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Confirmation of hilsa shad (*Tenualosa ilisha*) in Vietnamese waters: a morphological and genetic analysis

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Abstract

One specimen of tropical shad was caught from the Giang Thanh River, Kien Giang province, Vietnam in a survey on 16 October 2022. We identified the specimen as the hilsa shad, *Tenualosa ilisha* Hamilton, 1822 using morphological analysis, and further validated by its cytochrome oxidase subunit I (COI) sequence. The specimen was 418 mm long, 1428 g in weight, with a head length of 29.0% and pectoral fin length of 31.1% of its standard length. Notably, the presence of 34 scutes, a higher gill raker count and a caudal fin length within the moderate range for *Tenualosa* species distinguished it from *T. macrura*, *T. toli* and *T. reevesii*. The COI sequence of the sample matched closely to the *T. ilisha*. The results confirm that *T. ilisha* still endures Vietnamese water, where it was thought to be extinct. Climate change and Indo-Pacific Ocean currents may introduce expansion of distribution area of the *T. ilisha*. Further studies on distribution of the *T. ilisha* and other *Tenualosa* species and their dynamics are needed.

Introduction

The aquatic ecosystems of Southeast Asia harbour a rich biodiversity (Koh and Sodhi, 2010; Liu, 2013; Hughes, 2017), with various fish species contributing significantly to the region's ecological and economic dynamics (Todd *et al.*, 2010; Pomeroy *et al.*, 2019). *Tenualosa ilisha* is a highly valued fish species in South Asia and some Middle Eastern countries (Hossain *et al.*, 2019a; Hossain *et al.*, 2019b), where it has economic, cultural and ecological significance (Khan *et al.*, 2020; Bandara and Wijewardene, 2023). They are anadromous fish and migrate from marine to freshwater environments for spawning (Bhaumik, 2015a; Hossain *et al.*, 2016; Asaduzzaman *et al.*, 2019b; Asaduzzaman *et al.*, 2020). However, the distribution and population status of *T. ilisha* in different regions is poorly understood, especially in the Vietnamese water, where it was thought to be extinct due to overfishing, habitat degradation and climate change (Blaber *et al.*, 2023).

Previous studies on *T. ilisha* focused on its biology, ecology and fisheries management in the Bay of Bengal and the Persian Gulf (Bhaumik, 2017; Hossain *et al.*, 2019a, 2019b), where it is more abundant and accessible (Bhaumik, 2015a; Sarker *et al.*, 2023). However, consistent, reliable data on the occurrence, abundance and genetic diversity of *T. ilisha* in the South China Sea is lacking. Moreover, only one study documented the existence of *T. ilisha* in Vietnamese water but without support data (Nguyen and Nguyen, 1994; Turan *et al.*, 2004). We aimed to survey *T. ilisha* in Vietnamese water and confirm the sampled species using both morphological and molecular data.

Materials and methods

We set up six trawling trips and surveyed from offshore to the estuary area of the Giang Thanh River, Kien Giang Province, Vietnam (Figure 1). Temperature and salinity were determined using a conventional CTD profiler (Compact-CTD Lite, JFE Advantech, accuracy ± 0.03) (Miyata *et al.*, 2016). Only one individual of *Tenualosa* species was captured on 16 October 2022 (Figure 2). Morphometric characters of the specimen were measured following a methodology outlined in a previous study (Arai and Amalina, 2014).

Fin and tissue samples were preserved in 96% ethanol for subsequent analysis. DNA was extracted using an Ezup Column Animal Genomic DNA Purification Kit (Sangon, Shanghai, China). Cytochrome oxidase subunit I (COI) gene was amplified using standard COI gene primers designed for the Clupeiformes in our lab (COI-F GGAGCTACAATCCGCCGCTA and COI-R GGTTCGATTCCTYCCTTCTCGTT). Each PCR reaction contained 2.0 μ l of DNA sample, 2.5 μ l of each 10 μ M of each primer, 50 μ l of the QIAGEN Taq PCR Master Mix and 43 μ l of distilled water. The PCR reaction condition was as follows: initial denaturation: 94°C for 5 min; 32 cycles of 94°C for 30 s, primer annealing at 62.9°C for 30 s and extension at 72°C for 1 min; with a final extension at 72°C for 7 min. Finally, the PCR products were analysed by using 1.5% agarose gel electrophoresis with Biotium – Gel Red. The sequences were



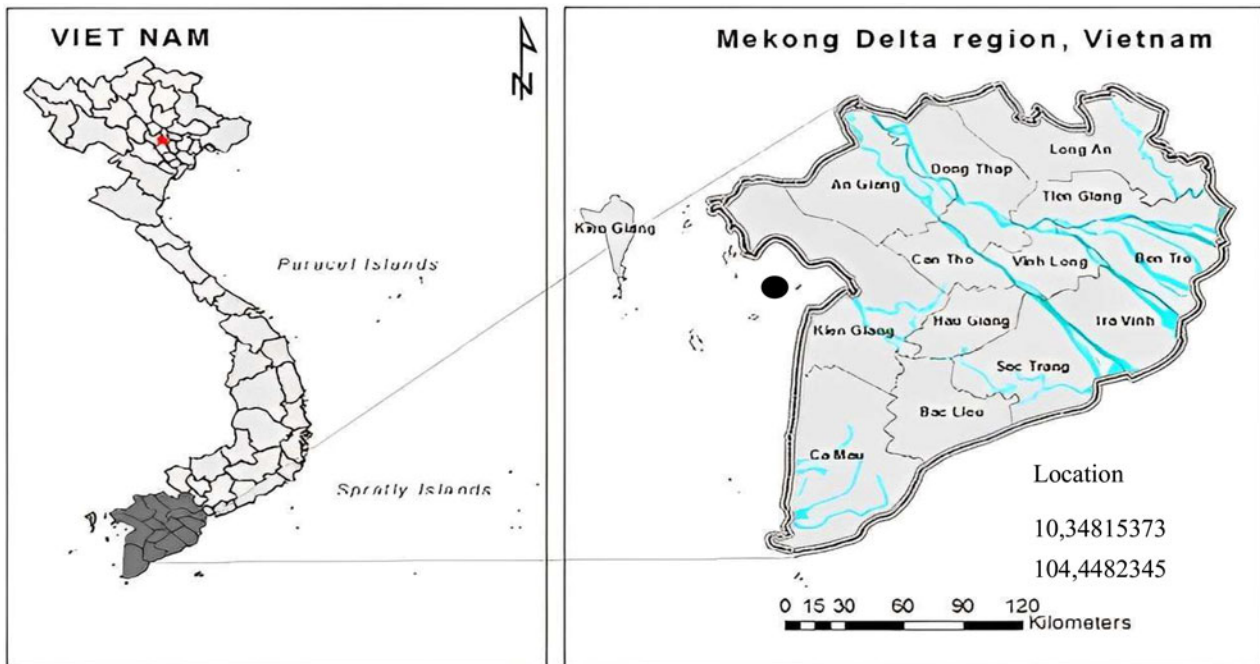


Figure 1. Collection sites of the *Tenulosa* specimen in the Kien Giang province of Vietnam. A black circle on the map indicates the sampling location.

determined through Sanger sequencing at Sangon Biotech. Chromatographs were used to check and edit sequences, which were assembled using Codon Code Aligner software (Centerville, MA, USA).

The COI gene sequence was lodged in NCBI as *T. ilisha* OR088067. The COI sequence was compared with the sequences of other *Tenulosa* for species identification using BLAST. The sequence obtained in this study also was aligned to other *Tenulosa* species (KX786670.1, KY751995.1, Nc 016682.1, NC 016719.1, MK572252.1) with *Gudusia chapra* (MK572252.1) as the outgroup using the MUSCLE algorithm. A neighbour-joining tree (NJ tree) was reconstructed under the Kimura 2-Parameter model selected by using MEGA XI (Mello, 2018).

Results

The water parameters at the sampling location: temperature ranged from 28.4 to 31.7°C and salinity from 25.0 to 28.0 ppt. The specimen was 418 mm in length and 1428 g in weight, showing a size-weight correlation within its species (Nima *et al.*, 2020). It had a head length of 29.0% and pectoral fin length of 31.1% of its standard length, indicative of its unique body proportions (Salini *et al.*, 2004; Hossain *et al.*, 2022). Notably, the presence of 34 scutes aided in species identification (Tint *et al.*, 2019). The specimen showed a higher gill rakers count of 283, and a caudal fin length within the moderate range for *Tenulosa* species (Table 1), distinguishing it from *T. macrura*, *T. toli* and *T. reevesii*.



Figure 2. Photograph showing the *Tenulosa ilisha* (418 mm in TL) collected in Vietnam.

The amplified COI gene of the specimen was 1532 bp in length and 98.76% match with *T. ilisha* sequences in GenBank (NC_016682.1). The reconstructed phylogenetic tree confirmed that the Giang Thanh River specimen is a *T. ilisha* (Figure 3). A close relationship between *T. ilisha* and *T. toli* was supported by a 100% bootstrap value.

Discussion

Prior research suggested that the *T. ilisha* was extinct in the South China Sea (Arjunaidi *et al.*, 2016; Blaber *et al.*, 2023). The discovery of them in Vietnamese Giang Thanh River suggests a broader migratory pattern or habitat adaptation within the Indo-Pacific region. The *T. ilisha* is an indigenous anadromous fish in the Indo-Pacific (Brierley and Kingsford, 2009; Hossain *et al.*, 2019a), inhabiting the coasts, estuaries and rivers of southern Asia countries (Sahoo *et al.*, 2018; Ghosh *et al.*, 2022). Its habitat preferences include extensive continental shelves (Hossain *et al.*, 2016; Dwivedi, 2019), monsoonal influences, significant precipitation and runoff (Naskar *et al.*, 2017; Leal Filho *et al.*, 2022), surface temperatures of 20–30°C (Kundu *et al.*, 2020), seasonally shifting currents (Hossain *et al.*, 2019b), moderate organic productivity (Sarker *et al.*, 2016) and coastal waters with lower salinity (Mohindra *et al.*, 2023). The water conditions at the sampling location are suitable for the *T. ilisha*'s growth and survival (Fernandes *et al.*, 2016; Das *et al.*, 2020; Dalpadado *et al.*, 2021). This finding is significant as it suggests that the Giang Thanh River could serve as a previously unrecognized habitat or migration pathway for this species. Nonetheless, further studies are essential to assess the population size, genetic variation and ecological impact of the *T. ilisha* in Vietnamese water.

The specimen has a shorter head and longer tail than *T. toli* and *T. reevesii*, similar head length and caudal fin length to *T. macrura*, but higher in the number of gill rakers than *T. toli* and *T. macrura* (Table 2). This variation possibly reflects its wide geographic range, ecological diversity, feeding habits and preferences (Borah *et al.*, 2022; Sarker *et al.*, 2023). These differences can distinguish *T. ilisha* from *T. macrura*, *T. toli* and *T. reevesii*, which often get confused due to their similar appearance

Table 1. Morphometric measure and meristic characters of the *T. ilisha* specimen

Character	Range
Body weight (B)	1428 g
Morphometric (mm)	
1. Total length (TL)	418
2. Fork length (FL)	357
3. Standard length (SL)	347
4. Pelvic fin length (PVFL)	33
5. Pectoral fin length (PFL)	54.7
6. Caudal fin length (CFL)	107
7. Predorsal length (PDL)	144
8. Preanal length (PAL)	234
9. Prepectoral length (PPCL)	63
10. Prepelvic length (PPVL)	142
11. Length of dorsal fin base (LDFB)	136
12. Length of anal fin base (LAFB)	138
13. Mouth height (MH)	46
14. Upper jaw length (UJL)	47
15. Lower jaw length (LJL)	39
16. Length of caudal peduncle (LAFB)	51
17. Depth of caudal peduncle (DCP)	35
18. Body depth (BD)	111
19. Body width (BW)	56
20. Snout length (SNL)	27
21. Eye diameter (ED)	23
22. Head length (HL)	76
23. Girth	305
24. HL% of SL	29%
25. CFL% of SL	31%
26. PVFL% of SL	9.51%
Meristic	
27. Dorsal fin ray (DFR)	18
28. Anal fin ray (AFR)	20
29. Pectoral fin ray (PCFR)	15
30. Pelvic fin ray (PVFR)	9
31. Prepelvic scutes (PrePVSC)	19
32. Postpelvic scutes (PostPVSC)	17
33. Total number of scutes (TSC)	34
34. Gill raker on lower arch of the first-gill arch	283

TL, total length; SL, standard length; g, grams.

and overlapping distribution (Bhaumik, 2015b). However, morphological identification alone may not be sufficient or accurate, and molecular genetic analysis is often needed to confirm the species identity and phylogenetic relationships of *Tenuulosa* species.

Although *T. ilisha* is found in Bruneian and Malaysian waters (Azri *et al.*, 2020), only one record *T. ilisha* was found in Vietnam in 1994, with no supported data (Nguyen and Nguyen, 1994). The complexity of visually identifying *Tenuulosa* species needs molecular genetic analysis for validation. The confusion in

morphological identification among these species can be attributed to their genetic similarities and differences (Rahman *et al.*, 2018; Abdullah *et al.*, 2021; Afrand *et al.*, 2023). The BLAST analysis revealed that the *T. ilisha* sample from Kien Giang closely matched the Indian hilsa species, with a 2708 score reflecting a high gene sequence similarity. The 98.76% query cover confirms extensive sequence overlap, suggests a significant genetic link and a common evolutionary background between the two populations. The NJ tree (Figure 3) also suggested that the Kien Giang sample is *T. ilisha*.

The phylogenetic analysis indicated *T. ilisha* and *T. toli* are closely related (Figure 3), as evidenced by a 10,000 bootstrap value, suggesting a strong genetic link between the two species. This close relationship implies they share similar appearances and structures, which leads to confusion when naming them based solely on morphology. On the other hand, *G. chapra*, the outgroup species, appears to be distantly related to *T. ilisha*, and shows significant genetic divergence (Egana *et al.*, 2018; Milec *et al.*, 2022). This genetic distance helps to clarify the evolutionary lineage of *T. ilisha* and its separation from the outgroup species (Sarker *et al.*, 2021; Sultana *et al.*, 2022).

The low genetic diversity and the presence of admixed individuals without precise grouping could further contribute to the morphological confusion (Jorde and Wooding, 2004; Slovák *et al.*, 2012; Holm *et al.*, 2018; Garmendia *et al.*, 2022). Recent studies highlighted the low genetic variation within *T. ilisha* populations, suggesting a single panmictic population with admixture from other populations (Sarker *et al.*, 2021). Moreover, the genetic population structure of *T. ilisha* is influenced by its highly migratory nature (Mohindra *et al.*, 2019; Habib *et al.*, 2022; Sultana *et al.*, 2022). The presence of distinct genetic barriers, limited gene flows and complex evolutionary processes has resulted in a significant population genetic and phylogeographic structure for *T. ilisha* (Asaduzzaman *et al.*, 2019a; Habib *et al.*, 2022). The genetic relationships and evolutionary history of *T. ilisha* are complex and influenced by various factors, including migration patterns, genetic diversity and population structure (Asaduzzaman *et al.*, 2019a, 2020). These factors play a crucial role in the morphological similarities and differences observed among *Tenuulosa* species and have important implications for their identification and conservation.

Climate change significantly affects species distribution, as warmer temperatures and altered sea conditions disrupt marine ecosystems and migration (Harley *et al.*, 2006; Brierley and Kingsford, 2009; Doney *et al.*, 2012). The presence of *Tenuulosa* in Vietnam's Kien Giang Sea is influenced by climate change (Mitra and Mitra, 2013), and ocean currents (Blaber, 2002; Habib *et al.*, 2022). The occurrence of *T. ilisha* in Malay and Brunei (Roberd *et al.*, 2019; Yakup *et al.*, 2019; Azri *et al.*, 2020) implies climate-driven range shifts explain its presence in the Kien Giang Sea. Genetic studies corroborate revealing the species' evolutionary links and possible migration routes (Asaduzzaman *et al.*, 2019b, 2020). Closeness of India to the Kien Giang Sea suggests a dispersal path, aided by ocean currents serving as natural passageways. Comprehending these elements and their interactions is crucial for understanding the effects of climate change on marine life diversity and formulating effective preservation measures.

Conclusion

Our study confirmed the presence of *T. ilisha* in Vietnamese waters, a species once considered extinct locally. Utilizing the COI gene for molecular identification, we emphasize the necessity of refined molecular techniques testing uncertain morphological traits. The detection of *T. ilisha* indicates potential novel

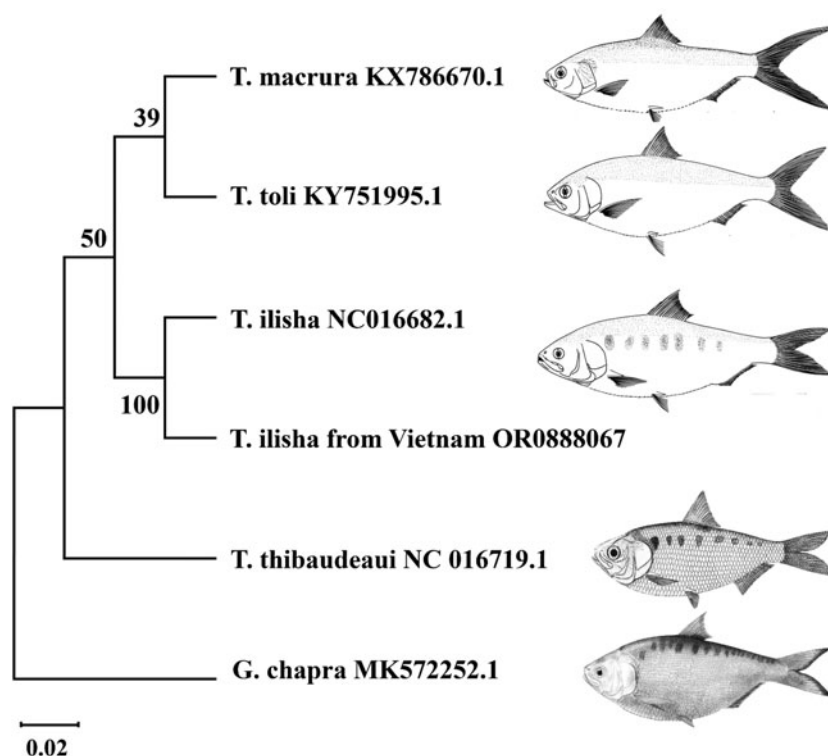


Figure 3. Phylogenetic tree of four species of the *Tenulosa* genus based on cytochrome oxidase subunit I (COI) gene sequences and *Gudusia chapra* from the same family as the outgroup. The neighbour-joining (NJ) tree was reconstructed using K2P model with 10,000 replications for bootstrap analysis.

Table 2. Distinctive biological characters and geographical distribution of five *Tenulosa* species found in Indo-Pacific region (Yakup *et al.*, 2019)

<i>T. ilisha</i>	<i>T. toli</i>	<i>T. macrura</i>	<i>T. reevesii</i>	<i>T. thibaudeai</i>
Caudal fin moderate, 25–31% of CFL % of SL	Caudal fin relatively short, 31–34% of CFL % of SL	Caudal fin long, 40–42% of CFL % of SL	Caudal fin moderate, 25–31% of CFL % of SL	Caudal fin moderate, about 25–30% of CFL % of SL
Gill rakers fine and numerous, about 100–250	Gill rakers fine but not numerous, 60–100	Gill rakers fine but not numerous, 60–75	Gill rakers fine and numerous, 80–250	Gill rakers fine and very numerous, 204–316
Indo-West Pacific	Indo-West Pacific	Western Central Pacific	Northwest Pacific	Mekong endemic, middle to the Delta

CFL % of SL, ratio of caudal fin length for standard length.

migratory routes, warranting further exploration of its movement and habitat choices, and reassessment of conservation tactics and the advocacy of sustainable fisheries to preserve its existence. Future research should target the ecological elements aiding endurance of *T. ilisha* in Vietnam and the development of collective management approaches with community, policy and research stakeholders.

Data availability. The data sets include morphological measurements and genetic sequences are available at NCBI: **OR088067** of *T. ilisha* specimen collected from Vietnamese waters.

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Author contributions. Vanthu Giap conceived the study, designed and coordinated the research, performed molecular genetic studies and sequence alignment and drafted the manuscript. Md Rashedur Rahman conducted molecular genetic experiments. Chenhong Li provided resources, reviewed and edited the manuscript, supervised the project and provided funding. All authors read and approved the final manuscript.

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Competing interest. None.

Ethical standards. The *Tenulosa ilisha* specimen was collected and examined under the ethical standards and guidelines of the Institute of Aquaculture, Nha Trang University, Vietnam, and in compliance with local regulations and permissions granted by the appropriate Vietnamese authorities. The specimen’s welfare and conservation were prioritized, and all ethical considerations, particularly regarding handling and identification, met international standards.

References

- Abdullah TA, Al-Noor SS and Javadmanesh A (2021) Genetic distance of anadromous *Tenulosa ilisha* (Hamilton, 1882) in Shatt al-Arab River based on partial sequencing of mitochondrial DNA. *Agriculture and Natural Resources* 55, 848–853.
- Afrand M, Sourinejad I, Shahdadi A and Vera M (2023) DNA barcoding for identification and discovery of fish species in the protected mangroves of Hormozgan, Iran. *Estuaries and Coasts* 46, 1–15.

- Arai T and Amalina R** (2014) New record of a tropical shad *Tenualosa ilisha* (Teleostei: Clupeidae) in Malaysian waters. *Marine Biodiversity Records* 7, e66.
- Arijunaidi NN, Zakaria MF, Aziz AHA, Shahreza MS, Jaafar TNAM, Seah YG and Asma AN** (2016) Authentication of *Tenualosa* species in Perak River, Malaysia: Application of morphological measurement and molecular analysis of partial CO1 and 16S genes to resolve species ambiguity. *Aquaculture, Aquarium, Conservation & Legislation* 9(6), 1355–1363.
- Asaduzzaman M, Igarashi Y, Wahab MA, Nahiduzzaman M, Rahman MJ, Phillips MJ, Huang S, Asakawa S, Rahman MM and Wong LL** (2019a) Population genomics of an anadromous hilsa shad *Tenualosa ilisha* species across its diverse migratory habitats: discrimination by fine-scale local adaptation. *Genes* 11, 46.
- Asaduzzaman M, Wahab MA, Rahman MJ, Nahiduzzaman M, Dickson MW, Igarashi Y, Asakawa S and Wong LL** (2019b) Fine-scale population structure and ecotypes of anadromous hilsa shad (*Tenualosa ilisha*) across complex aquatic ecosystems revealed by NextRAD genotyping. *Scientific Reports* 9(1), 16050.
- Asaduzzaman M, Wahab MA, Rahman MM, Nahiduzzaman M, Rahman MJ, Roy BK, Phillips MJ and Wong LL** (2020) Morpho-genetic divergence and adaptation of anadromous hilsa shad (*Tenualosa ilisha*) along their heterogenic migratory habitats. *Frontiers in Marine Science*, 7 Article 554.
- Azri A, Taha H, Metali F, Ahmad N and Arai T** (2020) Validation of occurrence and ecological implication of tropical shads *Tenualosa ilisha* and *T. toli* (Teleostei: Clupeidae) in Bruneian and Malaysian waters. *Thalassas: An International Journal of Marine Sciences* 36, 41–46.
- Bandara T and Wijewardene L** (2023) Global research effort on hilsa shad (*Tenualosa ilisha*) – insights from scientometrics. *Thalassas: An International Journal of Marine Sciences* 39(2), 1–16.
- Bhaumik U** (2015a) Migration of hilsa shad in the Indo-Pacific region – a review. *International Journal of Current Research and Academic Review* 3, 139–155.
- Bhaumik U** (2015b) Review of global studies on food, growth and maturity profile of Indian shad (*Tenualosa ilisha*). *International Journal of Current Research and Academic Review* 3, 127–139.
- Bhaumik U** (2017) Fisheries of Indian shad (*Tenualosa ilisha*) in the Hooghly–Bhagirathi stretch of the Ganga River system. *Aquatic Ecosystem Health & Management* 20, 130–139.
- Blaber S** (2002) 'Fish in hot water': the challenges facing fish and fisheries research in tropical estuaries. *Journal of Fish Biology* 61, 1–20.
- Blaber SJ, Milton DA, Brewer DT and Salini JP** (2023) Biology, fisheries, and status of tropical shads *Tenualosa* spp. in south and southeast Asia. Proceedings of the American Fisheries Society Symposium, 2003. American Fisheries Society, pp. 49–58.
- Borah S, Vaisakh G, Jaiswar A, Bhattacharjya B, Deshmukhe G, Sahoo A, Gogoi P, Meena D, Mohanty D and Das B** (2022) Food spectrum dynamics of anadromous hilsa, *Tenualosa ilisha* (Hamilton, 1822) inhabiting River Brahmaputra, India curtailing apprehension of food selectivity: an insight into its domestication. *Indian Journal of Geo-Marine Sciences (IJMS)* 51, 67–77.
- Brierley AS and Kingsford MJ** (2009) Impacts of climate change on marine organisms and ecosystems. *Current Biology* 19, R602–R614.
- Dalpadano P, Arrigo KR, van Dijken GL, Gunasekara SS, Ostrowski M, Bianchi G and Sperfeld E** (2021) Warming of the Indian Ocean and its impact on temporal and spatial dynamics of primary production. *Progress in Oceanography* 198, 102688.
- Das I, Lauria V, Kay S, Cazcarro I, Arto I, Fernandes JA and Hazra S** (2020) Effects of climate change and management policies on marine fisheries productivity in the north-east coast of India. *Science of the Total Environment* 724, 138082.
- Doney SC, Ruckelshaus M, Emmett Duffy J, Barry JP, Chan F, English CA, Galindo HM, Grebmeier JM, Hollowed AB and Knowlton N** (2012) Climate change impacts on marine ecosystems. *Annual Review of Marine Science* 4, 11–37.
- Dwivedi A** (2019) Morphometric variations between seasonal migrants of anadromous shad *Tenualosa ilisha* (Hamilton, 1822) from Hooghly Estuary, India. *Marine and Freshwater Research* 70, 1427–1435.
- Egana JP, Bloom DD, Kuo C-H, Hammerf MP, Tongnunuig P, Iglésiash SP, Sheavesi M, Grudpank C and Simonsb AM** (2018) Phylogenetic analysis of trophic niche evolution reveals a latitudinal herbivory gradient in Clupeoidei (herrings, anchovies, and allies). *Molecular Phylogenetics and Evolution* 124, 151–161.
- Fernandes JA, Kay S, Hossain MA, Ahmed M, Cheung WW, Lazar AN and Barange M** (2016) Projecting marine fish production and catch potential in Bangladesh in the 21st century under long-term environmental change and management scenarios. *ICES Journal of Marine Science* 73(5), 1357–1369.
- Garmendia A, Merle H, Sanía M, López C and Ferriol M** (2022) Morphologic, genetic, and biogeographic continua among subspecies hinder the conservation of threatened taxa: the case of *Centaurea aspera* ssp. *scorpiurifolia* (Asteraceae). *Scientific Reports* 12, 932.
- Ghosh P, Rajawat VS, Nazir A, Banerjee Y, Nath AK and Sakthivel T** (2022) Stable isotope on hilsa shad (*Tenualosa ilisha*) otoliths revealed migratory behavior of a population found in Hooghly River, West Bengal, India. *Environmental Biology of Fishes* 105, 1909–1918.
- Habib KA, Nam K, Xiao Y, Sathi J, Islam MN, Panhwar SK and Habib AS** (2022) Population structure, phylogeography and demographic history of *Tenualosa ilisha* populations in the Indian Ocean region inferred from mitochondrial DNA sequence variation. *Regional Studies in Marine Science* 54, 102478.
- Harley CD, Randall Hughes A, Hultgren KM, Miner BG, Sorte JC, Thornber CS, Rodriguez LF, Tomanek L and Williams SL** (2006) The impacts of climate change in coastal marine systems. *Ecology Letters* 9(2), 228–241.
- Holm AK, Elameen A, Oliver BW, Brandsæter LO, Floistad IS and Brurberg MB** (2018) Low genetic variation of invasive *Fallopia* spp. in their northernmost European distribution range. *Ecology and Evolution* 8, 755–764.
- Hossain M, Sharifuzzaman S, Chowdhury S and Sarker S** (2016) Habitats across the life cycle of hilsa shad (*Tenualosa ilisha*) in aquatic ecosystem of Bangladesh. *Fisheries Management and Ecology* 23, 450–462.
- Hossain MA, Das I, Genevier L, Hazra S, Rahman M, Barange M and Fernandes JA** (2019a) Biology and fisheries of hilsa shad in Bay of Bengal. *Science of the Total Environment* 651, 1720–1734.
- Hossain MS, Sharifuzzaman S, Rouf MA, Pomeroy RS, Hossain MD, Chowdhury SR and AftabUddin S** (2019b) Tropical hilsa shad (*Tenualosa ilisha*): biology, fishery and management. *Fish and Fisheries* 20(1), 44–65.
- Hossain MY, Rahman MA, Rahman O, Islam MA, Rahman MA, Hasan MR, Mawa Z, Tanjin S, Shakila M, Sarmin AN and Chowdhury AA** (2022) Morphological characteristics and length-weight relationships of hilsa shad *Tenualosa ilisha* (Hamilton, 1822) (Actinopterygii: Clupeidae) in the Ganges River, Bangladesh. *Acta Zoologica Bulgarica* 74, 75–83.
- Hughes AC** (2017) Understanding the drivers of Southeast Asian biodiversity loss. *Ecosphere* 8, e01624.
- Jorde LB and Wooding SP** (2004) Genetic variation, classification and 'race'. *Nature genetics* 36, S28–S33.
- Khan MA, Wahab MA, Haque AM, Nahiduzzaman M and Phillips MJ** (2020) Value chain impact of the increased hilsa shad (*Tenualosa ilisha*) harvest in Bangladesh. *International Food and Agribusiness Management Review* 23, 355–368.
- Koh LP and Sodhi NS** (2010) Conserving Southeast Asia's imperiled biodiversity: scientific, management, and policy challenges. *Biodiversity and Conservation* 19, 913–917.
- Kundu GK, Islam MM, Hasan MF, Saha S, Mondal G, Paul B and Mustafa MG** (2020) Patterns of fish community composition and biodiversity in riverine fish sanctuaries in Bangladesh: implications for hilsa shad conservation. *Ecology of Freshwater Fish* 29(2), 364–376.
- Leal Filho W, Nagy GJ, Martinho F, Saroar M, Erache MG, Primo AL, Pardo MA and Li C** (2022) Influences of climate change and variability on estuarine ecosystems: an impact study in selected European, South American and Asian countries. *International Journal of Environmental Research and Public Health* 19, 585.
- Liu J** (2013) Status of marine biodiversity of the China Seas. *PLoS ONE* 8, e05719.
- Mello B** (2018) Estimating TimeTrees with MEGA and the TimeTree Resource. *Molecular Biology and Evolution* 35, 2334–2342.
- Milec LJM, Vanhove MPM, Bukinga FM, De Keyzer EL, Kapepula VL, Masilya PM, Mulimbwa NS, Wagner CE and Raeymaekers JA** (2022) Complete mitochondrial genomes and updated divergence time of the two freshwater clupeids endemic to Lake Tanganyika (Africa) suggest intralacustrine speciation. *BMC Ecology and Evolution* 22, 1–17.
- Mitra A and Mitra A** (2013) Climate change and its impact on brackish water fish and fishery. *Sensitivity of Mangrove Ecosystem to Changing Climate*, pp 191–217.
- Miyata N, Mori T, Kagehira M, Miyazaki N, Suzuki M and Sato K** (2016) Micro CTD data logger reveals short-term excursions of Japanese sea bass from seawater to freshwater. *Aquatic Biology* 25, 97–106.
- Mohindra V, Divya BK, Kumar R, Singh RK, Dwivedi AK, Mandal S, Masih P, Lal KK and Jena JK** (2019) Genetic population structure of a highly

- migratory hilsa shad, *Tenualosa ilisha*, in three river systems, inferred from four mitochondrial genes analysis. *Environmental Biology of Fishes* **102**, 939–954.
- Mohindra V, Chowdhury LM, Chauhan N, Paul A, Singh RK, Kushwaha B, Maurya RK, Lal KK and Jena JK** (2023) Transcriptome analysis revealed osmoregulation related regulatory networks and hub genes in the gills of hilsa shad, *Tenualosa ilisha*, during the migratory osmotic stress. *Marine Biotechnology* **25**, 161–173.
- Naskar M, Chandra G, Sahu SK and Raman RK** (2017) A modeling framework to quantify the influence of hydrology on the abundance of a migratory Indian shad, the hilsa *Tenualosa ilisha*. *North American Journal of Fisheries Management* **37**, 1208–1219.
- Nguyen H and Nguyen N** (1994) Checklist of marine fishes in Vietnam. Vol. 2. Osteichthyes, from Elopiformes to Mugiliformes. *Science and Technics Publishing House, Vietnam*, 54–55.
- Nima A, Hossain MY, Rahman MA, Mawa Z., Hasan MR, Islam MA, Rahman MA, Tanjin S, Sabbir W, Bashar MA and Mahmud Y** (2020) Temporal variations of length, weight, and condition of Hilsa shad, *Tenualosa ilisha* (Hamilton, 1822) in the Meghna River, Southeastern Bangladesh. *Egyptian Journal of Aquatic Biology and Fisheries* **24**, 481–494.
- Pomeroy RS, Garces LR, Pido MD, Parks JE and Silvestre G** (2019) The role of scale within an ecosystem approach to fisheries management: policy and practice in Southeast Asian seas. *Marine Policy* **106**, 103531.
- Rahman A, Begum M, Reza H, Ahsan M and Ahmed M** (2018) Molecular characterization of hilsa shads in Bangladesh using cytochrome C oxidase subunit 1 (CO1) gene. *International Journal of Fauna and Biological Studies* **5**, 1–5.
- Roberd AA, Taha H, Metali F, Ahmad N and Arai T** (2019) Validation of occurrence of tropical shads, *Tenualosa ilisha* (Hamilton, 1822) and *T. toli* (Valenciennes, 1847) (Teleostei, Clupeidae), in Malaysian waters. *Check List* **15**, 65–69.
- Sahoo AK, Wahab MA, Phillips M, Rahman A, Padiyar A, Puvanendran V, Bangera R, Belton, B, De DK, Meena DK and Behera BK** (2018) Breeding and culture status of hilsa (*Tenualosa ilisha*, Ham. 1822) in South Asia: a review. *Reviews in Aquaculture* **10**, 96–110.
- Salini J, Milton D, Rahman M and Hussain M** (2004) Allozyme and morphological variation throughout the geographic range of the tropical shad, hilsa *Tenualosa ilisha*. *Fisheries Research* **66**, 53–69.
- Sarker MJ, Rashid F and Tanmay M** (2016) Assessment of coastal water habitat with reference to the variability of plankton during spawning season of Indian river shad in Greater Noakhali-Bangladesh. *Journal of Ecosystem & Ecography* **6**, 197.
- Sarker A, Jiang J, Naher H, Huang J, Sarker KK, Yin G, Baki MA and Li C** (2021) Cross-species gene enrichment revealed a single population of hilsa shad (*Tenualosa ilisha*) with low genetic variation in Bangladesh waters. *Scientific Reports* **11**, 11560.
- Sarker MJ, Sarker PK, Cahoon LB, Dipty AK, Bashar MA, Hasan MM, Mahmud Y and Sarker MM** (2023) Seasonal variation in the epibenthic feeding habits of hilsa shad (*Tenualosa ilisha*) in the Upper Meghna River Estuary, Bangladesh. *Fishes* **8**, 335.
- Slovák M, Kučera J, Marhold K and Zozomová-Lihová J** (2012) The morphological and genetic variation in the polymorphic species *Picris hieracioides* (Compositae, Lactuceae) in Europe strongly contrasts with traditional taxonomical concepts. *Systematic Botany* **37**, 258–278.
- Sultana S, Hasan MM, Hossain MS, Alim MA, Das KC, Moniruzzaman M, Rahman MH, Salimullah M and Alam J** (2022) Assessment of genetic diversity and population structure of *Tenualosa ilisha* in Bangladesh based on partial sequence of mitochondrial DNA cytochrome b gene. *Ecological Genetics and Genomics* **25**, 100139.
- Tint K, Ko Z and Oo N** (2019) Morphological identifications and morphometric measurements of genus *Tenualosa* spp. fowler, 1934 (Family Clupeidae) in Mon coastal areas, Myanmar. *Journal of Aquaculture & Marine Biology* **8**, 17–22.
- Todd PA, Ong X and Chou LM** (2010) Impacts of pollution on marine life in Southeast Asia. *Biodiversity and Conservation* **19**, 1063–1082.
- Turan C, Ergüden D, Gürlek M and Turan F** (2004) Genetic and morphologic structure of *Liza abu* (Heckel, 1843) populations from the rivers Orontes, Euphrates and Tigris. *Turkish Journal of Veterinary & Animal Sciences* **28**, 729–734.
- Yakup NF, Taha H, Metali F, Ahmad N and Arai T** (2019) Validation of occurrence of a tropical shad *Tenualosa toli* (Teleostei: Clupeidae) in Brunei Darussalam. *Tropical Ecology* **60**, 299–302.