

Landmark-based Morphometric and Meristic Variations in Emperors (*Lethrinus*, Lethrinidae, Percoidae) from Three Areas around Sulawesi (Indonesia) with Different Levels of Destructive Fishing

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Abstract

This study analysed the variation in morphometric and meristic characteristics among fishes in the genus *Lethrinus* from three areas around Sulawesi (Indonesia) with different levels of destructive fishing: Makassar, South Sulawesi, high; Manado, North Sulawesi, medium; and Wakatobi, Southeast Sulawesi, low. The research was conducted from June–November 2019. Morphometric characters (21) and meristic characters (8) of *L. erythropterus*, *L. semicinctus*, *L. obsoletus*, *L. ornatus*, and *L. harak* were measured (30 specimens/species/site). Morphometric characters were compared between areas using one-way analysis of variance (ANOVA) with post-hoc Tukey Test. Characteristic traits and similarities between species/areas were evaluated using Multivariate Discriminant Function Analysis (DFA) test and tree diagram (dendrogram) analysis. For the five lethriniid species studied there were statistically significant differences ($P < 0.05$) in morphometric characters between the Makassar population and the populations in Manado and Wakatobi. Interestingly, meristic count variability was greater in lethriniids from Makassar and Manado compared to those from the Wakatobi marine protected area. Differences in destructive fishing level between areas are one factor influencing lethriniid morphometric and meristic characters, which can also be influenced by other environmental conditions.

Keywords: Sulawesi, morphometric, meristic, destructive fishing, Lethrinidae

1. Introduction

Emperors (Perciformes: Lethrinidae) are a group of high-value coral reef-associated fishes found in tropical and sub-tropical waters. Emperors can be found from the back-reef area, including shallow seagrass beds, to the reef crest and slopes to depths of a few hundred meters (Carpenter and Allen, 1989). There are approximately 29 species of emperors in the Family Lethrinidae, of which 86% have been reported from Indonesian waters (Carpenter and Randall, 2003; Lo Galbo *et al*, 2002). The Lethrinidae are further divided into two subfamilies: the Lethrininae (with a single genus: *Lethrinus*) and the Monotaxinae (genera *Gnathodentex*, *Monotaxis* and *Wattsia*).

The high volume of exports and lack of regulation on the trade in fishes of the genus *Lethrinus* have given rise to concerns regarding the condition of these populations. Furthermore, in addition to heavy demand from the export market, *Lethrinus* populations are threatened by the various destructive fishing methods used to catch these valuable fish (Briggs, 2003). Destructive fishing is prevalent in the seas around Sulawesi, but severity is not

uniform between areas (Unsworth *et al.*, 2018; Briggs (2003) categorised the risk level as high in the waters off Makassar in South Sulawesi, medium in the waters off Manado in North Sulawesi, and low in the waters of the Wakatobi Archipelago in Southeast Sulawesi. The past 44 years have also seen changes in the coral cover of Sulawesi reefs (Nurdin *et al*, 2016; Nurdin *et al*, 2015; Edinger *et al*, 1998).

Fishing pressure and destructive fishing along with phenomena associated with global warming are increasing the pressure on fish communities (Andrés *et al*, 2013). Fishes of the genus *Lethrinus* are protogynous hermaphrodites (Marriott *et al*, 2010; Motlagh *et al*, 2010), changing from female to male after more than five years, at around 33 cm total length (Wassef, 1991). In addition to the high fishing mortality of small size classes, global warming phenomena are detrimental to fitness, with impacts at the population level including imbalance in the sex ratio of *Lethrinus* populations. This imbalance can lead to the emergence of cryptic species which can affect the population structure in multi-species *Lethrinus* communities, with the potential to severely affect the condition and even the survival of these fisheries resources, including changes in morphological characters.

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At an intra-species level, however, change in morphological characteristics is not always controlled principally by genetic factors, but rather by changes in the surrounding environment (Clayton, 1981). Phenotypic plasticity is strategy employed by many fishes to enable them to adapt to their environment through physiological and behavioural modifications which can lead to or entrain morphological and reproductive changes and alter survival rates in order to reduce the impacts of environmental change. Such strategies do not necessarily result in genetic changes within the population, and such morphological differences between populations cannot be used as proof of genetic differences (Meyer, 1987; Stearns, 1983).

In the context of stock management for fishes such as the genus *Lethrinus*, the analysis of differences in morphometric and meristic characters can enable the grouping of individuals or populations (Burhanuddin, 2014). Quantitative morphometric studies are an important key to determining sex and species (Brzesky and Doyle, 1988), describing the patterns of morphological traits which can differentiate between populations or species (Ballesteros-Córdova *et al*, 2016; Firawati *et al*, 2017), in taxonomic classification and the estimation of phylogenetic relationships, and in identifying new species (Burhanuddin and Iwatsuki, 2003). Landmark-based morphometric methods are increasingly used in the

identification, discrimination, and classification of fishery stocks, and can also indicate differences in growth and maturation rates because body form is a product of ontogeny (Hayward and Margraf, 1987; Roby *et al*, 1991; Cadrin, 2000). These considerations prompted this research with the aim of analysing the biodiversity and population structure of *Lethrinus* species in waters around Sulawesi using an approach based on morphometric characters. The results of this research will contribute to the scientific basis for forming policies and outlining effective strategies to manage and conserve *Lethrinus* communities.

2. Materials and Methods

This research was carried out from June to November 2019 in three sea areas around Sulawesi, Indonesia: the waters of Manado City in North Sulawesi Utara; the waters off Makassar City in South Sulawesi; and the waters of the Wakatobi District (Wakatobi Archipelago) in Southeast Sulawesi (Figure 1). Samples were collected and then analysed at the Marine Biology Laboratory, Faculty of Marine Science and Fisheries, Universitas Hasanuddin, in Makassar.

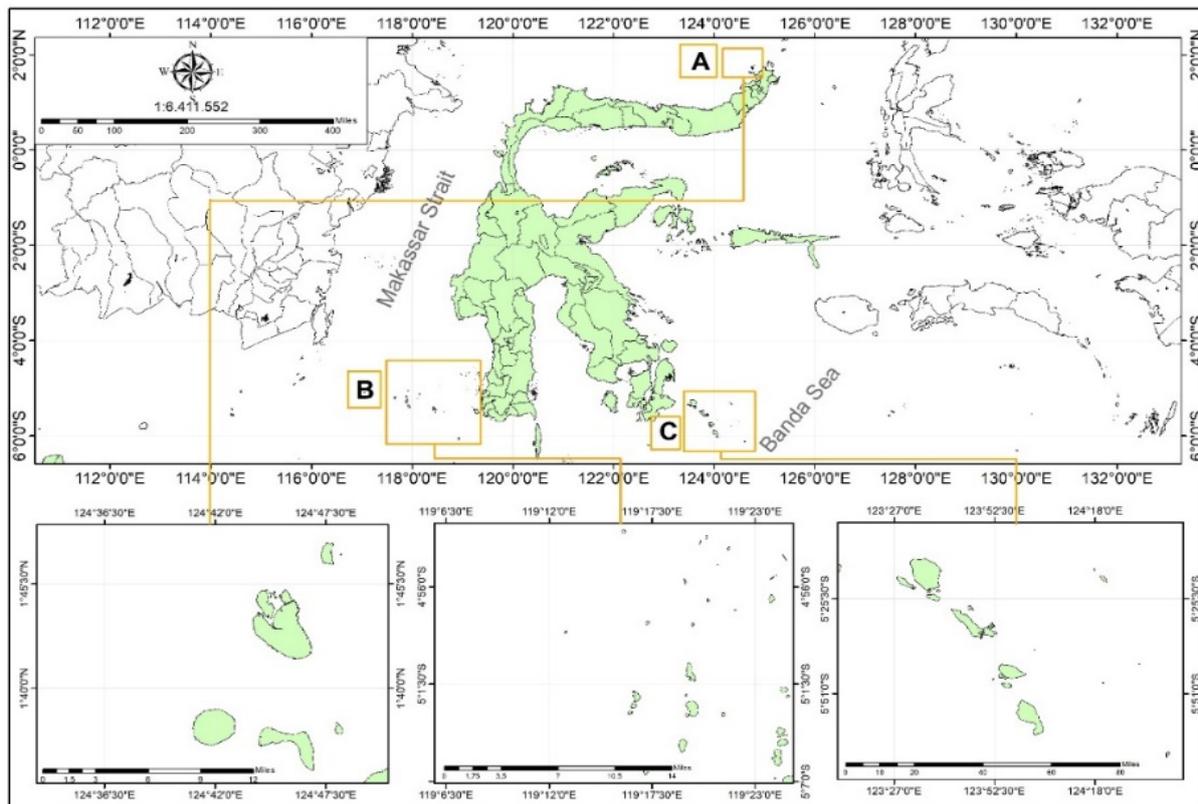


Figure 1. Sampling locations for Lethrinid fishes within Sulawesi waters: (A) Manado, North Sulawesi; (B) Makassar, South Sulawesi; (C) Wakatobi, Southeast Sulawesi.

The total number of fish sampled was 450 specimens, belonging to five species of the genus *Lethrinus*: *L. erythropterus*, *L. semicinctus*, *L. obsoletus*, *L. ornatus*, and *L. harak*. The measurement of morphometric and meristic characters mostly followed Brzesky and Doyle (1988) and

Hubbs and Lagler (1958) (Table 1, Figure 2), except for the number of gill-rakers (Burhanuddin *et al*, 2002). Measurements were made using digital callipers (WIPRO, WP-150B, precision 0.02 mm).

Table 1. *Lethrinus* morphometric characters measured, based on Brzesky and Doyle (1988).

Body Section	Code	Character Description
Head	A1	Posteriormost point of maxilla to origin of pelvic fin
	A2	Posteriormost point of maxilla to posteriormost point of eye
	A3	Posteriormost point of eye to origin of dorsal fin
	A4	Origin of pelvic fin to origin of dorsal fin
	A5	Posteriormost point of eye to origin of pelvic fin
	A6	Posteriormost point of maxilla to origin of dorsal fin
Anterior Body	B1	Origin of pelvic fin to origin of anal fin
	B3	Origin of dorsal fin to point between spinous and soft portions of dorsal fin
	B4	Origin of anal fin to point between spinous and soft portion of dorsal fin
	B5	Origin of dorsal fin to origin of anal fin
	B6	Origin of pelvic fin to point between spinous and soft portions of dorsal fin
Posterior Body	C1	Origin of anal fin to insertion of anal fin
	C3	Point between spinous and soft portions of dorsal fin to insertion of dorsal fin
	C4	Insertion of anal fin to insertion of dorsal fin
	C5	Point between spinous and soft portions of dorsal fin to insertion of anal fin
	C6	Origin of anal fin to insertion of anal fin
Tail	D1	Insertion of anal fin to anterior attachment of ventral membrane from caudal fin
	D3	Insertion of dorsal fin to anterior attachment of dorsal membrane from caudal fin
	D4	Anterior attachment of ventral membrane from caudal fin to anterior attachment of dorsal membrane from caudal fin
	D5	Insertion of dorsal fin to anterior attachment of ventral membrane from caudal fin
	D6	Insertion of anal fin to anterior attachment of dorsal membrane from caudal fin

The meristic characters counted were: (1) Dorsal fin-rays, (2) Anal fin-rays, (3) Pectoral fin-rays, (4) Pelvic fin-rays, (5) Lateral line scales, (6) Scales above lateral line, (7) Scales below lateral line, and (8) number of gill-rakers.

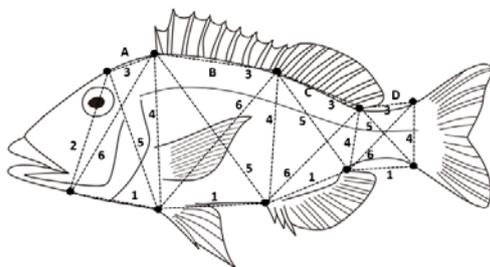


Figure 2. Morphometric truss for the genus *Lethrinus*, showing the location of the 10 anatomical points (landmarks) used and the morphometric distances measured for each individual (Brzesky and Doyle, 1988).

Before analysing the morphometric data, the data were standardised using the regression from Elliot *et al.* (1995). This model was used to remove the size component from the measurements of shape and homogenise the variation within the sample (Jolicoeur, 1963). The regression formula from Elliot *et al.* (1995) is:

$$M_s = M_o \left(\frac{L_s}{L_t} \right)^b$$

where M_s is the standardized measurement of the character, M_o is the original morphometric measurement (mm), L_s is the standard length of the fish, and L_t the mean of the standard length of all fish from all samples. The parameter b was estimated for each character from the observed data as the slope of the regression of $\log M$ on $\log L$, using all specimens.

The standardised morphometric data for the 450 specimens was compared using One-Way analysis of

variance (ANOVA) followed by post-hoc Tukey tests. Further analysis using Multivariate Discriminant Function Analysis (DFA) was used to identify characters specific (to a species or site), and resemblances between species or sites. These analyses were implemented in SPSS version 22.0. Principal Component Analysis (PCA) and tree (dendrogram) analysis were used to analyse the patterns of diversity between species at each site; these analyses were implemented in Minitab version 17.0.

3. Results

3.1. Morphometric Characters of *Lethrinus* spp.

The measurements of the morphometric characters of *Lethrinus* spp. species are given in Table 2. The results of the one-way analysis of variance followed by Tukey post-hoc tests (at 95% confidence level) are also shown in this table. The principle component analysis eigenvalues and coefficients are shown in Table 3. A scatterplot of the specimens along the first and second axes (roots) of the principle components analysis results is shown in Figure 3. The Discriminant Function Analysis (DFA) assignment of each specimen is shown in Table 4.

3.1.1. *Lethrinus erythropterus*

The majority of the 21 characters were observed significantly ($P < 0.05$) for *L. erythropterus* with the exception of the character A3 (the posteriormost point of the eye to the origin of the dorsal fin); however, there was significant grouping of *L. erythropterus* populations by site (Table 2). The Manado and Wakatobi populations resembled each other for the characters A2, A6, B1, B3, B4, C1, and C4. The Makassar *L. erythropterus* population

differed from the other two locations for morphometric characters A4, A5, B5, B6, C3, C5, C6, D1, D3, D4, D5, and D6.

Standardized coefficients of canonical variables (roots) 1 and 2 from the DFA showed 95.4% and 41.7% variation between the populations analysed, with 20 principal variables for discriminating between groups (Table 3). In canonical root 1, the variables with major effects were: A6 (Y=1.304), B1 (Y=0.659), B3 (Y=0.323), B5 (Y=0.674), C3 (Y=0.782), C5 (Y=-0.362), C6 (Y=-0.365), D4 (Y=-0.373), (Y=0.713), D6 (Y=0.713). For root 2, variables with major effects were: A2 (Y=-0.388), A3 (Y=-0.423), A4 (Y=-0.564), A5 (Y=1.328), B5 (Y=-0.347), C3 (Y=0.354), C4 (Y=-0.473), C5 (Y=0.391), D1 (Y=0.504), D3 (Y=0.495), D4 (Y=-538).

Predictive classification assigned 93.3% of the 90 *L. erythropterus* specimens to their population of origin (Table 4). The *L. erythropterus* collected from Manado contained 3 specimens assigned to the Wakatobi group and vice-versa. Meanwhile, the *L. erythropterus* from Makassar formed a distinct group (100% assignment to place of origin).

3.1.2. *Lethrinus semicintus*

The one-way ANOVA showed that certain characters contributed significantly ($p < 0.05$) to between population differences in *L. semicintus* (Table 2). The Tukey post-hoc test showed significant differences between populations, except for the character C1, the origin of the anal fin to the insertion of the anal fin ($P > 0.05$). The Manado and Wakatobi populations were similar for the characters A1, A2, A5, B4, B5, C4, C5, C6, D1, D3, D4, D5, and D6. The Makassar population was significantly different from the other two populations for characters A3, A4, A6, B1, B3, B6, while character C3 was similar for the Makassar and Wakatobi populations (Table 2).

The standardized coefficients of the canonical variable (root) 1 and 2 obtained from the DFA show 96.04% and 50.41% variation between the populations analysed, with 19 principal variables for discriminating between groups (Table 3). The morphometric characters influencing root 1 were: A4 (Y=-0.316), A6 (Y=1.078), B1 (Y=0.744), B5 (Y=0.587). The variables with the strongest influence on root 2 were: A2 the posteriormost point of the maxilla to the posteriormost point of the eye (Y=-0.840), A3 (Y=-0.448), A4 (Y=0.541), A6 (Y=0.322), B1 (Y=0.336), B5 (Y=0.683), B6 (Y=-0.895), C1 (Y=0.482), C4 (Y=-0.317), D1 (Y=0.333), D3 (Y=868), D4 (Y=0.542), D5 (Y=-0.531), D6 (Y=-0.565).

Predictive classification of individuals showed an overall 97.8% assignment of *L. semicintus* to population of origin (Table 4). The DFA assigned one individual from the Manado population of *L. semicintus* to the Wakatobi population and vice-versa, while the *L. semicintus* population from Makassar clustered apart from the other two populations with 100% assignment to site of origin.

3.1.3. *Lethrinus obsoletus*

The ANOVA showed a significant ($p < 0.05$) effect of population (site) on morphometric characters; the Tukey post-hoc test determined the level of significance for each parameter (Table 2). There was a significant difference ($P < 0.05$) between the three *L. obsoletus* populations for eight characters (A4, A5, A6, B1, B5, C6, D4, and D5).

However, the difference was not significant between the Manado and Wakatobi populations for characters A2, B3, B6, C1, C3, C5, D1, D3, D6, and between the Manado and Makassar populations for characters A1, A3, and C4.

The standardized coefficients of canonical variables (roots) 1 and 2 from the DFA for *L. obsoletus* showed 90.25% and 49% variation between the populations analysed, with 22 principal discriminant group variables. The variables with the greatest influence on Root 1 were: A1 (Y=0.587), A3 (Y=0.310), A4 (Y=0.318), A6 (Y=0.520), B1 (Y=0.544), B5 (Y=0.645), C1 (Y=0.621), C4 (Y=-0.449), D1 (Y=0.379), D3 (Y=0.672), D6 (Y=0.347). The variables with the greatest influence on Root 2 were: A2 (Y=0.587), A3 (Y=0.516), A4 (Y=0.988), A5 (Y=-1.072), B5 (Y=0.687), C3 (Y=-0.562), C4 (Y=0.625), C5 (Y=-0.509), D4 (Y=0.572), D5 (Y=-0.443).

Predictive classification assigned 94.4% of the 90 *L. obsoletus* sampled to their population of origin (Table 4). Two individuals from the Manado *L. obsoletus* population were assigned to the Wakatobi population, and vice-versa. One individual from the Makassar population was assigned to the Manado group.

3.1.4. *Lethrinus ornatus*

The one-way ANOVA showed a significant ($P < 0.05$) between-site difference for the 21 morphometric characters. The Tukey post-hoc test did not show significant variation between the Manado and Wakatobi populations of *L. ornatus* for characters A1, A2, A3, B1, C1, C3, C5, D1, D3, D5, D6, while for character D4 the difference between Makassar and Wakatobi populations was not significant. However, nine characters differed significantly between all three populations (A4, A5, A6, B3, B4, B5, B6, C4, and C6).

The standardized coefficient of DFA canonical variables (roots) 1 and 2 showed 90.25% and 32.49% variation between the three *L. ornatus* populations, with 14 principal discriminant variables. The morphometric characters influencing Root 1 were: A6 (Y=0.934), B1 (Y=-0.443), B4 (Y=-0.517), B6 (Y=0.353), C4 (Y=-0.370), C6 (Y=0.568), D1 (0.526). The characters with the greatest influence on Root 2 were: A1 (Y=0.342), B1 (Y=0.340), B6 (Y=-0.560), C1 (Y=0.408), C3 (Y=0.332), C6 (-0.370), and D3 (Y=0.409).

Predictive classification assigned 95.6% of the 90 *L. ornatus* individuals to their site of origin (Table 4). The Manado population of *L. ornatus* (93.3%) had 2 individuals assigned to the Wakatobi group and vice-versa. The Makassar population formed a distinct group with 100% assignment to site of origin.

3.1.5. *Lethrinus harak*

The one-way ANOVA of the 21 morphometric characters *L. harak* showed significant ($P < 0.05$) differences between the three populations at the 95% confidence level, indicating a significant effect of population on shape for this species. The Tukey post-hoc test (Table 2) showed that the Manado and Wakatobi population had similar values for seven characters (A1, A3, B1, B3, C4, D1, and D4), while Makassar and Wakatobi populations had similar values for three characters (C1, C3, and C5); however, character D3 differed significantly between the Makassar and Wakatobi populations. The values of ten characters (A2, A4, A5, A6,

B4, B5, B6, C6, D5, and D6) differed significantly between all three species.

The standardized coefficients of canonical components (roots) 1 and 2 from the DFA explained 90.25% and 32.49% of between population variation, with 14 principal discriminant group variables (Table 3). The morphometric characters influencing Root 1 values were: A6 (Y=0.934), B1 (Y=0.443), B4 (Y=-0.517), B6 (Y=0.353), C4 (Y=-0.370), C6 (Y=0.568), and D1 (Y=0.526). The main characters influencing Root 2 values were: A1 (Y=0.342),

B1 (Y=0.340), B3 (Y=-0.323), B6 (Y=-0.560), C1 (Y=0.408), C3 (Y=0.332), C6 (Y=-0.370), and D3 (Y=0.409).

Predictive classification assigned 91.1% of the 90 *L. harak* individuals to their site of origin (Table 4). From the Manado population, one individual was assigned to the Wakatobi population. From the Wakatobi population, four individuals were assigned to Manado and one to Makassar. Two individuals from Makassar were assigned to the Wakatobi group.

Table 2. Variation (mean and standard deviation) in the morphometric characters of *Lethrinus* spp. from Sulawesi, Indonesia

Code	<i>L. erythropterus</i>			<i>L. semicinctus</i>			<i>L. obsoletus</i>			<i>L. ornatus</i>			<i>L. harak</i>		
	Manado	Makassar	Wakatobi	Manado	Makassar	Wakatobi	Manado	Makassar	Wakatobi	Manado	Makassar	Wakatobi	Manado	Makassar	Wakatobi
A1	46.33 ± 2.69 ^a	51.69 ± 2.10 ^b	48.30 ± 4.36 ^c	47.37 ± 7.60 ^d	50.27 ± 1.69 ^e	45.89 ± 2.39 ^f	47.55 ± 1.45 ^g	48.56 ± 2.05 ^h	46.24 ± 2.35 ⁱ	41.84 ± 1.46 ^j	45.05 ± 2.26 ^k	41.55 ± 2.01 ^l	44.68 ± 3.57 ^m	48.81 ± 2.21 ⁿ	45.89 ± 2.58 ^o
A2	57.64 ± 3.47 ^a	64.60 ± 2.74 ^b	58.06 ± 3.04 ^c	49.61 ± 2.75 ^d	55.37 ± 1.21 ^e	49.03 ± 2.19 ^f	50.32 ± 3.49 ^g	52.94 ± 1.50 ^h	49.39 ± 1.44 ⁱ	50.40 ± 2.80 ^j	56.12 ± 2.17 ^k	49.21 ± 2.11 ^l	47.22 ± 3.86 ^m	53.40 ± 1.76 ⁿ	49.82 ± 2.20 ^o
A3	26.17 ± 8.76 ^a	28.44 ± 1.98 ^b	25.49 ± 1.91 ^c	22.49 ± 3.35 ^d	25.31 ± 1.44 ^e	20.93 ± 1.75 ^f	26.78 ± 6.67 ^g	25.90 ± 1.53 ^h	23.17 ± 1.32 ⁱ	23.41 ± 1.62 ^j	25.47 ± 2.12 ^k	22.40 ± 2.46 ^l	26.17 ± 4.21 ^m	30.10 ± 1.91 ⁿ	26.98 ± 2.77 ^o
A4	72.72 ± 2.03 ^a	83.75 ± 3.44 ^b	75.40 ± 3.70 ^c	57.96 ± 1.71 ^d	64.07 ± 2.40 ^e	56.55 ± 2.23 ^f	63.92 ± 1.29 ^g	65.59 ± 1.88 ^h	61.93 ± 2.27 ⁱ	65.96 ± 1.87 ^j	70.60 ± 2.92 ^k	62.89 ± 1.91 ^l	61.36 ± 5.05 ^m	69.88 ± 3.24 ⁿ	64.69 ± 3.69 ^o
A5	69.15 ± 1.93 ^a	77.97 ± 2.30 ^b	71.80 ± 3.64 ^c	56.86 ± 1.85 ^d	62.70 ± 2.11 ^e	55.78 ± 1.68 ^f	61.34 ± 1.44 ^g	62.91 ± 1.33 ^h	60.25 ± 1.85 ⁱ	63.12 ± 1.73 ^j	67.60 ± 2.16 ^k	60.92 ± 1.83 ^l	59.51 ± 5.32 ^m	67.21 ± 2.47 ⁿ	62.61 ± 3.33 ^o
A6	74.49 ± 4.93 ^a	86.77 ± 2.39 ^b	75.89 ± 3.94 ^c	65.39 ± 2.30 ^d	74.34 ± 1.58 ^e	64.21 ± 1.69 ^f	69.52 ± 2.55 ^g	73.50 ± 2.13 ^h	66.86 ± 1.72 ⁱ	67.11 ± 1.86 ^j	74.36 ± 2.45 ^k	64.61 ± 1.65 ^l	66.46 ± 5.48 ^m	75.09 ± 2.45 ⁿ	69.15 ± 3.84 ^o
B1	53.64 ± 3.45 ^a	58.90 ± 4.35 ^b	53.84 ± 2.93 ^c	48.93 ± 3.51 ^d	52.08 ± 2.77 ^e	46.92 ± 2.21 ^f	50.74 ± 2.21 ^g	54.44 ± 2.89 ^h	49.13 ± 2.17 ⁱ	46.57 ± 2.57 ^j	48.64 ± 3.11 ^k	45.57 ± 2.45 ^l	49.49 ± 3.98 ^m	56.63 ± 2.91 ⁿ	51.38 ± 2.53 ^o
B3	58.67 ± 2.37 ^a	65.86 ± 2.35 ^b	59.34 ± 3.21 ^c	52.63 ± 1.93 ^d	58.61 ± 3.63 ^e	49.72 ± 2.66 ^f	54.08 ± 1.41 ^g	56.07 ± 1.23 ^h	53.21 ± 2.25 ⁱ	52.97 ± 1.65 ^j	55.73 ± 2.00 ^k	50.87 ± 1.76 ^l	52.60 ± 3.73 ^m	57.44 ± 1.73 ⁿ	53.79 ± 3.44 ^o
B4	67.24 ± 1.79 ^a	76.56 ± 2.79 ^b	69.47 ± 5.40 ^c	50.78 ± 1.29 ^d	55.92 ± 1.25 ^e	50.32 ± 1.79 ^f	58.76 ± 1.22 ^g	59.80 ± 1.80 ^h	56.42 ± 7.37 ⁱ	60.73 ± 1.54 ^j	64.63 ± 2.74 ^k	59.24 ± 2.00 ^l	56.94 ± 4.44 ^m	64.55 ± 1.90 ⁿ	61.33 ± 3.84 ^o
B5	88.50 ± 1.92 ^a	101.06 ± 3.13 ^b	90.62 ± 3.51 ^c	73.14 ± 4.68 ^d	81.00 ± 1.50 ^e	72.43 ± 1.68 ^f	80.92 ± 1.63 ^g	83.11 ± 1.41 ^h	79.16 ± 1.91 ⁱ	81.07 ± 1.17 ^j	85.34 ± 3.98 ^k	78.94 ± 1.67 ^l	78.38 ± 5.54 ^m	86.84 ± 2.19 ⁿ	82.22 ± 4.24 ^o
B6	89.76 ± 1.98 ^a	101.10 ± 4.07 ^b	91.97 ± 3.44 ^c	74.08 ± 1.86 ^d	80.87 ± 2.40 ^e	70.93 ± 2.18 ^f	79.77 ± 1.78 ^g	82.97 ± 2.13 ^h	78.66 ± 3.30 ⁱ	80.11 ± 3.01 ^j	84.33 ± 2.89 ^k	76.18 ± 1.69 ^l	77.61 ± 5.98 ^m	88.52 ± 2.80 ⁿ	81.22 ± 4.54 ^o
C1	34.80 ± 3.09 ^a	39.05 ± 3.06 ^b	36.23 ± 1.74 ^c	31.41 ± 9.57 ^d	33.38 ± 1.01 ^e	30.15 ± 1.01 ^f	32.64 ± 0.77 ^g	33.85 ± 0.86 ^h	32.35 ± 0.89 ⁱ	32.48 ± 1.23 ^j	34.93 ± 1.21 ^k	32.86 ± 5.24 ^l	32.96 ± 2.98 ^m	36.54 ± 1.37 ⁿ	35.85 ± 2.07 ^o
C3	31.95 ± 0.96 ^a	36.61 ± 2.46 ^b	34.83 ± 3.25 ^c	29.85 ± 2.38 ^d	32.47 ± 1.49 ^e	32.41 ± 3.27 ^f	31.98 ± 0.85 ^g	33.08 ± 0.79 ^h	32.46 ± 1.31 ⁱ	32.99 ± 1.01 ^j	34.58 ± 2.15 ^k	33.08 ± 1.94 ^l	32.58 ± 2.80 ^m	37.01 ± 0.92 ⁿ	37.45 ± 3.33 ^o
C4	32.97 ± 1.47 ^a	37.24 ± 1.54 ^b	33.36 ± 1.59 ^c	28.14 ± 4.01 ^d	30.21 ± 3.32 ^e	26.35 ± 0.92 ^f	30.64 ± 0.86 ^g	30.96 ± 1.01 ^h	29.91 ± 1.09 ⁱ	29.33 ± 0.91 ^j	30.77 ± 1.20 ^k	28.51 ± 1.04 ^l	29.83 ± 2.86 ^m	32.79 ± 1.97 ⁿ	31.04 ± 1.95 ^o
C5	57.73 ± 1.63 ^a	65.36 ± 2.48 ^b	60.48 ± 3.21 ^c	48.20 ± 1.01 ^d	52.69 ± 1.12 ^e	49.16 ± 2.42 ^f	54.34 ± 1.02 ^g	55.36 ± 1.32 ^h	54.10 ± 1.57 ⁱ	54.92 ± 1.36 ^j	57.74 ± 2.30 ^k	53.99 ± 2.09 ^l	53.26 ± 4.12 ^m	60.63 ± 1.30 ⁿ	58.97 ± 3.83 ^o
C6	58.03 ± 1.29 ^a	65.56 ± 2.56 ^b	61.14 ± 8.25 ^c	47.14 ± 0.90 ^d	52.35 ± 1.38 ^e	46.58 ± 1.41 ^f	52.63 ± 1.14 ^g	54.37 ± 1.72 ^h	51.76 ± 1.18 ⁱ	52.46 ± 1.11 ^j	55.70 ± 1.70 ^k	50.72 ± 1.46 ^l	51.60 ± 4.70 ^m	57.90 ± 1.15 ⁿ	55.17 ± 4.01 ^o
D1	26.42 ± 2.26 ^a	32.70 ± 2.61 ^b	29.00 ± 1.89 ^c	28.70 ± 1.77 ^d	31.87 ± 1.99 ^e	28.64 ± 2.44 ^f	28.39 ± 1.59 ^g	31.32 ± 1.69 ^h	28.41 ± 1.49 ⁱ	26.40 ± 1.59 ^j	28.78 ± 1.74 ^k	25.95 ± 1.16 ^l	29.91 ± 3.28 ^m	33.12 ± 2.28 ⁿ	30.86 ± 2.36 ^o
D3	26.36 ± 2.04 ^a	30.04 ± 1.81 ^b	28.75 ± 2.37 ^c	27.07 ± 1.89 ^d	29.31 ± 1.70 ^e	28.10 ± 2.19 ^f	27.30 ± 1.74 ^g	30.48 ± 1.48 ^h	27.99 ± 1.42 ⁱ	25.99 ± 2.12 ^j	28.55 ± 2.42 ^k	26.58 ± 1.73 ^l	29.07 ± 2.84 ^m	31.13 ± 2.07 ⁿ	30.13 ± 2.17 ^o
D4	25.19 ± 1.35 ^a	29.03 ± 1.33 ^b	26.17 ± 1.21 ^c	19.61 ± 0.83 ^d	22.69 ± 1.20 ^e	19.95 ± 0.99 ^f	23.45 ± 0.82 ^g	24.61 ± 0.71 ^h	22.75 ± 0.77 ⁱ	22.64 ± 5.68 ^j	23.38 ± 1.01 ^k	21.08 ± 0.87 ^l	22.46 ± 2.21 ^m	25.51 ± 1.21 ⁿ	23.27 ± 2.12 ^o
D5	38.26 ± 1.55 ^a	44.33 ± 1.92 ^b	40.24 ± 2.50 ^c	35.43 ± 1.87 ^d	38.99 ± 1.04 ^e	34.50 ± 1.75 ^f	37.73 ± 1.01 ^g	40.74 ± 1.42 ^h	37.82 ± 1.45 ⁱ	35.55 ± 1.67 ^j	38.84 ± 1.45 ^k	35.30 ± 1.83 ^l	37.67 ± 3.49 ^m	42.27 ± 2.01 ⁿ	39.66 ± 2.83 ^o
D6	39.91 ± 1.57 ^a	46.57 ± 2.25 ^b	41.73 ± 1.49 ^c	37.15 ± 1.45 ^d	40.64 ± 1.41 ^e	36.54 ± 1.43 ^f	39.11 ± 1.76 ^g	42.12 ± 1.58 ^h	38.28 ± 1.30 ⁱ	35.97 ± 2.13 ^j	39.09 ± 1.88 ^k	35.42 ± 1.01 ^l	39.71 ± 3.42 ^m	43.67 ± 2.12 ⁿ	40.23 ± 1.99 ^o

*One-way ANOVA with Tukey post-hoc test; different superscript letters indicate significant difference at $\alpha=0.05$

Table 2. Eigenvalue, cumulative variance (%), canonical correlation, and standardized coefficients of the canonical variables produced by the principle components analysis of morphometric characters for *Lethrinus* species from Sulawesi, Indonesia

Species	<i>L. erythropterus</i>		<i>L. semicinctus</i>		<i>L. obsoletus</i>		<i>L. ornatus</i>		<i>L. harak</i>	
	Function		Function		Function		Function		Function	
	1	2	1	2	1	2	1	2	1	2
Eigenvalue	21.127	0.71	24.46	1.02	10.47	0.98	11.20	0.49	11.2	0.49
Cumulative% of variance	96.7	3.3	96	4	91.4	8.6	95.8	4.2	95.8	4.2
Canonical correlation	0.977	0.646	0.98	0.71	0.95	0.70	0.95	0.57	0.95	0.57
A1	.001	-.130	.249	-.083	.587	.070	.185	.342	.185	.342
A2	.264	-.388	-.241	-.840	.140	.587	.263	.198	.263	.198
A3	.678	-.423	-.071	-.448	.310	.516	.130	-.272	.130	-.272
A4	-.183	-.564	-.316	.541	.318	.988	-.273	-.106	-.273	-.106
A5	.199	1.32	-.251	-.012	-.248	-.1072	.062	.007	.062	.007
A6	1.304	-.024	1.078	.322	.520	.014	.934	.006	.934	.006
B1	.659	.149	.744	.336	.544	-.053	.443	.340	.443	.340
B3	.323	-.280	.128	-.010	-.244	-.270	.212	-.323	.212	-.323
B4	-.268	.092	-.024	-.085	-.203	-.111	-.517	.291	-.517	.291
B5	.674	-.347	.587	.683	.645	.687	.004	.100	.004	.100
B6	-.188	.090	.069	-.895	.058	-.294	.353	-.560	.353	-.560
C1	.189	.087	.717	.482	.621	-.267	-.049	.408	-.049	.408
C3	.782	.354	.165	.154	.250	-.562	.002	.332	.002	.332
C4	-.227	-.473	-.021	-.317	-.449	.625	-.370	-.041	-.370	-.041
C5	-.362	.391	-.060	.254	-.453	-.509	-.154	-.227	-.154	-.227
C6	-.365	.021	.508	.206	-.151	-.094	.568	-.370	.568	-.370
D1	.177	.504	.153	.333	.379	-.043	.526	.241	.526	.241
D3	-.216	.495	.157	.868	.672	-.021	.129	.409	.129	.409
D4	-.373	-.538	.156	.542	-.167	.572	.043	-.259	.043	-.259
D5	.270	.078	.289	-.531	-.002	-.443	.067	.197	.067	.197
D6	.713	-.109	-.002	-.565	.347	-.282	-.149	.246	-.149	.246

Table 4. Predictive classification of individuals for five *Lethrinus* species from Sulawesi

Species	Collection site	Number of specimens assigned			Assignment (%)		
		Manado	Makassar	Wakatobi	Manado	Makassar	Wakatobi
<i>L. erythropterus</i>	Manado	27	0	3	90.0	0.0	10.0
	Makassar	0	30	0	0.0	100.0	0.0
	Wakatobi	3	0	27	10.0	0.0	90.0
<i>L. semicinctus</i>	Manado	29	0	1	96.7	0.0	3.3
	Makassar	0	30	0	0.0	100.0	0.0
	Wakatobi	1	0	29	3.3	0.0	96.7
<i>L. obsoletus</i>	Manado	28	0	2	93.3	0.0	6.7
	Makassar	1	29	0	3.3	96.7	0.0
	Wakatobi	2	0	28	6.7	0.0	93.3
<i>L. ornatus</i>	Manado	28	0	2	93.3	0.0	6.7
	Makassar	0	30	0	0.0	100.0	0.0
	Wakatobi	2	0	28	6.7	0.0	93.3
<i>L. harak</i>	Manado	29	0	1	96.7	0.0	3.3
	Makassar	0	28	2	0.0	93.3	6.7
	Wakatobi	4	2	25	13.3	6.7	83.3

3.1.6. Graphical analyses of morphometric characters

The distribution of the specimens along PCA components (roots) 1 and 2 based on morphometric characters indicates a close relationship between the five *Lethrinus* species (Fig. 3), with considerable overlap between species. In general, *L. erythropterus* specimens

mostly grouped in the upper right-hand quadrant, while *L. semicinctus* predominantly grouped in the lower left-hand quadrant, *L. obsoletus* straddled the lower right and left quadrants, *L. ornatus* mostly grouped in the upper left-hand quadrant, and *L. harak* straddled the upper and lower right-hand quadrants.

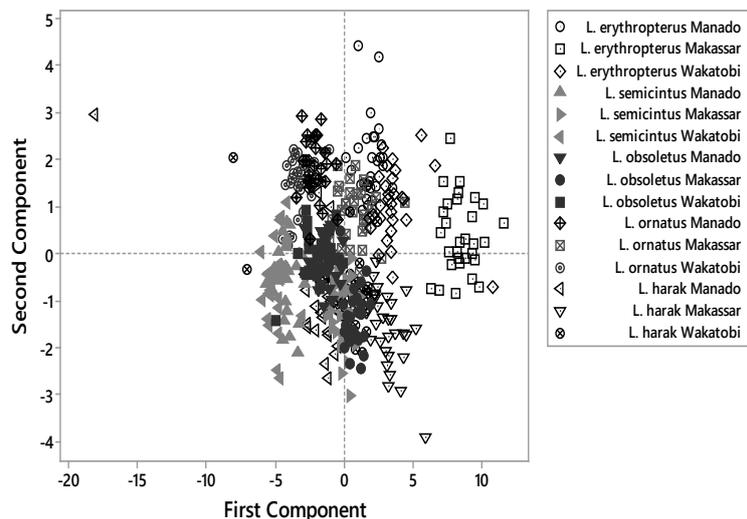


Figure 3. Scatterplot of the 420 specimens from three study locations and five species of the genus *Lethrinus* on the first component (Root 1) and second component (Root 2) of the principal component analysis based on 21 morphometric variables.

The tree analysis of the 21 morphometric variables (Fig. 4) shows distinct groupings based on the combination of species and study location. At the 66.67% level of similarity, four groups were formed: (1) *L. erythropterus* Manado, *L. erythropterus* Wakatobi, *L. harak* Makassar, *L. ornatus* Makassar; (2) *L. erythropterus* Makassar; (3) *L. semicinctus* Manado, *L. semicinctus* Wakatobi; (4) *L. semicinctus* Makassar, *L. obsoletus* Makassar, *L. obsoletus* Manado, *L. obsoletus* Wakatobi, *L. harak* Manado, *L. harak* Wakatobi, *L. ornatus* Manado, *L. ornatus* Wakatobi. Despite this somewhat unexpected structure, for each of the five species the Manado and Wakatobi populations were relatively closely grouped with each other, but were not closely grouped with conspecifics from Makassar.

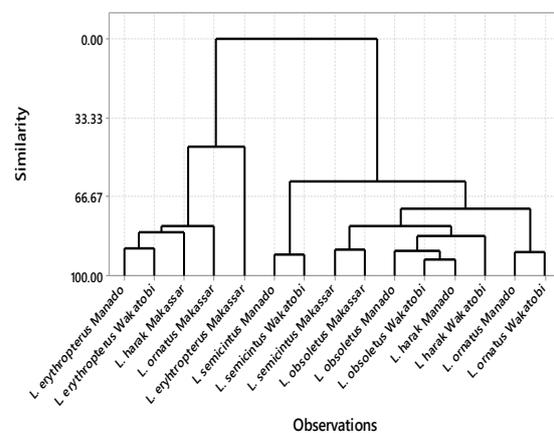


Figure 4. Dendrogram based on the similarity (Euclidean distance) of the 21 morphometric variables measured for five *Lethrinus* species from three study locations.

The canonical discriminant function analysis of group centroids showed a similar grouping pattern for the five species (Fig. 5). The Manado and Wakatobi specimens tended to be grouped to the left of the vertical axis, above or below the horizontal axis. Conversely, the Makassar populations were grouped to the right of the vertical axis.

The centroid positions indicate that the first component predominantly discriminates between the Makassar population and the other two populations, while the second component predominantly discriminates between the Wakatobi and Manado populations.

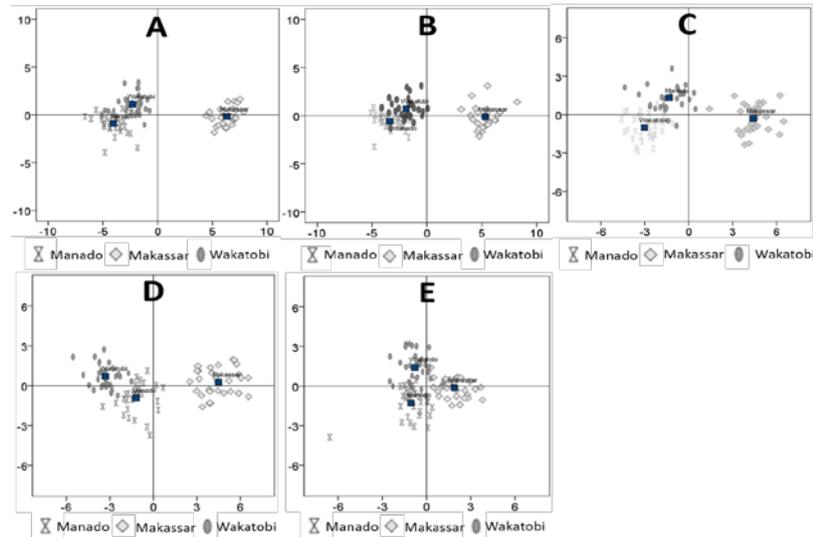


Figure 5. Distribution of the three *Lethrinus* populations studied based on discriminant analysis of morphometric characters for five species: (A) *L. erythropterus*; (B) *L. semicintus*; (C) *L. obsoletus*; (D) *L. ornatus*; (E) *L. harak*.

3.2. Meristic Character

The counts for the 8 meristic characters (Table 5) show that for four characters the five *Lethrinus* species had the same count range in all three study locations. These characters were: anal fin-rays, pectoral fin-rays, pelvic fin-rays, and number of gill-rakers. The dorsal spine count differed for *L. obsoletus* from Wakatobi with two values (IX, X), while for the remaining species and locations the dorsal spine count was always ten (X). The remaining three meristic counts (scales above lateral line, scales above lateral line, and scales below lateral line) varied between species and/or site.

Lateral line scale count varied more for *L. erythropterus* from Makassar (42-48) compared to the

Manado and Wakatobi populations. Conversely, the scales above lateral line count varied more in the Manado population (4-6) compared to the other two populations. The number of scales below the lateral line was also more varied in Makassar (14-17) compared to the Manado and Wakatobi populations which both had the same range (14-16).

For *L. semicintus*, the Manado population had the widest range of lateral line scale count (46-50). The number of scales above the lateral line was most varied in the Wakatobi population (5-7), followed by Manado and Makassar. The scales below the lateral line count varied more in Manado (13-17) followed by Wakatobi, with once again the lowest variation in Makassar.

Table 5. Meristic characters of *Lethrinus* species from Sulawesi

Species	Locality	Dorsal fin-rays	Anal fin-rays	Pectoral fin-rays	Pelvic fin-rays	Lateral line scales	Scales above lateral line	Scales below lateral line	Number of gill-rakers
<i>L. erythropterus</i>	Manado	X, 10	III, 9	12	I, 5	44-47	4, 6	14-16	4
	Makassar	X, 10	III, 9	12	I, 5	42-48	4, 5	14-17	4
	Wakatobi	X, 10	III, 9	12	I, 5	44-47	5, 6	14-16	4
<i>L. semicintus</i>	Manado	X, 10	III, 9	12	I, 5	46-50	5, 6	13-17	4
	Makassar	X, 10	III, 9	12	I, 5	46-49	4, 5	13-14	4
	Wakatobi	X, 10	III, 9	12	I, 5	46-49	5, 7	13-16	4
	Manado	X, 10	III, 9	12	I, 5	45-48	5, 7	14-16	4
<i>L. obsoletus</i>	Makassar	X, 10	III, 9	12	I, 5	46-48	5	14-15	4
	Wakatobi	IX, X, 10	III, 9	12	I, 5	46-48	5, 6	14-16	4
<i>L. ornatus</i>	Manado	X, 10	III, 9	12	I, 5	45-48	5, 6	13-15	4
	Makassar	X, 10	III, 9	12	I, 5	45-47	5	14-15	4
	Wakatobi	X, 10	III, 9	12	I, 5	46-48	4, 6	13-16	4
	Manado	X, 10	III, 9	12	I, 5	43-49	5, 6	13-16	4
<i>L. harak</i>	Makassar	X, 10	III, 9	12	I, 5	43-48	5, 6	14-15	4
	Wakatobi	X, 10	III, 9	12	I, 5	45-48	5, 6	14-16	4

The meristic counts for *L. obsoletus* were most varied in Manado, and least varied in Makassar. In Manado, the lateral line scale count range was 45-48, while scales above lateral line count range was 5-7. For the latter character, the Makassar population was homogenous, with all specimens having 5 scales above the lateral line. The range of scales below lateral line count was the same for Manado and Wakatobi (14-16), wider than for Makassar (14-15).

For *L. ornatus*, the range of lateral line scales was greatest in Manado (45-48), and lowest in Wakatobi. Conversely, the Wakatobi population had the highest variation in scales above lateral line (4-6), and scales below lateral line (13-16), with the Makassar population having the lowest variation in both these counts.

For *L. harak*, scales above lateral line had the same range (5-6) at all three sites. Lateral line scale count and scales below lateral line count varied most in the Manado population (43-49 and 13-16), followed by Makassar for the former count and Wakatobi for the latter.

4. Discussion

The one-way analysis of variance (ANOVA) followed by Tukey post-hoc test and discriminant function analysis (DFA) showed that for most characters measured the difference between the Manado and Wakatobi populations was not significant ($P > 0.05$), while the Makassar population differed significantly for most characters ($P < 0.05$). The principal components analysis (PCA) and tree (dendrogram) analysis gave a similar result, showing close groupings of the Manado and Wakatobi populations, with the Makassar population distinctly separate.

The similarity in characters between Manado and Wakatobi, and difference with Makassar could be related to the differences in fishing pressure at each location. While there is a risk of destructive fishing in all waters around Sulawesi, the frequency is highest in Makassar, South Sulawesi Selatan, followed by Manado, North Sulawesi, and lowest in the Wakatobi, Southeast Sulawesi Tenggara (Briggs, 2003).

However, change in the dorsal fin-ray count of the species *L. obsoletus* was detected in the Wakatobi, the study location with the lowest level of destructive fishing. Differences in morphometric and meristic characters can occur in populations of fish which are of the same species but live in different locations (Firawati *et al.*, 2017). Morphological changes in *Lethrinus* have been reported by Afrisal *et al.* (2018) who found changes in the morphological characters of *L. erythropterus* in the Spermonde Archipelago, Makassar City, in particular spinal malformations.

Morphometric variation can be associated with or related to genetic variation (Hebert *et al.*, 2003). Genetic analysis and research on parallel genetic structuring in the southwest Indian Ocean using the cytochrome c oxidase subunit I (COI) mtDNA gene and microsatellites (Healey *et al.*, 2018a) found cryptic species within the genus *Lethrinus*, with different populations of some species (including *L. harak*, *L. mahsena* and *L. nebulosus*) appearing to be in fact different species. The species *L. harak* in this study is strongly divided based on morphometric traits, as shown in the tree analysis dendrogram (Figure 4). Similarly, genetic research

revealed that *L. nebulosus* harvested in the Southwest Indian Ocean comprised in fact two cryptic species (Healey *et al.*, 2018b). The emergence of cryptic species is thought to occur due to various reasons, including topography (Krakau 2008), anthropogenic activity and food availability (Irmawati *et al.*, 2018).

The growth parameters have been calculated for *Lethrinus* species from different fishing grounds, including Southern Iran (Motlagh *et al.*, 2010), the Gulf of Aden (Mehanna *et al.*, 2014), the Persian Gulf (Raeisi *et al.*, 2011), the Egyptian Red Sea (Zaahkhouk *et al.*, 2017), and within Indonesia in the Thousand Islands (Sevtian, 2012), Spermonde Archipelago (Budimawan *et al.*, 2002), and Outer Kendari Bay (Nurdiansyah *et al.*, 2017). For most of these populations, the growth pattern was allometric negative, with the exception of the Egyptian Red Sea, and Outer Kendari Bay populations which had isometric growth patterns. The availability of food is a crucial factor in determining growth patterns, and can lead to morphological changes in fish (Clabaut *et al.*, 2007).

The results of this study indicate that destructive fishing may be a key driver of change in the morphometric characters of lethrinids in the waters around Sulawesi, and therefore that morphometric characters could serve as indicators of pressure from destructive fishing. Although destructive fishing activities may not affect individual lethrinids directly, there are several ways in which they could affect morphological characters. For example, the explosives used to catch fish can destroy around 0.5 – 2 m² per 1 kg of “fish bomb” (McManus *et al.*, 1997; Pet-Soede & Erdman, 1998). Destructive fishing can also cause mass mortality of fish and other marine organisms, which can lead to a reduction in biodiversity, local extinctions, and a reduction in predators, entraining changes in trophic structure as well as habitat modification (Bacalso and Wolff, 2014; Cinner, 2009). Degradation of coral reefs can promote increased algal growth, increasing food availability for herbivores while reducing the abundance of potential prey for carnivorous fishes (Piazzi *et al.*, 2012). Such changes will affect the food and feeding habitats of the carnivorous lethrinids (Cinner, 2009). These factors can induce modifications in the physiology, reproductive patterns and feeding habit of fishes, which in turn can induce changes in fish body shape, such as bodily proportions and spine/ray counts (Alonzo *et al.*, 2008; Unsworth *et al.*, 2007), as observed in the five lethrinids in this study.

5. Conclusion

For all five species of the genus *Lethrinus* included in this study, the Manado and Wakatobi populations were similar, with little between-population variation in morphometric characters, while the Makassar populations differed substantially from the other two populations. The meristic scale counts (scales along lateral line, scales above lateral line, and scales below lateral line) varied most in the Manado populations and least in Wakatobi populations. Differences in destructive fishing levels could be associated with differences in morphometric characters. The *Lethrinus* populations within the Wakatobi National Park, exposed to the lowest level of destructive fishing, had less variation in meristic characters compared to the other two populations and some individuals of *L. obsoletus*

had one less spine in the dorsal fin compared to other *Lethrinus* populations and species.

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