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An overview of grey mullet (Mugilidae) global occurrence and species- rich ecoregions, with indications of possible past dispersal routes within the family

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Abstract :

This review examines the published literature on the distribution and species richness of the family Mugilidae around six continents as well as their phylogenetic relationships in a time-calibrated tree. Three mugilid species-rich regions were identified globally, namely the Coral Triangle, southern Asia and southern Africa, all of which have between 16 and 18 morphologically recognized species. Two of the species hotspots are tropical, and only southern Africa incorporates temperate waters. The centre of mugilid evolution and then global dispersion appears to be located in the tropical waters of the Indo-Pacific. Speciation within the family was promoted mainly by plate tectonics, eustatic sea-level changes, tropical climate and high habitat diversity within this region. The number of these tropical species that radiated out to the coastal waters of Africa and America was clearly less than the number that remained in the central Indo-Pacific region. Nonetheless, access by tropical mugilid species was greater to Africa than the Americas because of the direct tropical and subtropical coastal connectivity to the former continent. This enabled more tropical mugilids to reach Africa than America, with the latter probably relying on Palaeocene “island hopping” or “rafting” to move eastwards across the Pacific Ocean. In addition, tropical mugilids were able to access warm western and central African coastal waters from the Pacific prior to the closure of the Tethys Sea gap in the eastern Mediterranean and prior to the development of the cool Benguela Current upwelling off the southwest African coast, and from America through at least two transatlantic rafting events.

Keywords : biogeography, distribution, evolution, hotspots, mugilids

Introduction

The Mugilidae, currently comprising 77 valid species and 26 valid genera, occur in most tropical and temperate coastal zones around the world. There is considerable uncertainty about the exact number of species related to mullet phylogeny, which is also reflected by the uncertainty around diversification time scales. However, a study by Santini et al. (2015) identified two major lineages of grey mullet that diverged during the Paleocene and Eocene, followed by a mainly Oligocene radiation across both tropical and subtropical coastal habitats. This radiation may have been facilitated by the abundant and widespread availability of food in the form of detritus and benthic microalgae, resources that are naturally concentrated in estuaries and shallow coastal shelf areas around the world. Since very few other fish families have the ability to 'telescope the food chain' and exploit this type of nutrition, the mugilids are able to exploit this broad niche with limited competition from other species (Whitfield & Blaber 1978).

Mugilids are found in a range of water turbidities in rivers, estuaries and the sea. This diversity of aquatic environmental occupation may have been one of the 'triggers' for allopatric speciation within the family. Mugilid spawning generally occurs in the marine environment but the juveniles often make extensive use of estuaries as nursery areas and also feeding grounds for adults of many species. Indeed, most species favour estuaries or the marine environment as a primary habitat, but there are some taxa that occur mainly in rivers, lagoons and lakes. Wherever mugilid species occur, they are often a dominant component of the local fish assemblage from a biomass perspective, primarily due to their detritivorous feeding mode which places them at the broad base of the aquatic food 'pyramid'.

The taxonomy and systematics of the Mugilidae is in a state of ongoing development, primarily due to recent DNA analyses of the genetic status and therefore phylogenetic relationships between the species (e.g. Heras et al. 2009, Durand et al. 2012a). Past taxonomic issues arising from misidentification and synonyms for morphologically similar species within the family are now being addressed by new approaches. However, there are several widely distributed species that have now been shown to consist of species complexes that have yet to be formally described (Durand & Borsa 2015). Using DNA barcoding in terms of species delimitation, a total of 129 putative species or barcode index number (BIN) are now registered in BOLD system (03/01/2023) for the family Mugilidae. This review is therefore based on our current understanding of the biology and taxonomy of species within the family and draws heavily on information provided by the book *Biology, Ecology and Culture of the Grey Mullet (Mugilidae)*, edited by Crosetti & Blaber (2016), as well as genetic results based on BINs registered in BOLD.

Mugilidae have been listed as occurring between latitudes 65°N to 50°S in Africa, Asia, Australia, Europe and New Zealand, and between 40°N to 37°S on the east coast and 30°N to 5°S on the west coast of America (Berra 1981). They therefore occur in tropical, subtropical and temperate biogeographic regions and follow the global estuarine fish species richness trend of a significant decline in species numbers from the equator to the poles (Pasquaud et al. 2015). *Mugil cephalus* Linnaeus 1758 is the only cosmopolitan species occurring between latitudes 42°N and 42°S globally (Whitfield et al. 2012) but is actually a species complex that has yet to be teased apart.

A recent review by Harrison & Whitfield (2022) has shown a major estuary-associated fish species hotspot in the tropical Indo-West Pacific. For the purposes of the current review, a mugilid 'hotspot' is defined as a coastal ecoregion where the number of recognised species exceeds 15. Although numerous studies have been conducted on grey mullet taxa globally, no attempt has been made to explore or document global hotspots in terms of species richness, or the reasons why such species rich ecoregions should occur where they do. In this review, mugilid species richness is documented for the continents and associated islands where the family is particularly well represented (viz. Asia and Australia/Oceania), as well as those continents were species richness is more limited (viz. Africa, America and Europe). We have adopted the 62 global coastal ecoregions of Spalding et al. (2007) to map mugilid species richness around the world and have then used this analysis to compare and account for why ecoregion 'hotspots' are located where they are, and why some have a higher species richness than others.

Global mugilid species occurrence and distribution

Most mugilids are primarily tropical or subtropical in terms of their core distribution. The five main continents selected for this review are Africa, America, Asia, Australia (Oceania) and Europe and only formally described species are included in the analyses below. Exotic mullets that have been introduced to a region for aquaculture purposes, e.g. *Planiliza haematocheilus* (Temminck & Schlegel 1845) in the Black Sea (Harrison 2004), are also excluded from this analysis.

The African continent ranges over 71° of latitude (37°N to 34°S), with a total coastline of 26 000 km and covering eight coastal ecoregions. Over the Atlantic, Mediterranean and Indian Ocean coasts (including the Red Sea) there are a total of 30 recognized species (Durand & Whitfield 2016, Table 1), belonging to 10 genera associated with the African continent, viz. *Agonostomus* (2 spp.), *Chelon* (10 spp.), *Crenimugil* (3 spp.), *Ellochelon* (1 sp.), *Mugil* (4 spp.), *Neochelon* (1 sp.), *Osteomugil* (2 spp.), *Parachelon* (1 sp.), *Planiliza* (5 spp.) and *Pseudomyxus* (1 sp.). Based on the published occurrence of mugilid species around Africa, a single hotspot comprising 16 species is identified in southern Africa.

The American continent, ranging over 127° of latitude (72°N to 55°S), covers 12 coastal ecoregions and has an approximately 14 000 km coastline along the Pacific Ocean alone. Along the Atlantic and Pacific coasts there are a total of 15 recognized species (Barletta & Dantas 2016, Table 2), belonging to four genera, viz. *Mugil* (12 spp.), *Dajaus* (1 sp.), *Chaenomugil* (1 sp.) and *Joturus* (1 sp.).

The Mediterranean, northeastern Atlantic coastline and Black Sea are included in the European analysis (Turan 2016). This region ranges over 20° of mainly temperate latitude waters (30°N to 50°N) and covers only four continental ecoregions. A total of eight species belonging to four genera (Table 3) have been recognised from this area (Turan 2016), viz. *Chelon* (4 spp.), *Mugil* (1 sp.), *Oedalechilus* (1 sp.), and *Planiliza* (2 spp.); with both *Planiliza* species being exotic to the Mediterranean, i.e. *Planiliza haematocheilus* was artificially introduced for aquaculture in the Black Sea and *Planiliza carinata* is a Lessepsian species (Harrison 2004, Bariche et al. 2015, Hasan et al. 2022). Based on the published occurrence of mugilid species in the European region, no mugilid hotspot could be identified.

The southeastern portion of the Asian continent and proximate islands (e.g. Sri Lanka), ranges over 30° of mainly tropical and subtropical latitude waters (5°N to 35°N), covering 11 coastal ecoregions. A total of 28 species belonging to 12 genera (Table 4) have been recognised from this area (Shen & Durand 2016), viz. *Cestraeus* (3 spp.), *Crenimugil* (4 spp.), *Ellochelon* (1 sp.), *Mugil* (2 spp.), *Minimugil* (1 sp.), *Osteomugil* (4 spp.), *Paramugil* (1 sp.), *Planiliza* (8 spp.), *Plicomugil* (1 sp.), *Rhinomugil* (1 sp.), *Squalomugil* (1 sp.) and *Sicamugil* (1 spp.).

The Australian continent and proximate islands are sometimes referred to as Oceania, which ranges over 55° of latitude (8°N to 47°S) and covers an area of some 8.5 million km^2, covering 11 coastal ecoregions. A total of 26 species belonging to 14 genera from Australia/Oceania and the adjacent Indo-Pacific islands (Table 5) have been recognised (Ghasemzadeh 2016), viz. *Aldrichetta* (1 sp.), *Cestraeus* (2 spp.), *Crenimugil* (4 spp.), *Ellochelon* (1 sp.), *Gracilimugil* (1 sp.), *Mugil* (1 sp.), *Myxus* (1 sp.), *Neomyxus* (1 sp.), *Osteomugil* (4 spp.), *Paramugil* (2 spp.), *Planiliza* (5 spp.), *Plicomugil* (1 sp.), *Squalomugil* (1 sp.), and *Trachystoma* (1 sp.).

Mugilid species richness in different coastal ecoregions around the world was assessed (Table 6). Based on this analysis, three broad regions of peak mugilid species richness were identified, namely the Coral Triangle, southern Asia and southern Africa. The former two regions are primarily tropical/subtropical and the latter one primarily subtropical/warm temperate.

Phylogeny and divergence time estimation

Phylogenetic relationships, as well as divergence time among genera and species of the Mugilidae family depicted in Figure 1, rely on the phylogenetic analyses provided by Santini et al. (2015). These authors mainly used the dataset published by Durand et al. (2012a) for phylogenetic reconstruction and were able to estimate absolute divergence times using fossil calibrations as prior probability densities relating to three internal nodes of mullet phylogeny (Santini et al. 2015). The original tree was modified by merging nodes that were not statistically supported, updating the genus name nomenclature according Durand et al. (2012b), and stressing the continental origin of specimens used in the tree. This latter information was used to infer the probable geographic origin of mullet ancestors.

Discussion

Africa

Most African mullet species are confined to either tropical or subtropical waters, with very few being present in temperate areas. A few species have an apparent broad latitudinal distribution (e.g. *Mugil cephalus* spp. or *Chelon dumerili* spp.), but these consist of evolutionary lineages with a more limited geographic distribution when the species complexes are eventually teased apart. Indeed, genetic evidence suggests that both the above lineages comprise species complexes which reduces latitudinal distribution even further (Durand et al. 2012a, 2012b; Durand & Borsa 2015).

Marine biogeographic boundaries between tropical and temperate zones in Africa often correspond to intense upwelling areas where cool upwelled water is a barrier to the dispersion of tropical and even some warm-temperate species (Henriques et al. 2016). Many of the tropical fish taxa, including the mugilids, recorded in subtropical southeastern African estuaries occur mainly in the more northern systems within this region (i.e. within the KwaZulu-Natal Province), with decreasing numbers being recorded in a south-westerly direction (i.e. towards the Western Cape Province) (Harrison 2005). Although some of these tropical mugilid taxa have been recorded from estuaries in the warm-temperate zone of southern Africa, they are usually only present as isolated stragglers (Whitfield 2019). Similarly, tropical species from the central west African coast are unable to penetrate south of Angola due to the presence of cool upwelled water from the Benguela Current (Figure 2, Hutchings et al. 2009, Whitfield 2005) and an absence of estuaries in the Namibian region. Ecological and physiological barriers also exist in the Cape Verde Archipelago and a stretch of coast from the western

Sahara to northern Mauritania (Ndoye et al. 2014). The cool Canary Current (Figure 2) flows southward as far as Senegal (Mittelstaedt 1991) is likely to prevent the northward dispersion of tropical mugilid species such as *Chelon bandialensis* (Diouf 1991), *Mugil bananensis* (Pellegrin 1927), *Mugil curema* (Valenciennes 1836), *Neochelon falcipinnis* (Valenciennes 1836) and *Parachelon grandisquamis* (Valenciennes 1836) that present their northern distribution limits in Banc d'Arguin (Mauritania) (see distribution maps in Durand & Whitfield 2016, Thieme et al. 2022).

Mugilid phylogenetic relationships (Figure 1) and their African evolutionary history indicate that African coastal waters were an important diversification centre for the Mugilidae (Durand & Whitfield 2016). Among the four subfamilies (Durand 2016, Xia et al. 2016), the Cheloninae subfamily consists, with one exception, of genera recorded exclusively in Africa or the coasts of the northeastern Atlantic. The exception is the specious Indo-Pacific genus *Planiliza* which is closely related to the eastern Atlantic genera *Chelon* and *Parachelon*, with *Chelon* exhibiting a very wide Indian Ocean, Mediterranean and East Atlantic distribution (Durand et al. 2012a,b, Xia et al. 2016). Time-calibrated phylogeny shows that genetic divergence of African *Chelon* and *Parachelon*, together with that of the Indo-Pacific *Planiliza*, probably occurred during the middle Oligocene (Figure 1). This is consistent with two major vicariant events, firstly the closure of the eastern Tethys Gateway (Hamon et al. 2013) which provided access for tropical mugilids to the region, and secondly the loss of a marine connection between the Indian Ocean and Mediterranean Sea (Durand & Whitfield 2016).

These events were followed by diversification of the genus *Chelon* (Durand et al. 2012b), mainly in temperate areas of the Mediterranean Sea and in southern Africa, which contrasts with the genus *Planiliza* which had maximum species diversity in tropical latitudes. The youngest vicariant event influencing the genus *Chelon* was probably linked to the formation of permanent upwellings off West Africa and off the western coast of South Africa and Namibia (Shannon 1985). This view is supported by the existence of three sibling species associated with either temperate or tropical environments, i.e. *Chelon labrosus* (Risso 1827)/*Chelon bispinosus* (Bowdich 1825), *C. bandialensis/Chelon tricuspiden*s (Smith 1935) and *Chelon dumerili* (Steindachner 1870)/*Chelon* sp. B (Durand & Whitfield 2016). For these last two sibling species, the estimated divergence date is congruent with the formation of the Benguela Current system that occurred less than 12 Mya (Shannon 1985). Consequently, *C. dumerili* is now limited to western and central Africa and *Chelon* sp. B (sensu Durand & Borsa 2015) to southern Africa.

The diversity of African mugilids has benefitted from colonization via both the western Atlantic and the Indo-Pacific regions. The genus *Mugil* probably originated in American waters, based on both the species and phylogenetic diversity within this region (Durand & Whitfield 2016) and the ancestral distribution range inferred from the mugilid phylogenetic tree (Figure 1). Table 2 shows that 12 of the 15 mugilid species from North and South America belong to the genus *Mugil*. Dispersion events across the mid-Atlantic Ridge would have been difficult due to the distance which would have to be covered between America and Africa without access to typical mugilid food resources. However, this dispersal event probably occurred at least twice during the evolutionary history of the genus *Mugil* (Durand & Whitfield 2016). The African ancestors of *Mugil capurrii* (Perugia 1892) and *M. bananensis* probably reached African waters during the Oligocene (Figure 1, Durand & Whitfield 2016), while the level of divergence of the *M. curema* and *M. cephalus* complexes suggest a much more recent connection during the Pliocene (Figure 1, Neves et al. 2020).

Rafting by fishes from the Caribbean to the northeastern Atlantic has been already suggested (Boehm et al. 2013) using the warm Gulf Stream which flows from Florida (USA) towards North Carolina and then eastwards towards north-west Europe where the southern stream eventually joins the Canary Current off West Africa (Figure 2). Mugilid postflexion larvae and early juveniles in the marine environment swim in small shoals in surface waters (AKW personal observation). Where floating macrophyte rafts or other debris such as wooden logs occur, these rafts would potentially provide some physical protection from pelagic predation and also be a source of microalgal food growing on the debris until landfall was reached. According Boehm et al. (2013), who proposed this trans-Atlantic route of dispersion, the European and West African populations of the seahorse *H. hippocampus* became isolated from Caribbean/North American populations around 3.35 Ma, a date consistent with the divergence recorded for *M. cephalus* and *M. curema* species complexes (Figure 1).

Dispersion and connectivity of Mugilidae from the tropical Indo-Pacific region into tropical East African waters (Figure 3) would have been easier considering the large distribution range of species belonging to *Ellochelon*, *Crenimugil* and *Osteomugil* genera (Durand & Whitfield 2016). Migration and settlement of the latter genus in southern African waters is certainly ancient, as indicated by the presence of the endemic *O. robustus* along the southeastern Indian Ocean coast and their high level of divergence when compared to other species of the genus *Osteomugil* (Figure 1). Dispersion of these tropical genera over considerable distances was certainly easier than crossing the mid-Atlantic Ridge, mainly because the Indian Ocean coastline is continuous from Asia to Africa and mostly tropical or subtropical in terms of water temperatures. However, potential connectivity restrictions would have existed in the form of the Indo-Pacific Barrier on the Indian Ocean western border and the mid-Indian Barrier (Randall 1998). In addition, most mugilids use estuaries as primary nursery areas and there are a limited number of such habitats along the Arabian Gulf and Horn of Africa coasts.

The southern African 'hotspot' (Figure 4) is unique in that it contains both tropical and temperate mullet species (Figure 5), some of which, e.g. *Chelon richardsonii* (Smith 1846) and *Pseudomyxus capensis* (Valenciennes 1836), are endemic to southern Africa. Although a total of only 16 mugilid species has been recorded from the southern African hotspot, it is important to note that this species richness far exceeds that on the African east, west or northern coastal areas.

America

Most of the North and South American mugilid species occur in the tropical Indo-West Atlantic region (Harrison 2002). Of the approximately 26 global mugilid genera, only 4 valid genera, comprising 15 recognised species, are found in the Americas. The genus *Mugil* currently comprise 12 species (80% of the species richness in America) which totally dominates the mugilid species richness on the continent. *Mugil curema* and *M. cephalus* in particular have a widespread American distribution and an unusual amount of variation exists between geographically distant populations (Harrison et al. 2007), indicating that the number of recognised *Mugil* species are likely to increase further in the future.

The mugilid species distribution patterns in the Americas fits a general model of transisthmian geminate pairs that were linked prior to the formation of the Isthmus of Panama approximately 3.5 million years ago (Lessios 2008). Following the separation of the tropical Pacific and Atlantic oceans by the isthmus, mugilids developed divergences between the Pacific and Caribbean lineages (Barletta & Dantas 2016), a feature that has persisted despite the completion of the Panama Canal in 1914 which reconnected tropical waters within the region. For example, mitochondrial studies on *Dajaus monticola* (Bancroft 1834) indicate four distinct lineages that arose in the mid-Miocene, two in the

Caribbean and Gulf of Mexico in the east and two along the Pacific coast in the west (McMahan et al. 2013).

Other physico-chemical features in the ocean basins of the Americas may also influence mugilid distribution and biogeographical patterns (Barletta & Dantas 2016). A number of soft barriers exist (e.g. eastern Pacific Barrier) and current patterns within the ocean basins also influence faunal distribution along the American coasts. For example, the southern portion of the eastern Pacific is influenced by the cool Humboldt Current off Peru (Figure 6) which prevents tropical waters from flowing further south (Briggs 1995). Similarly, the eastern Pacific coastal region is influenced by the California Current (Figure 6) which prevents tropical waters from flowing north of Baja California Sur. Both the above coastal upwellings have a major influence on the distribution of tropical mugilid species (Figures 7).

In the western Atlantic, the eastward portion of Brazil splits the tropical South Equatorial Current (Figure 2) into two branches, with the Brazilian Current (Figure 2) running southwards and the other running in a northwesterly direction parallel to the continental shore. The latter current is instrumental in supporting a tropical mugilid species concentration in the central American region, including the associated islands. Similarly the loop current (the northern tip of the South Equatorial Current) maintains a strong biogeographic barrier for some *Dajaus monticola* evolutionary lineages that show a clear spatial disconnection between the Caribbean and Gulf of Mexico (McMahan et al. 2013).

Europe

The evolutionary history of European mullet species is intimately link to species present in the West African tropical area. Different connection/isolation events occurred between the eastern tropical Atlantic and northeastern Atlantic. The first isolation between these regions during the Eocene has been linked to the origin of the monotypic genus *Oedalechilus* versus *Parachelon*/*Chelon* (Figure 1). Later secondary contacts occurred, since there are several sister species in these two areas belonging to the genus *Chelon*. What happened between Europe and West Africa mirrors what occurred between temperate South Africa and the eastern tropical Atlantic, i.e. initial connectivity between the warm South African/Namibian and Angolan coastal waters ceased with the development of the cool Benguela upwelling system, thus isolating the *Chelon dumerili* populations of South Africa and Angola.

For the purposes of this review, the eastern Atlantic region extends from the British Isles, through the Mediterranean and into the Black Sea (Turan 2016). To fully understand the current mugilid species richness in these areas it is necessary to briefly examine the geological and geomorphological history of the region.

The Mediterranean Sea forms part of what was once the Tethys Ocean, an initial eastward-opening equatorial sea that eventually surrounded northern Pangea during the Triassic. The Tethys Ocean was then connected, through an uninterrupted equatorial belt around north Africa, to both the Indo-Pacific Ocean and the Atlantic Ocean during the Cretaceous (Biju-Duval et al. 1977). During that time, the Tethys Sea contained a highly diverse tropical marine fauna, mainly from the Indo-West Pacific region (Bianchi & Morri 2000). Tropical estuary-associated fish species, including warm-water mugilids, were also able to transit across the incipient north African coastline into the adjacent western and eastern oceans and estuaries (Whitfield 2005). This conclusion was reached because of the number of identical tropical mugilid genera on the eastern and western African coasts, but the lack of identical tropical species on these two coasts (Whitfield 2005). This finding suggests that isolation since the Miocene had led to the evolution of new species of these tropical genera along the western African coastline in particular.

During the Miocene, plate collisions resulted in the formation of the Isthmus of Suez, thus separating the Indo-Pacific Ocean from the Mediterranean Sea. The connection between the Atlantic Ocean and the Mediterranean Sea was also closed at the end of the Miocene (Torfstein & Steinberg 2020), with the Mediterranean becoming an isolated marine system. The genus *Planiliza* underwent considerable speciation during the Miocene (Figure 1), with all current species restricted to Asia and East Africa and absent from the Mediterranean and Atlantic Ocean.

River inflow from surrounding catchments was not enough to maintain the level of the Mediterranean, which then dried out, probably resulting in the loss of mugilids from this region. In effect, the natural bridge for tropical mugilid species to transit across the northern coastal waters of the African continent also came to an end. After the natural re-opening of the Straits of Gibraltar at the beginning of the Pliocene (approximately 6 million years ago), the Mediterranean was populated by marine species of Atlantic origin (Briggs & Bowen 2012), thus losing its Indian Ocean biotic links.

Some changes in the Mediterranean fauna occurred after the opening of the Suez Canal in 1869, particularly in the south-eastern region of this sea. The Suez Canal connects two major water bodies, the Red Sea with the Mediterranean, each of which differs fundamentally in terms of fauna and hydrography with the other. The main physico-chemical difference between the two regions is water temperature, which is warmer in the tropical Red Sea and fluctuates less than in the subtropical and more seasonal Mediterranean (Berman et al. 2003). The fauna of the Red Sea is of tropical Indo-Pacific in origin, whereas that of the Mediterranean is primarily of temperate Atlantic origin, with most of the mullet species located in the Mediterranean being temperate taxa (Turan 2016). Although some tropical mugilid species, e.g. *Planiliza carinata* (Valenciennes 1836), have managed to transit the Suez Canal into the Mediterranean and boost temperate species numbers, overall there are no mugilid species 'hotspots' within this region.

Asia

There are 12 marine ecoregions of the world, and these are of importance in the analysis of, and comparison between, marine coastal biodiversity patterns (Spalding et al. 2007). Within these 12 marine realms, the central Indo-Pacific region appears to have the highest marine biodiversity. A variety of hypothetical centres of marine diversity have been suggested (e.g. Sanciangco et al. 2013) but most identify hotspots located between the Indo-Malayan and Philippine archipelagos.

The evolution of 'geological plate endemics' has received special attention in terms of fish biogeography (Springer 1982), with these species ranges appearing to be confined to particular tectonic plates. When these plates move to or from one another, so do their faunas, thus causing them to merge or to split from one another. India, southeast and east Asia lie on an intersection of four tectonic plates that experienced important volcanic activities during the Cenozoic era (Hall 1996). Therefore, a number of the islands in east and southeast Asia were created by these tectonic activities and volcanism which provided structural habitat diversity for marine biota, including fishes. This historical geomorphological process associated with current features, together with prevailing sea surface temperatures and water currents, are probably the primary factors that shaped the current species distribution of mugilids and other fish species in this region.

Considering the wide variety of processes, occurring at different spatial and temporal scales, and responsible for either vicariant or dispersal events, makes it difficult to interpret current Asian mullet species distribution patterns. Some species exhibit a distribution range limited to certain biogeographic provinces, e.g. *Planiliza haematocheilus, Planiliza lauvergnii* (Eydoux & Souleyet 1850) and *Planiliza klunzingeri* (Day 1888) (Hassan et al. 2021, 2022). Others, seem to present a more continuous and widespread distributional range such as *Osteomugil cunnesius* (Valenciennes 1836), *Crenimugil seheli* (Fabricius 1775), *Crenimugil buchanani* (Bleeker 1853), *Ellochelon vaigiensis* (Quoy & Gaimard 1825), *Planiliza subviridis* (Valenciennes 1836), *Planiliza macrolepis* (Smith 1846) and *Mugil cephalus*, all of which extend from Asia to southeastern Africa (Table 6, Whitfield 2019).

Recent DNA barcoding has highlighted cryptic diversity, probably corresponding to sister species within the distributional range and are defined by past and present biogeographic barriers (Durand & Borsa 2005; Hasan et al. 2021). However, in Asian mullet phylogeny, the oldest evolutionary event is perhaps not only related to these geological and climatic processes, since the presence in India, Bangladesh and Myanmar of three monotypic genera (i.e. *Rhinomugil, Minimugil* and *Sicamugil*) that share a common ancestor (Xia et al. 2016), and probably evolved in freshwater and not the coastal marine environment of this region.

The alternation between glacials and interglacials during the Pleistocene caused large scale eustatic sea-level changes globally, and had a major effect on continental shelves and shore lines in the Indo-Malayan region (Voris 2000) as well as marginal seas of the northwest Pacific (Wang 1999). Sea-levels fluctuated up to 120 m between these events, with vertical changes of up to 10-20 m per 1000 years being recorded (Siddall et al. 2003). Horizontal shoreline migrations across continental shelves was also prevalent, and exceeded 100 m per 10 years (Chappell & Thom 1977). Large shelf areas of the Indo-Malayan and Philippine archipelagos were exposed and therefore fish, including mugilids associated with such areas, probably experienced local marine extinctions and population disconnection during the Pleistocene sea-level regressions (Voris 2000).

Southeast Asian peninsulars and islands were above sea level during the Pleistocene epoch ice ages, and this emergent land area was named the Sundaland. The creation of Sundaland became a barrier for marine fish dispersal, as well as an opportunity for speciation through isolation (Sholihah et al. 2021). During the ice ages, five main refuges formed within this region, which probably influenced the present day distribution and diversity of fishes, including mugilids (Shen & Durand 2016). This was proposed as an explanation for the apparent antitropical distribution range of the cryptic *Mugil* species belonging to the *Mugil cephalus* L. species complex (Viet Tran et al. 2017), and the absence of *M. cephalus* species from Indonesian waters being confirmed by Delrieu-Trottin et al. (2020). Furthermore, northwestern Pacific marginal seas disconnections during ice ages have been largely invoked as an explanation for the high cryptic diversity flagged by phylogeographic studies on *Mugil cephalus* and *Planiliza haematocheilus* (Liu et al. 2007, Shen et al. 2011, Viet Tran et al. 2017, Bae et al. 2020).

In addition to past geological events being able to partially explain present day marine species richness and distribution in India and Asia, the high habitat diversity present in these regions is also an important factor to consider (Randall 1998). For example, mangroves are an important coastal habitat for fishes in southeast Asia that are latitudinally determined by the 20^{o}C winter isotherm (McCoy & Heck 1976). Mangroves promote high biotic diversity in southeast Asia (Giri et al. 2011) and provide a suitable habitat for many fish species, including mugilids (Kuo et al. 1999). For example, 62% of fish biomass and 41% of fish abundance in mangrove intertidal creeks in Iran were accounted for by Mugilidae (Shahraki et al. 2016).

Coral reefs are estimated to globally cover approximately 285 000 km^2 of coastal shelf waters, with the Indo-Pacific region accounting for approximately 92% of this area (Spalding et al. 2001). Reefs are topographically complex, with thousands of fish species living in association with these structures. There are a number of mugilids that are associated with coral reef habitats (Hiatt & Strasburg 1960), e.g. *Crenimugil seheli*, *Crenimugil buchanani*, *Crenimugil crenilabis* (Forsskål 1775) and *Ellochelon vaigiensis*. Therefore, coral reefs and mangroves, together with past and present environmental characteristics, have probably contributed to the high diversity of mugilids in southeast Asia.

Australia/Oceania

The islands of Oceania can be divided into four different subregions, based primarily on the geological processes that played a role in their physical evolution. The first and largest subregion is Australia, which is situated in the middle of the Indo-Australian Plate. The second category includes the islands formed at the collision boundaries between major crustal plates and are found specifically in the South Pacific, e.g. the collision boundary between the Indo-Australian and Pacific plates formed islands such as New Zealand and Papua New Guinea. Similar types of marine landscapes and islands are found along the Eurasian and Pacific plates in the northern Pacific region of Oceania. The third category of landscape types found in Oceania are volcanic islands, e.g. Fiji. These islands typically rise from the sea floor at places where a large amount of magma was extruded into the Pacific Ocean basin. Most of these landscapes consist of very small islands in terms of land area but with high mountain ranges. Coral reef islands and atolls are the last type of landscape found in Oceania and are low-lying features, some with enclosed lagoons (Ghasemzadeh 2016).

There are two major climatic zones that encompass most of Oceania, viz. tropical and temperate. Approximately half of Australia and all of New Zealand are within the temperate zone, whilst most of the northern part of Australia and the island areas in the Pacific are considered tropical. The presence of coral reefs, such as the Great Barrier Reef in the tropical region, have also promoted marine biodiversity and some coastal areas are classified as biodiversity hotspots (Ghasemzadeh 2016). Records of mugilids in Australia/Oceania indicate a high diversity and they inhabit the marine, estuarine and some inland freshwaters of the region. According to Ghasemzadeh (2016), 20 species of mullet belonging to 12 genera are found in Australian waters. The species *Trachystoma petardi* (Castelnau 1875), *Myxus elongatus* Günther 1861, *Gracilimugil argenteus* (Quoy & Gaimard 1825) and *Paramugil georgii* (Ogilby 1897) are restricted to Australian waters. Deep phylogenetic relationships among these endemic species (Durand et al. 2012, Santini et al. 2015, Xia et al. 2016) indicate a long isolation of these species and genera (Figure 1), thus emphasizing the ancient history of the Australian mugilids.

Harrison & Senou (1999) produced a comprehensive review on the mullets of Indo-West Pacific, recognizing 11 genera and 31 species from this region. Ghasemzadeh (2016) reported 27 species belonging to 14 genera from the Oceania region. The tropical waters and abundant mangrove habitat in the northern parts of Australia, together with the close proximity to the centre of mugilid evolution and distribution to the north of that continent, boosts the species richness of mugilids associated with this region.

Cosmopolitan versus endemic mugilids

Many tropical mullet species have a widespread coastal distribution covering many thousands of kilometres in tropical and subtropical waters of both the Pacific and Indian oceans, e.g. *Ellochelon vaigiensis* and *Crenimugil* species. In contrast temperate mullet species (e.g. *Chelon richardsonii*) tend to have a much more restricted coastal distribution and are limited to cooler, higher latitude waters. This supports the hypothesis that mugilids originally evolved in tropical waters, with temperate species representing examples of tropical ancestral species that became isolated as a result of climate change and then adapted to more temperate conditions during periods of global climate change.

Mugilids that are mainly restricted to inland waters of the world also tend to have restricted distributions and are therefore more endemic than wider ranging tropical marine taxa. There is one species, or species complex, that is truly cosmopolitan (*Mugil cephalus* spp.) which is well represented in tropical and temperate waters of all oceans between 34°N and 34°S (Whitfield et al. 2012). Part of the reason why *M. cephalus* spp. has a global distribution is because this species and its conspecifics have been able to disperse through both tropical and temperate waters, something purely tropical or temperate mugilids have been unable to achieve.

Freshwater-associated mugilids

It is apparent that a number of primarily freshwater-associated mugilid taxa, e.g. *Agonostomus catalai* (Pellegrin 1932), *Agonostomus telfairii* (Bennett 1832), *Dajaus monticola* (Bancroft 1834), *Cestraeus goldiei* (MacLeay 1883), *Cestraeus plicatilis* (Valenciennes 1836), *Cestraeus oxyrhynchus* (Valenciennes 1836), *Joturus pichardi* (Poey 1860), *Rhinomugil corsula* (Hamilton 1822), *Squalomugil nasutus* (De Vis 1883), *Minimugil cascasia* (Hamilton 1822), *Sicamugil hamiltonii* (Day 1870), and *Trachystomus petardi* (Castelnau 1875), are abundant in the rivers and lagoons of high rainfall areas in the African, Asian, Australian and American tropics, further enhancing the species richness of these regions.

Although two mugilids (*M. cephalus* and *P. capensis*) are associated with some rivers in temperate southern Africa (Bok 1979), neither species is restricted to these catchment areas, and are often more abundant in estuaries and the marine environment. The moderate to high rainfall areas of temperate Europe also host some freshwater-associated mugilid species (e.g. *C. labrosus*) but, once again, no entirely freshwater mullet species are recorded. This is probably a function of extensive ice sheets that formed over much of Europe during recurrent ice ages, the last one having reached a maximum 19 000 years BP. Overall, the richness of freshwater mugilid species in tropical waters, and absence of such species from temperate areas, reinforces the purported tropical/subtropical origin and centre of diversification for this family.

Conclusions

Three mugilid species hotspots are identified globally, namely the Coral Triangle, southern Asia and southern Africa. Two of the species hotspots are tropical/subtropical and only the southern African one is subtropical/temperate. The probable reason why this region has a richer mugilid representation than tropical America may be linked to both coastal connectivity with the Indo-Pacific and the contribution of temperate species, two of which (*Chelon richardsonii* and *Pseudomyxus capensis*) evolved on the subcontinent and are endemic to South Africa.

It would appear from the available circumstantial evidence, based primarily on species richness, that the centre of mugilid evolution and then global dispersion lies in the tropical waters of the Indo-Pacific.

The number of these tropical species that radiated out to the coastal waters of Africa and America were clearly less than the number that remained in the central Indo-Pacific region. Access by tropical mugilid species was greater to Africa than the Americas, primarily because of the direct tropical and subtropical coastal connectivity to the former continent. This would have enabled more tropical mugilids to reach Africa than America, with the latter probably relying on 'island hopping' and possible 'rafting', assisted by the Pacific Equatorial Counter Current, to move eastwards across the Pacific Ocean. In the absence of alternative explanations, the circumstantial evidence supports this hypothesis on how some of the mugilids may have reached the Americas.

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References

Bae, S.E., Kim J.K. & Li C. 2020. A new perspective on biogeographic barrier in the flathead grey mullet (Pisces: Mugilidae) from the northwest Pacific. Genes & Genomics: https://doi.org/10.1007/s13258-020-00942-8

Bariche, M., Torres, M., Smith, C., Sayar, N., Azzurro, E., Baker, R. & Bernardi, G. 2015. Red Sea fishes in the Mediterranean Sea: a preliminary investigation of a biological invasion using DNA barcoding. Journal of Biogeography 42: 2363-2373

Barletta, M. & Dantas, D.V. 2016. Chapter 3. Biogeography of distribution of Mugilidae in the Americas. In: Biology, Ecology and Culture of Grey Mullets (Mugilidae) (Crosetti, D. & Blaber, S.J.M., ed.), pp. 42-62. CRC Press, Boca Raton, USA.

Berman, T., Paldor, N. & Brenner, S. 2003. Annual SST cycle in the Eastern Mediterranean, Red Sea and Gulf of Elat. Geophysical Research Letters 30: https://doi.org/10.1029/2002GL015860

Berra, T.M. 1981. An Atlas of Distribution of the Freshwater Fish Families of the World. University of Nebraska Press, London. 197 pp.

Bianchi, N.C. & Morri, C. 2000. Marine biodiversity of the Mediterranean Sea: situation, problems and prospects for future research. Marine Pollution Bulletin 40: 367-376.

Biju-Duval, B., Dercourt, J. & Le Pichon, X. 1977. From the Tethys Ocean to the Mediterranean seas: a plate tectonic model of the evolution of the western Alpine system. International Symposium on the Structural History of the Mediterranean Basins (Biju-Duval, B. & Montadert, L., eds), pp. 143-158.

Boehm, J.T., Woodall, L., Teske, P.R., Lourie, S.A., Baldwin, C., Waldman, J. & Hickerson, M. 2013. Marine dispersal and barriers drive Atlantic seahorse diversification. Journal of Biogeography 40: 1839-1849.

Bok, A.H. 1979. The distribution and ecology of two mullet species in some freshwater rivers in the eastern Cape, South Africa. Journal of the Limnological Society of Southern Africa 5: 97-102.

Bray, D.J. 2018. Fishes of Australia, *Crenimugil heterocheilos.* https://fishesofaustralia.net.au/home/species/4536

Briggs, J.C. 1995. Global Biogeography. Developments in Paleontology and Stratigraphy, Vol. 14. Elsevier, Amsterdam.

Briggs, J.C. & Bowen, B.W. 2012. A realignment of marine biogeographic provinces with particular reference to fish distributions. Journal of Biogeography 39: 12-30.

Chappell, J. & Thom, B.G. 1977. Sea levels and coasts. In: Sunda and Sahul: Prehistoric Studies in Southeast Asia, Melanesia and Australia (Allen, J., Golson, J. & Jones, R., eds), pp. 275–291. Academic Press, London.

Crosetti, D. & Blaber, S. (eds) 2016. Biology, Ecology and Culture of Grey Mullet (Mugilidae). CRC Press, Boca Raton.

Delrieu-Trottin, E., Durand, J.D., Limmon, G., Sukmono, T., Kadarusman, K., Sugeha, H.Y., et al. 2020. Biodiversity inventory of the grey mullets (Actinopterygii: Mugilidae) of the Indo-Australian Archipelago through the iterative use of DNA-based species delimitation and specimen assignment methods. Evolutionary Applications 13: 1451-1467.

Durand, J.D. 2016. Implications of molecular phylogeny for the taxonomy of Mugilidae. In: Biology, Ecology and Culture of Grey Mullet (Mugilidae) (Crosetti, D. & Blaber, S.J.M., eds), pp. 22-41. CRC Press, Boca Raton, USA.

Durand, J.D**.** & Borsa, P. 2015. Mitochondrial phylogeny of grey mullets (Acanthopterygii: Mugilidae) suggests high proportion of cryptic species. C.R. Biologies 338: 266–277.

Durand, J.D., Shen, K.N., Chen, W.J., Jamandre, B.W., Blel, H., Diop, K., Nirchio, M., Garcia de Leon, F.J., Whitfield, A.K., Chang, C.W. & Borsa, P. 2012a. Systematics of the grey mullets (Teleostei: Mugiliformes: Mugilidae): Molecular phylogenetic evidence challenges two centuries of morphology-based taxonomy. Molecular and Phylogenetics Evolution 64: 73-92.

Durand, J.D., Chen, W.J., Shen, K.N., Fu, C. & Borsa, P. 2012b. Genus-level taxonomic changes implied by the mitochondrial phylogeny of grey mullets (Teleostei: Mugilidae). C.R. Biologies 335: 687-697.

Durand, J.D. & Whitfield, A.K. 2016. Chapter 6. Biogeography of mugilids in western, central and southern regions of Africa. In: Biology, Ecology and Culture of Grey Mullets (Mugilidae) (Crosetti, D. & Blaber, S.J.M., ed.), pp. 102-115. CRC Press, Boca Raton, USA.

Francis M.P. 2022. Checklist of the coastal fishes of Lord Howe, Norfolk and Kermadec Islands, southwest Pacific Ocean. Unpublished Technical Report.

Fukuchi, I. & Tachihara, K. 2020. Northernmost record of half-fringelip mullet*, Crenimugil heterocheilos* (Bleeker, 1885) (Teleostei: Mugilidae), from the Okinawa-jima Island, Ryukyu Archipelago, southern Japan. Biogeography 22: 21-25.

Ghasemzadeh, J. 2016. Chapter 5. Biogeography and distribution of Mugilidae in Australia and Oceania. In: Biology, Ecology and Culture of Grey Mullets (Mugilidae) (Crosetti, D. & Blaber, S.J.M., ed.), pp. 85-101. CRC Press, Boca Raton, USA.

Giri, C., Ochieng, E., Tieszen, L.L., Zhu, Z., Singh, A., Loveland, T., Masek, J. & Duke, N. 2011. Status and distribution of mangrove forests of the world using earth observation satellite data. Global Ecology and Biogeography 20: 154-159.

Golani, D. & Fricke, R. 2018. Checklist of the Red Sea Fishes with delineation of the Gulf of Suez, Gulf of Aqaba, endemism and Lessepsian migrants. Plazi.org taxonomic treatments database. Checklist dataset https://doi.org/10.11646/zootaxa.4509.1.1 accessed via GBIF.org on 2023-03-10.

Hall, R. 1996. Reconstructing Cenozoic SE Asia. In: Tectonic Evolution of SE Asia. (Hall, R. & Blundell, D., eds), pp. 203–224. Geological Society, London.

Hamon, N., Sepulchre, P., Lefebvre, V. & Ramstein, G. 2013. The role of eastern Tethys seaway closure in the Middle Miocene Climatic Transition (ca. 14 Ma). Climate of the Past 9: 2687-2702.

Harrison, I.J. 2002. Mugilidae. In: FAO Species Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central Atlantic, Vol. 2. Bony Fishes, Part 1 (Acipenseridae to Grammatidae) (Carpenter, K., ed.), pp. 1071-1085. FAO, Rome.

Harrison, I.J. 2004. Mugilidae. In: The Freshwater Fishes of Europe. Volume 8 (Miller, P.J., ed.), pp. 469-472. AULA-Verlag, Wiebelsheim.

Harrison, I.J., Nirchio, M., Oliveira, C., Ron, E. and Gaviria, J. 2007. A new species of mullet (Teleostei: Mugilidae) from Venezuela, with a discussion on taxonomy of *Mugil gaimardianus*. Journal of Fish Biology 71: 76-97.

Harrison, I.J. & Senou, H. 1999. Order Mugiliformes. In: The Living Marine Resources of the Western Central Pacific (Carpenter, K.E. & Niem, V.H., eds), pp. 2069-2790. FAO Species Identification Guide for Fisheries Purposes. FAO, Rome.

Harrison, T.D. 2005. Ichthyofauna of South African estuaries in relation to the zoogeography of the region. Smithiana Bulletin 6: 1-27.

Harrison, T.D. & Whitfield, A.K. 2022. Global biogeography of estuary-associated fishes. Journal of the Marine Biological Association of the UK: https://doi.org/10.1017/S0025315422000285

Hasan, A., Siddiqui, P.J.A., Amir, S.A. & Durand, J.-D. 2021. DNA barcoding of mullets (Family Mugilidae) from Pakistan reveals surprisingly high number of unknown candidate species. Diversity 13: 232. https://doi.org/10.3390/d13060232

Hasan M.E., Hasan A., Béarez P., Shen K.N., Chang C.W., Tran T.Y.V., Golani D., Al-Saboonchi A., Siddiqui P.J.A. & Durand J.D. 2022. *Planiliza lauvergnii* (Eydoux & Souleyet, 1850), a senior synonym of *Planiliza affinis* (Günther, 1861) with a re-evaluation of keeled back mullets (Teleostei: Mugilidae). Zootaxa 5194: 497-518.

Henriques, R., Potts, W.M., Sauer, W.H., Santos, C.V., Kruger, J., Thomas, J.A. & Shaw, P.W. 2016. Molecular genetic, life-history and morphological variation in a coastal warm-temperate sciaenid fish: evidence for an upwelling-driven event. Journal of Biogeography 43: 1820-1831.

Heras, S, Roldán, M.I. & Castro, M.G. 2009. Molecular phylogeny of Mugilidae fishes revised. Reviews in Fish Biology and Fisheries 19: 217-231.

Hiatt, R.W. & Strasburg, D.W. 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecological Monographs 30: 65-127.

Hutchings, L., van der Lingen, C.D., Shannon, L.J., Crawford, R.J.M., Verheye, H.M.S., et al. 2009. The Benguela Current: an ecosystem of four components. Progress in Oceanography 83: 15-32.

Kuo, S.R., Lin, H.J. & Shao, K.T. 1999. Fish assemblages in the mangrove creeks of northern and southern Taiwan. Estuaries 22: 1004-1015.

Larson, H.K., Williams R.S. & Hammer M.P. 2013. An annotated checklist of the fishes of the Northern Territory, Australia. Zootaxa 3696.

Lessios, H.A. 2008. The great American schism: divergence of marine organisms after the rise of the Central American Isthmus. Annual Review of Ecology, Evolution and Systematics 39: 63-91.

Liu, J., Gao, T.X., Wu, S. & Zhang, Y.A.P. 2007. Pleistocene isolation in the northwestern Pacific marginal seas and limited dispersal in a marine fish, *Chelon haematocheilus* (Temminck & Schlegel, 1845). Molecular Ecology 16: 275-288.

McCoy, E.D. & Heck, K.L. 1976. Biogeography of corals, seagrasses and mangroves: an alternative to the center of origin concept. Systematic Zoology 25: 201-210.

McMahan, C.D., Davis, M. P., Domínguez-Domínguez, O., García-de-León, F.J., Doadrio, I. & Piller, K.R. 2013. From the mountains to the sea: phylogeography and cryptic diversity within the mountain mullet*, Agonostomus monticola* (Teleostei:Mugilidae). Journal of Biogeography 40: 894-904.

Mittelstaedt, E. 1991. The ocean boundary along the African coast. Circulation and oceanographic properties at the sea surface. Progress in Oceanography 26: 307-455.

Neves, J.M.M., Almeida, J.P.F.A., Sturaro, M.J., Fabré, N.N., Pereira, R.J. & Mott, T. 2020. Deep genetic divergence and paraphyly in cryptic species of *Mugil* fishes (Actinopterygii: Mugilidae). Systematics and Biodiversity, 18:2, 116-128.

Ndoye S., Capet X., Estrade, B., Sow, B., Dagorne D., Lazar A., Gaye A. & Brehmer P. 2014. SST patterns and dynamics of the southern Senegal-Gambia upwelling centre. JGR Oceans 119: 8315-8335.

Pasquaud, S., Vasconcelos, R.P., França, S., Henriques, S., Costa, M.J. & Cabral, H. 2015. Worldwide patterns of fish biodiversity in estuaries: effect of global vs local factors. Estuarine, Coastal and Shelf Science 154: 122-128.

Randall, J.E. 1998. Zoogeography of shore fishes of the Indo-Pacific region. Zoological Studies 37: 227-268.

Sanciangco, J.C, Carpenter, K.E., Etnoyer, P.J. & Moretzon, F. 2013. Habitat availability and heterogeneity and the Indo-Pacific warm pool as predictors of marine species richness in the tropical Indo-Pacific. Plos One, https://doi.org/10.1371/journal.pone.0056245.

Santini, F., May, M.R., Carnevale, G. & Moore, B.R. 2015. Bayesian inference of divergence times and feeding evolution in grey mullets (Mugilidae). Plos One, https://doi.org/10.1101/019075.

Satapoomin, U. 2011. The fishes of southwestern Thailand, the Andaman Sea – a review of research and a provisional checklist of species. Phuket Marine Biological Center Research Bulletin 70: 29-77.

Shahraki, M., Saint-Paul, U., Krumme, U. & Fry, B. 2016. Fish use of intertidal mangrove creeks at Qeshm Island, Iran. Marine Ecology Progress Series 542: 153-166.

Shannon, L.V. 1985. The Benguela ecosystem. Part I. Evolution of the Benguela, physical features and processes. Oceanography and Marine Biology 23: 105-182.

Shen, K.-N. & Durand, J.D. 2016. Chapter 4. Biogeography and distribution of Mugilidae in India, South-East and East Asia. In: Biology, Ecology and Culture of Grey Mullets (Mugilidae) (Crosetti, D. & Blaber, S.J.M., ed.), pp. 63-84. CRC Press, Boca Raton, USA.

Shen, K.-N., Jamandre, B.W., Hsu, C.C., Tzeng, W.N. & Durand, J.D. 2011. Plio-Pleistocene sea level and temperature fluctuations in the northwestern Pacific promoted speciation in the globally-distributed flathead mullet *Mugil cephalus*. BMC Evolutionary Biology 11: 83.

Sholihah, A., Delrieu-Trottin, E., Condamine, F.L., Wowor, D., Rüber, L., Pouyaud, L., Agnèse, J.-F. & Hubert, N. 2021. Impact of Pleistocene eustatic fluctuations on evolutionary dynamics in southeast Asian biodiversity hotspots. Systematic Biology 70: 940-960.

Siddall, M., Rohling, E.J., Almogi-Labin, A., Hemleben, C., Meischner, D., Schmelzer, I. & Smeed, D.A. 2003. Sea-level fluctuations during the last glacial cycle. Nature 423: 853-858.

Siu, G., Bacchet, P., Bernardi, G., Brooks, A.J., Carlot, J., Causse, R., Claudet, J., Clua, E., Delrieu-Trottin, E., Espiau, B., Harmelin-Vivien, M., Keith, P., Lecchini, D., Madi-Moussa, R., Parravicini, V., Planes, S., Ponsonnet, C., Randall, J. E., Sasal, P., Taquet, M., Williams, J.T., Galzin, R. 2017. Shore fishes of French Polynesia. Cybium 41: 245-278.

Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A. & Robertson, J. 2007. Marine ecoregions of the world: a bioregionalization of coast and shelf areas. BioScience 57: 573-583.

Spalding, M.D., Ravilious, C. & Green, E.P. 2001. World Atlas of Coral Reefs. University of California Press and UNEP/WCMC ISBN 0520232550.

Springer, V.G. 1982. Pacific plate biogeography, with special reference to shore fishes. Smithsonian Contributions to Zoology 367: 1-182.

Thieme, P., Bogorodsky, S.V., Alpermann, T.J., Whitfield, A.K., Freitas, R. & Duramd, J.-D. 2022. Contributions to the taxonomy of the mugilid genus *Chelon* Artedi (Teleostei: Mugilidae), with a major review of the status of *C. persicus* Senou, Randall & Okiyama, 1995. Zootaxa 5188(1): 001-042.

Torfstein, A. & Steinberg, J. 2020. The Oligo-Miocene closure of the Tethys Ocean and evolution of the proto-Mediterranean Sea. Scientific Reports 10: Article No. 13817.

Trape, S. & Durand, J.D. 2011 First record of *Mugil capurrii* (Mugilidae, Perciformes) in the Gulf of Guinea. Journal of Fish Biology 78: 937-940.

Turan, C. 2016. Chapter 7. Biogeography and distribution of Mugilidae in the Mediterranean and the Black Sea, and North-East Atlantic. In: Biology, Ecology and Culture of Grey Mullets (Mugilidae) (Crosetti, D. & Blaber, S.J.M., ed.), pp. 116-127. CRC Press, Boca Raton, USA.

Viet Tran, T.T., Ke Phan, L. & Durand, J.D. 2017. Diversity and distribution of cryptic species within the *Mugil cephalus* species complex in Vietnam. Mitochondrial DNA (Part A) 28: 1-9.

Voris, H.K. 2000. Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. Journal of Biogeography 27: 1153-1167.

Wang, P. 1999. Response of Western Pacific marginal seas to glacial cycles: paleoceanographic and sedimentological features. Mar Geol 156:5-39

Whitfield, A.K. 2005. Preliminary documentation and assessment of fish diversity in sub-Saharan African estuaries. African Journal of Marine Science 27: 307-324.

Whitfield, A.K. 2019. Fishes of Southern African Estuaries: From Species to Systems. Smithiana Monograph No. 4: 495 pp.

Whitfield, A.K. & Blaber, S.J.M. 1978. Resource segregation among iliophagous fish in Lake St Lucia, Zululand. Environmental Biology of Fishes 3: 293-296.

Whitfield, A.K., Panfili, J. & Durand, J.D. 2012. A global review of the cosmopolitan flathead mullet *Mugil cephalus* Linnaeus 1758 (Teleostei: Mugilidae), with emphasis on the biology, genetics, ecology and fisheries aspects of this apparent species complex. Reviews in Fish Biology and Fisheries 22: 641-681.

Wirtz, P., Bingeman, J., Bingeman, J., Fricke, R., Hook, T.J. & Young, J. 2017. The fishes of Ascension Island, central Atlantic Ocean – new records and an annotated checklist. Journal of the Marine Biological Association of the United Kingdom 97: 783-798.

Xia, R., Durand J.D. & Fu, C. 2016. Multilocus resolution of Mugilidae phylogeny (Teleostei: Mugiliformes): Implications for the family's taxonomy. Molecular Phylogenetics and Evolution 96: 161-177.

Zajonz, U., Lavergne E., Bogorodsky, S.V., Naseeb Saeed, F., Sheikh Aideed, M. & Krupp, F. 2019. Coastal fish diversity of the Socotra Archipelago, Yemen. Zootaxa 4636: 001-108.

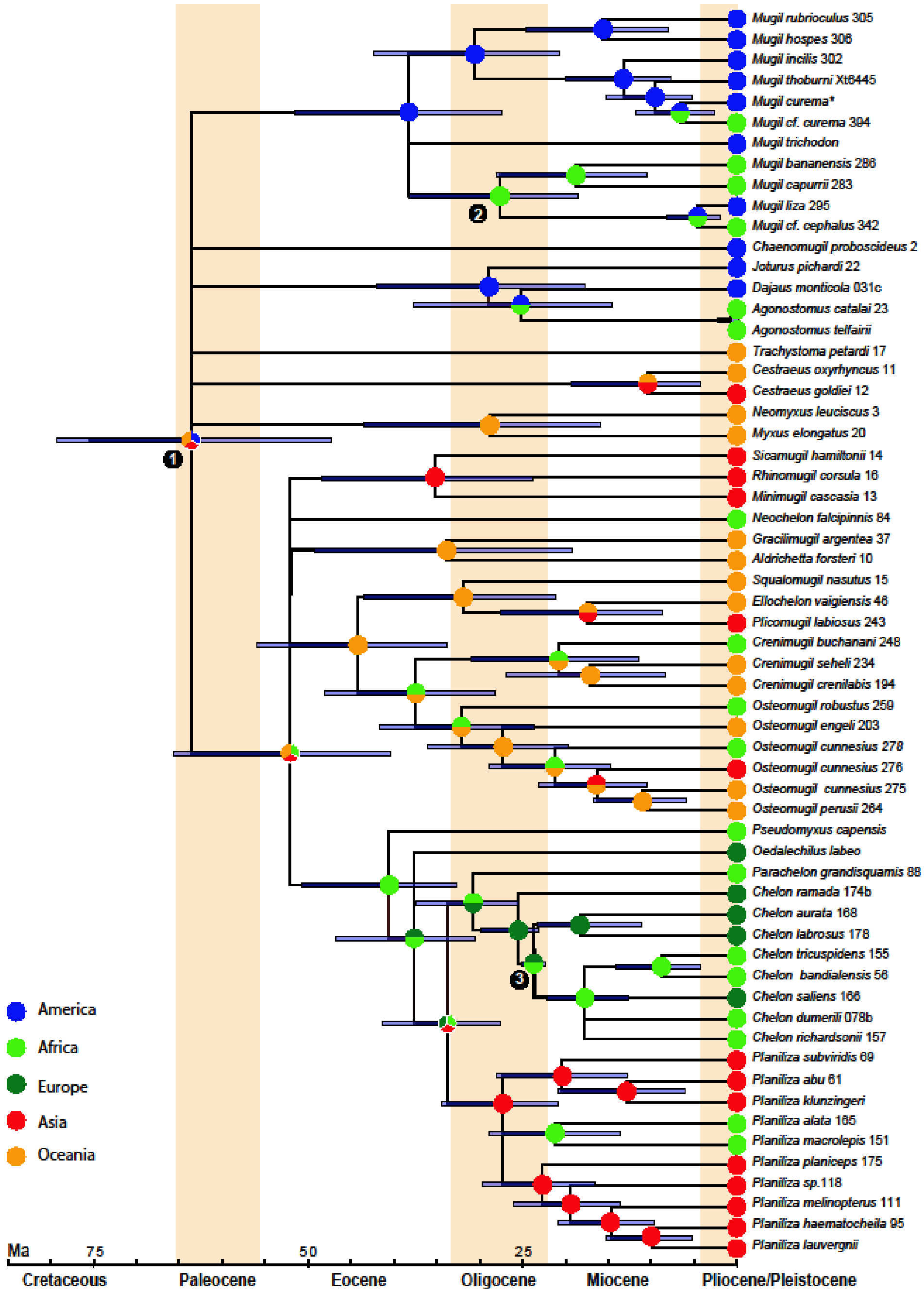

Figure 1. Baysian time-calibrated phylogenetic tree of the Mugilidae (adapted from Santini et al. 2015) based on genetic polymorphisms of three mitochondrial markers: Cytochrome Oxydase 1, Cytochrome b and 16S RNA. The numbered internal nodes indicate the location of the corresponding fossil calibrations (see Santini et al. 2015 for details) and bar plots on the nodes indicate the corresponding 95% HPD interval of divergence times. The number following each species name corresponds to the specimens analyzed in Durand et al. (2012a, b). The colour of dots indicate the geographic origin of the specimen used for phylogenetic reconstruction (at leaf) or ancestor level (internal nodes).

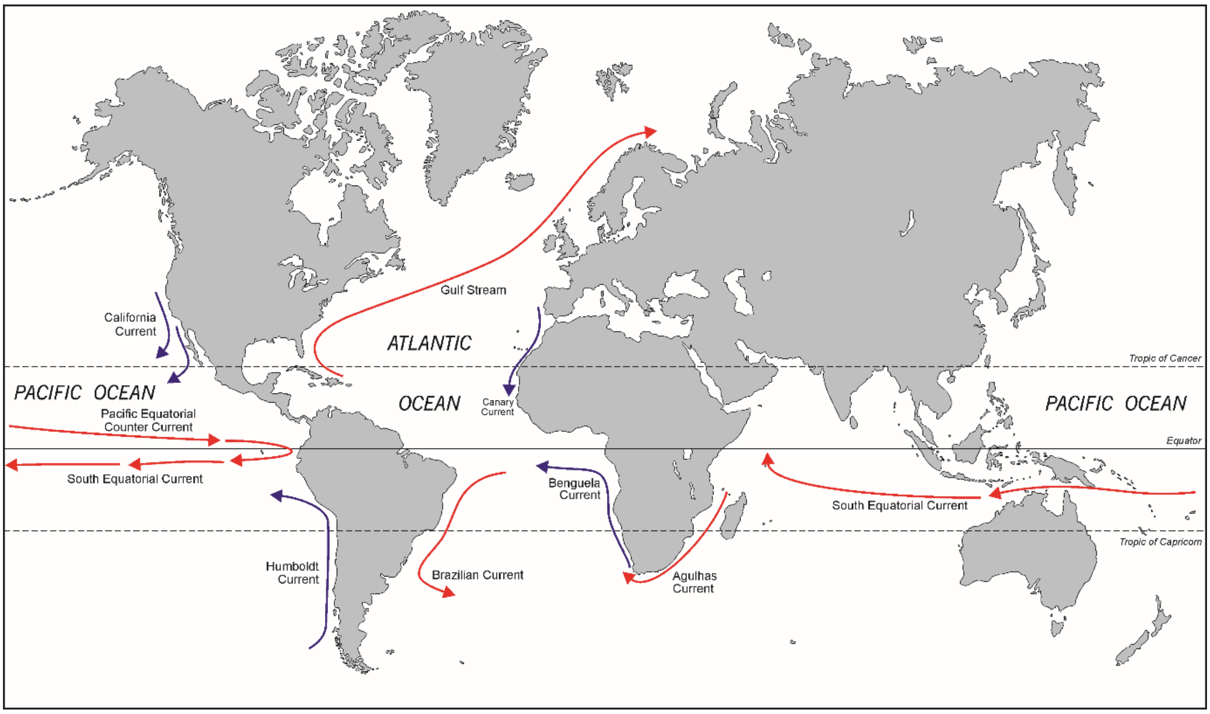

Figure 2. Global map showing ocean currents mentioned in the text of this review.

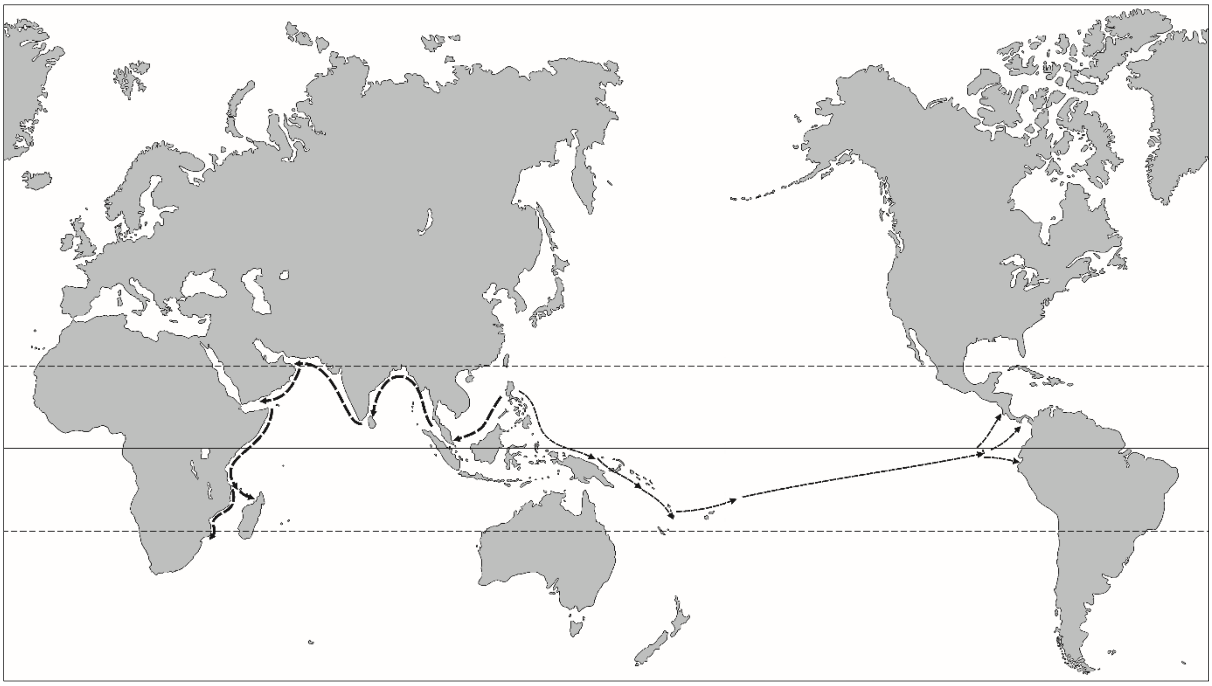

Figure 3. Global map showing the hypothetical dispersal routes for tropical mugilid species from the central Indo-Pacific towards Africa in the west and America in the east. The sizes of the arrows are slightly different because more species reached Africa than America. Note that coastal dispersion of tropical species to the east was not possible because coastal waters in the northern and southern Pacific are polar or cold temperate.

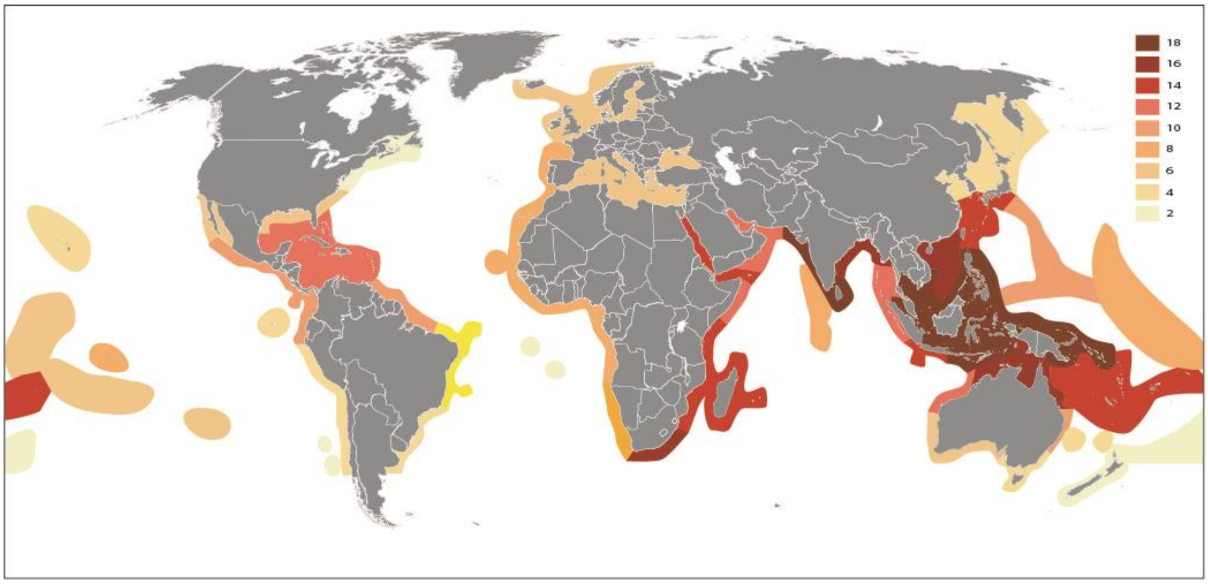

Figure 4. Mugilid species richness using the 62 ecoregions depicted by Spalding et al. (2007). The number of species recorded in each ecoregion are listed in Table 6 and visually depicted in this map. Three global mugilid species richness regions are recognised, based on this analysis, and include the Coral Triangle, southern Asia and southern Africa.

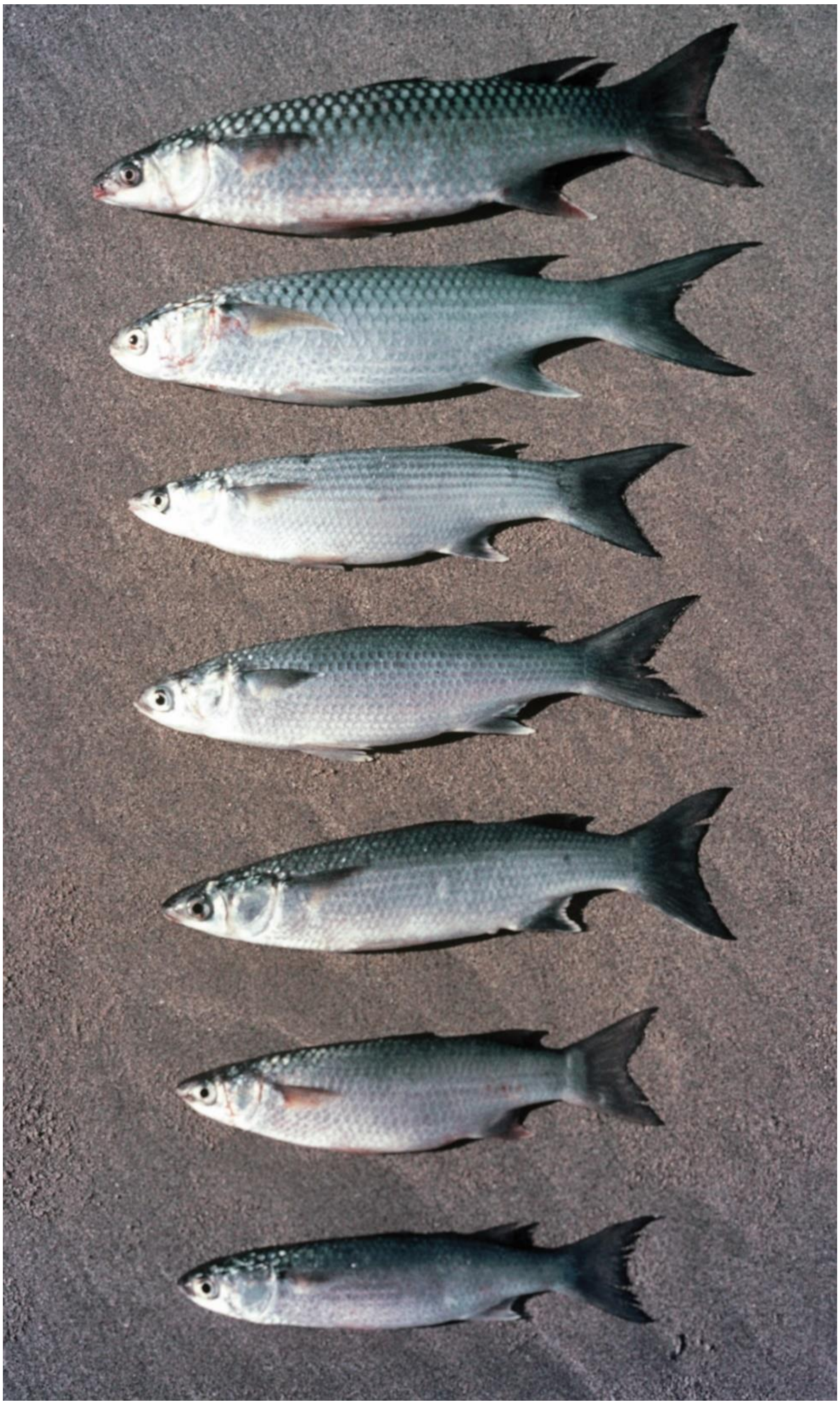

Figure 5. Seven mullet species captured in a single overnight gill net from the subtropical Msikaba Estuary on the South African south-east coast, illustrating the species richness and relative morphological conformity between species in this mugilid hotspot. From top to bottom the species are *Planiliza alata*, *Crenimugil buchanani*, *Chelon tricuspidens*, *Mugil cephalus*, *Pseudomyxus capensis*, *Planiliza macrolepis* and *Osteomugil robustus* (Photograph: © Alan Whitfield).

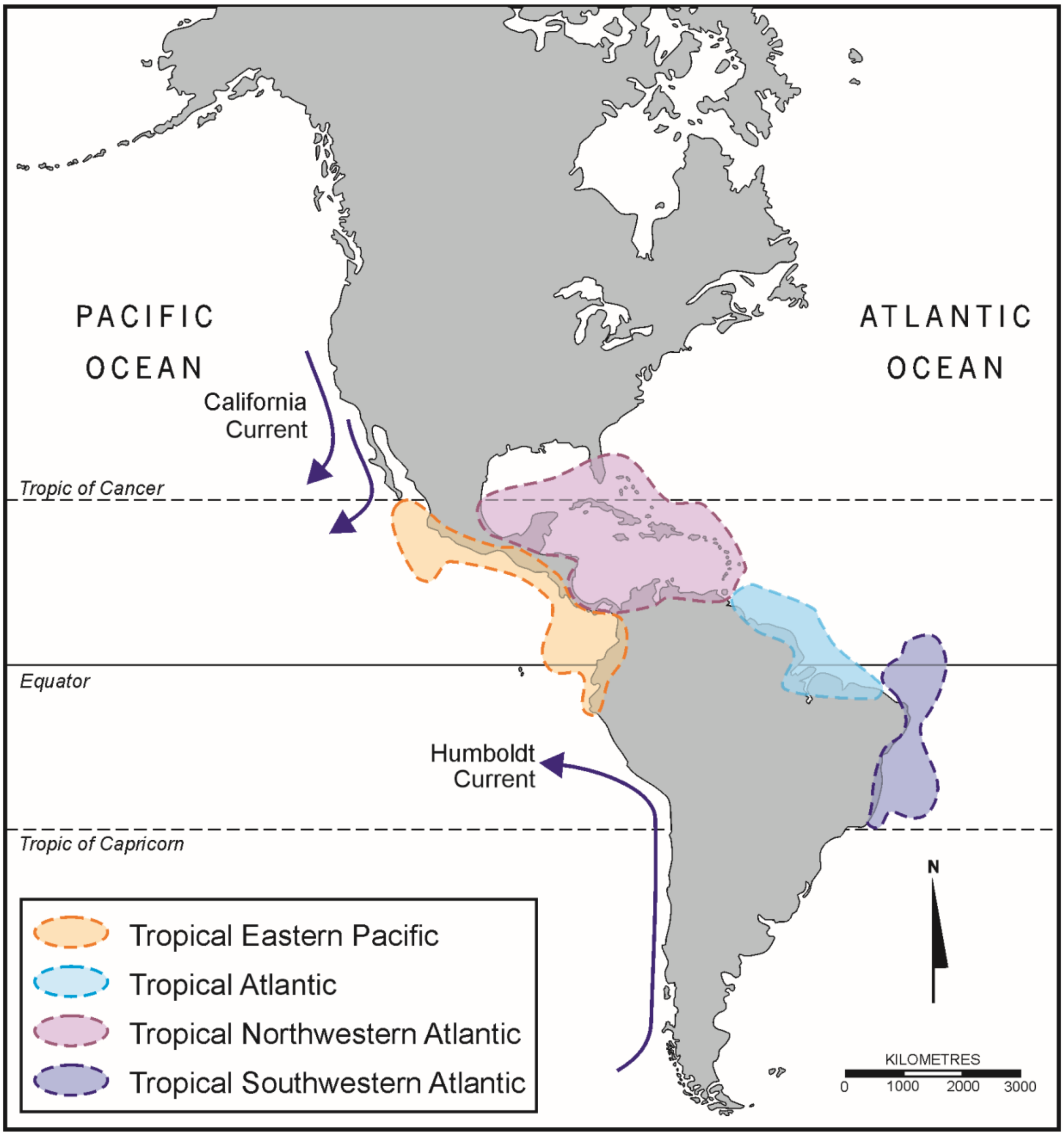

Figure 6. Primary tropical and temperate marine provinces along the east and west coasts of North, Central and South America (modified from Barletta & Dantas 2016).

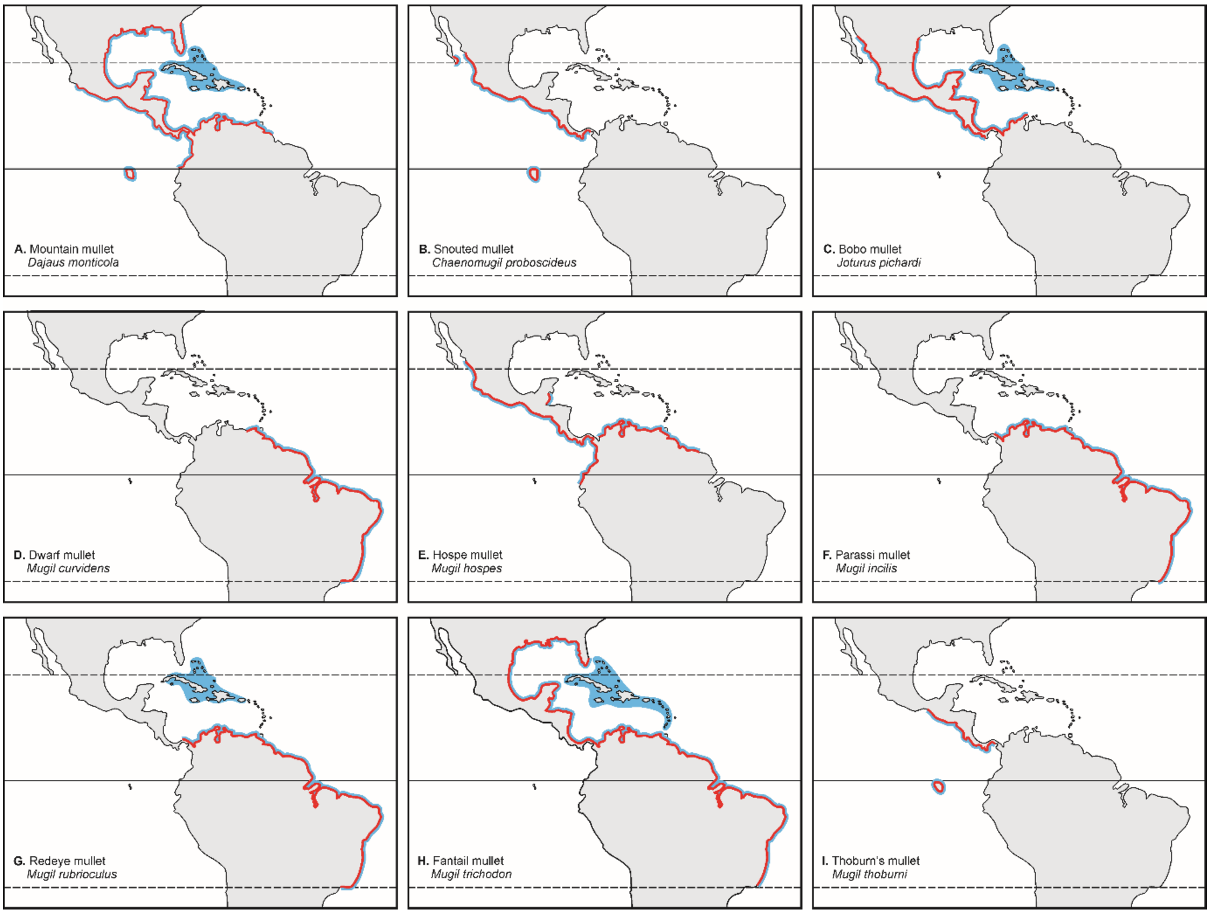

Figure 7. Biogeographic distribution of nine selected tropical mugilid species from America; A. Mountain mullet *Dajaus monticola*, B. Snouted mullet *Chaenomugil proboscideus*, C. Bobo mullet *Joturus pichardi*, D. Dwarf mullet *Mugil curvidens*, E. Hospe mullet *Mugil hospes*, F. Parassi mullet *Mugil incilis*, G. Redeye mullet *Mugil rubrioculus*, H. Fantail mullet *Mugil trichodon*, I. Thoburn's mullet *Mugil thoburni* (after Barletta & Dantas 2016).

Table 1. Mugilid species recorded in association with African coasts (information from Durand & Whitfield 2016, Thieme et al. 2022).

Mugilid species	**Common name**	**Biogeographic distribution**
Agonostomus catalai	Comoro mullet	Tropical
Agonostomus telfairii	Fairy mullet	Tropical
Chelon auratus	Golden mullet	Tropical, Subtropical, Temperate
Chelon bandialensis	Diassanga mullet	Tropical
Chelon bispinosus	Cape Verde mullet	Tropical
Chelon dumerili	Grooved mullet	Tropical, Subtropical, Temperate
Chelon labrosus	Thicklip mullet	Tropical, Subtropical, Temperate
Chelon persicus	Persian mullet	Tropical, Subtropical
Chelon ramada	Thinlip mullet	Temperate, Subtropical
Chelon richardsonii	Southern mullet	Temperate
Chelon saliens	Leaping mullet	Temperate, Subtropical
Chelon tricuspidens	Striped mullet	Temperate, Subtropical, Tropical
Crenimugil buchanani	Bluetail mullet	Tropical, Subtropical
Crenimugil crenilabis	Fringelip mullet	Tropical, Subtropical
Crenimugil seheli	Bluespot mullet	Tropical, Subtropical
Ellochelon vaigiensis	Squaretail mullet	Tropical
Mugil bananensis	Banana mullet	Tropical
Mugil capurrii	Leaping African mullet	Tropical, Subtropical
Mugil cephalus	Flathead mullet	Tropical, Subtropical, Temperate
Mugil curema	White mullet	Tropical, Subtropical
Neochelon falcipinnis	Sicklefin mullet	Tropical
Osteomugil cunnesius	Longarm mullet	Tropical, Subtropical
Osteomugil robustus	Robust mullet	Tropical, Subtropical
Parachelon grandisquamis	Largescaled mullet	Tropical
Planiliza alata	Diamond mullet	Tropical, Subtropical
Planiliza carinata	Keeled mullet	Tropical, Subtropical
Planiliza macrolepis	Largescale mullet	Tropical, Subtropical
Planiliza melinoptera	Giantscale mullet	Tropical, Subtropical

Planiliza subviridis	Greenback mullet	Tropical, Subtropical
Pseudomyxus capensis	Freshwater mullet	Temperate, Subtropical

Table 2. Mugilid species recorded in association with American coasts (information from Barletta & Dantas 2016).

Mugilid species	Common name	Biogeographic distribution
Dajaus monticola	Mountain mullet	Tropical, Subtropical
Chaenomugil proboscideus	Snouted mullet	Tropical, Subtropical
Joturus pichardi	Bobo mullet	Tropical, Subtropical
Mugil brevirostris	Ribeiro’s mullet	Tropical, Subtropical
Mugil cephalus	Flathead mullet	Tropical, Subtropical, Temperate
Mugil curvidens	Dwarf mullet	Tropical
Mugil curema	White mullet	Tropical, Subtropical, Temperate
Mugil hospes	Hospe mullet	Tropical, Subtropical
Mugil incilis	Parassi mullet	Topical, Subtropical
Mugil liza	Lebranche mullet	Tropical, Subtropical, Temperate
Mugil margaritae	Menezes’ mullet	Tropical
Mugil rubrioculus	Redeye mullet	Tropical, Subtropical
Mugil setosus	Liseta mullet	Tropical, Subtropical
Mugil trichodon	Fantail mullet	Tropical, Subtropical
Mugil thoburni	Thoburn’s mullet	Tropical

Table 3. Mugilid species recorded in association with the Mediterranean, Black Sea and north-eastern Atlantic coast, including the introduced *Planiliza haematocheilus* and Lessepesian species *Planiliza carinata* (information from Turan 2016).

Mugilid species	**Common name**	**Biogeographic distribution**
Chelon auratus	Golden mullet	Tropical, Subtropical, Temperate
Chelon labrosus	Thicklip mullet	Tropical, Subtropical, Temperate
Chelon ramada	Thinlip mullet	Temperate, Subtropical
Chelon saliens	Leaping mullet	Temperate, Subtropical
Mugil cephalus	Flathead mullet	Tropical, Subtropical, Temperate
Planiliza carinata	Keeled mullet	Tropical, Subtropical
Planiliza haematocheilus	So-iuy	Temperate, Subtropical
Oedalechilus labeo	boxlip mullet	Temperate

Table 4. Mugilid species recorded in association with the Asian coast (information from Shen & Durand 2016).

Mugilid species	**Common name**	**Biogeographic distribution**
Cestraeus goldiei	Goldie river mullet	Tropical
Cestraeus oxyrhrynchus	Sharp-nosed river mullet	Tropical
Cestraeus plicatilis	Lobed river mullet	Tropical
Crenimugil buchanani	Bluetail mullet	Tropical, Subtropical
Crenimugil crenilabis	Fringelip mullet	Tropical, Subtropical
Crenimugil heterocheilos	Half fringelip mullet	Tropical
Crenimugil seheli	Bluespot mullet	Tropical, Subtropical
Ellochelon vaigiensis	Squaretail mullet	Tropical, Subtropical, Temperate
Mugil broussonnetii	Broussonnet's mullet	Tropical, subtropical
Mugil cephalus	Flathead mullet	Tropical, Subtropical, Temperate
Minimugil cascasia	Yellowtail mullet	Tropical, Subtropical
Osteomugil cunnesius	Longarm mullet	Tropical, Subtropical
Osteomugil engeli	Kanda	Tropical, Subtropical
Osteomugil perusii	Longfinned mullet	Tropical, Subtropical
Osteomugil speigleri	Speigleri's mullet	Tropical
Paramugil parmatus	Broad-mouthed mullet	Tropical
Planiliza haematocheilus	So-iuy	Temperate, Subtropical
Planiliza klunzingeri	Klunzinger's mullet	Tropical, Subtropical
Planiliza lauvergnii	Eastern keeled back mullet	Tropical, Subtropical
Planiliza macrolepis	Largescale mullet	Tropical, Subtropical
Planiliza melinoptera	Giantscale mullet	Tropical, Subtropical
Planiliza parsia	Goldspot mullet	Tropical, Subtropical
Planiliza subviridis	Greenback mullet	Tropical, Subtropical
Planiliza tade	Fabricius' mullet	Tropical, Subtropical
Plicomugil labiosus	Hornlip mullet	Tropical, Subtropical
Rhinomugil corsula	Corsula	Tropical
Squalomugil nasutus	Shark mullet	Tropical
Sicamugil hamiltonii	Burmese mullet	Tropical

Table 5. Mugilid species recorded in association with Australia/Oceania coasts (information from Ghasemzadeh 2016).

Mugilid species	**Common name**	**Biogeographic distribution**
Aldrichetta forsteri	Yellow-eye mullet	Subtropical, Temperate
Cestraeus oxyrhrynchus	Sharp-nosed river mullet	Tropical
Cestraeus plicatilis	Lobed river mullet	Tropical
Crenimugil buchanani	Bluetail mullet	Tropical, Subtropical
Crenimugil crenilabis	Fringelip mullet	Tropical, Subtropical
Crenimugil heterocheilos	Half fringelip mullet	Tropical
Crenimugil seheli	Bluespot mullet	Tropical, Subtropical
Ellochelon vaigiensis	Squaretail mullet	Tropical, Subtropical, Temperate
Gracilimugil argenteus	Flat-tail mullet	Temperate, Subtropical
Mugil cephalus	Flathead mullet	Tropical, Subtropical, Temperate
Myxus elongatus	Sand grey mullet	Temperate
Neomyxus leuciscus	Acute-jawed mullet	Tropical, Subtropical
Osteomugil cunnesius	Longarm mullet	Tropical, Subtropical
Osteomugil engeli	Kanda	Tropical, Subtropical
Osteomugil perusii	Longfinned mullet	Tropical, Subtropical
Osteomugil speigleri	Speigleri's mullet	Tropical
Paramugil georgii	Silver mullet	Tropical, Subtropical, Temperate
Paramugil parmatus	Broad-mouthed mullet	Tropical
Planiliza alata	Diamond mullet	Tropical, Subtropical
Planiliza macrolepis	Largescale mullet	Tropical, Subtropical
Planiliza melinoptera	Giantscale mullet	Tropical, Subtropical
Planiliza subviridis	Greenback mullet	Tropical, Subtropical
Planiliza tade	Fabricius' mullet	Tropical, Subtropical
Plicomugil labiosus	Hornlip mullet	Tropical, Subtropical
Squalomugil nasutus	Shark mullet	Tropical
Trachystoma petardi	Pinkeye mullet	Subtropical, Temperate

Table 6. Mugilid species richness in 62 coastal marine provinces around the world (for details see Figure 2b and Box 1 in Spalding et al. 2007). Mullet species distribution patterns were primarily extracted from Barletta & Dantas (2016), Durand & Whitfield (2016), Ghasemzadeh (2016), Shen & Durand (2016), Thieme et al. (2022) and Turan (2016). Additional material on mugilid species occurrences in different regions was obtained from Fukuchi & Tachihara (2020)[1], Wirtz[2], Trape & Durand (2011)[3], Golani & Fricke (2018)[4], Zajonz (2019)[5], Satapoomin (2011)[6], Larson et al. (2013)[7], Bray (2018)[8], Francis (2022)[9], Siu et al. (2017)[10]. Translocated or non-native mugilid species in a particular region were not considered in the calculation of provincial species richness.

Marine provinces	**Mugilid species**	**Total number**
1. Arctic		
2. Northern European Seas	*Chelon auratus, Chelon labrosus, Chelon ramada, Chelon saliens, Mugil cephalus*	5
3. Lusitanean	*Chelon auratus, Chelon labrosus, Mugil capurrii, Chelon ramada, Chelon saliens, Mugil cephalus, Oedalechilus labeo*	7
4. Mediterranean Sea	*Chelon auratus, Chelon labrosus, Chelon ramada, Chelon saliens, Mugil cephalus, Oedalechilus labeo*	6
5. Cold Temperate Northwest Atlantic	*Mugil curema*	1
6. Warm Temperate Northwest Atlantic	*Dajaus monticola, Mugil cephalus, Mugil curema, Mugil trichodon*	4
7. Black Sea	*Chelon auratus, Chelon labrosus, Chelon ramada, Chelon saliens, Mugil cephalus*	5
8. Cold Temperate Northwest Pacific	*Mugil cephalus, Planiliza haematocheilus, Planiliza macrolepis, Planiliza lauvergnii*	4
9. Warm Temperate Northwest Pacific	*Crenimugil buchanani, Crenimugil heterocheilos*[1]*, Crenimugil crenilabis, Crenimugil seheli, Ellochelon vaigiensis, Osteomugil cunnesius, Osteomugil perusii, Osteomugil engeli, Planiliza macrolepis, Planiliza melinoptera, Planiliza subviridis, Planiliza lauvergnii, Planiliza haematocheilus, Plicomugil labiosus*	13
10. Cold Temperate Northeast Pacific	*Mugil cephalus*	1
11. Warm Temperate Northeast Pacific	*Mugil cephalus, Mugil curema*	2
12. Tropical Northwestern Atlantic	*Dajaus monticola, Joturus pichardi, Mugil cephalus, Mugil curema, Mugil curvidens, Mugil hospes, Mugil incilis, Mugil liza, Mugil margaritae, Mugil rubrioculus, Mugil trichodon*	11
13. North Brazil Shelf	*Dajaus monticola, Mugil brevirostris, Mugil curema, Mugil curvidens, Mugil hospes, Mugil incilis, Mugil liza, Mugil rubrioculus, Mugil trichodon, Mugil trichodon*	10
14. Tropical Southwestern Atlantic	*Mugil brevirostris, Mugil curema, Mugil curvidens, Mugil incilis, Mugil liza, Mugil rubrioculus, Mugil trichodon*	7
15. St Helena and Ascension Islands	*Mugil curvidens*[2]	1
16. West African Transition[3]	*Chelon aurata, Chelon bispinosus, Chelon labrosus, Mugil bananensis, Mugil curema, Mugil capurrii, Mugil cephalus*	7

17. Gulf of Guinea	*Mugil bananensis, Mugil capurrii*[3]*, Mugil curema, Mugil cephalus, Neochelon falcipinnis, Parachelon grandisquamis, Chelon dumerili,*	7
18. Red Sea and Gulf of Aden[4,5]	*Crenimugil buchanani, Crenimugil crenilabis, Crenimugil seheli, Chelon persicus, Mugil cephalus, Planiliza carinata, Planiliza subviridis, Planiliza macrolepis, Planiliza melinoptera, Planiliza tade, Plicomugil labiosus, Osteomugil cunnesius, Osteomugil speigleiri*	13
19. Somali/Arabian	*Chelon persicus, Crenimugil crenilabis, Crenimugil seheli, Planiliza klunzingerii, Planiliza subviridis, Planiliza macrolepis, Planiliza melinoptera, Planiliza tade, Mugil cephalus, Osteomugil cunnesius, Ellochelon vaigiensis, Planiliza abu*	12
20. Western Indian Ocean	*Chelon dumerili, Chelon persicus, Mugil cephalus, Crenimugil buchanani, Crenimugil crenilabis, Crenimugil seheli, Ellochelon vaigiensis, Osteomugil cunnesius, Osteomugil robustus, Planiliza alata, Planiliza macrolepis, Planiliza melinoptera, Agonostomus telfairii, Agonostomus catalai*	14
21. West and South Indian Shelf	*Crenimugil buchanani, Crenimugil crenilabis, Crenimugil seheli, Ellochelon vaigiensis, Mugil cephalus, Minimugil cascasia, Osteomugil cunnesius, Osteomugil perusii, Osteomugil speigleri, Planiliza klunzingeri, Planiliza macrolepis, Planiliza subviridis, Planiliza tade, Planiliza parsia, Planiliza mandapamensis, Planiliza melinoptera, Plicomugil labiosus, Rhinomugil corsula*	18
22. Central Indian Ocean Islands	*Crenimugil crenilabis, Crenimugil seheli, Ellochelon vaigiensis, Mugil cephalus, Planiliza macrolepis, Planiliza subviridis, Plicomugil labiosus*	7
23. Bay of Bengal	*Crenimugil buchanani, Crenimugil crenilabis, Crenimugil seheli, Ellochelon vaigiensis, Osteomugil cunnesius, Osteomugil engeli, Osteomugil perusii, Osteomugil speigleri, Planiliza parsia, Planiliza macrolepis, Planiliza subviridis, Planiliza tade, Planiliza melinoptera, Plicomugil labiosus, Rhinomugil corsula, Sicamugil hamiltonii, Minimugil cascasia*	17
24. Andaman[6]	*Crenimugil buchanani, Crenimugil crenilabis, Crenimugil seheli, Ellochelon vaigiensis, Osteomugil cunnesius, Osteomugil perusii, Planiliza macrolepis, Planiliza parsia, Planiliza subviridis, Paramugil parmatus, Plicomugil labiosus*	11
25. South China Sea	*Crenimugil buchanani, Crenimugil crenilabis, Crenimugil seheli, Ellochelon vaigiensis, Mugil cephalus, Osteomugil cunnesius, Osteomugil engeli, Osteomugil perusii, Osteomugil speigleri, Planiliza haematocheila, Planiliza lauvergnii, Planiliza macrolepis, Planiliza melinoptera, Planiliza subviridis, Planiliza tade, Plicomugil labiosus*	16
26. Sunda Shelf	*Crenimugil buchanani, Cestraeus goldei, Cestraeus oxyrhynchus, Crenimugil crenilabis, Crenimugil seheli, Mugil cephalus, Ellochelon vaigiensis, Osteomugil cunnesius, Osteomugil engeli, Osteomugil perusii, Osteomugil speigleri, Paramugil parmatus, Planiliza macrolepis, Planiliza melinoptera, Planiliza subviridis, Planiliza tade, Plicomugil labiosus*	17

27. Java Transitional	*Crenimugil buchanani, Crenimugil crenilabis, Crenimugil seheli, Ellochelon vaigiensis, Osteomugil cunnesius, Osteomugil engeli, Osteomugil perusii, Osteomugil speigleri, Paramugil parmatus, Planiliza macrolepis, Planiliza melinoptera, Planiliza subviridis, Planiliza tade, Plicomugil labiosus*	14
28. South Kuroshio	*Crenimugil buchanani, Crenimugil heterocheilos*[1]*, Crenimugil crenilabis, Crenimugil seheli, Ellochelon vaigiensis, Osteomugil cunnesius, Osteomugil perusii, Osteomugil engeli, Planiliza macrolepis, Planiliza melinoptera, Planiliza subviridis, Planiliza lauvergnii, haematocheilus, Plicomugil labiosus*	13
29. Tropical Northwestern Indo-Pacific	*Crenimugil crenilabis, Ellochelon vaigiensis, Osteomugil engeli, Osteomugil seheli, Mugil cephalus, Neomyxus leuciscus, Planiliza macrolepis, Plicomugil labiosus, Osteomugil cunnesius, Osteomugil engeli*	10
30. Western Coral Triangle	*Cestraeus goldiei, Cestraeus oxyrhynchus, Cestraeus plicatilis, Planiliza melinoptera, Crenimugil buchanani, Crenimugil crenilabis, Crenimugil seheli, Ellochelon vaigiensis, Mugil broussonnetii, Osteomugil cunnesius, Osteomugil engeli, Osteomugil perusii, Osteomugil speigleri, Paramugil parmatus, Planiliza macrolepis, Planiliza subviridis, Planiliza tade, Plicomugil labiosus*	18
31. Eastern Coral Triangle	*Cestraeus oxyrhynchus, Cestraeus plicatilis, Planiliza melinoptera, Crenimugil buchanani, Crenimugil crenilabis, Crenimugil heterocheilos, Crenimugil seheli, Ellochelon vaigiensis, Mugil cephalus, Osteomugil speigleri, Paramugil georgii, Paramugil parmatus, Planiliza tade, Planiliza macrolepis, Planiliza subviridis, Plicomugil labiosus, Squalomugil nasutus*	17
32. Sahul Shelf[7]	*Crenimugil buchanani, Crenimugil seheli, Ellochelon vaigiensis, Squalomugil nasutus, Osteomugil engeli, Osteomugil perusii, Osteomugil cunnesius, Paramugil parmata, Paramugil georgii, Planiliza ordensis, Planiliza macrolepis, Planiliza melinoptera, Planiliza tade, Planiliza subviridis, Plicomugil labiosus, Squalomugil nasutus*	16
33. Northeast Australian Shelf	*Crenimugil crenilabis, Crenimugil buchanani, Crenimugil heterocheilos*[8]*, Crenimugil seheli, Ellochelon vaigiensis, Gracilimugil argentea, Mugil cephalus, Osteomugil cf. cunnesius, Osteomugil engeli, Paramugil georgii, Planiliza macrolepis, Planiliza melinoptera, Planiliza ordensis, Planiliza tade, Planiliza subviridis, Squalomugil nasutus*	16
34. Northwest Australian Shelf	*Crenimugil buchanani, Crenimugil seheli, Ellochelon vaigiensis, Mugil cephalus, Osteomugil cunnesius, Osteomugil perusii, Paramugil georgii, Planiliza ordensis, Planiliza melinoptera, Planiliza tade, Planiliza subviridis, Squalomugil nasutus*	12
35. Tropical Southwestern Pacific	*Cestraeus oxyrhyncus, Cestraeus plicatilis, Crenimugil buchanani, Crenimugil crenilabis, Crenimugil seheli, Ellochelon vaigiensis, Mugil cephalus, Osteomugil cunnesius, Osteomugil perusii, Planiliza macrolepis, Planiliza melinoptera, Planiliza subviridis, Plicomugil labiosus*	13
36. Lord Howe and Norfolk Islands[9]	*Crenimugil crenilabis, Crenimugil seheli, Mugil cephalus, Myxus elongatus*	4
37. Hawaii	*Mugil cephalus, Neomyxus leuciscus, Osteomugil engeli*	3

38. Marshall, Gilbert and Ellis Islands	*Mugil cephalus, Neomyxus leuciscus, Crenimugil crenilabis, Crenimugil seheli, Osteomugil cunnesius, Osteomugil engeli, Planiliza macrolepis, Planiliza subviridis*	8
39. Central Polynesia[10]	*Ellochelon vaigiensis, Mugil cephalus, Neomyxus leuciscus, Crenimugil crenilabis, Osteomugil engeli, Planiliza macrolepis*	6
40. Southeast Polynesia[10]	*Neomyxus leuciscus, Crenimugil crenilabis, Osteomugil engeli, Ellochelon vaigiensis, Mugil cephalus*	5
41. Marquesas	*Neomyxus leuciscus, Crenimugil crenilabis, Crenimugil seheli, Osteomugil engeli, Planiliza macrolepis, Planiliza melinoptera, Planiliza alata*	7
42. Easter Island	*Crenimugil crenilabis*	1
43. Tropical East Pacific	*Dajaus monticola*, *Chaenomugil proboscideus*, *Joturus pichardi*, *Mugil cephalus*, *Mugil curema*, *Mugil hospes*, *Mugil setosus*, *Mugil thoburni*	8
44. Galapagos	*Chaenomugil proboscideus*, *Mugil galapagensis*, *Mugil thoburni*	3
45. Warm Temperate Southeastern Pacific	*Mugil cephalus*, *Mugil curema*	2
46. Juan Fernández and Desventuradas	*Mugil curema*	1
47. Warm Temperate Southwestern Atlantic	*Mugil brevirostris*, *Mugil curema*, *Mugil liza*	3
48. Magellanic		
49. Tristan Gough		
50. Benguela	*Chelon richardsonii*, *Chelon tricuspidens*, *Pseudomyxus capensis*, *Mugil cephalus*,	4
51. Agulhas	*Chelon richardsonii*, *Chelon dumerili*, *Chelon persicus*, *Chelon tricuspidens*, *Crenimugil buchanani*, *Crenimugil crenilabis*, *Crenimugil seheli*, *Ellochelon vaigiensis*, *Pseudomyxus capensis*, *Mugil cephalus*, *Osteomugil cunnesius*, *Osteomugil robustus*, *Planiliza alata*, *Planiliza macrolepis*, *Planiliza melinoptera*, *Planiliza subviridis*	16
52. Amsterdam-St Paul		
53. Northern New Zealand	*Mugil cephalus, Aldrichetta forsteri*	2
54. Southern New Zealand	*Mugil cephalus, Aldrichetta forsteri*	2
55. East Central Australian Shelf	*Aldrichetta forsteri*, *Crenimugil buchanani, Crenimugil seheli, Gracimugil argenteus, Mugil cephalus, Myxus elongatus*, *Osteomugil cf. cunnesius*, *Plicomugil labiosus, Planiliza subviridis, Trachystoma petardi*	10
56. Southeast Australian Shelf	*Aldrichetta forsteri*, *Gracimugil argenteus, Mugil cephalus, Myxus elongatus*	4
57. Southwest Australian Shelf	*Aldrichetta forsteri*, *Gracimugil argenteus, Ellochelon vaigiensis, Mugil cephalus, Myxus elongatus, Trachystoma petardi*	6
58. West Central Australian Shelf	*Aldrichetta forsteri*, *Ellochelon vaigiensis*, *Mugil cephalus*, *Myxus elongatus*, *Osteomugil perusii*	5
59. Subantarctic Islands		
60. Scotia Sea		

61. Continental High Antarctic		
62. Subantarctic New Zealand		