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Morphological patterns of oblong slipmouth *Photolateralis stercorarius* populations in the Makassar Strait, Indonesia

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Abstract. *Umar MT, Omar SBA, Amir F, Hidayani AA, Parenrengi A, Moore AM. 2025. Morphological patterns of oblong slipmouth* Photolateralis stercorarius *populations in the Makassar Strait, Indonesia. Biodiversitas 26: 1675-1690.* Slipmouths or ponyfishes (Leiognathidae) are important fisheries commodities in Indonesia. Morphological identification of leiognathids can be challenging, with ongoing taxonomic revisions including recent recognition of the genus *Photolateralis*. The purpose of this study was to describe and compare (between sites and by sex) the morphological traits of slipmouths (30 males and 30 females per site) from two sites in the Makassar Strait, South Sulawesi, Indonesia. Qualitative and quantitative (morphometric and meristic) morphological traits were recorded. Statistical analyses included Bray-Curtis dissimilarity (PAST v4.17) and discriminant analysis (XLSTAT 2019.2.2.). All specimens were identified as the oblong slipmouth *P. stercorarius*. The analyses showed that *P. stercorarius* is sexually dimorphic; males displayed a bluish longitudinal line just below the body midline, and on average females were longer than males (fork length and standard length). Meristic traits did not differ significantly by sex or between sites. Both dissimilarity and discriminant function analyses showed significant differences between the sites and between males and females at each site. The results reveal morph variation in Makassar Strait *P. stercorarius* populations, indicating the populations at each site may belong to a demographically separated and/or genetically distinct stock. This has implications for fisheries management, as fish stocks should be managed separately, entailing the need to determine stock boundaries.

Keywords: Leiognathidae, morph variation, morpho-meristic, sexual dimorphism, South Sulawesi

INTRODUCTION

The Makassar Strait is an important fishing ground in Indonesian Fisheries Management Area (FMA) 713, with fisheries commodities including demersal fishes such as groupers and snappers, large and pelagic species such as tunas and small pelagic fishes such as slipmouths (Suprapto 2014; Khumaera et al. 2019; Khaerah et al. 2021; Nadiarti et al. 2021; Saruran 2023). Ponyfishes or slipmouths (Leiognathidae: Actinopterygii) are predominantly marine euryhaline demersal fish widely distributed across the Indo-West Pacific region (Pauly 2018a, b; Alavi-Yeganeh et al. 2021; Froese and Pauly 2025), reported from shallow waters including seagrass and mangrove ecosystems (SPC 2011) to depths below 70 m (Pauly 2018a, b). Juveniles are often found in estuarine environments (Borah et al. 2018; Guerreiro et al. 2021). The Leiognathidae comprise 10 recognized genera with over 50 species (Fricke et al. 2025; Froese and Pauly 2025) and display bioluminescence (Sparks et al. 2005; Chauvin 2022). Locally important fisheries commodities in many southeast Asian countries including Vietnam Malaysia, and Indonesia (Seah et al. 2012; White et al. 2013; Pauly 2018b; Halim et al. 2020; Klangnurak and True 2022; Kazara-Belja 2023), slipmouths are caught with trawls, gillnets, trammel nets, lift-nets, set nets, traps and beach seines (Woodland et al. 2001; Pauly 2018b), and valued by-catch in many trawl fisheries (Giat et al. 2008; Klangnurak and True 2022). In Indonesia, slipmouths are commercial target species (Midrar 2020; Syahailatua et al. 2023) with recorded catches of 69,000-93,000 tonnes from 2000 to 2014 (Halim et al. 2020), providing affordable high-quality protein (Pauly 2018b; Yusfiandayani et al. 2023).

Many gears are operated in the Makassar Straits, such as large set nets and fixed traps (local name sero); various small trawling gears with Indonesian or local names in brackets, e.g. beach trawls, small bottom trawls (dogol), and Danish seines (payang**)** (Suprapto 2014; Setianto et al. 2019; Nadiarti et al. 2021; Ihsan et al. 2022); and larger trawls (cantrang) including locally-based and Java-based vessels (Suuronen et al. 2020; Nadiarti et al. 2021; Rustam 2022). Lift-nets (fixed and mobile) operating at night with lights (Khumaera et al. 2012; Sudirman et al. 2020; Azakhrah et al. 2022; Fatma et al. 2022; Kurnia et al. 2023) catch predominantly juvenile fish of many species (including slipmouths), representing a substantial opportunity loss to fisheries targeting adult fish life-stages (Khumaera et al. 2012). Unselective and/or habitat-damaging gears and overfishing symptoms have raised concerns regarding fish populations and ecosystem health (Coll et al. 2008; Khumaera et al. 2012; Suprapto 2014; Pauly 2018b; Suuronen et al. 2020; Nadiarti et al. 2021;

Cheng 2022; Saruran 2023; Leadbitter et al. 2024). In 2022, a high exploitation rate (E: 0.56) was reported for a Makassar Strait slipmouth population (Saruran 2023).

Responsible approaches to fisheries management aiming to balance human needs and protect the environment (Suuronen et al. 2020; Malvarosa et al. 2023) typically rely heavily on the concept of stocks as fisheries management units and the availability of adequate data (Cadrin 2020; Suuronen et al. 2020). Identifying stocks present within each FMA is vital to enable stock and fisheries status evaluation (Muawanah et al. 2018; Cadrin et al. 2023). Slipmouth can be hard to distinguish from each other (Suzuki and Kimura 2024). Intraspecies morphological differences due to sex, environmental, and other factors can further complicate identification (Chakrabarty et al. 2010; Harrisson et al. 2017; Pauly 2018a; Lehnen et al. 2021; Klangnurak and True 2022; Verba et al. 2022; Pasisingi et al. 2024). Morphometrics (body dimensions, proportions and shape) can help identify, describe and understand morphological variation (To and Anumudu 2015; Trail 2021). Taxonomic, species distribution, and fisheries data are limited for Indonesia generally (Syahailatua et al. 2023). Studies on slipmouths in Indonesia mostly focused on species diversity and distribution (Asriyana et al. 2011; Suyatna et al. 2016; Wedjatmiko et al. 2017), or reproductive biology and life history (Sharif et al. 2018; Permatasari et al. 2022; Wardhani et al. 2024), while data on morphology (morpho-meristic traits) are lacking.

Around 11 to 16 slipmouth species can be found in the Makassar Strait (Suyatna et al. 2010; Wardhani et al. 2024). Revisions in Leiognathidae phylogeny include the description of the genus *Photolateralis*, distinguished by the presence of a translucent flank stripe (Sparks and Chakrabarty 2015) with four currently recognized species: *P. antongil*; *P. moretoniensis*; *P. polyfenestrus*; *P. stercorarius* (Froese and Pauly 2025; WoRMS Editorial Board 2025). The limited data on slipmouth populations in the Makassar Strait do not cover the genus *Photolateralis*, although this genus has been observed during studies on other taxa. Determination and sustainable management of slipmouth stock(s) in the Makassar Strait requires verification of the species present, and an understanding of phenotypic and genotypic variation in slipmouth populations, in order to map species distributions and delimit stocks. Therefore, the purpose of this study was to describe and compare the morphological and morpho-meristic traits of male and female slipmouth of the genus *Photolateralis* landed at two sites on the Makassar Strait coast of South Sulawesi, Indonesia.

MATERIALS AND METHODS

Sampling site and sample collection

Slipmouth specimens of the genus *Photolateralis* were obtained from first level traders who buy fish directly from fishermen at two Fish Landing Sites (FLS) on the Makassar Strait coast of South Sulawesi, Indonesia: the Beba FLS in Galesong, Takalar District and the Maccini Baji FLS, in Pankajene and Kepulauan (Pangkep) District (Figure 1). At each site the sample collected comprised 30 male and 30 female slipmouths. The traders had already divided their catch into groups of fish with similar morphology, and the samples were selected from groups which were preliminarily identified as belonging to the genus *Photolateralis*. The samples were placed in cool-boxes filled with crushed ice for transport to the Fisheries Biology Laboratory at Universitas Hasanuddin in Makassar, Indonesia.

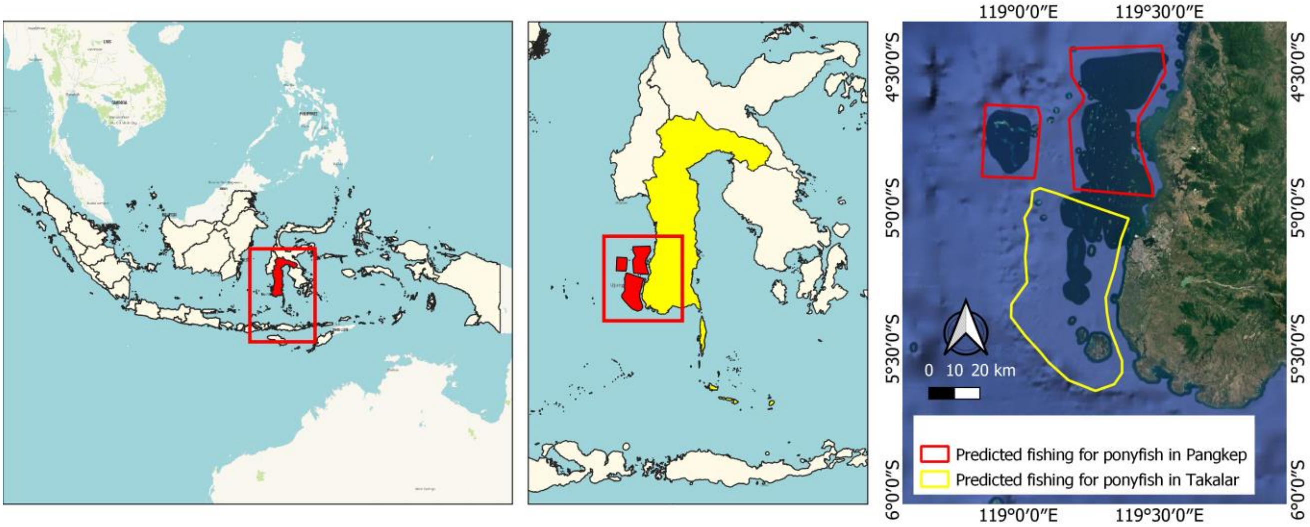


Figure 1. Slipmouth sample collection sites and approximate fishing area of fishers from Fish Landing Sites (FLS) on the Makassar Strait, Indonesia coast on of South Sulawesi, Indonesia: Beba FLS in Takalar District (yellow marker) and Maccini Baji FLS in Pankajene and Kepulauan (Pangkep) District (red marker)

Procedures

Morphological identification

Morphological identification to genus level was carried out in situ at each sampling site in the Makassar Strait based on their morphological characteristics. Detailed analysis was performed in the Fisheries Biology Laboratory. All *Photolateralis* specimens collected for this study (Figure 2) were identified as based on the FAO species identification guide for fishery purposes section on Leiognathidae (Woodland et al. 2001) and other references (Kimura et al. 2003; Sparks 2006; Sparks and Chakrabarty 2015, 2019). Two male and two female specimens from each site were preserved as voucher specimens and deposited in the Aquatic Macrofauna Biodiversity and Conservation (AMBIoC) research group collection at Universitas Hasanuddin, with the reference numbers UNH24-PAN001 to UNH24-PAN004 (Pangkep District) and UNH24-TAK001 to UNH24-TAK004 (Takalar District).

Morphometric and meristic traits

Each specimen was weighed (digital scales, precision 0.01 g) and measured. Morphometric measurements, defined as the straight distance between two anatomical landmark points, were based on Wiadnya et al. (2015) and Seth et al. (2019). The 19 morphometric traits recorded for each specimen were: Standard Length (SL), Fork Length (FL), Dorsal Body Depth (DBD), Anal Body Depth (ABD), Pre-Dorsal Length (PDL), Pre-Anal Length (PAL), Pre-Ventral Length (PVL), Pre-Pectoral Length (PPL), Upper Caudal Peduncle Length (UpCL), Lower Caudal Peduncle Length (LoCL), Dorsal Fin Base (DFB), Anal Fin Base (AFB), Head Length (HL), Nuchal Length (NL), Snout Length (SNL), Orbit Diameter (OBD), Upper Maxilla Length (UpML), Lower Maxilla Length (LoML), and Post-Orbital Length (POL). These were measured (digital calipers, 0.1 mm precision) based on the points shown in Figure 3 as detailed in Table 1.

Morphometric trait measurements were standardized to reduce bias due to differences in the size of individual specimens using the following equation (Elliott et al. 1995; Umar et al. 2024):

$$\mathrm{Ms} = \mathrm{Mo}\left(\frac{\mathrm{Ls}}{\mathrm{Lo}}\right)^{b}$$

Where, Ms: Standardized measurement; Mo: Measured trait length; Ls: Mean Standard Length (SL) of all fish in each group (4 groups, divided by sex and site); Lo: specimen SL; b: regression coefficient calculated from the linear regression of log(Mo) on log(Lo) for the sex-location group in question, with all measurements in mm unit. These standardized measurements were used to calculate the ratios used as morphometric traits.

The slipmouth meristic traits counted were: the number of anal fin spines (A-s) and rays (A-r); the number of caudal fin rays (C); the number of dorsal fin spines (D-s), and rays (D-r); the number of pectoral fin rays (P); the number of ventral fin spines (V-s) and rays (V-r) (Acharya and Naik 2015). Spine counts were given in Roman numerals, and ray counts in Arabic numerals. The meristic formula was determined based on spine and ray counts.

Figure 2. Oblong slipmouth *Photolateralis stercorarius* specimen from the Makassar Strait, South Sulawesi, Indonesia

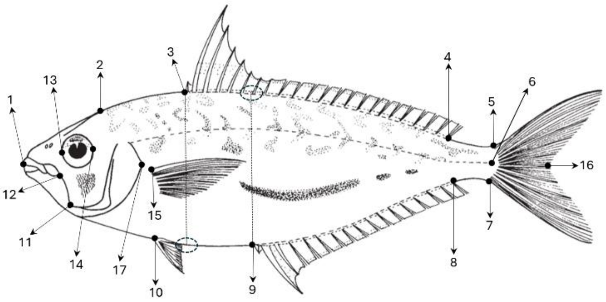


Figure 3. Anatomical waypoints used to measure slipmouth morphometric traits (modified from Woodland et al. 2001; Wiadnya et al. 2015): 1. Rostral tip of premaxilla; 2. Posterior end of nuchal spine; 3. Anterior base of dorsal fin; 4. Posterior base of dorsal fin; 5. Dorsal base of caudal fin; 6. Midpoint of caudal border of hypural plate; 7. Ventral base of caudal fin; 8. Posterior base of anal fin; 9. Anterior base of anal fin; 10. Anterior base of pelvic fin; 11. Ventral end of lower jaw articulation; 12. Posterior end of maxilla; 13. Anterior margin of orbit midline; 14. Posterior margin of orbit midline; 15. Dorsal base of pectoral fin; 16. Centre of the fork in the tail/posterior end of the middle caudal rays, and 17. Posterior point of operculum

Table 1. Slipmouth morphometric traits recorded (mm) based on waypoints in Figure 3 (Woodland et al. 2001; Wiadnya et al. 2015)

Code	Description
SL	Straight distance from point 1 to 6
FL	Straight distance from point 1 to 16
DBD	Body depth at point 3
ABD	Body depth at point 9
PDL	Straight distance from point 1 to 3
PAL	Straight distance from point 1 to 9
PVL	Straight distance from point 1 to 10
PPL	Straight distance from point 1 to 15
UpCL	Straight distance from point 4 to 5
LoCL	Straight distance from point 7 to 8
DFB	Straight distance from point 3 to 4
AFB	Straight distance from point 8 to 9
HL	Straight distance from point 1 to 17
NL	Straight distance from point 1 to 2
SNL	Straight distance from point 1 to 13
OBD	Straight distance from point 13 to 14
UpML	Straight distance from point 1 to 12
LoML	Straight distance from point 1 to 11
POL	Straight distance from point 14 to 17

The length-weight relationship $W = aL^b$ (Froese 2006) was calculated for each site-sex group, by site, and by sex. The growth pattern was determined based on the coefficient b: values significantly different from 3 indicate an allometric negative growth pattern if $b<3$ and allometric positive pattern if $b>3$, while values not significantly different from 3 indicate an isometric growth pattern. The coefficients a and b were obtained through linear regression of the log-transformed standard length (FL) and weight (W).

Data analysis

The data was tabulated in Microsoft Excel 365. Descriptive statistical analyses of morphometric and meristic data were conducted, and box plot graphics were produced in PAST v4.17 (Hammer et al. 2001). Standardized morphometric and meristic values for the 120 specimens were analyzed by population group (based on site and sex) using forward stepwise Discriminant Function Analysis (DFA) using XLSTAT 2019.2.2 (Addinsoft) to determine which combination of morphometric characters performed best in discriminating between the site-sex groups. Differences between group centroids were analyzed based on the Bray-Curtis Dissimilarity Index in PAST v4.17.

RESULTS AND DISCUSSION

Typical morphological characteristics

All 120 specimens were identified as *P. stercorarius*. This name is a recent combination, due to the description of the genus *Photolateralis* in 2015 to resolve the non-monophyletic status of the genus *Leiognathus* (Sparks and Chakrabarty 2015). The original name of this species described in 1907 was *L. stercorarius* (Evermann and Seale 1907). Distinguishing morphological characteristics of *P. stercorarius* (Figure 4) include ventral body silvery white, dorsal body brownish, dark and indistinct irregular oblique lines on dorsal body surface, yellow stripes on dorsal and anal fins, black spot-on snout (Sparks and Chakrabarty 2015); anal fin between second and third spines and anterior fin margin yellow; in males, a bluish longitudinal flank stripe just below midline (Woodland et al. 2001; Sparks and Chakrabarty 2015; Bray 2022).

Other diagnostic traits of the species *P. stercorarius* (listed as *L. stercorarius*) in the key provided in the FAO identification guide (Woodland et al. 2001) include fine scribbly lines on the upper half of the body. Additional traits of *P. stercorarius* observed in the specimens collected from the two study sites include an extensible mouth which points forward or downward when extended; an almost straight lower jaw profile; small, slender teeth set in a single row on the jaw; scales on the cheek, thorax and abdomen; non-elongated dorsal and anal fin spines; and numerous “windows” in the translucent mid-lateral stripe (Woodland et al. 2001; Seah et al. 2009; Sparks and Chakrabarty 2015; Bray 2022).

The genus name has been revised at least twice. In 2005, the genus *Photoplagios* was proposed for several species including *L. stercorarius* (Sparks et al. 2005). In 2008, the genus *Equulites* was proposed as a senior synonym of *Photoplagios* (Kimura et al. 2008) and subsequently subdivided into *Equulites* and *Photolateralis* (Sparks and Chakrabarty 2015). The now obsolete synonyms of *P. stercorarius* can be found in older literature on this species (e.g. *L. stercorarius* in Woodland et al. 2001) and the synonym is still encountered in more recent literature, as well as the Indonesian fisheries database (MMAF 2021). However, the combination *P. stercorarius* has been formalized (Chakrabarty and Sparks 2015) and is retained in a recent Leiognathidae phylogenic study focused on the genus *Equulites* (Suzuki and Kimura 2024).

Morphometric and meristic traits

Morphometric characters of oblong slipmouth *P. stercorarius* from two landing sites in the Makassar Strait (Table 2) are presented as range (mean) values along with secondary data from two studies. These data reveal considerable intra-species variability among individuals, overall and within each of the four site/sex groups. On average, the fish from the Pangkep site were larger (mean SL 85.92 mm for males, 91.15 mm for females) compared to those from Takalar (mean SL 75.20 mm for males, 78.10 mm for females). Mean Fork Length (FL) differed significantly between all sex-site groups (ANOVA, α: 0.05, $p<0.001$). The combined between-sex difference in mean length (Female: 95.55 mm FL; male 90.35 mm FL) and the combined (male and female) between-population difference in mean lengths (Takalar 100.39 mm FL; Pangkep 85.51 mm FL) were significant at the 95% confidence level (Student’s t-test, α: 0.05, $p<0.001$). The mean length of female *P. stercorarius* was significantly longer (ANOVA, α: 0.05, $p<0.001$) than that of male fish overall and in each group. Most traits measured differed significantly between male and female *P. stercorarius* (Table 2). The Pangkep female group had the highest mean values for 7 traits.

The fin spine and ray counts of male and female *P. stercorarius* from the two sampling sites (Beba in Takalar District and Maccini Baji in Pangkep District) are shown in Table 3 together with secondary data for this species (Evermann and Seale 1907; Seah et al. 2009). Six meristic characters were identical for all specimens, and consonant with the counts reported in the initial description (Evermann and Seale 1907) from a Philippine population and from a population in the waters off southeastern Peninsular Malaysia in the South China Sea (Seah et al. 2009). The two counts which varied between individuals (pectoral and caudal fin rays) did not vary significantly between sites or between male and female *P. stercorarius* or with the data from other studies in Table 3. No records for caudal fin ray counts were found in the literature on this species. The meristic formula was: D, VIII+16; A, III+14; P, 16-18; V, I+5.

The oblong slipmouth *P. stercorarius* is laterally compressed and elongated, with somewhat convex dorsal and ventral profiles, with the body depth greater than the length of the head. In addition to the secondary data in

Table 2, Woodland et al. (2001) gives an aspect ratio of 2.8 to 3.6, corresponding to a body depth to standard length ratio of 27.8% to 35.7%, while according to Seah et al. (2009) the body is elongated, and the body depth is 33-35% of the standard length. According to Evermann and Seale (1907), the aspect ratio is 2.6-3.9 times the body depth giving a body depth to standard length ratio of 25.6-38.5%. Although it is not clear whether body depth in these studies corresponds to DBD, ABD, or some point in between, this is similar to the ranges for both body depth ratios calculated in this study. Notably, the aspect ratio is also similar to that of the recently described congener *P. polyfenestrus* (Sparks and Chakrabarty 2019).

Length-weight relationship

The length-weight relationship ($W = aL^b$) was calculated for all four sex-size groups (Figure 5.A) as well as for the four sex-site groups combined (Figure 5.B), by sex (Figures 5.C and 5.D) and by site (Figure 5.E and 5.F). The value of the growth exponent b varied between groups. For males and the population as a whole, the values were close to 3 indicating an isometric growth pattern. This was also the case for the combined-sex relationship at the Pangkep site. Values significantly larger than 3 (Figur 5.C) indicate a positive allometric growth pattern in females overall and a negative allometric growth pattern showed at the Takalar site (values of b significanly lower than 3; Figure 5.E). The high correlation coefficient ($R>0.5$) for overall the relationship indicates a good fit and strong correlation.

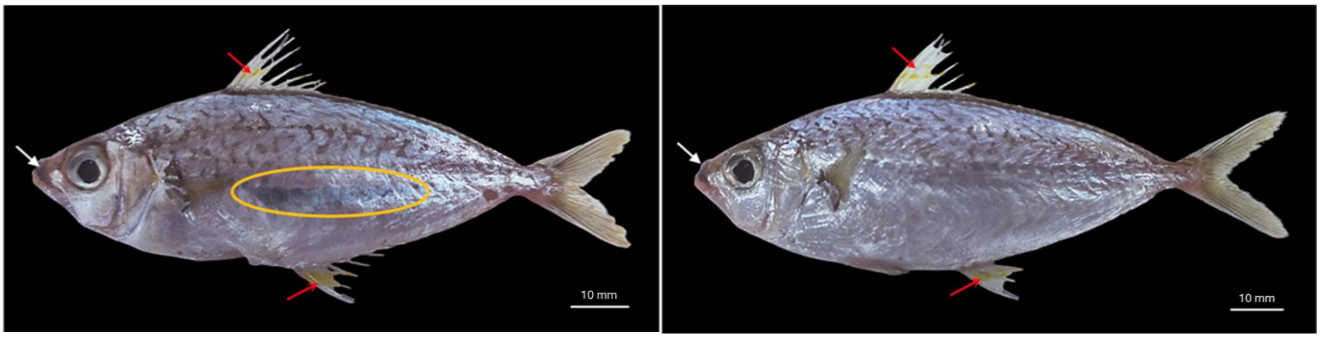


Figure 4. Morphology of oblong slipmouth *Photolateralis stercorarius* from the Makassar Strait, South Sulawesi, Indonesia. A. Male (orange ellipse outlines the bluish longitudinal stripe); B. Female. In both sexes, red arrows show yellow stripes on dorsal and anal fins; white arrows point to a black spot on the snout

Table 2. Standard Length (SL), Fork Length (FL), weight and standardized morphometric traits of the oblong slipmouth *Photolateralis stercorarius* from two Makassar Strait, Indonesia landing sites[a] and mean values of morphometric traits reported from previous studies on *P. stercorarius* and *P. polyfenestrus*

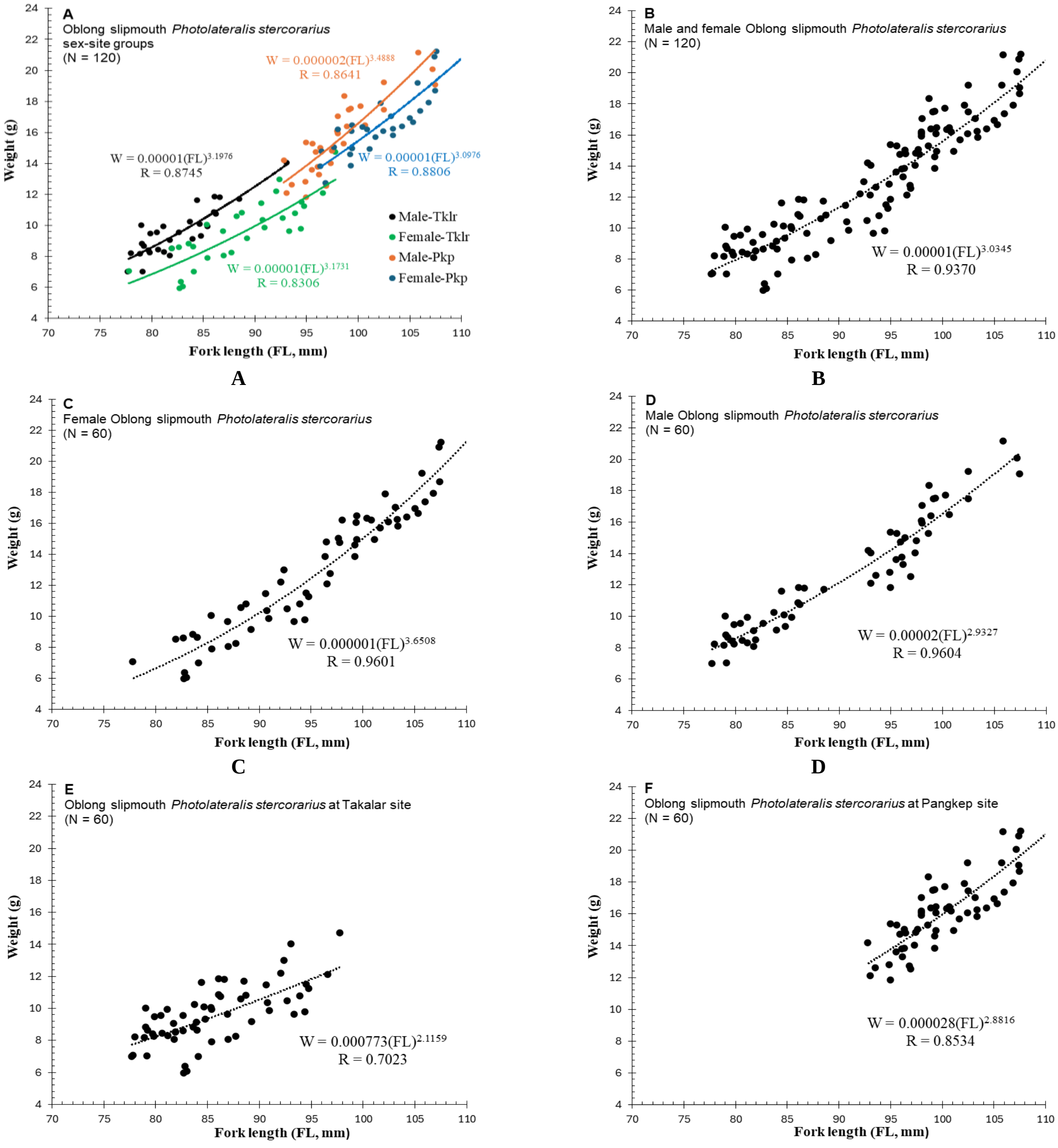
Morphometric trait (unit)	Male- Takalar n: 30	Female- Takalar n: 30	Male- Pangkep n: 30	Female-Pangkep n: 30	South China Sea [b] n: 48	*Photolateralis polyfenestrus* [c]
SL (mm)	70.3-88.4 (75.20	70.1-86.3 (78.1)	79.6-93.0 (85.9)	84.2-103.9 (91.2)	100.22	66.8
FL (mm)	77.7-93.0 (82.5)	77.8-97.8 (88.5)	92.8-107.4 (98.2)	96.3-111.0 (102.6)	no data	no data
Weight (g)	7.01-14.05 (9.57)	5.96-14.74 (9.63)	11.84-21.17 (15.71)	12.75-23.98 (16.85)	no data	no data
DBD (%SL)	29.7-37.4 (32.5)	27.8-37.9 (33.7)	25.9-36.3 (33.4)	31.6-36.8 (33.7)	33-35	35.9
ABD (%SL)	32.2-39.9 (34.7)	31.5-38.9 (35.4)	31.4-37.2 (34.8)	32.9-37.9 (34.8)	no data	no data
PDL (%SL)	39.9-44.8 (42.21	20.2-46 (42.0)	15.6-44.9 (40.2)	35.0-44.4 (41.1)	42	41.5
PAL (%SL)	37.4-54.9 (50.1)	32.2-56.5 (52.3)	50.2-58.5 (55.1)	49.9-57.5 (54.7)	no data	53.4
PVL (%SL)	30.0-36.6 (33.4)	27.1-36.9 (33.3)	31.3-37.9 (35.0)	32.5-39.6 (35.3)	no data	33.1
PPL (%SL)	25.2-31.7 (28.6)	25.6-32.3 (29.4)	26.0-31.3 (29.0)	27.1-31.2 (28.9)	no data	no data
UpCL (%SL)	5.2-6.6 (5.9)	5.1-6.3 (5.8)	3.7-5.1 (4.4)	4.2-6.2 (4.9)	6	5.4
LoCL (%SL)	5.2-6.6 (5.9)	5.1-6.3 (5.8)	3.7-5.1 (4.4)	4.2-6.2 (4.9)	no data	no data
DFB (%SL)	54.3-63.8 (57.2)	49.3-63.7 (57.3)	53.9-60.0 (56.8)	48.6-61.9 (56.5)	57	no data
AFB (%SL)	38.0-47.5 (42.2)	29.6-53.6 (40.8)	38.6-44.4 (42.19)	33.2-47.9 (42.3)	45	no data
HL (%SL)	24.6-29.2 (27.5)	25.6-29.8 (28.4)	24.0-28.7 (26.6)	25.8-28.9 (27.3)	29	27.7
NL (%HL)	44.6-62.1 (53.6)	43.9-60.5 (52.7)	57.7-69.2 (63.4)	60.5-77.5 (68.1)	no data	no data
SNL (%HL)	28.1-36.4 (31.8)	28.6-35.7 (31.8)	31.5-37.9 (34.1)	28.5-37.4 (32.7)	32	33
OBD (%HL)	24.5-32.7 (29.0)	24.6-33.1 (28.8)	27.3-33.6 (30.7)	28.1-33.2 (30.7)	33	34.6
UpML (%HL)	22.0-36.9 (30.3)	25.3-35.1 (30.2)	30.6-38.1 (34.5)	29.2-44.4 (37.4)	no data	22.7
LoML (%HL)	46.0-59.6 (52.6)	42.6-55.1 (48.5)	35.1-50.2 (40.7)	42.1-55.6 (47.4)	no data	58.4
POL (%HL)	31.9-41.6 (36.4)	32.5-45.8 (38.6)	31.4-38.7 (35.0)	29.6-42.0 (34.8)	32	30.8

Note: [a] Takalar: Takalar District; Pangkep: Pankajene and Kepulauan District; [b] Seah et al. (2009); [c] Sparks and Chakrabarty (2019)

Table 3. Meristic characters of oblong slipmouth *Photolateralis stercorarius* from two landing bases in the Makassar Strait[a], Indonesia and other studies

Meristic trait code[b]	Male-Takalar n: 30	Female-Takalar n: 30	Male-Pangkep n: 30	Female-Pangkep n: 30	Philippines[c] n: 7	South China Sea[d] n: 48
D-s	VIII	VIII	VIII	VIII	VIII	VIII
D-r	16	16	16	16	16	16
A-s	III	III	III	III	III	III
A-r	14	14	14	14	14	14
P	16-17	16-17	16-18	16-18	16-18	17
V-s	I	I	I	I	no data	I
V-r	5	5	5	5	no data	5
C	23-26	24-26	26-26	24-26	no data	no data

Note: [a] Takalar: Takalar District; Pangkep: Pankajene and Kepulauan District. [b] D-s: Dorsal fin spines; D-r: Dorsal fin rays; A-s: Anal fin spines; A-r: Anal fin rays; P: Pectoral fin rays; V-s: Ventral fin spines; V-r: Ventral fin rays; C: Caudal fin rays. [c] Evermann and Seale (1907). [d] Seah et al. (2009)



A B C D E F

Figure 5. Length-weight relationship of oblong slipmouth *Photolateralis stercorarius* from two Makassar Strait, Indonesia landing sites. A. By sex-site group; B. All groups combined; C. Female fish; D. Male fish; E. Combined-sex at Takalar; F. Combined-sex at Pangkep

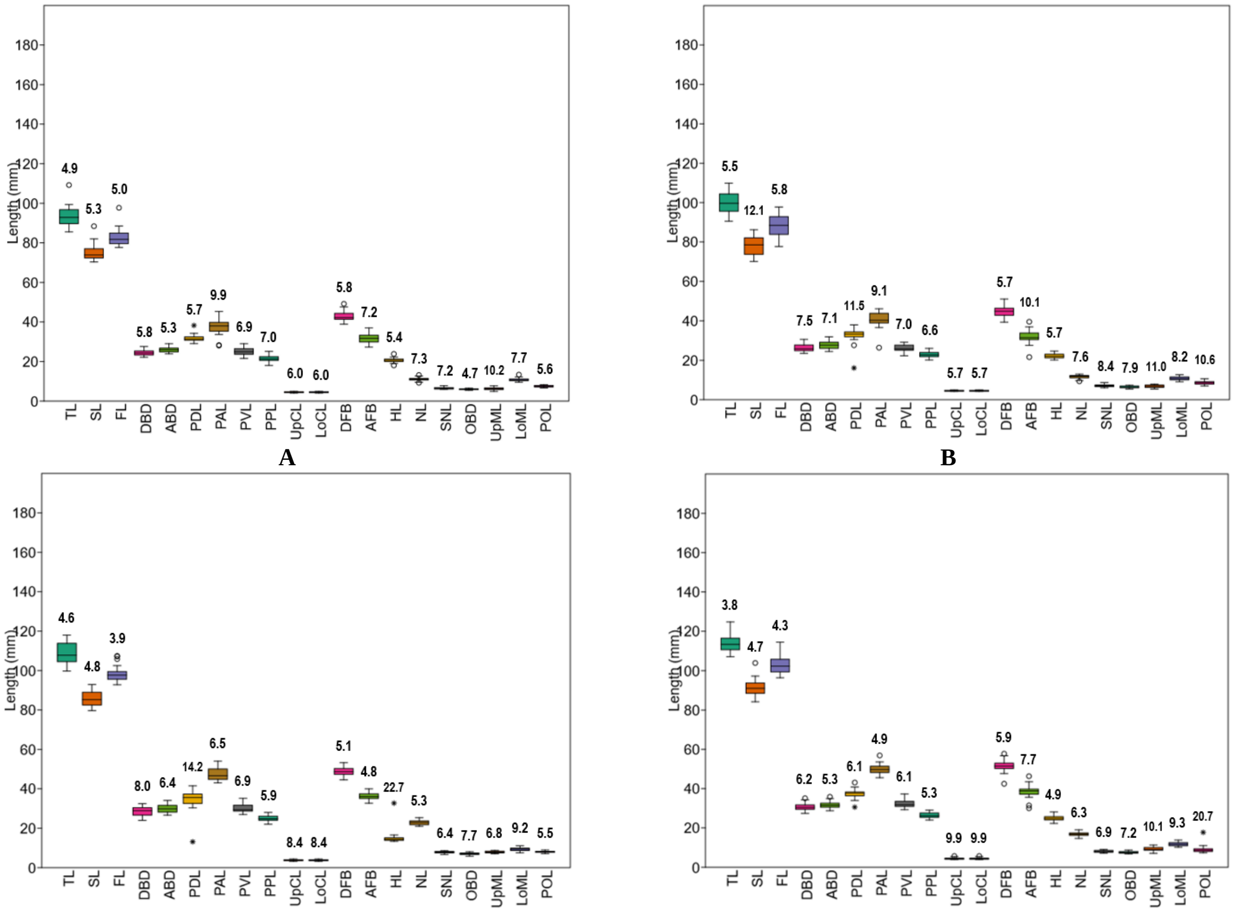
Discriminant analysis

The distribution of morphometric traits for each site/sex group of *P. stercorarius* from the Makassar Strait is shown as a box plot in Figure 6. The box plots clearly show outliers for some morphometric traits, including extreme data points, especially in the female-Pangkep group. The Coefficient of Variation values (CV) above each trait in the plot box are high and indicate that the dataset should be standardized to reduce bias in the discriminant analysis and cluster analysis (Elliott et al. 1995; Umar et al. 2024).

The Canonical Discriminant Function (CDF) plot (Figure 7) based on the standardized values of the morphological traits explains 96.27% of variation within the dataset. The majority of the variation (over 93%) is described by the first function (F1, X axis) and around 5% is explained by the second function (F2, Y axis). This plot shows strong clustering in each site-sex group. The centroids of each group are well separated along the F1 axis, with greater between-site than between-sex separation. The male and female Pangkep group centroids and distributions are strongly separated along the F2 axis, and separated by the Takalar site groups, with very little difference between males and female on F2 at this site. The 90% probability ellipses overlap between sexes at each site but not between sites, with very few outliers and few individuals within the opposite sex clusters.

Pairwise between-group analysis based on Fisher distances between the four site-sex groups revealed significant between-group phenotypic differences (Table 4). While the CDF indicated greater separation between sites than by sex, the phenotypic distance analysis indicates highly significant differences between the sexes. Both analyses indicate greater differences between male and female fish in the Pangkep population compared to the Takalar population.

Morphological traits that differed between groups and could be used as identifiers (potential discriminant traits) were first evaluated using a unidimensional test of equality of the means. All 19 characters measured differed significantly between the four site-sex groups at the 95% confidence level ($p<0.05$). However, the discriminant analysis found nine characters that could be characterized as discriminators (Table 5).



A

B

C

D

Figure 6. Box plots of the morphometric characters of oblong slipmouth *Photolateralis stercorarius* in the Makassar Strait, Indonesia. A. Male-Takalar; B. Female-Takalar; C. Male-Pangkep; D. Female-Pangkep. Coefficient of Variation (CV) values shown above the boxes; o: Outlier; ●: Extreme data point

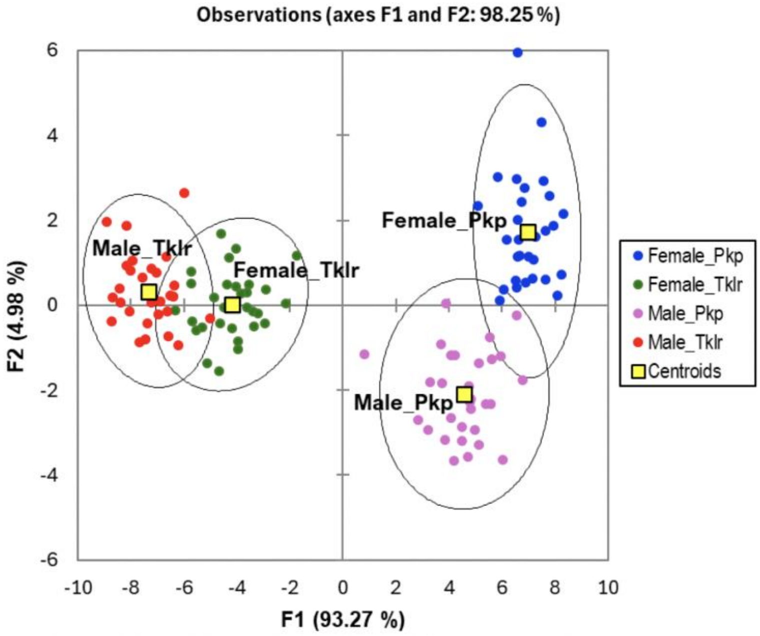


Figure 7. Canonical Discriminant Function (CDF) biplot of oblong slipmouth (*Photolateralis stercorarius*) from Makassar Strait, Indonesia grouped according to site and sex. Takalar: Takalar District; Pangkep: Pankajene and Kepulauan District; 90% probability ellipses shown for each group

Table 4. The phenotypic distance between oblong slipmouth *Photolateralis stercorarius* populations based on morphometric characters

Sex-Site		**Female-Pangkep**	**Female-Takalar**	**Male-Pangkep**	**Male-Takalar**
Female-Pangkep	Fd	0	200.09	31.51	320.62
	Sig.	1	< 0.0001	< 0.0001	< 0.0001
Female-Takalar	Fd	200.09	0	129.70	23.28
	Sig.	< 0.0001	1	< 0.0001	< 0.0001
Male-Pangkep	Fd	31.51	129.704	0	230.01
	Sig.	< 0.0001	< 0.0001	1	< 0.0001
Male-Takalar	Fd	320.62	23.28	230.01	0
	Sig.	< 0.0001	< 0.0001	< 0.0001	1

Note: Takalar: Takalar District; Pangkep: Pankajene and Kepulauan District; Fd: Fisher distance; sig.: Significance (p-value)

Table 5. Equality of means test results (p-value) for 19 morphometric traits of Makassar Strait, Indonesia oblong slipmouth *Photolateralis stercorarius* from four site-sex groups and discriminator traits identified

Morphometric trait (standardized)[a]	**Wilks' Lambda**	**F**	**df1**	**df2**	**p-value**
SL	0.305	88.269	3	116	< 0.0001
FL	0.067	536.390	3	116	< 0.0001
DBD	0.262	108.883	3	116	< 0.0001
ABD	0.2	154.452	3	116	< 0.0001
PDL	0.643	21.493	3	116	< 0.0001
PAL	0.217	139.392	3	116	< 0.0001
PVL	0.188	167.137	3	116	< 0.0001
PPL	0.249	116.603	3	116	< 0.0001
UpCL	0.505	37.901	3	116	< 0.0001
LoCL	0.505	37.901	3	116	< 0.0001
DFB	0.227	131.906	3	116	< 0.0001
AFB	0.371	65.451	3	116	< 0.0001
HL	0.206	149.045	3	116	< 0.0001
NL	0.105	330.491	3	116	< 0.0001
SNL	0.324	80.558	3	116	< 0.0001
OBD	0.27	104.447	3	116	< 0.0001
UpML	0.231	128.491	3	116	< 0.0001
LoML	0.463	44.832	3	116	< 0.0001
POL	0.657	20.231	3	116	< 0.0001

Note: [a] Bold font: Discriminant analysis discriminator trait

The Predicted Group Membership (PGM) analysis (Table 6) shows that the discriminant classification function produced by the discriminant analysis mostly assigned both female and male *P. stercorarius* collected from the two locations to the correct sex-site group. The classification function (Table 7) achieved 96.67% overall accuracy in assigning individual specimens to the correct group. This accuracy varied between groups, with 100% accuracy for female-Pangkep and male-Takalar groups. One male-Pangkep individual was mistakenly classified as female-Pangkep, and three female-Takalar individuals were incorrectly classified as male-Takalar. No individuals were assigned to the wrong site. The Bray-Curtis Dissimilarity Index between centroids of the *P. stercorarius* groups showed that the distance between centroids based on site was greater than the distance based on sex (Figure 8). However, the distance between male and female individuals at each site was still clearly visible and was greater for the Pangkep site than the Takalar site.

Discussion

Morphological traits

Understanding taxonomic classifications and evolutionary (phylogenetic) relationships is essential for understanding biodiversity at multiple levels, and the quest for a more accurate monophyletic taxonomy is important for the conservation and sustainable management of this fish family (Chakrabarty and Sparks 2015; Sparks and Chakrabarty 2015; He et al. 2022; Suzuki and Kimura 2024). In 1977, around 30 Leiognathidae species were recognized; 15 species were known to occur in Indonesia prior to 1975, of which 13 were identified during a 1975 trawl survey in eastern Indonesia, and a further three had been reported from Ambon (Pauly 2018b). Historically most Leiognathidae were assigned to the genus *Leiognathus*, as evidenced in the 1977 list of 18 Indonesian slipmouths (Sparks and Chakrabarty 2015; Pauly 2018b). Since then, taxonomic revisions in the Leiognathidae have been quite extensive, largely based on improved understanding of leiognathid evolutionary dynamics and relationships through the use of classic morphology-based and molecular methods (Sharifuzzaman et al. 2021; Omar et al. 2021; Suzuki and Kimura 2024). In particular, the genus *Leiognathus* has been shown to be non-monophyletic (Sparks and Chakrabarty 2015). For example, the taxon (listed as *Leiognathus splendens*) which comprised over 90% of leiognathid trawl catch in eastern Indonesia in the 1970’s (Pauly 2018b) was originally described as *Equula splendens* and is now recognized as *Eubleekeria splendens* (Kimura et al. 2008). Several new Indo-Pacific Leiognathidae taxa have been described in recent decades, including new species and new genera, some due to the recognition of cryptic species (e.g. Kimura et al. 2003, 2008; Chakrabarty et al. 2010; Sparks and Chakrabarty 2015). While several species can be hard to distinguish from each other (Suzuki and Kimura 2024), slipmouths can exhibit considerable intraspecies morphological differences, for example multiple phenotypes or morphs are described in genetically homogenous *Photopectoralis bindus* populations (Klangnurak and True 2022). Morphological differences between the sexes have also contributed to the complexity of species identification and caused taxonomic confusion (Chakrabarty et al. 2010). In groups such as the slipmouths where many species and even genera can share similar morphological traits, there is a non-negligeable risk of species (or even genus level) misidentification (Giat et al. 2008; Chakrabarty et al. 2009; Seah et al. 2012; Klangnurak and True 2022). Habitat may also influence traits such as color, in particular counter-shading, and variation in the intensity of bioluminescent light emission with depth (Pauly 2018a). In slipmouths, identification can be further complicated by within-species morph variations in phenotypes (Klangnurak and True 2022). Changes in both phenotype and genotype can be driven by many factors, including exploitation and environmental change (Harrisson et al. 2017; Lehnen et al. 2021; Klangnurak and True 2022; Verba et al. 2022; Pasisingi et al. 2024).

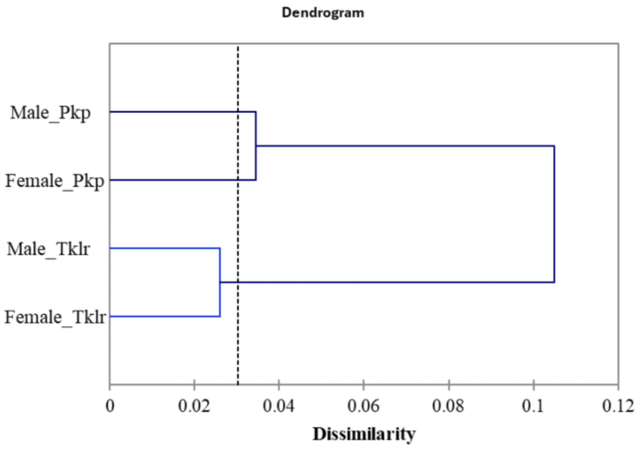


Figure 8. Bray-Curtis dissimilarity dendrogram for oblong slipmouth *Photolateralis stercorarius* from two sites in the Makassar Strait, Indonesia grouped by site and sex

Table 6. Cross-validation of Predicted Group Membership (PGM) discriminant function for sex-site groups of oblong slipmouth *Photolateralis stercorarius* from two sites[a] in the Makassar Strait, Indonesia

From\to	Female-Pangkep	Female-Takalar	Male-Pangkep	Male-Takalar	Total	% Correct
Female-Pangkep	30	0	0	0	30	100.0%
Female-Takalar	0	27	0	3	30	90.0%
Male-Pangkep	1	0	29	0	30	96.67%
Male-Takalar	0	0	0	30	30	100.0%
Total	31	27	29	33	120	96.67%

Note: [a]Takalar: Takalar District; Pangkep: Pankajene and Kepulauan District

Table 7. Discriminant function for Predicted Group Membership (PGM) of male and female oblong slipmouth *Photolateralis stercorarius* from two landing sites[a] in the Makassar Strait, Indonesia

Discriminator (normalized trait)	Trait code	Female-Pangkep	Female-Takalar	Male-Pangkep	Male-Takalar
Intercept		-2141.66	-1571.71	-1947.42	-1394.29
Standard length	SL	5.118	4.379	4.826	4.218
Fork length	FL	24.844	21.268	24.261	19.833
Upper caudal peduncle length	UpCL	22.993	28.932	18.612	30.410
Anal fin base	AFB	14.238	11.768	13.925	11.321
Head length	HL	36.015	32.162	34.621	29.758
Nuchal length	NL	4.649	-0.999	2.329	-0.854
Upper maxilla length	UpML	12.852	5.351	12.395	4.073
Lower maxilla length	LoML	-30.506	-23.447	-32.208	-20.181
post-orbital length	POL	-14.227	-8.783	-12.849	-10.261

Note: [a] Takalar: Takalar District; Pangkep: Pankajene and Kepulauan District

This study focused on the recently described slipmouth genus *Photolateralis*, classified within the tribe Equulitini and the subfamily Gazzinae (Sparks and Chakrabarty 2019). Of the four recognized species within the recently described genus *Photolateralis*, one (*P. polyfenestrus*) was described in 2019 (Sparks and Chakrabarty 2019) while the other three species were initially described under other genera: *P. antongil* was originally assigned to the genus *Photoplagios* (Sparks 2006); *P. moretoniensis* (Ogilby 1912); and *P. stercorarius* (Evermann and Seale 1907) to the genus *Leiognathus.* Members of the genus *Photolateralis* are remarkable for their distinctive elongated, laterally compressed and shallow body shape and bioluminescence (Chakrabarty and Sparks 2015). These traits, all present in the specimens collected (see Figure 4), promote strong swimming ability and influence their ecological interactions with the aquatic environment (Sparks and Chakrabarty 2019).

Arguably the most visually striking feature of the genus *Photolateralis* is the translucent stripe running along the mid-lateral flank, serving as a visual hallmark with species-specific variations that aid in their identification (Chakrabarty and Sparks 2015). These differences likely reflect evolutionary pressures faced by each species and the intricate relationships between fishes and the ecosystems in which they live. For example, in *P. stercorarius* and *P. moretoniensis*, the mid-lateral stripe is segmented into numerous small, independent translucent windows, while it is unbroken in *P. antongil* (Sparks and Chakraborty 2015). The intricacy of the windows in the lateral stripe of *P. stercorarius* creates a mosaic effect that can change with the angle of light and may play a crucial role in survival strategies. This windowed appearance may enhance their visual allure or conversely aid in camouflage and predator avoidance in their natural habitat, where light patterns are constantly shifting, and could play a role in recognition of and social interactions among conspecifics including schooling behavior (Sparks and Chakrabarty 2015). Sexual dimorphism is well-marked in the genus *Photolateralis*, with males having a well-developed lateral stripe, while females either lack this stripe or have considerably less developed stripes (Sparks and Chakrabarty 2019). As in slipmouths more generally, this striking difference likely serves as a visual cue for mate selection and may play a crucial role in reproductive success and survival strategies (Sparks et al. 2005). Understanding the nature and roles of these differences can provide valuable insights into the evolutionary pressures that shape mating behaviors and ecological adaptations within this genus (Thorson 2023).

The slipmouths (Leiognathidea) display bioluminescence due to the presence of symbiotic bacteria hosted in special organs situated at the distal end of the esophagus as well as other abdominal structures enabling the control of light intensity, direction, and dispersion (Sparks et al. 2005; Chauvin 2022). The light organ is a distinguishing feature in slipmouths and enables males to emit species-specific luminescence signals from their flanks (Sparks et al. 2005). In the genus *Photolateralis* the light organ is characterized by its moderate enlargement and unique donut shape; has conspicuous spots that enhance its visibility; extends slightly into the gas bladder (an evolutionary adaptation specific to this genus); and may play a role in buoyancy as well as communication (Sparks and Chakrabarty 2019). In contrast, males of the closely related genus *Equulites* exhibit significantly different light organ morphology with larger, heavily pigmented dorsolateral lobes that extend further into the gas bladder (Chakrabarty et al. 2010). The differences between *Photolateralis* and *Equulites* can provide valuable insights into the evolutionary pressures and ecological niches that have shaped their respective anatomical features (Suzuki and Kimura 2017, 2024). Such modifications suggest differences in functional capacity or ecological roles for this organ, highlighting the diversity of adaptations that can be found within closely related taxa.

The length-weight relationship varied between the four site-sex groups (Figure 5) but Figures 5.A and 5.B show a similar overall growth pattern for the population as a whole, albeit with considerable variation. The correlation coefficient was highest (R>0.92) for the combined site single-sex relationships, indicating that sex is a better growth pattern predictor than population (site). The value of the growth exponent (b: 2.933<3) in the male-only relationship was not significantly less than 3 and indicates that male *P. stercorarius* generally display an isometric growth pattern, possibly with a slight negative allometric tendency. In the female-only relationship, the value of the exponent (b: 3.651>3) shows a clear positive allometric trend. Combined with the significant between-sex differences in mean length, these results indicate a difference in growth pattern between male and female *P. stercorarius* with females growing larger in terms of length and having proportionally higher weight gain with length compared to males. Higher b values in females than males have been reported in several fish, including *Amblypharyngodon mola* (Gupta and Banerjee 2015), *Anabas testudineus* (Ndobe et al. 2019), and *Mystus tengara* (Mitu et al. 2019). These patterns could reflect differences in body shape (subtle sexual dimorphism, as discussed above), but could also be related to sexual maturity and gonad development (Gupta and Banerjee 2015; Mitu et al. 2019; Ndobe et al. 2019).

Intra-species variation

Morphometric characteristics and meristic counts are helpful in the identification, classification, fish species, alone or in combination with genetic studies (Andriyono et al. 2020; Hossain et al. 2022). In contrast to morphometrics which emphasizes the measurement and proportions of body parts, meristic involves calculating the number of body parts (Oetama et al. 2020). Morphometric and meristic characters can also be useful in comparing life histories, identifying morphological trends in fish populations, and evaluating individual fish welfare (Rahman et al. 2019). Intra-species variations in fish morphology, including sexual dimorphism, can be caused by genetic and other factors that affect phenotype (Seah et al. 2009; Parés-Casanova et al. 2022). Sexual dimorphism can be caused by evolutionary forces because the two sexes may have different habits and/or habitat leading to functional adaptations to their respective primary environments, as well as sexual selection based on mate preference for certain traits (Connallon 2015; Servedio and Boughman 2017; Cooney et al. 2019; Lindsay et al. 2019; Ansai et al. 2024). Ontogenetic changes in morphology (e.g. color, shape) can also occur; these can be marked or more subtle (Sibly et al. 2015; Cortesi et al. 2016; Duarte et al. 2017; Higham et al. 2018). It is possible that some of the outliers in this could be related to temporary shifts in morphology related to reproductive cycles (e.g. ripe or spent adults). The few individuals mis-assigned based on sex could be juveniles or sub-adults where sex-related traits might not be fully developed, especially as this mostly occurred in the Takalar population where the average size was smaller (Tables 2 and 6). However, ontogenetic effects are unlikely to account for the clear between-site separation observed in Figure 6 as there was a considerable overlap in size between the two populations, and therefore most likely reflects true between-population differences in morphology.

In morphometric studies, the Coefficient of Variation (CV) is a mean-standardized measure of variation calculated by taking the ratio of the standard deviation to the mean, resulting in a dimensionless number that allows for comparisons among traits with varying units or scales (Pélabon et al. 2020). The CV can serve as an important quantitative tool for analyzing trait variation within and between different groups (e.g. populations) and across different environments, and high CV values can indicate traits that are influenced by environmental factors or fish habitat type. Therefore, environmental factors that can individually or collectively influence observed variability need to be taken into account in order to draw meaningful conclusions about the ecological and evolutionary implications of trait variation in fish populations (Ahmadia et al. 2018; Pélabon et al. 2020). The CV values for 19 *P. stercorarius* morphometric traits (Figure 6) show that different traits had the highest coefficients of variation in each group. In the male-Takalar group, these traits were UpML, PAL, and LoML while in the female-Takalar group they were SL, PDL, and UpML. In the male-Pangkep group, they were HL, PDL, and LoML, while in the female-Pangkep group they were POL, UpML, and either UpCL or LoCL. The UpML ranks among the three traits with the highest CV value in three of the four groups (the exception being the male-Pangkep group). This indicates that upper jaw length is an important trait for characterizing *P. stercorarius* populations in the Makassar Strait. Evolutionary and individual changes in jaw morphology can be related to environmental factors and ecological niches (Cristescu et al. 2010; Ma et al. 2016; Riley et al. 2023) and could be an important trait to consider in ecological studies and in monitoring this species.

The lack of or minimal variation in meristic counts observed in this and other studies (Evermann and Seale 1907; Seah et al. 2009) suggests minimal influence of geographical origin or sex on these traits. Meristic traits of fish species tend to remain constant throughout their lives and are generally not dependent on body size (Rochmatika et al. 2023). Although small, the differences in two meristic counts between *P. stercorarius* populations in the four sex-site groups could be related to habitat characteristics and/or genetic differences and their effects on phenotype. It is also possible that additional sampling in more locations could reveal greater variability in some meristic traits. However, the paucity of published data on both morphometric and meristic traits in *P. stercorarius* (and its congeners) highlights the importance of collecting and publishing morpho-meristic data in aquatic studies, to elucidate patterns at regional as well as global levels.

The Canonical Discriminant Function (CDF) biplot and Predicted Group Membership (PGM) cross-validation analyses both indicate that each of the four *P. stercorarius* sex-site groups has unique characteristics. All specimens clustered with their site of origin, although a few specimens were more similar to individuals from the opposite sex in the CDF plot, while the discriminant function was nearly 97% accurate in assigning sex and 100% accurate in assigning individuals to their site of origin. Mean values of morphometric trait values of male and female *P. stercorarius* differed at statistically significant levels, while half the standardized traits measured were identified as discriminant function predictors. Heterogeneous environmental conditions such as climate regime, exposure to severe weather, substrate type, and food availability can vary greatly between locations, and can lead to changes in fish morphology due to phenotypic plasticity (Winkler et al. 2017; Donelson et al. 2019; Manna et al. 2019; Caiger et al. 2021). Some environmental parameters may differ between the two study sites, and the strong between-site dissimilarity could indicate a substantial degree of demographic separation between the populations.

Many factors can impede reproductive connectivity between populations (Selkoe et al. 2016). Studies have indicated potential barriers to genetic flow within the Makassar Strait, and even within the Spermonde Archipelago (Umar et al. 2019; Lu et al. 2023). If confirmed, a genetic and/or demographic barrier could be related to seasonal water movement patterns. Despite the overall southward water mass transport of the Indonesian Throughflow, surface and shallow-water current direction in the Makassar Strait can vary between monsoonal seasons (Wainwright et al. 2018), with northwards flows of varying strength in the northern hemisphere winter, especially in the southern reaches of the Makassar Strait (Gordon et al. 2019). Water movement can also be influenced by interaction with the complex bathymetry of the Makassar Strait (Brackenridge et al. 2020). This question might be resolved through population genetics research; however, incomplete demographic and reproductive isolation across a putative barrier might not be detected as very few exchanges (individuals mating, recruiting or migrating between populations) are needed to maintain genetic connectivity compared to demographic connectivity (Hohenlohe et al. 2021), and results could indicate past rather than current connectivity patterns (Hellberg 2007; Lehnen et al. 2021).

Insights for fisheries management and biodiversity research

In some countries, slipmouths are mostly most caught as commercially important by-catch in trawl fisheries primarily targeting other species (Giat et al. 2008; Klangnurak and True 2022) and often considered as trash fish; although eaten by local people, most are used for fish or poultry feed and manure (Pauly 2018b; Klangnurak and True 2022). However, in Indonesia slipmouths are considered commercially important fisheries species in their own right, as the fishery and trade make a substantial contribution to local economies as well as to meeting nutritional needs and food security (Pauly 2018b; Midrar 2020; Syahailatua et al. 2023; Yusfiandayani et al. 2023). It is therefore clearly important to manage the slipmouth stocks in a sustainable manner, in particular in the Makassar Strait.

Although trawls can cause overfishing, arguments have been put forward that proper fishing practices and management could reduce negative impacts (Ayling 2015; Suuronen et al. 2020; Zhang 2023). Many countries have applied strict regulations and modern technology to monitor fish populations and protect natural habitats (Zagorodniuk 2022), however these are not always implemented effectively (Leadbitter et al. 2024). Indonesia has adopted the Ecosystems Approach to Fisheries Management (EAFM) within the framework of the Fisheries Management Areas (FMAs) established under Ministerial Regulation 18/PERMEN- KP/2014 (Muawanah et al. 2018; Nadiarti et al. 2021). There are few regulations on small-scale multi-species artisanal fisheries such as most fisheries catching slipmouths in the Makassar Strait. Regulations do include a ban on trawlers (Ministerial Regulation 2/2015) issued in 2015 (MMAF 2015). Despite enforcement efforts (MFS 2019), this ban has not been very effective due *inter alia* to the (sometimes deliberate) confusion over gear nomenclature and vessel classification, and limited surveillance resources (MFS 2019; Nadiarti et al. 2021; Leadbitter et al. 2024). It is also worth noting that the Indonesian fisheries database (MMAF 2021) does not include *P. stercorarius* under any of its names and lists some other slipmouths under obsolete names; also, as mentioned above, there may be doubts regarding the identity of the taxa reported by existing sources. One reason for the lack of species-level data on slipmouth is that, when catch or other fisheries data are collected and recorded, many locally important (but generally non-export) species are often aggregated into categories such as “small pelagic”, or into the catch-all “other” category (Leadbitter et al. 2024) They may also be aggregated at higher taxonomic levels (e.g. genus, family, order), including local common names such as “*ikan peperek*”, an Indonesian term which covers all slipmouths (Suprapto 2014; Wardhani et al. 2024). Other local names in Indonesia include *bete-bete*, *pepetek*, and *petek* (Wardhani et al. 2024).

The oblong slipmouth *P. stercorarius* was recently assessed as Least Concern based on the IUCN Red List criteria (Kimura et al. 2024). The assessment was based on limited data, noting that the species has a wide distribution and can be common in some parts of its range, specifically Malaysia and the Philippines. Although the assessment states that “exploitation and mangrove degradation are not suspected to be causing a global population decline of 30% at this time”, it also notes that current population trends are unknown. The assessment does not include data or references on Indonesia populations, and notes on exploitation (fisheries) are limited to Malaysia and the Philippines. The paucity of data in the assessment highlights the need for research on this species. Responsible fisheries management aims to conserve fisheries resources and ensure they are utilized in a sustainable manner (Jhariya et al. 2022). Assuming the assessment is reasonably accurate, despite the limited data, the Least Concern status means that *P. stercorarius* stocks should be able to sustain well-managed fisheries. However, sustainable fisheries management requires fostering awareness and promoting environmentally responsible fishing practices through effective collaboration between government, fishermen, and non-governmental organizations (Giacomarra et al. 2021). Environmental change needs to be taken into account, whether it is due to the local impacts of global climate change, or to more readily identifiable factors affecting water quality and causing habitat degradation, in particular because such factors can also influence genetic diversity and dominant traits (Boulanger et al. 2022; Verba et al. 2022), as well as phenotypic traits identifiable through biometrics, and examining morphometric and meristic characters (Deyrestani et al. 2015; Seth et al. 2019). The impacts of environmental change on fish genetic diversity are often but not always negative (Mendoza-Portillo et al. 2023).

Adaptation can trigger evolution and increase genetic diversity, albeit generally over long time-scales (Chen et al. 2018; Dayi 2022). Degradation of water quality and other habitat characteristics can create new opportunities for resistant or tough species or strains to develop, which can enrich ecosystem functionality and increase overall genetic variation (Banks-Leite et al. 2020; Millette et al. 2020). Therefore, despite the challenges, environmental change can also produce positive dynamics in fish genetic diversity (Folio et al. 2021). Some fish species, including pony fish, may have a high capacity to adapt to change climate and changing environmental conditions as well as to fishing pressure (Rodriguez-Dominguez et al. 2019), potentially giving them a competitive advantage. This could be through any combination of phenotypic plasticity, exploiting existing genetic variability, and selection-driven evolution (Harrisson et al. 2017; Verba et al. 2022; Pasisingi et al. 2024). In addition to understanding morphological variation, it is therefore also important to evaluate genetic variation in exploited fish populations such as the Makassar Strait slipmouth stocks, and in particular *P. stercorarius*. Such an exploration should take an integrative approach, including oceanographic dynamics and morphology as well as genetics (To and Anumudu 2015; Ottenburghs et al. 2019; Lehnen et al. 2021; Trail 2021). Furthermore, there is a need to improve the recording of fisheries catch data in terms of taxonomic resolution.

In conclusion, morphometric characters between male and female *P. stercorarius* sampled from two sites in the Makassar Strait differ significantly from each other. Females had an allometric growth pattern and were, on average, longer than males at both sites, while male growth patterns were isometric. Meristic counts did not differ significantly between site or sex. The results demonstrate that *P. stercorarius* exhibits more subtle sexual dimorphism in body shape, in addition to the highly visible lateral stripe which is more marked and bluish in males. Between-site differences in morphometric traits and body shape were more marked than between-sex differences, indicating the two populations sampled may belong to separate stocks. The indication of between-population morph variation in Makassar Strait *Photolateralis stercorarius* calls for multidisciplinary research including an exploration of genetic diversity to help elucidate the number and extent of *P. stercorarius* stocks in this waterway and in FMA 713 as a whole.

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