Will the High Biodiversity of Eels in the Coral Triangle be Affected by Climate Change?

M J Miller*1, S Wouthuyzen2, J Aoyama3, H Y Sugeha2, S Watanabe4, M Kuroki1, A Syahailatua2, S Suharti2, S Hagihara5, F Y Tantu6, Trianto2, T Otake1, K Tsukamoto1

1 Department of Aquatic Bioscience, Graduate School of Agricultural and Life Sciences, The University of Tokyo, 1-1-1, Yayoi, Bunkyo, Tokyo 113-8657, JAPAN
2 Research Centre for Oceanography, Indonesian Institute of Sciences, Jl. Pasir Putih I, Ancol Timur, Jakarta 14430, INDONESIA
3 International Coastal Research Center, Atmosphere and Ocean Research Institute, The University of Tokyo, Akahama, Otsuchi, Iwate 028-1102, JAPAN
4 Department of Fisheries, Faculty of Agriculture, Kindai University 3327-204 Nakamachi, Nara, 631-8505, JAPAN
5 Atmosphere and Ocean Research Institute, the University of Tokyo, 5-1-5 Kashiwanoha, Kashiwa, Chiba 277-8564, JAPAN
6 Department of Aquaculture, Faculty of Animal Husbandry and Fishery, Tadulako University, Jalan Soekarno-Hatta Km 9, Kampus UNTAD Tondo, 94118 Palu, INDONESIA
7 Research Centre for Limnology, Indonesian Institute of Sciences, Jl. Raya Bogor Km. 46 Cibinong, West Java 16911, INDONESIA

*Corresponding author: michael.miller@marine.fs.a.u-tokyo.ac.jp

Abstract. The Indonesian Seas are at the center of the Coral Triangle, which has the highest marine biodiversity in the world, and the region is under threat from climate change. Freshwater habitats in the region have a high number of anguillid eels compared to other regions of the world, but it is more difficult to capture marine eels to assess their biodiversity. Catches of leptocephali from 5 internationally collaborative surveys for eel larvae (leptocephali) in the Coral Triangle have collected about 126-169 species of larvae, which indicates that the Coral Triangle region likely has the highest marine eel biodiversity in the world based on comparisons to similar larval surveys in the Indian, Pacific, and Atlantic oceans (29-107 species). These marine eel species inhabit a wide range of benthic and pelagic habitats, but how they might be affected by climate changes such as ocean warming has not been considered. Anguillid eels in the Coral Triangle region could be affected mainly by changes in rainfall patterns that could affect their freshwater growth stage or their reproductive maturation patterns and migration. Effects on marine eels would depend on the types of habitats where they live, with the least impacts occurring for deep benthic or pelagic species. Marine eels that live in shallow habitats would be most affected if warming seas and coral bleaching reduce the types of prey species they depend on. Based on their possible association with coral reef habitats, eels of the families Muraenidae and Chlopsidae appear to the most likely types of eels to be impacted by changes in community structure resulting from coral bleaching. All leptocephali species live in the ocean surface layer where they feed on marine snow, so warmer
ocean temperatures might reduce the amount or quality of marine snow that is available, resulting in lower larval survival rates. Further studies on eel biodiversity and habitat use will provide more insight into the possible loss of endemic species in the Coral Triangle due to climate change, but presently it is unclear how many species of eels may be directly affected by climate change.

1. **Introduction**

The region referred to as the “Coral Triangle” has the highest marine biodiversity in the world because of the presence of high species richness for most types of marine animals [1], including coral reef and coastal marine fishes, and other species [2-5]. The Coral Triangle also appears to have the highest biodiversity of marine eels in the world, based on sampling surveys for eel larvae[6-8] in the waters of the Indonesian Archipelago [9,10]. Figure 1 shows how coral reefs are widely present across most areas of the Coral Triangle, as can also be seen in maps of the coral reefs of the region [11]. This region includes several countries and the marine resources are of great economic importance [12], so impacts from climate change are a critical concern [13,14]

The Indonesian Seas form the central region of the Coral Triangle, and the waters around the 18,000 islands of Indonesia have at least 10,850 species of marine algae, mangroves, and other organisms [15] These diverse habitats of Indonesia include at least 2057 species of coral reef fishes belonging to 113 families compared to about 4000 species of fishes in the entire Indo-Pacific region [16]. Figure 2 shows imagery of two regions that may have particularly high biodiversity that include the Togian Islands, which have some genetically distinct populations [17-20], but are under pressure from fishing [21,22], and the Banggai Islands that also have distinctive atolls and fringing reefs. Both areas have been assessed for their species compositions and biodiversity [23,24].

![Figure 1](http://ctatlas.reefbase.org/mapgallery.aspx)

**Figure 1.** Map of the Coral Triangle region (from Philippines to eastern Java and east to the Solomon Islands off the map) that shows bathymetry (dark: deep, light: shallow) and coral reef areas (red color). The square over northern Sulawesi Island shows the area shown in figure 2. Bathymetry imagery was obtained from the NOAA Marine Geology and Geophysics Center. The coral reef location imagery was modified from maps obtained from The Coral Triangle Atlas and then overlaid on the bathymetry map [25] (http://ctatlas.reefbase.org/mapgallery.aspx).

Although coral reef habitats and their biodiversity and fisheries attract the most attention in the Coral Triangle, this region may also be important for having the highest biodiversity of eels of the Anguilliformes. These species include the highest number of catadromous anguillid eels of the genus *Anguilla* to be found in one region, which have various distributions and life history characteristics
Some species such as Anguilla bornensis and A. celebesensis have relatively limited geographic ranges of distribution compared to others, such as A. marmorata, the two subspecies A. bicolor bicolor and A. bicolor pacifica, and A. interioris that have wider distribution areas [28]. These anguillid species live in the freshwater rivers and lakes of the region during their yellow eel stage, and some appear to use estuarine areas [29,30]. When they reach maturity the silver eels migrate downstream into the ocean and begin their oceanic spawning migrations. Species such as A. bornensis, A. celebesensis, and A. interioris, spawn locally after a short spawning migration [27], but A. marmorata migrate to the north to spawn in the North Equatorial Current region, where the Japanese eel, A. japonica, also spawns [31]. The seasonality of when anguillid eels begin their maturation and make their spawning migrations may be related to the occurrence of rainy seasons, which can differ among areas of Indonesia [26,32].

Although there are only 6 freshwater eel species living in the Indonesian Seas region and 19 total species and subspecies in the world [33], there are almost 1000 marine eel species worldwide [34], and a rich fauna of at least 118 documented species of marine eels are present in Indonesian waters [16]. Unlike freshwater eels, which use a limited range of habitats, marine eels have diversified to live from shallow water to deep in the ocean. Some families live in coastal or continental shelf habitats, some live deeper on the continental slope and benthic environments down to about 5000 m, and others live in the mid-water meso- and bathy- pelagic zones of the ocean [35]. However, their leptocephalus larvae all mix together in the upper few hundred meters of the ocean [36]. Most leptocephali are found primarily in the upper 100 m at night [36-38] and some move deeper during the day [36,39].

Figure 2. Images of the Togian Islands (a-c) that are located inside Tomini Bay of Sulawesi Island (upper rectangle in d), and images of some coastal areas (e) of the Banggai Islands (lower rectangle in d) and nearby reef atolls (f-h). The rectangles in (c) show the locations of the enlarged images (a,b).

Leptocephali can be easily collected when large plankton nets are fished at night, but in contrast, marine eels in coastal and continental shelf habitats are typically nocturnal and fossorial, which makes them difficult to observe or collect. Therefore, it is possible that the diversity of eel species, such as of moray eels (Muraenidae) and false moray eels (Chlopsidae) that live in coral reef and other habitats
have been underestimated in visual surveys of fish diversity or normal types of fish collections. This is also likely to be true for other eel species such as ophichthids (Ophichthidae), congrids (Congridae) and moringuids (Moringuidae) that burrow in soft sediments [7,35] and this is supported by greater numbers of eel species being suggested to be present based on surveys for leptocephali [9,10] than are known from surveys for fishes. Part of this discrepancy is likely due to some types of eels only being able to be collected by invasive methods, such as ichthyocide sampling that are not frequently used in recent years.

The larval surveys in the Indonesian Seas (figure 3) have collected higher numbers of species of leptocephali than those in other parts of the world, but this has not been carefully compared. There have been surveys for leptocephali in coastal Japan [40,41], the East China Sea [42], the Indonesian Seas [9,10], in the Indian Ocean off Sumatra [43-45] and east of Madagascar [46], in the western South Pacific [46], and in the Atlantic Ocean Sargasso Sea region [48-50], the Gulf of Mexico [39,51] and other Atlantic regions [52-55] that can be compared for their taxonomic compositions.

It has been hypothesized that the larval survival rate of anguillid eels might be influenced by changes in productivity associated with ocean-atmosphere changes [56,57] or that rainfall changes might affect the downstream migration of silver eels in continental waters [58], but how marine eels might be affected by factors such as coral bleaching [59] has not yet been considered.

The present paper is designed to evaluate the numbers of species of leptocephali that have been collected in the Indonesian Seas region of the Coral Triangle in comparison to other areas of the world and to make a first assessment of how the apparently high biodiversity of eels that is indicated by the larval surveys in the Coral Triangle might be affected by climate change. What effects climate change might have on anguillid eels living in freshwater is also considered. Marine eels consist of a wide range of taxonomic groups that utilize different habitats and depths, so the objective of this overview of subjects related to eels and climate change is to outline the various factors involved with considering climate change and eel biodiversity.

Figure 3. Maps of the IKMT sampling stations (red circles) for collecting leptocephali during the 5 surveys of BJ-01-1 in 2001 (a), KH-02-4 in 2002 (b, upper), BJ-02-2 in 2002 (c, right), BJ-03-2 in 2003 (c, left), Leg 7 of KH-09-5 in 2010 (b, lower). The surveys were conducted by the R/V Baruna Jaya VII (BJ) of LIPI, Indonesia, and by the R/V Hakuho Maru (KH) of JAMSTEC, Japan.
2. Materials and Methods

Some of the data on the biodiversity of leptocephali in the Indonesian Seas and off west Sumatra were obtained during 3 cruises conducted by the R/V *Baruna Jaya VII* of the Research Center for Oceanography of the Indonesian Institute of Sciences (LIPI) (figure 3). Those 3 surveys used an 8.7 m² mouth opening Isaacs-Kidd Midwater trawl (IKMT) with 0.5 mm mesh. The first 2 surveys sampled at stations distributed at various locations mostly around Sulawesi Island, including in Tomini Bay in May 2001 [9,60] and in Sept-Oct 2002 [61]. In June 2003, a survey was conducted off west Sumatra [61]. All 3 surveys of the *Baruna Jaya VII* deployed the IKMT in the same way that consisted of both an oblique and a step tow being conducted at each station, usually with 2 stations being sampled each night, with no sampling during the day as described previously.

Two cruises were also conducted by the R/V *Hahuho Maru* of JAMSTEC in Japan that consisted of IKMT sampling mostly in the northern Celebes Sea and in the Sulu Sea in November 2002 and sampling in the Celebes Sea and in Tomini Bay in March 2010 (figure 3) [10,27]. The 2002 Sulu Sea survey deployed the IKMT at one station each night using single oblique tows that mostly fished in the upper 150 m. The 2010 survey fished the IKMT in various styles during night and day as described previously [10].

During all surveys of both the *Baruna Jaya VII* and the *Hakuho Maru*, the same onboard processing and identification of leptocephali were used. The larvae were first sorted fresh out of the IKMT plankton samples and held in cold seawater before being measured to the nearest 1 mm total length (TL) and identified to the lowest possible taxonomic level using various resources [7,63,64]. Unlike in areas such as the western North Atlantic where the types of leptocephali have been matched with their adult species, the marine eel leptocephali in the Indo-Pacific have mostly not been matched with their adult species yet [7,65]. Different species or taxa can be separated using their morphological features even if they cannot be matched with an adult species. A system has been developed to separate likely different species using a combination of meristic (counts of myomeres/muscle segments) and pigmentation characteristics. The resulting numbers of species are estimates, but for convenience, they will usually be referred to as the number of species in this paper.

![Figure 4](image-url)  
**Figure 4.** Map showing the areas of sampling surveys for leptocephali that are used in the present study to compare the numbers of species of leptocephali in the Indo-Pacific region (all sampling conducted with IKMT plankton trawls) and in the Atlantic Ocean (IKMT sampling in the Sargasso Sea, various plankton nets in other areas) as shown in figure 5.
This system to distinguish different species has enabled the number of species of leptocephali collected during our internationally collaborative surveys to be estimated across a wide geographic area of the Indo-Pacific, and these numbers of species can be compared to what was caught in sampling surveys in several areas of the Atlantic Ocean (figure 4). In the Indo-Pacific, single surveys are used for off-Sumatra, the western South Pacific (WSP), and the Sulu Sea, 2-4 surveys were used in for the other areas of Indonesian Seas (Indo-Seas; 4 surveys), and western Indian Ocean (WIO; 2 surveys).

Only studies with intensive sampling using large trawls or many tows of smaller nets are used for these regional taxonomic comparisons. These individual surveys and the number of species of leptocephali that were collected during each study are described in the next section.

3. Results

3.1 Number of eel species in the Coral Triangle

The first IKMT sampling survey of this study that was conducted in the Indonesia Seas was BJ-01-1 in May 2001 (figure 3a) and 2084 leptocephali of 136 species were collected (figure 5a) at 25 stations around Sulawesi Island [9]. In September of the next year during the BJ-02-2 cruise, 2312 leptocephali of 132 species were caught around Sulawesi Island and in the eastern Java Sea (figure 3c). Later in November 2002 during the KH-02-4 cruise, leptocephali of 169 species were collected mostly in the Sulu Sea (figure 3a). The next year in June 2003, the BJ-03-2 survey collected leptocephali of 143 species off West Sumatra (Fig. 3c; [43-45]. The most recent cruise was Leg 7 of KH-09-5 that was conducted in March 2010 in both the Celebes Sea (78 species, 973 larvae) and Tomini Bay (105 species, 1094 larvae) [10] of northern Sulawesi Island and 126 species were collected during the entire survey (figure 3b). This showed that more than 125 species of marine eel larvae and a few other taxa (tarpon, ladyfish, bonefish, and notacanths), were collected during each of the surveys that were conducted using IKMT sampling to specifically target leptocephali in the Indonesian Seas region.

3.2 Numbers of eel species in other Indo-Pacific regions

IKMT sampling in other regions of the Indo-Pacific included sampling for leptocephali in the East China Sea, coastal Japan, and the Kuroshio gyre and these surveys are pooled together as the “East Asia” region (figure 4). At least 71 species were collected in these studies in the East Asia region, but in areas such as in a nearshore area of northeastern Japan, only 5 species were collected [40]; about 45 were collected along the outer continental shelf in the East China Sea, and 51 were collected in the Kuroshio Extension and northern subtropical gyre [66]. There were 66 species collected in transects across the North Equatorial Current (NEC) just to the south [38]. The other regions in the Indo-Pacific that have been sampled with an IKMT (figure 4) included long transects of stations in the WSP during the KH-95-4 survey when 94 species were estimated to be among the leptocephali that were collected [47]. Far to the west in the WIO to the east of Madagascar and near the Mascarene Plateau, two sampling surveys (KH-06-4; KH-09-5, Leg 5) collected about 82 species [46].

3.3 Numbers of eel species in Atlantic Ocean studies

The present study includes the numbers of species of leptocephali that were collected in 5 general areas of the Atlantic Ocean (figure 4). In the western North Atlantic (WNA), IKMT sampling was conducted in the Sargasso Sea and Florida Current (6 surveys) to study the distribution of the leptocephali of the two Atlantic anguillid eels (A. anguilla, A. rostrata) and then the marine eel larvae from those surveys were analyzed later [48,49]. Those surveys collected at least 50 species of leptocephali offshore and 77 in the southwestern Sargasso Sea region (figure 5b), with the biodiversity of species being greatest in the Northern Bahamas area. Other sampling occurred with rectangular nets just inshore of the Florida Current along the western edge of the Sargasso Sea, which collected 63
species. Similar gear was used at several locations of the Gulf of Mexico (GOM) that collected 59 species [51]. A more intensive series of surveys in a large grid of stations was then conducted in the northern GOM that collected 107 species of anguilliform leptocephali and 11 species of other groups of elopomorph leptocephali [39]. That study also included some sampling with a 10 m² mouth opening MOCNESS trawl and it included more intensive sampling in deeper layers 200-1000 m, which resulted in higher numbers of rare species being collected. There has been a total of 156 species of anguilliform leptocephali described in careful identification research efforts in the WNA region (figure 5b), although some species of the Muraenidae could not be separated [67]. In comparison, 174 species of adult eels have been described in the WNA [35].

![Figure 5](image-url)  
**Figure 5.** Plots of the estimated numbers of species of leptocephali that were collected during IKMT surveys in areas of the Indo-Pacific (a) and by various other types of plankton net sampling gears in areas of the Atlantic Ocean (b). See the text for details. The dotted lines show the 100 species level for visual comparison between the upper and lower panels.

Farther south and to the east, leptocephali were collected with various types of gears during 4 different years at Barbados at the eastern edge of the Caribbean Sea (figure 4), resulting in 68 species being collected [54]. Much farther to the southeast in the Gulf of Guinea of West Africa, about 10,000 leptocephali were collected with small plankton nets over a ten-year period resulting in 68 species being distinguished [52,55]. On the other side of the South Atlantic, 29 species of leptocephali were collected off eastern Brazil [53].

4. **Discussion**

4.1 **Highest eel biodiversity is in the Coral Triangle**

The comparison of the number of species among areas of the Indo-Pacific and the Atlantic Ocean clearly indicated that greater numbers of species of leptocephali were collected during each of the surveys within the Coral Triangle and off West Sumatra than in other areas. The highest number of species of leptocephali occurred during the Sulu Sea survey that collected about 169 species, which is more than all the described species of leptocephali in the entire WNA region [35]. The main reason for such a high number of species in the Sulu Sea survey was that 74 species of Ophichthidae leptocephali were distinguished among the large catch of those larvae (compared to 54 total ophichthid species in the WNA [35]. Most of those larvae were identified in the laboratory after the cruise, in comparison to
larvae being identified onboard during a survey when there is limited time available, which might suggest the numbers of ophichthid species have been typically underestimated during our Indo-Pacific surveys. This is likely also true for the leptocephali of the Muraenidae, which were distinguished in more detail (44 species) during the 2010 survey in Tomini Bay [10], compared to only 34 species being distinguished in the Sulu Sea survey, or just > 15 species in the 2001 survey around Sulawesi Island [9].

Based on adults, 61 species of Muraenidae have been reported from Indonesian waters (compared to 24 total species in the WNA [75], but fewer species of difficult to collect adult eels such as ophichthids, congrid, and chlopsids have been reported [16]; so our larval collections indicate there is undocumented biodiversity of eels in the region. Combining larval and adult eel information, it was recently estimated that there could be at least 170 species of marine eels in the Indonesian Seas region [10]. Regardless of the difficulty and likely underestimates of the number of species based on capturing juveniles and adults, and separating likely different larval taxa only on morphology and pigmentation (or meristics in some cases), the present analysis indicates more species of marine eels are present in the Indonesian Seas region than anywhere else in the world. In fact, where careful research has been ongoing, 207 species of marine eels have been reported from Taiwan that included 71 Muraenidae, 60 Ophichthidae, 29 Congridae, and 17 Synaphobranchidae species [68], which is higher than the total number of species including many other families in the WNA [35]. This indicates that the biodiversity of eels in the Coral Triangle and nearby areas is clearly higher than areas such as the WNA. These marine eels have a wide range of body sizes, shapes, and color patterns, and few examples are shown in figure 6; although their close relatives within the Elopomorpha, which also have leptocephalus larvae, have fish-like body forms (figure 6g).

Figure 6. Photographs of eels or elopomorphs of 6 different families that are the Muraenidae that typically live in coral reefs or other shallow areas (a), Moringuidae that are burrowers (b), Ophichthidae, that are also burrowers (c), the blacklip conger eel, Conger cinereus (d), garden eels that protrude their bodies from burrows to feed on plankton (e), Chlopsidae (f), and a tarpon (g). Photographs were taken by John E. Randall, and are adapted from Miller and Tsukamoto [7].
The higher number of marine eel species is likely related to the overall higher biodiversity of marine animals in the Coral Triangle that has probably resulted from a variety of factors that have been discussed previously [2-5]. The structural diversity of habitats and the number of coral reef habitats are likely some reasons that such high biodiversity has occurred in this region. One example of the diversity of habitats is the Togian Islands in Tomini Bay of Sulawesi Island as shown in figure 2a-c. Tomini Bay is a unique large (59,500 km²), deep (>1500 m in the central bay, >3000 m in the outer bay) [69] semi-enclosed bay that is considered to be a functional seascape or ecoregion distinguished from surrounding areas [70,71]. Small banks with coral reefs or coral atolls are also found in many areas along the shorelines of Tomini Bay (figure 2a-c; [11,81]). The Togian Islands mainly consist of 3 larger closely spaced islands and 60 smaller islands stretching across a distance of 90 km [34] that have a diverse fauna of corals (~264 species; [73]), mollusks [74], and fishes (~800 species; [23]) in fringing reefs, platform/patch reefs, atolls, and barrier reefs. These habitats also appear to have a unique phylogeographic history and unusually diverse faunas of groups such as Acropora corals, and there are some genetically distinct populations, including 6 apparently endemic fish species [16-20].

Similarly diverse habitats also appear to be present in the Banggai Islands region just to the southeast (figure 2e-h). A survey of reef fishes at 47 sites including 19 in the Banggai Islands and 24 in the Togean Islands found that Banggai sites (average 176 species) usually had more species than Togean sites (average 166 species) [23]. Among the two areas, a total of 819 species were observed or collected, but an extrapolation method suggests there are at least 1,023 reef fish species in the region [23]. Both of these areas, and also many areas of the Coral Triangle include the typical types of habitats that are used by various taxa of marine eels, but very few eels were included in the fish species counts in those surveys even though they were likely present. Moray eels of the family Muraenidae are common components of coral reef habitats, so the distribution of coral reefs shown in figure 1 directly represents appropriate habitats for moray eels and likely some chlopsid eels. Furthermore, shallow sandy habitats around coral reefs or in other areas (figure 2) are habitats for the burrowing eels of the diverse family Ophichthidae. Some shallow-water species of the Congridae are also burrowing species, but others live deeper over the slope. The many coastlines and islands of the Coral Triangle would likely provide a diversity of suitable habitats for these shelf and slope congrids.

The most abundant species of congrid eel larvae in all of the surveys in the Indonesian Seas is the small-sized tropical conger, Ariosoma scheelei [75], which appears to primarily inhabit very shallow soft-sediment sheltered bays or lagoons, as has been collected by ichthyocide sampling [76,77]. Ariosoma scheelei was also the most abundant species of leptocephali in the Northwest Coral Sea [77]. Because these small congrid eels burrow in soft sediments and are nocturnal, they are rarely seen or collected without ichthyocides, so their abundance in tropical areas may be greatly underestimated [77].

The same could also be true for the small eels of the Chlopsidae, at least regarding their presence and number of species in each area. For example, the larval collections indicate that more than 10 species could be present, but this appears to be more than the 4 adult species that have been documented to be present in the Coral Triangle, with 2 species having been reported from the Togian Islands and only another 2 species having been reported from throughout Indonesia [16,24]. The survey of reef fishes in the Togean and Banggai Islands only reported 2 species of ophichthids and 11 species of muraenids, and most of these species were only collected with ichthyocide (rotenone) [24], which highlights the difficulty of surveying for the presence and abundances of marine eels. It seems likely that there could be a very large unknown biodiversity of eel species in the Coral Triangle that has only been detected through the larval sampling.

4.2 Possible climate change effects on marine eels in the Coral Triangle
The marine habitats of the Indonesian Seas are under threat from a variety of anthropogenic activities such as overfishing by local fishermen, the live fish aquarium trade, and destructive fishing practices [77-80], and also from land-based pollution and sedimentation [82,83]. Additional impacts from
climate change could make these problems even worse. Intensive harvesting of some fisheries species can drastically reduce their numbers in particular areas [84-86], which affects the community structure. Both anthropogenic activities and coral bleaching have affected many reef areas around Sulawesi Island [80,87] and these areas are considered to be highly threatened [88]. Destructive fishing practices [21,80,88] and coral bleaching have also been problems in the Togian Islands in Tomini Bay, because water temperatures can reach 30-33ºC [89]. The survey of the Togean and Banggai Islands that was mentioned previously for marine fishes, also examined other groups of marine species and it was found that coral bleaching had occurred at almost every site in the Togian Islands, but only at one site in the Banggai Islands [24,89].

These impacts related to climate change and other threats to the marine biodiversity from human activities in the Indonesian Seas and the wider Coral Triangle region may significantly affect the ecological communities in which marine eels live. The severe coral bleaching events in the region have been associated with El Niño events and at least 4 of these events have occurred in Indonesian waters that have been recorded [90]. Rising sea surface temperatures (SST) cause coral bleaching that can destroy coral reefs if it becomes severe, such as during a 2010 coral bleaching event in the Indonesian Seas [91]. Wouthuyzen et al. [90] analyzed the SST data acquired by the Aqua MODIS Satellite and showed that the coral bleaching events of both 2010 and 2016 started and finished in the same periods of Mar-Jun. Field observations and various sources showed that coral bleaching events occurred in many areas of the Coral Triangle region as shown in figure 7 overlain on maps of SST patterns plotted as degree heating weeks (DHW), which is the duration that a sea temperature occupies a water body. Various other studies have been published about coral bleaching issues in the Coral Triangle region that provide other information about this problem [92-95]. Coral bleaching also occurred in 2016 and 2017 in parts of the Great Barrier Reef off northeastern Australia [96,97] as well as during 1998 and 2002 [59]. The 1998 and 2010 bleaching events also affected the southeast Bay of Bengal region of the eastern Indian Ocean areas [98] to the west of the Coral Triangle. If these events cause long-term changes to the coral reef communities, this could affect some types of marine eels.

![Maps of sea surface temperature expressed as degree heating weeks (DHW) during the same two-month periods [90], which show areas where warm water remained for extended periods of time in the Coral Triangle during the El Niño events of 2010 and 2016. The black circles show areas where coral bleaching was reported, as described by Wouthuyzen et al. [90].](image_url)
The community structure of reef areas can change after coral bleaching occurs, such as by having dead corals become overgrown by algae after they collapse, which causes a loss of structural complexity and changes in the assemblages of fishes [99,100]. Climate change is likely to be accompanied by a wide range of impacts on both the marine and terrestrial environments that are linked through rainfall and levels of storm activities etc. [101]. These types of drastic habitat changes such as those from coral bleaching or other damage to marine habitats could have major impacts on some types of eels that live in those habitats. Changes in community structure and reductions in the abundances of prey species, such as small fishes and invertebrates could reduce the growth and survival of marine eels in coral reef habitats. Eels that live in sandy or seagrass areas or in slope habitats might be less affected unless warmer water temperatures or excess sedimentation affects those communities. Mesopelagic eels that live in the midwater below 200 m depths are likely to be less affected by global warming, or might not be affected at all, unless through effects on their larvae that live in the surface layer as discussed later.

Little is known about the biology of most shallow-water marine eels, however, so exactly how changes such as warmer sea temperatures or loss of coral reef habitats will affect them is presently mostly a matter of speculation. Some studies have been conducted on various behavioral aspects of moray eels in areas outside the Coral Triangle, but very little is known about most other taxa. The depth/habitat zones where marine eels live were documented in Hawaii, which suggested that some habitat segregation occurs among species of moray or ophichthid eels [102] and some studies have been conducted on the movements, habitat use, or abundances of moray eels mostly in the Atlantic Ocean [103-106]. Studies on the diets of moray eels have shown that some species eat fishes such as wrasses, small crabs, and octopus in the shallow backreef habitat of a barrier reef with some species specializing on a particular type of prey, such as fish versus crabs [104]. Morays typically appear to feed at night when crabs and shrimp come out to feed, or when they can find small fishes hiding at night [107]. There is less information about the diets of other families such as Congridae, Ophichthidae, and Moringuidae, but polychaetes in addition to fish or crustaceans have been found in some cases, and some burrowing species of the latter 2 families may forage within the sediment [107]. Congrids have also been found to eat stomatopods (mantis shrimp) and echinoids (starfish), but crabs may be the main food source for some species, while large individuals of other species feed only on fishes or octopus [108]. Along the Mediterranean Sea coast of Italy, the diet of a congrid species of Gnathophis and a smaller-sized species of Chlopsidae (Chlopsis bicolor) were examined from the bottom trawl-caught specimens caught at night [109]. The Gnathophis species showed dietary changes with size by shifting from amphipods to decapods, cephalopods, and then to mostly eating fishes, but the Chlopsis eels shifted from amphipods to decapods, with some echinoderms also eaten, but they never shifted to include fish in their diet. Garden eels of the family Congridae only feed on planktonic organisms such as zooplankton or eggs [108,110], which is a unique feeding style among benthic eels, because they protrude their bodies out of their burrows to feed on plankton drifting past them figure 6e.

The amount of information about what marine eels feed on is very limited however, in terms of the number of species and number of individuals that have been examined, but what is known can be used to consider how changes in community structure due to climate change and other ecological impacts on the marine environment might affect marine eels. Reductions in the abundances of some types of reef fishes that are susceptible to eel predation, and reductions in crabs, shrimp, polychaetes, and octopuses, appear to have the potential to have direct negative impacts on the growth or survival of marine eels. How those reductions might be linked to coral bleaching and marine habitat degradation needs to be the subject of future studies. One possibility is that the degradation of pristine tropical habitats such as coral reefs and seagrass beds could favor eel species that are adapted to more disturbed or muddy habitats, where they also feed on the fishes and crustaceans that are adapted to those environments [108,111], while other eel and prey species with more specific habitat requirements will decline. Another concern is that it is possible that there are some rare and less abundant and possibly endemic species of eels that could greatly be affected by even minor changes to
marine communities due to competition for food with more abundant eel species or other types of consumers. In the Indonesian Seas, the Chlopsidae is one family that may have unique undocumented diversity in the region as mentioned previously. These are very secretive eels that are essentially never seen, and almost nothing is known about their biology. A species of the chlopsid genus *Kaupichthys* was collected from a small coral head area of Amami Island Japan [112], so damage to corals could be harmful to those eels. If there are endemic chlopsid species present for example, they could be vulnerable to changes in community structure due to climate change-related impacts. A recent study has suggested there is cryptic genetic diversity among some coral reef species including the genus *Kaupichthys* in the Coral Triangle [113], so much remains to be learned about these species.

### 4.3 Possible global warming effects on eel larvae

Many species of marine eels such as those living below 1000 m may be unaffected by climate change, but almost all eel larvae live in the upper few hundred meters and their food source is directly linked to primary production factors that could be affected by climate change. Leptocephali appear to feed on marine snow particles as their primary food source [114,115], and these particles are produced by materials released by phytoplankton and from various sources of detrital materials from planktonic organisms [116]. Therefore, because primary production of eukaryotic phytoplankton appears to be reduced by warm water conditions [116,118], there may be reductions of marine snow production when ocean surface layer temperatures become warmer as a result of global warming. For example, correlations have been found between anguillid eel recruitment levels and fluctuations in SST, primary production or ocean-atmosphere indicators [56, 119,120] as was overviewed by Miller et al. [57, 121]. Reductions of marine snow production resulting from ocean-atmosphere changes have been hypothesized to reduce the larval survival of species such as anguilid eels that produce many larvae in their spawning areas during limited periods of time [56], so reductions of marine snow abundances in areas that have high abundances of leptocephali, such as the Indonesian Seas could also reduce larval survival and cause slower growth rates. This might have a greater effect on species that are less abundant and produce fewer larvae, so the combination of reduced growth and survival of both the eels and larvae of these species should be considered regarding the question of how climate change might affect eels and their regional biodiversity and abundances.

### 4.4 Possible climate change effects on anguilid eels

Climate change is thought to be one of the threats to anguilid eels worldwide [122], but the possible effects on catadromous eels inhabiting freshwater and estuarine habitats would be very different than those on marine eels, except for the effects on their oceanic larvae. The tropical anguilids living in the freshwater and estuarine habitats of the Coral Triangle must feed and grow there during their yellow eel stage until they start the process of reproductive maturation into the silver eel stage. For the eels living in the inland freshwater rivers, streams, and lakes, a possible disruption could be climatic changes that affect patterns of rainfall, which might affect the timing of the silvering/reproductive maturation process and the timing of downstream migration of the silver eels. Reductions in rainfall patterns as a result of climate change were considered to possibly have contributed to the declines of the European eel, and the resulting water shortages can cause increases in dam construction that reduce the available habitats for anguilid eels [58].

Regions within the Coral Triangle have seasonal patterns of monsoon rainfall that may be affected by climate change [123] through disruptions from ocean-atmosphere events such as El Niño [124-126]. Indonesia has several different rainfall regions where seasonal patterns of rainy seasons may influence the timing of downstream migration and spawning of anguilid eels [26,32]. Some clear evidence of seasonality of spawning migrations has been seen in the anguilid eels that migrate out of Poso Lake and into Tomini Bay [61, 127], and this has been linked to the presence of larvae of *Anguilla celebesensis* that spawns in the bay [27]. Therefore, seasonal changes in patterns of rainfall or severe droughts could affect the reproductive success of anguilid eels in the Indonesian Seas region. It is beyond the scope of this paper to evaluate how warming freshwater temperatures might affect the
juvenile growth and survival of yellow eels, but large water temperature increases might affect community structure in some habitats and affect the feeding success of the eels.

Another factor to consider though is what effects increased CO₂ absorption in the ocean might trigger in the future, because that causes ocean acidification, which can alter marine communities [128]. A recent study has suggested that ocean acidification might have the potential to affect the ability of recruitment-stage glass eels to detect or be attracted to freshwater habitats [129]. Fish larvae may also be particularly vulnerable to ocean acidification [130], and this might be especially true for leptocephali, which are quite fragile, so studies on the early life history stages of eels in relation to ocean acidification may be important subjects to consider for future studies.

4.5 Future perspectives on understanding eel biodiversity and climate change
It appears very likely that the Coral Triangle region has the highest biodiversity of shallow-water marine eels in the world, but how these species will be affected by climate change is not known. A first step towards beginning to try to answer that question is to gather more information about this diversity of eel species. This includes determining what species are present, where they live, and understanding their ecology. With eels, however, gathering these kinds of information is not easy due to the nocturnal and secretive nature of most marine eel species. Therefore, an important step would be to document the diversity of eel species that are present using genetic techniques with the more easily collected larvae in various regions of the Coral Triangle. This might begin to determine if there are endemic species in some areas, which could suggest particular habitats that are priorities for conservation or reef rehabilitation efforts if coral bleaching continues to be a recurring problem due to climate change. A greater understanding of the seasonality of spawning of anguillid eels in the region is also needed to help understand how those species might be affected by climate change factors such as changes in rainfall patterns.

Acknowledgments
We are grateful to the many captains and crews of the R/V Baruna Jaya VII of LIPI in Indonesia and R/V Hakuho Maru of ORI/AORI/JAMSTEC in Japan for assisting with the operation of the sampling gear during the collections of leptocephali, and the technicians and scientists who helped sort the leptocephali from plankton samples. All coauthors had direct contributions to collecting the data used in the study and the writing and evaluation of its contents.

References
[1] Hoeksema BW 2007 Delineation of the Indo-Malayan centre of maximum marine biodiversity: the Coral Triangle. In: Renema W (ed) Biogeography, time, and place: distributions, barriers, and islands. Springer, Netherlands, pp 117–178
[2] Randall JE 1998 Zoogeography of shore fishes of the Indo-Pacific region. Zool. Stud. 37 227–267
[3] Roberts CM, McClean CJ, Veron JEN, Hawkins JP, Allen GR, McAllister DE, Mittermeier CG, Schueler FW, Spalding M, Wells F, Vynne C, Werner TB 2002 Marine biodiversity hotspots and conservation priorities for tropical reefs. Science 295 1280–1284
[4] Carpenter KE and Springer VG 2005 The center of the center of marine shore fish biodiversity: the Philippine Islands. Environ. Biol. Fish. 72 467–480
[5] Allen GR 2008 Conservation hotspots of biodiversity and endemism for Indo-Pacific coral reef fishes. Mar. Freshw. Ecosystems 18 541–556
[6] Smith DG 1989 Introduction to leptocephali. Fishes of the Western North Atlantic. Böhlke EB (ed), pp. 657–668, Part 9, Volume 2, Sears Foundation for Marine Research, New Haven
[7] Miller MJ and Tsukamoto K 2004 An introduction to leptocephali: Biology and identification. Tokyo: Ocean Research Institute, University of Tokyo 96 pp
[8] Miller MJ 2009 Ecology of anguilliform leptocephali: remarkable transparent fish larvae of the
ocean surface layer. *Aqua-BioSci Monogr.* **2**(4) 1–94

[9] Wouthuyzen S, Miller MJ, Aoyama J, Minagawa G, Sugeha YH, Suharti S, Inagaki T and Tsukamoto K 2005 Biodiversity of anguilliform leptocephali in the central Indonesian Seas. *Bull. Mar. Sci.* **77** 209–224

[10] Miller MJ, Wouthuyzen S, Sugeha HY, Kuroki M, Tawa A, Watanabe S, Syahailatua A, Suharti S, Tantu FY, Otake T, Tsukamoto K and Aoyama J 2016 High biodiversity of leptocephali in Tomini Bay Indonesia in the center of the Coral Triangle. *Reg. Stud. Mar. Sci.* **8** 99–113

[11] Spalding MD, Ravilious C and Green EP 2001 World Atlas of Coral Reefs. University of California Press, Berkeley, CA

[12] Asian Development Bank 2014 Regional State of the Coral Triangle. Coral Triangle Marine Resources: Their Status, Economies, and Management. 94 pp

[13] Hoegh-Guldberg O, Hoegh-Guldberg H, Veron JEN, Green A, Gomez ED, Lough J, King M, Ambarionyanto Hansen L, Cinner J, Dews G, Russ G, Schuttenberg HZ, Peñaff or EL, Eakin CM, Christensen TRL, Abbey M, Areki F, Kosaka RA, Tewfi KA and Oliver J 2009 The Coral Triangle and Climate Change: Ecosystems, People and Societies at Risk. WWF Australia, Brisbane, 276 pp

[14] Barange M, Merino G, Blanchard JL, Scholtens J, Harle J, Allison EH, Allen Ji, Hol J and Jennings S 2014 Impacts of climate change on marine ecosystem production in societies dependent on fisheries. *Nature Clim. Change* **4** 211–216

[15] Hutomo M and Moosa MK 2005 Indonesian marine and coastal biodiversity: Present status. *Indian J. Mar. Sci.* **34** 88–97

[16] Allen GR and Adrim M 2003 Coral reef fishes of Indonesia. *Zool. Stud.* **42** 1–72

[17] Wallace CC 1999 The Togian Islands: coral reefs with a unique coral fauna and hypothesized Tethys Sea signature. *Coral Reefs* **18** 162

[18] Wallace CC, Paulay G, Hoeksema BW, Bellwood DR, Hutchings PA, Barber PH, Erdmann M, Wolstenholme J 2000 Nature and origins of unique high diversity reef faunas in the Bay of Tomini, Central Sulawesi: The ultimate “center of biodiversity”? *Proc. 9th Internat. Coral Reef Symp.*, Bali, Indonesia

[19] Barber PH, Palumbi, SR, Erdmann MV and Moosa MK 2002 Sharp genetic breaks among populations of *Haptosquilla pulchella* (Stomatopoda) indicate limits to larval transport: patterns, causes, and consequences. *Mol. Ecol.* **11** 659–674

[20] Knittweis L, Kraemer WE, Timm J, and Kochzius M 2009 Genetic structure of *Heliofungia actiniformis* (Scleractinia: Fungiidae) populations in the Indo-Malay Archipelago: implications for live coral trade management efforts. *Conserv. Genet.* **10** 241–249

[21] Lowe C 2002 Who is to blame? Logics of responsibility in the live reef food fish trade in Sulawesi, Indonesia. *SPC Live Reef Fish Inform. Bull.* **10** 7–16

[22] Moore A and Ndobe S 2008 Reefs at risk in Central Sulawesi, Indonesia - status and outlook. *Proc. 11th Internat. Coral Reef Sympos.* **18** 840–844

[23] Allen GR 2001 Reef Fishes of the Togean and Banggai Islands, Sulawesi, Indonesia. Pages 44-53 In: Allen GR and McKenna SA editors, A Marine Rapid Assessment of the Togean and Banggai Islands, Sulawesi, Indonesia. Conservation International, Washington, DC

[24] Allen GR and McKenna SA 2001 A Marine Rapid Assessment of the Togean and Banggai Islands, Sulawesi, Indonesia. RAP Bulletin of Biological Assessment 20, Conservation International, Washington, DC

[25] Cros A, Ahamad Fatani N, White A, Teoh, SJ, Tan S, et al. 2014 The coral Triangle Atlas: An Integrated Online Spatial Database System for Improving Coral Reef Management. *PLoS ONE* **9**(6) e96332

[26] Sugeha HY, Suharti SR, Wouthuyzen S and Sumadhiharga K 2008 Biodiversity, distribution, and abundance of the tropical anguillid eels in the Indonesian waters. *Mar. Res. Indones.* **33** 129–137
[27] Aoyama J, Wouthuyzen S, Miller MJ, Sugeha HY, Kuroki M, Watanabe S, Syahailatua A, Tantu FY, Haihara S, Triyanto, Otake T and Tsukamoto K 2018 Reproductive ecology and biodiversity of freshwater eels around Sulawesi Island Indonesia. Zool. Stud. 57 30

[28] Watanabe S 2003 Taxonomy of the freshwater eels, genus Anguilla Schrank, 1798. In: Aida K, Tsukamoto K, Yamauchi K (eds) Eel Biology. Springer, Tokyo, pp. 3–18

[29] Chino N and Arai T 2010 Habitat use and habitat transitions in the tropical eel, Anguilla bicolor bicolor. Environ. Biol. Fish. 89 571–578

[30] Arai T and Chino N 2018 Opportunistic migration and habitat use of the giant mottled eel Anguilla marmorata (Teleostei: Elopomorpha). Sci. Rep. 8 1–10

[31] Kuroki M, Aoyama J, Miller MJ, Yoshinaga T, Shinoda A, Hagihara S and Tsukamoto K 2009 Sympatric spawning of Anguilla marmorata and Anguilla japonica in the western North Pacific Ocean. J. Fish Biol. 74 1853–1865

[32] Aldrian E and Susanto RD 2003 Identification of three dominant rainfall regions within Indonesia and their relationships to sea surface temperature. Int. J. Climatol. 23 1435–1452

[33] Tsukamoto K, Kuroki M and Watanabe S 2020 Common names for all species and subspecies of the genus Anguilla. Environ. Biol. Fish. 103 985–991

[34] Eschmeyer WN and Fong JD 2016 Species by Family/Subfamily in the Catalog of Fishes. California Academy of Sciences, Institute for Biodiversity Science and Sustainability. http://researcharchive.calacademy.org/research/ichthyology/catalog/SpeciesByFamily.asp. Accessed 26 Feb. 2021

[35] Böhlke E 1989a Orders Anguilliformes and Saccopharyngiformes. Fishes of the Western North Atlantic. Mem. Sears Found. Mar. Res. 1(9) 1–655

[36] Castonguay M and McCleave JD 1987 Vertical distributions, diel and ontogenetic vertical migrations and net avoidance of leptocephali of Anguilla and other common species in the Sargasso Sea. J. Plankt. Res. 9 195–214

[37] Miller MJ 2015 Nighttime vertical distribution and regional species composition of eel larvae in the western Sargasso Sea. Reg. Stud. Mar. Sci. 1 34–46

[38] Onda H, Miller MJ, Takeshige A, Miyake Y, Kuroki M, Aoyama J and Kimura S 2017 Vertical distribution and assemblage structure of leptocephali in the North Equatorial Current region of the western Pacific. Mar. Ecol. Prog. Ser. 575 119–136

[39] Moore JA, Fenolio DB, Cook AB and Sutton TT 2020 Hiding in plain sight: elopomorph larvae are important contributors to fish biodiversity in a low-latitude oceanic ecosystem. Front. Mar. Sci. 7 169

[40] Kimura Y, Miller MJ, Minagawa G, Watanabe S, Shinoda A, Aoyama J and Tsukamoto K 2006 Evidence of a local spawning site of marine eels along northeastern Japan, based on the distribution of small leptocephali. Fish. Oceanogr. 15 183–190

[41] Minagawa G, Miller MJ, Kimura Y, Watanabe S, Shinoda A, Aoyama J and Tsukamoto K 2007 Seasonal differences in catches of leptocephali in the East China Sea and Suruga Bay, Japan. Estuar. Coast. Shelf Sci. 71 730–740

[42] Miller MJ, Otake T, Minagawa G, Inagaki T, Tsukamoto K 2002 Distribution of leptocephali in the Kuroshio Current and East China Sea. Mar. Ecol. Prog. Ser. 235 279–288

[43] Miller MJ, Wouthuyzen S, Ma T, Aoyama J, Suharti SR, Minegishi Y and Tsukamoto K 2011 Distribution, diversity and abundance of garden eel leptocephali off west Sumatra, Indonesia. Zool. Stud. 50 177–191

[44] Miller MJ, Yamaguchi M, Wouthuyzen S, Aoyama J, Suharti S, Ma T, Yoshinaga T, Minegishi Y, Kawakami Y and Tsukamoto K 2013 Ariosoma-type leptocephali (Congridae: Bathymyrinae) in the Mentawai Islands region off western Sumatra, Indonesia. Zool. Stud. 52 26

[45] Miller MJ, Wouthuyzen S, Feunteun E, Aoyama J, Watanabe S, Syahailatua A, Kuroki M, Robinet T, Hagihara S, Otake T and Tsukamoto K 2019 Contrasting biodiversity of eel
lakes across the central Indian Ocean subtropical gyre. Deep-Sea Res. II 161 120–131

[46] Miller MJ, Feunteun E, Aoyama J, Watanabe S, Kuroki M, Lecomte-Finiger R, Minegishi Y, Robinet T, Reveillac E, Gagnaire P-A, Berrebi P, Tsukamoto K and Otake T 2015 Biodiversity and distribution of leptocephali west of the Mascarene Plateau in the southwestern Indian Ocean. Progr. Oceanogr. 137 84–102

[47] Miller MJ, Aoyama J, Mochioka N, Otake T, Castle PHJ, Minagawa G, Inagaki T and Tsukamoto K 2006 Geographic variation in the assemblages of leptocephali in the western South Pacific. Deep-Sea Res. I 53 776–794

[48] Miller MJ and McCleave JD 1994 Species assemblages of leptocephali in the subtropical convergence zone of the Sargasso Sea. J. Mar. Res. 52 743–772

[49] Miller MJ and McCleave JD 2007 Species assemblages of leptocephali in the southwestern Sargasso Sea. Mar Ecol. Progr. Ser. 344 197–212

[50] Ross SW, Casazza TL, Quattrini AM and Sulak KJ 2007 Anguilliform larvae collected off North Carolina. Mar. Biol. 150 681–695

[51] Quattrini AM, McClain-Counts J, Artabane SJ, Roa-Varon A, McIver TC, Rhode M and Ross SW 2019 Assemblage structure, vertical distributions, and stable isotopic compositions of anguilliform leptocephali in the Gulf of Mexico. J. Fish Biol. 94 621–647

[52] Blache J 1977 Leptocephales des poissons Anguilliformes dans la zone sud du Golfe de Guinée. Faune Tropicale 10 1–381 (in French)

[53] De Castro MS and Bonecker ACT 2005 Leptocephali collected off the eastern coast of Brazil (12°–23°S). Zootaxa 935 1–28

[54] Richardson DE and Cowen RK 2004 Diversity of leptocephalus larvae around the island of Barbados (West Indies): relevance to regional distributions. Mar. Ecol. Prog. Ser. 282 271–284

[55] Miller MJ and Robinet T 2018 Life history and morphology of eel larvae in the Gulf of Guinea of western Africa: Revisiting Jacques Blache’s research (1960-1977) 40 years later. Rev. Fish. Biol. Fish. 161 120–131

[56] Bonhommeau S, Chasso, E, Planque B, Rivet E, Knap AH and Le Pap O 2008 Impact of climate on eel populations of the Northern Hemisphere. Mar. Ecol. Progr. Ser. 373 71–80

[57] Miller MJ, Feunteun E and Tsukamoto K 2016 Did a “perfect storm” of oceanic changes and continental anthropogenic impacts cause Northern Hemisphere anguillid recruitment reductions? ICES J. Mar. Sci. 73 43–56

[58] Kettle AJ, Vøllestad LA and Wibig J 2011 Where once the eel and the elephant were together: decline of the European eel because of changing hydrology in southwest Europe and northwest Africa? Fish and Fisheries 12 380–411

[59] Hughes TP, Kerry JT and Wilson SK 2017 Global warming and recurrent mass bleaching of corals. Nature 543 373–377

[60] Aoyama J, Wouthuyzen S, Miller MJ, Inagaki T and Tsukamoto K 2003 Short-distance spawning migration of tropical freshwater eels. Biol. Bulletin 204 104–108

[61] Wouthuyzen S, Aoyama J, Sugeha YH, Miller MJ, Kuroki M, Minegishi Y, Suharti S and Tsukamoto K 2009 Seasonality of spawning by tropical anguillid eels around Sulawesi Island, Indonesia. Naturwissenschaften 96 153–158

[62] Aoyama J, Wouthuyzen S, Miller MJ, Minegishi Y, Minagawa G, Kuroki M, Suharti SR, Kawakami T, Sumardiharga KO and Tsukamoto K 2007 Distribution of leptocephali of the freshwater eels, genus Anguilla, in the waters off west Sumatra in the Indian Ocean. Environ. Biol. Fish. 80 445–452

[63] Tabet O and Mochioka N 1988 Leptocephali. In Okiyama M ed An atlas of the early stage fishes in Japan. Tokyo: Tokai University Press, pp 15–64 (in Japanese)

[64] Mochioka N and Tabet O 2014 Leptocephali. pp 2–89, In Okiyama M ed. An atlas of the early
stage fishes in Japan, Second Edition. Tokai University Press, Minamiyama. (in Japanese)

[65] Miller MJ and Tsukamoto K 2006 Studies on eels and leptocephali in Southeast Asia: a new research frontier. *Coast. Mar. Sci.* **30** 283–292

[66] Miller MJ, Itoh S, Watanabe S, Shinoda A, Saruwatari T, Tsukamoto K and Yasuda I 2020 Distribution of leptocephali and wintertime hydrographic structure in the Kuroshio Extension and northern subtropical gyre. *Deep-Sea Res. I.*

[67] Böhlke EB (ed.) 1989b Leptocephali. Fishes of the Western North Atlantic. Mem. *Sears Found. Mar. Res.* **1(9)**

[68] Ho H-C, McCosker JE, Smith DG and Shao KT 2015a Introduction to the systematics and biodiversity of eels (orders Anguilliformes and Saccopharyngiformes) of Taiwan. *Zootaxa* **4060** 5–18

[69] Kusnida D and Subarsyah 2008 Deep sea sediment gravity flow deposits in Gulf of Tomini, Sulawesi. *J. Geol. Indon.* **3** 217–225

[70] Green AL and Mous PJ 2008 Delineating the Coral Triangle, its ecoregions and functional seascapes. Version 5.0. *TNC Coral Triangle Program Report* **1/08** 44 pp

[71] Veron JEN, Devantier LM, Turak E, Green AL, Kininmonth S, Stafford-Smith M and Peterson N 2009 Delineating the coral triangle. *Galaxea, J. Coral Reef Stud.* **11** 91–100

[72] Burke L, Selig E and Spalding M 2002 Reefs at risk in Southeast Asia. World Resources Institute, Washington, DC

[73] Miller MJ, Wouthuyzen S, Minagawa G, Aoyama J and Tsukamoto K 2006 Distribution and ecology of leptocephali of the congrid eel, *Ariosoma scheelei*, around Sulawesi Island, Indonesia. *Mar. Biol.* **148** 1101–1111

[74] Johannes RE and Riepen M 1995 Environment, economic and social implications of the live fish trade in Asia and the western Pacific. *Rep. Nature Conser. Forum Fisheries Agency.* 83 pp

[75] Bryant D, Burke L, McManus J and Spalding M 1998 Reefs at Risk. A Map-based Indicator of Threats of the World’s Coral Reefs. World Resources Institute, Washington DC 27
[86] Lane JW and Limbong D 2015 Catastrophic depletion of reef-associated sea cucumbers: resource management/reef resilience issues for an Indonesian marine park and the wider Indo-Pacific. Aquat. Conserv. 25 505–517

[87] Nontji A 2000 Coral reefs of Indonesia: past, present and future. Proceed. 9th Internat. Coral Reef Symp. I 17–27

[88] Burke L, Selig E and Spalding M 2002 Reefs at risk in Southeast Asia. World Resources Institute, Washington, DC

[89] Yusuf S and Allen GR 2001 Condition of Coral Reefs in the Togean and Banggai Islands, Sulawesi, Indonesia. Pages 27-37 In: Allen GR and McKenna SA editors, A Marine Rapid Assessment of the Togean and Banggai Islands, Sulawesi, Indonesia. Conservation International, Washington, DC

[90] Wouthuyzen S, Abrar M, and Lorwens J 2018 A comparison between the 2010 and 2016 El-Niño induced coral bleaching in the Indonesian waters. IOP Conf. Series: Earth and Environm. Sci. 118 012051

[91] Wouthuyzen S, Abrar M, and Lorwens J 2015 Coral bleaching incidents of 2010 in Indonesian waters revealed through analysis of sea surface temperature. Oceanologi dan Limnologi di Indon. 1(3) 305

[92] Brown BE and Suharsono 1990 Damage and recovery of coral reefs affected by El Niño related seawater warming in the Thousand Islands, Indonesia. Coral Reefs 8(4) 163–170

[93] Rudi E, Iskandar T, Fadli N and Hidayati H 2012 Impact of mass coral bleaching on fish reef community and fishermen catches at Sabang, Aceh Province, Indonesia. AACL Bioflux 5(5) 309–320

[94] Sutthacheep M, Pongsakun S, Yucharoen M, Klinthong W, Sangmanee K, Yeemin T 2013 Impacts of the mass coral bleaching events in 1998 and 2010 on the Western Gulf of Thailand. Deep Sea Research II 96 25–31

[95] Garpe KC, Yahya SAS, Lindahl U and Öhman C 2006 Long-term effects of the 1998 coral bleaching event on reef fish assemblages. Mar. Ecol. Prog. Ser. 315 237–247

[96] López-Pérez A, Guendulain-García S, Granja-Fernández R, Hernández-Urraca V, Galván-Rowland L, Zapata-Vilchis R and López-López D 2016 Reef community changes associated with the 2009–2010 El Niño in the Southern Mexican Pacific. Pacific Sci. 70 175–190

[97] Hoegh-Guldberg O, Hoegh-Guldberg H, Veron JEN, Green A, Gomez ED, Lough J, King M, Ambariyanto Hansen L, Cinner J, Dew G, Russ G, Schuttenberg HZ, Peñafl or, EL, Eakin CM, Christensen TRL, Abbey M, Areki F, Kosaka RA, Tewfik, A and Oliver J 2009 The Coral Triangle and Climate Change: Ecosystems, People and Societies at Risk. WWF Australia, Brisbane 276 pp

[98] Gosline WA 1965 Vertical zonation of inshore fishes in the upper water layers of the Hawaiian Islands. Ecology 46 823–831

[99] Abrams R., Abrams MD and Schein MW 1983 Diurnal observations on the behavioural ecology of Gymnothorax moringa (Cuvier) and Muraena miliaris (Kaup) on a Caribbean coral reef.
[104] Young RF and Winn HE 2003 Activity patterns, diet, and shelter site use for two species of moray eels, *Gymnothorax moringa* and *Gymnothorax vicinus*, in Belize. *Copeia* **2003** 44–55

[105] Gilbert M, Rasmussen JB and Kramer DL 2005 Estimating the density and biomass of moray eels (Muraneidae) using a modified visual census method for hole-dwelling fauna. *Environ. Biol. Fish.* **73** 415–426

[106] Basset D and Montgomery J 2011 Home range use and movement patterns of the yellow moray eel *Gymnothorax prasinus*. *J. Fish Biol.* **79** 520–525

[107] Hiatt RW and Strasburg DW 1960 Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecol. Monogr.* **30** 65–127

[108] Randall JE 1967 Food habits of reef fishes of the West Indies. *Stud. Trop. Oceanogr.* **5** 665–847

[109] Carpentieri P, Colloca F and Ardizzone G 2007 Rhythms of feeding activity and food consumption of two Mediterranean burrowing fishes: *Gnathophis mystax* (Delaroche) and *Chlopsis bicolor* Rafinesque. *Mar. Ecol.* **28** 487–495

[110] Vigliola L, Galzin R, Harmelin-Vivien ML, Mazeas F and Salvat B 1996 *Les Heterocongrinae* (Teleostei: Congridae) de la pente externe de Moorea (Ile de la Société, Polynésie Française): distribution et biologie [The heterocongrinae (Teleostei: Congridae) of the outer slope of Moorea (Society Islands, French Polynesia) distribution and biology]. *Cybium* **20** 379–393

[111] Santos FB and Castro RMC 2003 Activity, habitat utilization, feeding behaviour, and diet of the sand moray *Gymnothorax ocellatus* (Anguilliformes, Muraenidae) in the south western Atlantic. *Biota Neotropica* **3** 1–7

[112] Mastubara K and Asano H 1959 A new eel of the genus *Kaupichthys*. *Copeia* **1959(4)** 293–297

[113] Hubert N, Meyer CP, Bruggemann HJ, Gue´rin F, Komeno RJL et al. (2012) Cryptic diversity in Indo-Pacific coral-reef fishes revealed by DNA-barcoding provides new support to the centre-of-overlap hypothesis. *PLoS ONE* **7**(3) e28987

[114] Miller MJ, Hanel R, Feunteum E and Tsukamoto K 2020 The food source of Sargasso Sea leptocephali. *Mar. Biol.* **167** 57

[115] Tsukamoto K, and Miller M 2020 The mysterious feeding ecology of leptocephali: a unique strategy of consuming marine snow materials. *Fisheries Sci.* **87** 11–29

[116] Allardredge AL and Silver MW 1988 Characteristics, dynamics and significance of marine snow. *Progr. Oceanogr.* **20** 41–82

[117] Behrenfeld MJ, O’Malley RT, Siegel DA, McClain CR, Sarmiento JL, Feldman GC, Milligan AJ et al. 2006 Climate-driven trends in contemporary ocean productivity. *Nature* **444** 752–755

[118] Boyce DG, Lewis MR and Worm B 2010 Global phytoplankton decline over the past century. *Nature* **466** 591–596

[119] Knights B 2003 A review of the possible impacts of long-term oceanic and climate changes and fishing mortality on recruitment of anguillid eels of the Northern Hemisphere. *Sci. Tot. Environ.* **310** 237–244

[120] Friedland KD, Miller MJ and Knights B 2007 Oceanic changes in the Sargasso Sea and declines in recruitment of the European eel. *ICES J. Mar. Sci.* **64** 519–530

[121] Miller MJ, Kimura S, Friedland KD, Knights B, Kim H, Jellyman DJ and Tsukamoto K 2009 Review of ocean-atmospheric factors in the Atlantic and Pacific oceans influencing spawning and recruitment of anguillid eels. *Amer. Fish. Soc. Symp.* **69** 231–249

[122] Drouineau H, Durif C, Castonguay M, Mateo M, Rochard E et al. 2018 Freshwater eels: A symbol of the effects of global change. *Fish Fish.* **19** 903–930

[123] Loo YY, Billa L and Singh A 2015 Effect of climate change on seasonal monsoon in Asia and its impact on the variability of monsoon rainfall in Southeast Asia. *Geosci. Front.* **6** 817e823
[124] Hendon HH 2003 Indonesian rainfall variability: Impacts of ENSO and local air–sea interaction. J. Clim. 16 1775–1790

[125] Giannini A, Robertson AW and Qian J-H 2007 A role for tropical tropospheric temperature adjustment to El Niño–Southern Oscillation in the seasonality of monsoonal Indonesia precipitation predictability. J. Geophys. Res. 112 D16110

[126] D’Arrigo R and Wilson R 2008 El Niño and Indian Ocean influences on Indonesian drought: implications for forecasting rainfall and crop productivity. Internat. J. Climatol. 28 611–616

[127] Sugeha HY, Aoyama J and Tsukamoto K 2006 Downstream migration of tropical anguillid silver eel from Lake Poso, central Sulawesi Island, Indonesia. Limnotec XIII 18–25

[128] Fabry VJ, Seibel BA, Feely RA and Orr JC 2008 Impacts of ocean acidification on marine fauna and ecosystem processes. ICES J. Mar. Sci. 65 414–432

[129] Borges FO, Santos CP, Sampaio E, Figueiredo C, Paula JR, Antunes C, Rosa R and Grilo TF 2019 Ocean warming and acidification may challenge the riverward migration of glass eels. Biol. Lett. 15 20180627

[130] Muller C, Childs A-R, James NC and Potts WM 2021 Effects of experimental ocean acidification on the larval morphology and metabolism of a temperate sparid, Chrysoblephus laticeps. Oceans 2 26–40