high level of fishing pressure. This study presents the first comprehensive analysis of all ontogenetic stages of *T. mediterraneus* in the northern Black Sea, assesses the current population status, and provides a basis for forecasting future dynamics under climate change.

Introduction

T. mediterraneus is a commercially significant pelagic marine fish species belonging to the family Carangidae. Its distribution ranges from the eastern Atlantic Ocean, from the English Channel to Morocco, throughout the Mediterranean Sea, and extends into the Sea of Azov. In the Black Sea, *T. mediterraneus* inhabits both shallow coastal waters and offshore areas, exhibiting distinct migratory behavior (Ivanov and Beverton, 1985; Vasil'eva, 2007). In spring, the species migrates to the northern Black Sea for breeding and feeding, during which it enters the Kerch Strait and the central part of the Sea of Azov. In summer, it resides in the upper quasi-homogeneous layer (UQHL) above the thermocline. In autumn, *T. mediterraneus* migrates to wintering grounds located along the coasts of Crimea, the Caucasus, and Anatolia, as well as in parts of the Marmara Sea (Kasapoglu, 2018; Georgieva et al., 2019).

Climate change occurring from the 1990s to the present has significantly affected the hydrological regime of the seas, with pronounced seasonality. These changes have substantially altered habitat conditions, influencing the life cycles of aquatic organisms, spawning phenology, spatial distribution, and trophic relationships (Edwards and Richardson, 2004; Auth et al., 2017). The thin oxygen layer in surface waters of the open Black Sea contributes to the instability of its pelagic ecosystem (Turan et al., 2016; Markova et al., 2021).

Changes in hydrological patterns and thermohaline characteristics of the Black Sea over the past three decades are comparable to those observed in the 1960s and 1970s; however, recent years have witnessed greater variability. Hydrological cycles have shifted: during the summer season, dynamic activity in coastal and shelf waters has intensified due to a weakening of the Black Sea Rim Current (BRC). Furthermore,

thermohaline conditions in the upper 100 m have changed. Salinity has increased by 0.18‰ per decade, and sea surface temperature has risen by 0.5 – 0.6°C per decade (Sakalli and Basusta, 2018; Belokopytov and Zhuk, 2024).

In the Black Sea, the spawning season for warm-water and temperate-water fish species has lengthened, while the size and weight of their larvae have decreased (Klimova et al., 2022; 2023). *T. mediterraneus* is a common pelagic fish of considerable commercial value and ecological importance, serving as a key component of the marine food web (Turan, 2004; Alheit and Pitcher, 2012; Erbay, 2022; ICES, 2023; Păun et al., 2025). In the Black Sea ecosystem, *T. mediterraneus* ranks third in annual catches, following European sprat *Sprattus sprattus* and European anchovy *Engraulis encrasicolus* (Kozhurin et al., 2018; Shlyakhov et al., 2018). A substantial body of literature addresses the biological characteristics of *T. mediterraneus* across various regions of the Black Sea (Păun et al., 2019, 2020; Kutsyn, 2021; Dürrani, 2023; Melnikova et al., 2023; Samsun, 2023; Donchik, 2025; Păun et al., 2025).

Existing studies on the biology of *T. mediterraneus* typically focus on individual life cycle stages, which precludes a holistic understanding of recruitment mechanisms, the cumulative impact of environmental factors across generations, and the species' adaptation to changing climatic conditions. Data on reproduction, distribution, size-mass characteristics, and feeding during early ontogenetic stages remain scarce and fragmented. Yet it is during these early stages that the fundamental properties of a population are established—including the species' capacity for range expansion, adaptation to novel environmental conditions, and the parameters that determine the abundance of future generations (Arhipov, 2015). This critical role of early ontogeny underscores the scientific importance of comprehensive studies on this aspect of the species' biology.

Although *T. mediterraneus* has been extensively studied in the Black Sea, many questions regarding its intrapopulation structure and the spatial and temporal variability of its biological indicators remain unresolved. As demonstrated by Donchik (2025), size characteristics and growth rates are heterogeneous not only across the species' entire range but also within the Black Sea basin. This finding is of considerable interest for comparative regional analyses as well as for investigating interannual dynamics.

This study presents the first comprehensive analysis encompassing all major ontogenetic stages of *T. mediterraneus* in the northern Black Sea. This integrated approach enables an assessment of the current population status across all life cycle stages, an evaluation of the impacts of climatic changes on key biological parameters, and, consequently, a prediction of their variability to enhance the efficiency of biological resource utilization. Analyzing the influence of environmental factors on biological variability

contributes to understanding the mechanisms of evolutionary adaptation.

The aim of this study is to investigate the current status of the *T. mediterraneus* population in the northern Black Sea across different stages of its life cycle.

Materials and Methods

The material on ichthyoplankton was collected on the shelf (depths <200 m) and in deep-water areas (≥200 m) of the northern Black Sea within the Russian EEZ, along the Crimean Peninsula and the Caucasian coast. Sampling was conducted on July 11–August 3, 2019, during the 108th cruise of the R/V Professor Vodyanitsky, and on June 29–August 9, 2021, during the 117th cruise of the same vessel. Ichthyoplankton was sampled using a reverse-conical Hensen net and a BR-80/113 net (mouth area 0.7 and 0.8 m², respectively; mesh size 400 μm). At shallow-water stations, tows were carried out from the bottom to the surface. At deep-water stations, tows were conducted from the lower boundary of the oxygen layer ($\sigma_t = 16.2$, based on data from an IDRONAUT OCEAN SEVEN 320 PlusM CTD probe) to the surface. In 2019, a total of 230 eggs and 112 larvae were examined; in 2021, 148 eggs and 100 larvae were examined. All samples were fixed in a 4% neutral formaldehyde solution and processed in a shore-based laboratory using an MBS-9 microscope at 8×2 and 8×4 magnifications. Ichthyoplankton was identified following Dekhnik (1973). Larvae of *T. mediterraneus* were divided into four size groups based on morphological parameters and feeding type (Sinyukova, 1964): (1) total length (*TL*) <2.2 mm, yolk feeding; (2) *TL* 2.3 – 3.5 mm, mixed feeding; (3) *TL* 3.6 – 5.5 mm, mixed feeding with a predominance of exogenous nutrition; (4) *TL* 5.6 – 10 mm, exogenous feeding.

Material for the analysis of growth, size–age structure, onset of maturation, spawning period, and mortality was collected from June 2020 to December 2021 in coastal waters off southern Crimea, between Matyushenko Bay and Kruglaya Bay (Figure 1). Fish were captured using fixed gill nets (12 mm mesh) at depths of 4 – 18 m. Biological analysis was performed on 1,714 individuals. The following measurements were recorded with the specified precision: total body length (*TL*) to 0.1 cm, total body weight (*W*) to 0.1 g, and gonadal mass (*GW*) to 0.001 g. Gonadal maturity was assessed on a five-point scale; individuals with gonads at maturity stage III or higher were considered sexually mature (Manual, 1975). Sexual maturation was analyzed using a logistic regression model (Shiraishi et al., 2010):

$$Y_{TL} = 100 / [1 + e^{-a(TL - b)}]$$

Where *Y_{TL}* is the proportion of mature individuals at length *TL*, *a* is the slope coefficient, and *b* is the inflection point corresponding to the length at which 50% of individuals reach maturity (*TL₅₀*). The

gonadosomatic index (*GSI*) was calculated as the ratio of gonad weight to total body weight:

$$GSI = GW \times 100/W \text{ (Barber \& Blake, 2006).}$$

Feeding intensity was assessed using the index of gut fullness

$$(IF): IF = (w / W) \times 10.000$$

Where *w* is the weight of the food bolus (g) and *W* is fish weight (g) (Zapletal et al., 2012).

The condition factor (*CF*) was determined using Fulton’s condition factor:

$$CF = (W \times 100) / SL^3$$

Where *W* is fish weight (g) and *SL* is standard length (cm) (Datta et al., 2013; Savin et al., 2022). Food digestion stages were categorized following Manko (2016): 1–stomach empty; 2–traces of prey; 3–<50% intact; 4–50–75% intact; 5–75–100% intact; 6–no digestion. The degree of stomach fullness was categorized as follows (Garrido et al., 2008; Manko, 2016): 1–empty; 2–<50% full; 3–>50% full; 4–bursting.

Age was determined for 341 individuals by counting translucent and opaque zones (annuli) on otoliths. These data were used to construct growth models and calculate mortality rates. Linear growth was modeled using the von Bertalanffy equations (Bertalanffy, 1938; Mina & Klevezal’, 1976; Ricker, 1979):

$$L = L_{\infty}(1 - e^{-k(t-t_0)})$$

$$W = W_{\infty}(1 - e^{-k(t-t_0)})^b$$

Where L_{∞} and W_{∞} are the asymptotic length and weight, respectively; k is the growth coefficient, determining the rate of approach to L_{∞} ; t_0 is the theoretical age at zero length; and b is the exponent from the length–weight relationship

$$W = aL^b$$

Growth rate was analyzed by calculating the initial instantaneous growth rate (Gallucci & Quinn, 1979):

$$G_{init} = kL_{\infty}$$

As well as the growth performance indices (Pauly et al., 1988):

$$\phi' = \lg k + 2\lg L_{\infty} \text{ (linear growth index) and } \phi = \lg k + (2\lg W_{\infty})/3 \text{ (weight growth index).}$$

Total mortality rate (*Z*) was estimated using linear regression (Cadima, 2003):

$$\ln N_t = a + bt$$

Where *t* is age and *N_t* is the number of individuals at age *t*

$Z = -b$. Natural mortality rate (*M*) was estimated using Pauly’s empirical equation (Pauly, 1980):

$$\log M = -0.0066 - 0.279\log L_{\infty} + 0.6543\log k + 0.463\log T,$$

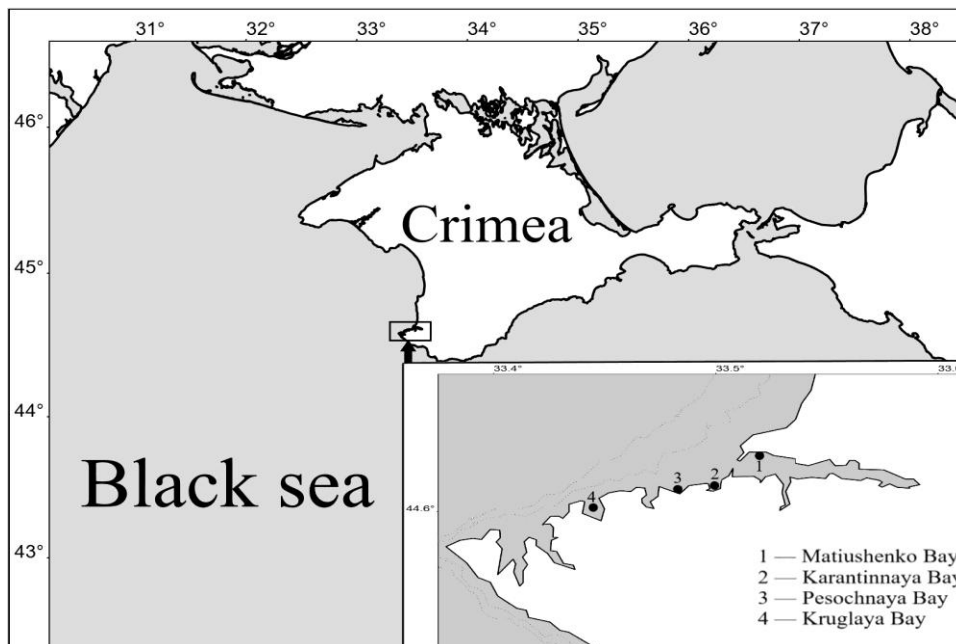


Figure 1. Map of the study area for adult *T. mediterraneus*: (•) sampling sites: 1—Matiushenko Bay, 2—Karantinnaya Bay, 3—Pesochnaya Bay, 4—Kruglaya Bay.

where T is the mean annual sea surface temperature. Fishing mortality (F) was calculated as the difference between total and natural mortality:

$$F = Z - M \text{ (Ricker, 1979).}$$

Exploitation rate (E) was determined as $E = F / Z$ (Gulland, 1971).

Results

Reproductive Biology

The reproductive behavior of *T. mediterraneus* can be described by the logistic function $Y_{TL} = 100 / [1 + \exp(-0.84(TL - 11.09))]$, where TL_{50} is the length at which 50% of individuals reach maturity. According to the logistic model, 50% of *T. mediterraneus* individuals mature at a length of 11.09 cm (Figure 2), which corresponds to the first year of life (Table 1) and is

consistent with the findings of Kutsyn (2021). Based on GSI dynamics, the spawning period of Black Sea *T. mediterraneus* extends from early June to late August, with a peak value of 4.1% in July (Figure 3), in agreement with previously published data (Melnikova, 2020; Kutsyn, 2021).

Ichthyoplankton

In 2019, ichthyoplankton samples were collected in the northern Black Sea near the Crimean Peninsula and the Caucasus coast during the summer hydrological season, between July 11 and August 3. Sea surface temperature (SST) ranged from 22.4 to 26.6°C, with an average of 24.8°C. Eggs and larvae of *T. mediterraneus* were found throughout the study area at depths ranging from 16 to 2150 m (Figure 4).

The abundance of *T. mediterraneus* eggs and larvae increased from the shelf edge toward the continental slope and then sharply decreased toward

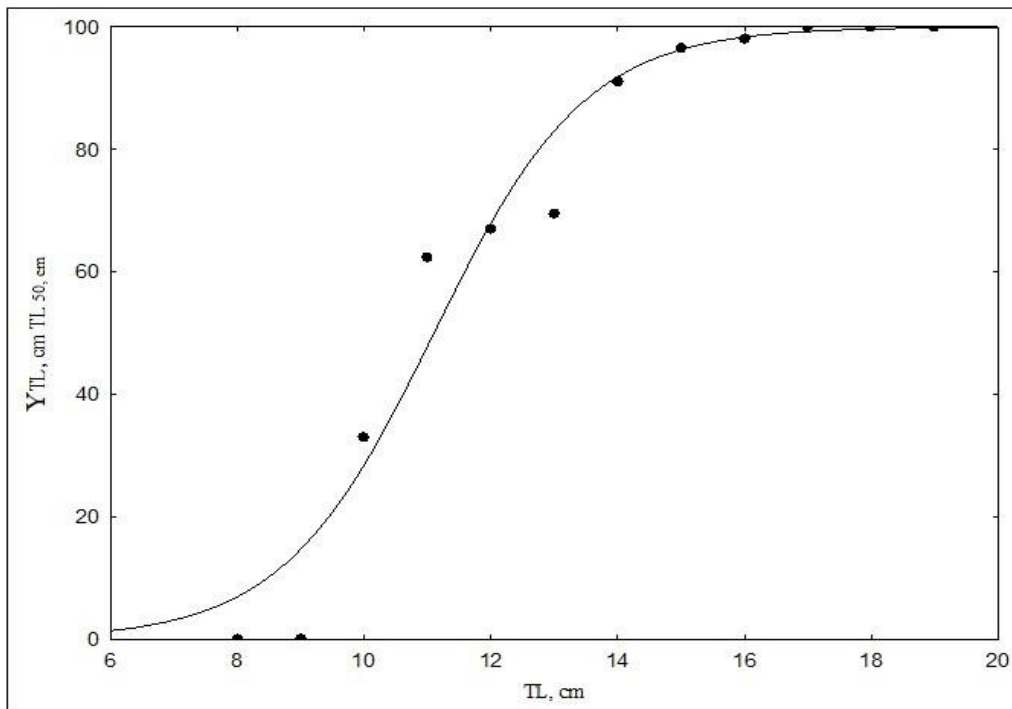


Figure 2. The proportion of mature individuals (YTL) of *T. mediterraneus*, depending on the length (TL), in the coastal waters of southwestern Crimea.

Table 1. The total length (TL) and weight (W) of the *T. mediterraneus* (M ± SE) in different age groups in the coastal waters of southwestern Crimea.

Age, year	Length (TL), cm	Weight (W), g	n, ind.
1	11.78±0.12	14.06±0.3	101
2	14.54±0.07	25.98±0.39	157
3	15.89±0.19	29.99±0.78	52
4	16.51±0.22	36.24±1.49	20
5	18.96±0.47	45.1±2.78	8
6	21.85±0.75	77.21±9.74	2
7	23.3	90.03	1

M±SE, mean value and standard error.

the deep-sea area. The maximum abundance was recorded in the 0–100 m layer at a depth exceeding 636 m, where egg abundance reached 69.9 ind./m² (36 specimens per catch) and larval abundance reached 46.5 ind./m² (24 specimens per catch). The distribution of eggs and larvae across different depths was uneven and exhibited a "patchy" pattern, as indicated by the low reliability of the polynomial trend line approximation: $R^2 = 0.1427$ for eggs and $R^2 = 0.2018$ for larvae.

In 2021, ichthyoplankton was collected in the same study area from June 29 to August 8. Sampling was conducted over two periods: June 29–July 7 and July 30–August 8. During this time, the average SST was

25.8°C. In the open waters of the northern Black Sea, eggs and larvae of *T. mediterraneus* were found at depths ranging from 25 to 2130 m (Figure 5).

The first sampling period occurred during the initial phase of the summer hydrological season, which lasted until the end of the first decade of July. Increased cyclonic activity in June delayed the formation of the upper quasi-homogeneous layer (UQHL), which had a thickness of 6–9 m. SST ranged from 19 to 24°C, conditions favorable for the onset of *T. mediterraneus* spawning. However, northerly and northeasterly winds intensified to 12–15 m/s, generating storms of up to 4 Beaufort force. Consequently, the proportion of dead

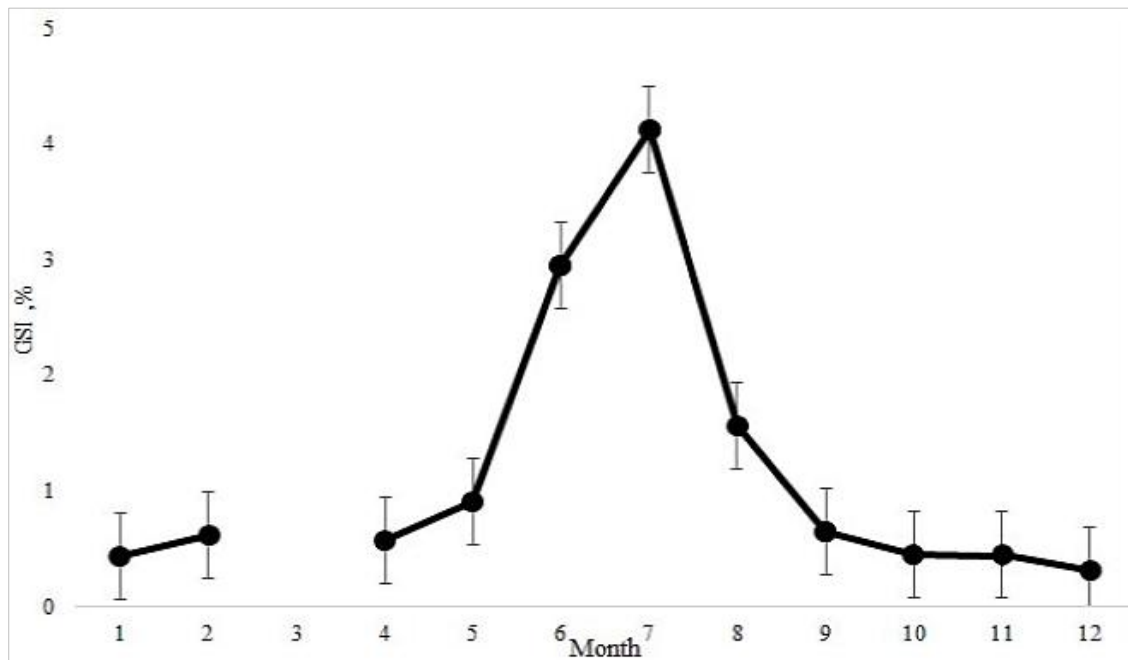


Figure 3. Dynamics of gonadosomatic indices of the *T. mediterraneus* in the coastal waters of southwestern Crimea during the year.

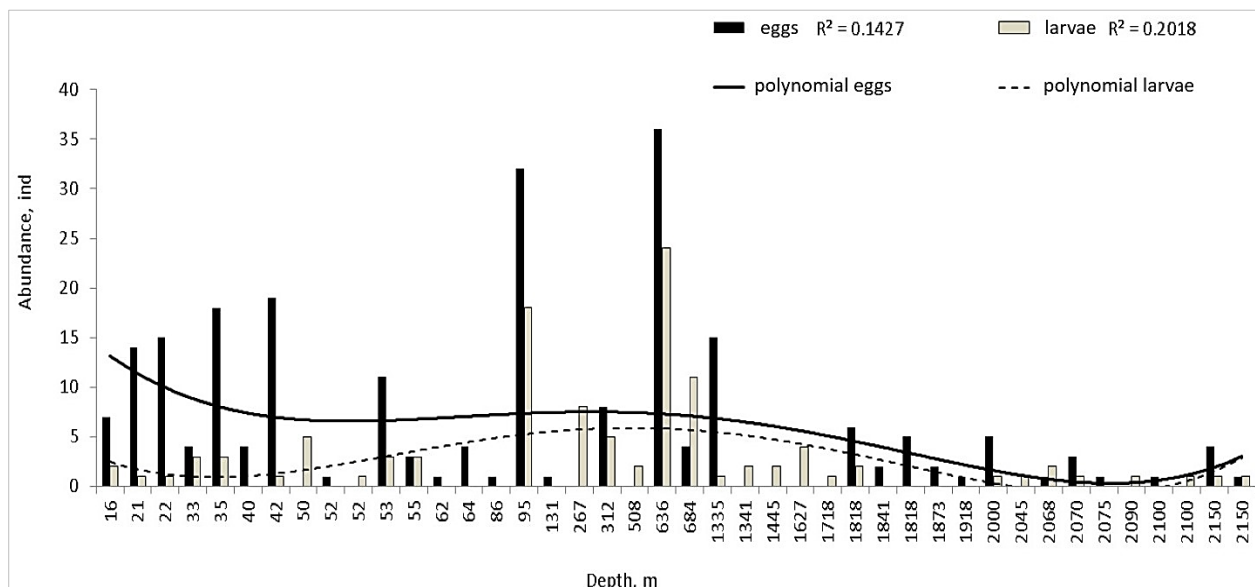


Figure 4. Spatial distribution of *T. mediterraneus* eggs and larvae at different research depths in July 2019.

eggs increased dramatically, ranging from 62% to 100% and averaging 84%. No larvae were found in the samples during this period.

The second sampling period took place between July 30 and August 8, during the peak of the summer hydrological season. Conditions were predominantly partly cloudy, and SST rose from 25 to 28°C. The thickness of the UQHL in the coastal shelf area increased to 16–17 m. A total of 148 fish larvae were collected. The maximum number of larvae (30 per catch, or 78 ind./m² of sea surface) was observed at a depth of 84 m. The maximum number of eggs (13 per catch, or 33.8 ind./m² of sea surface) was recorded at a shallow-water station at a depth of 25 m off the Caucasus coast. The proportion of dead eggs averaged 46% in the Caucasus region, where sea waves reached up to 2 Beaufort force, and 75% off the Kerch Peninsula, where wave heights reached 3–4 Beaufort force (Klimova et al., 2024).

High water temperatures (26°C) during embryonic development may also contribute to increased egg mortality (Dekhnik, 1973). Eggs were found only sporadically throughout the study area. Larvae were collected at a single station in the coastal zone. Maximum abundance was observed over the continental slope, with larvae subsequently found in low numbers at deep-sea stations down to a depth of 2100 m (Klimova et al., 2024). As in 2019, the distribution of eggs and larvae was patchy. The reliability of the polynomial approximation improved for both eggs ($R^2 = 0.2581$) and larvae ($R^2 = 0.3317$).

Diet

In 2019, the diet of *T. mediterraneus* larvae (TL range 2.5–11.4 mm) consisted primarily of copepod juveniles. Calanoida dominated the diet across all larval size groups, with Acartiidae contributing significantly more than Cyclopoida. The contribution of Cladocera to

the diet increased with larval growth; in some areas, Cladocera consumption reached up to 36% of all prey items (Zagorodnyaya et al., 2022). Small copepods (≤ 0.2 mm) constituted a substantial portion of the diet for larvae up to 5.5 mm TL, accounting for 50% to 63% of total copepod consumption.

In 2021, the diet of larvae measuring 2.3–5.5 mm TL consisted mainly of *Acartia* (*A. tonsa* and *A. clausi*). *Paracalanus parvus*, *Pseudocalanus elongatus*, and the cladoceran *Penilia avirostris* played secondary roles. The number of prey items per gut ranged from 1 to 3. In larger larvae (5.6–10 mm TL), copepod juveniles (Calanoida) remained dominant, accounting for 62% of total prey items, while the contribution of Cladocera increased to 38%. The number of prey items per gut ranged from 1 to 4 (Klimova et al., 2024).

Thus, favorable conditions for the development of *T. mediterraneus* larvae were observed in the northern Black Sea and off the Caucasus coast during 2019–2021. Larvae at all developmental stages were present in the samples. The dominance of small copepods in the larval diet indicates favorable growth and survival conditions, consistent with previous studies (Zagorodnyaya et al., 2022; Klimova et al., 2024).

The diet of *T. mediterraneus* during the winter hydrological season of 2023 was also examined. Samples were collected off the coast of Sochi (40 individuals in January) and off the Crimean coast in Laspi Bay (34 individuals in February). During the summer hydrological season, in June 2024, 28 individuals were collected off the Crimean coast in Karantinnaya Bay. The number and parameters of fish examined for diet are presented in Table 2.

In winter, the diet of *T. mediterraneus* (TL range 8.1–11.6 cm) consisted of adult and juvenile stages of the copepod *Calanus helgolandicus*, as well as highly digested fish remains. Notably, large numbers of fish scales, primarily from *Sprattus sprattus*, were found in

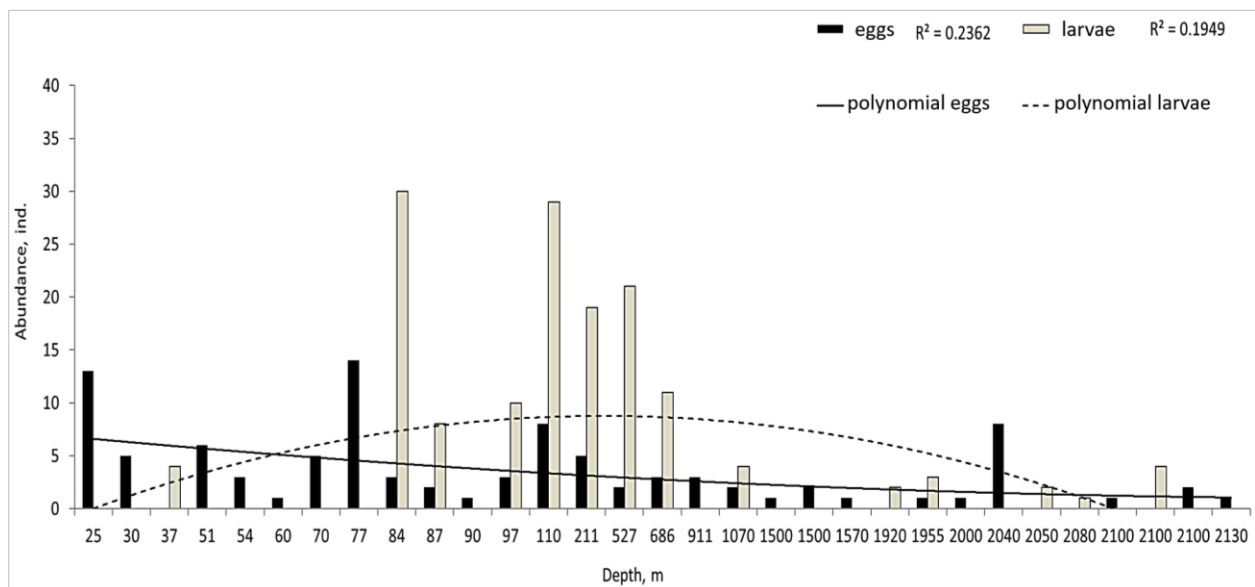


Figure 5. Spatial distribution of *T. mediterraneus* eggs and larvae at different depths in July 2021.

the digestive tracts, compressed into dense masses and coated with mucus.

In summer, the diet of *T. mediterraneus* (TL range 8.2 – 14.6 cm) consisted primarily of fish, represented by heavily digested remains such as scales and bones. Most of these remains belonged to *Mullus barbatus*. In one individual (TL 13 cm), a juvenile *M. barbatus* (4.5 cm in length) was found in the gut with a digestion stage of 4. The prey was folded in half and lacked a scaly covering. In two individuals (TL 14.6 and 14.4 cm), *T. mediterraneus* larvae measuring 2.8, 2.6, and 3.0 mm were found in the guts. Parasitic isopods *Elaphognathia bacescoi*, ranging from 3.1 to 3.4 mm in length, were found in the digestive tracts of four *T. mediterraneus* individuals. Digestion stages for *C. helgolandicus* ranged from 2 to 5, and for fish remains from 2 to 4. The degree of stomach fullness ranged from 1 to 3. The proportion of individuals with empty guts was high: 76% in winter and 86% in summer, exceeding values reported for other areas of the Black Sea (Georgieva et al., 2019).

Growth

A comparative analysis of the length distribution of *T. mediterraneus* larvae revealed changes compared to the mid-20th century. In July 2019, larvae at all developmental stages were present in samples, with lengths ranging from 1.4 to 11 mm. The proportion of larvae smaller than 2.2 mm was 40–50% in both shallow and deep-sea areas (Zagorodnyaya et al., 2022), higher than the 5–30% recorded in the 1960s (Dekhnik, 1970). Larvae were represented at all developmental stages, from 1.4 to 11 mm. In the mid-20th century, the highest concentrations of *T. mediterraneus* eggs and larvae were observed in July, with spawning activity typically declining by August, accompanied by a decrease in egg and larval abundance (Dekhnik, 1970). During our August 2019 sampling, no such decline in spawning activity was observed, and the proportion of small larvae (<2.2 mm) on the shelf was 69% (Zagorodnyaya et al., 2022). In 2021, larvae ranged in length from 1.5 to 10.2 mm. The proportions of larvae by feeding type were: yolk-feeding –24%, mixed feeding–66%, and exogenous feeding–10% of the total larval count.

The most rapid increase in body size occurs during the first year of life. The average linear increase is 11.78±0.12 cm, with a weight of 14.06±3 g (Table 1). The greatest increase in body weight was observed in the

oldest age groups. The relationship between body weight (*W*, g) and length (*TL*, cm) is described by the power equation $W=0.0097 \times TL^{2.91}$, $R^2=0.91$, indicating nearly isometric growth ($t=4.16$, $P<0.05$). Linear and weight growth are described by the following von Bertalanffy equations (Figure 6): $L_{\infty}=21.8[1 - e^{-0.25(t + 2.46)}]$; $W_{\infty}=77.2[1 - e^{-0.25(t + 2.46)}]^{2.91}$. The growth coefficients are: $k=0.25 \text{ year}^{-1}$, $t_0=-2.46$, $Ginit=5.45 \text{ cm/year}$, $\phi'=2.07$, $\phi=0.65$.

Mortality

The total mortality rate for *T. mediterraneus* in the coastal waters of southwestern Crimea is 1.03 year⁻¹, with natural mortality estimated at 0.49 year⁻¹ and fishing mortality at 0.54 year⁻¹. The exploitation rate (*E*) is 0.53, indicating a high level of fishing pressure ($E>0.50$). It should be emphasized that these results are preliminary. The conventional method used to estimate *E* does not account for factors such as gear selectivity, natural recruitment variability, or interannual differences between year classes, all of which may affect the accuracy of the estimates.

Discussion

In the Black Sea, a documented increase in sea surface temperature (SST) is correlated with a reduction in oxygen levels (Gül, Ceylan, & Dalgıç, 2025). This phenomenon is considered a potential stressor that may threaten ecosystem balance by reducing the availability of suitable habitat for marine organisms. Furthermore, the ongoing trend of rising average annual temperatures in the region could influence the Black Sea ecosystem, potentially driving adaptive changes in the life-history strategies of *T. mediterraneus*.

Within established physiological frameworks (Jørgensen et al., 2007), accelerated gonadal maturation under warmer conditions may promote an earlier onset and extended duration of spawning. Similarly, accelerated growth during early life stages could lead to a shift in energy allocation, favoring reproductive investment over somatic growth. This trade-off may result in a reduction in body size at maturation. It is hypothesized that such adjustments in reproductive strategy represent an adaptive response aimed at enhancing population resilience and ensuring long-term persistence in a changing environment.

Table 2. Length and weight parameters of *T. mediterraneus*; IF–index of gut fullness ‰; CF–Condition factor; (min÷max/Xcr±SD)

Parameter	Winter	Summer
Number, ind.	75	28
TL, cm	8.1–11.6/9.9±0.7	8.2–14.6/10.6±1.5
SL, cm	7.6–10.9/8.8±0.6	7.2–12.1/9.2±1.3
W_{fish} , g	3.5–11.8/7.4±1.8	2.7–26.3/7.3±5.7
Share of fish with food, %	24	14
CF	0.6–1.8/1.1±0.2	0.4–1.6/0.9±0.3
IF, ‰	208–721/460±100	86–917/419±214

During the summer spawning season, pelagic eggs and larvae of *T. mediterraneus* are typically distributed throughout the upper quasi-homogeneous layer (UQHL) of the Black Sea. They can be found both in narrow coastal areas, where they dominate samples, and in open waters, where they are second in abundance to *Engraulis encrasicolus* (Dekhnik, 1973).

In recent years, as a result of the weakening of the Rim Current during the summer hydrological season, anticyclonic eddies have been observed to form between the narrow coastal zone and the Rim Current jet. These eddies facilitate the movement of planktonic organisms between coastal and deep-water zones. Consequently, an expansion has been observed in the species composition and abundance of plankton, as well as in the larval and juvenile fish that feed on it (Klimova et al., 2022; Morozov & Mankovskaya, 2023; Belokopytov & Zhuk, 2024).

In 2019, *T. mediterraneus* larvae accounted for 10.5% of the total larval abundance in shallow waters and 16.2% in deep-sea areas. In 2021, they represented 8.9% of total fish larvae in shallow waters and 7.1% in deep-sea areas. Active cyclonic activity in the eastern part of the sea during June and July 2021 caused the Black Sea Rim Current (BRC) to intensify into a more pronounced flow than is typical for that time of year.

The displacement of the BRC toward the coastal shelf area facilitated the transport of warm-water fish larvae into this zone. Consequently, the average larval abundance on the shelf increased to 452 ind./m², five times higher than the average in deep-sea areas, with a maximum abundance of 936 ind./m². The timing of the spawning season, as well as the survival of eggs and pre-

larvae, is primarily influenced by abiotic environmental factors such as temperature, salinity, and anthropogenic pollution. In contrast, the survival of fish larvae and juveniles depends largely on food availability. Climate change, particularly the rapid warming of surface waters, may contribute to an earlier onset of the reproductive cycle for summer-spawning fish species and an increase in food availability (Zagorodnyaya et al., 2022). Thus, favorable conditions for the development of *T. mediterraneus* larvae were observed in the northern Black Sea and off the Caucasus coast during 2019 – 2021. Larvae at all developmental stages were present in the samples. Small copepods dominated the larval diet, indicating favorable growth and survival conditions. These findings are consistent with previous studies conducted in recent years (Zagorodnyaya et al., 2022; Klimova et al., 2024). The high abundance of *T. mediterraneus* larvae and eggs recorded during the summer (July and August) of 2019 during research aboard the R/V Professor Vodyanitsky was consistent with the spawning period as indicated by GSI data. The predominance of 1–2-year-old individuals in the 2020–2021 catches (Table 1) may reflect successful spawning and relatively high juvenile survival from preceding spawning seasons.

The diet of *T. mediterraneus* during the winter of 2023 and the summer of 2024 consisted mainly of fish, with crustaceans recorded only in winter. The proportion of individuals with empty guts was high: 76% in winter and 86% in summer. These values exceed those reported for other areas of the Black Sea. For instance, in the southwestern Black Sea during spring, the proportion of empty guts among fish measuring

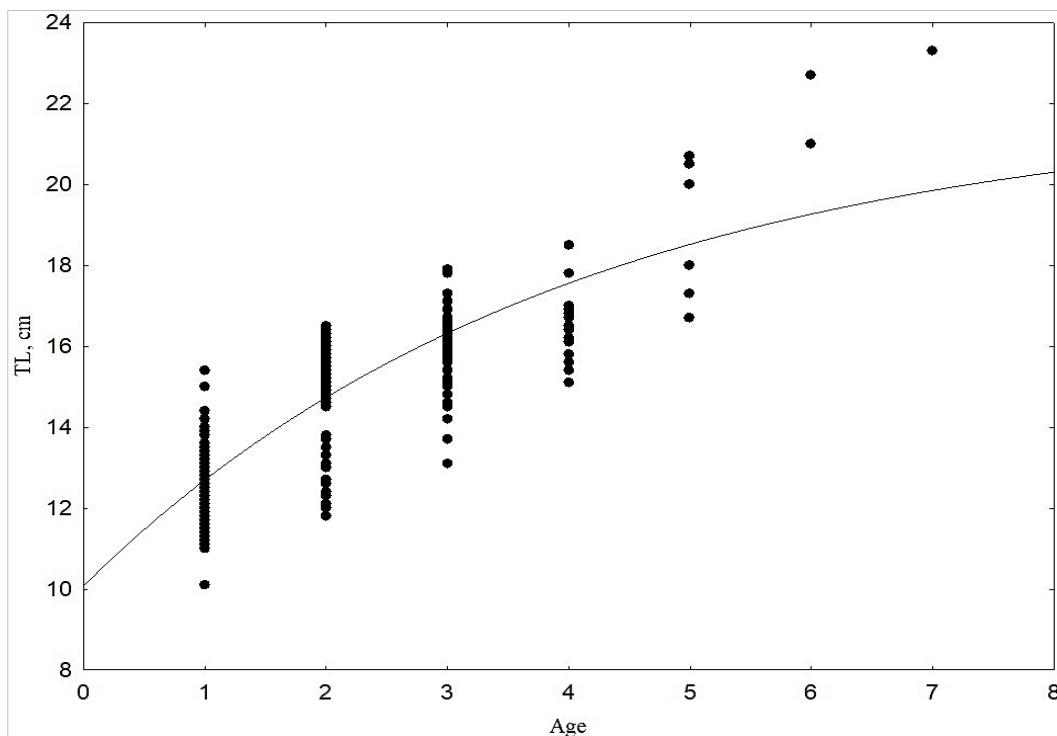


Figure 6. Linear growth curves for *T. mediterraneus* at the south-eastern coast of the Crimea, approximated with the von Bertalanffy equation.

10–18 cm in length reached 47%, decreasing to 39% in summer. In that region, the diet of *T. mediterraneus* included polychaetes, crustaceans, and fish, and varied seasonally: benthic organisms were preferred in spring, while fish became a significant dietary component in autumn. Zooplankton, benthic prey items, and fish were also consumed in summer (Georgieva et al., 2019). These findings are consistent with our observations of zooplankton and fish consumption by *T. mediterraneus*; however, benthic prey items were not recorded in our samples.

The average condition factor (CF) varied considerably, ranging from 0.6 to 1.8 in winter and from 0.4 to 1.6 in summer. Meanwhile, the index of gut fullness (IF) showed high values in both seasons, averaging 460‰ in winter and 419‰ in summer (Table 2). The high proportion of fish with empty guts may therefore not reflect a lack of food availability, but rather be influenced by factors such as age, season, circadian rhythms, and other determinants of feeding behavior.

The total length and weight values obtained for different age groups in this study, together with the estimated L_{∞} and W_{∞} values, were slightly higher than those previously reported for *T. mediterraneus* off the southwestern coast of Crimea during 2003–2019 (Kutsyn, 2021). Differences in total length, depending on age group, ranged from 0.5 cm to over 3 cm. A similar trend was observed for asymptotic sizes: L_{∞} = 21.8 cm and W_{∞} = 77.2 g in the present study, compared to L_{∞} = 19.0 cm and W_{∞} = 57.8 g in the earlier study.

Melnikova et al. (2023) examined the long-term variability of certain biological indicators in relation to increases in mean annual sea surface temperature (SST) in the Black Sea. Their study revealed an increase in asymptotic size parameters (L_{∞} and W_{∞}) as well as growth rate parameters (k , ϕ' , and ϕ). Between 2000 and 2007, asymptotic sizes were L_{∞} = 18.8 cm and W_{∞} = 56.8 g; between 2008 and 2013, they increased to L_{∞} = 19.5 cm and W_{∞} = 60.8 g; and between 2014 and 2020, they reached L_{∞} = 20.8 cm and W_{∞} = 66.1 g. Comparison of these values with those obtained in the current study reveals a continuing positive trend in the asymptotic size of *T. mediterraneus* off the Crimean coast.

The observed increase in growth rate and maximum length of *T. mediterraneus* may be partly attributable to rising mean annual sea surface temperatures in the Black Sea. As a subtropical,

thermophilic, and migratory species, its biology is likely influenced by temperature changes. Moreover, given the pronounced seasonality of the Black Sea, this species undertakes long-distance migrations to warmer areas within its range (Ivanov & Beverton, 1985). Should the current warming trend continue, it is plausible that *T. mediterraneus* will undertake shorter migrations, thereby reducing its wintering period. Such a shift could result in reduced energy expenditure, increased productivity, improved survival, and decreased winter mortality.

It is important to note that, according to the temperature-size rule (TSR), populations inhabiting warmer environments typically exhibit accelerated growth and earlier maturation, accompanied by reductions in maximum body size and life expectancy. Consequently, the observed increase in asymptotic sizes (L_{∞} and W_{∞}) may represent a temporary phenomenon. In the longer term, a decrease in these parameters is expected in accordance with the TSR. Continued climate warming is therefore likely to lead to increased growth rates alongside reductions in maximum body size and maximum life span of *T. mediterraneus* in the Black Sea.

The variability in biological parameters observed in our study correlates with an increase in mean annual sea surface temperature, which may contribute to elevated mortality rates. Specifically, our findings are consistent with the established model that posits a positive relationship between the natural mortality coefficient (M) and ambient temperature. This relationship is attributed to fundamental processes such as increased metabolic rates (Pauly, 1980) and reduced dissolved oxygen concentrations (Cheung et al., 2013). Consequently, a further increase in M values can be expected if the current warming trend persists. In the long term, this may lead to a reduction in population biomass due to decreased individual size and a declining proportion of older age groups, in accordance with the temperature-size rule (TSR).

With regard to fishing pressure, an analysis of available literature data (Table 3) indicates that high exploitation rates (E) for *T. mediterraneus* in the Black Sea suggest excessive fishing pressure. This conclusion is supported by findings from several regional studies. For example, Salihoglu et al. (2017) project a decline in stocks if intensive fishing continues. Research by Erbay (2022), based on acoustic surveys in the southeastern Black Sea, documents a significant decrease in *T. mediterraneus* abundance and notes that a substantial

Table 3. Mortality rates and exploitation coefficient of *T. mediterraneus* from different regions of the Black Sea

Region	Total Mortality (Z)	Natural Mortality (M)	Fishing Mortality (F)	Exploitation Rate (E)	Sources
Black Sea, northern part	1.03 year ⁻¹	0.49 year ⁻¹	0.54 year ⁻¹	0.53	This study
Black Sea, southeastern part	1.02 year ⁻¹	0.31 year ⁻¹	0.71 year ⁻¹	0.69	Samsun, 2023
Black Sea, southeastern part	1.08 year ⁻¹	0.43 year ⁻¹	0.65 year ⁻¹	0.6	Kasapoğlu, 2018
Black Sea, southeastern part	1.2 year ⁻¹	0.47 year ⁻¹	0.73 year ⁻¹	0.61	Özdemiretal. 2009
Black Sea, central part	1.71 year ⁻¹	0.84 year ⁻¹	0.87 year ⁻¹	0.51	Samsun et al, 2018
Black Sea, western part	2.99 year ⁻¹	1.08 year ⁻¹	1.91 year ⁻¹	0.64	Yankova,2013

proportion of the catch consists of immature individuals. A decline in *T. mediterraneus* stocks off the Romanian coast has also been reported (Păun et al., 2025), accompanied by a sharp annual decrease in catch biomass.

It is important to note that our data do not allow for a quantitative separation of the contributions of climatic factors from fishing pressure to the observed population changes. This constitutes a key methodological limitation of the present study. Nevertheless, given that *T. mediterraneus* is a major target species and a crucial component of the Black Sea trophic web, our results underscore the need for enhanced monitoring and the revision of fisheries management measures. Sustained monitoring of the status and abundance of *T. mediterraneus* stocks in the Black Sea is essential for ensuring sustainable fisheries management. Given the observed increase in natural mortality (*M*) and the persistently high exploitation rate (*E*), management measures such as increasing mesh size could be considered to alleviate fishing pressure on the younger age classes of *T. mediterraneus*. This recommendation follows the precautionary approach, aiming to mitigate potential growth overfishing.

Conclusions

Future research priorities should include monitoring the species composition and abundance of ichthyoplankton, as well as quantifying the effects of temperature on the reproductive biology, size-at-age, growth rates, diet, and mortality of *T. mediterraneus*. We hypothesize that analyzing the influence of environmental variability on life-cycle parameters will provide insight into key mechanisms of evolutionary adaptation. Ultimately, such data are expected to form the basis for developing more rational fisheries management strategies, thereby improving the efficiency of resource use and enabling better prediction of shifts in biological parameters under ongoing climate change.

Ethical Statement

Animal protocols were approved by the Bioethics Commission of the Kovalevsky Institute of Biology of the Southern Seas of Russian Academy of Sciences, Sevastopol, Russia (Protocol No.4(9)/24) 09 December 2024).

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Author Contribution

P.D., concertualization, methodology, writing, data analysis, editing, original draft; **I.V.**, writing, data analysis, diet of fish; **T.K.**, writing, editing, data analysis, Identification of ichthyoplankton.

Conflict of Interest

The authors declare that they have no known competing financial or non-financial, professional, or personal conflicts that could have appeared to influence the work reported in this paper.

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