

Article

An Analysis of Adriatic Ichthyofauna—Ecology, Zoogeography, and Conservation Status

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Abstract: The paper presents an analysis of biogeographic and habitat distribution patterns, and the conservation status data of Adriatic fishes, based on the last published checklist and evidence-based critical analyses of species presence. The total number of species recorded in the Adriatic is 449. The Adriatic has 58.8% of Mediterranean species richness, 76.1% of its families, and 87.8% of its orders. Among species discovered in the Adriatic after 2010, twelve species were attributed to biological invasion, mostly Atlantic immigrants or alien species, and ten species were attributed to improved research on the native ichthyofauna of the Adriatic area. About 58% of species are native species of Atlanto-Mediterranean origin, 21% are native species of wider global occurrence, 15% are Mediterranean or Mediterranean and Black Sea endemics and 5% originated outside Mediterranean Sea. The majority of species inhabit the benthic environment (71.9%), while others occur in the pelagic environment (20.7%) or are euryhaline (7.3%). The benthic littoral species are the most numerous Adriatic fishes, representing 40% of all species richness, whereas pelagic fishes are mainly eurybathic or epipelagic; only 3.6% of species are deep pelagic species. A Red Book of marine fishes of the Adriatic Sea is urgently needed to assess their conservation status, covering the entire Adriatic Sea and reviewing all fish species to assess their conservation status.

Keywords: Adriatic ichthyofauna; evidence-based approach; zoogeography; habitat distribution; biological invasion; meridionalisation



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1. Introduction

Marine biodiversity in the Adriatic is attributed to its geological history, limited by its present bathymetric, hydrographic, and climatic characteristics, and influenced by present geographical connectivity and anthropogenic processes [1]. These characteristics have been crucial in shaping the peculiarities of Adriatic ichthyofauna. Although the Adriatic Sea is a part of the Mediterranean, it is an independent biogeographical and ecological subunit, which is evident in the composition and properties of its biological communities [2].

The marine biodiversity of the Mediterranean Sea is currently facing substantial changes in its flora and fauna [3]. It is rapidly changing due to the increasing arrival of non-indigenous fishes and other taxa [4–7]. Such changes have also been recorded in the Adriatic Sea. During the last few decades, various factors including climate change, anthropogenic activity, and “Lessepsian migration” have changed the composition of Adriatic ichthyofauna [5–10]. While “Lessepsian migration” is responsible for the arrival of non-indigenous species through the Suez Canal, climate change has caused northward spreading of southern, thermophilous species, a process known as meridionalisation [7–10]. Furthermore, extensive investigations carried out in recent decades have recognized species that have not been recorded in this area previously or led to the description of new species [2,5,7,11].

The only existing analysis of the zoogeographic distribution of Adriatic fishes was published about forty years ago by Jardas [12]. In addition to this time span, the number

of geographic categories in Jardas [12] was restricted, and the methodology for their establishment and delimitation was not well-documented. Since this paper, the number of known fish species in the Adriatic has increased, as has the knowledge on the biogeography and ecology of individual species. Furthermore, numerous taxonomical changes caused qualitative changes to fish species composition. To date, there are no published analyses of the depth and habitat distribution of Adriatic ichthyofauna. After Jardas [12], only Lipej and Dulčić [7] have published a paper on Adriatic fish biodiversity. The paper was descriptive, explaining the trends and developments of Adriatic ichthyofauna and reviewing existing knowledge. The recently updated and cleared list of Adriatic fishes, based on the evidence approach, increased the reliability of checklists and provided a base for the current research. The list consists of 444 fishes with confirmed records in the Adriatic Sea [13]. The aim of this paper is to analyse Adriatic fish species richness, taxonomy, conservation status, and zoogeographical and habitat distribution patterns, using the updated critically assessed list of Adriatic fishes [13].

2. Materials and Methods

2.1. Study Area

The Adriatic Sea is part of the Mediterranean Sea, occupying only 5.5% of its surface area. This semi-enclosed sea is the northernmost part of the Mediterranean, which influences some important physical properties of the Adriatic Sea. Together with the Gulf of Lion, the Adriatic Sea is the coldest part of the Mediterranean with winter temperatures below 10 °C in its northern part [14]. The Adriatic Sea is also a shallow sea compared to the rest of the Mediterranean. Three quarters of the sea bottom, about 102,415 km², is less than 200 m deep [15]. The depth gradually decreases from south to north [15]. The Jabuka/Pomo pit (280 m) and the South Adriatic pit (1330 m) are the only areas deeper than 200 m. Therefore, most of the bottoms are on the continental shelf and a significantly smaller part is on the continental slope (>200 m deep). In the south, the Adriatic Sea is separated from the Ionian Sea by the 72 km wide Strait of Otranto [16].

The Adriatic Sea is generally divided into three geographic subregions: the North Adriatic, the middle Adriatic, and the South Adriatic (Figure 1), which differ by their bathymetric and hydrographic properties [17]. The North Adriatic is very shallow and strongly influenced by the rivers of northern Italy, the river Po in particular. The North Adriatic is a young sea. During the Last Glacial Maximum 24–18 thousand years (ka) ago, the sea level was more than 120 m lower than today [18] and the North Adriatic was desiccated. The sea level rise was slow, from 21 to 17 ka, keeping the Adriatic sea level about 100 m lower than today and the Adriatic coastline still at the boundary between the present north and central Adriatic, followed by the higher average rate of rise in the following 10 ka, which was more or less completed by about 7 ka, when the coastlines of the North Adriatic were more or less the same as the current ones [18,19].

The rich river inflows over the shallow shelf of the North Adriatic and the mixing of bottom sediments make this area one of the most productive in the Mediterranean, while the central and South Adriatic are less productive, despite their exposure to the influence of the North Adriatic and the periodically stronger influence of Mediterranean waters [20]. The eastern Adriatic channel areas are also more productive compared to the open sea given that they are influenced by fresh water inflow, coves, bays and river mouths, and lower depths; mean gross primary production ranges between 60 and 150 g·C·m⁻²·year⁻¹, while in the open sea it is 55 g·C·m⁻²·year⁻¹ [21].

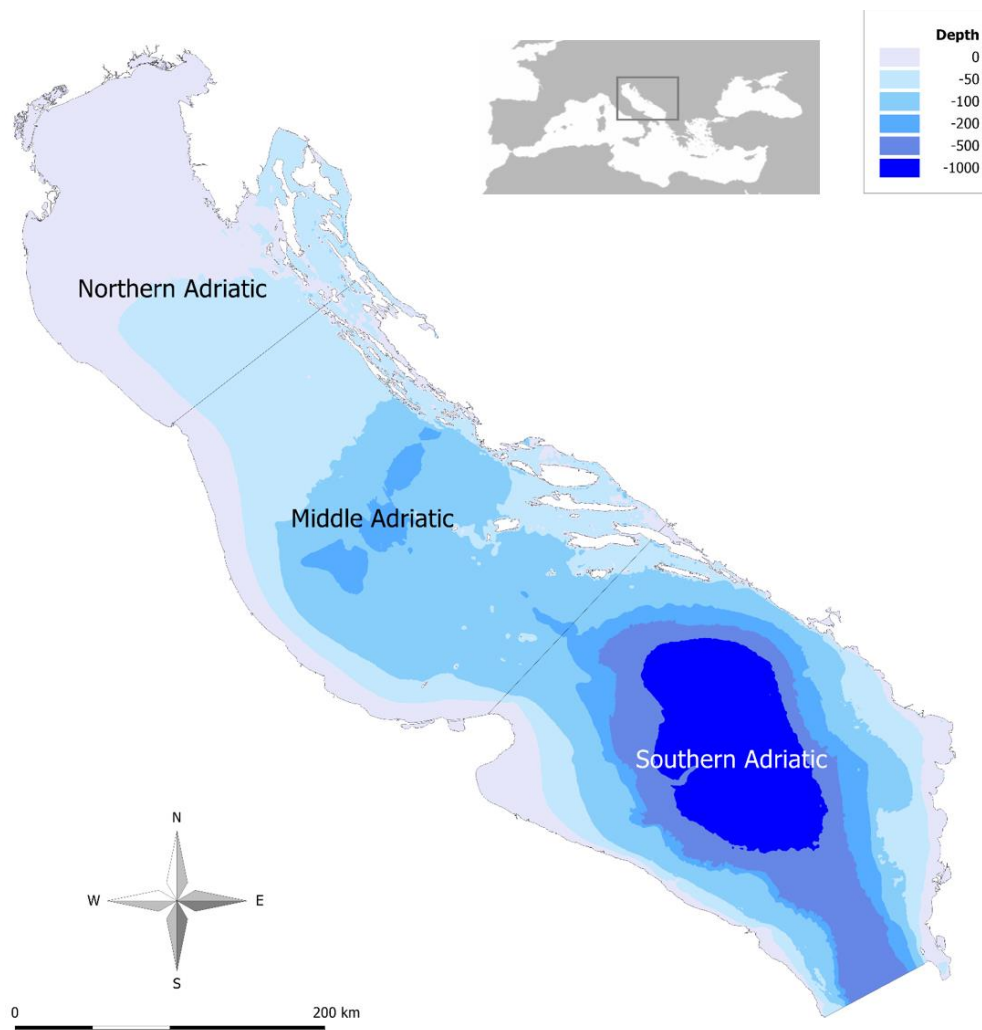


Figure 1. The division of the Adriatic Sea and its position in the Mediterranean Basin.

2.2. Species Richness and List of Adriatic Fish Species

The present list of Adriatic fishes is based on a published checklist [13]. This Adriatic fish fauna checklist critically assessed Adriatic fish fauna using an evidence-based approach [13]. The presence of fish species in the Adriatic was defined by at least one positive record of the species in the area, while the present and historical species status in the area, e.g., extant vs. extinct, native vs. alien, established population vs. casual visitor, etc., were not evaluated. The protocol consisted of several steps in the search for evidence, starting from the most direct and simplest evidence to gradually less strong and less convincing records. If any step was applicable to a certain species but the data were doubtful, then its status for the Adriatic was changed from confirmed to unconfirmed. If none of the protocol steps were applicable to a species, the species was excluded from the checklist and the reason for the decision was given. The additional species were added based on recent descriptions of new species and new Adriatic species records published after the checklist publication, again according to the evidence-based approach [13]. The date of the last update of the new published Adriatic fish species records based on the best authors' knowledge in present work was 1 December 2021.

2.3. Geographic Distribution

Geographical distribution of fish species was assigned based on distribution Point maps in Froese et al. [22]. The non-good points as defined in Froese et al. [22] and descriptive geographic distributions in the Distribution chapter of Froese et al. [22] were not taken

into account. Geographic distribution categories are based on the groupings of Realms and Provinces of coastal and shelf areas of Spalding et al. [23], covering all expected combinations of the fish species currently known to exist in the Mediterranean Sea. The list of possible categories was first applied to all fish species and then the categories with no fish species in the Mediterranean were excluded, and similar categories with only a few fish species were pooled in order to define a reasonable number of categories in Table 1. Corresponding bathyal and pelagic provinces are only given in Table 1 for each category, for reasons of comparison as the Bathyal provinces of Watling et al. [24] and the Pelagic provinces of Spalding et al. [25] are much broader and the biogeography is simpler compared to coastal and shelf areas [23]. Biogeographic boundaries were considered in a strict sense, e.g., a generally Mediterranean species also recorded outside the Strait of Gibraltar was not classified as a Mediterranean endemic species (M), but as a Warm temperate East Atlantic-Mediterranean (WEAM) species, found both in the Mediterranean and Lusitanian provinces. Species assigned to a particular regional category are present in all coastal and shelf provinces listed in that category. In the geographically broad categories, including the worldwide categories, with numerous coastal and shelf realms or with the numerous bathyal and pelagic provinces, the species does not have to be distributed in every listed area in order to fit the category, but all and shelf realms or bathyal and pelagic provinces within the geographic borders of a particular category are listed in Table 1 solely for the purpose of area delimitations.

Table 1. The geographic distribution categories and definitions. The abbreviations consist of the first letters of geographic distribution categories for later use in the text and tables. Coastal and Shelf Realms in bold and Provinces in regular. The bathyal province codes are from Watling et al. [24] and explained by the accompanied province names.

Mediterranean Status	Geographical Distribution Grouping Category	Geographical Distribution Category	Abbreviation	Definition	Spalding et al. [23] Coastal and Shelf Realms (in bold) or Provinces	Corresponding Bathyal Provinces of Watling et al. [24]	Corresponding Pelagic Provinces of Spalding et al. [25]
	Mediterranean	Mediterranean	M	Mediterranean endemic species	Mediterranean Sea	BY4 North Atlantic	Mediterranean
	Mediterranean and Black Sea	Mediterranean and Black Sea	MB	Mediterranean and Black Sea endemic species	Mediterranean Sea and Black Sea	BY4 North Atlantic	Mediterranean, Black Sea
		East Atlanto-Mediterranean	EAM	Species distributed in east Atlantic Ocean and Mediterranean	North European Seas, Lusitanian, West African Transition, Gulf of Guinea, Mediterranean Sea, Benguela	BY4 North Atlantic, BY13 South Atlantic	Mediterranean, North Atlantic Current, Canary Current, Equatorial Atlantic, Guinea Current, Benguela Current
Native Mediterranean	Mediterranean-East Atlantic	North and Tropical East Atlanto-Mediterranean	NTAM	Species distributed in tropical east and cold and warm temperate or just tropical east and warm temperate North east Atlantic Ocean and Mediterranean	North European Seas, Lusitanian, West African Transition, Gulf of Guinea, Mediterranean Sea	BY4 North Atlantic, BY13 South Atlantic	Mediterranean, North Atlantic Current, Canary Current, Equatorial Atlantic, Guinea Current
		Northeast Atlanto-Mediterranean	NEAM	Species distributed in temperate North east Atlantic Ocean and Mediterranean	North European Seas, Lusitanian, Mediterranean Sea	BY4 North Atlantic	Mediterranean, North Atlantic Current, Canary Current
		Warm temperate East Atlantic-Mediterranean	WEAM	Species distribution restricted to warm temperate north east Atlantic, Lusitania and Mediterranean	Lusitanian, Mediterranean Sea	BY4 North Atlantic	Mediterranean, North Atlantic Current, Canary Current

Table 1. Cont.

Mediterranean Status	Geographical Distribution Grouping Category	Geographical Distribution Category	Abbreviation	Definition	Spalding et al. [23] Coastal and Shelf Realms (in Bold) or Provinces	Corresponding Bathyal Provinces of Watling et al. [24]	Corresponding Pelagic Provinces of Spalding et al. [25]
Native Mediterranean	Mediterranean-amphiatlantic	Atlanto-Mediterranean	AM	Species widespread amphiatlantic in temperate northern Atlantic and tropical Atlantic and in Mediterranean, present or not in temperate south Atlantic	Temperate Northern Atlantic, Tropical Atlantic, Benguela	BY4 North Atlantic, BY13 South Atlantic	Mediterranean, North Atlantic Current, North Central Atlantic, Canary Current, Equatorial Atlantic, Guinea Current, Benguela Current
		North Atlantic-Mediterranean	NAM	Species amphiatlantic, distribution restricted to North Atlantic, cold and warm temperate or just warm temperate and Mediterranean	Temperate Northern Atlantic	BY4 North Atlantic	Mediterranean, North Atlantic Current, North Central Atlantic, Canary Current
		Tropical Atlantic-Mediterranean	TAM	Species amphiatlantic, distribution restricted to Tropical Atlantic and Mediterranean	Tropical Atlantic, Mediterranean	BY4 North Atlantic, BY13 South Atlantic	Mediterranean, Equatorial Atlantic, Guinea Current
	Indopacific-Atlantomediterranean	West Pacific, Indian Ocean and Atlanto-Mediterranean	PIAM	Species distributed in Mediterranean, Atlantic, Indian ocean and West Pacific	Temperate Northern Atlantic, Tropical Atlantic, Temperate South America, Temperate Southern Africa, Western Indo-Pacific, Central Indo-Pacific, Eastern Indo-Pacific, Temperate Northern Pacific, Temperate Australasia	BY4 North Atlantic, BY13 South Atlantic, BY11 Indian, BY6 New Zealand-Kermadec, BY12 West Pacific, BY14 North Pacific	See Spalding et al. [25] for 22 pelagic provinces overlapping with the defined area

Table 1. Cont.

Mediterranean Status	Geographical Distribution Grouping Category	Geographical Distribution Category	Abbreviation	Definition	Spalding et al. [23] Coastal and Shelf Realms (in Bold) or Provinces	Corresponding Bathyal Provinces of Watling et al. [24]	Corresponding Pelagic Provinces of Spalding et al. [25]
Native Mediterranean	Indopacific-Atlantomediterranean	Indian Ocean and Atlanto-Mediterranean	IAM	Species distributed in Mediterranean, Atlantic and Indian ocean	Temperate Northern Atlantic, Tropical Atlantic, Temperate South America, Temperate Southern Africa, Western Indo-Pacific	BY4 North Atlantic, BY13 South Atlantic, BY11 Indian	See Spalding et al. [25] for 16 pelagic provinces overlapping with the defined area
		West Indian Ocean and Atlanto-Mediterranean	WIAM	Species distributed in Mediterranean, Atlantic and West Indian ocean	Temperate Northern Atlantic, Tropical Atlantic, Temperate Southern Africa, Temperate South America, Western Indo-Pacific	BY4 North Atlantic, BY13 South Atlantic, BY11 Indian	See Spalding et al. [25] for 14 pelagic provinces overlapping with the defined area
	Mediterranean-circumworld	Circumglobal including Mediterranean	CG	Cosmopolite species in all seas or in all seas except polar	All 12 realms or 10 realms without Arctic and Southern Ocean	See Watling et al. [24] for 9 to 14 bathyal provinces overlapping with the defined area	See Spalding et al. [25] for 31 to 37 pelagic provinces overlapping with the defined area
		Bitemperate	BT	Species worldwide distributed restricted to south and north cold and warm or just warm temperate zone	Temperate Northern Atlantic, Temperate South America, Temperate Southern Africa, Temperate Northern Pacific, Temperate Australasia	BY4 North Atlantic, BY13 South Atlantic, BY12 West Pacific, BY3 Northern Pacific Boreal, BY6 New Zealand-Kermadec, BY5 Southeast Pacific Ridges, BY8 Nazca Plate	See Spalding et al. [25] for 17 pelagic provinces overlapping with the defined area

Table 1. Cont.

Mediterranean Status	Geographical Distribution Grouping Category	Geographical Distribution Category	Abbreviation	Definition	Spalding et al. [23] Coastal and Shelf Realms (in Bold) or Provinces	Corresponding Bathyal Provinces of Watling et al. [24]	Corresponding Pelagic Provinces of Spalding et al. [25]
	Mediterranean-circumworld	Circumnorth temperate	CNWT	Species worldwide distributed restricted to north temperate zone	Temperate Northern Atlantic, Temperate Northern Pacific	BY4 North Atlantic, BY12 West Pacific, BY3 Northern Pacific Boreal	See Spalding et al. [25] for 10 pelagic provinces overlapping with the defined area
		Circumtropical and warm temperate including Mediterranean	CTT	Species worldwide distributed restricted to warm temperate and tropical zones	All realms except Arctic and Southern Ocean, 10 realms	See Watling et al. [24] for 9 bathyal provinces overlapping with the defined area	See Spalding et al. [25] for 27 pelagic provinces overlapping with the defined area
Non Mediterranean	non Mediterranean East Atlantic	Temperate and tropical East Atlantic	TTEA	Species distribution restricted to North and tropical east Atlantic	North European Seas, Lusitanian, West African Transition, Gulf of Guinea	BY4 North Atlantic, BY13 South Atlantic	North Atlantic Current, Canary Current, Equatorial Atlantic, Guinea Current
		Tropical East Atlantic	TREA	Species distribution restricted to tropical east Atlantic	West African Transition, Gulf of Guinea	BY13 South Atlantic	Equatorial Atlantic, Guinea Current
		Temperate North East Atlantic	TEA	Species distribution restricted to cold and warm temperate North east Atlantic, i.e., European Atlantic	North European Seas, Lusitanian	BY4 North Atlantic	North Atlantic Current, Canary Current
		Warm temperate East Atlantic	WTEA	Lusitanian endemic species	Lusitanian	BY4 North Atlantic	North Atlantic Current, Canary Current

Table 1. Cont.

Mediterranean Status	Geographical Distribution Grouping Category	Geographical Distribution Category	Abbreviation	Definition	Spalding et al. [23] Coastal and Shelf Realms (in Bold) or Provinces	Corresponding Bathyal Provinces of Watling et al. [24]	Corresponding Pelagic Provinces of Spalding et al. [25]
Non Mediterranean	non Mediterranean amphiatlantic	Atlantic	A	Species amphiatlantic	Temperate Northern Atlantic, Tropical Atlantic , Benguela	BY4 North Atlantic, BY13 South Atlantic	North Atlantic Current, North Central Atlantic, Canary Current, Equatorial Atlantic, Guinea Current, Benguela Current
		North Atlantic	NA	Species amphiatlantic, distribution restricted to North Atlantic, cold and warm temperate or just cold or just warm temperate	Temperate Northern Atlantic	BY4 North Atlantic	North Atlantic Current, North Central Atlantic, Canary Current
		Tropical Atlantic	TA	Species amphiatlantic, distribution restricted to Tropical Atlantic	Tropical Atlantic	BY13 South Atlantic	Equatorial Atlantic, Guinea Current
		Western Atlantic	W	Species distribution restricted to Western Atlantic	Temperate Northern Atlantic, Tropical Atlantic, Temperate South America	BY4 North Atlantic, BY13 South Atlantic	Gulf Stream North Atlantic Current, North Central Atlantic, Equatorial Atlantic, South Central Atlantic

Table 1. Cont.

Mediterranean Status	Geographical Distribution Grouping Category	Geographical Distribution Category	Abbreviation	Definition	Spalding et al. [23] Coastal and Shelf Realms (in Bold) or Provinces	Corresponding Bathyal Provinces of Watling et al. [24]	Corresponding Pelagic Provinces of Spalding et al. [25]
Non Mediterranean	non Mediterranean Indopacific	Indo-Pacific	IP	Species distributed in both Indian and Pacific Ocean	Western Indo-Pacific, Central Indo-Pacific, Eastern Indo-Pacific, Temperate Northern Pacific, Temperate Australasia, Temperate South America, Tropical eastern Pacific	BY11 Indian, BY6 New Zealand-Kermadec, BY12 West Pacific, BY14 North Pacific, BY3 North Pacific Boreal, BY7 Cocos Plate, BY5 Southeast Pacific Ridges, BY8 Nazca Plate	See Spalding et al. [25] for 19 pelagic provinces overlapping with the defined area
		Indo-Western Pacific	IWP	Species distributed in both Indian and Western Pacific Ocean	Western Indo-Pacific, Central Indo-Pacific, Eastern Indo-Pacific, Temperate Northern Pacific, Temperate Australasia	BY11 Indian, BY6 New Zealand-Kermadec, BY12 West Pacific, BY14 North Pacific	See Spalding et al. [25] for 13 pelagic provinces overlapping with the defined area
		Indian	I	Species distributed in Indian Ocean or just West Indian Ocean	Western Indo-Pacific	BY11 Indian	Red Sea, Somali Current, Northern Indian Ocean, Agulhas Current, Southern Indian Ocean, Leeawin Current
		Red Sea	R	Red Sea and Gulf of Aden province	Red Sea and Gulf of Aden	BY11 Indian	Red Sea
		Western Pacific	WP	Species distribution restricted to Western Pacific Ocean	Central Indo-Pacific, Eastern Indo-Pacific, Temperate Northern Pacific, Temperate Australasia	BY6 New Zealand-Kermadec, BY12 West Pacific, BY14 North Pacific	Indonesian Through-flow, South China Sea, Kuroshio-Ovashio Current, Southwest Pacific, Equatorial Pacific, North Central Pacific, South Central Pacific

Table 1. Cont.

Mediterranean Status	Geographical Distribution Grouping Category	Geographical Distribution Category	Abbreviation	Definition	Spalding et al. [23] Coastal and Shelf Realms (in Bold) or Provinces	Corresponding Bathyal Provinces of Watling et al. [24]	Corresponding Pelagic Provinces of Spalding et al. [25]
	non Mediterranean Atlantic and Indo-Pacific	West Pacific, Indian Ocean and Atlanto-Mediterranean	PIA	Species distributed in Atlantic, Indian ocean and West Pacific	Temperate Northern Atlantic, Tropical Atlantic, Temperate South America, Temperate Southern Africa, Western Indo-Pacific, Central Indo-Pacific, Eastern Indo-Pacific, Temperate Northern Pacific, Temperate Australasia	BY4 North Atlantic, BY13 South Atlantic, BY11 Indian, BY6 New Zealand-Kermadec, BY12 West Pacific, BY14 North Pacific	See Spalding et al. [25] for 22 pelagic provinces overlapping with the defined area

2.4. Taxonomy

The nomenclature matches that of Fricke et al. [26]. The classification follows Van der Laan et al. [27]; both sources belong to Eschmeyer's Catalogue of Fishes online database by California Academy of Sciences.

2.5. Life Zonation

Definitions of marine life environments and of depth zones for pelagic environments were modified from Lally [28] (Table 2). Definitions for benthic depth zones were combined from Bellan-Santini et al. [29] for benthic littoral and from Emig's [30] revision for benthic bathyal (Table 2). The data for environment and depth range are from Froese et al. [22]. The entire recorded depth range was taken to define species depth zone.

Table 2. The depth zonation categories and definitions. The abbreviations consist of the first letters of depth zone categories for later use in the text and the tables.

Life Environment	Depth Zone Category	Abbreviation	Definitions of Depth Zones for Pelagic Environment Modified from Lally [28] and for Benthic Environment Modified from the Zonations of Bellan-Santini et al. [29] and Emig [30], Data Source for Environment and Depth Range from Froese et al. [24]
Pelagic Marine	Epipelagic occurrence	EP	Epipelagic zone is a euphotic zone where light is sufficient to support the growth and reproduction of plants, usually from surface down to 200 m depth.
	Mesopelagic occurrence	MP	Mesopelagic zone is a disphotic zone where light is too low for positive net photosynthesis, but still present and sensed by animals usually from 200 m down to 1000 m depth.
	Bathypelagic occurrence	BP	Bathypelagic zone is the shallowest of the aphotic zones where light cannot be detected by biological systems, usually from 1000 m down to 4000 m depth.
	Mesopelagic and bathypelagic occurrence	MBP	See mesopelagic and bathypelagic definitions.
	Epipelagic and mesopelagic occurrence	EMP	See epipelagic and mesopelagic definitions.
	Mesopelagic occurrence with epipelagic migrations	MP(EP)	See mesopelagic and epipelagic definitions.
Benthic Marine	Mediolittoral occurrence	ML	Mediolittoral zone is a continental shelf zone extending from the uppermost high tide line to the lowermost low tide line, it is regularly daily exposed and submerged.
	Infralittoral occurrence	IL	Infralittoral zone is a continental shelf zone extending from the lowermost low tide line to the deepest occurrence of photophilic algae and marine phanerogams which depends on the water transparency and in the Adriatic Sea usually ranges from 20 to 40 m.
	Circalittoral occurrence	CL	Circalittoral zone is a continental shelf zone extending from the deepest occurrence of photophilic algae and marine phanerogams, which depends on the water transparency and in the Adriatic Sea usually ranges from 20 to 40 m, to the deepest occurrence of multicellular algae which usually matches the shelf break at 100 to 150 m.
	Mediolittoral and infralittoral occurrence	MIL	See mediolittoral and infralittoral definitions.
	Infralittoral and circalittoral occurrence	ICL	See infralittoral and circalittoral definitions.

Table 2. Cont.

Life Environment	Depth Zone Category	Abbreviation	Definitions of Depth Zones for Pelagic Environment Modified from Lally [28] and for Benthic Environment Modified from the Zonations of Bellan-Santini et al. [29] and Emig [30], Data Source for Environment and Depth Range from Froese et al. [24]
Benthic Marine	Middle bathyal occurrence	MB	Middle bathyal zone is a continental slope zone extending from 160 to 300 m depth where the middle bathyal mud first occurs to the continental slope to continental rise boundary which is in the Mediterranean at 1900 to 2200 m depth.
	Upper and middle bathyal occurrence	B	Upper bathyal zone is continental slope zone extending from deepest occurrence of multicellular algae, which usually matches the shelf break at 100 to 150 m, down to depth of between 160 to 300 m where the middle bathyal mud replace the upper bathyal detritic sand and mud bottoms, see middle bathyal definition.
	Infralittoral, circalittoral and upper bathyal occurrence	ICUB	See infralittoral, circalittoral and upper bathyal definitions.
	Circalittoral and upper bathyal occurrence	CUB	See circalittoral and upper bathyal definitions.
	Infralittoral, circalittoral and upper and middle bathyal occurrence	ICB	See infralittoral, circalittoral, upper, and middle bathyal definitions.
	Circalittoral and upper and middle bathyal occurrence	CB	See circalittoral, upper, and middle bathyal definitions.
Euryhaline	Anadromous	A	Living in the sea and going to the fresh water to spawn.
	Catadromous	C	Living in fresh water and going to the sea to spawn.
	Transitional water infralittoral occurrence	EIL	Infralittoral habitats with brackish water, e.g., river and stream mouths, brackish lagoons, and underwater and coastline springs.
	Infralittoral occurrence and transitional water infralittoral occurrence	EILand IL	See infralittoral and transitional water infralittoral definitions.

2.6. Conservation Status

The conservation status is based on the Red List of Threatened Species categories and criteria [31] of the International Union for Conservation of Nature (IUCN). The conservation status is therefore considered as an indicator of whether a species still exists and how likely it is for a species to become extinct in the near future. The published regional Red lists and Red books of marine fishes covering the Adriatic Sea area were used to evaluate the conservation status of Adriatic fish. The only sources considered were those published by the International Union for Conservation of Nature (IUCN) or by regional state or non-governmental partners of IUCN, according to the categories and criteria of IUCN's Red List of Threatened Species [31].

3. Results

3.1. Known and Historical Species Richness of Adriatic Sea Fishes

To date, the total number of known fish species recorded in the Adriatic is 449, according to Kovačić et al. [13], later published descriptions of new species [32,33], and new Adriatic records [34–36] (Figure 2) (Supplementary Material). The Adriatic Sea can be considered as a well-studied Mediterranean area with centennial tradition in ichthyology [7]. Since the first ichthyological works published almost 200 years ago by Naccari [37], Nardo [38], and other scientists [2,7,13,15,39–43], the number of recorded fish species for

the area started with less than a hundred known species and gradually increased with new discoveries and research (Figure 2).

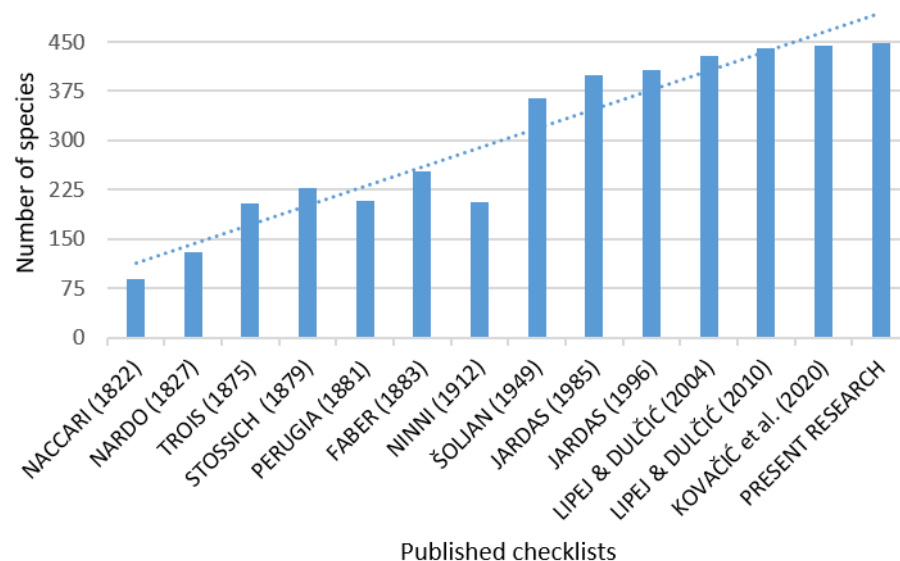


Figure 2. Number of Adriatic fish species according to various checklists of Adriatic fish and current data.

In a monograph on fish of the Adriatic Sea, Šoljan [43] describes 365 fish species. Almost half a century later, Jardas [15] published a list of 407 fish species in his book on Adriatic ichthyofauna. Due to the arrival of new fish species in the Adriatic Sea, associated with the biological invasion and meridionalisation processes, and also to the increase in scientific effort in studies of native ichthyofauna, the list of Adriatic fish species increased to 444 fish species [13]. Despite the numerous new recorded species, the increase in total known Adriatic fish biodiversity has slowed down in the last decade due to the evidence-based approach revision of Kovačić et al. [13]. In Kovačić et al. [13], the increase from the added fish species not listed in Lipej and Dulčić [2] were compensated by 19 species from Lipej and Dulčić [2] shown to be unconfirmed or even excluded by evidence as not recorded in the Adriatic Sea (3 of 22 excluded or unconfirmed by Kovačić et al. [13] were from sources other than Lipej and Dulčić [2]) leading to a total of 444 species in Kovačić et al. [13]). In any case, 23 fish species were reported in the Adriatic Sea by Kovačić et al. [13] that were not previously listed in Lipej and Dulčić [2]. Excluding two species reported before 2010, but missed by Lipej and Dulčić [2], 21 records of new species for the period were summarized in Kovačić et al. [13]. By adding the recently described species [32,33] and the species recently recorded in the Adriatic Sea [34–36], 26 new Adriatic fish species were reported from 2010 to 2021, which represents an annual average addition of 2.1 species (Table 3). The annual average increase from Jardas [15] to Lipej and Dulčić [2] was 2.4 species and annual average increase from Šoljan [43] to Jardas [15,44] was 0.9 species. The rate of increase in the Adriatic fish biodiversity is not showing signs of slowing down, having an annual average increase of over two species since the end of the last century.

The 26 new added species to the known fish biodiversity of the Adriatic Sea from 2010 are new Atlantic immigrants or alien species (for twelve species the cause of finding was biological invasion, Table 3) or are Mediterranean species or recently discovered native ichthyofauna of the Adriatic area (for ten species the cause of finding was improved research, Table 3). Atlantic species influx, contributing with three species, was the most effective vector, although for many species the vector was not clear (Table 3). *Paranthias furcifer* is known to drift with oil platforms [45]. Some species are native Adriatic species overlooked due to lack of targeted research and were found in the Adriatic Sea using appropriate methods, e.g., *Speleogobius llorisi* (Kovačić, Ordines and Schliewen, 2016) or overlooked due to their similarity to already known Adriatic fish, e.g., *Lepadogaster purpurea*

(Bonnaterre, 1788), or just recently described in the Adriatic Sea (*Gobius incognitus* Kovačić and Šanda, 2016) [46,47]. The most successful research improvements were cryptobenthic fish sampling and genetic studies revealing cryptic species, both with three species discovered (Table 3).

The total number of known fish species recorded in the Adriatic to date (449 species) is very close to the number of species reported by Psomadakis et al. [48] for the Ligurian Sea (454 species), the northern Tyrrhenian (426), and the southern Tyrrhenian Sea (447). All these seas have similar fish species richness, ranging from 56.3% to 60.1% of total Mediterranean fish biodiversity (759 fish species [49]). According to the number of fish species, the Adriatic Sea is one of the richest parts of Mediterranean, sharing this high fish diversity with the rest of the North Mediterranean [49].

Table 3. Species first time found in the Adriatic Sea in the period 2010–2021 and the factors which facilitated their detection for the Adriatic Sea or caused their arrival in the Adriatic Sea. Legend: FR—first record, SD—species description.

Species	Reference of Species Recognition in Adriatic	Year of Finding	Kind of Recognition	Cause of Finding	Vector/Research Improvement
<i>Abudefduf saxatilis</i> (Linnaeus, 1758)	Lipej et al. [34]	2020	FR	Biological invasion	-
<i>Alopias superciliosus</i> (Lowe, 1841)	Madiraca and Davidov [50]	2012	FR	Improved researches	Vagrant
<i>Apletodon dentatus</i> (Facciola, 1887)	Brandl et al. [51]	2010	FR	Improved researches	Cryptobenthic fish sampling
<i>Bregmaceros nectabanus</i> Whitley, 1941	Dulčić et al. [35]	2019	FR	Biological invasion	-
<i>Caranx rhonchus</i> Geoffroy St. Hilaire 1817	Kožul and Antolović [52]	2012	FR	-	-
<i>Chrysiptera cyanea</i> (Quoy and Gaimard, 1825)	Lipej et al. [53]	2014	FR	Biological invasion	Aquarium release
<i>Dipturus nidarosiensis</i> (Storm, 1881)	Carbonara et al. [54]	2010	FR	Improved researches	Deep water sampling
<i>Enchelycore anatina</i> (Lowe, 1838)	Lipej et al. [55]	2007	FR	Biological invasion	Atlantic influx
<i>Gaidropsarus granti</i> (Regan 1903)	Bello [56]	1997	FR	Improved researches	Atlantic influx
<i>Gobius incognitus</i> Kovačić and Šanda, 2016	Kovačić and Šanda [47]	2016	SD	Improved researches	Phylogeny revealed cryptic species
<i>Gouania adriatica</i> Wagner, Kovačić and Koblmüller 2021	Wagner et al. [33]	2021	SD	Improved researches	Phylogeny revealed cryptic species
<i>Hexanchus nakamurai</i> Teng, 1962	Bakiu et al. [57]	2017	FR	Casual record	Vagrant
<i>Holacanthus ciliaris</i> (Linnaeus, 1758)	Dulčić and Dragičević [58]	2011	FR	Biological invasion	Drift
<i>Lagocephalus sceleratus</i> (Gmelin, 1789)	Sulić Šprem et al. [59]	2012	FR	Biological invasion	Lessepsian migration
<i>Lepadogaster purpurea</i> (Bonnaterre, 1788)	Wagner et al. [60]	2014	FR	Improved researches	Cryptobenthic fish sampling
<i>Lobotes surinamensis</i> (Bloch, 1790)	Dulčić and Dragičević [61]	2010	FR	Range expansion	Atlantic influx
<i>Oplegnathus fasciatus</i> (Temminck and Schlegel 1844)	Ciriaco and Lipej [62]	2015	FR	Biological invasion	Sea chest or ballast waters
<i>Parablennius pilicornis</i> (Cuvier, 1829)	Santin and Willis [63]	2005	FR	Biological invasion	-
<i>Paranthias furcifer</i> (Valenciennes 1828)	Dulčić and Dragičević [45]	2013	FR	Biological invasion	Drift
<i>Pomadasys incisus</i> (Bowdich, 1825)	Đodo and Dulčić [64]	2015	FR	Biological invasion	-

Table 3. Cont.

Species	Reference of Species Recognition in Adriatic	Year of Finding	Kind of Recognition	Cause of Finding	Vector/Research Improvement
<i>Pterois cf. miles</i>	Dragičević et al. [36]	2021	FR	Biological invasion	-
<i>Rhizoprionodon acutus</i> (Rüppell, 1837)	Bakiu [65]	2019	FR	Casual record	Vagrant
<i>Salmo marmoratus</i> Cuvier, 1829	Soldo [66]	2008	FR	Improved researches	-
<i>Siganus luridus</i> (Rüppell, 1829)	Poloniato et al. [67]	2010	FR	Biological invasion	Lessepsian migration
<i>Speleogobius llorisi</i> Kovačić, Ordines et Schliewen, 2016	Kovačić and Glavičić [46]	2018	FR	Improved researches	Cryptobenthic fish sampling
<i>Zebrus pallaoroi</i> Kovačić, Šanda, Čekovská, Soukupová and Vukić 2021	Kovačić et al. [32]	2016	SD	Improved researches	Phylogeny revealed cryptic species

3.2. Taxonomic Characterization of Adriatic Ichthyofauna

Adriatic ichthyofauna belongs to four classes out of the eight recognized ones [27]: class Petromyzonti is represented by one species in the Adriatic, class Elasmobranchii by 55 species, class Holocephali by one species, and class Actinopteri by 392 species. Adriatic ichthyofauna is assigned to 43 out of 78 recognized fish orders, and to 141 out of 613 fish families [26]. Perciformes are the richest Adriatic order with 116 fish species recorded, while the Gobiidae (48), Sparidae (23), Labridae (17), Blenniidae (17), and Myctophidae (15) families have the highest number of species in the Adriatic Sea. As regards class Elasmobranchii, Rajidae is the richest family with 12 species. Compared to the Mediterranean [13], the Adriatic Sea has 58.8% of Mediterranean species richness, 76.1% of families and 87.8% of orders present in the Mediterranean. Gobiidae is the richest family, as it is for the Mediterranean and world in general [13,26]. The Adriatic Sea shares the same order of species richest families with the Mediterranean, except that in the Mediterranean families Carangidae and Serranidae have more known species than Myctophidae.

3.3. Zoogeographic Characterization of Adriatic Ichthyofauna

Detailed characterization of fish species according to geographic distribution categories is summarized in broader groups (Figure 3), see Supplementary Material for details on each category.

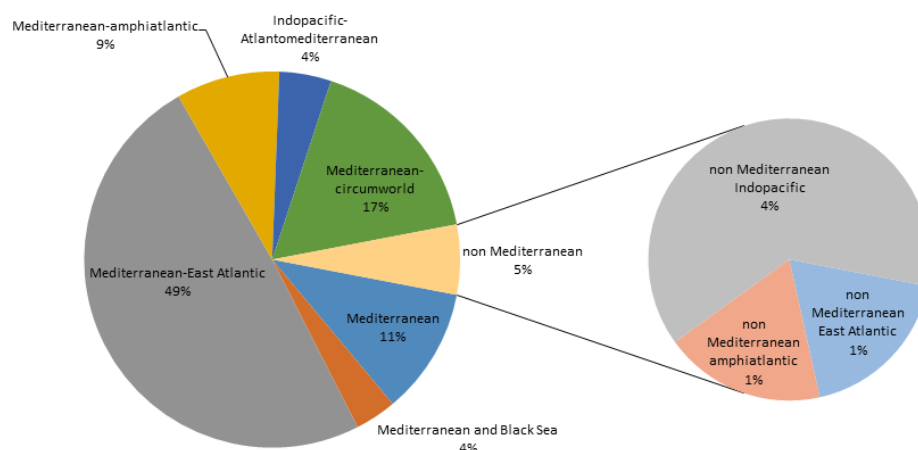


Figure 3. Zoogeographic origin of fish species recorded in the Adriatic Sea.

About 58% of all species presently known in the Adriatic are of Atlanto-Mediterranean origin, 21% are of wider global occurrence, 15% are Mediterranean or Mediterranean and Black Sea endemics, while the origin of 5% of the species is outside Mediterranean Sea (Figure 3). Most of the Atlanto-Mediterranean species (49%) are restricted to the Eastern Atlantic, only 9% being amphiatlantic (Figure 3). Most of the native Mediterranean fishes with wider global occurrence are of some kind of circumglobal occurrence (17%), mostly cosmopolite (50 species), but also circumtropical and warm temperate (21 species) and rarely bitemperate (4 species), or circumnorth temperate (1 species) (Figure 3, Supplementary Material).

Only 4% of all species are native to the Mediterranean and of wider global occurrence, but limited to the Indo-Pacific and Atlantic. They mostly penetrate from the Atlantic Indo-Pacific to the West Indian Ocean (12 species), though rarely crossing the entire Indian Ocean (5 species), or the West Pacific (3 species) (Figure 3).

There are more Mediterranean endemics in the Adriatic Sea, in the narrow sense (11%), than Mediterranean and Black Sea endemics (4%) (Figure 3).

To date, the zoogeographic origins of non-Mediterranean fish recorded in the Adriatic Sea are: Indo-Pacific species (17 species), Eastern Atlantic species (5 species), and amphiatlantic species (5 species) (Figure 3). Among non-native fishes, 20 genera and 10 families were not present earlier in the Adriatic Sea, while all non-Mediterranean species belonged to orders already present in the Adriatic Sea, mostly to order Perciformes.

Among the currently known Adriatic ichthyofauna, four species seem to be restricted to the Adriatic and could be true Adriatic endemics, namely, *Acipenser naccarii* (Bonaparte, 1836), *Syngnathus taenionotus* (Canestrini, 1871), *Knipowitschia panizzae* (Verga, 1841), and *Ninnigobius canestrinii* (Ninni, 1883), all of them euryhaline species.

Each of the three Adriatic subregions, North, Central, and South Adriatic, has different ichthyofauna to some degree. Thus, the North Adriatic is characterized by species extending from the warm and cold temperate Eastern Atlantic to the Mediterranean but these are rare in the rest of Adriatic, such as *Sprattus sprattus* (Hector, 1872) and *Platichthys flesus* (Linnaeus, 1758) [12]. The Central and South Adriatic share more similar composition of ichthyofauna due to similar depth and sea water temperature, with more thermophilic elements [15], such as *Thalassoma pavo* (Linnaeus, 1758), *Sparisoma cretense* (Linnaeus, 1758), *Brama brama* (Bonnaterre 1788), and bathyphilic elements [12]. The Central Adriatic is characterized by the Jabuka Pit, where thermophilic fish and some of the species extended to cold temperate Eastern Atlantic are complemented by some bathyphilic fish. Finally, the deep South Adriatic has a distinct bathyphilic ichthyofauna composed of mesopelagic and bathypelagic fish and bathyal fish from the continental slope, and also numerous thermophilic elements, many of which only occur in this region.

3.4. Adriatic Ichthyofauna Life zone Distribution

Detailed characterization of fish species by depth zone categories (Table 2, Supplementary Material) is summarized in broader groups in Figure 4.

The great majority of species is attributed to the marine benthic environment (71.9%); the remaining species occur in a marine pelagic environment (20.7%) or are euryhaline (7.3%) (Figure 4). Most of the fishes related to the benthic environment are benthic littoral species, representing 56% of all benthic fish diversity and 40% of total Adriatic fish diversity, followed by species occurring both in the littoral and in bathyal area representing 37% of all benthic fish diversity and 27% of total Adriatic fish diversity, and exclusive bathyal species representing 7% of all benthic fish diversity and 5% of total Adriatic fish diversity) (Figure 4). Comparing fish families with the largest number of representatives in each zone, it is clear that the family with most benthic littoral representatives (Gobiidae) is several times more numerous in species number than families with the most benthic bathyal species (Macrouridae), the most epipelagic species (Scombridae), or the most mesopelagic species (Myctophidae). Moreover, in the littoral zone, there are several other families (Sparidae, Labridae, and Blenniidae) outnumbering any family from other zones.

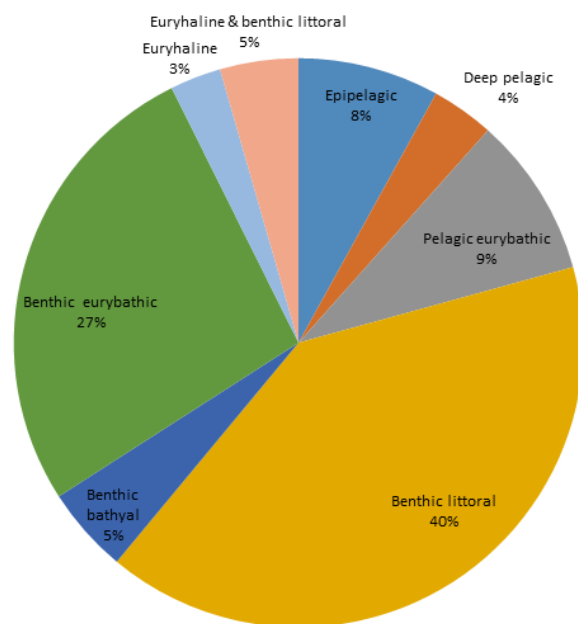


Figure 4. Life environment and depth zonation of fish species recorded in the Adriatic Sea.

Among benthic species restricted to the continental shelf, infralittoral species (83 species) and species of widespread littoral occurrence are common in both the infralittoral and circalittoral zones (87 species) (Supplementary Material). Only few species are exclusively circalittoral (6 species) or enter the mediolittoral zone (5 species). Exclusively bathyal species are rare: 19 species have widespread bathyal occurrence, 3 species are restricted to the middle bathyal zone, and no species is restricted to the upper bathyal zone. The small difference between two bathyal zones as regards to the occurrence of deep water species indicates their lack of depth specialization. Eurybathic species occurring both in the littoral and bathyal zones are mostly present on the entire shelf and upper bathyal zone (42 species), or on the entire bathyal and lower shelf, i.e., circalittoral (48 species). Thus, the delimitation in fish species composition of two bathyal zones is almost only based on the presence limited to upper bathyal of shelf species extending to the bathyal.

Fishes with more restricted (circalittoral and upper bathyal-9 species) or more extended depth range (entire continental shelf and entire bathyal-21 species) are less common (see Supplementary Material).

Pelagic fish are mostly eurybathic (41 species) or epipelagic (36 species). Eurybathic species are mostly epipelagic fish also occurring deeper (24 species) or are mesopelagic fish with daily vertical migration (17 species). Deep pelagic species are mostly restricted to the mesopelagic zone (11 species), with only 5 species occurring in bathypelagic zone as well. Species exposed to euryhaline conditions mostly live both in the marine and transitional water environment (20 species); 5 species are found exclusively in transitional waters, while 8 are diadromous fish switching between the marine and freshwater environments.

Considering overall species richness in each zone of the benthic and pelagic environment, a clear decrease of diversity with increased depth is apparent in both realms, except for the mediolittoral zone, where only a few species, amphibious blennies and clingfishes living in intertidal gravel, are adapted to extreme conditions of diurnal dry periods (Figures 5 and 6).

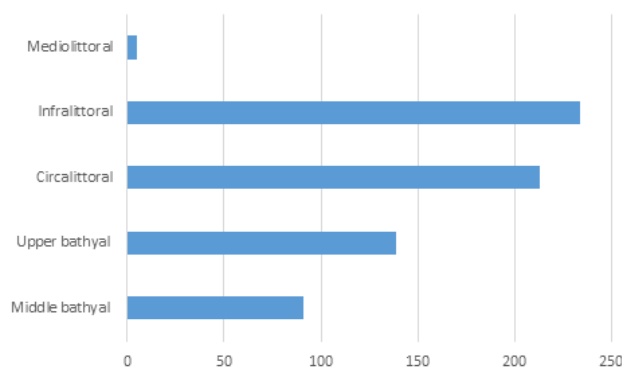


Figure 5. Number of fish species in each depth zone of the Adriatic Sea benthic environment.

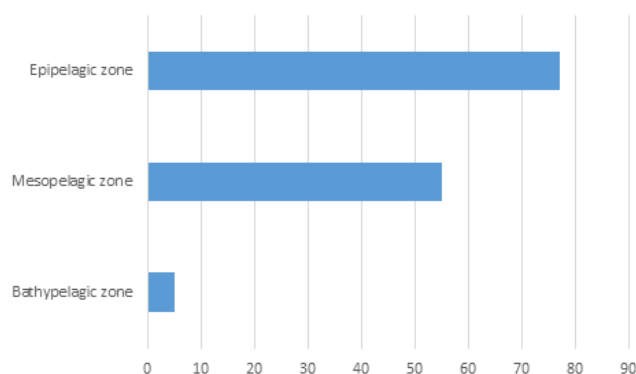


Figure 6. Number of fish species in each depth zone of the Adriatic Sea pelagic environment.

Comparing the pelagic and benthic environments, the ratio of deep water species is clearly higher in the pelagic than in the benthic environment (17.2% of pelagic species were deep pelagic vs. 6.8% of bathyal benthic species). As regards eurybathic species, the difference between realms is less clear (44.1% in the pelagic environment vs. 37.2% in the benthic environment).

Among 27 non-Mediterranean fish species, 66.7% are benthic littoral species, 14.8% benthic eurybathic, and 18.5% pelagic species. Compared to total Adriatic fish diversity of benthic littoral species (40%), it is clear that benthic littoral species are more present among the newcomers, while other categories are underrepresented or absent

3.5. Conservation Status of Adriatic Ichthyofauna

The review of published regional Red lists and Red books of marine fishes revealed that there is no published regional Red list of marine fish conservation status covering the entire Adriatic Sea. Only a Red book of marine fishes covering the Croatian part of the Adriatic Sea [68] has been published. The authors dealt with 123 species taxa that represent roughly a quarter of all Adriatic fish species. Three species, *Acipenser sturio* (Linnaeus, 1758), *Argyrosomus regius* (Asso y del Rio, 1801), and *Squatina oculata* (Bonaparte, 1840) were considered as regionally extinct species [68]. Five species, four sharks and one ray, were listed as critically endangered species. Another five sharks and three bony fishes were listed as endangered species. For many of the mentioned species, their inclusion in the specific IUCN category is justified; however, recent evidence shows that some of them should be checked as to whether they still fit the assigned category. Certain shark species, such as *Isurus oxyrinchus* (Rafinesque, 1810), *Lamna nasus* (Bonnaterre, 1788), and *Squatina squatina* (Linnaeus, 1758), were recently observed entangled in fishing nets, or sighted in some parts of the Adriatic Sea [69–71]. The other three IUCN categories of evaluated fish species are more or less equal in percentage of assigned fishes (near threatened, least concern, and data deficient). In comparison with the Mediterranean Red list of marine fishes [72], the percentage of endangered species among those assessed (in categories such

as critically endangered, endangered, and vulnerable species) is considerably higher in the Adriatic Sea than in the region as a whole (Figure 7).

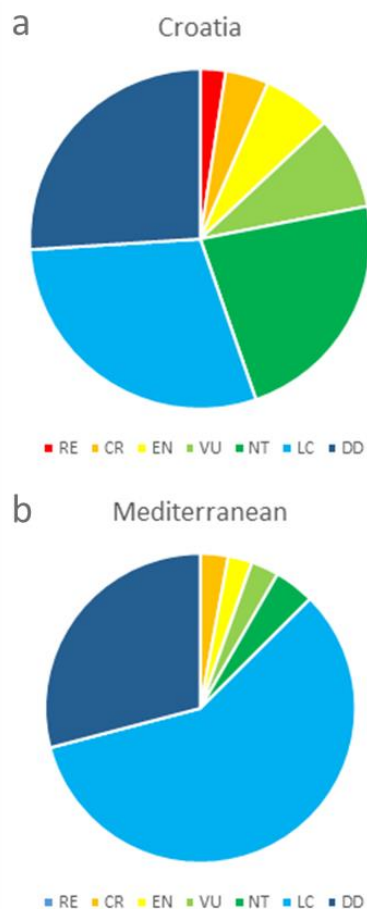


Figure 7. Red List of native marine fish species (including both bony and cartilaginous fishes) known to occur in the Croatian part of the Adriatic Sea (a) [68], (the assessment was performed for only a quarter of all Adriatic fish species) and in the Mediterranean Sea (b) [72]. Legend: RE—regionally extinct, CR—critically endangered, EN—endangered, VU—vulnerable, NT—nearly threatened, LC—lower concern, and DD—data deficient.

However, as the assessment was performed for only a quarter of all Adriatic fish species, the final picture, with all Adriatic fish species assessed by Jardas et al. [68] and re-evaluated, could be quite different. As only a quarter of all Adriatic fish species were evaluated in terms of vulnerability, it is clear that the majority of Adriatic ichthyofauna is rather poorly studied and many of them could become data deficient in the new evaluation. This is especially true for mesopelagic and bathypelagic species, cryptobenthic species, and vagrant species. In addition, some species were recorded on only one or a few occasions. Finally, some species have not been recorded for more than fifty years, raising doubts about their recent occurrence in the Adriatic Sea. Such is the case of the blenny *Salaria basilisca*, which was recorded only once in Piran (northern Adriatic Sea, Slovenia) [73]. A Red book of marine fishes of the Adriatic Sea to assess their conservation status, covering the entire Adriatic Sea and reviewing all fish species to assess their conservation status, is urgently needed.

4. Discussion

4.1. Known Species Richness of Adriatic Sea Fishes

The species richness of Adriatic Sea fishes has increased during the last two centuries, as evidenced by the Adriatic fish checklists (Figure 2). Taking into account newly recorded

species exclusively, the rate of increase in Adriatic fish species richness is high, with an annual average increase of over two species since the end of the last century. The Adriatic Sea is, with 449 species recorded, one of the richest parts of Mediterranean and shares this high fish diversity with the rest of the North Mediterranean [49]. Among the new recorded species, shortly after their first records, second records of *Lobotes surinamensis* (Bloch, 1790), *S. luridus*, *Enchelycore anatina* (Lowe, 1838), and *Lagocephalus sceleratus* (Gmelin, 1789) followed [74–76], thus confirming their presence. Additionally, findings of juveniles of *F. commersonii* and *S. luridus* and immature specimens of *Caranx crysos* (Mitchill, 1815) in the South Adriatic might indicate the establishment of populations of these species [75]. Furthermore, it is unclear whether *E. anatina* is a previously established, but overlooked inhabitant of the Adriatic Sea or only a recent immigrant [55,76]. Two records of *L. sceleratus* from two distinct areas of the eastern Adriatic may indicate an early phase of colonization, especially considering a rather fast spreading of this species in the Mediterranean Sea [77]. Among the species considered rare or very rare in the Adriatic Sea, new findings of *Tylosurus imperialis* (Rafinesque, 1810) and *Ruvettus pretiosus* (Cocco, 1833) were recorded [78]. A second record and northward expansion was observed for *Stephanolepis diaspros* (Fraser-Brunner, 1940) [79]. Northward expansion was also observed for *L. surinamensis* [80]. Even some meganehton species were reported for the very first time. Such is the case of a captured big-eye thresher shark (*A. superciliosus*), reported by Madiraca and Davidov [50] close to the island of Mamula (Montenegro). Finally, a specimen of the alien fish *Oplegnathus fasciatus* was caught in the waters of Trieste (Italy, north Adriatic Sea) by a local fisherman [62].

The cooperation of citizen scientists was crucial for recording newcomers [34,36], but also for the detection of many rare and less-known fish species [7]. However, the increasing number of fish should be also attributed to new research approaches and improved field techniques applied by scientists [7]. Nowadays, marine fauna and flora, and habitat types as well, could be sampled by non-destructive techniques such as the visual census method [81,82]. Another technique that is specialized in cryptobenthic fish species, which generally hide under stones, in cracks, crevices, and cavities of rocky habitats, combines SCUBA diving (including cave diving and deeper diving by accelerated decompression and trimix) with anaesthetic and collecting gear for small fishes [83,84]. This method has allowed the description of new species [32] and new records of cryptobenthic fish species in the Adriatic [46].

One of the reasons known to cause an increase in species in the area is biotic globalisation, due to two different reasons: the first is related to the phenomenon of meridionalisation, and the other to the phenomenon of biological invasion. Meridionalisation of the Adriatic Sea is a temperature-related factor that causes changes in fish species distribution [5,6]. The warm-water fish species spread from southern to northern areas in different parts of the Mediterranean [85] and the Adriatic Sea [5,7] due to temperature fluctuations. Changes in fish distributions are a good indicator of the effect of temperature change, as fishes are unable to regulate their temperature independently of the surrounding water [86]. For example, *Balistes carolinensis* (Gmelin, 1789), *Pomatomus saltatrix* (Linnaeus, 1766), and *Thalassoma pavo* (Linnaeus, 1758), which expanded their area of distribution northwards, are indicators of meridionalisation in the Adriatic [5]. As regards the last decade, there is evidence of regular occurrence of the dolphin fish, *Coryphaena hippurus* (Linnaeus, 1758), in the North Adriatic, a fish previously considered as a South Adriatic species [87]. Increased occurrence and also abundance was noted for *Sardinella aurita* (Valenciennes, 1847) [88] in the northern Adriatic Sea. The latter seems to be an indicator of water warming in the Mediterranean Sea [89].

Biological invasion is a process that can be associated with different factors (temperature, but also salinity, other hydrological conditions, unsaturated ecological niches, and other) [90]. It refers to a (non-indigenous) newcomer species, originating from another biogeographic area (donor area) that is transported to the recipient area by a vector [10,91,92]. The non-indigenous species have mostly arrived in the new area from Erythrean province through the Suez Canal [91–93]. This process is known as Lessepsian migration and is the

main vector of introduction for Indo-pacific fish species into the Mediterranean Sea and consequently the Adriatic Sea [7,9,11,13,49]. Among the 14 Lessepsian migrants that have been recorded in the Adriatic, *Fistularia commersonii* (Rüppell, 1838) and *Siganus luridus* (Rüppell, 1829) proved to be successful invaders for its southern part [74,75]. Other important vectors of introduction, such as mariculture, aquarium pets, and ballast waters and ballast sediments, are of minor importance in delivering new fish species to the area [53].

4.2. Taxonomy and Zoogeography of Adriatic Ichthyofauna

Adriatic ichthyofauna includes about a quarter of the total number of fish families in the world and about half of the total number of fish orders [26]. Moreover, it hosts three fifths of Mediterranean species richness, three quarters of its families, and nine tenths of its orders [49]. Gobiidae is the largest fish family, both in the Mediterranean and the world in general [26,49]. The largest families in the Adriatic Sea are quite similar to those of the Mediterranean; only families Carangidae and Serranidae in the Mediterranean have more known species than family Myctophidae. Traditionally, in the literature, up to 40% of Adriatic fishes had been assigned to boreal fauna, and explained by the cold character of the Adriatic Sea [12]. The “boreal” characteristic of Adriatic fish, which means that they belong to the eastern Atlantic boreal zone, has been disproved, as no Adriatic fish species has disjunct distribution restricted to cold temperate north east Atlantic, i.e., boreal zone, and the Mediterranean while being missing from warm temperate Atlantic Lusitanian province. Furthermore, among 221 fishes restricted to the Eastern Atlantic and Mediterranean, only about 20% of all Adriatic fish extend in continuous distribution through warm temperate Eastern Atlantic to cold temperate Eastern Atlantic, while the rest extends only to warm temperate Eastern Atlantic, have Eastern Atlantic range from warm temperate zone on north to the south along African coast, or have wide ranges along Eastern Atlantic (Supplementary Material). Most of the geographic distribution categories that have roughly similar geographic range in the present research and in Jardas [12] have quite different species richness, which is expected considering different methodology and considering the accumulated differences in the species composition over forty years. The list of Adriatic Sea fish endemics has varied dynamically since Jardas [12] due to the marine species described in the Adriatic that were “endemic” until they were found elsewhere in the Mediterranean. The only present marine fish species restricted to the Adriatic Sea is the recently described *Zebrus pallaoroi* (Kovačić, Šanda, Čekovská, Soukupová, and Vukić, 2021) [32]. However, contrary to marine fishes, among euryhaline fauna, four species seem to have a native range restricted to the Adriatic and could be true Adriatic endemics, namely, *Acipenser naccarii* (Bonaparte, 1836), *Syngnathus taenionotus* (Canestrini, 1871), *Knipowitschia panizzae* (Verga, 1841), and *Ninnigobius canestrinii* (Ninni, 1883). The Adriatic Sea and the western Mediterranean share similar fish species composition, sharing similar lower sea temperatures with the north western Mediterranean rather than the rest of the Mediterranean, although the Adriatic is both geographically and physiographically part of the eastern Mediterranean [12]. However, those differences are becoming less prominent due to global changes [49].

4.3. Life Zonation of Adriatic Ichthyofauna

The majority of Adriatic fish species are benthic (about 72% of total marine and euryhaline Adriatic diversity); the rest occur in a marine pelagic environment (about 21%) or are euryhaline (about 7%) (Figure 4). Unfortunately, there have been no comparable regional or global fish diversity data for all marine and euryhaline environments and depth zones since Cohen [94]. A comparison of Adriatic data with Cohen’s [94] recalculated ratios shows globally higher benthic (about 88% of total marine and euryhaline world diversity) and lower pelagic (about 11%) and euryhaline (about 1%) contribution to species richness, which could be explained by global contribution of tropical marine shore and continental shelf fish diversity to total fish diversity. Benthic littoral species are the most numerous Adriatic fishes, representing 40% of all Adriatic fish species richness and, together with

species occurring in both the littoral and bathyal zones, 67% of all Adriatic fish species richness. Globally, benthic littoral species also dominate marine and euryhaline species richness, but with even higher contribution of 77% [94], again the most likely explained by the tropical marine shore and continental shelf contribution to total fish diversity. Exclusively deep-water benthic fishes are rare, representing 7% of Adriatic fish species richness and about 11% of global marine and euryhaline richness [94]. The difference is most likely due to the Adriatic Sea depth limits.

Adriatic eurybathic fish species occurring both in the littoral and bathyal zones are mostly present on the shelf and upper bathyal, or on the bathyal and lower shelf, i.e., circalittoral. Thus, the delimitation in the fish species composition of the two bathyal zones is based primarily on the boundaries to the upper bathyal of the shelf species, which extend to the bathyal, while the deep-water species show no depth specialization when the two bathyal zones are considered.

Pelagic fishes are mainly eurybathic or epipelagic; only about 3.6% of total marine and euryhaline Adriatic diversity consists of deep pelagic species, compared to 8.6% globally, the difference again being most likely due to the Adriatic Sea depth limits. The clear decrease of species richness with depth is visible both in benthic and pelagic environments, with the exception of the mediolittoral zone (Figures 5 and 6). While benthic fish species richness globally is also much lower on the continental slope and in deep sea compared to coastal areas and the continental shelf (a ratio of approximately 7 to 1), global deep pelagic fish species richness is four times higher than global epipelagic fish species richness [94]. In the mediolittoral, contrary to the oceans and many seas, the small tide in the Adriatic Sea and mostly soft sediment or steep bedrock bottoms in the tidal zones rarely shape mediolittoral basins during low tide. Thus, contrary to the coasts with large tides, the Adriatic fish present in the mediolittoral zone should be able to survive for a limited time above the water surface on exposed rock or under gravel or boulders, which greatly limits the fish diversity of the Adriatic mediolittoral zone. Compared to total Adriatic fish diversity, newcomers consist of many more benthic littoral species, while other categories are either underrepresented or absent. The success of benthic littoral newcomers indicates either much higher diversity of benthic littoral species in the donor sea compared to other categories (large potential on the “supply” side), or better transport or settlement characteristics.

4.4. Conservation Status of Adriatic Ichthyofauna

The IUCN Red List and fish stock assessments address different issues. The IUCN is concerned with extinction risk, whereas fisheries assessments involve fish stock studies and are concerned with their sustainable exploitation [95]. However, sustainable fishery in Europe was proven to be consistent with low extinction risk [95]. For European marine fishes, fishing was the most common threat causing extinction risk to marine fishes, both for species in targeted fisheries and as bycatch [96]. Other observed threats to endangered European marine fish species include pollution, coastal development, climate change, energy production and mining [95]. All Adriatic fish stocks among those studied by Fernandes et al. [95] were overexploited and depleted, as in the rest of the Mediterranean and Black Sea, contrary to other European seas reviewed in the same work. Annual catches of fish and other sea organisms in the Adriatic Sea comprises about 15% of the total catch in the Mediterranean [97], which is disproportional with the surface area of the Adriatic Sea, which covers only 5.5% of the Mediterranean surface area. Since 1983, the quantity of fish caught is decreasing. It should be noted that the decline of the most vulnerable megafauna (elasmobranchs and other large-sized fish species) commenced as early as the beginning of industrialisation of fisheries [98]. Changes in the stocks of fish and edible invertebrates, manifested as changes in quantitative and qualitative catch structure, are due to various reasons, and intensive fishing in particular [99]. Tremendous fishing effort in the Adriatic Sea, considering its size, causes overfishing. Considering large vessels alone, there are about 8000 trawlers, purse seiners, etc., in the Adriatic Sea [100]. Fishing activities

also affect many non-target fishes, which are subject to severe by-catch in the Adriatic Sea. This is especially true for many sharks and batoid species entangled in fishing nets. There are known cases of entanglement of many rare and endangered shark species such as the basking shark (*Cetorhinus maximus* (Gunnerus, 1765)) [101], sixgill shark (*Hexanchus griseus* (Bonnaterre, 1788)) [102], common thresher shark (*Alopias vulpinus* (Bonnaterre, 1788)) [103], the sandbar shark (*Carcharhinus plumbeus*, (Nardo, 1827)) [104–106], and many others. Overall, the Adriatic Sea should be considered an overfished sea. Indirect damages caused to the environment by fishing, trawling activities in particular, are very evident as well [107].

Apart from unreasonable and uncontrolled fishing, the influence of other threats (pollution, coastal development, climate change, energy production, and mining), listed as causing extinction risk to European marine fish species in Nieto et al. [96], is hard to estimate for Adriatic fishes. The main Adriatic source of nutrient pollution is the Italian river Po, which contributes more than 50% of the total inflow of nutrients into the Adriatic [108]. Eutrophication represents a threat to fishes and marine life in general. It changes biological communities, degrading fish habitats, such as sea grass meadows [109,110] or *Cystoseira* forests [111], and can be manifested even by anoxia that can cause almost total mortality of marine organisms in the community [112]. Coastal development degrades and alters coastal and shallow sea habitats. Currently, about two thirds of the Mediterranean coastline is urbanised, and more than half of the Mediterranean coasts are dominated by concrete [113]. Data are not available for the Adriatic, but the situation is probably similar. The coastal habitats have been so degraded in the Mediterranean that they are no longer available or adequate to provide nursery, feeding, or reproductive functions for fishes, with negative consequences on the production and renewal of populations [114]. Substantial changes in environmental conditions often affect competitive interactions among species. Anthropogenic impacts can alter an environment so drastically that even native species may end up in an environment that is just as novel as it is to a non-indigenous species [115]. Climate change due to increased temperature is the most important abiotic factor determining the dispersal of invasive species as already discussed above. There is no published data on energy production and mining as a threat to Adriatic fishes; the threat in the Adriatic Sea is limited to gas production platforms, with production recently in decline.

5. Conclusions

The known total Adriatic fish species richness has been following an upward trend during the two centuries since the first Adriatic fish checklists were published, with an average increase of over two species per year since the end of the last century. Among the species discovered in the Adriatic after 2010, twelve species are attributed to biological invasion, mostly by Atlantic immigrants or alien species, and ten species are attributed to improved research of the native Adriatic ichthyofauna. Most of the Adriatic fish species, about 58%, are native species of Atlanto-Mediterranean origin, 21% are native species of wider global occurrence, 15% are Mediterranean or Mediterranean and Black Sea endemics, and 5% originate outside the Mediterranean Sea. The “boreal” characteristic of Adriatic fish fauna is disproven as, among 221 Atlanto-Mediterranean fishes restricted to the Eastern Atlantic, none has disjunct boreal–Mediterranean distribution, and only 88 extend their distribution from the warm-temperate Eastern Atlantic to the cold-temperate Eastern Atlantic. Mediterranean endemics, in the narrow sense, represent 11% of Adriatic fish species. Only four species seem to have a native range restricted to the Adriatic and could be true Adriatic endemics, all four being euryhaline fish. The majority of the Adriatic fish species are benthic (about 72% of total marine and euryhaline Adriatic diversity), the remaining species occur in the marine pelagic environment (about 21%) or are euryhaline (about 7%), matching the worldwide dominance of marine benthic fishes. Benthic littoral species are the most numerous Adriatic fishes and, together with the species occurring both in the littoral and bathyal zones, represent two thirds of all Adriatic fish species richness. The delimitation in fish species composition of two bathyal zones is based mainly on only

upper bathyal presence of shelf species extending to the bathyal, while deep water species show lack of intrabathyal depth specialization. The higher number of benthic littoral species among newcomers and the underrepresentation or absence of other categories indicate either much higher diversity of benthic littoral species in the donor sea compared to other categories (large potential on the “supply” side), or better transport survival or settlement characteristics. The only regional Red list or Red book of marine fishes published for the Adriatic Sea is limited to the territorial waters of the Republic of Croatia and covers only about a quarter of all Adriatic fish species. A Red book of marine fishes is urgently needed for the entire Adriatic Sea, with an assessment of all Adriatic fish species in order to evaluate their conservation status.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/fishes7020058/s1>.

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