

Length–weight relations of ten freshwater fish species (Actinopterygii) from Abashiri River basin, eastern Hokkaido, Japan

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Abstract

Length–weight relations (LWRs) were estimated for ten freshwater fish species such as gin-buna, *Carassius langsdorffii* Temminck et Schlegel, 1846; lake minnow, *Rhynchocypris percunura* (Pallas, 1814); Siberian loach, *Barbatula toni* (Dybowski, 1869); Japanese smelt, *Hypomesus nipponensis* McAllister, 1963; masu salmon, *Oncorhynchus masou* (Brevoort, 1856); rainbow trout, *Oncorhynchus mykiss* (Walbaum, 1792); whitespotted char, *Salvelinus leucomaenis* (Pallas, 1814); ninespine stickleback, *Pungitius pungitius* (Linnaeus, 1758); hana-kajika, *Cottus nozawae* Synder, 1911; and a species of goby *Rhinogobius* sp. Specimens were collected once a month except in the snow season from the Abashiri River basin, eastern Hokkaido, between June 2007 and November 2011. Fishes were captured by an electrofishing device (Smith–Root Inc., Model 12-b). The estimated allometric coefficient b values ranged from 2.790 (ninespine stickleback) to 3.294 (hana-kajika), and r^2 values ranged from 0.772 (lake minnow) to 0.994 (goby). All the LWRs were highly significant, with $P < 0.001$. Besides, the study provides the first estimates of LWRs for the Siberian loach, Japanese smelt, masu salmon, whitespotted char, hana-kajika, and the goby.

Keywords

LWRs, gin-buna, goby, lake minnow, ninespine stickleback, hana-kajika, Siberian loach, rainbow trout

Introduction

Length–weight relations (LWRs) are important for morphological comparisons between different congeneric species and populations from different geographical areas (Herath et al. 2014; Panda et al. 2016; Roul et al. 2017a, 2017b, 2018; Tran et al. 2021). Several freshwater fishes inhabit the Abashiri River basin in Hokkaido. However, the species' primary biological parameters,

such as LWRs, have been poorly studied or have not been studied at all. Hence, the presently reported study aimed to provide the first estimates of LWRs for gin-buna, *Carassius langsdorffii* Temminck et Schlegel, 1846 (Cyprinidae); Siberian loach, *Barbatula toni* (Dybowski, 1869) (Balitoridae) (Figs. 1 and 2); Japanese smelt, *Hypomesus nipponensis* McAllister, 1963 (Osmeridae); masu salmon, *Oncorhynchus masou* (Brevoort, 1856) (Salmonidae); whitespotted char, *Salvelinus leucomaenis*



Figure 1. Siberian loach, *Barbatula toni* collected from the Abashiri River, Japan.



Figure 2. Siberian loach, *Barbatula toni* collected from the Kemichappu River in the Abashiri River basin, Japan.



Figure 3. Hana-kajika, *Cottus nozawae* (16.3 cm TL, 72.7 g) collected from the Chimikeppu River in the Abashiri River basin, Japan.

(Pallas, 1814) (Salmonidae); hana-kajika, *Cottus nozawae* Synder, 1911 (Cottidae) (Figs. 3 and 4); and a goby *Rhinogobius* sp. (Gobiidae). In addition, this study was intended to provide a new estimate of LWRs for alien rainbow trout, *Oncorhynchus mykiss* (Walbaum,

1792) (Salmonidae), exploited in eastern Hokkaido, Japan, and new estimates of LWRs for lake minnow *Rhynchocypris percnura* (Pallas, 1814) (Cyprinidae) and ninespine stickleback *Pungitius pungitius* (Linnaeus, 1758) (Gasterosteidae) inhabiting Asia.



Figure 4. Hana-kajika, *Cottus nozawae* collected from the Abashiri River, Japan.

Materials and methods

The fishes were collected once a month except in the snow and snow-melt season from June 2007 to November 2011, from Abashiri River basin (i.e., Abashiri River, Horokama-hashiri stream, Kemichappu River, Chimikeppu River, and Tsubetsu River; 43°28′–44°01′N, 143°48′–144°16′E). All fishes were captured by an electrofishing device (Smith–Root Inc., Model 12-b). Fishes were measured in the field after being anesthetized by the clove oil (Anderson et al. 1997). In gin-buna, lake minnow, Japanese smelt, and salmonid fishes the fork length (FL) was measured while in other fishes the principal measurement was the total length (TL) and a fish measuring board with 0.1 cm accuracy was used. Total body weight (BW) was determined by an electronic balance with 0.1 g accuracy.

The length–weight relations (LWRs) for all species were calculated using the equation

$$\log(\text{BW}) = \log(a) + b \log(\text{FLorTL})$$

where BW is the total body weight [g], FL is the fork length [cm], TL is the total length [cm], $\log(a)$ is the intercept related to body form and b is the coefficient indicating allometric growth. The parameters of a and b were estimated by a simple linear regression after logarithmic transformation of length and weight data. Extreme outliers were removed from the regression analysis by performing a log-log plot of the length–weight pairs (Froese 2006). The 95% confidence interval (CI) of parameters a and b and coefficient of determination (r^2) were estimated.

Results

The details on length–weight relations (LWRs) of all species are given in Table 1. All the LWRs showed highly significance levels ($r^2 > 0.772$, $P < 0.001$). The formula of LWRs were estimated to be $\text{BW} = 0.0213\text{FL}^{2.9353}$ for gin-buna, $\text{BW} = 0.0139\text{FL}^{2.9953}$ for lake minnow, $\text{BW} = 0.0076\text{TL}^{2.9797}$ for Siberian loach, $\text{BW} = 0.0089\text{FL}^{2.8731}$

Table 1. LWRs parameters for 10 freshwater fish species collected from Abashiri River basin, eastern Hokkaido, Japan.

Species	<i>n</i>	Fork length [cm]	Total length [cm]	Weight [g]	<i>a</i>	95%CI _{<i>a</i>}	<i>b</i>	95%CI _{<i>b</i>}	<i>r</i> ²
<i>Carassius langsdorffii</i>	764	2.1–29.7	—	22.4–410.0	0.0213	0.0176–0.0258	2.9353	2.8713–2.9991	0.915
<i>Rhynchocypris percunura</i>	58	5.3–9.7	—	1.6–13.5	0.0139	0.0058–0.0334	2.9953	2.5685–3.4221	0.772
<i>Barbatula toni</i>	4611	—	2.0–19.8	0.1–121.0	0.0076	0.0074–0.0079	2.9797	2.9635–2.9960	0.966
<i>Hypomesus nipponensis</i>	13	5.3–10.9	—	0.9–7.4	0.0089	0.0012–0.0636	2.8731	2.0411–3.7051	0.789
<i>Oncorhynchus masou</i>	8208	1.9–21.9	—	0.1–161.5	0.0106	0.0103–0.0109	3.0397	3.0245–3.0550	0.949
<i>Oncorhynchus mykiss</i>	3410	2.0–40.0	—	0.1–800.0	0.0117	0.0114–0.0120	2.9970	2.9854–3.0094	0.987
<i>Salvelinus leucomaenis</i>	3314	2.3–52.0	—	0.1–1700.0	0.0121	0.0117–0.0126	2.9424	2.9273–2.9558	0.978
<i>Pungitius pungitius</i>	9	—	3.0–6.8	0.2–3.0	0.0119	0.0028–0.0507	2.7901	2.0579–3.5222	0.873
<i>Cottus nozawae</i>	38	—	5.4–17.3	1.7–76.8	0.0071	0.0050–0.0099	3.2937	3.1593–3.4282	0.985
<i>Rhinogobius</i> sp.	3	—	6.0–9.0	2.2–8.4	0.0063	0.0001–0.7084	3.2860	2.9194–3.6526	0.994

n = number of individuals studied, *a* = intercept of relation, *b* = slope of relation, CI = confidence interval, *r*² = co-efficient of determination.

for Japanese smelt, $BW = 0.0106FL^{3.0397}$ for masu salmon, $BW = 0.0117FL^{2.9970}$ for rainbow trout, $BW = 0.0121FL^{2.9424}$ for whitespotted char, $BW = 0.0119TL^{2.7901}$ for ninespine stickleback, $BW = 0.0071TL^{3.2937}$ for hana-kajika, and $BW = 0.0063TL^{3.2860}$ for *Rhinogobius* sp.

Discussion

In addition to the fishes mentioned in the results, the following species were collected during the investigation: lampreys (especially ammocoetes larva), *Lethenteron reissneri* (Dybowski, 1869) and *Lethenteron camtschaticum* (Tilesius, 1811), and redfins, *Pseudaspius hakonensis* (Günther, 1877) and *Pseudaspius sachalinensis* (Nikolskii, 1889), these were difficult to identify in the field and were excluded from this study.

This study was the first report to determine LWRs of Siberian loach, Japanese smelt, masu salmon, whitespotted char, hana-kajika, and *Rhinogobius* sp. These LWRs were not found in the FishBase (Froese R, Pauly 2022) except for Russian sea-run form of masu salmon. However, Kato (1992) reported the LWR of whitespotted char in Japan; the formula was $BW = 0.01389SL^{3.0181}$, where SL is the standard length. Besides, Kato (1991) reported the LWR of subspecies of masu salmon, *O.masou ishikawai* in Japan; the formula was $BW = 0.00220SL^{3.66}$. Both reports using SL were not directly comparable to this study's results using FL. On the other hand, there are some reports of the LWRs of alien rainbow trout,

Oncorhynchus mykiss, in Europe and western Asia (Esmaceli and Ebrahimi 2006; Erguden and Goksu 2008; Verreycken et al. 2011), but there has been no report from eastern Asia. In addition, the LWRs for lake minnow and ninespine stickleback were studied at Lake Baikal in Russia (IGFA 2001) and Lake Superior in the USA (Devine 2002), respectively. These LWRs of this study were the first records in Asia. Furthermore, since the LWRs of gin-buna were recorded from only one individual (IGFA 2001), the results of this study enriched the database. As for the goby, its species identity has not yet been determined, and according to Nakabo (2013), it is probably a species included in *Rhinogobius kurodai* (Tanaka, 1908), but *R. kurodai* is not listed in FishBase. These results that provide primary data for further biological research will be useful for fishery conservation in the Abashiri River basin.

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First record of the batfish, *Halieutaea indica* (Actinopterygii: Lophiiformes: Ogcocephalidae), from the Red Sea

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Abstract

The Indian handfish or batfish, *Halieutaea indica* Annandale et Jenkins, 1910, is recorded for the first time from the Red Sea. This report constitutes also the first record of the family Ogcocephalidae from this region.

Keywords

batfish, *Halieutaea indica*, handfish, Red Sea

Introduction

The batfishes (Ogcocephalidae) are benthic marine fish species found in tropical and sub-tropical regions. They are found on soft bottoms of the continental slope, most species between 200 and 1000 m depth, while a few species live in shallower waters among rocks or reefs (Bradbury 2003). Their diet includes small snails, small clams and scallops, a variety of worms and small crustaceans, and occasionally small fishes. As far as we know, eggs, larvae, and postlarvae are all pelagic, the postlarvae transparent, globular in shape, sometimes reaching 25 to 30 mm, metamorphosing upon settling to the bottom (Bradbury 2003). Nelson et al. (2016) estimated 78 species in ten genera, but later Prokofiev (2019 and 2020) added another two species. Fricke et al. (2021a) counted 90 valid species in ten genera. The genus *Halieutaea* Valenciennes, 1837, round batfish or handfishes include eleven valid species with a wide Indo–west Pacific distribution from South Africa east to the Hawaiian Islands, north to southern Japan, south to northern Australia (Prokofiev 2020; Fricke et al. 2021b). It was characterized by Bradbury (1967) as hav-

ing, among other characters, the disk very flat and rounded, isolated lateral-line organs on ventral surface of tail present, teeth absent from palate, frontal bones forming a groove, but absence of small scales on ventral surface of tail, pupillary opercula, or bucklers.

While sorting old material from the Hebrew University Fish Collection, we were surprised to find a specimen of Batfish belonging to the family of Ogcocephalidae that was collected in February 1958 in the southern Red Sea. Consequently, it was identified as the Indian handfish, *Halieutaea indica* Annandale et Jenkins, 1910. This report constitutes the first record of this species and family in the Red Sea. The specimen was deposited in the Fish Collection of the Hebrew University (HUJ) and received the catalogue number HUJ 10625.

Materials and methods

Measurements and counts follow Hubbs and Lagler (1947). The vertebrae were counted using an X-ray. The classification follows Fricke et al. (2021b); family

authorship follows Van der Laan et al. (2014). Abbreviations used: HJ = The Hebrew University of Jerusalem, Israel; MNHN = Muséum national d'histoire naturelle, Paris, France; SMNS = Staatliches Museum für Naturkunde in Stuttgart. SL = standard length.

Comparative material. *Halieutaea fumosa*: SMNS 24740 (1, 68 mm SL), Taiwan, Kueishan Island. *Halieutaea indica*: MNHN 1986-0004 (1, 82 mm SL), 27 Feb. 1973, depth 445–455 m, Madagascar, 23°36'0"S, 043°31'1.2"E; MNHN 1986-0005 (1, 85 mm SL), 2 Feb. 1973, depth 445–455 m, Madagascar, 23°36'0"S, 043°31'1.2"E; MNHN 1986-0104 (1, 82 mm SL), 4 Mar. 1973, depth 70–74 m, Madagascar, 25°4'1.2"S, 047°6'3.6"E. *Halieutaea stellata*: SMNS 23752 (1), Loyalty Islands, Lifou; SMNS 24623 (1, 135 mm SL), Taiwan, Kueishan Island; SMNS 25863 (2), China; SMNS 25886 (1), China.

Results

Family Ogcocephalidae Gill, 1893

- Halieutaea indica* Annandale et Jenkins, 1910 (their figs. 1, 2, and 3)
Halieutaea indica Annandale et Jenkins, 1910: 19, pl. 2 (fig. 4) (Bay of Bengal, off Orissa coast, India).
Lophie faujas Lacepède, 1798: 318, pl. 11 (figs. 2–3) (no locality; appeared as vernacular name only; not available, nomen nudum).
Lophius muricatus Shaw, 1804: 382, pl. 162 (no locality; based on the “*Lophie faujas*” of Lacepède 1798; not treated as valid after 1900).
Astrocanthus stellatus Swainson, 1839: 331, fig. 108 (no locality stated; based on the “*Lophie faujas*” of Lacepède, 1798; preoccupied by *Lophius stellatus* Vahl, 1797 when both are in *Halieutaea*).
Halieutaea sinica Tchang et Chang, 1964: 156, pl. 1 (figs. 1–3) (Swamei, Guangdong Province, China).
Halieutea spicata Smith, 1965: 39, pl. 11 (fig. A) (Isipingo, KwaZulu-Natal, South Africa, southwestern Indian Ocean).

Material. HJ 10625, 1 specimen, 77.2 mm SL, Eritrea, Southern Red Sea, Coll. O. Oren, Feb. 1958,

Description of HJ 10625. Head and body round and depressed, width subequal to length. Upper surface and tail densely covered with broad-base tubercle spines, most of them bicuspid or tricuspid. Ventral surface sparsely covered with minute spinules. Tail round in cross section, its length four times in SL. Mouth with small fine teeth, its width 4.7 in SL. Eyes in dorsal position, their diameter 10.9 times in SL. Interorbital slightly depressed, 6.3 times in SL. Small dorsal fin in posterior position with four rays. Pectoral fins with shape of “elbow” with ten rays well distanced from each other, their length 3.1 times in SL. Prepectoral length 1.5 times in SL. Ventral fins with a single spine and four rays, its length 4.2 times in SL. Preventral distance 2.6 times in SL. 22 vertebrae.

Color. Dorsal surface grayish-brown, spines lighter in color, ventral surface light grayish-beige, pectoral and ventral fins brown.

Table 1. Measurements and counts of *Halieutaea indica* (HJ 10625) from Eritrea, southern Red Sea.

Character	Measurement [mm]	Count
Total length	90.1	
Standard length	77.2	
Body width	55.3	
Mouth width	16.3	
Interorbital	12.1	
Distance between gill openings	15.9	
Predorsal length	57.2	
Prepectoral length	50.8	
Prepelvic length	29.8	
Snout to gill opening	46.6	
Pectoral-fin length	25.6	
Pelvic-fin length	18.2	
Caudal-fin length	20.0	
Distance between pectoral-fin bases	18.8	
Distance between pelvic-fin bases	9.0	
Dorsal fin		4
Anal fin		4
Pectoral fin		12
Pelvic fin		5
Caudal fin		7

Discussion

The characters of the Red Sea ogcocephalid specimen well agree with those of *Halieutaea indica* (see Table. 1).

Halieutaea indica was originally described by Annandale and Jenkins (1910: 19, pl. 2 (fig. 4), based on 9 syntypes from the Bay of Bengal, off Orissa coast, India, northeastern Indian Ocean. The species is distinguished from its congeners by having the following combination of characters: broad-based, thorn-like spines on dorsal surface of disc long, closely-spaced, nearly uniform in size; those on tail as long as on disc; underside of disc sparsely covered by small bucklers (broad-based thorns); tooth patches on ceratobranchials-5 with long and pointed inner posterior extension; dorsal surface of disc with irregular patches of pigment or without pattern; pectoral fin unpigmented (Prokofiev 2020).

This taxon was first described and illustrated as “*La Lophie Faujas*” by Lacepède (1798: 318, pl. 11, figs. 2–3), without a stated locality. The holotype is still extant (MNHN A.4542), but the name is not available, as it was based on a vernacular name only. The first Latinization was the description of *Lophius muricatus* by Shaw (1804: 382, pl. 162); this name is treated as a nomen oblitum, as it was not treated as valid after 1900, and its priority is reversed in favor of *Halieutaea indica* Annandale et Jenkins, 1910 (which is here declared a nomen protectum). The subsequent description of *Astrocanthus stellatus* by Swainson (1839: 331, fig. 108) is a secondary homonym and preoccupied by *Lophius stellatus* Vahl, 1797 when both are in *Halieutaea*.

The batfishes (Ogcocephalidae) are marine fish species found in tropical and sub-tropical regions. Nelson et al. (2016) enumerated 78 species in ten genera, but later Prokofiev (2019 and 2020) added another two species. The family Ogcocephalidae was not known

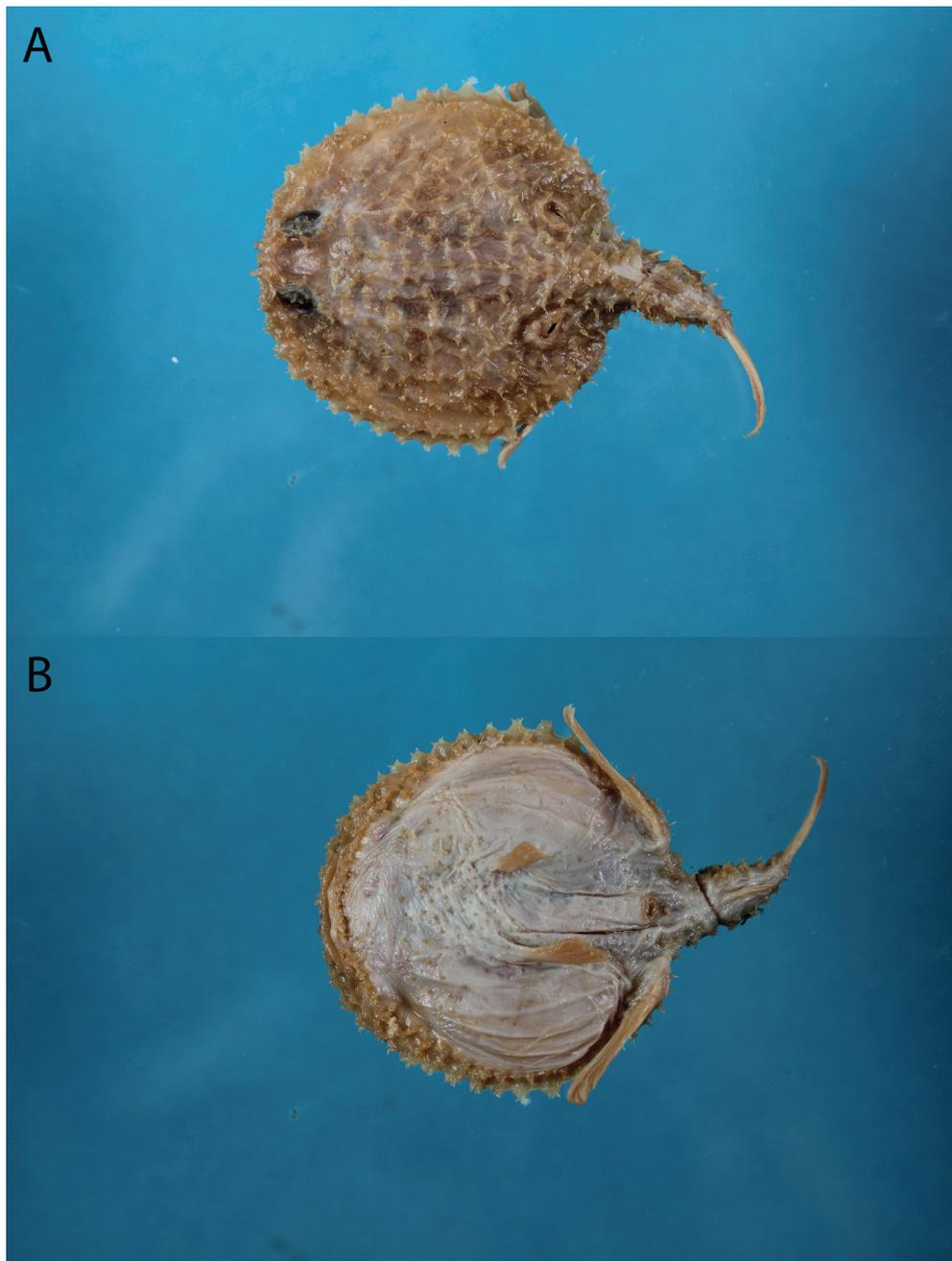


Figure 1. *Halieutaea indica* HUI 10625, 77.2 mm SL, Eritrea, southern Red Sea. (A) dorsal view, (B) ventral view (photograph: D. Golani).

hitherto from the Red Sea. The genus *Halieutaea* Valenciennes, 1837, round batfish or handfishes include eleven valid species with wide Indo–Pacific distribution from south Africa to Japan, Hawaii, and Australia (Prokofiev 2020).

Halieutaea indica has a wide Indo–west Pacific distribution from the western Indian Ocean, South Africa, Seychelles (Smith 1965), and recently recorded from the Gulf of Oman (Owfi et al. 2021) to northern Australia, China (Tchang and Chang 1964) and Japan (Kailola 1987; Kuitert and Tonzuka 2001) (Fig. 3). *Halieutaea indica* is a demersal species mostly found on muddy

substrate to depths of 500 m. It “walks” on the sea floor using its “elbow-shape” pectoral fins. The IUCN Red List designated this species to be in the category of “Least Concern”.

The family Ogcocephalidae was not known hitherto from the Red Sea. *Halieutaea indica* is apparently very rare in the Red Sea, since in the past six decades no other specimen has been collected. Alternatively, this can also be explained by its occupying a niche that has been rarely sampled. This is an interesting addition to the Red Sea ichthyofauna; this finding illustrates that the fish diversity of the southern Red Sea is still poorly known.

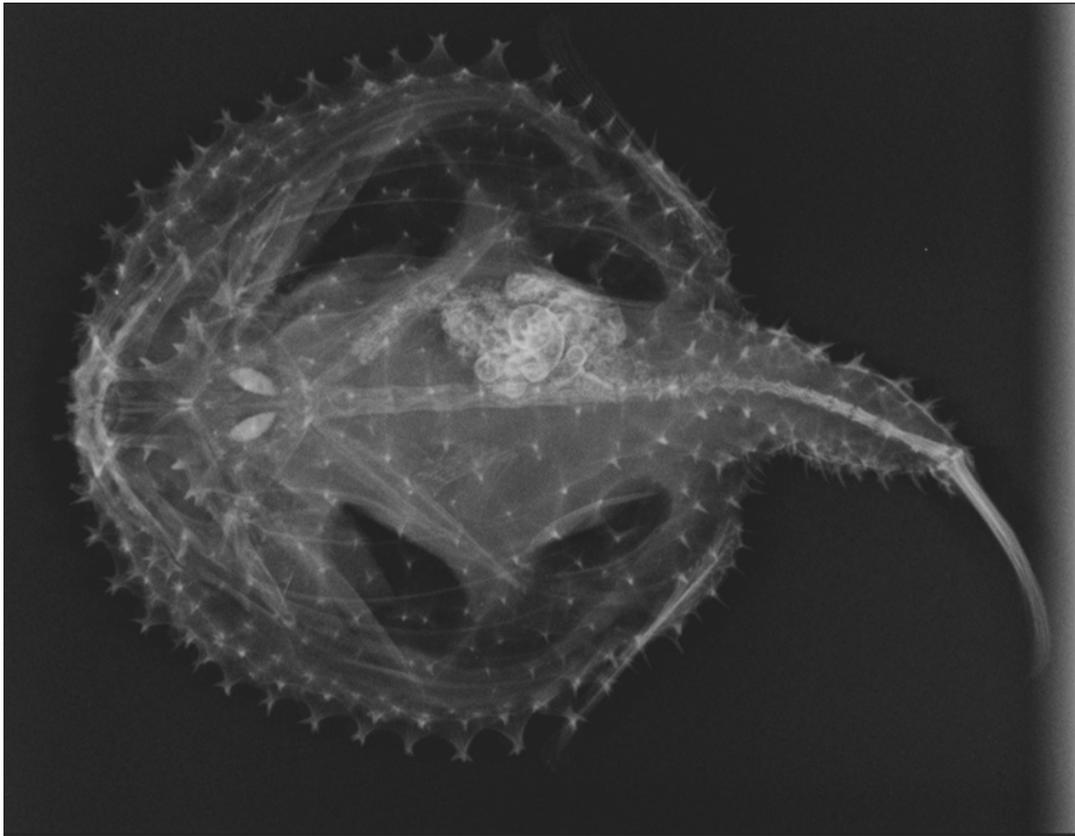


Figure 2. X-ray radiograph of *Halieutaea indica*, HUI 10625, 77.2 mm, Eritrea, southern Red Sea. Dorsal view (photograph: I. Aizenberg).

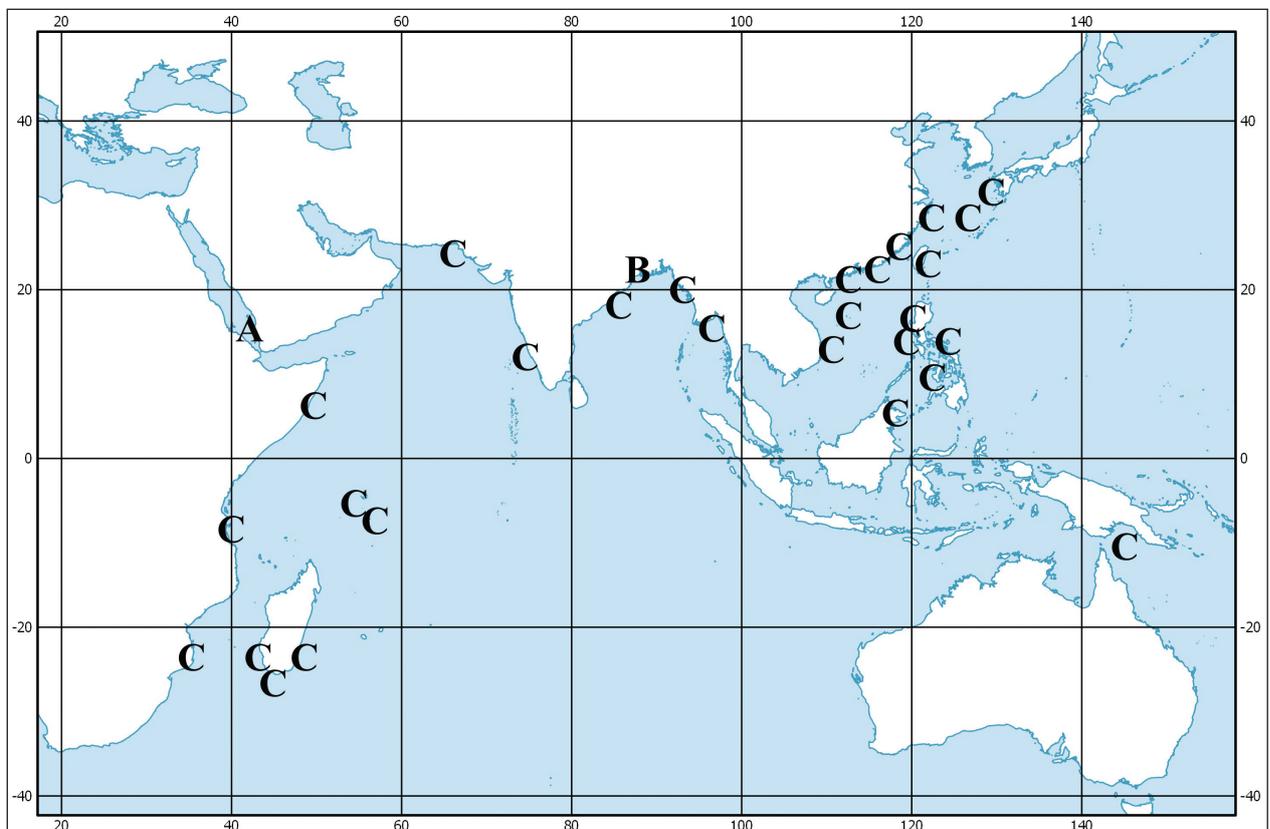


Figure 3. Geographical distribution of *Halieutaea indica*. (A) New record from southern Red Sea. (B) Type locality. (C) Other records based on literature and material in collections.

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First record of the Philippine snubnose halfbeak, *Melapedalion breve* (Actinopterygii: Beloniformes: Hemiramphidae), from Bangka Belitung Islands, Indonesia

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Abstract

A single specimen (117.1 mm standard length) of *Melapedalion breve* (Seale, 1910) collected off Lepar Island, Bangka Belitung Islands, Indonesia, represents the first record of *M. breve* from Indonesian waters and the southernmost record of the species. *Melapedalion breve* has previously been recorded from the Sulu Sea (southwestern Philippines) and eastern central South China Sea.

Keywords

distribution, southernmost record, South China Sea, Sulu Sea

Introduction

The monotypic genus *Melapedalion* (Beloniformes, Hemiramphidae), represented by the Philippine snubnose halfbeak, *Melapedalion breve*, was originally described by Seale (1910) as *Oxyporhamphus brevis*, based on specimens collected from Paawacan, Palawan Island, Philippines. Subsequently, Fowler (1934) and some later authors (e.g., Collette 1974, 1999, 2000, 2004; Parin et al. 1980; Kottelat 2013) treated the species as *Melapedalion breve*.

A single short-beaked hemiramphid specimen, collected off Lepar Island, Bangka Belitung Islands, Indonesia and recently found in the collections of the Research Center for Oceanography, Jakarta (NCIP), was identified as *M. breve*, a species previously known only from the Sulu

Sea and eastern central South China Sea (Collette 1999, 2000, 2004). Representing the first record of *M. breve* from Indonesian waters and southernmost record of the species, the specimen is described below.

Methods

Methods for counts and proportional measurements followed Collette and Su (1986). Gill rakers were counted on the right side of the head, and the preorbital canal type confirmed by removing anterior scales from the right side orbit. Standard length is expressed as SL. Descriptive characters are based on the Indonesian specimen. The specimen was transferred to the Museum Zoologicum Bogoriensis, Bogor, Indonesia (MZB), and re-cataloged.

Results

Family Hemiramphidae Gill, 1859

Melapedalion Fowler, 1934

Melapedalion breve (Seale, 1910)

(Figs. 1 and 2)

Material examined. MZB.26439, 117.1 mm SL, Lepar Island, Bangka Belitung Islands, Indonesia, 02°53'16.2"S, 106°48'35.5"E, 1 m depth, beach seine, Fahmi, 1 October 2010.

Description. Dorsal fin rays 16; anal fin rays 15; pectoral fin rays 12; pelvic fin rays 6; gill rakers on first gill arch 8 + 20 = 28; pre-dorsal scales ca. 37. Morphometrics (expressed as percentage of SL): head length 23.9% of SL; snout length 7.8% of SL; upper jaw length 6.4% of SL; upper jaw width 6.2% of SL; lower jaw length 3.0% of SL; preorbital length 7.8% of SL; orbit diameter 6.4% of SL; pectoral fin length 13.0% of SL; distance from base of uppermost pectoral-fin ray to base of anteriormost pelvic-fin ray 34.1% of SL; distance from base of anteriormost pelvic-fin ray to base of caudal fin 44.4% of SL; dorsal-fin base length 15.7% of SL; anal-fin base length 12.0% of SL.

Body elongate, subcylindrical; dorsal profile rising slowly from snout tip to above pectoral fin insertion, thereafter parallel to body axis to dorsal fin origin before lowering slowly to upper caudal-fin base; ventral profile sloping gradually from tip of lower jaw to below posterior margin of opercle, thereafter parallel with body axis to anal fin, before elevating gradually to lower caudal-fin base. Upper jaw short, triangular in dorsal view; dorsal surface covered with scales. Lower jaw slightly longer than upper jaw, with distinct symphyseal knob. Jaws with short, minute, dense, conical teeth.

Dorsal and anal fins located on posteriormost quarter of body. Origin of first dorsal-fin ray above anus; base of dorsal fin slightly longer than that of anal fin; posteriormost point of dorsal-fin base slightly posterior to posteriormost point of anal-fin base. Origin of first anal-fin ray below origin of fourth dorsal-fin ray. Pelvic fin short, posteriorly depressed fin not reaching anus; located slightly anterior to mid body length; distance from upper insertion of pectoral-fin base to origin of pelvic fin less than that from origin of pelvic fin to caudal-fin base. Pectoral fins short, not reaching posterior nasal pit when folded forward; uppermost part of pectoral-fin base distinctly higher than snout tip; located slightly posterior to dorso-posterior margin of opercle. Caudal fin deeply forked; lower lobe longer than upper lobe.

Nasal papillae short, rounded, length less than half pupil diameter. Preorbital canal T-shaped, with posterior branch. Preorbital ridge well developed. Posterior margins of preopercle and opercle smooth. Body scales cycloid. Scales on dorsal surface of snout. Lateral line with one branch ascending toward pectoral fin origin.

Color when fresh (Fig. 1A). Head greenish dorsally, whitish ventrally. Upper and lower jaws reddish. Body whitish, with silvery and narrow dark lateral stripes. Pectoral and pelvic fins uniformly translucent whitish; a black spot on base and upper insertion of pectoral fin. Dorsal, anal, and caudal fins translucent yellowish; anterior tips of dorsal and anal fins, and upper and lower caudal-fin lobes distinctly black.

Color of preserved specimen (Fig. 1B). Head blackish dorsally, with silvery lacrimal and operculum. Body yellowish-brown, with silvery and narrow dark lateral stripes. All fins whitish, with distinct dark spot on upper insertion of pectoral fin, anterior dorsal and anal fins, and upper and lower caudal-fin lobes.



Figure 1. Photographs of *Melapedalion breve* collected from Lepar Island, Bangka Belitung Islands, Indonesia. (A) fresh and (B) preserved specimens of MZB.26439, 117.1 mm SL.



Figure 2. Distributional records of *Melapedalium breve*, based on Collette (1999) (red shading) and the presently reported study (star).

Discussion

The Bangka Island specimen agreed closely with the diagnostic characters and morphological description of *Melapedalium breve* (Seale, 1910) given by Collette (1999): e.g., pectoral fin short (13.0% of SL); pectoral-fin rays 12; nasal papillae rounded; scales present on dorsum of snout; preorbital ridge well developed; gill rakers on first gill arch 28; lateral line with one branch ascending toward pectoral fin origin; lower jaw short, only slightly longer than upper jaw; preorbital canal T-shaped, with posterior branch; caudal fin deeply forked, with slightly elongate lower lobe.

The monotypic genus *Melapedalium* is most similar to two other monotypic genera, *Arrhamphus* Günther, 1866 and *Chriodorus* Goode et Bean, 1882, as well as *Oxyporhamphus* Gill, 1864, in having greatly reduced lower jaw length (Collette 2004). However, the latter is distinguished from the three former genera in having the anterior margin of the upper jaw straight (not forming a prominent triangular anterior projection) and a longer pectoral fin (Collette 1999, 2004). Detailed comparisons between *Melapedalium breve* and *Arrhamphus* and *Chriodorus* were given by Collette (1974), the former being distinguished from

the others as follows: preorbital canal with a posterior branch (vs. preorbital canal simple, without a posterior branch); distinct black tips on upper and lower caudal-fin lobes, and on anterior dorsal and anal fins (vs. no distinct black spots on fins); greater number of gill rakers [this study: 28 (vs. 21–25)]; and greater number of vertebrae.

Melapedalium breve has previously been recorded from the Sulu Sea (southwestern Philippines) and eastern central South China Sea (Collette 1999: unnumbered fig; Fig. 2). The specimen described herein, representing the first record of *M. breve* from Indonesia and southernmost record of the species (Fig. 2), suggests that *M. breve* is widely distributed in the South China Sea. The specimen was collected together with silverbiddy (genus *Gerres*) and silverside (genus *Atherinomorus*) fishes in a coastal area (1 m depth) characterized by a sandy bottom with patchy seagrass beds.

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Comparison of technical measures in the Aegean Sea to support harmonization of fisheries management policies

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Abstract

The Aegean Sea features an important archipelago in the Eastern Mediterranean, consisting of 60 inhabited islands, more than 1400 uninhabited islands, about 60–70 commercial marine taxa, along many vulnerable species. Fisheries are mainly coastal and are exploited by Greek and Turkish fishers. The multi-species and multi-gear fisheries operate within each country's 6-nautical mile territorial sea and in the international waters of the Aegean Sea. As the fisheries resources are currently declining in this region, it is clear that current management initiatives are ineffective and would benefit from a new regime aiming to improve the state of the commercial marine resources. This study offers a comparative analysis of certain fishing gear technical measures applied by Greece and Turkey in the Aegean Sea. Identified differences can provide clear and helpful insights for decision-makers for the development of a new and productive management approach in Aegean waters. The fishery regulations were shown to be highly variable, sharing few similarities and stressing many more differences, thus rendering the current management of the shared fish stocks unsustainable. The resources of both states would greatly benefit from the harmonization of management measures focusing on an ecosystem approach to fisheries, and incorporating fishers as stakeholders.

Keywords

Aegean Sea, co-management, fishing gears, Greece, Turkey

Introduction

The Aegean Sea, lies in the Eastern Mediterranean Sea between Greece and Turkey, and comprises GSA 22 of the General Fisheries Commission of the Mediterranean (GCFM). The long coastlines, numerous bays, more than 1450 islands and islets of the area render the Aegean a key fishing region in the Mediterranean. Due to its rich ichthyofauna (449 species for the Turkish coast and 510

species for Hellenic Seas including the Aegean Sea) (Bilecenoğlu et al. 2014; Papaconstantinou 2014) and a large number of artisanal fishers, it collectively supports two of the largest fishing fleets in the Mediterranean which combined represent >18% of the total of the Mediterranean commercial fishing fleet. From 2016 to 2018, 8% of total Mediterranean and Black Sea catches were from the Aegean Sea (FAO 2020). Greece reported 70 commercial taxa in 2018, and Turkey reported 60 commercial taxa

from this sea (GFCM 2021). Both countries' territorial seas in the Aegean extend to 6 nm from their coasts. Currently, 48% of the marine area falls under the national jurisdiction of the two countries, exercised by each State within its respective territorial sea. The remaining area is international waters and, thus, beyond national jurisdiction (Öztürk et al. 2002).

Fisheries in the Eastern Mediterranean are characteristic for targeting multiple species using several different types of gear (from here on multi-species and multi-gear), much like in many other Mediterranean regions (Papaconstantinou et al. 2007; Ünal and Göncüoğlu 2012). In fact, in this region, 42 taxa constitute more than 90% of catches (FAO 2020). Thus, the applications of single-species management measures are mostly ineffective, except when they are highly selective, such as bluefin tuna (*Thunnus thynnus*).

The gear types most commonly used in the Aegean Sea by Greek and Turkish fisheries are towed and dragged gears (bottom trawl, dredges), static gears (gillnets, trammel nets, longlines, pots, hook and line), and encircling gears (purse seine, small surrounding nets) (Nedelec and Prado 1990; Tokaç et al. 2010).

In 2018, 11 580 Greek vessels and 4007 Turkish vessels were operating in the Aegean Sea. Of those, 95% of the Greek vessels and 96.5% of the Turkish vessels were small-scale (TURKSTAT 2019; Conides et al. 2020), which is far greater than the 83% Mediterranean average for the entire small-scale fleet (FAO 2020). Thus, small-scale fisheries (SSF) greatly dominate the marine capture fisheries industry in the Aegean Sea, in terms of the number of vessels and fishers, in both Greece and Turkey (Conides et al. 2020; Ünal and Ulman 2020). The small-scale vessels mainly use gillnets, trammel nets, longlines, fyke nets and surrounding net types, and some traps. The large-scale vessels are trawlers (including otter trawlers), purse seiners, and drifting longliners, while Turkey has 25 additional carrier vessels used in purse seine fishing (HRMRDAF 2019). Greece authorized 356 vessels to fish in the international waters of the Mediterranean in 2018, and Turkey authorized 243 bottom trawlers to fish in international waters in 2018 (GDFA 2020a).

Fisheries in the Aegean Sea are of high importance for both countries in terms of production, food security, and, most importantly, job security and provision in coastal rural areas where alternative employment options are scarce. Around 90% of Greece's (61 955 t) and 15% of Turkey's (42 613 t) total wild marine fishery catches in 2018 were provided by fishing activities in the Aegean Sea (ELSTAT 2019; TURKSTAT 2019). A total of 20 565 employees are directly employed in the fisheries sector in Greece (ELSTAT 2019); the corresponding number in Turkey amounts to 30 878 employees, of which 21% or 6542 fishers work in the Aegean region (TURKSTAT 2019). Furthermore, Greece is the leading country employing fisherwomen, accounting for 7% of total female fishers in the EU (Elliott 2002). However, in Turkey, the official data claims only 1% of the fishers are women

(TURKSTAT 2019), but more localized studies from the Datça-Bozburun Peninsula have shown this percentage to be much higher-up to 20% (Ünal et al. 2015).

Effective fisheries management measures are essential for maintaining stock renewability and fisheries sustainability. Classically, fishery management is divided into two main typologies of capture control: input and output controls. Input controls regulate fishing effort in some manner (e.g., in number of licenses or maximum vessel lengths). Output controls regulate the amount of the catch being withdrawn from the sea (e.g., in catch composition, commercial minimum landing sizes, quotas) (Pope 2009; Bellido et al. 2020). Along with input and output controls, fishery management is also based on the adoption of technical measures that regulate the catchability of fishing gears by limiting features of the gears (Bjorndal 2002) or by their spatial or temporal regulations (Hall 2009). With the exception of large pelagics, the current fishery management regime of the Mediterranean Fisheries is predominantly based on the input control approach along with the adoption of technical measures for fishing gear (Fiorentino and Vitale 2021). The regulations and technical measures implemented by the two countries fishing in the Aegean Sea vary a great deal, forming the basis of this study. Since the two countries share their fisheries resources, many of which move freely between jurisdictions, we propose that technical measures are harmonized between Greece and Turkey, which would require both countries to work jointly to achieve this.

Greece, a member of the European Union, the Common Fishery Policy (CFP) and the relevant EU legislations apply, in addition to their National Legislations (NL) (consisting of Royal decrees-RD, Legislative decrees-LD, and Presidential decrees-PD) aim to regulate fishing effort with appropriate technical measures (Papaconstantinou et al. 2007; OECD 2008). In Turkey, the Fishing Notification is the main regulatory basis for fisheries. The most recent notification (Notification 5/1) adopted on 1 September 2020, is active for four years (GDFA 2020b). Both countries have set mandatory rules for fishing in their territorial waters and international waters of the Aegean Sea. Greek fishing vessels are permitted to fish in international waters after a specific fishing authorization is issued for a fishing license, provided that it is compliant with specific requirements pertaining to national and EU legislation, as well as international regulations on fish stock management (HRMRDAF 2019). In Turkey, unless otherwise decided by the national management authority, the same fisheries laws apply to both territorial and international waters in the Aegean Sea (GDFA 2020b).

Despite regulatory measures enforced in both states, Aegean fisheries have been declining for over two decades, demonstrating that the state of the fisheries has not benefitted under the current management framework. The total annual catches of both Greece and Turkey in the Aegean Sea follow the exact same trends, increasing with the modernization of their fisheries until efforts were maximized, before catches began to decline; although for Greece, the maximum total catch peaked four years earlier

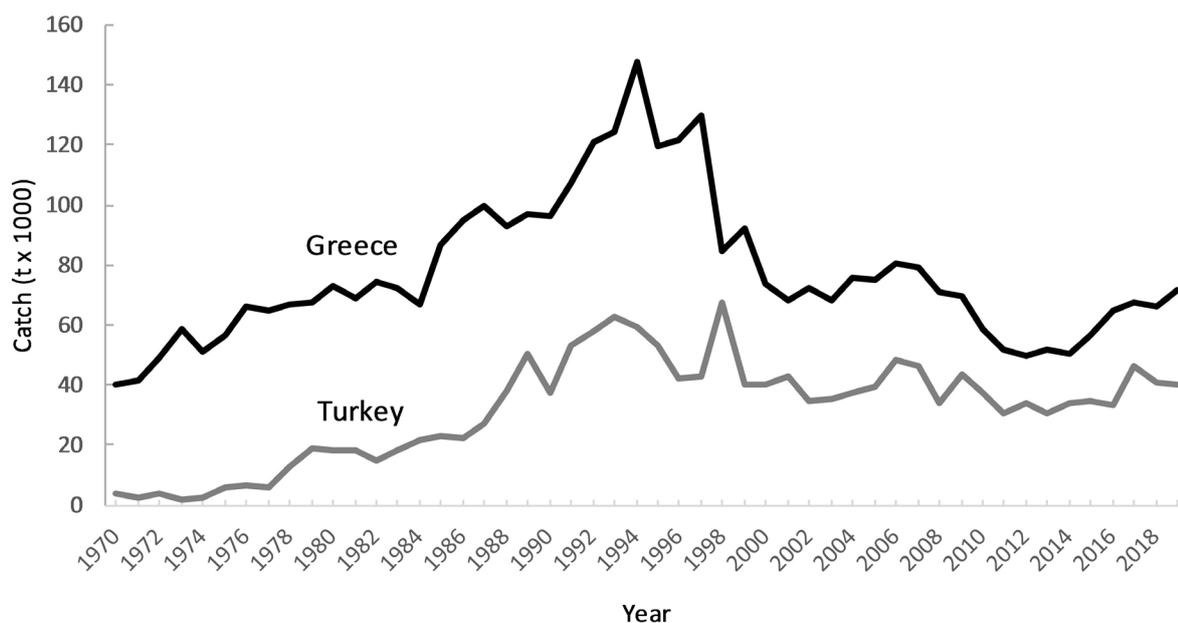


Figure 1. Greek and Turkish total marine wild fisheries catches from the Aegean Sea (1970–2019). Source: GFCM database.

than the Turkish (Fig. 1). In fact, from their peaks until 2019, Greek Aegean catches declined by 51 percentage points, and Turkish Aegean catches declined by 41 percentage points. The small increase in Greek catches in recent years was due to reporting amendments from 2017 that included smaller vessels with engines below 14.17 kW (ELSTAT 2019). A sharp decline in the Fishing-in-Balance (FiB) Index shows declining catches and marine trophic levels, signifying high overexploitation and unsustainable fisheries negatively affecting both ecosystem structure and function (Dimarchopoulou et al. 2021).

The aim of this study was to highlight the current discrepancies in the national fisheries management measures for Greece and Turkey relating to technical measures in terms of fishing gear regulations and spatial and temporal restrictions of fishing activities. We then suggest that a harmonized fisheries management system in the Aegean Sea would benefit the future of the fisheries in the Aegean Sea.

Methods

A literature review of the current fisheries technical regulations was undertaken for both Greece and Turkey. Specifically, the laws that were reviewed for technical comparisons include the relevant EU regulations (Council Regulation EC No. 1967/2006 and Regulation EU 2019/1241) applicable in Greece, as well as Greek National Legislation (NL) (RD: Royal decrees, LD: Legislative decrees, and PD: Presidential decrees) (EU 2006; Papaconstantinou et al. 2007; EU 2019) and the most recent Fishing Notification 5/1 issued by Turkey in 2020 (GDFA 2020b).

The revised International Standard Statistical Classification of Fishing Gear (ISSCFG Revision 1) (FAO 2016) was carefully considered before proceeding to the evaluation of similarities and differences of applicable

technical measures. More specifically, regulations concerning the fishing gear used were examined and compared in relation to the mesh size, net length, height, circumference, and material, as well as the maximum number of permitted gear (types) on board. Moreover, the rules prescribing fishing prohibitions and restrictions for habitats, areas, seasons, species, light sources, soak time, depth, or distance were also evaluated along with provisions pertaining to the monitoring and tracking systems used by fishing vessels. Technical and operational differences were also evaluated for fishing gear. Specifically, Greek and Turkish regulations are compared for each of the 20 different gear types. The fishing gear categorical abbreviation codes and the standard abbreviations of fishing gears used are in unison with ISSCFG.

Comparisons of technical measures of both countries are presented in Tables 1–5. References to additional measures reported in the relevant legislations of only one of the two countries are made prior to the respective Table where applicable. Measures for which no commonalities exist are instead mentioned in the main text, without the need for a table.

Results

Fisheries with surrounding nets. The information presented in Table 1 describes the regulations for surrounding nets for Greece and Turkey, in particular purse seines (PS) (01.1), which greatly contribute to total catches of both countries. Both countries implement technical measures regarding the maximum net height, minimum operating depth or distance from the coast, along with seasonal and spatial prohibitions, and light use. Greece applies three additional measures regarding a minimum mesh size of 14 mm, maximum net length of 800 m, with prohibited

Table 1. Technical measures for purse seine (PS) (01.1) fisheries in the Aegean Sea.

Parameter	Greece	Turkey
Maximum height	120 m (except tuna purse seine nets)	164 m (except tuna purse seine nets)
Minimum depth or distance	Min. distance: 300 m distance Min. depth: 50 m; 70% of purse seine's height 100 m min distance from coast line, irrelevant of depth (PD 25/93)	Min. depth: 24 m
Seasonal prohibition	NL: 15 Dec–28 Feb (for night seines) (PD 25/93) 1 Jul–31 Aug (for day seines) (PD 25/93) Saturdays and those Sundays following full moon (for both day and night seine) (LD 4711/2020 and LD 4691/2020)	15 Apr–31 Aug
Prohibited area	NL: Fishing prohibited in areas closer than 1000 m from entrance to sea farms when they are open for harvest and in areas closer than 500 m measured radially outward from permanent fishing establishments of <i>almadrabas</i> nets (a type of stationary uncovered pound nets) when they operate (PD 25/93). Special spatial prohibitions exist for night seines (PD 23.3/53)	Many spatial prohibitions detailed in fisheries notification
Light use	NL: use of underwater lights by night seines permitted only while lifting nets Use of artificial light more intense than 2000 lumens (> 133.3 W of incandescent light, or > 33.3 W led light) per drifting lighting unit prohibited (PD 25/93) Use of more than five drifting lighting units prohibited (PD 25/93) Fishing with drifting lighting units having light emitting lamp uncovered prohibited (light should be only directed at sea) (PD 25/93)	Lighting permitted only above sea level; use of white light prohibited Light prohibited in shallow waters less than 30 meters and less than 300 meters from fish farm cages 8 additional areas prohibit use of light Only one boat permitted to have light generator; light power up to 100 W does not require permission; total light power of main vessel, auxiliary vessels, and transfer vessel in light fishing allowed areas shall not exceed 8 kW; distance between light boats shall not be closer than 200 m

NL = Greek national legislation, LD = Legislative decrees, PD = Presidential decrees.

areas including seagrass beds (although derogations may be authorized within management plans if the lead-line or the hauling ropes do not touch the seagrass beds), and in all Natura 2000 sites, all specially protected areas and all specially protected areas of Mediterranean interest (SPAMI). Turkey does not yet have any Natura 2000 protected sites but is currently working towards establishing some under EU Guidance. Surrounding nets without purse lines (LA) (01.2) in Greece operate only on the basis of a management plan, and no such plan is currently in force; these gears are not prohibited in Turkey, but Turkish fishers do not use them.

Fisheries with seine nets. Beach seines (SB) (02.1) are prohibited in all Greek and Turkish waters. Fishing with beach seines above seagrass beds and coralligenous habitats and mäerl beds and in all Natura 2000 sites, all specially protected areas, and all specially protected areas of Mediterranean interest (SPAMI) are prohibited in Greece. Boat seines (SV) (02.2) are prohibited in Turkey. Seine nets can be put in operation only on the basis of a management plan in Greece, but no such plan is in force.

Fisheries with trawls. There are detailed regulations for single boat bottom otter trawlers (OTB) in both countries, which are compared in Table 2. A management plan (MD 271/2576/2014 ‘National Management Plan for Bottom Trawl Net Fishing’) specific for bottom otter trawls, approved by the European Commission, has been in force since early 2014 and is implemented throughout Greece (MRDF 2014; HRMRDAF 2019). Greece (as opposed to Turkey) implements measures relating to net characteristics and habitat protection; A balloon codend is prohibited in trawl nets; and within any single codend the number of

equal-sized meshes around any circumference of the codend shall not increase from the front end to the rear end. The circumference of the rearmost part of the trawl body or of the extension piece shall not be smaller than the circumference of the front end of the codend *sensu stricto*. For a square mesh codend, the circumference of the rearmost part of the trawl body or of the extension piece shall be from two to four times the circumference of the front end of the codend *sensu stricto*. As the habitat protection concerns trawling on seagrass beds and coralligenous habitats and mäerl beds and in all Natura 2000 sites, all specially protected areas and all specially protected areas of Mediterranean interest (SPAMI) are prohibited. The minimum mesh size for the codend is 40 mm for square mesh in both countries, while it is 50 mm for diamond mesh in Greece and 44 mm in Turkey. Turkish legislation, on the other hand, requires that the mesh of the trawl body must not be smaller than the codend. In Greece and Turkey for the Aegean Sea, the use of mid-water pelagic trawls (PTM) (03.22) and beam trawls (TBB) (03.11) are prohibited (Papaconstantinou et al. 2007; GDFA 2020b).

Fisheries with towed and mechanized dredges. Technical measures for towed dredges (DRB) (04.1) are in force in Greece, but the use of towed dredges is prohibited in the Turkish Aegean fisheries. Two dredge types are used in Hellenic fisheries, one called *argaleios*, for bivalve mollusks (smooth scallop *Flexopecten glaber*; brown venus *Callista chione* and the bearded horse mussel *Modiolus barbatus*) and another called *gagava* for sponge-fishing which is a traditional fishing method in the Dodecanese region (southeastern Aegean Sea) (Papaconstantinou et al. 2007). Greek measures include: maximum sizes of 3 m breadth (except for sponge fishing), minimum depth,

Table 2. Technical measures for single boat bottom otter trawls (OTB) (03.12) in the Aegean Sea.

Parameter	Greece	Turkey
Minimum mesh size	40 mm square mesh or 50 mm diamond mesh	40 mm square mesh or 44 mm diamond mesh
Codend	120 mm (if codend mesh smaller than 60 mm)	Mesh size of protective bag must not be smaller than 2 times of codend mesh size
Protective bag		
Material	Use of netting with twine thickness > 3 mm or with multiple twines; or netting with twine thickness > 6 mm in any part of bottom trawl prohibited	Use of monofilament material prohibited in codend of bottom trawl
Minimum depth or distance	Use of multiple twines prohibited on any towed net in net and codend Beyond 3 nm distance from coastline or beyond 50 m isobath (whichever comes first); in any case, bottom trawl net fishing prohibited at any distance < 1.5 nm from coast, regardless of depth (MD 271/2576/2014, EU Reg. 1967/2006 art. 13: 1 and 2)	Min. depth: 200 m (Area 40.3) Min. distances: 1.5 nm (Areas 40.2; 40.4; 40.6) 2 nm (Area 40.1) 3 nm (Areas 40.5; 40.7; 40.8; 40.9)
Maximum depth	1000 m	1000 m
Season prohibition	NL: 1 Jun–30 Sep 24–31 May 24–31 Dec (MD: 271/2576/2014: G.G B 58; par. 9-a) 24 May–15 Jul (for all international waters in Aegean Sea) 16 Jul–30 Sep (in international waters west of 25 th meridian in GFCM subregion GSA 22)	15 Apr–31 Aug (Trawl fleets can fish in international waters with permission from authorities between 15 Jul and 31 Aug)
Prohibited area	NL: many prohibited areas, mainly gulfs and bays (PD: 739/79, PD: 988/80, PD: 228/2006; PD: 68/2009; MD 271/2576/2014)	Many prohibited areas, mainly gulfs and bays specified in notification

NL = Greek national legislation, PD = Presidential decrees, MD = National management plan.

and distance requirements of 50 m isobath or 0.3 nm distance, but can be used within 3 nm (when shellfish catch is $\geq 90\%$ of the total live weight of the catch) and 50 m isobath or 0.5 nm distance from the coast (for sponge fishing); maximum depth of 1000 m; habitat restrictions where fishing with dredges above seagrass beds and coralligenous habitats and mäerl beds and in all Natura 2000 sites, all specially protected areas and all specially protected areas of Mediterranean interest (SPAMI) are prohibited; and national seasonal prohibitions from 1 August through 31 October (for *Venus verrucosa*), from 1 April through 30 June (for *Callista chione*, *Ostrea edulis*, *Modiolus barbatus*, *Donax trunculus*, *Ruditapes decussatus*, *Aequipecten opercularis*), from 1 April through 31 October (for *Flexopecten glaber*), and from 1 November

through 31 March (for *Mytilus galloprovincialis*) (PD 227/2003). Mechanized dredges (DRM) (04.3) are prohibited under Greece and Turkish regulations.

Fisheries with gillnets and trammel nets. Comparisons of technical measures for gillnets (GNS) and trammel nets (GTR) are presented in Table 3. Greece has one additional prohibited area regulation mostly pertaining to closed bays under national legislation (PD 497/88, PD 338/80, PD 986/80, PD 189/78); Turkey, meanwhile, has additional regulations for soak time where gillnets (used for *Sarda sarda*, *Lichia amia*, and *Seriola dumerili*) are prohibited between 07:00 and 19:00 in the Aegean Sea (Güllük and Gökova Gulfs), and are prohibited 500 m from fixed lift nets between 20:00 and 01:00; and

Table 3. Technical measures for set gillnets (anchored) (GNS) (07.1) and trammel nets (GTR) (07.5) in the Aegean Sea.

Parameter	Greece	Turkey
Minimum mesh size	16 mm NL: 20 mm (PD 174/2013) 100 mm (for red sea bream fishing); 68 mm (for <i>Solea</i> spp. fishing) (in Alexandroupolis area and within 3 nm from coast) (PD 986/1980); 36 mm (in Thessaloniki and Thermaikos Gulfs) (PD 189/1978); 64 mm (in part of Maliakos Gulf) (PD 338/1980); 40 mm (within 1.5 nm from coasts of Mesolongi Lagoon) (PD 68/2006); 48 mm (for trammel nets) (228/2006); and 56 mm (for trammel nets used in June in Kalimnos–Kos) (228/2006)	80 mm (for sole and flounder fishing)
Maximum length and height	Max length: 6000 m for gillnets and trammel nets Max height: 10 m for gillnets and 4 m for trammel nets	Max length: 6000 m
Material	> 0.5 mm twine thickness prohibited NL: monofilament nets prohibited (PD: 1094/1977)	Monofilament and multi-monofilament nets prohibited
Species	Bottom-set nets shall not be used to catch following species: albacore, bluefin tuna, Ray's Sardines can be caught with bream, swordfish; sharks (<i>Hexanchus griseus</i> , <i>Cetorhinus maximus</i> , Alopiidae, Carcharhinidae, Sphyrnidae, Isuridae, Lamnidae) Incidental catches of no more than three specimens of shark species pertaining to a certain list of shark species may be retained on board or landed provided that they are not protected species under EU law NL: European hake (in February) (MD 271/2576, GG B/58/2014)	gillnets all year round

NL = Greek national legislation, PD = Presidential decrees, MD = National management plan. Sea bream = *Pagellus bogaraveo*; albacore = *Thunnus alalunga*; bluefin tuna = *Thunnus thynnus*; Ray's bream = *Brama brama*; swordfish = *Xiphias gladius*; European hake = *Merluccius merluccius*.

gillnets must be marked by a surface buoy during the day and a lighted buoy at night and information must be marked on the buoy or on a visible place of the gear indicating the license number of the fishing vessel. Turkey has additional seasonal and spatial restrictions for *alamana* nets, which are prohibited from 15 April through 15 May, also called *voli* nets, which can be equipped with or without trammel nets, without eyebolts and wires, or any pursing mechanism.

Table 4 presents a comparison of regulations for combined gillnets and trammel nets (GTN) in the Aegean Sea, while Greece has an additional length regulation stating that a combined bottom-set net has a maximum length of 500 m and may have a maximum height of 30 m. It is also prohibited to have on board or use more than 2500 m of combined bottom-set nets when the 10 m height limit is exceeded. The use of drift gillnets (GND) (07.2) is prohibited in both countries' fisheries in the Aegean Sea.

Table 4. Technical measures for combined gillnets–trammel nets (GTN) (07.6) in the Aegean Sea.

Parameter	Greece	Turkey
Maximum length and height	Max. length: 2500 m Max. height: 10 m	Max. length: 6000 m Max. height: 22 m for <i>alamana</i> nets when purse seine nets prohibited
Material	Greater than 0.5 mm twine thickness prohibited	Mono and multi monofilament nets prohibited

Fisheries with pots and fyke nets. Greece has several measures for pots (FPO) (08.2) in the Aegean Sea. Greek regulations include: minimum size regulations of 10 mm for eel fishing, named *volkos* (RD 805/1968), 56 mm for crustaceans (PD 157/2004), and 40 mm (within 1.5 nm from the coasts of Mesolongi Lagoon) (PD 68/2006); size restrictions of: Diameter < 1 m, height < 50 cm, opening > 13 cm diameter (for fish cylindrical traps), and length and width restrictions of < 80 cm, height < 45 cm (for crustacean traps) (PD 157/2004), with a maximum number of 250 pots and a minimum depth of 10 m (PD 157/2004, GG A/126/2004). Greece has a 10 m minimum depth measure (PD 157/2004, GG A/126/2004) for fyke nets (FYK) (08.3), while Turkey only prohibits their use for white grouper fishing.

Table 5. Technical measures for harpoons and spearfishing (HAR) (10.1), hand implements (MHI) (10.2), and diving (MDV) (10.8) in the Aegean Sea.

Parameter	Greece	Turkey
Season prohibition	NL: 1 Jun–31 Oct (for bait collection) 1 Jan–31 Mar (for coral fishing) (PD 324/194) 1 May–31 Oct (for sea cucumbers) (PD 48/2018)	1 Jun–31 Oct (for sea cucumbers) 15 Apr–31 Aug (for <i>Donax trunculus</i>)
Soak time	Spear-guns prohibited with scuba gear and at night (PD: 471/1978) NL: Divers prohibited to fish for mollusks at night	Divers prohibited from sunset to dawn for sea cucumbers
Species	NL: Scuba divers and rebreather systems permitted only for mollusk, sponges, and coral fishing but must operate in pairs (PD: 324/94, PD: 86/98)	Commercial fishing for fish using SCUBA, nargile (surface supplied air diving operation), mask, snorkel and spearguns forbidden Special certificates needed to hunt species other than fish by diving Octopus cannot be hunted using scuba, nargile, or any artificial air source Sponge, <i>Donax trunculus</i> and sea cucumbers (latter only in certain areas) can be caught by diving

NL = Greek national legislation, PD = Presidential decrees.

Fisheries with longline. For set longlines (LLS) (09.31), Greece has much more advanced regulations than Turkey in the Aegean Sea. In Greece, there is a minimum hook length of 3.95 cm, and width of 1.65 cm (the latter only applicable for sea bream, *Pagellus bogaraveo*), there are maximum hook numbers: 1000 hooks per person onboard, 5000 hooks per vessel, 7000 hooks per vessel (for vessels fishing more than 3 days), while vessels fishing more than two days can have an equivalent number of spare hooks on board (for surface-set longlines), and there are two prohibited geographic areas, mainly closed bays (PD 435/70, PD 189/78). In the Turkish Aegean Sea, there is a minimum hook width (Turkish *ağız açıklığı*) of 0.72 cm, longlines must be marked using a signal flag (buoy) during the day and lighted buoy at night, and the license number of the fishing vessel must be visibly displayed on the buoy or gear at the surface. It is obligatory to show information (on the buoy or in a visible place of the gear) indicating the license code number of the fishing vessel to which it belongs.

For drifting longline (LLD) (09.32) regulations, both countries apply highly different measures. Greece applies maximum hook numbers (2500 hooks per vessel for swordfish fishing, 5000 hooks per vessel for albacore fishing, and 2000 hooks per vessel for bluefin tuna), with a maximum 70 km main line length measure, and prohibits swordfish fishing in December by Ministerial Decision No. 3265/60504/2018 (HRMRDAF 2019), while vessels out fishing for more than two days can have an equivalent number of spare hooks on board. Turkey applies a 2.8 cm minimum hook width for swordfish only and longlines must be marked using buoys during the day and lighted buoys at night.

Fisheries with harpoons, spear guns, and diving. Comparisons of technical measures for harpoons (HAR) (10.1), hand implements (MHI) (10.2), and diving (MDV) (10.8) are presented in Table 5. Harpoons are used for traditional swordfishing in Turkey. Spearfishing for commercial purposes is prohibited in both states and is only permitted in recreational fishing. Greece has an additional 10 m maximum depth for mollusks, and Turkey prohibits diving using lights in lagoons, areas outside Map 59 for sea cucumber fishing, and prescribes a total annual catch

for sea cucumber fishing, and sponge fishing is permitted only in the north Aegean coast between where the Meriç River flows into the sea and Babakale. In Greece, divers fishing for mollusks use handheld gear named *tsougrana* which must have three ‘teeth’, each one a maximum of eight cm long, with a minimum distance of two cm between them. Turkey also has minimum mesh size technical measures for in hand implements (wrenching gear, clamps, tongs, rakes, spears) for sieves used in grooved carpet shell (Turkish *akivades*), *Ruditapes decussatus* (as 24 mm), warty venus (Turkish *kidonya*), and *Venus verrucosa* (as 30 mm).

Comparative summary of measures

The only similarities found between the two sets of management measures of both states include the following: the prohibition of using driftnets, mid-water pelagic trawls, beam trawls, spearfishing, beach seine, mechanized dredges, otter trawl fishing during summer months and in water deeper than 1000 m, and monofilament materials in gillnet fishing, gillnets longer than 6000 m, lights by skin divers during nocturnal hunting, and the adoption of the minimum 40 mm square mesh codend opening.

As shown in the following paragraph, from the comparison of the national regulations of the two countries regarding certain gear types, many highly diverse technical measures were shown, the most striking of which relate to the complete ban of certain fishing gear types in one country, and not the other, and also maximum net lengths and maximum number of hooks in one country and not the other.

The use of towed dredges is permitted in the Greek Aegean fisheries, while prohibited under Turkish regulations. Otter trawling in Greece is prohibited within a 3 nm minimum distance from the coast or within the 50 m isobath where that depth is reached at a shorter distance. While according to the respective Turkish regulation for the Aegean, the distance determination varies between 200 m (for a very small area), to 1.5 nm, 2 nm, and 3 nm. In both states the overall cumulative timespan for seasonal closures is roughly the same, amounting to approximately 4.5 months; however, the exact time periods do not coincide. Specifically, Greek bottom trawlers are prohibited from fishing from 1 June through 30 September, with additional temporal restrictions from 24 December through 31 December and 24 May through 31 May, while in Turkey trawling is prohibited from 15 April through 31 August. Greek bottom trawlers fish in international waters after issuance from a relevant fishing authorization which is valid for one year. The authorization determines the exact geographical sub-area of the General Fisheries

Commission for the Mediterranean (GFCM) where fishing is permitted, the targeted species and the gear to be used. The use of the authorization is prohibited in GSA 22 from 24 May through 15 July and west of the 25th meridian of GSA 22 from 16 July through 1 October (MRDF 2014). Finally, the minimum mesh size of the diamond mesh in the codend of the trawl is 50 mm in Greece, and 44 mm in Turkey.

In Greece, day and night purse seine maximum net lengths are set at 800 m and the minimum mesh size at 14 mm according to the EU regulation. Turkey, on the other hand, has not yet adopted any such rules on the subject. For purse seine, there are seasonal prohibition differences. Consequently, some key species can be targeted during their reproductive seasons in one of the littoral states, while the other protects this period under diverging regulations; for example, according to Greek legislation, the use of the night purse seine is prohibited during the winter period (15 December–28 February), in order to protect sardine spawning stocks, but catch anchovy in their spawning season in summer (Papaconstantinou et al. 2007). However, in Turkey, the respective seasonal purse seine prohibition (15 April–31 August) incorporates the anchovy spawning season with the aim of protecting their spawning stocks. Fishing for European pilchard is permitted by Turkish law during their spawning season (December–February), but is prohibited in Greece during the same period (Akyol et al. 1996; Cihangir unpublished*). This demonstrates that these two important migratory pelagic stocks can still be targeted by one country’s fleet during their spawning period. Another key distinction is that the minimum operating depth for purse seines is set at 50 m in Greece, and is less than half that depth in Turkey at 24 m; thus, the Turkish purse seine fleet can fish at depths between 24 m and 50 m. This lower minimum depth limit increases the risk of adverse effects on certain benthic habitats of Turkey’s shores, as it permits fishing up to depths of 164 m (equivalent to 90 fathoms). Greece applies additional minimum mesh size, maximum net length, and protected habitats regulations for purse seines, which are absent from the respective Turkish legislation. Specifically, the additional minimum mesh size restrictions are aimed at reducing juvenile mortality within multispecies fisheries (NEMC 1985), and consequently, many of Turkey’s main fished stocks are plagued by both growth and recruitment overfishing. From a fishing effort (in days at sea) perspective, the seasonal prohibitions allow Greek purse seiners to fish in the Aegean for 260 days per year (for day seines) and 248 days per year (for night seines), while Turkish regulations only permit purse seiners to operate for 225 days per year.

Gillnets and trammel nets used by Greek vessels must have a minimum mesh size of 20 mm; with the exception of gillnets targeting *Atherina boyeri* which have a minimum mesh size of 16 mm, and 68 mm for common

* Cihangir B (1991) Ege Denizi’nde sardalya (*Sardina pilchardus* Walbaum, 1792)’nin üreme biyolojisi ve büyümesi. [Growth and reproduction of sardine (*Sardina pilchardus* Walbaum, 1792) in the Aegean Sea.] PhD Thesis, Dokuz Eylül University, İzmir, Turkey. [In Turkish]

sole (*Solea solea*) and European flounder (*Platichthys flesus*), in addition to several other regulations according to species and regions detailed in Table 3, whereas no minimum mesh size regulations exist in Turkey aside from one 80 mm measure for set net targeted sole and flounder. Greece and Turkey both have 6000 m maximum gillnet and trammel net lengths, whereas Greece has additional height and material (twine thickness) restrictions for gillnets and trammel nets. Turkey on the other hand has a maximum soak time and signal regulations in place to identify the owner for gillnets and trammel nets.

The use of pots has many Greek restrictions such as the maximum number of pots, while Turkey only prohibits their use for white grouper. However, fish pots are used for targeting groupers (*Epinephelus* spp.) in the Dodecanese region (southeastern Aegean Sea) by Greek vessels (Papaconstantinou et al. 2007).

The use of set longlines is better regulated in Greece where provisions are made for minimum hook width and the maximum number of hooks, in relation to the species targeted. There is a huge difference between the minimum hook width sizes, of 3.95 cm in Greece, and 0.72 cm in Turkey generally, however for set longlines, Turkey has the same 3.95 cm min. hook width size as Greece but does not impose any regulations for the maximum number of hooks.

The use of drifting longlines is regulated in more detail in Greece compared to Turkey, the latter which has no maximum number of hooks nor maximum total longline length prescribed, with only an implementation for a 2.8 cm minimum hook width regulation for swordfish. This presents another huge disparity, with Greek fishers only permitted to have 5000 hooks per fisher, with Turkish fishers unregulated in this regard.

With scuba diving, all mollusks, sponges and coral can be collected in Greece (except for at night), while only *Donax trunculus* and sea cucumbers can be collected in Turkey, since the catch of fish and octopus with the use of scuba is prohibited, and sponge and corals are nationally protected. For hand-held gears, Greece has maximum size and minimum distance measures for mollusk fishing, whereas Turkey has minimum mesh sizes applied to sieves used for the grooved carpet shell, *Ruditapes decussatus*, and warty venus, *Venus verrucosa*, fishing.

For special habitats, Greece prohibits the use of purse seining, bottom otter trawls, dredging, beach and boat seining above seagrass beds and in some special habitats (in all Natura 2000 sites, all specially protected areas and all specially protected areas of Mediterranean interest-SPAMI) under EU legislation. Also, bottom otter trawling, beach seining, and dredging are prohibited above coralligenous habitats, and mäerl beds in Greece. While in Turkey, industrial fishing is also prohibited in several special habitats such as *Posidonia* beds, coralligenous habitats and mäerl beds, and both beach and boat seine are already prohibited in the Aegean Sea to protect the benthic habitat, indirectly compensating their lack of more specific habitat protection, such as Natura 2000 sites, which are to be implemented in the near future.

The different mesh size regulations and hook length and width features of the two countries have highly different selectivities which diversely affect the marine resources, and such discrepancies can further negatively affect juveniles in areas where the regulations are more relaxed or non-existent.

Discussion

This study highlights numerous differences and fewer similarities existing in the technical measures of the two fishing states in the Aegean Sea which undermines the efficacy of either state to improve the overall state of fisheries. Even though Greece and Turkey apply a few similar technical measures, the many more differences detected after comparing the technical measures applied to fisheries in the two countries, pose particular (and even divergent) hurdles to the overall sustainable management goal of the shared commercial fish stocks of the Aegean Sea which compromise current management goals. As the small-scale fishers are already a highly marginalized group, especially in the Eastern Mediterranean, imposing more regulations on them towards harmonization of measures will not be favourable for many, but are of extreme importance in securing a viable future for this sector, which is currently at high risk of being compromised.

The declining state of the Aegean fisheries clearly reveals the ineffectiveness of the current management system, heavily based on technical measures, and rarely incorporating scientific advice into decision-making (Stergiou et al. 1997). Science should absolutely be used as the basis for stock rebuilding, and also needs to shift its focus to protect new recruits, juveniles, spawning grounds, and to synchronize an effective reduction of effort in both seas. The multi-species and multi-gear nature of the fisheries in the Aegean Sea poses a challenge to the current management effectiveness. The fish stocks shared by both Aegean Sea fishing states fall under highly diverse regulatory systems, and their current status corroborates the 'Tragedy of the commons' scenario, where one party typically aims to maximize their gains at the expense of community interest (Berkes 1985; Hardin 1994). Empirical studies have shown that fish stocks shared between two countries have a 7 percentage points higher chance of being overfished and are 14 percentage points more likely to be depleted than a stock fished by one country (McWhinnie 2009). However, we stress that the system can be remodeled for success by the adaptation of a new paradigm of community co-management which at the very least should include the harmonization of fisheries technical measures, stakeholder rights and an ecosystem focus. The joint exploitation of living resources in the Aegean Sea has been examined in other studies, which also suggest that these two Aegean Sea fishing countries should strive for co-operation and co-management (Aquarone 1995; Van Dyke 1996; Pratt and Schofield 2000). While for the management of small pelagics here, based just on sardine and anchovy,

the adoption of catch quota systems could be introduced with relative ease to manage these fisheries to ensure their sustainability (Fiorentino and Vitale 2021).

Fisheries management in the Mediterranean would benefit from incorporating in-depth expert fishing knowledge of fishers in the decision-making processes at regional, national and international levels (Bilgin unpublished*). The dominance and importance of the small-scale fisheries in this region needs to be reflected in management initiatives. According to the EU Mediterranean Community Action Plan (EU 2002), regional cooperation for shared resources with non-EU countries, like Turkey, needs to be improved upon. The strong imbalances on both sides vary greatly.

About 78% of assessed Mediterranean and the Black Sea stocks are currently fished beyond sustainable levels, although the situation has slightly improved since 2014 (from 88%). In terms of trends, many priority species in the Mediterranean, especially sardines, show an increase in negative exploitation rate in recent years (FAO 2020). Similarly, the major commercial fish stocks continue to decline in both countries, and these important stocks are direly in need of innovative and effective management regimes directed at their rebuilding. In this context, the FAO promotes the ecosystem approach to fisheries as an appropriate application for the sustainable management of fisheries. Recently, Vasconcellos and Ünal (2022) reported best practices based on case studies and lessons learned on how the ecosystem approach to fisheries was considered, developed and implemented in many Mediterranean fisheries. In fact, one of the good practices discussed in the report from the southern Aegean Sea of Turkey indicates that the use of new practices can lead to improved fisheries management capabilities in the Aegean Sea.

There are too many fishers chasing around a reduced amount of fish, and their combined effort and technological sophistication level is much too high in the region. Greece adopted, in accordance with EU Reg. 1380/2013, a multiannual Operational Programme for Fisheries and Sea (2014–2020), currently under review prior to implementation for the period 2021–2027, on the basis that the total number of fishing vessels has substantially decreased. In addition, Greece granted financial *de minimis* aid to commercial vessel owners (up to €25 000) for the withdrawal of boat seines (SB) (MD 145/296596/202 GG Vol. B no. 4680 (2020) implementing EU Reg. 717/2014. Turkey practiced five fisheries buy-back programs and withdrew 1253 vessels longer than 10 m from their entire fleet between 2013 and 2018 (Ünal and Göncüoğlu-Bodur 2018), but the overall fishing effort still remains about three times higher than needed to achieve optimal catch per unit effort (Ulman and Pauly 2016). Fleet mobility makes it difficult to establish the balance between fish stocks and fishing effort. To better address this, aside from technical measures

for fishing gear, the number of days the large-scale fishing fleet is permitted to fish at sea has also been restricted. However, success has not been achieved in protecting both shared and local fish stocks. In this regard, we suggest the preparation of the regional fisheries management plan in the GSA 22 area with the cooperation and coordination of both countries and the GFCM.

For Greek Aegean fish stocks, a new stock assessment method- AMSY (Abundance Maximum Sustainable Yield) tested abundance trends from scientific assessments both for commercial and non-commercial species (Tsikliras et al. 2021); Out of 74 assessed species, 20 of which were commercial species, and the others non-targeted species normally landed as commercial bycatch, 70% of the commercially targeted taxa were found to have unhealthy stock trends, and surprisingly, even 19% of non-targeted stocks were also deemed unhealthy demonstrating negative ecosystem effects on even non-commercial taxa, as secondary effects of fishing. While using the method CMSY (Catch Maximum Sustainable Yield) to assess Turkish stocks, 90% of 21 assessed Turkish Levantine stocks were found to be exploited beyond safe limits, ten of those critically (Demirel et al. 2020).

Some management measures are designed to work congruently with other measures for efficacy, especially that of minimum mesh size requirements for fishing nets, and ‘Minimum Conservation Reference Size’ (commonly used in the EU) or ‘Minimum Landing Sizes’ (MLS, commonly used elsewhere) for regulated species. The goals of both these measures are to protect juvenile fish so they can at least spawn once, and to catch the species at an optimum size. The minimum fish sizes are normally scientifically based on the female minimum length of maturity (L_{mat}). In a study on Turkish MLS sizes, it was found that several of the MLS sizes are prescribed at sizes much lower than the L_{mat} (Yildiz and Ulman 2020). For Greek fisheries, a study by Stergiou et al. (2004) found that catches from trawlers resulted in a higher percentage of juvenile fish in the catch compared to artisanal vessels, while the use of all gear types still had juvenile fish representing the majority of catches below the optimum exploitation length (L_{opt}) for Greek fisheries. Future work is needed to compare the Minimum Conservation Reference Sizes or MLS for both Greece and Turkey, as these measures also need aligning in order to help improve the health of the Aegean Sea resources.

Regional management framework

Currently, both countries are members of the General Fisheries Commission for the Mediterranean and are responsible for implementing the GFCM’s rules. GFCM membership is an advantage for the sustainability of

* Bilgin B (2008) Türkiye’nin Akdeniz’de balıkçılık yönetimi çerçevesinde Avrupa Birliği ortak balıkçılık politikasına uyumu. [Harmonization of Turkey with the European Union common fisheries policy within the framework of Mediterranean fisheries management.] EU Expertise Thesis, Ministry of Agriculture and Rural Affairs, Ankara, Turkey. [In Turkish]

the living marine resources of both countries. European Union (EU) legislation, the other common denominator between the two countries, is fully implemented in the member country Greece, and not yet applied to Turkey. However, some progress pertaining to harmonization provides hope that the discrepancies may be resolved. For instance, the recent report (EC 2021) published by the European Commission states that Turkey made good progress on fisheries in implementing the fisheries law, resources and fleet management, and inspection and control. The GFCM adopted its 2030 strategy for the Mediterranean and the Black Sea on 6 November 2021. The 2030 strategy included 35 GFCM recommendations and resolutions translating the objectives and targets of the strategy into concrete actions. The recommendations include important measures to improve fisheries management and control in the Adriatic and Black Seas, better protect sensitive species and habitats, and consolidate the monitoring and control framework, including combatting illegal, unreported, and unregulated (IUU) activities in both the Mediterranean and the Black Sea.

For the Mediterranean Sea, the key forum is the Barcelona Convention (BC), of which both Greece and Turkey are contracting parties. The Contracting Parties to the Barcelona Convention developed a set of ecological objectives, operational objectives, and indicators, which reflect Mediterranean priorities and are also coherent with the EU's Marine Strategy Framework Directive (MSFD) (2008/56/EC) (EPPA 2019). One of the key requirements of the MSFD is that EU Member States must take a coordinated approach to implementation, cooperating with other states within the appropriate marine region or sub-region, and ensure coherent and coordinated strategies (EPPA 2019). However, Turkey, unlike Greece, is not an EU member state, and, thus, it is not bound by the obligation to implement the MSFD.

Accompanying the MSFD was a set of criteria and standards to assist the implementation of the plan, which were revised in 2017 with the new Commission Decision on Good Environmental Status. Annex III is of special interest here, which was also amended in 2017 to better link ecosystem components, anthropogenic pressures, and marine environmental impacts with 11 descriptors. A 2020 report on the first implementation of the MSFD showed that although highly ambitious, the framework can be improved to tackle the main issues such as overfishing. The EU-funded Capacity Building on Marine Strategy Framework Directive in Turkey Project (MARinTURK) supports the possible adoption and implementation of the MSFD in the near future. As part of the initial assessment, the economic and social analysis of the different marine water uses has been completed.

The parties are signatory to the overarching BC goal of protecting the marine environment of the Mediterranean by boosting regional and national plans, which now includes 104 protected and 79 endangered species inhabiting the Aegean Sea. The most threatened groups are the largest species, which are crucial in their contributions to

ecosystem regulation and control, namely the top-tiered sharks, rays, fishes, and mammals (Katağan et al. 2015).

In 2008, Turkey completed an institutional twinning program to support the country's legal and institutional alignment to the EU *acquis* for fisheries policy during their candidacy process (Ünal and Göncüoğlu 2012). This process is aimed at harmonizing Turkish fisheries management measures in line with the EU, in order to be able to implement the Common Fisheries Policy (CFP). Short-term and medium-term objectives included aligning fisheries management with those of the European Union. Although the accession process is currently frozen, its framework is still maintained. One principal aim of both the MSFD and CFP is the progressive implementation of an ecosystem-based approach to fisheries management (Gros et al. 2008). Greece, which joined the European Union in 1981, therefore had EU regulations directly transcribed into national legal order and provisions are applied directly and can be enforced. EU Directives provide for the framework regulatory text in reference to a certain subject matter. In order for Directives to be transcribed into national law, further national action is required (additional implementing legislation). EU legislation doesn't exclude differentiated national legislation on the same subject, so long as national rules are stricter and under requirements.

The main issue is that the very important Aegean Sea fisheries are severely threatened and require drastic new measures if they are to remain a viable activity into the future. Ecosystems are now understood to represent the correct scale within which scientific knowledge and the management of renewable resources should be based on. The Ecosystem Approach to Fisheries (EAF) offers a long-term vision for the management of marine biodiversity: sustainable exploitation of resources while respecting the marine ecosystem (Cury et al. 2016). According to the FAO (2003), the EAF is a management planning process that was adopted by the FAO Committee on Fisheries (COFI) as the appropriate and practical way to implement the FAO Code of Conduct for Responsible Fisheries. It is well known that this code established principles and standards applicable to the conservation, management, and development of fisheries. Under such an approach, it is obvious that the allowance of sponge and coral collection in Greece needs to be reconsidered, as these are key components of the ecosystem upon which many other species depend on. Both countries would also benefit from protecting the same vulnerable and overexploited species under the protection of Key Biodiversity Areas or similarly important habitat types for birds, marine mammals, and elasmobranchs.

Another management suggestion applicable to ecoregions such as the Aegean Sea is that they be managed by using conservation targets such as sensitive habitat types including *Posidonia oceanica*, coralligenous formations, and marine cave habitats, which better represent the functional diversity of the area and can improve ecosystem resilience in the face of heightened environmental change (Giakoumi et al. 2013). Also, the creation of networks

of marine protected areas, also focusing on ecosystems can also concurrently be applied (Browman and Stergiou 2004; Papaconstantinou et al. 2007). Results have shown that partial protection of protected areas along with adaptive co-management plans involving fishers, scientists, and managers at the core can benefit the fisheries and alleviate overfishing; and it should be stressed that fisher involvement is one of the most important criteria for successful management (Guidetti and Claudet 2010).

As stated in Tsikliras (2014), the majority of pelagic fish stocks move freely between the limits of both states, and the majority of fisheries are hence shared; therefore, management measures need to be common in order to be equitable. Collective management may be more fruitful when both states share responsibilities, especially sharing their knowledge of the ecosystem and taking into consideration how their actions affect one another, and actually develop harmonized common management measures.

Conclusions

Under the Common Fisheries Policy, fisheries management regulations including technical measures, catch quotas, managing fleet capacity, market rules and support for fisheries and coastal communities are prescribed (EC 2022). Greece is a member of the EU, while Turkey is still a candidate country that is working on aligning its policies under the EU framework. Since they share many fish stocks, and the Aegean Sea basin is a highly important fisheries subregion in the Mediterranean, co-management of the marine resources, especially implementing the same rules, with a focus on rebuilding the fisheries and the ecosystems that support them should be the ultimate

priority for both parties. It is recommended that co-management, involving the adoption and application of the same, or similar, measures and the implementation of the EAF, should constitute the foundations of an Aegean fisheries management framework. First, the management measures for the sustainable exploitation of fishery resources in the Mediterranean Sea provided for in Council Regulation (EC) No 1967/2006 should be implemented by both countries, and secondly, joint action should be taken under the guidance of the FAO Code of Conduct for Responsible Fisheries (CCRF). Both states should review and harmonize not only their technical measures for their fisheries but also their management approaches for their shared stocks and fishing areas. For this purpose, abiding by the FAO-CCRF and the EAF should be the first step toward developing harmonized management strategies. Vasconcellos and Ünal (2022) provide current information about the transition to an ecosystem approach to fisheries in the Mediterranean through a review of case studies and lessons learned in the region that can serve as a guide for managerial transitions. In conclusion, as long as Turkey is a candidate country of the EU, it will continue to harmonize (some of) its fisheries policy measures with those of the EU; thus, harmonization should be easy under this context. The recent amendment to the main Fisheries Law in Turkey will help to harmonize the code implementing the European Community rules as necessary (GDFA 2019). The same applies to the technical measures regulating the fisheries. In this context, the implementation of the EC No 1967/2006 by Turkey would fill most of these gaps, and Turkey is already taking some measures to harmonize its fisheries legislation according to the EC system for the management and conservation of the fish stocks in the Mediterranean.

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Estimating somatic growth of fishes from maximum age or maturity

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Abstract

Growth in body size is a key life-history trait that has coevolved and is interlinked with maturation, maximum age, mortality, generation time, and the intrinsic rate of population growth. Growth parameters are therefore required inputs in the majority of assessment models used in conservation or fisheries management. However, because of the difficulties involved in the proper aging of individuals, growth parameters are unknown for the vast majority of species. Here, two new data-limited methods are presented to estimate somatic growth from maximum length combined with either length or age at maturation or with maximum age. A comparison with existing growth parameters of fishes (Actinopterygii and Elasmobranchii) shows that the estimates of the new methods fall within the range of established methods. The new methods apply to species with indeterminate growth, such as fishes or invertebrates, and were used here to produce the first growth parameter estimates for 110 species of fishes.

Keywords

age at first maturity, asymptotic length, maximum age, maximum length recruitment, von Bertalanffy growth equation

Introduction

The speed by which organisms increase in body size determines how fast they reach maturity and maximum size, i.e., the adult size and age range. The mean age of parents when their offspring are born defines generation time, which itself is linked to the intrinsic rate of population growth (Pianka 2000). The somatic growth rate is thus a central life-history parameter, especially in species like fishes or invertebrates which grow throughout their lives. Growth parameters are of key importance in population dynamic analyses for conservation or fisheries management (Ricker 1975). For example, the ratio ($M:K$) between natural mortality M and growth parameter K plays a central role in determining sustainable catch levels (Beverton and Holt 1957) or the optimum body size for capture (Froese et al. 2016).

The first-principle equation that is most widely used to estimate growth is the one proposed by von Bertalanffy

(1938, 1951) building on the work of Pütter (1920). It describes the growth in body length (L) as a function of asymptotic length L_{∞} , a parameter K indicating how fast L_{∞} is approached, and a parameter t_0 indicating the hypothetical age t at zero length, given that larvae or pups have a length larger than zero at hatching or birth, where L_t is the predicted length L at age t

$$L_t = L_{\infty} (1 - e^{-K(t-t_0)}) \quad [\text{Eq 1}]$$

The hypothetical age at zero length t_0 typically has a negative value which is small compared to the maximum age. Different values of t_0 shift the growth curve along the age-axis without changing the values of L_{∞} or K . For the sake of simplicity in data-limited methods, t_0 is assumed here to be zero and is omitted from the subsequent equations. Also, for easy comparison among species, length in fish is measured in centimeters and age in years, which

implies that K has the unit year^{-1} . Note that the type of length, such as total length (TL), fork length (FL), standard length (SL), pre-anal length, or body width (WD) does not affect the estimate of K as long as the species grows roughly isometrically and thus changes its proportions during growth only in a minor way.

While measuring lengths in one of the above length types is straightforward in most species of fish, determining age e.g. from counting rings in hard structures such as scales, otoliths, vertebrae or spines is more demanding and prone to error. As a result, sufficiently large and reliable data sets for fitting Equation 1 [Eq 1] are missing for the majority of species (Froese and Binohlan 2003, Froese and Pauly 2021). The purpose of this study was to explore two less data-demanding methods, which use Equation 1 in a deterministic fashion, estimating growth parameters from maximum length combined with a maximum age, with length and age at maturation, or with any known length-at-age, such as the mean length of an outstanding year class.

Material and methods

Data on asymptotic length (L_∞), maximum length (L_{\max}), maximum age (t_{\max}), and length (L_m) and age (t_m) at first maturity were extracted from FishBase 08/2021 (Froese and Pauly 2021). Values for t_m were direct observations and not estimated from L_m and known growth parameters. Similarly, t_{\max} values were based on direct observations and not derived from growth parameters. Values that had been marked as doubtful by FishBase staff were excluded from the analysis.

Solving Equation 1 for K and omitting t_0 gives Equation 2

$$K = -\frac{\ln\left(1 - \frac{L_t}{L_\infty}\right)}{t} \quad [\text{Eq 2}]$$

To estimate growth from the maximum length and maximum age, Equation 3 replaces age t with reported maximum age for a population and assumes that t_{\max} is reached and reported at about 95% of L_∞ (Taylor 1958, Froese and Binohlan 2000). Following this reasoning, a proxy for asymptotic length is obtained as $L_\infty = 1.05L_{\max}$ (Pauly 1984)

$$K = -\frac{\ln(1-0.95)}{t_{\max}} = \frac{3.0}{t_{\max}} \quad [\text{Eq 3}]$$

If several estimates of t_{\max} are available for a population, e.g., as the oldest fish observed during periods of one or 5 years over the last 20–40 years, then these numbers can be used to derive a mean estimate of t_{\max} with 95% confidence limits. Since the main source of uncertainty in Equation 3 is the estimate of t_{\max} , its lower and upper confidence limits can be inserted in the equation to derive approximate confidence limits

for K . Alternatively, plausible ranges of uncertainty can be derived by assuming that maximum age will be observed and reported in individuals with a body length between 90% and 99% of L_∞ . Replacing 0.95 in Equation 3 with 0.90 and 0.99, respectively, then yields plausible ranges of K between $2.3/t_{\max}$ and $4.6/t_{\max}$. For example, for an observed $t_{\max} = 15$ years, Equation 3 would predict $K = 0.20$. Applying the alternative rules for uncertainty gives plausible ranges of K as 0.15–0.31.

To estimate growth from length and age at maturation, Equation 4 replaces age t in Equation 2 with the age where individuals have reached sexual maturity (t_m), L_t with the corresponding length L_m , and L_∞ with $L_{\max}/0.95$

$$K = -\frac{\ln\left(1 - 0.95 \frac{L_m}{L_{\max}}\right)}{t_m} \quad [\text{Eq 4}]$$

Similar to Equation 3, approximate 95% confidence limits of K can be obtained from observed confidence limits of t_m or L_m . Alternatively, plausible ranges of K can be obtained from the observation that in species that mature e.g., on average at 3 years of age, some mature already at two and some at four years of age. Based on this common observation, a typical uncertainty range in the estimate of t_m can be construed as $0.67t_m - 1.33t_m$. For example, for observed values of $t_m = 3$ years, $L_m = 40$ cm and $L_{\max} = 110$ cm, Equation 4 would predict $K = 0.14$. Setting t_m to $0.67*3$ and $1.33*3$, respectively, gives a plausible range for K of 0.11–0.21.

Equation 4 can be used more generally for any case where a combination of length and age is known, such as an unusually large year class with a strong visible peak in length-frequency plots, see the example below.

Estimates of K resulting from the new methods are shown with only two significant decimals to avoid the impression of unrealistic high precision, given that these are data-limited methods with wide ranges of uncertainty.

All data and code used in this study are available from <https://oceanrep.geomar.de/id/eprint/55916>.

Results

Growth estimates derived from maximum length and length and age at maturation. The MATURITY table in FishBase 08/2021 (Froese and Pauly 2021) contained 170 records with reported age and length at first maturity as well as an estimate of the corresponding maximum length in the population, for altogether 120 species of fishes (Froese and Pauly 2021). Of these, 15 species had no previous growth estimates in FishBase (Table 1). For the remainder, a comparison with the 880 existing growth estimates showed that the new estimates of K fell within the previously observed range, without obvious bias (Fig. 1).

Table 1. List of fifteen species with first estimates of growth parameters (L_{∞} , K), as derived from age (t_m) and length (L_m) at first maturity and maximum length (L_{max}), with indication of family, locality of the population, and type of length measurements. TL stands for total length, SL for standard length, and WD for body width. Plausible ranges of K were calculated from an assumed uncertainty range of t_m of $\pm 33\%$. See the supplement data (<https://oceanrep.geomar.de/id/eprint/55916>) and the MATURITY table in FishBase (Froese and Pauly 2021) for additional information and references.

Family	Species	Locality	Sex	t_m	L_m	L_{max}	Type	L_{∞}	K	95% CL
Acipenseridae	<i>Acipenser dabryanus</i>	Yangtze River	F	9	106	250	TL	263	0.06	0.04–0.09
Ariidae	<i>Sciades herzbergii</i>	Ceará	F	2.5	50.8	94.2	TL	98.9	0.29	0.22–0.43
Bothidae	<i>Bothus constellatus</i>	Gulf of Tehuantepec	F	5.5	10.1	15.7	TL	16.5	0.17	0.13–0.26
Characidae	<i>Gymnocharacinus bergii</i>	Valcheta	M	1	3.7	7.5	TL	7.88	0.63	0.48–0.95
		Valcheta	F	1	3.8	7.5	TL	7.88	0.66	0.49–0.98
Cichlidae	<i>Chaetobranchius flavescens</i>	Rupununi River	F	1	17	26	TL	27.3	0.97	0.73–1.46
Clupeidae	<i>Nematalosa erebi</i>	Murray River	U	2.5	19.9	39	TL	41	0.27	0.20–0.40
Gaidropsaridae	<i>Ciliata septentrionalis</i>	Severn estuary and Bristol Channel	M	1	7.18	12.2	SL	12.8	0.82	0.62–1.23
Gobiidae	<i>Knipowitschia longicaudata</i>	Caspian, Azov, and Black Sea basins	U	0.75	2	5	TL	5.25	0.64	0.48–0.96
Mobulidae	<i>Mobula birostris</i>	Indo–Pacific	F	6	445	680	WD	714	0.16	0.12–0.24
Muraenolepididae	<i>Muraenolepis microps</i>	South Georgia	M	4	24	35	TL	36.8	0.26	0.20–0.40
Notopteridae	<i>Chitala chitala</i>	Ganga River	F	3	75.5	122	TL	128	0.30	0.22–0.44
Pentaceroptidae	<i>Pentaceros wheeleri</i>	Emperor Seamount	M	6	27	44	TL	46.2	0.15	0.11–0.22
		Emperor Seamount	F	7	28	44	TL	46.2	0.13	0.10–0.20
Salmonidae	<i>Stenodus nelma</i>	Arctic Ocean	Mx	12	75	150	SL	158	0.05	0.04–0.08
Triakidae	<i>Mustelus griseus</i>	Taiwan	F	5.65	72	101	TL	106	0.20	0.15–0.30
Triakidae	<i>Mustelus punctulatus</i>	Mediterranean	F	1.95	95	190	TL	200	0.33	0.25–0.50

F = female, M = male, Mx = mixed, U = unsexed.

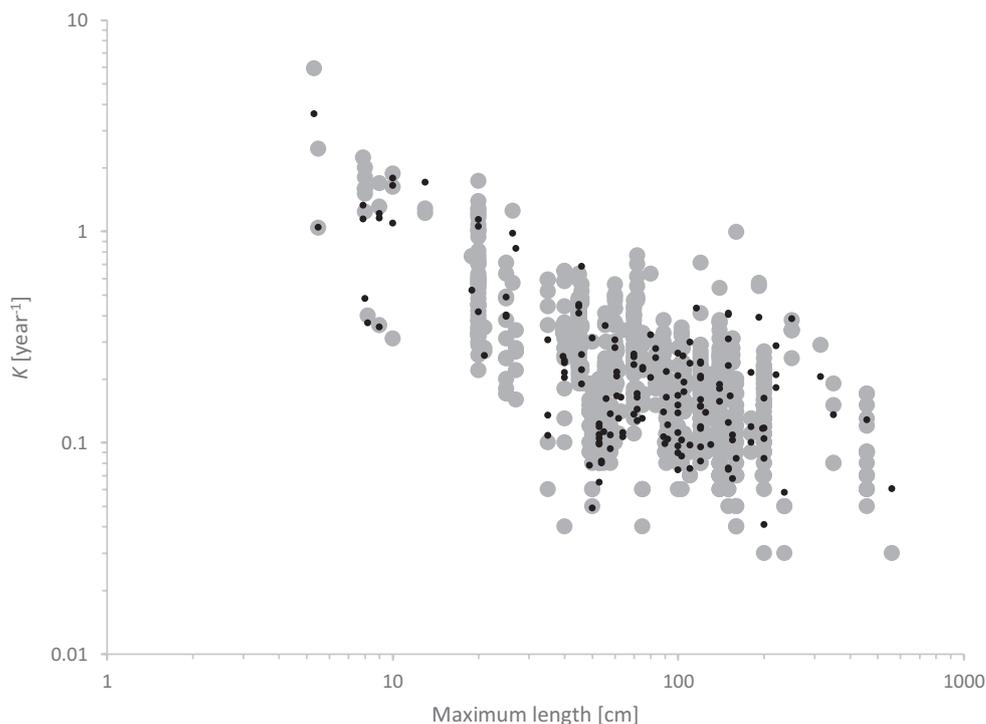


Figure 1. Comparison of 880 existing estimates of growth parameter K (grey dots) with 153 newly derived estimates from length and age at first maturity (black dots), plotted over the maximum length for 105 analyzed species, in log-log space.

The variability in Fig. 1 is wide because different species may be plotted over the same maximum length. In order to compare predictions of Equation 4 with growth estimates from accepted other methods at the species level, the six species with the highest number of independent growth estimates were selected (Fig. 2). This method of selecting species for the comparison was chosen for objectivity and in order to demonstrate the typical wide

spread of growth parameter estimates. The estimates of parameter K derived from maximum age overlapped with the independent estimates in all six species.

Growth estimates derived from maximum length and maximum age. The POPCHAR table in FishBase 08/2021 contained 744 records with reported maximum age and the corresponding maximum length in the

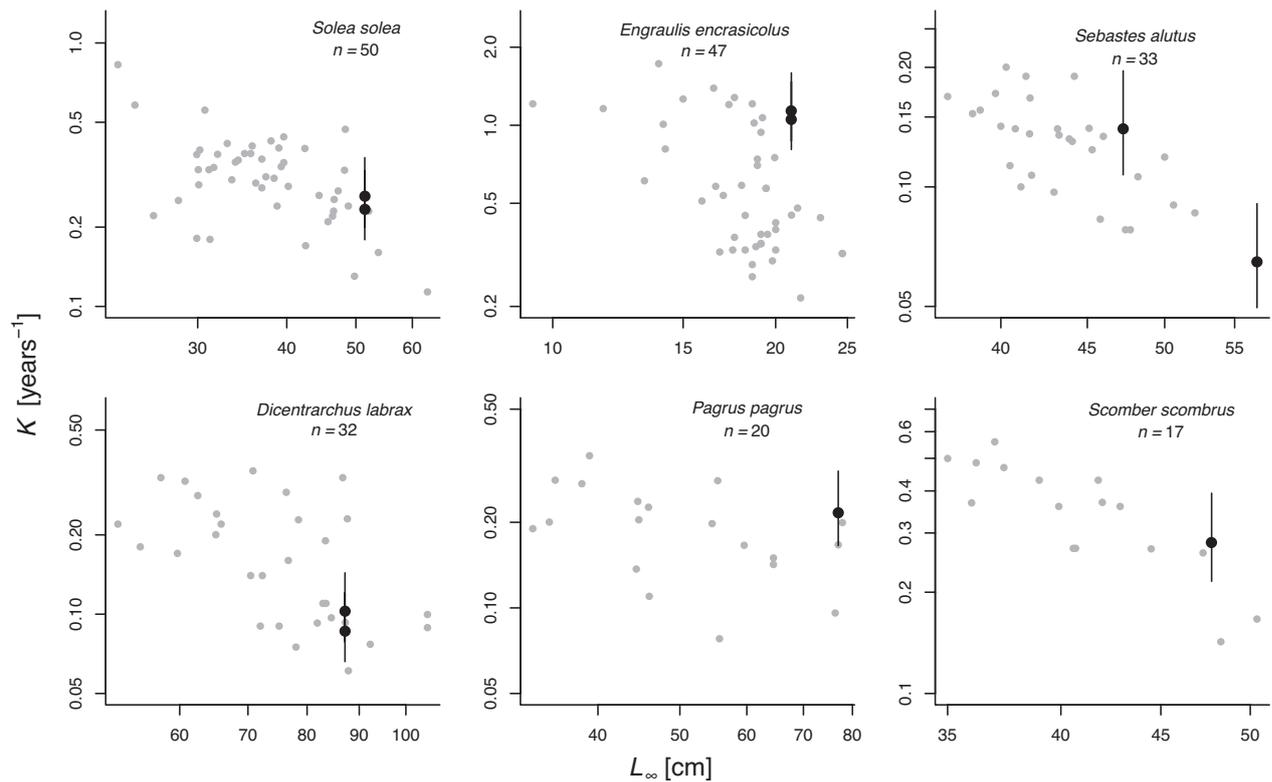


Figure 2. Comparison of growth parameters L_{∞} and K derived with various data-rich methods (gray dots) and from maximum length and length and age at maturation (black dots with indication of plausible ranges), in log-log space. The double-dots in some of the species are caused by records with different length or age at maturation for the same population and the same maximum length.

population, for, altogether, 573 species (Froese and Pauly 2021). Of these, 105 species had no previous growth estimates in FishBase (Table 2). For the remainder, a comparison with the 2814 existing growth estimates in

FishBase showed that the new estimates of K derived from maximum age fell within the previously observed range (Fig. 3), albeit with a slight tendency towards lower K values (see Table 3 and Discussion below).

Table 2. List of 105 species with first estimates of growth parameters (L_{∞} , K), as derived from maximum age (t_{\max}) and maximum length (L_{\max}), with indication of family, locality of the population, sex, and type of length measurements, where TL stands for total length, SL for standard length, FL for fork length, and WD for body width. The plausible ranges of K (CL) were derived from assuming that t_{\max} was observed between 0.9 and 0.99 L_{∞} . See the supplement data (<https://oceanrep.geomar.de/id/eprint/55916>) and the POPCHAR table in FishBase (Froese and Pauly 2021) for additional information and references.

Family	Species	Locality	Sex	t_{\max}	L_{\max}	L_{∞}	Type	K	CL
Acipenseridae	<i>Acipenser sinensis</i>	Yangtze River (below Gezhouba Dam)	F	33	346	363.3	TL	0.09	0.07–0.14
Adrianichthyidae	<i>Oryzias sinensis</i>	East Asia	U	1	3	3.15	SL	3.00	2.30–4.60
Agonidae	<i>Hemirhamphus bolini</i>	Bering Sea and Aleutian Islands	U	23	83	87.2	TL	0.13	0.10–0.20
Alepocephalidae	<i>Alepocephalus bairdii</i>	Southern Brittany	Mx	38	93	97.7	SL	0.08	0.06–0.12
Aphaniidae	<i>Aphanius baeticus</i>	Spain	U	2	3	3.15	SL	1.50	1.15–2.30
Bagridae	<i>Coreobagrus ichikawai</i>	Tagiri River	M	3	10.8	11.3	SL	1.00	0.77–1.53
Bagridae	<i>Coreobagrus ichikawai</i>	Tagiri River	F	4	9.35	9.8	SL	0.75	0.58–1.15
Bathymasteridae	<i>Bathymaster derjugini</i>	Sea of Okhotsk	U	8	18.1	19.0	TL	0.37	0.29–0.58
Bathymasteridae	<i>Bathymaster signatus</i>	N Kurils and SE Kamchatka	F	9	36	37.8	TL	0.33	0.26–0.51
Berycidae	<i>Centroberyx gerrardi</i>	Southern Australia	U	71	66	69.3	TL	0.04	0.03–0.06
Blenniidae	<i>Salaria fluviatilis</i>	Mediterranean (Europe)	U	5	13	13.7	SL	0.60	0.46–0.92
Carcharhinidae	<i>Carcharhinus galapagensis</i>	Circumtropical	F	24	370	388	TL	0.12	0.10–0.19
Carcharhinidae	<i>Negaprion brevirostris</i>	Eastern Pacific to Eastern central Atlantic	F	25	320	336	TL	0.12	0.09–0.18
Catostomidae	<i>Ictiobus cyprinellus</i>	Ontario	U	26	157	165	TL	0.12	0.09–0.18
Cebidichthyidae	<i>Cebidichthys violaceus</i>	Oregon–California	U	18	76	79.8	TL	0.17	0.13–0.26
Centrarchidae	<i>Ambloplites rupestris</i>	Ontario	U	13	43	45.2	TL	0.23	0.18–0.35
Characidae	<i>Astyanax mexicanus</i>	Tinaja cave	U	8	9	9.5	TL	0.37	0.29–0.58
Clupeidae	<i>Alosa killarnensis</i>	Lake Lough Lene	U	5	20	21	SL	0.60	0.46–0.92
Clupeidae	<i>Clupeonella abraui</i>	Lake Abrau	U	2	8	8.4	SL	1.50	1.15–2.30
Clupeidae	<i>Nematalosa erebi</i>	Lower Murray River	U	10	48	50.4	SL	0.30	0.23–0.46
Cobitidae	<i>Cobitis elongatoides</i>	Danube River	F	5	13	13.7	SL	0.60	0.46–0.92

Table continues on next page

Table 2. (Continuation)

Family	Species	Locality	Sex	t_{\max}	L_{\max}	L_{∞}	Type	K	CL
Cobitidae	<i>Cobitis ohridana</i>	Moraca River basin	F	3.5	8.3	8.7	TL	0.86	0.66–1.31
Cottidae	<i>Gymnocanthus herzensteini</i>	Primorye	F	17	42	44.1	TL	0.18	0.14–0.27
Cottidae	<i>Hemilepidotus jordani</i>	Bering Sea and Aleutian Islands	U	30	65	68.3	TL	0.10	0.08–0.15
Cyprinidae	<i>Barbus caninus</i>	Europe	U	5	25	26.3	SL	0.60	0.46–0.92
Cyprinidae	<i>Gymnocypris firmispinatus</i>	Anning River	M	9	16.3	17.1	TL	0.33	0.26–0.51
Cyprinidae	<i>Gymnocypris firmispinatus</i>	Anning River	F	13	24.2	25.4	TL	0.23	0.18–0.35
Cyprinidae	<i>Luciobarbus graellsii</i>	Spain	U	16	65	68.3	SL	0.19	0.14–0.29
Cyprinidae	<i>Onychostoma barbatulum</i>	Taiwan	U	7	26	27.3	TL	0.43	0.33–0.66
Fundulidae	<i>Fundulus heteroclitus</i>	East coast of North America	U	4	10	10.5	SL	0.75	0.58–1.15
Galaxiidae	<i>Galaxias olidus</i>	Australia: Goulburn, Torbreck, Howqua, and Tagerty rivers	U	4	13	13.7	SL	0.75	0.58–1.15
Gobiidae	<i>Acentrogobius pflaumii</i>	Swan–Canning estuary	Mx	3.9	9.6	10.1	TL	0.77	0.59–1.18
Gobiidae	<i>Amblygobius phalaena</i>	Pioneer Bay, Orpheus I.	M	1.17	10.2	10.7	TL	2.56	1.97–3.93
Gobiidae	<i>Amblygobius phalaena</i>	Pioneer Bay, Orpheus I.	F	1.17	10.5	11.0	TL	2.56	1.97–3.93
Gobiidae	<i>Babka gymnotrachelus</i>	Black, Azov, and Caspian Sea basins	U	5	16	16.8	SL	0.60	0.46–0.92
Gobiidae	<i>Economidichthys trichonis</i>	Lake Trichonis, Lysimachia	U	1.8	2.5	2.6	SL	1.66	1.28–2.56
Gobiidae	<i>Knipowitschia caucasica</i>	Eurasia	U	2	5	5.3	SL	1.50	1.15–2.30
Gobiidae	<i>Knipowitschia croatica</i>	Bosnia–Herzegovina, Croatia	U	2	4.7	4.9	SL	1.50	1.15–2.30
Gobiidae	<i>Knipowitschia longicaudata</i>	Caspian, Azov, and Black Sea basin	U	2	4	4.2	SL	1.50	1.15–2.30
Gobiidae	<i>Knipowitschia milleri</i>	Acheron River (lower stretch)	U	2	2.6	2.7	SL	1.50	1.15–2.30
Gobiidae	<i>Stiphodon percnopterygius</i>	Okinawa Island	F	2	3.5	3.7	SL	1.50	1.15–2.30
Gobiidae	<i>Stiphodon percnopterygius</i>	Okinawa Island	M	2	3	3.15	SL	1.50	1.15–2.30
Gobiidae	<i>Trimma benjamini</i>	Helen Reef (Hotsarihie Reef), Hatohobei State	U	0.39	2.29	2.4	SL	7.68	5.90–11.8
Gobiidae	<i>Valenciennea muralis</i>	Pioneer Bay, Orpheus I.	M	1	11.6	12.2	TL	3.00	2.30–4.60
Gobionidae	<i>Romanogobio albigimatus</i>	Northern Caspian basin (Volga, Ural)	U	5	11.5	12.1	SL	0.60	0.46–0.92
Gobionidae	<i>Romanogobio belingi</i>	Eastern Europe	U	5	11.5	12.1	SL	0.60	0.46–0.92
Gobionidae	<i>Romanogobio benacensis</i>	Italy, Slovenia	U	4	10	10.5	SL	0.75	0.58–1.15
Gobionidae	<i>Romanogobio ciscaucasicus</i>	Caspian Sea	U	6	11	11.6	SL	0.50	0.38–0.77
Gobionidae	<i>Romanogobio kesslerii</i>	Europe	U	5	11	11.6	SL	0.60	0.46–0.92
Gobionidae	<i>Romanogobio tanaiticus</i>	Don River drainage	U	5	10	10.5	SL	0.60	0.46–0.92
Gonostomatidae	<i>Cyclothone braueri</i>	Rockall Trough, NE Atlantic (near 55°N, 12°W)	F	1.25	3.8	3.99	SL	2.40	1.84–3.68
Heptapteridae	<i>Pimelodella kronoi</i>	Southeastern region of Brazil	U	15	15	15.8	TL	0.20	0.15–0.31
Hexagrammidae	<i>Pleurogrammus azonus</i>	Northern Sea of Japan	U	12	50	52.5	TL	0.25	0.19–0.38
Latridae	<i>Latris lineata</i>	Tasmania	M	29	81.5	85.6	FL	0.10	0.08–0.16
Latridae	<i>Latris lineata</i>	Tasmania	F	43	95	99.8	FL	0.07	0.05–0.11
Lestidiidae	<i>Lestrolepis japonica</i>	Kagoshima Bay	U	4	19	19.9	SL	0.75	0.58–1.15
Leuciscidae	<i>Anaocypris hispanica</i>	Guadiana drainage (Spain, Portugal)	U	3	6	6.3	SL	1.00	0.77–1.53
Leuciscidae	<i>Pelagus minutus</i>	Europe	U	6	5	5.25	SL	0.50	0.38–0.77
Leuciscidae	<i>Tropidophoxinellus hellenicus</i>	Peloponnese	U	4	9.3	9.8	SL	0.75	0.58–1.15
Liparidae	<i>Liparis fabricii</i>	Barents Sea	U	6	21	22.1	TL	0.50	0.38–0.77
Liparidae	<i>Palmoliparis beckeri</i>	Pacific off the North Kuril Islands	U	8	42	44.1	TL	0.37	0.29–0.58
Lutjanidae	<i>Etelis radiosus</i>	Lihir Island group (seamount)	U	14	70	73.5	SL	0.21	0.16–0.33
Lutjanidae	<i>Paracaesio stonei</i>	Lihir Island group (seamount)	U	15	37	38.9	SL	0.20	0.15–0.31
Mobulidae	<i>Mobula birostris</i>	India	U	20	680	714	WD	0.15	0.12–0.23
Mobulidae	<i>Mobula japonica</i>	Punta Arenas de la Ventana (24°03'N, 109°49'W), SE Baja California	Mx	14	240	252	WD	0.21	0.16–0.33
Muraenidae	<i>Muraena augusti</i>	Northeastern Central Atlantic	Mx	17.9	90	94.5	TL	0.17	0.13–0.26
Myctophidae	<i>Diaphus suborbitalis</i>	Suruga Bay	U	2.5	6.7	7.0	SL	1.20	0.92–1.84
Myctophidae	<i>Diaphus theta</i>	South Kurile region	U	6	11.7	12.3	SL	0.50	0.38–0.77
Myctophidae	<i>Lampanyctus macdonaldi</i>	Rockall Trough, NE Atlantic (near 55°N, 12°W)	U	6	13.5	14.2	SL	0.50	0.38–0.77
Oreosomatidae	<i>Allocyttus niger</i>	Tasmanian waters	U	100	47	49.4	TL	0.03	0.023–0.046
Oreosomatidae	<i>Allocyttus niger</i>	Chatham Rise and Puysegur-Snares	U	153	45.5	47.8	TL	0.02	0.015–0.030
Oreosomatidae	<i>Allocyttus verrucosus</i>	Western coasts of Australia	U	100	42	44.1	TL	0.03	0.023–0.046
Oreosomatidae	<i>Neocyttus rhomboidalis</i>	Australia (all states)	U	100	47	49.4	TL	0.03	0.023–0.046
Pentacerotidae	<i>Pentaceropsis recurvirostris</i>	Esperance (33°45'S, 121°55'E), Western Australia	M	43	55.3	58.1	TL	0.07	0.05–0.11
Pentacerotidae	<i>Pentaceropsis recurvirostris</i>	Esperance (33°45'S, 121°55'E), Western Australia	F	55	64.5	67.7	TL	0.05	0.04–0.08
Pentanchidae	<i>Galeus melastomus</i>	Rockall Trough	M	7	64	67.2	TL	0.43	0.33–0.66
Percichthyidae	<i>Nannoperca australis</i>	Australia	U	5	8.5	8.9	TL	0.60	0.46–0.92
Percichthyidae	<i>Nannoperca variegata</i>	Australia	U	4	6.2	6.5	TL	0.75	0.58–1.15
Percichthyidae	<i>Percilia irwini</i>	Andalién and Biobío rivers basins	Mx	4	9.6	10.1	TL	0.75	0.58–1.15
Percidae	<i>Gymnocephalus schraetser</i>	Danube River drainage	U	15	25	26.3	SL	0.20	0.15–0.31
Polynemidae	<i>Polydactylus macrochir</i>	Northwestern Australia	U	20	170	178	FL	0.15	0.12–0.23
Polyprionidae	<i>Stereolepis gigas</i>	California (off Santa Cruz Island)	U	62	220	231	TL	0.05	0.04–0.07
Pomacentridae	<i>Stegastes rectifraenum</i>	Lower Baja Peninsula, Gulf of California	U	11	12	12.6	SL	0.27	0.21–0.42
Salmonidae	<i>Coregonus danneri</i>	Lake Traunsee	U	6	22	23.1	SL	0.50	0.38–0.77
Salmonidae	<i>Coregonus lucinensis</i>	Lake Breiter Luzin	U	6	16	16.8	SL	0.50	0.38–0.77
Salmonidae	<i>Coregonus renke</i>	Germany	U	7	29	30.5	SL	0.43	0.33–0.66

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Table 2. (Continuation)

Family	Species	Locality	Sex	t_{max}	L_{max}	L_{∞}	Type	K	CL
Salmonidae	<i>Coregonus vandesius</i>	UK	U	10	20	21	SL	0.30	0.23–0.46
Salmonidae	<i>Salmo ferax</i>	British Isles	U	23	80	84	SL	0.13	0.10–0.20
Salmonidae	<i>Salvelinus alpinus</i>	Circumpolar	U	32	110	115	SL	0.09	0.07–0.14
Salmonidae	<i>Salvelinus gracillimus</i>	Lake Leynavatn, on Stremoy Island	U	8	35	36.8	SL	0.37	0.29–0.58
Salmonidae	<i>Salvelinus murta</i>	Lake Thingvalla	U	18	48	50.4	SL	0.17	0.13–0.26
Salmonidae	<i>Salvelinus struanensis</i>	Loch Rannoch and Loch Ericht	U	8	36	37.8	SL	0.37	0.29–0.58
Salmonidae	<i>Salvelinus thingvallensis</i>	Lake Thingvalla	U	17	24	25.2	SL	0.18	0.14–0.27
Salmonidae	<i>Salvelinus youngei</i>	UK Scotland	U	9	25	26.3	SL	0.33	0.26–0.51
Schindleriidae	<i>Schindleria praematura</i>	nearshore (27°10'S, 109°20'W)	U	0.25	2.09	2.19	SL	11.98	9.20–18.4
Sciaenidae	<i>Cynoscion othonopterus</i>	Colorado River delta, Gulf of California, Sonora	Mx	8	101	106	TL	0.37	0.29–0.58
Scorpaenidae	<i>Scorpaena loppei</i>	Balearic Islands	M	5	12.8	13.4	TL	0.60	0.46–0.92
Serranidae	<i>Cephalopholis miniata</i>	Kuwait	U	26	34	35.7	TL	0.12	0.09–0.18
Serranidae	<i>Cephalopholis miniata</i>	Great Barrier Reef	U	30	47.5	49.9	TL	0.10	0.08–0.15
Serranidae	<i>Epinephelus bleekeri</i>	Kuwait	U	24	65	68.3	TL	0.12	0.10–0.19
Serranidae	<i>Epinephelus polylepis</i>	Kuwait	U	41	74	77.7	TL	0.07	0.06–0.11
Serranidae	<i>Plectropomus pessuliferus</i>	Red Sea	U	19	96	100.8	TL	0.16	0.12–0.24
Somniosidae	<i>Somniosus microcephalus</i>	Greenland	F	392	502	527	TL	0.01	0.006–0.012
Sparidae	<i>Calamus brachysomus</i>	North Peru	F	15	44	46.2	TL	0.20	0.15–0.31
Sparidae	<i>Calamus brachysomus</i>	North Peru	M	15	51	53.6	TL	0.20	0.15–0.31
Sparidae	<i>Sparodon durbanensis</i>	Tsitsikamma and Bird Is.	M	26	95	99.8	FL	0.12	0.09–0.18
Squalidae	<i>Squalus megalops</i>	Canary Islands	F	32	88	92.4	TL	0.09	0.07–0.14
Syngnathidae	<i>Phyllopteryx taeniolatus</i>	Aquarium of the Pacific, Long Beach, CA	U	3.5	38.6	40.5	SL	0.86	0.66–1.31
Syngnathidae	<i>Syngnathus abaster</i>	Eastern Atlantic	U	4	19	19.9	SL	0.75	0.58–1.15
Tincidae	<i>Tinca tinca</i>	Eurasia	U	20	60	63	SL	0.15	0.12–0.23
Triakidae	<i>Mustelus californicus</i>	Eastern Pacific	F	12	163	171	TL	0.25	0.19–0.38
Trichomycteridae	<i>Trichomycterus itacarambiensis</i>	Olhos d'Água Cave, Itacarambi, Mina Gerais	U	7	8.3	8.7	SL	0.43	0.33–0.66
Valenciidae	<i>Valencia hispanica</i>	Catalonia	M	3	6.7	7.0	TL	1.00	0.77–1.53
Valenciidae	<i>Valencia hispanica</i>	Catalonia	F	4	7.1	7.5	TL	0.75	0.58–1.15
Valenciidae	<i>Valencia letourneuxi</i>	Albania/western Greece	U	3	7	7.4	SL	1.00	0.77–1.53

F = female, M = male, Mx = mixed, U = unsexed.

The variability in Fig. 3 is wide because different species may be plotted over the same maximum length. In order to compare predictions of Equation 3 with growth estimates from accepted other methods at the species level, the six species with the highest number of independent growth estimates were selected (Fig. 4). The estimates of parameter K derived from maximum age overlapped with the independent estimates in all six species. In three species t_{max} -based estimates are also the ones with the highest estimate of L_{∞} , which is not a bias of the method but of data reporting, with lower estimates of maximum age being less likely to be published (see Discussion below).

Discussion

The growth parameter estimates derived with the new methods proposed in this study were applicable to a wide range of species, sizes, and habitats (Tables 1 and 2). The estimates of K derived from length and age at maturation fell within the ranges from previous studies (Figs. 1 and 2), with a median K which included the median K of previous studies for these species within its 95% confidence limits (Table 3). The estimates of K derived from maximum age also fell within the ranges from previous studies (Figs. 3 and 4) albeit with a median K which was lower (0.2 vs. 0.24) and which did not include the median K of previous studies within its 95% confidence limits

(Table 3). This may be caused by a bias in (or lack of) publishing (and compilation in FishBase) of maximum ages that are less than an already published highest reported maximum age for a given species. Such underreporting (and under-compilation) of lower maximum ages may explain that the presented growth estimates derived from t_{max} apply mostly to long-lived populations with lower values of K compared to K values derived from short-lived populations. This may serve as a reminder that the quality of the results of the new methods (Equations 3 and 4) fully depends on the quality and applicability of the few input data, which should be therefore carefully researched and discussed.

Table 3. Comparison of new and previous median estimates of K , where n is the number of estimates for the same species.

Parameter	K	
	from L_m and t_m	from t_{max}
n new	153	628
Median new	0.174	0.200
95% confidence limits	0.149–0.231	0.187–0.230
n previous	880	2814
Median previous	0.19	0.243
95% confidence limits	0.18–0.19	0.235–0.250

If data for maturation and maximum age are available for a given population and are deemed equally reliable, then Equations 3 and 4 can be combined

$$K = \frac{\left(\frac{3.0}{t_{\max}} - \frac{\ln\left(1 - 0.95 \frac{L_m}{L_{\max}}\right)}{t_m} \right)}{2} \quad [\text{Eq 5}]$$

For example, maximum age ($t_{\max} = 20$ years) and maturation ($t_m = 6$ years, $L_m = 445$ cm WD, $L_{\max} = 680$ cm WD) data are available for the Giant manta *Mobula birostris* from the Indo-Pacific (Tables 1 and 2). Solving Equation 5 for these values gives $K = 0.16$. Deriving uncertainty from $2.3/t_{\max}$ and $4.6/t_{\max}$ gives a plausible range of $K = 0.14$ – 0.20 , assuming that uncertainty is higher in the estimation of maximum age compared to length and age at maturation.

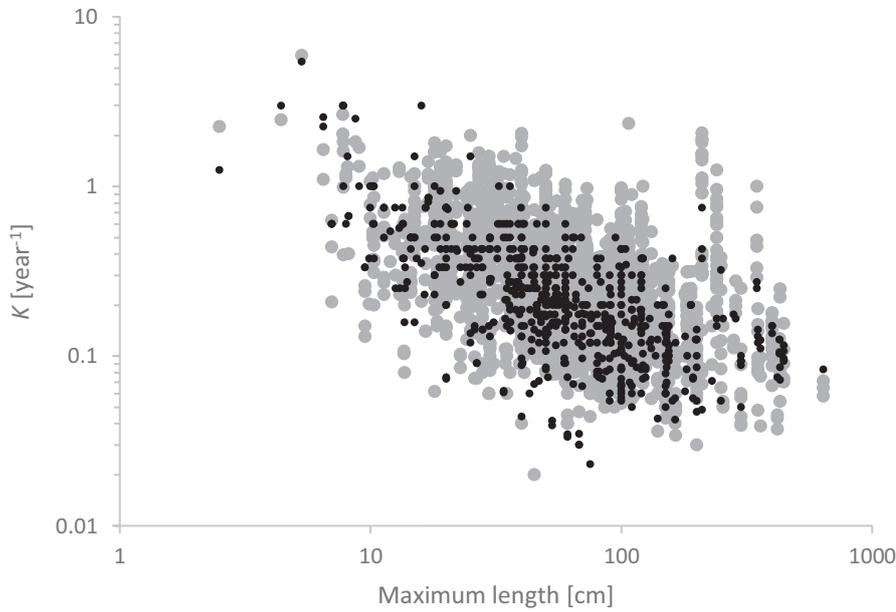


Figure 3. Comparison of 2814 existing estimates of growth parameter K (grey dots) with 628 newly derived estimates from maximum age (black dots), plotted over the known maximum length for 467 species.

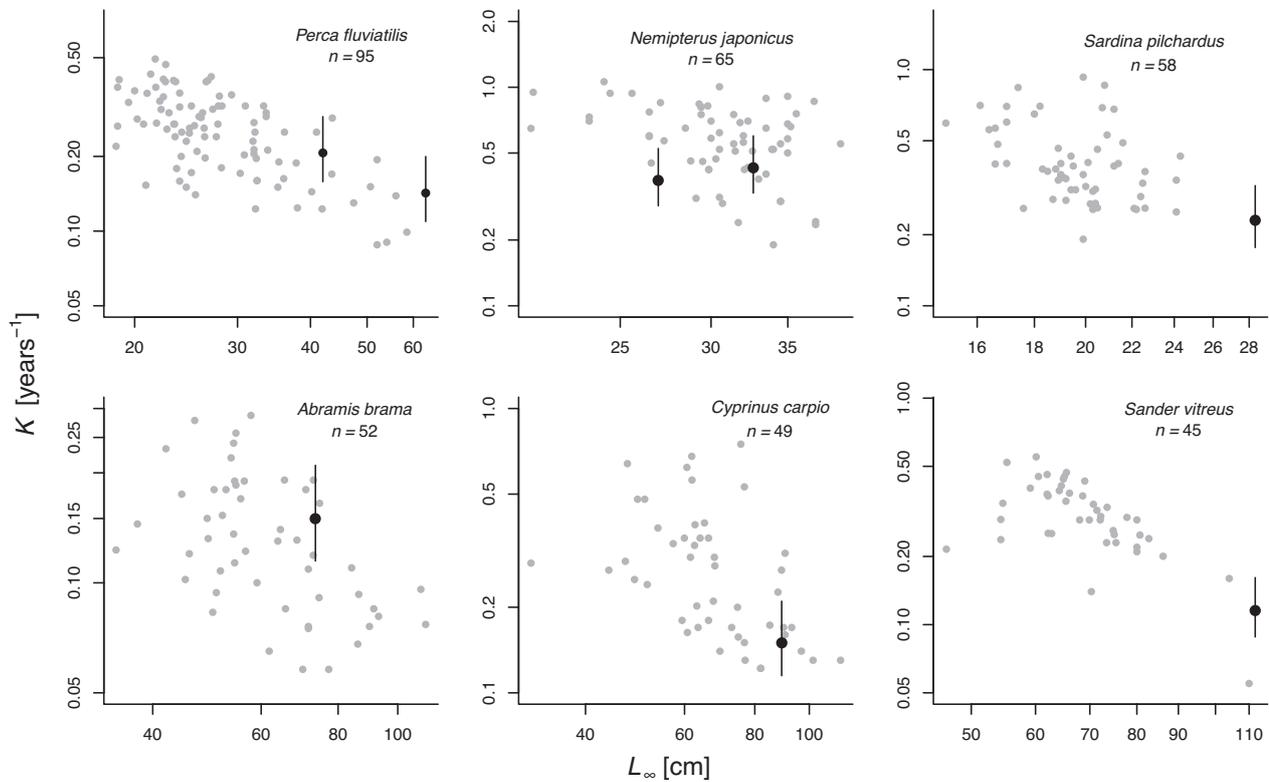


Figure 4. Comparison of growth parameters L_{∞} and K derived with various data-rich methods (gray dots) and from maximum length and maximum age (black dots with indication of plausible range), in log-log space.

The method of estimating growth from the maximum length and a smaller length for which the corresponding age is known is not limited to length and age at maturation (Equation 4) but can be applied to all cases where age is known for a certain length. This also means that Equation 4 is applicable to early maturing species, such as many gadoids, as well as late maturing species, such as sharks. For example, cod (*Gadus morhua*) in the western Baltic Sea had a string of years (2014–2020) with very bad reproductive success, however, with one intermediate year (2016) where reproductive success was close to the mean value of previous years (Froese et al. 2020; ICES 2021). A plot of length frequencies from a commercial trawl fisher in Kiel Bight in spring 2021 (Froese et al. 2022) shows a clear peak of 5-year-old individuals of the 2016 year class, with a mean length

of 76.6 cm length (CL = 75.6–77.6 cm, SD = 6.7, $n = 186$) and a maximum length of 106 cm (Fig. 5). Inserting these numbers into Equation 4 gives $K = 0.23$. Since there is little doubt about the age of the fish, the spread of lengths in the 5-year-old fish was used to derive approximate 95% confidence limits by inserting mean length plus-minus 2 SDs in Equation 4, resulting in a plausible range of $K = 0.17$ – 0.33 . A proxy for L_{∞} was obtained as $1.05 L_{\max} = 114$ cm. An independent study based on survey data from 2000–2012 gives growth parameters of the western Baltic cod as $L_{\infty} = 119$ cm and $K = 0.15$ (Froese and Sampang 2013, p. 31), i.e., with a similar asymptotic length but with a lower rate of increase. Given the absence of other year classes, the faster growth of the 2016 year class could result from the reduced intraspecific competition (Froese et al. 2022).

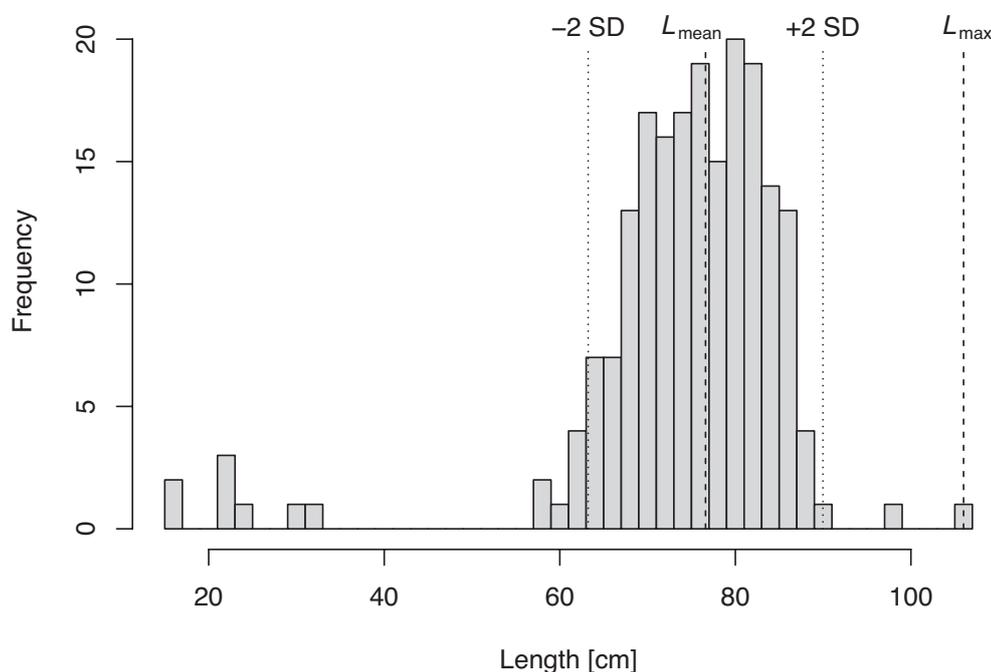


Figure 5. Length-frequencies of trawl catches of cod in Kiel Bight in spring 2021, with indication of maximum length L_{\max} , mean length L_{mean} of the cohort of 2016, and two standard deviations SD around the mean.

Overall, the growth estimates derived with the new methods presented in this study appear suitable for consideration and preliminary guidance in applications for conservation or management (Figs. 1–4, Table 3). The results are flagged as preliminary because of the few data behind the equations. Thus, users are advised to collect additional size-at-age data and perform standard fits of Equation 1, where the results of the methods presented in this study can be used as the required start values for non-linear regressions or as priors in Bayesian analyses.

Journals should accept growth estimates performed with the new methods as new knowledge if they are the first for a given species. In order to facilitate the conservation and management of natural resources, FishBase

(Froese and Pauly 2021) will continue to compile growth parameters, including results obtained with the new methods presented in this study.

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First record of the speckled Maori wrasse, *Oxycheilinus arenatus* (Valenciennes, 1840) (Actinopterygii: Perciformes: Labridae), from Indian coastal waters

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Abstract

The labrid fish species *Oxycheilinus arenatus* (Valenciennes, 1840) is recorded for the first time from India's southeast coast. A total of three specimens were collected as trawl bycatch at Tuticorin, Tamil Nadu, southeast coast of India, in December 2021. The standard length of the specimens ranged from 15.42 to 19.5 cm SL. The presently reported finding of this species from the southeastern coast of India expands and confirms the known distribution range of *O. arenatus*, which was previously not known from India.

Keywords

new record, Tamil Nadu, Teleostei, trawl bycatch, wrasses

Introduction

The fish family Labridae, commonly called wrasses, is a diverse, highly conspicuous, and important component of the ichthyofauna; most of the species (82%) are found in the tropical and subtropical Indo-Pacific region (Thresher 1991; Bellwood and Wainwright 2002). The Labridae is the second largest family of marine fishes in the world (after Gobiidae), with 565 species in 67 genera (Fricke et al. 2022a). Labridae fishes include some of the smallest (<40 mm total length) to the largest (>1 m) fishes on reefs, which feed on a range of invertebrates and also include species that feed exclusively on coral polyps or mucus (Randall et al. 1998). The genus *Oxycheilinus* was originally described by Gill (1862) who designated *Cheilinus arenatus* Valenciennes, 1840 as the type species. Westneat (1993) provided

characters to distinguish it from *Cheilinus*, and it is now accepted as valid by most recent authors (Randall et al. 2003). Westneat (1993) diagnosed *Oxycheilinus* as sharing the following unique characters: lower pharyngeal jaw with posterior shelf, hyomandibula with smooth lateral rim, horizontal color stripe present, and pattern of pelvic-fin pigmentation; also, the following homoplastic features: lateral processes on raised mesethmoid, three to five holes in neural arch of preural centrum 2, lower pharyngeal jaw with concave ventral surface, urohyal with single spike, and dorsal fin with anterior dark spot. In Indian waters, fishes of the genus *Cheilinus* have usually been reported from coral-reef and seagrass ecosystems, especially in the Gulf of Mannar and Palk Bay region (Murugan and Durgekar 2008). The Indo-Pacific labrid genus *Oxycheilinus* includes ten valid species (Fricke et al. 2022b), characterized by dor-

sal-fin rays IX, 10, anal-fin rays III, 8, a moderately shallow body, thin mid-lateral stripe, and elongated blotch at front of dorsal fin between 1st and 3rd spines, interrupted lateral line, 6 predorsal scales, cheek and opercle with two rows of scales, ventral and posterior margins of pre-opercle naked, body covered with relatively large scales, large canine teeth in the front of jaws, and anterior tip of lower jaw extending beyond anterior tip of upper jaw (Gill 1862; Westneat 2001; Randall and Khalaf 2003; Kuitert 2012; Fukui et al. 2017).

During our surveys on the fish diversity of Tamil Nadu coastal waters, India, we collected three specimens of *Oxycheilinus arenatus* (Valenciennes, 1840) for the first time from the bycatch of trawl landings at Tuticorin, southeast coast of India. These specimens are described in the present paper.

Materials and methods

The field surveys were conducted on a monthly basis at various major trawl fish landing centers in the Gulf of Mannar, Tamil Nadu, India (Fig. 1) during December 2020. Three specimens of *O. arenatus* (15.42–19.5 cm SL) were collected from the bycatch of bottom trawlers targeting shrimp (code end mesh size range, 18–25 mm) at Tuticorin (08°52'46.42"N, 078°26'05.49"E). The trawling was carried out on nearshore and offshore fishing grounds at depths ranging from 40–100 m, at a distance of 1–50 km from the shore. After the collection, the fish were photographed, and preserved in a 10% formaldehyde solution. The specimens were deposited in the Centre of Advanced Studies in Marine Biology, Annamalai University, Reference Museum, Parangipettai, India (CASMBAURM). The comparative material was borrowed from the Canadian Museum of Nature, Ottawa, Canada (CMNFI), the Museum of Comparative Zoology, Harvard College, Cambridge, MS, USA (MCZ), and the Muséum national d'histoire naturelle, Paris, France (MNHN). Morphometric measurements were

carried out using a digital Vernier caliper of 0.01 mm accuracy. The vertebrae numbers were counted using X-ray images. The specimens were identified to species level by following previously published keys Fischer and Bianchi (1984), Westneat (2001), Parenti and Randall (2018), and Dewa et al. (2020, 2021). Measuring methods follow Randall and Khalaf (2003), Randall et al. (2003), and Fukui and Motomura (2015, 2016). The results were expressed in % of standard length (SL), and measuring the head length (HL) follows Greenfield and Randall (2018). The genus and species classification follows Fricke et al. (2022b); the family classification follows van der Laan et al. (2014).

Materials examined. CASMBAURM/232116487-89, 3 specimens (17.7–19.5 cm SL), Tuticorin fishing harbor, Tamil Nadu, India, depth below 40 m, coll. A. Murugan, 15–24 December 2020. Comparative material: CMNFI 1973.0244.40, 1 specimen, Comoros, Grande Comore Island, 1973; MCZ 5854, 1 specimen, Mauritius, leg. Nicholas Pike; MNHN A-8284, holotype of *Cheilinus arenatus* Valenciennes, 1840, La Réunion, leg. Eydoux et Souleyet; MNHN A-8285, 1 specimen, Madagascar.

Results

Systematics

Family Labridae Cuvier, 1816

Genus *Oxycheilinus* Gill, 1862

Oxycheilinus arenatus (Valenciennes, 1840)

Figs. 1–3; Table 1

Cheilinus arenatus Valenciennes, 1840: 101, pl. 397 (Réunion, western Mascarenes, southwestern Indian Ocean).

Cheilinus notophthalmus Bleeker, 1853: 493 (Jakarta, Java, Indonesia).

Description. Apart from the presence of the generic characters mentioned above, the specimens are diagnosed by the following characters: Dorsal fin IX, 10–11; anal fin III, 8–9; pelvic-fin rays I, 5; pectoral-fin rays of left and right sides 11/11–12/12 (2 uppermost rays unbranched); caudal-fin rays 13–14 (upper and lower 2 rays unbranched); pored lateral-line scales 22 (13 on anterior lateral line, 9 on posterior lateral line); vertical scale rows 2 + 7; number of scales on black streak 19; pored scales on black streak 8; predorsal scales 6; gill rakers 5 + 6 = 11; branchiostegal rays 5; vertebrae 10 + 12 = 22 (Fig. 2). Body elongate, laterally compressed. Snout short, profile moderately rounded. Eye small; pupil slightly elongate. Interorbital space slightly convex, naked. Head and body covered with scales. Predorsal scales reaching anterior end of orbit. Opercular margins scaleless. Last scale of anterior lateral line located just below base of 4th dorsal-fin soft ray. First scale of posterior lateral line located just above base of 2nd anal-fin soft ray. Head laterally compressed, mouth terminal, gape oblique; posterior margin of lower lip extending beyond vertical through that of upper

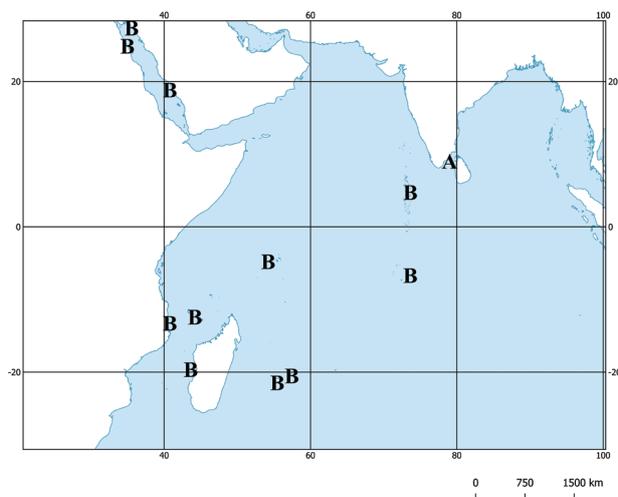


Figure 1. Geographical distribution of *Oxycheilinus arenatus* in Indian Ocean, (A) New record from Tuticorin, India and (B) Previous records.

lip; posterior margin of maxilla extending beyond vertical through anterior margin of orbit; teeth in jaws affixed to outer edge of bony ridge; 2 pairs of large, slender, curved canine teeth anteriorly in each jaw; 16–18 small conical teeth fixed posteriorly on each bony plate behind upper- and lower-jaw canine teeth. Tongue slender, rounded, its upper surface covered with small papillae. Gill rakers thick, short, compressed; rakers on upper limb slightly shorter than those on lower limb; gill membranes free from isthmus. Posterior end of pectoral fin not reaching anus. Pelvic-fin origin and dorsal-fin origin almost on same vertical. Caudal fin truncate, with central part of medium edge slightly rounded, and upper and lower rays elongate. 9th dorsal-fin spine and 7th soft dorsal-fin ray longest; 3rd anal-fin spine and 4th soft anal-fin ray longest; 1st pelvic-fin soft ray longest (Table 1).

Color. Upper part of body light red, abdomen white. Sides with mottled pattern reaching from upper side of head to upper back, consisting of small, scattered orange or dark brown spots at low density. Dark vertical black band at center of body extending from posterior margin of eye to caudal-fin base. Small white spots scattered at high density above vertical band. Large black spot on membranes of first four dorsal-fin spines. Membranes between first four dorsal-fin soft rays otherwise pale green, with white lines and irregularly arranged white spots. Membranes between 4–10 dorsal-fin soft rays whitish translucent. Pectoral-fin base bright yellow, fin membranes transparent. Pelvic-fin base and anal-fin membranes white, fins mottled with light red. Medium caudal-fin membranes white-translucent, mottled with light red, upper and lower lobes yellow (Fig. 3).

Remarks. *Oxycheilinus arenatus* (Valenciennes, 1840), commonly known as speckled Maori wrasse, is known from the Red Sea and the Indo–West Pacific: East Africa, Seychelles, Madagascar, and Mascarenes east to Marshall Islands and Samoa, north to Ryukyu Islands (Japan). Generally, from the conservation point of view, they are considered ‘Least concern’ (Liu and To 2010). In the Red Sea and Indian Ocean, the species was previously recorded from La Réunion (Valenciennes 1839, as *Cheilinus arenatus*; Fricke et al. 2009), Chagos Archipelago (Winterbottom et al. 1989, as *Cheilinus arenatus*), Mauritius (Günther 1862, as *Cheilinus arenatus*), Seychelles (Smith and Smith 1963, as *Cheilinus arenatus*), Maldives (Randall and Anderson 1993, as *Cheilinus arenatus*; Anderson et al. 1998), Mozambique (Gell and Whittington

2002), Red Sea (Randall and Khalaf 2003; Golani and Fricke 2018), Madagascar (Fricke 1999; Fricke et al. 2018). The current findings represent a range extension of ca. 700 km to the northeast of the closest previously known region (Maldives), and the first record of this species from India. *Oxycheilinus arenatus* is widespread in the Indo–West Pacific and was probably previously overlooked in Indian waters. Apparently, the species is very rare in India.

This species is found in caves of steep outer reef drop-offs from 25 to at least 46 m with rich invertebrate growth such as large gorgonians or soft corals (Froese and Pauly 2022). It is naturally rare and has been rarely documented due to its cryptic occurrence in deep reefs. The lower

Table 1. A comparison of morphometric characters of *Oxycheilinus arenatus* collected from Indian coastal waters and from Amami-oshima island, Ryukyu Islands, Japan.

Character	This study (<i>n</i> = 3)				Dewa et al. 2021 (<i>n</i> = 1)	
	Absolute value [mm]		%SL		Abs. value [mm]	%SL
	Range	Mean	Range	Mean		
Total length (TL)	177–195	186				
Standard length (SL)	142–157	151			128.7	
Head length			37.32–38.85	38.02		39.2
Head depth			28.16–29.29	28.64		
Snout length			14.08–15.28	14.65		14.1
Snout to end of preoperculum			27.46–28.02	27.73		
Orbit diameter			7.04–7.64	7.30		9.9
Upper-jaw length			10.56–12.10	11.31		12.9
Lower-jaw length			11.97–12.73	12.42		13.3
Caudal-peduncle depth			16.90–18.44	17.54		14.4
Caudal-peduncle length			12.67–14.01	13.37		12.9
Pectoral-fin length			14.78–16.56	15.64		16.4
Pelvic-fin length			12.67–14.64	13.84		11.3
Dorsal-fin length			4.90–5.70	5.30		
Dorsal-fin base length			50.70–53.50	52.17		53.6
Anal-fin base length			4.90–5.70	5.30		
Pelvic-fin base length			4.20–5.00	4.66		
Anal-fin length			26.76–26.82	26.67		
Anal-fin width			35.21–35.32	35.35		
Opercular length			9.80–11.46	10.66		
Interorbital width			14.08–15.28	14.66		
Predorsal length			45.19–47.75	46.53		
Prepectoral length			38.02–41.54	39.74		
Prepelvic length			45.07–47.88	46.49		
Preanal length			69.71–72.21	70.76		
1 st anal-fin spine length			4.90–5.70	5.33		5.1
2 nd anal-fin spine length			7.04–7.64	7.30		10.4
3 rd anal-fin spine length			9.80–11.97	10.62		11.2

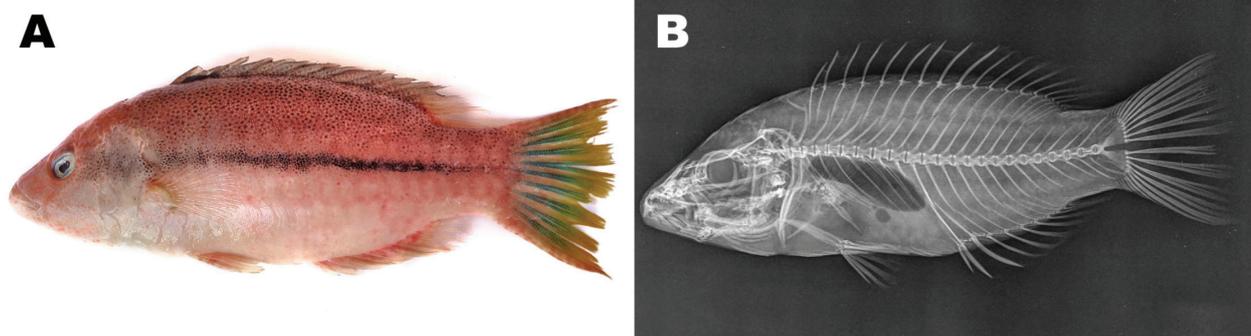


Figure 2. Freshly preserved *Oxycheilinus arenatus* (A) (CASMBAURM/232116489) and (B) X-ray of the adult Speckled Maori wrasse with 22 vertebrae (10 abdominal + 12 caudal).

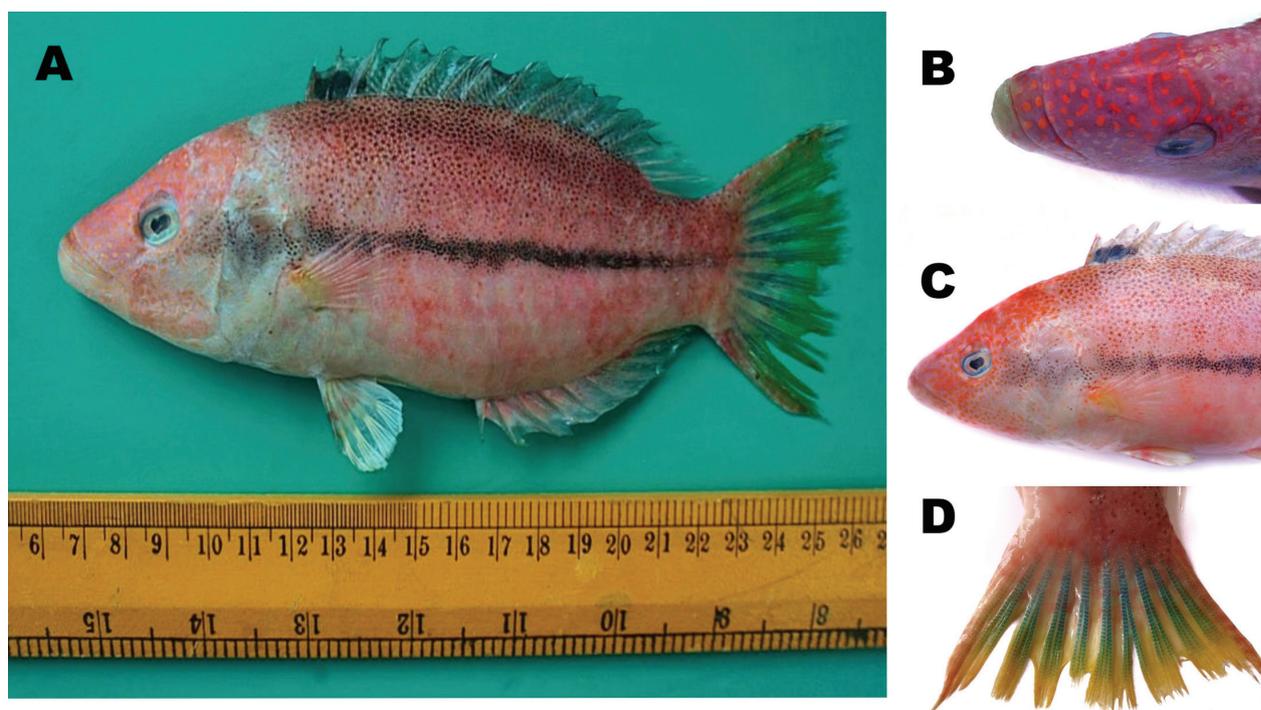


Figure 3. *Oxycheilinus arenatus* (A) collected from Tuticorin, India (CASMBAURM/232116487); (B) Head; (C) Dorsal fin and (D) Caudal fin.

extent of the depth distribution range is unknown. The collecting depth of the Indian specimens below 40 m well agrees with the previously known depth range.

Conflict of interest

The authors declare that they have no conflict of interest.

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First record of butterflyfish, *Roa haraguchiae* (Actinopterygii: Perciformes: Chaetodontidae), from northeast Taiwan

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Abstract

A recently-described butterflyfish, *Roa haraguchiae* Uejo, Senou et Motomura, 2020, is herewith for the first time reported from northeast Taiwan. In Taiwan, the genus *Roa* has been known represented by a single species, *Roa modesta* (Temminck et Schlegel, 1844). This study presents a comparison of *R. haraguchiae* with its congeners and includes diagnostic characters on the basis of morphology and genetic differences by life-barcoding. Our specimens have some differences that may be attributed to the individual variations, which are compared and discussed.

Keywords

CO1 sequence, mitochondrial DNA, morphology, taxonomy, white-spine butterflyfish

Introduction

The family Chaetodontidae is commonly referred to as butterflyfishes and its representatives inhabit tropical and subtropical sea areas, which are mainly distributed in the Indo–West Pacific. They live on coral reef substrate and are characterized by their colorful skin. According to Nelson et al. (2016), the family Chaetodontidae is represented by 12 genera and 129 species; whereas, according to Fricke et al. (2022), the family currently contains 12 genera and about 136 species in the world with seven genera and 46 species records in Taiwan (Shao 2022).

The genus *Roa* Jordan, 1923 represents the family Chaetodontidae and it can be separated from other butterflyfishes by having three distinct bands on the body, with the first band passing behind the eye and ending at the lower edge of the preopercle. According to Matsunuma and Motomura (2022), the genus includes the following

eight valid species: *Roa modesta* (Temminck et Schlegel, 1844); *Roa excelsa* (Jordan, 1921); *Roa jayakari* (Norman, 1939); *Roa australis* Kuitert, 2004; *Roa rumsfeldi* Rocha, Pinheiro, Wandell, Rocha et Shepherd, 2017; *Roa haraguchiae* Uejo, Senou et Motomura, 2020; *Roa semilunaris* Matsunuma et Motomura, 2022; and *Roa uejoi* Matsunuma et Motomura, 2022. The genus *Roa* was originally described as *Loa* with a type species *Loa excelsa* Jordan, 1921. Quite soon, however, Jordan (1923) changed the genus name to *Roa* because of its homonymy with *Loa* Stiles in Stiles et Hassall, 1905, which is a genus of nematodes belonging to Filariidae. For a long time, the majority of authors have considered the genus *Roa* to be a subgenus of the genus *Chaetodon* Linnaeus, 1758. Kuitert (2004) was the first researcher to confirm the generic rank of *Roa* following an unpublished thesis of Blum, mentioned in Blum (1989). He also described *Roa australis* Kuitert, 2004 as the only *Roa* species distributed

in the Southern Hemisphere. He also moved *Chaetodon modestus* to *Roa* as *R. modesta*, which is the only *Roa* species reported from Taiwan by Shen (1993). Recently, Matsunuma and Motomura (2022) described two new species of *Roa*—*Roa semilunaris* and *Roa uejoi*, which are respectively distributed in the southwestern Indian Ocean and the Mariana Islands.

Species of the genus *Roa* inhabit waters deeper than 200 m and are often caught by bottom trawl nets. Those fishes have been recorded from different environments. The ecosystems where *Roa rumsfeldi* was found vary from sheltered rocky outcroppings heavily covered by fine sediment to areas exposed to strong currents (Rocha et al. 2017). Uejo et al. (2020) mentioned that the *Roa* specimens from the East China Sea were all taken using bottom trawls, indicating a sandy bottom habitat, while all of the underwater photographs were taken in rocky bottom areas in fairly deep water.

The type locality of *Roa haraguchiae* is in the East China Sea, Japan (146–162 m), with a paratype collected at Iloilo, Panay Island, the Philippines. It was also found in the Izu Peninsula, the Pacific coast of Japan; Suruga Bay and Sakurajima in Kagoshima Bay, southern Kyushu (37–70 m) (Uejo et al. 2020).

In this study, the first record of *Roa haraguchiae* in Taiwan has been described, including the diagnostic characters on the basis of morphology, genetic differences from its congeners and a key for species of the genus *Roa*. The specimens collected in Taiwan have some differences that may be attributed to the individual variations, which are also compared and discussed.

Methods

Counts, measurements, and terminology generally follow Pyle and Kosaki (2016) and Uejo et al. (2020). Body depth is measured as a vertical straight line from the front edge of the pelvic-fin spine base to the insertion point of the first dorsal-fin spine. Postorbital length is the distance from the posterior edge of the bony orbit to the posterior edge of the fleshy flap near the end of the gill opening.

The radiographs on the skeleton of butterflyfish specimens were obtained using the X-ray equipment of the National Marine Museum of Biology and Aquarium (NMMB, Taiwan). All specimens were deposited at the Laboratory of Aquatic Ecology of the National Taiwan Ocean University (TOU-AE).

The cytochrome *c* oxidase subunit 1 (CO1) barcoding method follows Chang et al. (2016). PCR amplification of the 5' region of the CO1 gene (approximately 650 bp) was performed and all the successfully amplified sequences were aligned (Clustal W), trimmed, constructed, and saved as FASTA format by using BioEdit ver. 7.2.5 (Hall 1999), followed by the construction of a Neighbor-Joining (NJ) tree with 10 000 bootstrap-replicated K2P distance using MEGA ver. 10.0.5 (Kumar et al.

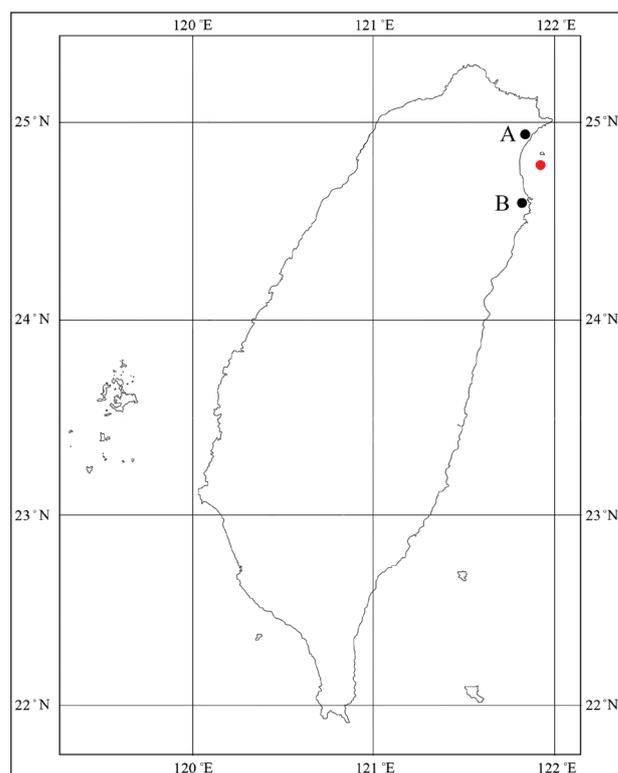


Figure 1. Distribution records of *Roa haraguchiae* from Taiwan. Black point symbols collection port, A = Da-xi, B = Nan-fang-ao. Red point means fishing location.

2018). Nine sequences from five species were used as the ingroup and one of *Chaetodon octofasciatus* Bloch, 1787 (KU944212) served as the outgroup. All of the accession numbers are listed in Table 1. Due to some differences in the appearance of these four specimens and given that they are the only vouchers with muscle tissue from this batch, we can only use them as the materials for the molecular analysis.

Our *Roa haraguchiae* specimens were all collected by bottom trawls at a depth of 100–300 m from northeast Taiwan (Fig. 1), including sandy and rocky bottom habitats.

Table 1. List of accession numbers of the species of *Roa* and *Chaetodon* (as outgroup) in GenBank and one specimen in BOLD.

Specimen No.	Scientific name	Accession number	
TOU-AE8100	<i>Roa haraguchiae</i>	OM365890	This study
TOU-AE8354	<i>Roa haraguchiae</i>	OM365891	This study
TOU-AE8355	<i>Roa haraguchiae</i>	OM365892	This study
TOU-AE8379	<i>Roa haraguchiae</i>	OM365893	This study
PNM15198	<i>Roa rumsfeldi</i>	MF995631	Rocha et al. 2017
CIFE:FGB-RJ-001	<i>Roa jayakari</i>	KF268176	
ASIZP0805725	<i>Roa modesta</i>	KU944230	Chang et al. 2016
ASIZP0802360	<i>Chaetodon octofasciatus</i>	KU944212	Chang et al. 2016
NMV A 29675-001	<i>Roa australis</i>	FOAG413-08. COI-5P	

Bold font denotes sequence ID from BOLD.

Results

Taxonomical status

Family Chaetodontidae Rafinesque, 1815
Roa Jordan, 1923

Roa haraguchiae Uejo, Senou et Motomura, 2020

Figs. 1–2, Table 2

English name: white-spine butterflyfish

New Chinese name: 原口氏羅蝶魚

Specimens examined. (six specimens) TOU-AE8100, 72.22 mm SL, Da-xi, NE Taiwan, bottom trawl, 8 May

2021; TOU-AE8354, 96.27 mm SL, Nan-fang-ao, NE Taiwan, bottom trawl, 1 Aug 2021; TOU-AE8355, 108.59 mm SL, sharing the same collecting information with TOU-AE8354; TOU-AE8379, 96.78 mm SL, Da-xi, NE Taiwan, bottom trawl, 13 Aug 2021; TOU-AE8491, 90.21 mm SL, Da-xi, NE Taiwan, bottom trawl, 26 Oct 2021; TOU-AE8492, 98.25 mm SL, sharing the same collecting information with TOU-AE8491.

Comparative material. *Roa modesta* (26 specimens): TOU-AE7862, 89.70 mm SL, Da-xi, NE Taiwan, date unknown; TOU-AE7863, 96.11 mm SL, Da-xi, NE Taiwan, date unknown; TOU-AE7876, 76.96 mm SL, Ba-dou-zi, NE Taiwan, 15 Aug 2020; TOU-AE7877, 84.71 mm SL and TOU-AE7878, 90.11 mm SL sharing the same

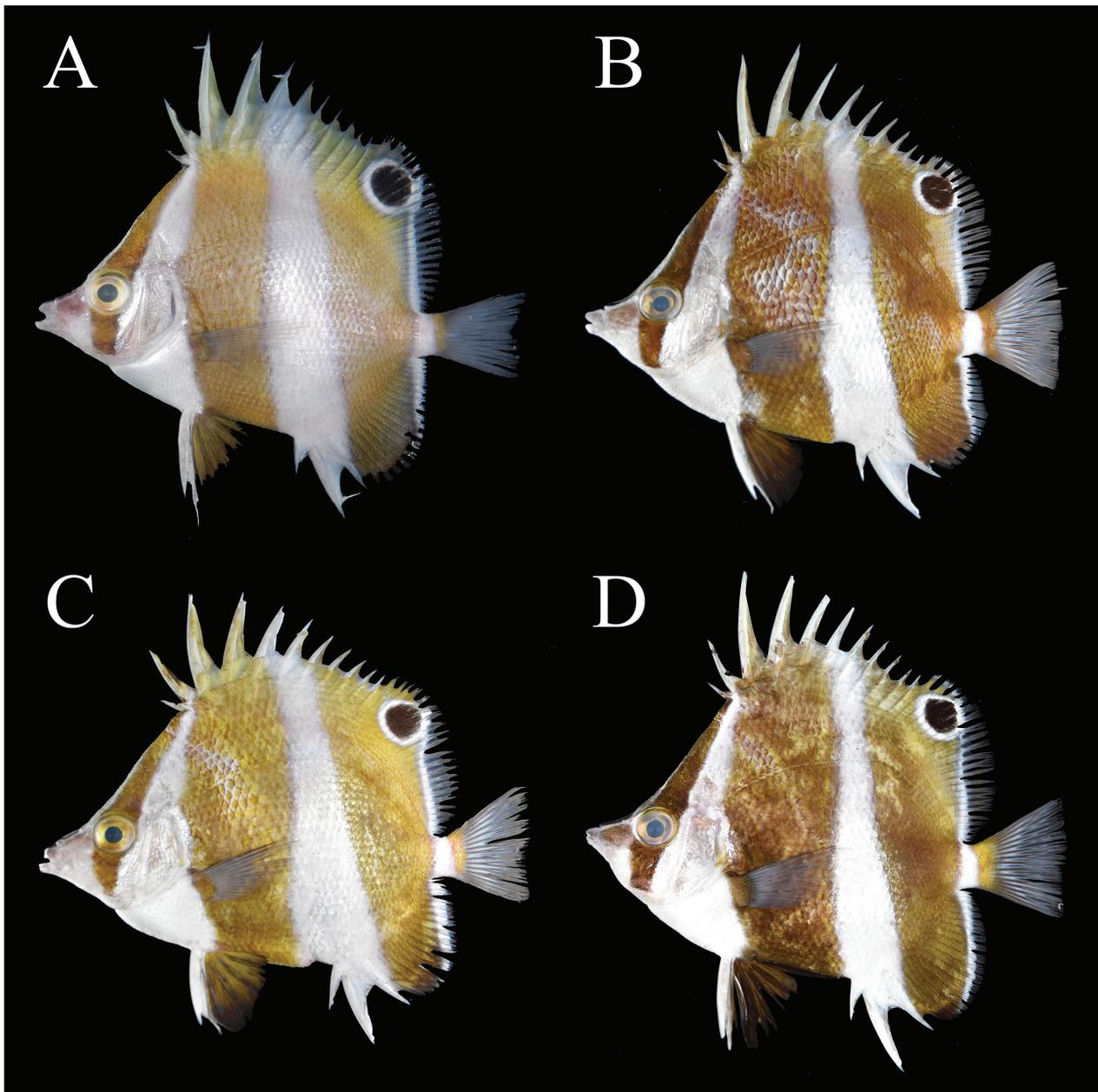


Figure 2. Comparison of the morphological differences of the fresh specimens of *Roa haraguchiae* in Taiwan, for which CO1 genes were sequenced. A. TOU-AE 8100, 72.22 mm SL; B. TOU-AE 8354, 96.27 mm SL; C. TOU-AE8355, 108.59 mm SL; D. TOU-AE 8379, 96.78 mm SL. Photo by J.-F. Huang.

collecting information with TOU-AE 7876 ; TOU-AE7995, 80.30 mm SL, Dong-gang, S Taiwan, 2 Jan 2021; TOU-AE7999, 86.50 mm SL, Dong-gang, S Taiwan, 23 Jan 2021; TOU-AE8000, 75.58 mm SL, Ke-tzu-liao, S Taiwan, 24 Jan 2021; TOU-AE8011, 43.91 mm SL sharing the same collecting information with TOU-AE8000; TOU-AE8109, 86.78 mm SL, Kan-zi-ding Fish Market, N Taiwan, 27 Apr 2021; TOU-AE8110, 92.98 mm SL sharing the same collecting information with TOU-AE8109; TOU-AE8131, 95.76 mm SL, Da-xi, NE Taiwan, 26 Jul 2020; TOU-AE8132, 91.31 mm SL sharing the same collecting information with TOU-AE8131; TOU-AE8133, 97.54 mm SL, Da-xi, NE Taiwan 1 May 2021; TOU-AE8241, 63.40 mm SL, Ke-tzu-liao, S Taiwan, 24 Jan 2021; TOU-AE8242, 54.87 mm SL, Ke-tzu-liao, S Taiwan, date unknown; TOU-AE8243, 72.98 mm SL and TOU-AE8244, 79.78 mm SL, Ke-tzu-liao, S Taiwan, date unknown; TOU-AE8287, 91.96 mm SL, Da-xi, NE Taiwan, 26 Jul 2021; TOU-AE8288, 90.82 mm SL sharing the same collecting information with TOU-AE8287; TOU-AE8322, 98.68 mm SL, Nan-fang-ao, NE Taiwan, 1 Aug 2021; TOU-AE8323, 94.74 mm SL and TOU-AE8324, 98.55 mm SL sharing the same collecting information with TOU-AE8322; TOU-AE8372, 74.76 mm SL, Ba-dou-zi, NE Taiwan, 2 Aug 2021; TOU-AE8373, 71.30 mm SL sharing the same collecting information with TOU-AE8372; TOU-AE8426, 77.42 mm SL, Da-xi, NE Taiwan, 13 Aug 2021.

Diagnosis. Specimens of *Roa haraguchiae* in Taiwan with the following combination of characters: pored lateral-line scales 39–42; non-pored lateral-line scales 4–6; scale rows above lateral line 11–13, scale rows below lateral line 20–24; scale rows under longer axis of black blotch on dorsal-fin soft-rayed portion 10–12; longer snout length 2.8–3.0 in HL; shorter caudal-peduncle depth 8.8–10 in SL; shorter dorsal-fin soft-rayed portion base length 2.7–2.9 in SL; longer 2nd anal-fin spine length 3.7–4.0 in SL; anterior margin of second body band not reaching anteroventrally to pelvic-fin spine base; first pelvic-fin soft ray white and extended; membranes associated with first and second dorsal-fin spines are respectively blackish completely and distally.

Description of Taiwanese specimens. Counts and proportional measurements as a percentage of SL and HL are given in Table 2. Data for the specimens in Taiwan, followed by data for the other congeners. Dorsal-fin XI, 20–21; anal-fin III, 16–17; pelvic-fin rays I, 5; pectoral-fin rays 14; pored lateral-line scales 39–42; Non-pored lateral-line scales 4–6; Scale rows above lateral line 11–13; Scale rows below lateral line 20–23; Scale rows in longer axil of black blotch on dorsal-fin soft-rayed portion 11–12; gill rakers 3–4 + 11–12 (14–16); vertebrae 11 + 13 = 24; caudal rays 12 + 11 = 23.

Body strongly deep and compressed, its depth 1.5–1.7 in SL and width 6.4–7.2 in SL; head length 2.6–2.8 in SL; orbit diameter slightly shorter than snout length, its length 3.0–3.3 in HL; snout length 2.8–3.0 in HL; postorbital length 2.8–3.1 in HL; interorbital region narrow, bony width 3.5–

4.0 in HL. Mouth small, terminal, and slightly protractile. Numerous bristle-like teeth in both jaws. Opercular membranes narrowly attaching to isthmus, slightly projecting at posterior margin of operculum; gill rakers short. Two pairs of nostrils closely symmetric, anterior to eye.

Scales on body ctenoid, also scattered on head, abdomen, and part of upper jaw, except lower jaw. Lateral line scales ascending from posterior edge of gill opening to divide between white and brown bands below base of eleventh dorsal-fin spine and then gradually declining to end of dorsal-fin.

Dorsal-fin spinous portion base length 2.5–2.7 in SL, soft-rayed portion base length 2.7–2.9 in SL; origin of dorsal-fin at vertical through base of pectoral-fin, well at origin of pelvic-fin. First dorsal-fin spine shortest, its length 11.9–14.7 in SL; second dorsal-fin spine length 5.1–8.3 in SL; third dorsal-fin spine slightly shorter than fourth spine, its length 2.9–3.2 in SL; fourth dorsal-fin spine longest, its length 2.8–3.2 in SL; after that, spine length becomes shorter when spine number increasing.

First dorsal-fin soft ray length 4.1–4.9 in SL. Pectoral-fin moderately long, its length 3.1–3.5 in SL, first ray not segmented, second or third ray longest and reaching through posterior edge of second band. Pelvic-fin origin below pectoral-fin base origin, its spine length 3.7–4.7 in SL; its soft ray length 3.1–4.0 in SL. Second anal-fin spine longest, its length 3.7–4.0 in SL; longest anal-fin soft ray length 4.0–4.6 in SL. Caudal-fin truncated, its length 4.1–5.1 in SL.

Coloration. In fresh specimens (Figs. 2A–D): head and body white, with three main brown bands. First band starting from origin of dorsal fin and descending through eye to lower edge of preopercle, with width slightly shorter than orbit diameter. Second band extending from base of second to seventh dorsal-fin spines down to base of pelvic-fin soft rays, posterior margin to anus. Third band starting from base of tenth dorsal-fin spine to terminal end of dorsal-fin, downwards almost covering soft anal fin, between third or fourth soft rays and terminal end of anal-fin. Two additional narrow brown bands also visible; one on anterior margin of body, extending from tip of upper snout through interorbital, approximately half of predorsal-fin length. Another narrow band on posterior margin of caudal-peduncle in form of black blotch with white edge between first and seventh dorsal-fin soft rays. Dorsal-fin spines and soft rays whitish, except for those blackish banded areas and membranes associated with first and second dorsal-fin spines. Anal-fin spines and soft rays whitish, except those banded areas. Caudal-fin and pectoral-fin greyish. Pelvic-fin spine and first soft ray whitish, while others brownish.

When preserved (Fig. 3): Head and body change from whitish to slightly yellowish, with three brown bands becoming lighter. Opercle brownish; opercular membrane yellowish; membranes associated with first and second dorsal-fin spines blackish; blotch on soft-rayed portion blackish, with still obvious whitish margin. The fin color is approximately the same as described above in color when fresh.

Table 2. Counts and measurements of *Roa haraguchiae*, *Roa modesta*, and *Roa rumsfeldi*.

Character	<i>Roa haraguchiae</i>		<i>Roa modesta</i>	<i>Roa rumsfeldi</i>
	This study n = 6	Uejo et al. 2020 n = 7	This study n = 26	Uejo et al. 2020 ASIZP 68098
Standard length [mm]	72.2–108.6	63.2–92.8	43.9–98.7	51.2
Counts				
Dorsal-fin rays	XI, 20–21	X–XI, 21	XI, 21–23	XI, 20
Anal-fin rays	III, 16–17	III, 16–17	III, 16–18	III, 17
Pelvic-fin rays	I, 5	I, 5	I, 5	I, 5
Pectoral-fin rays	14	13–15	14–15	15
Caudal-fin rays	12+11		12+11	
Pored lateral-line scales	39–42	38–42	40–44	32
Non-pored lateral-line scales	4–6	5–7	3–5	13
Scale rows above lateral line	11–13	11–12	12–13	8
Scale rows below lateral line	20–23	22–28	24–25	19
Scale rows in longer axil of black blotch on dorsal-fin soft-rayed portion	11–12	10–12	9–11	8
Gill rakers (upper + lower limbs)	3–4 + 11–12	3–5 + 9–11	3–4+9–10	3+9
Vertebrae (precaudal + caudal)	11+13		11+13	
Measurements [% SL]				
Body depth	60.1–66.9	56.5–66.6	64.1–70.6	60.2
Body width	13.8–15.7	14.5–16.7	13.4–17.4	15.4
Head length	35.9–38.0	34.3–38.7	32.3–39.8	39.3
Head depth	47.8–53.2	46.2–54.9	49.4–55.5	51.6
Predorsal-fin length	49.5–53.7	47.1–54.8	46.6–53.5	53.1
Prepelvic-fin length	42.0–48.5	39.7–46.2	43.1–49.1	44.9
Preanal length	65.0–66.7	67.3–72.0	61.0–67.1	69.1
Preanal-fin length	72.7–78.5	72.3–77.0	69.3–75.8	73.8
Snout length	12.4–13.8	12.6–13.6	9.2–12.4	12.7
Orbit diameter	10.8–13.3	11.1–13.5	10.7–14.1	14.6
Postorbital length	12.4–13.4	12.1–14.1	10.6–14.1	13.7
Interorbital width	9.2–11.3	9.2–11.3	9.3–11.6	10.2
Caudal-peduncle depth	10.0–11.4	10.8–11.3	11.1–13.9	10.0
Caudal-peduncle length	4.3–5.3	5.4–8.0	3.3–6.3	7.8
Caudal-fin length	19.7–24.5	20.1–24.2	20.1–25.0	23.8
Pectoral-fin length	28.7–31.8	27.9–30.5	26.2–32.8	32.4
Dorsal-fin spinous portion base length	37.4–40.4	34.0–39.9	35.7–40.1	33.4
Dorsal-fin soft-rayed portion base length	34.7–36.4	29.4–34.8	36.8–40.1	28.5
1 st dorsal-fin spine length	6.8–8.4	8.6–10.3	6.1–11.7	9.6
2 nd dorsal-fin spine length	12.0–19.8	19.0–25.0	13.6–24.4	22.9
3 rd dorsal-fin spine length	30.9–34.9	31.6–39.5	24.6–33.9	35.4
4 th dorsal-fin spine length	31.6–35.8	34.4–41.0	27.5–36.3	37.5
5 th dorsal-fin spine length	30.2–33.9	29.9–36.2	28.4–35.6	35.5
6 th dorsal-fin spine length	28.8–32.0	29.2–34.0	27.7–35.6	33.0
7 th dorsal-fin spine length	26.3–30.5	25.6–30.5	25.7–33.8	NA
8 th dorsal-fin spine length	23.9–27.8	24.0–27.6	22.7–31.2	29.9
9 th dorsal-fin spine length	21.9–25.4	22.2–26.4	20.6–29.5	26.2
10 th dorsal-fin spine length	20.3–22.9	21.5–24.5	20.9–27.2	NA
11 th dorsal-fin spine length	19.3–21.8	21.5–24.5	19.3–26.8	18.8
1 st dorsal-fin soft ray length	20.4–24.5	20.9–27.4	19.4–27.9	25.0
Anal-fin base length	33.4–37.0	20.6–34.8	34.5–41.6	32.6
1 st anal-fin spine length	10.7–12.8	11.6–15.0	9.7–13.4	11.3
2 nd anal-fin spine length	25.2–27.1	26.8–30.1	17.9–23.7	25.4
3 rd anal-fin spine length	20.5–24.3	20.4–26.2	17.9–23.1	24.4
Longest anal-fin soft ray length	21.8–24.9	21.8–29.4	18.2–24.2	NA
Pelvic-fin spine length	21.9–25.9	23.7–27.2	19.1–26.0	27.0
Pelvic-fin length	24.8–32.3	28.0–38.3	25.5–36.6	38.5
Measurements [% HL]				
Body depth	162.8–177.7	163.6–174.7	172.5–208.7	153.2
Body width	37.4–43.6	39.3–45.2	33.5–51.8	39.3
Head height	131.5–139.8	133.9–143.4	139.4–163.8	131.3
Predorsal-fin length	131.8–141.7	129.4–143.1	129.5–155.8	135.3
Prepelvic-fin length	113.6–128.8	112.6–121.3	122.9–139.3	114.4
Preanal length	166.1–184.2	178.4–203.8	161.5–199.2	176.1
Preanal-fin length	188.4–211.4	189.5–224.2	182.1–228.2	188.1
Snout length	33.4–36.3	33.2–38.7	25.3–33.4	32.3
Orbit diameter	30.0–33.7	31.4–35.0	30.9–37.1	37.3
Postorbital length	32.6–36.3	33.3–36.3	32.7–37.9	34.8
Interorbital width	24.9–28.2	25.0–29.2	27.1–33.7	25.9



Figure 3. Preserved specimens of *Roa haraguchiae*. The band coloration turns slightly brownish and the blackish part has remained.

Discussion

Roa haraguchiae, compared to *Roa modesta*, have a longer snout length 33.4–36.3 (vs. 25.3–33.4) in HL; a shorter caudal-peduncle depth of 10.0–11.4 (vs. 11.1–13.9) in SL; shorter dorsal-fin soft-rayed portion base length 34.7–36.4 (vs. 36.8–40.1) in SL; longer 2nd anal-fin spine length 25.2–27.1 (vs. 17.9–23.7) in SL. The second band extends from the base of the second to the seventh dorsal-fin spines (fourth to eighth). Shorter 2nd/3rd dorsal-fin spine length 53.1% (vs. 65.9%); pelvic first soft ray whitish and

others darkish (vs. all yellow). The main three bands on the lateral side are brownish without blackish margin (vs. yellowish with blackish margin); the eye band is equal to the eye diameter (vs. narrower than the eye diameter); the anterior margin of the second band reaching the gill opening where the lateral-line scale begins (vs. not reaching, through the fifth lateral-line scale) (Fig. 4).

A comparison of the four specimens in Taiwan shows the following: according to the results of CO1 sequencing, it was confirmed that TOU-AE 8100, TOU-AE 8354, TOU-AE 8355, and TOU-AE 8379 are the same species. An NJ tree constructed by partial CO1 gene sequences (552 bp after being processed by BioEdit software) of six species (Table 1) supports the separation of these species (Fig. 5). Besides, in Table 3, the K2P distance matrix reveals that there is no great distance amongst the same species, the distance ranging from 0.038 to 0.129 amongst the five *Roa* congeners and the outgroup shows the distance ranging from 0.191 to 0.220. The width of the eye band is equal to the eye diameter, except that TOU-AE 8355 narrows down. The second dorsal-fin spine of TOU-AE 8354 is shorter than the others (12% compared to the mean value of 17.4%) and the membrane-associated with second dorsal-fin spines is blackish completely (others are blackish distally). The band color from yellowish-brown to dark brown in fresh specimens has been observed to be the same in the preserved specimen.

The other six *Roa* species are not mentioned herein for they can be clearly separated from morphological features. Compared to *R. australis*, the second band reaching the posterior edge of the opercular membrane (vs. not reaching), is shown to be brownish (yellowish) in color. Compared to *R. excelsa*, the longest dorsal-fin

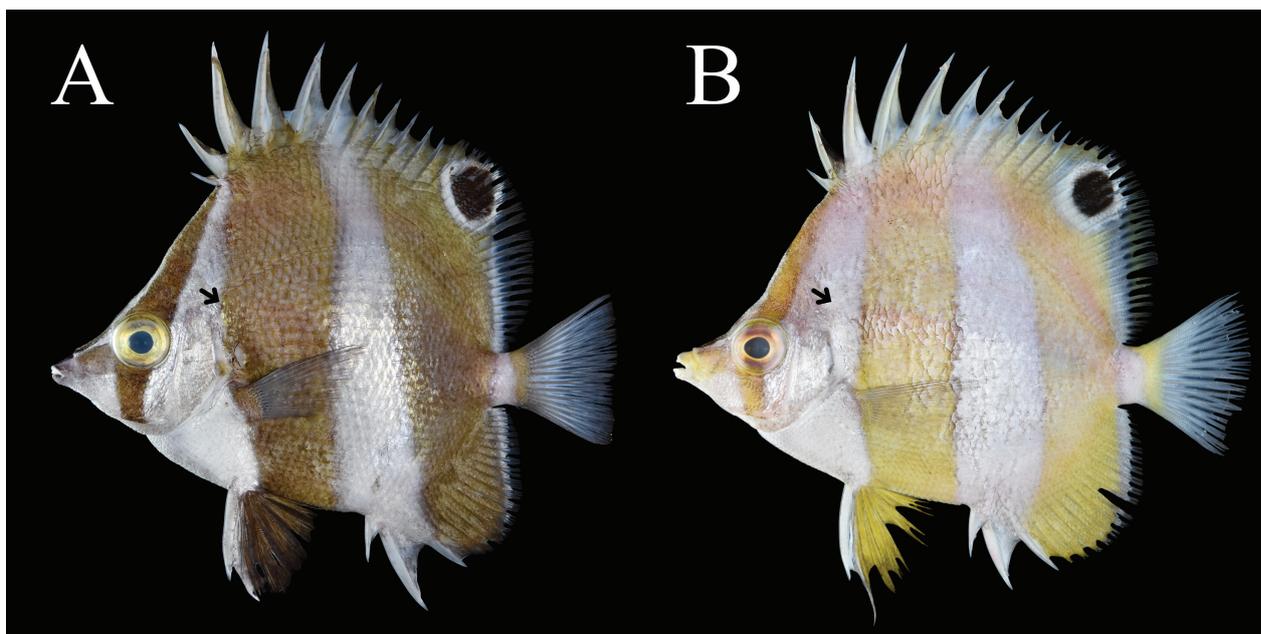
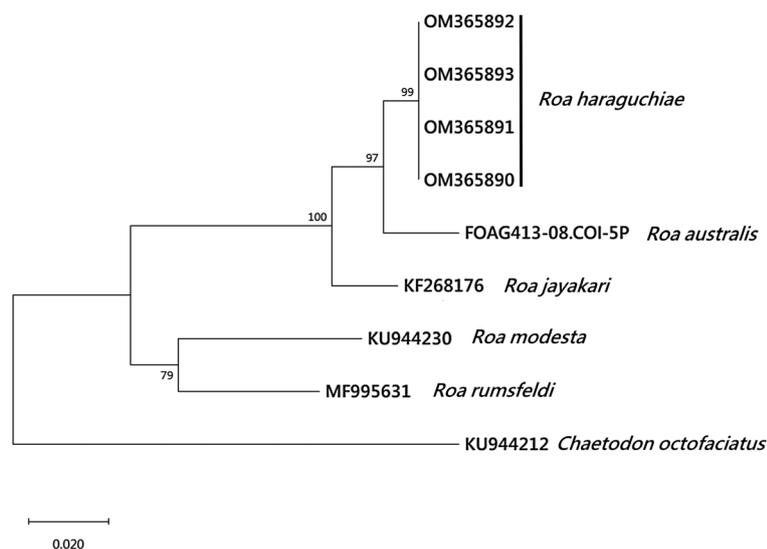


Figure 4. Comparison of the dorsal-fin spine and band coloration of two species in Taiwan. A. *Roa haraguchiae*, TOU-AE 8491, 90.21 mm SL; B. *R. modesta*, TOU-AE 8426, 77.42 mm SL. The arrow shows the differences where the second band reaches the anterior edge.

Table 3. Matrix of Kimura-2-parameter distances of the 9 CO1 sequences used to construct the NJ tree in the presently reported study. (1) to (8) are 8 specimens of five *Roa* congeners and (9) was taken as an outgroup, respectively.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
(1) <i>Roa haraguchiae</i> (TOU-AE8100)	0.000								
(2) <i>Roa haraguchiae</i> (TOU-AE8354)	0.000	0.000							
(3) <i>Roa haraguchiae</i> (TOU-AE8355)	0.000	0.000	0.000						
(4) <i>Roa haraguchiae</i> (TOU-AE8379)	0.000	0.000	0.000	0.113					
(5) <i>Roa rumsfeldi</i> (MF995631)	0.113	0.113	0.113	0.113	0.124				
(6) <i>Roa jayakari</i> (KF268176)	0.038	0.038	0.038	0.038	0.129	0.122			
(7) <i>Roa modesta</i> (KU944230)	0.129	0.129	0.129	0.129	0.077	0.122	0.138		
(8) <i>Roa australis</i> (FOAG413-08.COI-5P)	0.027	0.027	0.027	0.027	0.129	0.048	0.138	0.220	
(9) <i>Chaetodon octofasciatus</i> (KU944212)	0.213	0.213	0.213	0.213	0.194	0.205	0.191	0.220	

Bold font denotes sequence ID from BOLD.

**Figure 5.** NJ tree, based on CO1 sequences, constructed using four specimens mentioned in the presently reported study. The bar indicates the evolutionary distances which were computed using the Kimura 2-parameter method with 10 000 bootstrap-replicated.

spine is the fourth (third) and membranes associated with the first and second dorsal-fin spines are blackish (vs. whitish or yellowish). Compared to *R. jayakari*, the eye band under the eye is equal to the eye diameter (vs. narrower than the eye diameter). Compared to *R. rumsfeldi*, the specimens have more pored lateral-line scales 39–42 (32) (Table 2) and the anterior margin of the sec-

ond band does not reach anteroventrally to the pelvic-fin spine base (vs. reaching). Compared to *R. semilunaris*, the origin of the second band is from the base of the second to the seventh dorsal-fin spines (vs. third to sixth). Compared to *R. uejoi*, membranes associated with the first and second dorsal-fin spines are blackish (vs. whitish or yellowish).

Key to species of genus *Roa*

- 1a Second body band approximately same width as eye diameter, its anterior edge not passing through pectoral-fin base *R. australis*
- 1b Second body band two or more times wider than eye diameter, its anterior edge reaching to pectoral-fin base ...2
- 2a Pored lateral-line scales 26–32; pelvic fin spine brownish *R. rumsfeldi*
- 2b Pored lateral-line scales 36–41; pelvic-fin spine whitish 3
- 3a Body bands yellowish with distinct dark edges *R. modesta*
- 3b Body bands entirely blackish without dark edges 4
- 4a Whitish or yellowish membranes associated with first and second dorsal-fin spines; longest dorsal-fin spine on third 5
- 4b Blackish membranes associated with first and second dorsal-fin spines; longest dorsal-fin spine on fourth 6

- 5a Ratio of third and second dorsal-fin spine length in SL more than 2.0 (include 2.0) *R. excelsa*
 5b Ratio of third and second dorsal-fin spine length in SL less than 2.0 *R. uejoi*
 6a First band under eye equal to eye diameter *R. haraguchiae*
 6b First band under eye narrower than eye diameter 7
 7a Second body band broad, whitish space between second and third bands narrow, with 3–5 pored lateral-line scales at lateral line level *R. jayakari*
 7b Second body band narrow, whitish space between second and third bands broad, with 9 or 10 pored lateral-line scales at lateral line level *R. semilunaris*

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Intraspecific morphological variation in shads, *Dorosoma anale* and *D. petenense* (Actinopterygii: Clupeiformes: Clupeidae), in the Mexican Grijalva and Usumacinta river basins

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<https://zoobank.org/696CBE49-2B29-424D-9C3A-2281CD477D93>

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Abstract

Historical hydrological changes and the environmental characteristics of northern Middle America have promoted diversification and determined the distribution of fishes in the Grijalva and Usumacinta river basins of Mexico. In several taxa with wide distributions, cryptic diversity has been identified through molecular and morphological analyses. This study evaluated the intraspecific morphological variation of *Dorosoma anale* Meek, 1904 and *Dorosoma petenense* (Günther, 1867) along the Grijalva and Usumacinta river basins through geometric morphometric and linear biometric analyses. Little intraspecific differentiation was detected for either species. However, differences were identified between populations in the Grijalva basin and those from the upper Usumacinta River basins with respect to body height, head size, pelvic fin position, and anal fin size. The phenotypic expression of these attributes appears to be closely related to habitat type and geographic isolation. The morphological differences within *D. petenense* support the molecular hypothesis of two lineages existing in the Usumacinta River basin.

Keywords

body shape variation, geometric morphometrics, Middle-American fish, phenotypic differentiation

Introduction

The highly diverse ichthyofauna of northern Middle America has a complex biogeographic history. Frequent geological, volcanic, and climatic events from the Late Cretaceous to the Miocene and Pleistocene determined the diversification and distribution of fishes in the region

(Elías et al. 2021). Biogeographic patterns and a large amount of endemism among freshwater species represent the clearest evidence of the hydrological history of northern Middle America (Albert et al. 2020; Elías et al. 2021).

The Grijalva–Usumacinta hydrological system provides an excellent model for understanding the effects of geological and climatic events on the evolution of

fish communities in northern Middle America. This hydrological system is characterized by its diversity of fish species and large amount of endemism, which is predominantly observed in the Cichlidae and Poeciliidae families (Gómez-González et al. 2015; Velázquez-Velázquez et al. 2016; Soria-Barreto et al. 2018; Sánchez et al. 2019; Álvarez-Pliego et al. 2021). Constant events involving vicariance resulting from the capture of rivers and changes in sea level favored the diversification of several lineages through geographic isolation (Albert et al. 2020; Elías et al. 2021). The construction of dams on the Grijalva River can be considered an example to test the recent effects of hydrological and environmental changes on the dynamics of fish populations, particularly the consequences of a reduction or interruption in genetic flow for morphological and functional differentiation (Sánchez et al. 2019).

The lower regions of the Grijalva and Usumacinta basins share many species of the same ichthyofauna (Macossay-Cortez et al. 2011; Soria-Barreto et al. 2018). Nevertheless, the structure of the community in the upper regions of these rivers notably differs (Gómez-González et al. 2015; Velázquez-Velázquez et al. 2016; Soria-Barreto et al. 2018). Studies of systematic, biogeography and population genetics have revealed that the upper regions of the two basins have independent evolutionary histories (Elías et al. 2021; Beltrán-López et al. 2021; Terán-Martínez et al. 2021). The presence of relic endemic species such as the catfish of Chiapas (*Lacantunia enigmatica* Rodiles-Hernández, Hendrickson et Lundberg, 2005) and the livebearer (*Xenodexia ctenolepis* Hubbs, 1950) of the upper Usumacinta are evidence of the region's unique biogeographic history (Rodiles-Hernández et al. 2005; Hrbek et al. 2007; Elías et al. 2021).

Although cichlids and poeciliids are the most diverse and abundant fish families within the Grijalva–Usumacinta system, other families also reflect the effects of the region's historic events. Such is the case of the genus *Dorosoma*, for which genetic evidence shows that cryptic diversity exists throughout the distribution of the species *Dorosoma petenense* (Günther, 1867) in Middle America, which consists of several lineages (Elías et al. 2021). Two of these lineages converge in the Grijalva–Usumacinta basins. The lineage with the broadest distribution inhabits the region from the Río Grande to the lower Grijalva and Usumacinta rivers in Mexico and Guatemala, while the other is restricted to the upper Usumacinta River and Petén Itzá Lake in Guatemala (Elías et al. 2021). Curiously, in other *Dorosoma* species with similar distribution patterns, no significant genetic differences have been found (Elías et al. 2021). In this sense, the migratory behavior and salinity tolerance of each species could help to explain differences in genetic segregation and morphological differentiation (Bloom and Egan 2018). *Dorosoma petenense* is the most widespread and tolerant of different salinity ranges (Elías et al. 2021). In contrast, *Dorosoma anale* Meek, 1904 is considered a freshwater fish with little tolerance for salinity changes (Castro-Aguirre et al. 1999; Elías et al. 2021).

Based on the biogeographic and molecular precedents of the ichthyofauna in northern Middle America, we proposed an analysis of the intraspecific morphological variation of the shads *Dorosoma anale* and *D. petenense* throughout the Grijalva and Usumacinta rivers in Mexico. This study used linear biometric and geometric morphometric methods. Notably, both analyses are complementary and have been widely used in ichthyology to identify intra- and interspecific morphological differences and describe patterns of variation (Kerschbaumer and Sturmhuber 2011; Tripathy 2020; Lishchenko and Jones 2021). Morphological differentiation was expected due to historical vicariance events that occurred during river separation and sea level changes in northern Middle America. Furthermore, recent biological, environmental, and hydrological changes caused by human activities were expected to affect the phenotypic expression of morphological differences.

Methods

A total of 262 adult specimens were analyzed, corresponding to the species *Dorosoma anale* ($n = 136$, 71 males and 65 females) and *D. petenense* ($n = 126$, 44 males, 82 females). The specimens were deposited in the Fish Collection of El Colegio de la Frontera Sur (ECO-SC; Table 1). The specimens originated from 18 sites distributed throughout the Grijalva and Usumacinta basins in Mexico (Fig. 1 and Table 2). For the Grijalva basin, specimens from sites located in the middle region were used. For the Usumacinta basin, specimens were selected from representative sites of the upper, middle, and lower regions, following the criteria proposed by Soria-Barreto et al. (2018; see Table 2). Sexual maturity was determined by reviewing the gonads.

Specimens were photographed from the left side of the body with a Sony DSC-HX300 digital camera (10 megapixels) using a 10 mm reference scale. To characterize the body shape, we used a configuration of 18 fixed landmarks (Fig. 2 and Table 2) digitalized using tpsDig2 software, version 2.16 (Rohlf 2015).

Morphometric and statistical analyses. To analyze geographic intraspecific variation, specimens were classified into four groups according to the collection site. One group consisted of specimens from the Grijalva basin, while the other three were from the upper, middle, and lower regions of the Usumacinta basin (Fig. 1 and Table 2).

An analysis of geometric morphometrics was conducted using MorphoJ software, version 1.07a (Klingenberg 2011). Based on the coordinates obtained from digitization, a generalized procrustes analysis was performed (Rohlf and Slice 1990; Dryden and Mardia 1998) to eliminate variation among the configurations of the reference points due to the effects of position, orientation, and specimen size. Additionally, to eliminate the effect of allometry due to variation in specimen size, multivariate regression was conducted based on the procrustes coordinates

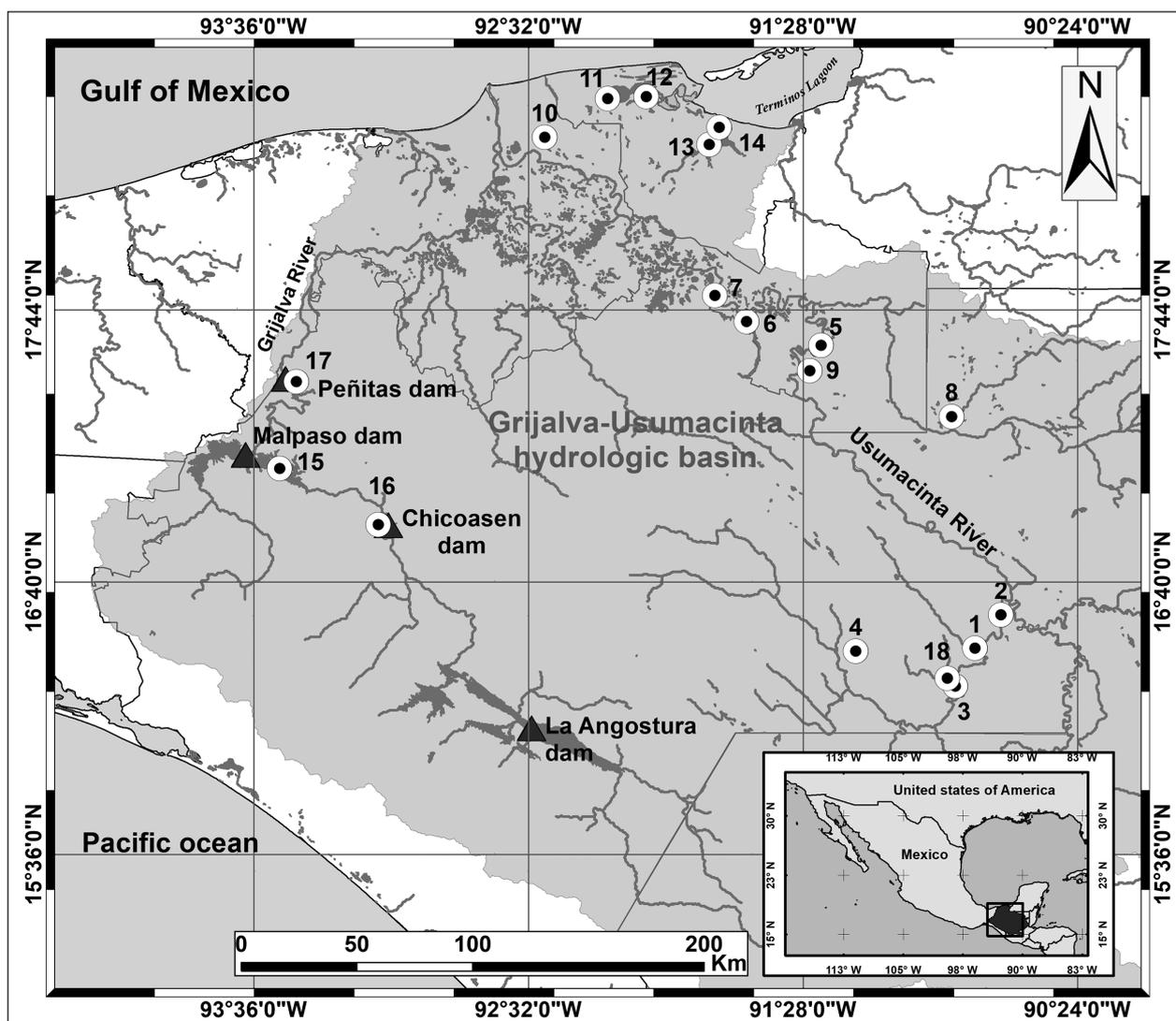


Figure 1. Sample sites location of *Dorosoma anale* and *D. petenense* in the Grijalva and Usumacinta basins: 1 = Lacantún River, 2 = Lacanja River, 3 = San Leandro Lagoon, 4 = Miramar Lagoon, 5 = Canitzán Lagoon, 6 = Chacamax River, 7 = Nueva Esperanza Lagoon, 8 = San Pedro River, 9 = Usumacinta River, 10 = San Isidro Lagoon, 11 = Pom Lagoon, 12 = Palancares Lagoon, 13 = Vapor Lagoon, 14 = Boca Chica estuary, 15 = Malpaso dam, 16 = Chicoasén dam, 17 = Peñitas dam, 18 = Tzendales River. Black triangles indicate the dams.

Table 1. Location of the sampling sites and samples sizes of *Dorosoma anale* and *D. petenense* in Grijalva and Usumacinta basins.

Site	Region	Coordinates	<i>D. anale</i> (n = 136)	<i>D. petenense</i> (n = 126)
1 Lacantun River	U	16°32'13"N, 090°41'52"W	10	1
2 Lacanja River	U	16°24'21"N, 090°47'54"W	10	3
3 San Leandro Lagoon	U	16°15'28"N, 090°52'31"W	17	10
4 Miramar Lagoon	U	16°23'40"N, 091°15'44"W	—	13
5 Canitzan Lagoon	M	17°35'34"N, 091°23'46"W	7	10
6 Chacamax River	M	17°41'08"N, 091°41'11"W	9	2
7 Nueva Esperanza Lagoon	M	17°47'16"N, 091°48'30"W	10	—
8 San Pedro River	M	16°18'48"N, 090°53'23"W	—	15
9 Usumacinta River	M	17°29'34"N, 091°26'26"W	8	—
10 San Isidro Lagoon	L	18°24'26"N, 092°28'09"W	10	10
11 Pom Lagoon	L	18°33'33"N, 092°13'31"W	10	10
12 Palancares Lagoon	L	18°33'58"N, 092°04'33"W	10	—
13 Vapor Lagoon	L	18°22'42"N, 091°49'52"W	—	10
14 Boca Chica estuary	L	18°26'46"N, 091°47'33"W	—	8
15 Malpaso dam	G	17°06'38"N, 093°29'59"W	32	12
16 Chicoasén dam	G	16°53'26"N, 093°07'00"W	3	9
17 Peñitas dam	G	17°27'02"N, 093°26'03"W	—	9
18 Tzendales River	U	16°17'20"N, 090°54'23"W	—	4

U = Upper, M = Middle, L = Lower, G = Grijalva.

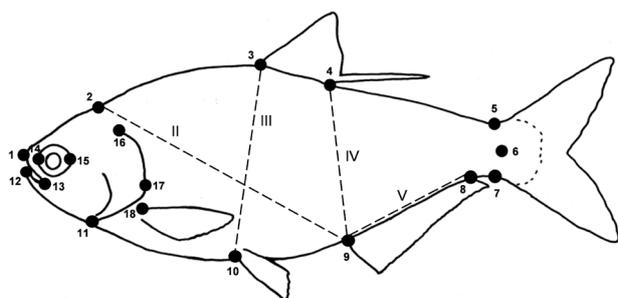


Figure 2. Location of fixed landmarks in two species of the *Dorosoma* genus (image modified from Hubbs and Lagler 1947, Whitehead 1985, and Farré et al. 2016). 1 = Anterior end of the upper maxilla, 2 = End of the supraoccipital bone, 3 = Start of the dorsal fin, 4 = End of the dorsal fin, 5 = Upper boundary of the caudal fin, 6 = Center of the caudal fin, 7 = Base of the caudal fin, 8 = End of the anal fin, 9 = Origin of the anal fin, 10 = Origin of the pelvic fin, 11 = Cleitral fusion, 12 = Anterior end of the lower maxilla, 13 = Posterior end of the maxilla, 14 = Left extreme of the sphenotic orbit, 15 = Right extreme of the sphenotic orbit, 16 = Upper end of the operculum, 17 = Most posterior end at the operculum, 18 = Dorsal insertion of the pectoral fin. The dashed lines are the intraspecific linear discriminant measures.

Table 2. Procrustes distances values (above diagonal) and *P*-values (below diagonal) to pairwise comparison test between all sections of the Grijalva–Usumacinta rivers basin to *Dorosoma anale* and *D. petenense*.

		Procrustes distances			
<i>D. anale</i>		Lower	Middle	Upper	Grijalva
	Lower	—	0.0075	0.0109	0.0142
	Middle	0.4219	—	0.0121	0.0136
	Upper	0.064	0.0083	—	0.0164
Grijalva	0.0012	<0.0001	<0.0001	—	
<i>D. petenense</i>		Lower	Middle	Upper	Grijalva
	Lower	—	0.0111	0.0272	0.0137
	Middle	0.0295	—	0.0228	0.0139
	Upper	<0.0001	<0.0001	—	0.0324
Grijalva	0.0004	0.0008	<0.0001	—	

Bold font indicates statistically significant *P*-values.

(shape variables) with the values of the logarithm of the centroid (size variable).

With the residual values of the multivariate regression, a principal components analysis (PCA) was performed to evaluate intraspecific variation. The first two principal components were used to explore the distribution of the specimens in the morphospace and describe variation in body shape based on the deformation grids. Later, we conducted a canonical variate analysis (CVA) to determine whether significant differences in body shape exist among the four groups. Additionally, we carried out paired comparisons based on the procrustes distances. Finally, we applied a discriminant function analysis (DFA) to perform cross-validation to determine the percentage of classification of the specimens in each group based on the Mahalanobis distances. All tests subjected the data to 10,000 permutations, when appropriate.

Additionally, based on the deformation grids, we identified the body sections for which greater variation existed. We then took linear measurements to evaluate whether they are discriminant among the four groups. Measurements were obtained by using the CoordGen8 program (IMP; Sheets 2014) with the photographs. The configuration of landmarks used in the geometric morphometric analysis followed the protocols of Hubbs and Lagler (1947), Whitehead (1985), and Farré et al. (2016). Measurements were standardized according to the method of Elliott et al. (1995) to eliminate the effect of allometry caused by variation in specimen size. Later, we conducted statistical analyses (ANOVA and Kruskal–Wallis) and *a posteriori* tests (Tukey, Mann–Whitney) to determine whether significant differences existed among the groups. For the measurements showing significant differences, box plots were elaborated to visualize their variation, which was expressed in proportions with respect to the standard length. For statistical analyses and the elaboration of box plots, we used the PAST program, version 3.14 (Hammer et al. 2001).

Museum catalog information. Catalogue number of the specimens used in the morphometric analysis. *Dorosoma anale*: ECOSC 612, 658, 1286, 1737, 3492, 4426, 6708, 6714, 10713, 10714, 11748, 11752, 12549, 12555, 12665, 12790, 13521, 13533 al 13535, 13546, 13549, 13561, 13564, 13565, 13976, 14290, 14300; *D. petenense*: ECO-SC 7339, 8698–8707, 9882–9891, 12616, 12619, 12657, 12669, 12716, 12722, 13702, 13723, 13738, 14547, 14679, 14680.

Results

Intraspecific variation in *Dorosoma anale*. In the PCA, the first two components explained 42.5% of the total variance. In the morphospace, no formation of groups was observed given the extensive overlap among specimens (Fig. 3A). Throughout PC1 (28.35%), greater variation was obtained for specimens from the upper region were the most broadly distributed throughout this component. Although much less variation occurred for PC2 (14.18%), it was not possible to distinguish groups (Fig. 3A). Based on the deformation grids for PC1, specimens in the negative axis were observed to have larger heads, shorter caudal peduncles, and anteriorly displaced dorsal and pelvic fins. For the positive axis, specimens had shorter heads, longer caudal peduncles, and dorsal and pelvic fins that were slightly more forward (Fig. 3A). For PC2, the most evident variations were in body height and the fact that specimens reached maximum body depth on the positive axis, while they tended to be less deep toward the negative axis (Fig. 3A).

Meanwhile, the CVA and paired tests revealed significant differences among groups ($P < 0.05$). Nevertheless, the only differences among the four groups were between the Grijalva group and the three groups of the Usumacinta basin. For the Usumacinta groups, only the middle and up-

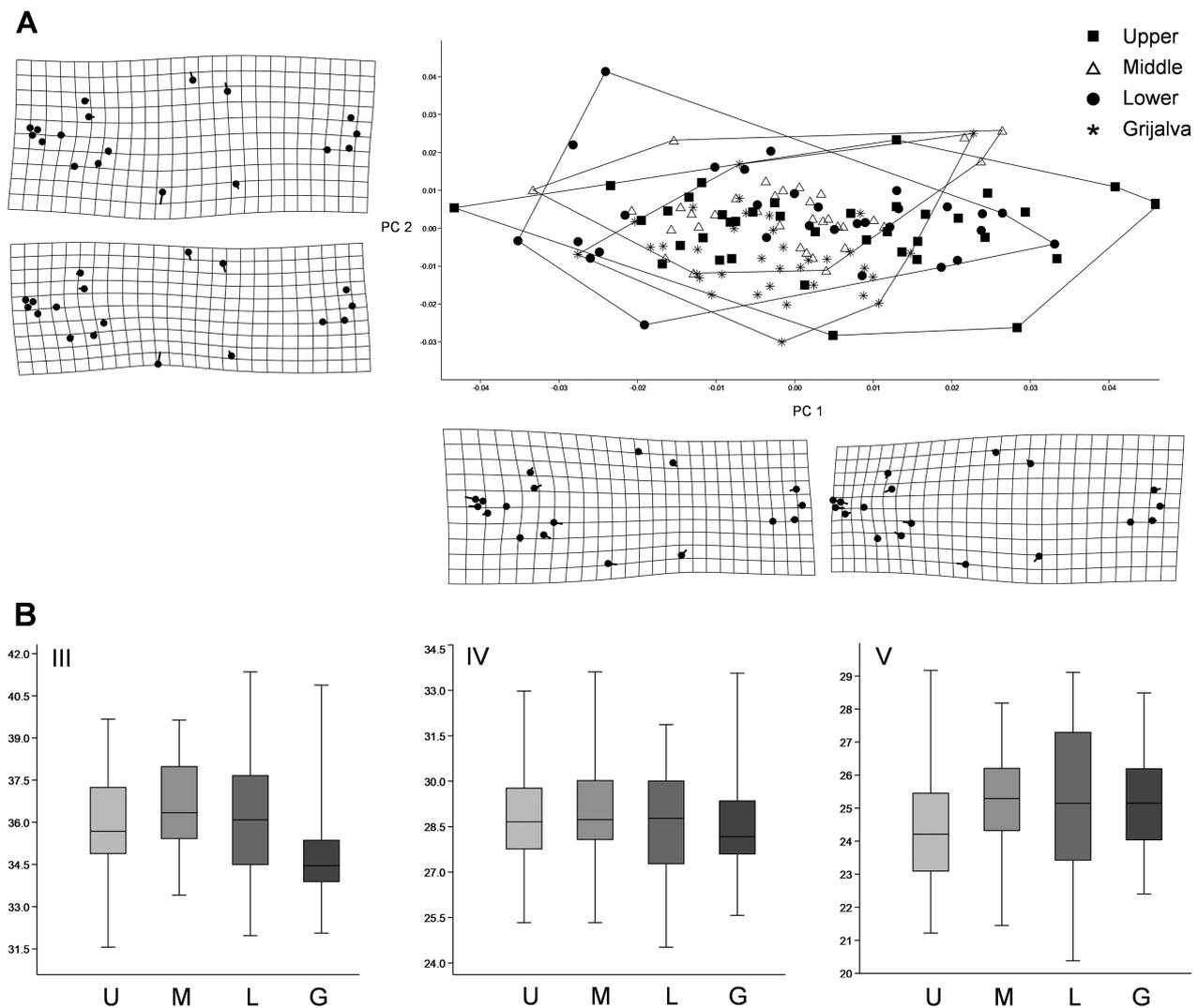


Figure 3. (A) Morphospace formed by PC1 (36.20%) and PC2 (18.94%) for *Dorosoma anale*. Squares represent the upper region, triangles represent the middle region, dots represent the lower region and stars represent the Grijalva region. Deformation grids are associated to the most negative and positive values of the PC1 and PC2. (B) discriminatory linear measures expressed in percent for *D. anale*. U = Upper, M = Middle, L = Lower, G = Grijalva.

per regions were significantly different ($P < 0.05$; Table 2). Cross-validation based on the DFA indicated that the assignment percentages were highest in the Grijalva group, while the highest percentages for the Usumacinta basin were found in the group of the upper region (Table 3).

Based on the variation in body shape observed in the deformation grids, we selected five linear measurements to evaluate their capacity to discriminate among the groups. The selected measurements were as follows: I) anterior margin of the upper mandible to the posterior margin of the operculum (landmarks 1–17); II) posterior margin of the supraoccipital crest to the anterior insertion of the anal fin (2–9); III) anterior insertion of the dorsal fin to the anterior insertion of the pelvic fin (3–10); IV) posterior insertion of the dorsal fin to the anterior insertion of the anal fin (4–9); V) anterior insertion of the anal fin to the posterior insertion of the anal fin (8–9).

In *D. anale*, the statistical analyses (ANOVA, Kruskal–Wallis) and respective *a posteriori* tests (Tukey, Mann–Whitney) revealed that only the following three measure-

ments could discriminate at least one of the groups ($P < 0.05$): I) anterior margin of the upper mandible to the posterior margin of the operculum (1–17); III) anterior insertion of the dorsal fin to the anterior insertion of the pelvic fin (3–10); IV) posterior insertion of the dorsal fin to the anterior insertion of the anal fin (4–9). The box plot of these three measurements (expressed in proportions) allowed us to determine that the groups with the greatest variation were from the upper regions of the Usumacinta and Grijalva basin (Fig. 3B).

Intraspecific variation in *Dorosoma petenense*. In the PCA, the first two components explained 42.73% of the total variance. In PC1 (25.19%), we observed a substantial overlap of the four groups on the negative axis. However, on the positive axis, specimens from the upper Usumacinta appeared to diverge, especially from Site 4 (Miramar Lagoon, Fig. 4A). Although no clear separation was found among the groups in PC2 (17.53%), the majority of specimens from the upper Usumacinta were located

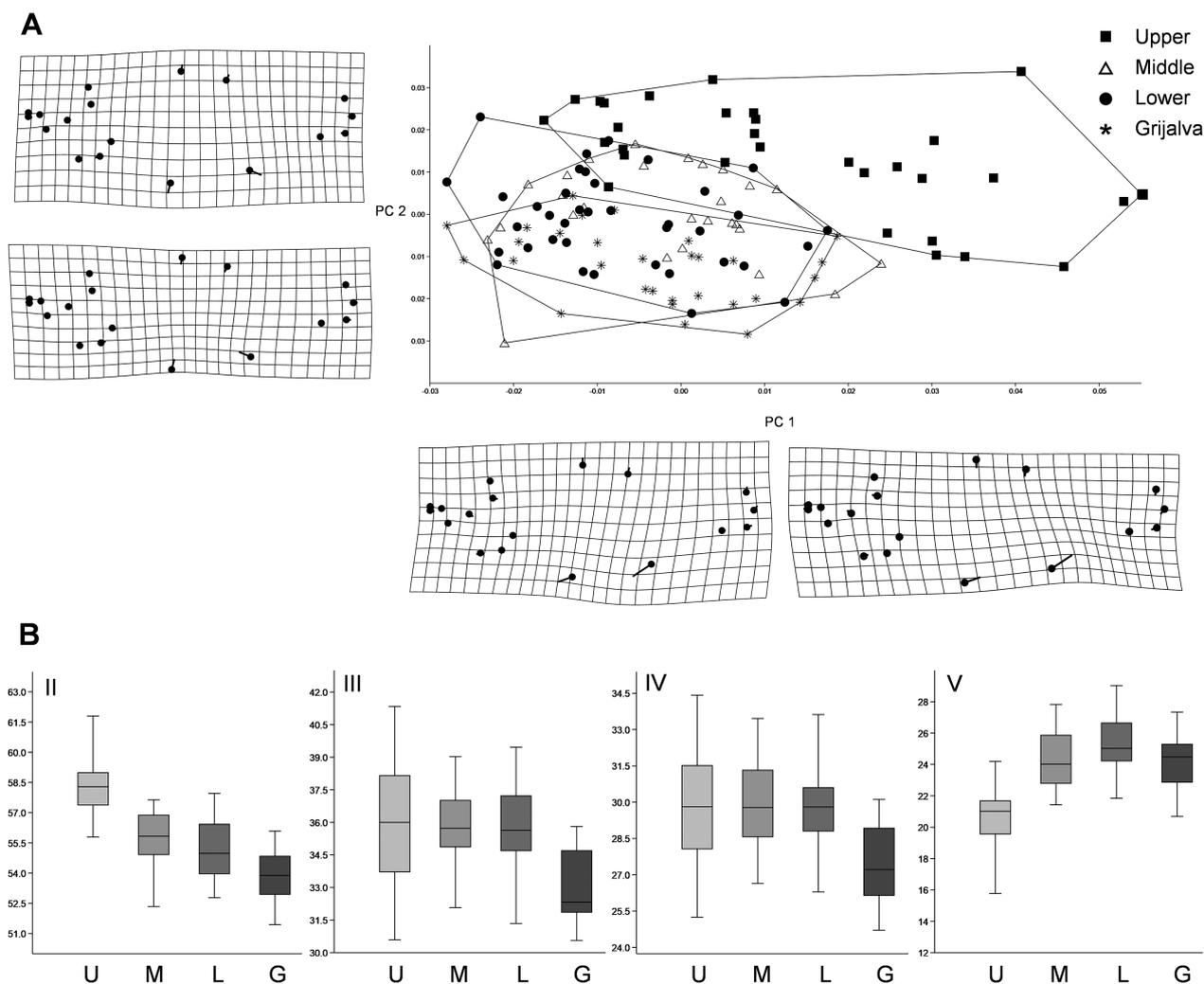


Figure 4. (A) Morphospace formed by PC1 (25.1%) and PC2 (17.5%) for *Dorosoma petenense*. Squares represent the upper region, triangles represent the middle region, dots represent the lower region and stars represent the Grijalva region. Deformation grids are associated to the most negative and positive values of the PC1 and PC2. (B) discriminatory linear measures for *D. petenense*. U = Upper, M = Middle, L = Lower, G = Grijalva.

Table 3. Percentage of *Dorosoma anale* and *D. petenense* correctly classified to their a priori groups based on the discriminant function analysis.

<i>D. anale</i>	<i>n</i>	Lower	Middle	Upper	Grijalva
Lower	30	72.2	56.7	76.7	83.3
Middle	34	64.7	72.6	73.5	79.4
Upper	37	70.3	70.3	77.48	91.9
Grijalva	35	82.9	85.7	88.6	85.7
Total	136				
<i>D. petenense</i>	<i>n</i>	Lower	Middle	Upper	Grijalva

n = number of specimens; Lower, Middle, Upper, and Grijalva are respective sections in the Grijalva–Usumacinta rivers basin.

toward the positive extreme (Fig. 4A). The negative end of PC1 represented specimens with relatively deep bodies and fins that were anteriorly displaced relative to specimens that possessed positive scores (Fig. 4). In the defor-

mation grids of PC2, shallow-bodied specimens were in the negative axis, while deeper-bodied specimens were located toward the positive part (Fig. 4B).

The CVA and paired tests showed significant differences among the four groups ($P < 0.05$; Table 3). The greatest procrustes distances were obtained for the upper Usumacinta group (Table 2). The DFA corroborated that the specimens of the upper Usumacinta were the most different, while the cross-validation revealed that they had the highest percentage of allocation (Table 3).

Multivariate analyses (ANOVA, Kruskal–Wallis) of the five linear measurements and the corresponding *a posteriori* tests showed that four measurements are discriminant ($P < 0.05$): II) posterior margin of the supraoccipital crest to the anterior insertion of the anal fin (2–9); III) anterior insertion of the dorsal fin to the anterior insertion of the pelvic fin (3–10); IV) posterior insertion of the dorsal fin to the anterior insertion of the anal fin (4–9); V) anterior insertion of the anal fin to the posterior insertion of the anal fin (8–9). Statistical differences were observed in the groups of the upper Usumacinta

and the Grijalva. The diagrams of the four measurements (expressed in proportions) suggest that the groups that differed most were from the upper Usumacinta and the Grijalva (Fig. 4B).

Discussion

Little intraspecific morphological differentiation was observed within *Dorosoma anale* and *D. petenense* throughout their distribution in the Grijalva and Usumacinta basins. Nevertheless, patterns of variation and morphological differences were identified in some of the geographic groups, which allowed us to assume that some regional historic and/or ecological processes were involved in creating and maintaining the phenotypic differentiation in both species. In the Clupeiformes and other fish taxa, migratory behavior and tolerance to salinity could have important implications for morphological differentiation (Aguirre and Bell 2012; Bloom and Egan 2018; Jiménez-Prado and Aguirre 2021). While it was difficult to test this hypothesis based on our results, this possibility should not be discarded.

In the morphospace of *D. anale*, no separation among groups by geographic location was observed. However, among specimens of the upper Usumacinta basin, variation existed in terms of head size, body depth, and fin position. This could be related to the type of habitat since the separation was observed among specimens from the river (sites 1, 2, and 18) and lake habitats (sites 3 and 4). Additionally, comparisons among geographic groups based on the statistical tests showed that the specimens of the Grijalva basin were differentiated by having shallower bodies.

A similar pattern of variation was observed in the morphospace of *D. petenense*, while the overlap between the four geographic groups was also found. Nevertheless, specimens of the upper Usumacinta tended to be differentiated from the rest of the groups by having a deeper body. Within the upper Usumacinta group, the separation from specimens of the Miramar Lagoon was notable (Fig. 1 and Table 1). The latter had shorter anal fins and their pelvic fins were further back along the body. Statistical tests confirmed that the upper Usumacinta group was the most different; however, specimens from the Grijalva tended to exhibit slender bodies.

In both species, the greatest intraspecific morphological variation was principally observed in body shape, head size, and fin position. For many diverse species of fish, it has been demonstrated that variation in these anatomic attributes has functional importance and has been correlated with environmental factors such as water current speed, habitat structure, and the presence of predators (Langerhans 2008; Langerhans et al. 2003; Bravi et al. 2013; Araújo et al. 2014; Peris-Tamayo et al. 2020). This has also been documented in certain fishes of Middle America, such as characins (Santos and Araújo 2015; Garita-Alvarado et al. 2018, 2021), cichlids (Feilich 2016; Barrientos-Villalobos et al. 2018; Gómez-González et al. 2018; Aguilar-Contreras et al. 2021), and poeciliids (Araújo et

al. 2014; Jourdan et al. 2016). In many fish taxa, phenotypic plasticity is an important precursor to morphological differentiation through adaptation to changing environmental conditions (Oufiero and Whitlow 2016).

Nevertheless, despite morphological evidence indicating that ecological-environmental factors may be promoting phenotypic differentiation in both species between the Grijalva and upper Usumacinta groups, the effect of geographic isolation and distance should also be considered—particularly for specimens of the Grijalva, which are the most geographically isolated (Sánchez et al. 2019). Furthermore, the specimens analyzed come from dams on the principal course of the Grijalva River. Notably, there is evidence of environmental changes and reductions in gene flow being caused by dam construction, which may induce rapid morphological modifications in fish (Michel et al. 2008; Franssen 2011; Perazzo et al. 2019; Gilbert et al. 2020). Additionally, while the Grijalva and Usumacinta basins share some biological and ecological characteristics, each basin has an independent biogeographical history (Elías et al. 2021). Likewise, they have been subjected to different modifications and anthropic activities (Lázaro-Vázquez et al. 2018; Sánchez et al. 2019). Also, it should be noted that hydrogeomorphological and habitat changes can affect the migratory behavior of these species—especially in the lower regions of both basins (Bloom and Egan 2018).

The morphological differentiation among *D. petenense* specimens in the upper Usumacinta appears to corroborate part of the hydrological history of the basin (Rosen 1967, 1970, 1979; Elías et al. 2021). Although this geographic group was the most highly differentiated within the study area, a notable separation among specimens from the Miramar Lagoon was evident in this group. This morphological evidence supports the hypothesis that diverse lineages exist within *D. petenense* in the Usumacinta basin (Elías et al. 2021). As presented in other biogeographic studies of the fish of northern Middle America, the territory that includes the upper Usumacinta has a particular independent evolutionary history characterized by geological events that promoted the geographic isolation of fish populations (Elías et al. 2021), such as the reversal of river current, collapse of stream beds, and underground connectivity among rivers (Rosen 1967, 1970, 1979).

Although morphological variation in the same anatomical attributes was found in both species, *D. anale* is less variable than *D. petenense*, mainly observed in the upper Usumacinta populations. Contrary to our expectations, despite being closely related and having similar ecological requirements, the magnitude and direction of morphological changes were distinct. This has also been found for other groups of fish for which the level of morphological variation among species is related to the level of dietary specialization (Ornelas-García et al. 2018; Kentao and Jearraaiprepame 2021). Regarding cichlids, generalist species were found to have greater variation in body shape than specialists (Kassam et al. 2004; Gilbert et al. 2020). It is also known that changes in head size and eye position may be related to dietary conduct, especially in terms of size and diet type (Haas et al. 2010; Kentao and Jearraaiprepame 2021).

Differences in the patterns of variation found in *D. anale* and *D. petenense* once again demonstrated that the phenotypic expression of morphological characteristics is a product of the interaction among diverse biological, environmental, and historic processes (Michel et al. 2008; Franssen et al. 2013; Bracciali et al. 2016). Thus, there is a need to continue conducting studies of the fish communities within the Grijalva and Usumacinta basins. As previously demonstrated, northern Middle America is an extraordinary natural laboratory for evaluating and understanding past and recent processes that have promoted morphological diversification among diverse species of Neotropical fish.

Conclusion

There is little intraspecific variation in body shape in *D. anale* and *D. petenense*. However, we uncovered statistically significant differences between specimens of both species from the Grijalva basins and the upper Usumacinta. Morphological differentiation was based on body height, head length, pelvic fin position, and anal fin length. Nevertheless, even though variation was observed for the same attributes in both species, the direction and magnitude differed. Since the variation in these morphological attributes seems to be related to biological, environmental, and geographic factors, it could serve to define ecotypes. For both species, morphologi-

cal differences among specimens from the Grijalva basin could be due to geographic isolation. Meanwhile, differentiation among *D. petenense* specimens from the upper Usumacinta appears to support the hypothesis regarding the existence of two lineages in the Usumacinta basin. Additionally, in *D. petenense*, differentiation was detected among specimens from the Miramar Lagoon. Notably, there is a need for further taxonomic and biogeographic studies of the ichthyofauna in northern Middle America to better comprehend their diversity and the processes related to their evolution—particularly in the Grijalva and Usumacinta basins, which possess some of the most interesting and complex fish communities of the Neotropics.

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First record and otolith morphometric description of an adult lightfish, *Ichthyococcus ovatus* (Actinopterygii: Stomiiformes: Phosichthyidae), caught in the Strait of Sicily (central Mediterranean Sea)

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Abstract

On July 2018, one specimen of *Ichthyococcus ovatus* (Cocco, 1838) was caught in the Strait of Sicily during the International Bottom Trawl Survey in the Mediterranean (MEDITS). The adult *I. ovatus* measured 49 mm in total length and weighed 1.44 g. In this context, the presently reported study constitutes the first and deepest record of an adult of *I. ovatus* as well as the morphometric description of its sagittal otoliths. In addition, we provide an age estimation as well as an update of the geographical distribution of this bathypelagic species around the Mediterranean Sea. Based on the growth increments of sagittal otoliths, the estimated age was five years. Specifically, the otolith from the presently reported specimen of *I. ovatus* tended to be elliptic in shape related to aspect ratio and high rectangularity while circularity showed high complexity of otolith contour complexity. The absence of economic value of rarely reported species may underestimate their abundance. Therefore, more studies and research surveys would be necessary to fill the information gap on the biology of these deep-water species.

Keywords

Mediterranean deep sea, otolith, rare species, MEDITS, Strait of Sicily, trawl survey

Introduction

The family Phosichthyidae of the order Stomiiformes (Froese and Pauly 2022) comprises lightfishes that produce bioluminescence by ventrally located photophores (Schaefer et al. 1986). Specifically, this family constitutes a monophyletic group characterized by members with the

advanced characters of three pectoral fin radials, which are further reduced in some genera with extremely small pectoral fins, and type gamma photophores having a lumen and duct (Weitzman 1974). Actually, earlier workers believed Phosichthyidae performed active diel vertical migration (Clarke 1971), which recent workers considered to range from the mesopelagic to epipelagic zones (Goçalo et

al. 2011). However, only a few species of Phosichthyidae such as *Vinciguerria poweriae* (Cocco, 1838), *Vinciguerria attenuata* (Cocco, 1838), and *Pollichthys maui* (Poll, 1953) have shown active diel migration (Badcock, 1984). Furthermore, fishes belonging to this family perform pelagic spawning, which allows them to deliver planktonic eggs and larvae (Ahlstrom and Ball 1954). However, not all genera of the family Phosichthyidae have been well studied. In particular, the genus *Ichthyococcus* Bonaparte, 1840 appears more evolute than the other congeneric species that are relatively primitive (Weitzman 1974). The genus *Ichthyococcus* includes 8 species (Froese and Pauly 2022), wherein *Ichthyococcus ovatus* (Cocco, 1848) has been singled out as an almost cosmopolitan bathypelagic species, found across a wide range of waters from the North Eastern Atlantic to the western/central Mediterranean basin (Lin et al. 2018; GBIF 2022). Moreover, it is worth mentioning that *I. ovatus* appears to be the only species of the genus *Ichthyococcus* reported within the Mediterranean Basin (Lin et al. 2018; GBIF 2022).

In relation to the Mediterranean Sea, the authors herein could only find the study of Battaglia et al. (2010) who reported the otolith morphology relations between some mesopelagic and bathypelagic species from the Strait of Messina. Otoliths are calcified structures (CaCO_3) located in the inner ear of fish providing sensory information about balance as well as hearing (Campana and Thorrold 2001; Popper et al. 2005). In particular, otoliths are demonstrated to continuously grow throughout the life of the fish (Chilton and Beamish 1992) along with absence of resorption or short-time variation (Cadrin and Friedland 2005). Such characteristics make otolith a powerful tool for age determination, and this activity entails reading (i.e., counting) the growth bands laid down as zones of opaque and translucent material (Ross et al. 2005; Rodríguez Mendoza 2006). Notably, the appearance, as well as shape of otolith (most often, the sagitta) in fish specimens remain species specific and can differ between populations of the same species in different locations (Lombarte et al. 2006; Ozpicak et al. 2018). This makes the otolith morphometry/shape a valuable tool for the identification of fish species. Additionally, the interspecific variations of otolith are considered useful for the identification of the stock as well as assessment of environmentally induced variation (Campana 2005; Rodríguez Mendoza 2006). More so, the form factor, roundness, and rectangularity are among such parameters that characterize the shape of the otolith's parts (Russ 1990).

Apart from the geographical distribution and nictemeral migration, the biological information about lightfishes appears limited. Furthermore, relevant information regarding the otoliths of *I. ovatus* specific to the Strait of Sicily (central Mediterranean Sea), to our best knowledge, is not available. Therefore, to supplement existing information, the presently reported study presents the first record and otolith morphometric description of an adult lightfish, *I. ovatus*, caught in the Strait of Sicily. In addition, we provide an age estimation as well as an update of the geographical distribution of this bathypelagic species around the Mediterranean Sea.

Materials and methods

Sample collection, identification, and biometrics. On July 2018, one specimen of *Ichthyococcus ovatus* (trawl haul points: $36^{\circ}36.89'N$, $013^{\circ}21.24'E$) was caught, at a depth of about 547 m, during the International Bottom Trawl Survey in the Mediterranean (MEDITS) (Bertrand et al. 2002) in the Strait of Sicily. The sample was transported to the laboratory of CNR-IRBIM of Mazara del Vallo. The identification of the specimen was conducted following descriptions of Badcock (1984). The biometric data involved total length (TL), standard length (SL), head length, eye diameter, total weight, as well as dorsal, pectoral, ventral, and anal fin lengths. In addition to weight with an accuracy of 0.01 g, the length measurement was conducted to the nearest 0.1 mm using a vernier caliper. In particular, photophores were counted as follows:

- entire ventral photophores row extending from anterior end of isthmus to posterior termination of this row on caudal peduncle (IC);
- ventral series of pelvic and anal photophores, part of IC extending between a vertical line at insertion of posterior pelvic fin ray and anal fin origin or to end of row (VAV + AC);
- entire lateral series photophores on body side (OA).

Age estimation and otolith morphometry. The otoliths' extraction was performed based on the procedures recommended by Secor et al. (1992), which entailed the cleaning of the blood, otic sac, and other membranes using distilled water, subsequently stored in labelled vials and thereafter, allowed to air-dry for 48 h. More so, the weight of each otolith was measured to 0.0001 mg using an analytical balance (Entris® II Advanced Line; Sartorius AG, Göttingen, Germany). Whole otoliths were placed in a dish with tap water and a black background and viewed under reflected light through a stereomicroscope (Leica Wild Mz12.5; Leica Microsystems GmbH, Wetzlar, Germany) at $1.0\times$ magnification. The contrast between opaque and translucent zones was enhanced by Adobe Photoshop software (v. 22.0, Adobe, San Jose, USA). The examination of whole otoliths required viewing the distal surface as shown in Fig. 1A. The age estimation was assigned independently by two readers using the views of whole otoliths and without additional information. Importantly, the growth zones of the otoliths were visible across the height (dorsal–ventral) as well as the length (anterior–posterior) surfaces, whereas the presumptive annuli were identified and counted from the core to margin along the longest axis of otoliths (Fig. 1B). Additionally, the opaque zones were counted.

The morphometric data of the otoliths were collected, which included area (A_o), perimeter (P_o), length (L_o , maximal distance from the anterior tip to the posterior edge, parallel to the sulcus (Harvey et al. 2000)) and width (W_o , maximal distance from the dorsal otolith edge to the ventral one, perpendicular to the sulcus). The morphometric parameters were measured using the ImageJ v.1.53f51

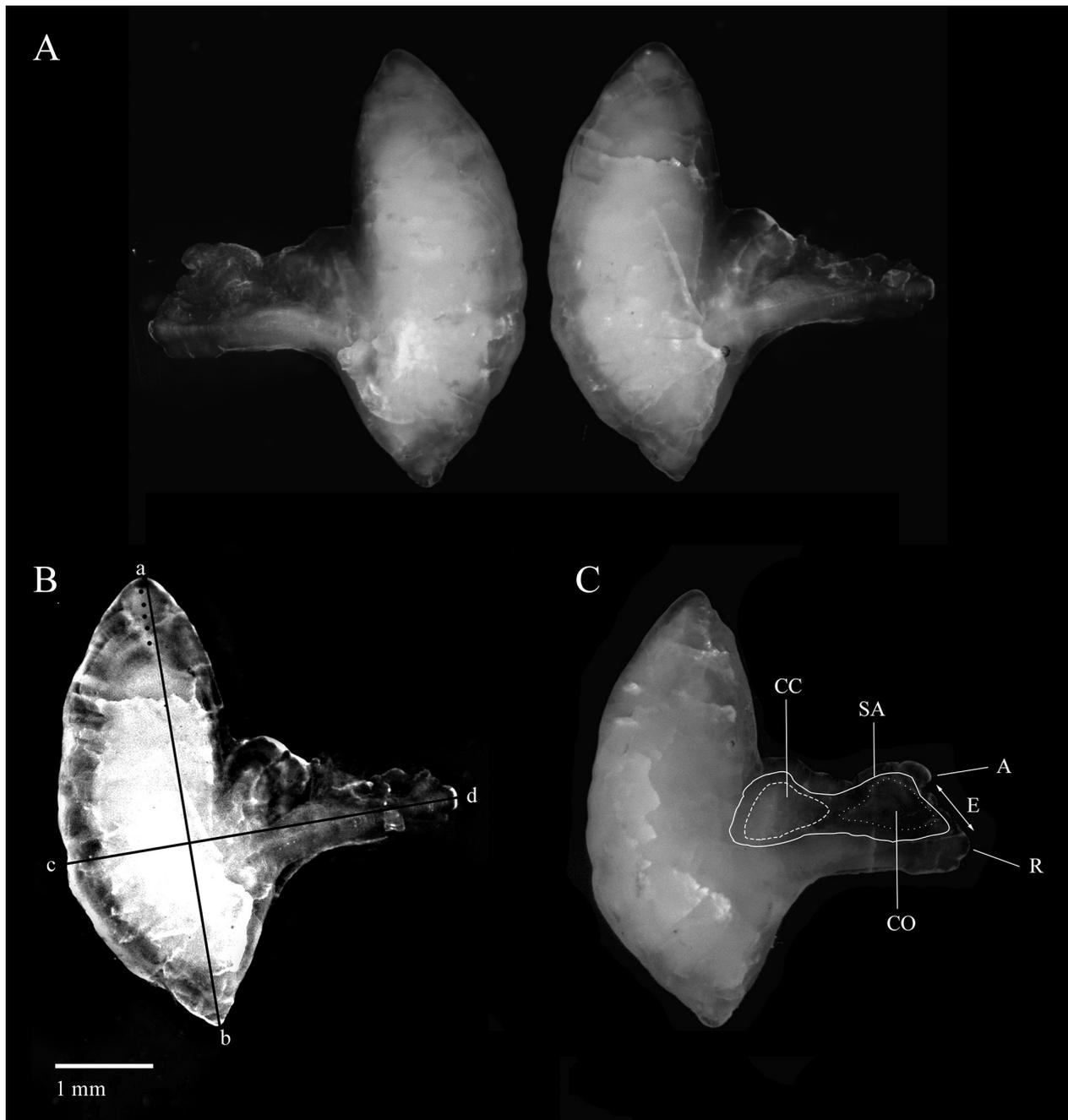


Figure 1. (A) Distal surface of the sagittal otoliths from *Ichthyococcus ovatus*. (B) Enhanced image of the right otolith used to count presumptive annuli for age estimation. Black dots represent the growth rings; the distance between a and b is the otolith width while the distance between c and d is the otolith length; (C), proximal surface of the left otolith showing rostrum (R), antirostrum (A), excisura ostii (E), sulcus acusticus (SA, continuous line), colliculum ostii (CO, dotted line), colliculum caudii (CC, dashed line).

software (Wayne Rasband (NIH), Bethesda, USA), which cumulatively enabled such dimensionless shape indices like otolith relative length ($100(L_o/TL)$, $100(L_o/SL)$), otolith relative size ($1000(A_o/TL^2)$), aspect ratio (Ar, shape tendency of otolith, L_o/W_o), form factor (Ff, its values range from 0 to 1 where a value of 1 corresponding to a perfect circle, $4\Pi A_o/P^2$ where Π is the pi, i.e. about 3.14), ellipticity (El, values close to 0 indicating a tendency towards circularity, $(L_o - W_o)/(L_o + W_o)$), roundness (Ro, the larger it is the more the otolith shape approximates that of a disk, $4A_o/\Pi L_o^2$), rectangularity (Re, a value of 1 indicating a perfect rectangle or square, $A_o/(L_o \times W_o)$) and

circularity (Ci, complexity of otolith contour, P^2/A_o) (Russ 1990; Tuset et al. 2003; Pavlov 2016). In addition, a pictorial comparison with the extant literature was performed.

Geographical distribution and mapping. The geographical distribution of this lightfish species has been prepared by compiling all existing scientific literature concerning reported records of *I. ovatus* with particular reference to the Mediterranean Sea. Every published article we found that contained reports of *I. ovatus* in the Mediterranean Sea was scrutinized in order to extract the spatial data. In addition, the Mediterranean

Table 1. Comparison of biometric and meristic characters of the presently reported *Ichthyococcus ovatus* from the Strait of Sicily with those provided by selected literature sources.

Character	This paper <i>n</i> = 1			Lombarte et al. 2006 <i>n</i> = 1	Battaglia et al. 2010 <i>n</i> = 40	
	Absolute		Relative	Meristic	Absolute	
	[mm]	[g]	[%SL]		mm	mm [g]
Total length	59			45		
Standard length	49				16.9–38.1	
Head length	14		28.6			
Eye diameter	4		8.2			
Total weight		1.44				0.11–1.27
Dorsal fin length	9		18.4			
Pectoral fin length	7		14.3			
Ventral fin length	4		8.2			
Anal fin length	7		14.3			
Dorsal fin rays				11		
Pectoral fin rays				8		
Ventral fin rays				7		
Anal fin rays				16		
Vertebrae				42		
IC				46		
VAV + AC				21		
OA				23		

%SL = percentage of the standard length; IC = Summary of photophores of the ventral series (isthmus to caudal fin base), VAV = Ventral series photophores (pelvic fin base to the caudal fin base), AC = posterior part of IC series, OA = entire lateral series photophores on body side (OA).

records of this species lacking in the literature were found using the Global Biodiversity Information Facility (GBIF 2022). In particular, all the records not verified in GBIF were excluded. Lastly, the records of *I. ovatus* were mapped via the help of Quantum GIS software (QGIS 2020).

Results

The photographic image of the *Ichthyococcus ovatus* specimen caught in the Strait of Sicily is shown in Fig. 2. The biometric and meristic measurements of individual *I. ovatus* specimen are showed in Table 1.

The examination of the whole otoliths by the distal surface as shown in Fig. 1. Considering the visibility of the growth zones (Fig. 1B), an age estimation and gross morphology of the otolith of the *I. ovatus* specimen appeared feasible. Thus, the putative age was estimated at five years. According to the terminology used by Smale et

**Figure 2.** *Ichthyococcus ovatus* specimen that was caught in the Strait of Sicily.

al. (1995) and Tuset et al. (2008), the gross morphology was described as follows: **Shape:** high and approximately triangular, entire to sinuate margins; **Thickness:** moderately thick; **Form:** Mesial slightly concave, Lateral very convex; **Sulcus acusticus:** pseudo-ostial, median, dorsal and ventral area similar sized; crista superior absent; crista inferior with a low ridge-like along entire sulcus acusticus. **Ostium:** elliptic, confined to antero-dorsal part of rostrum. **Cauda:** round-oval. **Ostio-cauda differentiation:** slight ventral constriction. **Anterior region:** peaked to notched with irregular margin, extended rostrum, very short and round antirostrum, excisura narrow with a shallow notch. **Posterior region:** entire to sinuate margins (Fig. 1C). The shape parameters and indices mea-

Table 2. Shape parameters and indices from otolith of *Ichthyococcus ovatus* from the Strait of Sicily, described in the presently reported study.

Shape parameters	Value
Area (A_o) [mm ²]	8.89
Perimeter (P_o) [mm]	17.01
Mass (M_o) [mg]	0.0154
Length (L_o) [mm]	3.99
Width (W_o) [mm]	4.68
Shape indices	
Otolith relative length (TL)	6.76
Otolith relative length (SL)	8.14
Otolith relative size	2.55
Aspect ratio (Ar)	0.85
Form factor (Ff)	0.39
Ellipticity (El)	0.07
Roundness (Ro)	0.71
Rectangularity (Re)	0.48
Circularity (Ci)	32.54

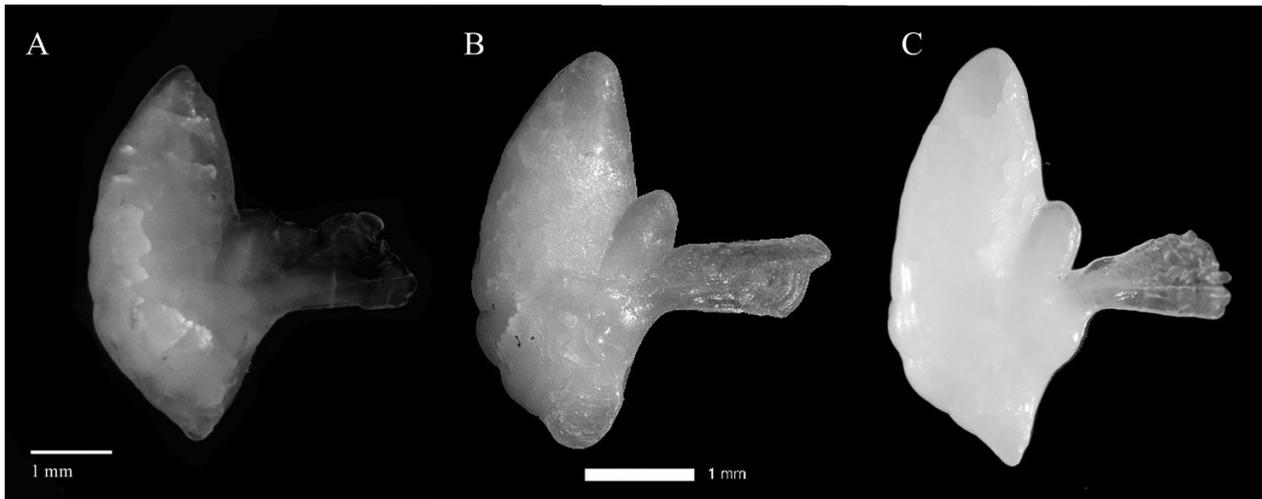


Figure 3. *Ichthyococcus ovatus* otolith (A) proximal view of the left sagitta from the Strait of Sicily, (B) otolith from the Canary Islands, (C) otolith from the Strait of Messina.

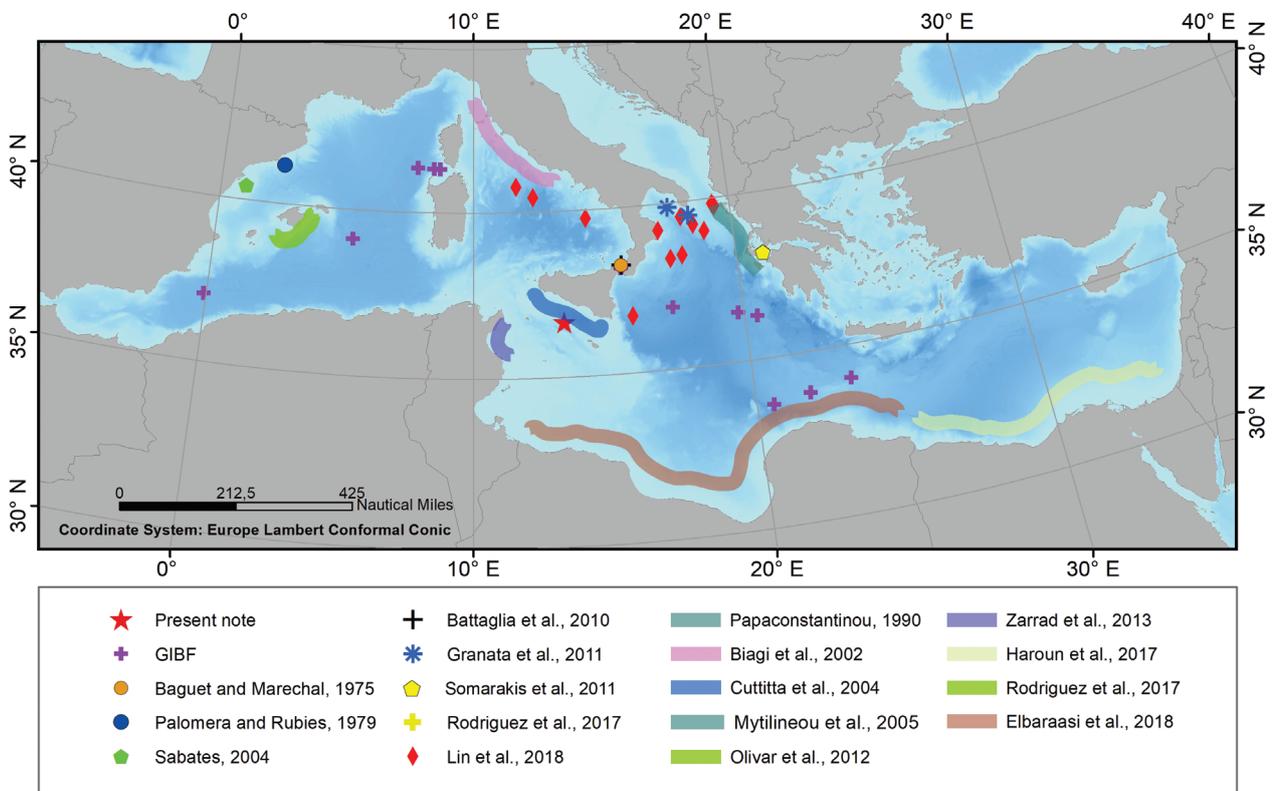


Figure 4. Map showing the geographical distribution of *Ichthyococcus ovatus* based on the previous and the presently reported study within the Mediterranean Basin. Specific records include: green, blue, violet, pink, stripes, and green pentagon as larvae; brown and light green stripes as the probable catch areas for specimens of Libyan, and Egyptian waters, respectively.

sured from the left sagittal otolith of *I. ovatus* caught in the Strait of Sicily can be seen in Table 2.

Overall, the otolith of the presently reported study tended to be elliptic in shape related to aspect ratio (Ar) and high rectangularity (Re) while circularity (Ci) showed high complexity of otolith contour (Table 2). Moreover, comparing the sagitta otoliths of this work (Fig. 3A) with those of published literature (Fig. 3B and 3C), there appears to be a somewhat but slight observable difference. Specifically, the otoliths of Canary Islands and Strait of

Messina possess rather shallower notches between the rostrum and antirostrum. Further, the rostrum appear somewhat prominent, whereas much less so for the antirostrum, and with different shapes in the Canary Islands and Strait of Messina.

Map comparing the geographical distribution of *I. ovatus* of the presently reported study with those of other previous studies within the Mediterranean Basin is shown in Fig. 4, which suggests the widespread nature of this lightfish species.

Discussion

Consistent with the features described by Badcock (1984), this *Ichthyococcus ovatus* specimen physically appeared dark in the back, silvery-translucent to the flanks and with the fin rays speckled basally. The photophores, biometrics and meristic counts of the *I. ovatus* specimen appear consistent with information provided by Badcock (1984). Notably, the nature and patterns of photophores are of high importance for discrimination of *Ichthyococcus* spp. as well as identifying larvae and adults (Ahlstrom et al. 1984). In particular, symphyseal photophores were absent whereas photophores of the ventral series, from the pectoral fin base to the pelvic fin base and from the anal fin base to caudal fin base, were in a straight line when viewed from below and continuous, respectively. According to Badcock (1984), the photophores development complete at about 15–17 mm of SL. Thus, our specimen might be ascribed as an adult of *I. ovatus*. As we have considered the putative age of the *I. ovatus* specimen to be estimated at five years, it is feasible to treat the specimen as an adult. However, the periodicity in the formation of the rings would need to be established. In addition, age validation studies would be required if a more accurate age determination of this lightfish species is to be realized. Additionally, the pictorial comparison with the extant literature might show a possibility of differentiation between the population of *I. ovatus* in the Canary Islands (Atlantic Ocean), Strait of Sicily, and Strait of Messina.

Environmental factors are believed to influence the otolith shape such as the depth, temperature, substrate type, salinity, and feeding conditions (Lombarte and Leonart 1993; Torres et al. 2000). Besides, the different variations in otolith shape would at times be interpreted to result from habitat differentiation (Morat et al. 2012). For instance, Vignon and Morat (2010) showed that contrasting environmental factors induce an overall change in otolith shape, but genetically induced changes locally affect the otolith shape in the area of the rostrum and antirostrum for bluestripe snapper *Lutjanus kasmira* (Forsskål, 1775). However, to clearly establish the specific details, it is necessary that a proper shape analysis (and more otoliths) be performed. Indeed, the literature on the biology and distribution of deep-water species is scarce. In addition, relevant information concerning the size at maturity, feeding strategy, sexual dimorphism, and growth of *I. ovatus* appears scanty.

The widespread nature of this lightfish species is demonstrated by its geographical distribution within the Mediterranean Sea. The records in the waters off Libya (Elbaraasi et al. 2019; GBIF 2022) and western coasts of Egypt (Akel and Karachle 2017; GBIF 2022) suggest that the geographical range of *I. ovatus* can extend to the Levantine basin of the Mediterranean Sea. Other workers found it as reported at different areas, for example, the Western and Central basin such as the Catalan Sea, Balearic Sea, Corsican Sea, Tyrrhenian Sea, Ionian Sea, Gulf of Hammamet, and Strait of Messina (Palomera and Rubies 1979; Papaconstantinou 1990; Biagi et al.

2002; Sabatés 2004; Mytilineou et al. 2005; Battaglia et al. 2010; Somarakis et al. 2011; Olivar et al. 2012; Rodríguez et al. 2013; Zarrad et al. 2013; Lin et al. 2018; GBIF 2022). Further, the occurrence of *I. ovatus* within the Mediterranean Sea would reach depths, ranging from 40 up to 1100 m (Granata et al. 2011; Olivar et al. 2012; Rodríguez et al. 2013; Zarrad et al. 2013). In particular, the records up to a depth of 200 m were ascribed as fish larvae (Sabatés 2004; Cuttitta et al. 2004; Somarakis et al. 2011; Zarrad et al. 2013). According to Watanabe et al. (1999), diel vertical migration is known to occur in several groups of fish and their larvae, especially in species with light organs. Further, *I. ovatus* vary in bathymetric range from the mesopelagic zone at a depth of about 200–500 m (Schaefer et al. 1986) to the deeper waters of the bathypelagic zone (Yang et al. 1996). It is important to mention here that the first record of *I. ovatus*, specifically at its larval stage, in the Strait of Sicily, was reported by Cuttitta et al. (2004) and since then, there appears to have been no other published report. Therefore, this presently reported study shows the first occurrence of an adult *I. ovatus* specimen in the Strait of Sicily. Besides, the *I. ovatus* specimens in the presently reported study represented the deepest record of this species in the Strait of Sicily.

Conclusions

The first record and morphometric description of sagittae otoliths in an adult *Ichthyococcus ovatus* specific to the Strait of Sicily has been presented in this communication. It also included an updated geographical distribution of this deep-water species around the Mediterranean Sea. As we have considered the putative age of the *I. ovatus* specimen estimated at five years, the periodicity in the formation of the rings must be established and age validation studies are required for accurate age determination of this lightfish species. This presently reported study is preliminary and lays a baseline for the future study of this *I. ovatus* species, which are not commonly caught by trawling likely because of its bathymetric distribution. A more robust study involving age validation and shape analysis will require the collection of more *I. ovatus* species samples. Indeed, the absence of economic value of rarely reported species may actually underestimate their presence/abundance in the Mediterranean basin (Sardo et al. 2020). Besides improving the sampling design (Falsone et al. 2017; Geraci et al. 2019), more research surveys involving the collection of meso- and bathypelagic fish fauna would be necessary in order to fill the information gap on the biology of these Mediterranean deep-water species.

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Records of the eel-goby, *Taenioides snyderi* (Actinopterygii: Gobiiformes: Gobiidae), from Taiwan

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Abstract

Four gobiid specimens collected from the western coast of Taiwan were identified as *Taenioides snyderi* Jordan et Hubbs, 1925, being characterized by 51–55 (total) dorsal-fin rays, 44–46 (total) anal-fin rays, 17–19 pectoral-fin rays, 10 + 21 = 31 vertebrae, 3 paired barbels on the chin surface, the pelvic-fin base fused by membrane to the abdomen, and the pattern of the dermal folds with sensory papillae on the head and body. *Taenioides snyderi* has been recorded to date only from Japanese waters, although the likelihood of a wider distribution has been suggested by molecular analysis. This study represents the first specimen-based records of the species outside Japan, with data adding to our knowledge of a poorly known fish group.

Keywords

distribution, morphology, range extension, specimen-based records

Introduction

Taenioides Lacepède, 1800, a genus of mud-dwelling eel-gobies inhabiting bays and estuaries, is characterized by dermal folds on the scaleless head and body, barbels on the chin, the first and second dorsal fin connected, the posteriormost rays of the dorsal and anal fins unbranched (rarely branched), and a Y-shaped second anal-fin pterygiophore (Murdy and Shibukawa 2001; Murdy 2011, 2018; Shibukawa and Murdy 2012; Koreeda and Motomura 2021). Although the relations of nominal species of *Taenioides* have not yet been resolved, the validity of *Taenioides anguillaris* (Linnaeus, 1758), *Taenioides gracilis* (Valenciennes, 1837), *Taenioides kentalleni* Murdy et Randall, 2002, *Taenioides purpurascens* (De Vis, 1884), and *Taenioides snyderi* Jordan et Hubbs, 1925 have been recently confirmed (Kurita and Yoshino 2012; Murdy 2018).

Four museum specimens of *Taenioides* previously collected from the western coast of Taiwan were identified as *Taenioides snyderi*, a species originally described from Wakayama Prefecture, Japan (Jordan and Hubbs 1925). Although recorded only from Japan to date (Jordan and Hubbs 1925; Kurita and Yoshino 2012; Koreeda and Motomura 2021), Koreeda and Motomura (2021) suggested that the species may also be distributed off China and Taiwan, following comparisons of molecular studies. The specimens from Taiwan are therefore the first verified records of *T. snyderi* from Taiwan, supported by voucher specimens.

Methods

Counts and measurements followed Murdy (2018), with the following exceptions: distance of posterior end of pelvic-fin base to anterior margin of anus (P–A length) was

measured from posterior margin of membrane between the pelvic fin and the abdomen to anterior margin of the anus. Terminology of sensory-papillae rows followed Koreeda and Motomura (2021). Relations of dorsal-fin pterygiophore and neural spine (P–V) followed Akihito (1984). Dorsal- and anal-fin rays, vertebrae, and pterygiophores were counted from X-ray photographs. Standard length is abbreviated as SL. Institutional codes are as follows: Kagoshima University Museum, Kagoshima (KAUM); National Museum of Marine Biology and Aquarium, Pingtung (NMMB-P).

Results

Family Gobiidae Cuvier, 1816

Taeniooides Lacepède, 1800

Taeniooides snyderi Jordan et Hubbs, 1925

Figs. 1–2; Table 1

Material examined. NMMB-P5491, male, 150.7 mm SL, Chiayi, Taiwan, bottom trawl, 30 Aug. 1965; NMMB-P6090, 137.1 mm SL, Anping Fishing Harbor, Tainan, bottom trawl, 23 Mar. 2003; NMMB-P32256, 2 specimens, 156.8–160.9 mm SL, off mouth of Tseng-Wen River, Tainan, Taiwan, 4 Apr. 1995.

Description. Counts and measurements are shown in Tables 1 and 2 and Fig. 3. Body elongated, subcylindrical, compressed posteriorly. Head slightly depressed. Snout longer than interorbital space. Eye small, embedded in anterodorsal head. Anterior nostril just behind upper lip, with short tube, reaching to or slightly over (NMMB-P32256) upper lip. Posterior nostril in front of eye, forming

oblique crest, size similar to eye diameter. Mouth terminal, forming angle of 60° with body axis, gape relatively wide; maxilla extending posteriorly to slightly in front of eye; upper lip well developed below anterior nostril, extending posteriorly with small flap-like projections; lower lip covering posteroventral margin of lower jaw, smaller than upper lip, smooth. Gill opening narrow, extending from behind posterior margin of preopercle to just below upper part of pectoral-fin base. Anus located at anterior one-third of body.

Sensory canals and pores absent. Three paired slender barbels on chin surface to lower margin of mandible; anteriormost pair on tip of chin; middle pair midway along lower jaw; posteriormost pair slightly before mouth corner. Dermal folds with single row of sensory papillae on head and body (damaged in some areas on specimens, especially NMMB-P 6090); row 14 well developed, extending slightly below row 9 (Fig. 2); row 17 comprising two transverse rows, the anterior row the longer (Fig. 2); anteriormost low lv located on antero-lateral trunk.

First and second dorsal fins connected by membrane; all first dorsal-fin spines flexible; all second dorsal-fin rays segmented; second dorsal fin continuous with caudal fin, with distinct notch between them. All anal-fin rays segmented, height subequal to second dorsal fin, continuous with caudal fin with distinct notch between them. Pectoral fin rounded, just behind gill opening, less than half length of pelvic fin; all rays segmented and branched (except upper and lowermost); free ray absent. Pelvic-fin origin below pectoral-fin base, posterior end reaching midway along trunk; spine covered with skin; all soft rays branched and segmented; fifth soft ray longest, anterior half connected by membrane to adjacent



Figure 1. Preserved specimens of *Taeniooides snyderi* from Taiwan. **A:** NMMB-P5491, male, 150.7 mm SL, Chiayi; **B:** one of NMMB-P32256, male, 156.8 mm SL, Zengwen River; **C:** one of NMMB-P32256, female, 160.9 mm SL, Zengwen River.

Table 1. Counts and measurements of *Taenioides snyderi* from Taiwan.

	NMMB-P			
	5491 Male	32256 Male	32256 Female	6090 Unknown
Standard length [mm]	150.74	156.8	160.9	137.1
Counts				
Total dorsal-fin rays	VI, 49	VI, 47	VI, 45	VI, 45
Total anal-fin rays	46	45	44	44
Pectoral-fin rays	19/17	18/17	18/17	17/19
Pelvic-fin rays	I, 5	I, 5	I, 5	I, 5
Caudal fin rays	10 + 8	9 + 8	11 + 8	—
Barbel arrangement	2-2-2	2-2-2	2-2-2	—
Teeth in upper jaw	14	16	13	10
Teeth in lower jaw	7	12	10	7
Vertebrae	10 + 21	10 + 21	10 + 21	10 + 21
P-V	3-12210/8-9	3-12210/8-9	3-12210/8-9	3-12210/8-9
AP	3	3	3	3
Measurements [%SL]				
Head length	12.9	13.6	12.5	14.1
Head depth	6.1	7.0	6.1	6.5
Head width	6.5	7.7	6.6	6.3
Snout length	3.2	3.4	3.4	4.3
Upper-jaw length	3.5	3.9	3.9	3.5
Body depth at pelvic-fin origin	7.2	6.8	6.7	6.7
Body depth	6.9	7.5	8.3	7.6
Body depth at anal-fin origin	—	7.0	7.2	6.6
Nape width	5.0	5.9	5.6	5.4
Body width at pectoral-fin base	5.4	5.7	5.3	4.7
Body width	5.2	6.3	7.6	5.1
P-A length	12.8	11.1	11.6	11.3
Preanal length	30.5	30.0	31.3	30.8
Predorsal-fin length	19.6	20.3	21.1	19.5
Preanal-fin length	32.0	31.8	34.0	33.6
Pectoral-fin length	3.4	4.5	3.6	3.9
Pelvic-fin length	13.0	12.4	12.9	13.2
Caudal-fin length	11.2	12.6	13.1	12.7
Measurements [%HL]				
Head depth	31.3	32.5	30.3	33.6
Head width	33.1	36.1	33.0	32.4
Snout length	16.4	16.0	16.8	22.3
Upper-jaw length	18.0	18.4	19.3	18.0
P-A length	65.6	51.9	57.9	58.5
Pectoral-fin length	17.4	21.2	17.7	20.0
Pelvic-fin length	66.7	58.1	64.2	68.2
Caudal-fin length	57.3	59.1	65.1	65.6

AP = Number of anal-fin pterygiophores anterior to anteriormost hemal spine.

ray; left and right fins connected by membrane; pelvic frenum present, smooth with slightly concave posterior margin; half length of longest ray fused to abdomen by

membrane; posterior margin of membrane between pelvic fin and abdomen located slightly behind anteriormost sensory papillae row lv. Caudal fin pointed, slightly shorter than pelvic fin.

Scales absent. Teeth in each jaw flat, conical, outer teeth larger than inner teeth; upper jaw with 10–16 slender outer teeth, distributed irregularly almost across entire jaw edge; lower jaw with 7–12 outer teeth (slightly longer than upper jaw teeth), distributed over slightly narrower to two-thirds width of jaw edge; inner teeth of each jaw less than one-third length of outer teeth. First hemal spine vertical. Other hemal spines slenderer than first spine, angled posteriorly. Second anal-fin pterygiophore Y-shaped.

Color in alcohol (Fig. 1). Body grayish-pink to pale pink, tail brownish. Dorsal fin light grayish-brown to grayish-brown with narrow white subtranslucent margin. Anal fin paler than dorsal fin, light grayish-brown to beige. Pectoral and pelvic fins paler than anal fin, pale beige to beige. Caudal fin darker than dorsal fin, dark yellowish-brown.

Distribution. *Taenioides snyderi* has been recorded to date only from southern Japan; Tokyo Bay to Kochi Prefecture (Pacific coast), Fukuoka Prefecture (East China Sea), Seto Inland Sea, Ariake Bay, Yatsushiro Sea, and Kagoshima Bay (Jordan and Hubbs 1925; Kurita and Yoshino 2012; Koreeda and Motomura 2021). The presently reported specimens, from the western coast of Taiwan, represent the first record outside of Japanese waters.

Remarks. Identification of examined specimens was based on the following combination of characters, which closely matched the diagnostic features of *Taenioides snyderi* given by Kurita and Yoshino (2012), Murdy (2018), Kanagawa et al. (2018), and Koreeda and Motomura (2021): total dorsal-fin rays 51–55, total anal-fin rays 44–46, pectoral-fin rays 17–19, vertebrae 10 + 21 = 31, barbel arrangement 2-2-2, sensory papillae row 14 developed and extending just below row 9, row 17 comprising two transverse rows, pelvic-fin base fused to the abdomen by a membrane to anteriormost sensory papillae row lv (half-length of pelvic fin), and brownish second dorsal fin with narrow white subtranslucent margin.

The pelvic-fin posterior end to anus (P-A) length/head length of the Taiwanese specimens of *T. snyderi* was less than 65.6%, being slightly shorter than in

Table 2. Comparison of *Taenioides snyderi* from Japan and Taiwan, and *T. anguillaris*.

Species	Locality	Total dorsal-fin rays										Pectoral-fin rays				
		47	48	49	50	51	52	53	54	55	56	16	17	18	19	20
<i>T. snyderi</i>	SJ					5	6	14	19	13	4		11	29	24	2
<i>T. snyderi</i>	T					2		1		1			1 (3)	2 (0)	1 (1)	
<i>T. anguillaris</i>	J-Ch	1	1	4	3	2						2	9	2		
		Anal-fin rays										Total vertebrae				
		40	41	42	43	44	45	46	47	48	49	29	30	31	32	
<i>T. snyderi</i>	SJ				1	6	13	16	19	5	3			7	51	
<i>T. snyderi</i>	T					2	1	1						4		
<i>T. anguillaris</i>	J-Ch	1	2	2	4	2		1				10	2			

SJ = southern Japan, T = Taiwan, J-Ch = Japan and China; Meristic data (except for Taiwanese specimens) from Kurita and Yoshino (2012), Koreeda and Motomura (2021), and Miyahira and Tachihara (2022); data for paralectotype of *T. snyderi* and holotype of *T. anguillaris* (indicated by **bold font**) also from Murdy (2018). Counts of pectoral fins on the right side of Taiwanese specimens are shown in parentheses.

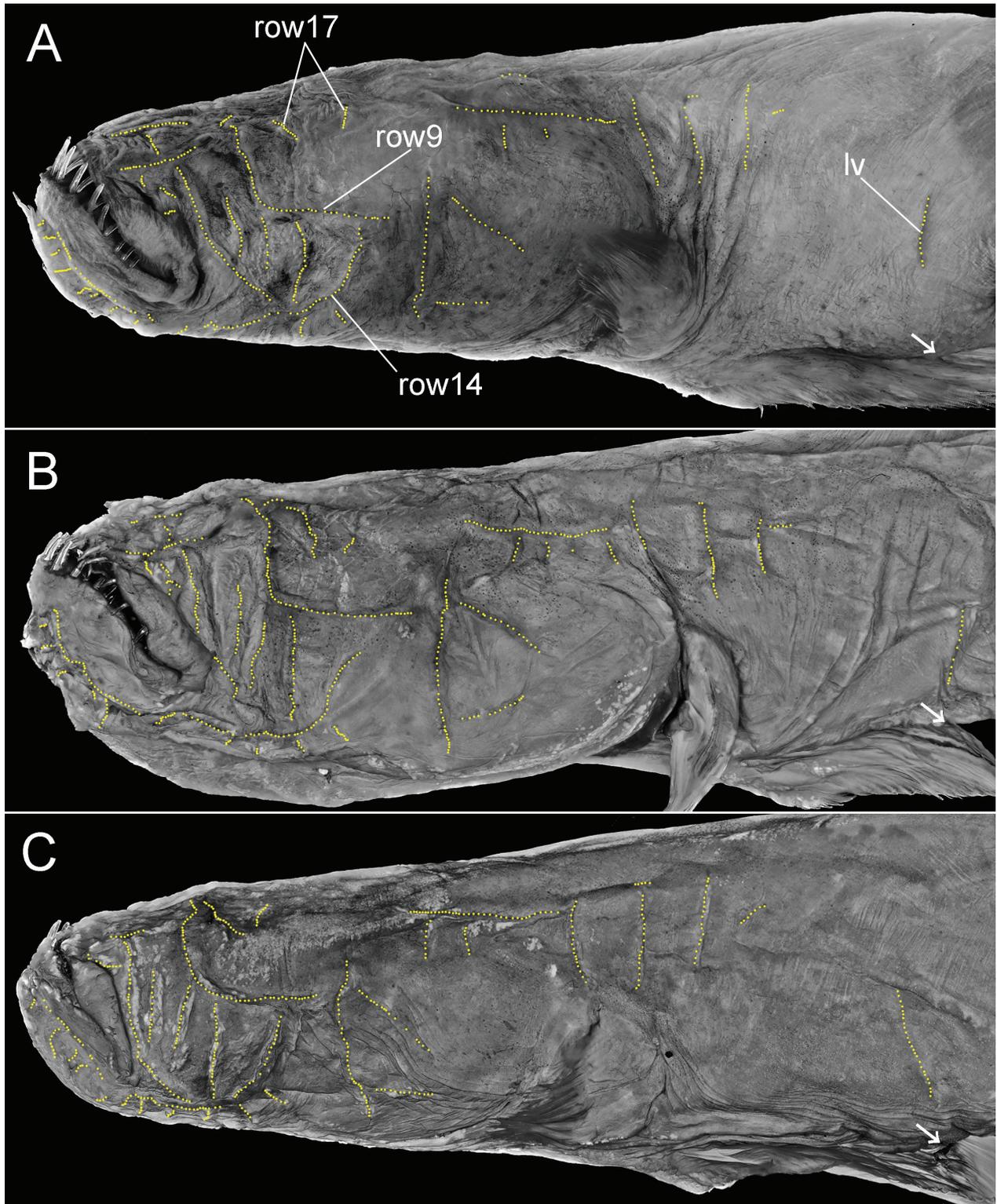


Figure 2. Head view of *Taenioides snyderi* from Taiwan, showing sensory papillae rows on the dermal fold (individual papillae indicated by yellow spots). White arrows indicate posterior end of pelvic-fin base. **A:** NMMB-P5491, 150.7 mm SL, Chiayi; **B:** one of NMMB-P32256, 156.8 mm SL, Zengwen River; **C:** one of NMMB-P32256, 160.9 mm SL, Zengwen River.

Japanese specimens (Fig. 3). The proportion is variable depending on the degree of fusion of the pelvic fin to the abdomen. Koreeda and Motomura (2021) reported that the pelvic-fin base of *T. snyderi* from southern Japan was strongly fused to the abdomen by a membrane,

the posterior end of the base being located below the anteriormost sensory papillae row IV. In the Taiwanese specimens, the pelvic-fin base fusion extended slightly behind the anteriormost row IV. The significance of this difference remains unclear.

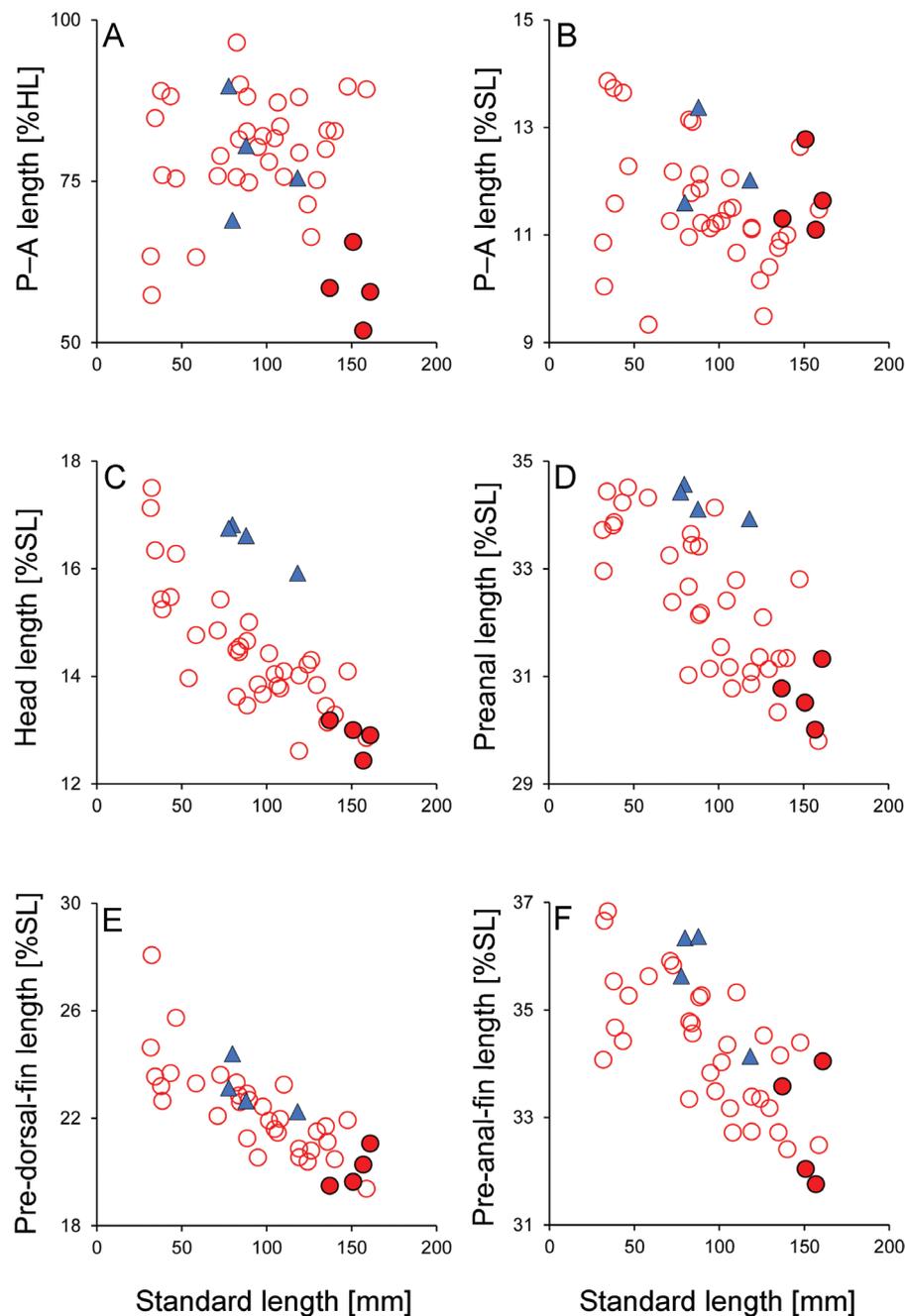


Figure 3. Relations of P–A length (A), as % of head length (mm), and P–A length (B), head length (C), Pre-anal length (D), pre-dorsal-fin length (E), and preanal-fin length (F) as % of standard length [mm] of *Taenioides anguillaris* and *T. snyderi*. Closed red circles: *Taenioides snyderi* (Taiwan); open red circles: *T. snyderi* (Japan); blue triangles: *T. anguillaris* (Japan). Data for *T. anguillaris* and *T. snyderi* from Koreeda and Motomura (2021) and Miyahira and Tachihara (2022).

Discussion

Although Koreeda and Motomura (2021) reported that *Taenioides snyderi* had been recorded only from Japan, they suggested that the species may have a wider distribution. Kurita and Yoshino (2012) reported four species of *Taenioides* from Japanese waters, based on partial sequences of the mitochondrial ND 2 and 16S rRNA genes, their *Taenioides* sp. A, *Taenioides* sp. B, *Taenioides* sp. C, and *Taenioides* sp. D which they deduced as possibly being *T. anguillaris*, *T. snyderi*, *T. gracilis*, and *T. kentalleni*,

respectively. Subsequently, Chen and Wen (2016) reported the complete mitochondrial genome of *Taenioides cirratus* (Blyth, 1860) from Chiku Lagoon, Tainan, Taiwan, and Wei et al. (2015) reported the complete mitochondrial genome of *T. anguillaris* from Xinghua Bay, Fujian Province, China. Koreeda and Motomura (2021) noted that *T. cirratus* of Chen and Wen (2016) and *T. anguillaris* of Wei et al. (2015) were included in the clade of *Taenioides* sp. B proposed by Kurita and Yoshino (2012), following Murdy's (2018) identification of *Taenioides* sp. B sensu Kurita and Yoshino (2012) as *T. snyderi*. This study has

confirmed, on the basis of morphological characters, that *T. snyderi* occurs in Taiwanese waters.

Taenioides anguillaris is known to have head length longer than the pelvic-fin posterior end to anus (P–A) length (e.g., Shen and Wu 2011). However, Koreeda and Motomura (2021) and the presently reported study found that *T. anguillaris* and *T. snyderi* shared that character, and consequently the record of *T. anguillaris* in Taiwan cannot be confirmed, pending examination of additional specimens. Although *T. anguillaris* is very similar to *T. snyderi* in sharing 3 paired barbels on the chin, a well-developed sensory papillae row 14 reaching closely below row 9, row 17 comprising two transverse dermal folds bearing sensory papillae, and a dark purple to reddish-brown body, it differs in the following: total dorsal-fin rays 48–51 (51–56 in *T. snyderi*), total anal-fin rays 41–46 (43–49), pectoral-fin rays 16–18 (17–20), vertebrae 29 or 30 (31 or 32), the posterior end of the fused pelvic fin base well forward of the anteriormost sensory papillae row lv (approximately level with or slightly

behind anteriormost row lv) (Kurita and Yoshino 2012; Murdy 2018; Koreeda and Motomura 2021; this study: Figs. 2–3).

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