A preliminary life history traits analysis of sharks in the Sea of Marmara (Türkiye), where deoxygenation and habitat deterioration are raising concerns

Hakan KABASAKAL¹, Serdar SAKINAN², Lovrenc LIPEJ³, Danijel IVAJNŠIČ⁴

ABSTRACT

Life history traits of 17 species of sharks occurring in the Sea of Marmara were analysed based on Gower’s distances, Principal Coordinate Analyses, and hierarchical clustering. The analysis shows that the sharks of the Sea of Marmara can ecologically be divided into several clusters. The increasing occurrence of sharks on the Marmara continental shelf, especially in the last few years, suggests that the expected habitat compression due to deoxygenation has begun to take place. This situation, which can be considered as a “habitat trap” for sharks, should be considered as a threat that may lead to shark mortalities due to the intensification of bycatches or even the intentional killing of sharks. Available results are sufficient to predict a disturbing future for sharks of the Sea of Marmara if the factors (deoxygenation, habitat loss, bycatch, etc.) threatening the overall ecosystem do not improve.

Keywords: PCoA, Ecology, Sharks, Habitat compression, Mortality
Introduction

The Sea of Marmara is the center of the hydrographic structure called the Turkish Straits System (Öztürk and Öztürk, 1996). Connected to the Mediterranean Sea via the Dardanelles Strait and the Black Sea via the Bosphorus Strait, the species composition of the fish fauna of the region represents the faunal characteristics of both seas (Eryılmaz and Meriç, 2005). Recent studies showed that the fish fauna of the Sea of Marmara includes 263 species of teleost fishes, representing 78 families (Artüz and Fricke, 2019) and 17 species of sharks, representing 11 families (Kabasakal, 2022a). According to Kabasakal (2022a) presence statuses of 3 out of 17 species of sharks, are currently being considered questionable.

Since it is on the way of one of the most intense maritime trade routes in the world, the Sea of Marmara has been exposed to serious pollution from ships (Erlevent and Kum, 2022). The fact that a significant part of Turkey’s population lives in large cities surrounding the Sea of Marmara, as well as the intense industrialization around the region and the drainage waters of agricultural areas carried by the rivers emptying into the marine area, have caused serious marine pollution in the inland sea during the last 40 years (Salıhoğlu et al., 2022). Especially in the deep sea trenches of the region, the fact that the oxygen level has decreased below 80 micromolar, which is considered the “hypoxia” limit (Mantıkçı et al., 2022), forces the fauna in these zones to live in extreme conditions. In a recent review, Kabasakal (2022b) pointed out that continued deoxygenation, particularly in the deep-sea region, could lead to “vertical habitat compression”, forcing bathydemersal shark species to ascend in the shallows of the continental shelf and inhabit these zones, which could increase bycatch of deep-sea sharks. In the present article, which is a follow-up study of Kabasakal’s (2022b) review, the authors aim to provide a preliminary life history traits analysis to a better understanding of the ecological status of the sharks of the Sea of Marmara. The Authors also aim to evaluate the available data regarding the deoxygenation and habitat loss in the Sea of Marmara to project possible consequences of such ecological conditions on the survival of sharks, based on the present analysis of life history traits of species occurring in the region.

Material and Methods

General Characteristics of the Study Area

Based on Kocatas et al. (1993) and Öztürk and Öztürk (1996), the general characteristics of the Sea of Marmara (Figure 1) can be summarized as follows: although it is a very small inland sea with an area of 11,500 km² and a volume of 3,378 km³, the Sea of Marmara occupies an important place in Turkey’s fishing economy. Three neighboring deep-sea trenches, (or deep depressions), a narrow continental shelf in the north and a relatively wider continental shelf in the south are the main geomorphological formations that stand out in the bottom structure of the Sea of Marmara (Figure 1). The deep depression zone, which is located in the middle region and reaches 1,335 m in depth, is the deepest place in the Sea of Marmara. A dual current system is dominated the current dynamics in the inland sea, which is connected to the Black Sea via the Bosphorus Strait, and to the Aegean and Mediterranean seas via the Dardanelles Strait. Considering the temperature and salinity stratification, three different water layers, which are surface, bottom, and transitional layers, fill the Marmara basin. The renewal time of the volume of water in the Sea of Marmara, with the oxygen-rich flow from the Mediterranean and Aegean, was estimated at 6 to 7 years (Kocataş et al., 1993).

Data Gathering and Analysis

Life history traits of 17 species of sharks, which are included in the current species list with confirmed or questionable occurrence (Kabasakal, 2022a), were gathered from the relevant literature (Compagno, 1984a,b; Serena, 2005; IUCN, 2007; Ebert and Stehmann, 2013; Froese and Pauly, 2022). In order to test whether the life history traits of the species could help to explain spatial variation in the Sea of Marmara a total of 18 functional traits with subcategories were assigned to each species, and the definitions of these traits (Pimiento et al., 2020) are shown in Table 1. Based on the definition that “any shark species with a total length (TL) >200 cm are classified as a large shark” (Ferretti et al., 2008), maximum sizes of examined species are arbitrarily divisioned into those with TL ≤200 cm and those with >200 cm.

To visualize the trait characteristics occupied by the selected shark species we conducted Principal Coordinate Analysis (PCoA) on Gower’s distances of the species by trait matrix (Ladds et al., 2018). Convex hulls were created and colour-coded based on vector overlays to show traits that are important for shark species separation in trait space. In order to compute Gower’s distances, based on the life history traits of 17 shark species, a “dissimilarity” matrix was computed with “dist.ktab” function of the “ade4” package of R (Pimiento et al., 2020). Since the data matrix is based on binary coding (1, presence; 0, absence), the “dichotomous – D” variable type is selected for computation. PCoA was performed with “pcoa” function of the “ape” package (Pimiento et al., 2020), and results were visualised with the “ggplot” library. Furthermore,
in order to illustrate the clustering of examined shark species, agglomerative cluster analysis, based on Gower’s distances, was performed (Akay and Yüksel, 2017). All analyzes were performed in an R environment.

Figure 1. Position of the Sea of Marmara on the globe and the bathymetric map depicting continental shelf and deep-depression zones
Table 1. Definitions of life history traits used in the present analysis

<table>
<thead>
<tr>
<th>Traits</th>
<th>Definition</th>
<th>Nature</th>
<th>Modality/Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum size, TL</td>
<td>Maximum reported total length for each species gathered from relevant literature; TL of examined species arbitrarily categorized as TL ≤200 cm and TL &gt;200 cm, based on definition of large elasmobranchs (Ferretti et al., 2008)</td>
<td>Binary</td>
<td>cm</td>
</tr>
<tr>
<td>Thermoregulation</td>
<td>The trait of mesothermy was assigned to two species of thresher sharks (Alopias superciliosus and A. vulpinus)</td>
<td>Binary</td>
<td>Mesothermy</td>
</tr>
<tr>
<td>Terrestriality</td>
<td>A ‘land’ trait designation was assigned to two angel sharks (Squatina oculata and S. squatina) and Mustelus asterias, since their juveniles or adults may occur in very shallow depths (eg. 5 m), coastal bays, estuaries and brackish water areas</td>
<td>Binary</td>
<td>Coastal bays, Shallow water, Estuarine, Brackish</td>
</tr>
<tr>
<td>Habitat zone and vertical position</td>
<td>Habitat was categorized in accordance where organisms occur based on the zone where they occur as adults (i.e., trait designations: continental shelf, slope, offshore, some of these, or all). The vertical position was assigned based on the most frequent part of the water column where they feed (i.e., trait designations: benthic or demersal, pelagic or both). These data were gathered from the relevant literature</td>
<td>Binary</td>
<td>Shelf, Slope, Coastal, Offshore, Demersal, Pelagic</td>
</tr>
<tr>
<td>Migration</td>
<td>Migration was assigned to define the seasonal coastal occurrences of Squatinid angel sharks, and seasonal migrations of Alopid thresher sharks and Galeorhinus galeus, based on relevant literature</td>
<td>Binary</td>
<td>Seasonal</td>
</tr>
<tr>
<td>Diet</td>
<td>Diet was categorized based on the information gathered from relevant literature</td>
<td>Binary</td>
<td>Fish, Cephalopods, Crustaceans, Polychaetes, Marine, Mammals</td>
</tr>
<tr>
<td>Reproduction</td>
<td>Since egg-laying oviparous Scyliorhinid sharks depend on bottom structures to fix their egg-cases, mode of reproduction was assigned to each species to identify the location of reproduction; viviparity includes species with or without a yolk-sac placenta</td>
<td>Binary</td>
<td>Oviparous, Viviparous</td>
</tr>
</tbody>
</table>

Results and Discussion

Life history traits of the following sharks species were analysed: Hexanchidae, Hexanchus griseus (Bonnaterre, 1788); Alopiidae, Alopias superciliosus (Lowe, 1841), A. vulpinus (Bonnaterre, 1788); Pentanchidae, Galeus melastomus Rafinesque, 1810; Scyliorhinidae, Scyliorhinus canicula (Linnaeus, 1758), S. stellaris (Linnaeus, 1758); Triakidae, Galeorhinus galeus (Linnaeus, 1758), Mustelus asterias Cloquet, 1819, M. mustelus (Linnaeus, 1758); Dalatiidae, Dalatias licha (Bonnaterre, 1788); Oxyotidae, Oxytus centrina (Linnaeus, 1758); Centrophoridae, Centrophorus uyato (Rafinesque, 1810); Squalidae, Squalus acanthias Linnaeus, 1758, S. blainville (Risso, 1827); Echinorhinidae, Echinorhinus brucus (Bonnaterre, 1788); and Squatinidae, Squatina oculata Bonaparte, 1840, S. squatina (Linnaeus, 1758).

PCoA analysis and hierarchical cluster analysis, based on Gower’s distances showed that 17 species of sharks occurring in the Sea of Marmara were divided into several clusters. Graphical illustrations of PCoA analysis and hierarchical clustering of the examined species are depicted in separate plots (Figures 2 and 3). The first cluster includes A. superciliosus and A. vulpinus, the last pelagic lamniform sharks still occurring in the Sea of Marmara, due to their pelagic migratory characteristics, and thermoregulation abilities. The second cluster includes predominantly demersal shark species.
and redimensioned in several subclusters including *H. griseus*, all of the squaliform sharks, representing in Dalatiidae, Oxy-
notidae, Centrophoridae, Squalidae and Echinochiridae fami-
lies; squatinid angel sharks, and the triakid *G. galeus* (Figure 3). Due to its’ specialized feeding modes, *O. centrina*, a spe-
cialized polychaete feeder, differs from other species of the second cluster. Although, included in the second cluster, *H. griseus*, the largest demersal shark occurring in the Sea of Marmara, is differentiated from other subclusters due to its large size and extensive depth distribution covering both bathyal and shallow shelf waters, as well as the fact that in its stomach contents remains of marine mammals could be found. Angels sharks (*S. oculata* and *S. squatina*) representing terrestriality and form another subcluster. The oviparous (egg-laying) pentanchid (*G. melastomus*) and scyllorhinid sharks (*S. canicula* and *S. stellaris*) were grouped in the third cluster. The fourth cluster is formed by *M. asterias* and *M. mustelus*, and they differed from other demersal species due to their durophagous feeding habits, since they mainly prey on crustaceans.

As Mouillot (2007) emphasizes, biodiversity is being lost rapidly in an increasingly changing world due to human ac-
tivities. Therefore, we urgently need to identify the factors that control the coexistence of species and thus sustain re-
gional biodiversity and the threats to them. Measurements of species dissimilarities or distances between them, which is a critical step in functional ecology studies, is an important milestone in understanding the factors that make the coexis-
tence of these species possible (Pavoine et al., 2009). Hierar-
chical clustering methods based on dissimilarities or differ-
ences, such as Gower’s distances, can help to understand di-
versity (Pavoine et al., 2009; Ladds et al., 2018). This pio-
neering study, in which the functional distances or dissimi-
larities of shark species occurring in the Sea of Marmara were revealed for the first time, showed that 17 species of sharks form distinct clusters that are not far apart. Thus, apart from 7 specialized species, 10 other species (58.8% of total spe-
cies) share similar niches.

Since sharks are apex predators, they play a fundamental role in maintaining a balanced food chain in the marine ecosys-
tem, and are indicators of healthy oceans (Stevens et al., 2000; Fowler et al., 2005; Motivarash et al., 2020). Despite the vital functional roles they play in the ecosystem, sharks are increasingly exploited in bycatch worldwide (Dulvy et al., 2021), and due to the nature of their K-selective life history, the effects of untargeted removal of these top predators from the marine ecosystem are still not fully understood (Stevens et al., 2000). Bycatch, causing more than half of shark and other cartilaginous fish mortalities worldwide (67.3%; Dulvy et al., 2021), is also the main threat targeting sharks in the Sea of Marmara (see Kabasakal, 2022a for relevant references). Moreover, habitat loss and deterioration as well as pollution are considered as raising threats that seriously affect the survival of sharks (Dulvy et al., 2021).

Since the survival of sharks (and cartilaginous fish in gen-
eral), which play a decisive role in the health of marine life, depends on perfectly functioning ecosystems (Fowler et al., 2005), studies dealing on the potential effects of habitat loss and deterioration, as well as pollution-related threats on sharks and possible consequences on the ecosystem, are of critical importance. In a recent review, Consales and Marsili (2021) considered habitat loss and environmental contamina-
tion as major hazards threatening sharks. However, pollution and the relevant stressors affecting sharks are the least inves-
tigated and evaluated threats, as well (Consales and Marsili, 2021; Lipej et al., 2022). Regarding the survival of sharks, critical habitats (e.g. shallow estuaries, bays, gorgonian reefs, deep-sea areas etc.) can play crucial roles in certain periods of life cycles (e.g. reproduction and development) of elasmo-
branches, and anthropogenic environmental pressures on crit-
ical habitats may have devastating consequences (Fowler et al., 2005). Those expected devastating consequences, which threaten the survival of sharks, have begun to occur with in-
creasing frequency in the Sea of Marmara, especially in re-
cent years, as well.

Deoxygenation, mucilage outbreaks and deterioration of ben-
thic habitats in the Sea of Marmara, which has undergone great changes in the last 40 years due to human pressures, severely threaten the entire ecosystem (Topçu and Öztürk, 2015; Özalp, 2021; Çınar et al., 2021; Aksu et al., 2022; Karadurmuş and Sari, 2022; Mantıkçı et al., 2022; Salihoğlu et al., 2022). Kabasakal (2022b) emphasized that ‘vertical habitat compression’ may occur in the Sea of Marmara due to deox-
ygenation and ‘dead zone’ formation, especially in the deep 
trenches, and as a result of this situation, deep-sea sharks can be encountered in the shallow continental shelf region more frequently than they used to be in the past. Fishing records of the last 10 years revealed that captures of deep-sea sharks have been increasingly concentrated in the shallower waters of the continental shelf (<100 m depth) (Bayhan et al., 2006; Kabasakal, 2013, 2017;). Mass mortalities of *Raja clavata*, and *Dasyatis pastinaca* were recorded for the first time in the Sea of Marmara during the mucilage outbreak in the summer of 2021 (Karadurmuş and Sari, 2022). Although not yet ob-
served, mass mortalities of demersal sharks can also be ex-
pected, if the current deoxygenation continues.

So, what could be the effects of deterioration of benthic hab-
itats on sharks in the Sea of Marmara? As a result of mucil,

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the sea, the gorgonian reefs in the Sea of Marmara have been severely damaged in recent years (Topçu and Öztürk, 2015). These reefs are considered to be among the important breeding areas of oviparous scyliorhinid catsharks, and the deterioration of these areas will possibly result in the loss of breeding grounds for *S. canicula* and *S. stellaris*. According to Cappé (2008), *O. centrina* is a specialized suction feeder that preys on worm-like prey such as polychaetes that constitute 60% of its diet, and the deterioration of the benthos can have dramatic consequences on the diet of this species. Crustaceans experienced the most severe mass mortalities during the mucilage outbreak in the Sea of Marmara (Karadurmuş and Sari, 2022). This situation threatens the diet of crustacean feeders among sharks such as *M. asterias* and *M. mustelus*. Young and adult individuals of *M. asterias* and *S. squatina* inhabit estuarine brackish areas, especially during the breeding and development period (Ebert and Stehmann, 2013). Such areas are inhabited also by some rare species such as *G. galeus* in the Sea of Marmara (Kabasakal and Türretken, 2021). The coastal destruction and human-induced pollution caused the deterioration of the estuarine regions, (Aksan and Ergül, 2022; Tan and Demirtaş, 2022) which subsequently resulted, in habitat loss for the sharks inhabiting these regions.

![Figure 2.](image)

**Figure 2.** Gower’s distances showing differences among shark species of the Sea of Marmara recorded in terms of their species traits. Coloured polygons were determined based on Principal Coordinate Analysis.
Most pelagic sharks are ram ventilators and can only tolerate moderate hypoxia for a short time (Sims, 2019). These species, which are obligatory swimmers, face a remarkable vertical and horizontal habitat compression in the pelagic realm, as a result of deoxygenation (Vedor et al., 2021). Lamnid sharks, such as *Carcharodon carcharias*, that seasonally migrated into the Sea of Marmara in the past following tuna, *Thunnus thynnus*, have disappeared from the region since the mid-1980s, following the extirpation of tuna populations due to overfishing and marine pollution (Kabasakal, 2016). Although it is currently unpredictable how *A. superciliosus* and *A. vulpinus*, the last remaining pelagic lamniform sharks in the Sea of Marmara, will respond to the increasingly severe deoxygenation, their concentration in habitable oxygenated areas may create a “habitat trap” (Sims, 2019) and can be caused with the increase of pelagic sharks’ bycatch.

Mittlebach and Schemske (2015) define the ‘mass effect’ as the immigration of individuals into a community in a way that influences the recipient community’s dynamics. In terms of functional ecology, we do not yet have basic data predicting how the recipient community dynamics in these regions may be affected as a result of the sharks being trapped in the habitable oxygenated areas and shallow continental shelf in the Sea of Marmara. Since the continental shelf of the Sea of Marmara is a region where commercial fishing is intense, as a result of increased predatory pressure on commercial species due to habitat compression, fisher-shark competition may dramatically intensify in the future. For example, *E. brucus*, which normally occurs at depths of 200-1,214 m (Kabasakal et al., 2005; Ebert and Stehmann, 2013), has been observed frequently in the Marmara continental shelf in recent years in areas shallower than 100 m and especially in the fishing grounds of the commercial shrimp species *Parapenaeus longirostris* (Kabasakal pers. obs.). The beam-trawl used in *P. longirostris* fishery produces significant amounts of bycatch in the Sea of Marmara (Bayhan et al., 2006; Bök et al., 2011). Although for the moment, most shrimp fishermen are releasing the sharks that have entered the beam trawl (Figure 4), as the economic losses due to predator pressure increase, will fishermen’s conservationist perceptions shift towards to intentionally killing of the bycaught sharks over time? Moreover, in the context of the assumption that economic pressures on any ecosystem will eventually turn into a biodiversity problem (Perrings and Walker, 1995), increasing economic losses in shrimp catches (as well as for other commercial species and fishing gears), can trigger a possible fisher-shark competition which could result in the loss of sharks in the Sea of Marmara. This concern, which has just begun to attract attention, seems to intensify if the threats on the Marmara ecosystem continue.
Figure 4. Releasing the bramble shark, *E. brucus*, which was incidentally captured by a commercial beam-trawler catching shrimp, *P. longirostris*, in the shallows (<100 m) of northern shelf of Sea of Marmara. Images were captured from a video footage.

**Conclusion**

On the basis of Gower’s distances, Principal Coordinate Analysis and hierarchical clustering, it can be suggested that 17 species of sharks occurring in the Sea of Marmara mostly share very close niches. The increasing occurrence of sharks on the Marmara continental shelf, especially in the last few years, suggests that the expected habitat compression due to deoxygenation has begun to take place. This situation, which can be considered as a “habitat trap” for sharks, should be considered as a threat that may lead to shark mortalities due to the intensification of bycatches or even the intentional killing of sharks. Unfortunately, this situation can only be resolved with an integrated rehabilitation in the Marmara ecosystem. Available results are sufficient to predict a disturbing future for sharks of the Sea of Marmara if the factors (deoxygenation, habitat loss, bycatch etc.) threatening the overall ecosystem do not improve.

**Compliance with Ethical Standards**

**Conflict of interests:** The authors declare that for this article they have no actual, potential, or perceived conflict of interest.

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**Disclosure:** -
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