



Research article

Morphological investigation and length-weight relationships of long-snouted pipefish *Doryichthys boaja* (Syngnathidae) from two different environments

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Abstract

Importance of the work: Stock identification is fundamental knowledge for fisheries biology and management of any fishing-targeted species.

Objectives: To discriminate stocks of long-snouted pipefish *Doryichthys boaja* from lentic and lotic environments by using morphological characters.

Materials and Methods: Fish were collected from Songkhla Lake and Bangpakong River, Thailand. Sampled individuals were evaluated for weight, seven meristic characters, and 16 morphometric characters. Multivariate methods *viz.*, permutational multivariate ANOVA, principal component analysis and linear discriminant function analysis were applied for stock discrimination. The length-weight relationship and condition factor were also examined.

Results: The sample of *D. boaja* comprised 297 individuals from Songkhla Lake and 110 from Bangpakong River. Permutational multivariate ANOVA revealed significant differences by sex and environment ($p < 0.05$). Except for tail length, morphometric and meristic characters all showed high loadings to the principal component axes. The linear discriminant function analysis predicted high accuracy in separating the two stocks. However, low success in prediction was found when using the meristic characters to distinguish the samples in combination of sex and environment. Results from the length-weight relationship indicate positive allometric growth of the stock from Songkhla Lake, and negative allometric growth for Bangpakong River; hence, the former appears healthier and with better growth.

Main finding: The morphometric characters provide a more accurate stock determination of *D. boaja* than the meristic characters. Difference in the length-weight relationship implies the effects by geographical and environmental conditions

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Introduction

A stock is a sub-population of a fish species that commonly occupies its own geographic range and in which the number is large enough to be essentially self-reproducing. Individuals within the stock present similar growth, mortality and reproductive rates (Begg and Waldman, 1999; Cadrin, 2000). Besides evolutionary and systematic studies, correct understanding of the boundaries of fish stocks is important for fisheries managers to determine how each stock may respond to harvest, in order to balance sustainability and maximum productivity (Pope et al., 2010). Fish stocks are identified on the basis of quantitative differences in characters, commonly caused by the environment and genetic factors (Begg and Waldman, 1999). Identifying fish stocks of a targeted species can be carried out by various approaches such as genetic and molecular analysis, otolith shape and microchemistry, stable isotopes, protein electrophoresis and study of life history traits, including parasite tags (International Council for the Exploration of the Sea, 2016).

Apart from the methods already mentioned, morphological investigation is commonly used for stock identification. This technique, which applies traditional morphometric distances, has been used in some fish species including European anchovy and Japanese threadfin bream (Cuttrita et al., 2015; Sreekanth et al., 2015). Morphological investigation provides meristic and continuous measurable morphometric variables that could be used to examine intraspecific as well as interspecific variability (Takács et al., 2016; Gammanpila et al., 2017; Shuai et al., 2018). Furthermore, compared to other methods, this classic body morphological technique is inexpensive and requires no sophisticated equipment but has substantial separative power (Cadrin, 2000; Parson et al., 2003; Takács et al., 2016).

The length-weight relationship (LWR) is fundamental to understanding each stock of a targeted fish species. The relationship differs among fish species, mostly due to body shape and physiological factors, which are governed by genetics, habitat and environmental conditions (International Council for the Exploration of the Sea, 2016). The LWR can be expressed using a power function but is also commonly presented using a log-log transformation function (Froese, 2006). The LWR is normally applied for two purposes: 1) in fish stock assessments for estimating fish weight using a given length (and vice versa); and 2) for examining fish well-being. The well-being value or condition factor of a fish is generally a ratio between the actual weight of the individual and the estimated weight from its length using the LWR. This factor is equal to one for a typical fish; a value greater than one implies a healthier fish and a value less than one indicates a fish in poorer condition (Froese, 2006; Jisr et al., 2018). Both the LWR and condition factor provide information about the growth and fitness of population of a fish stock in a particular habitat.

The long-snouted pipefish *Doryichthys boaja* (Bleeker, 1850; Fig. 1) is a doryrhamphine (trunk-pouch) pipefish and a freshwater member of the Family Syngnathidae, in which most species inhabit marine environments (Froese and Pauly, 2021). Commonly found in freshwater and sometimes brackish water environments of Southeast Asia, *D. boaja* is the largest of the pipefishes and individuals can reach 44 cm in total length (Kuiter, 2000). Halwart and Bartley (2007) reported that *D. boaja* can even survive in harsh aquatic environments such as rice fields. Currently, this species is considered “Data Deficient” by the IUCN Red List of Threatened Species. Thailand is known as a major trader of dried seahorse and pipefish (Lam et al., 2016). The major pipefish fishing ground is Songkhla Lake in southern Thailand. The harvest of *D. boaja*

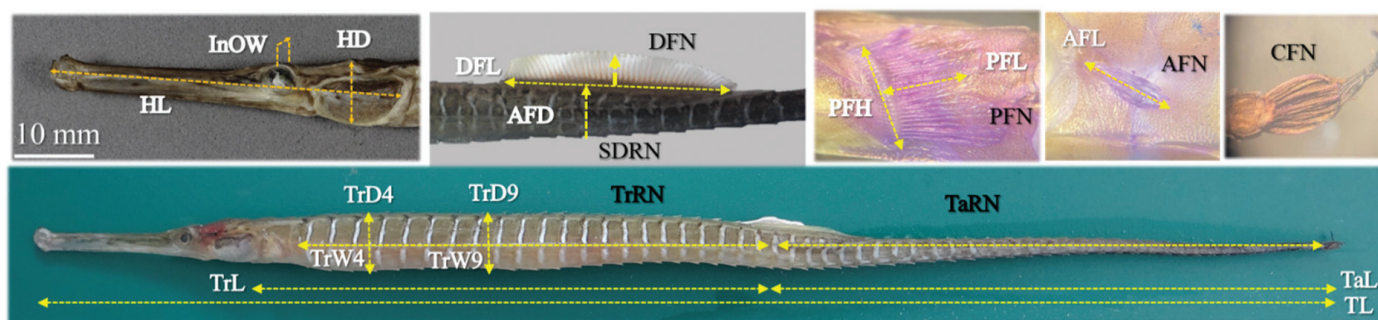


Fig. 1 Long-snouted pipefish *Doryichthys boaja* (Bleeker, 1850), where DFN = number of dorsal fin rays, PFN = number of pectoral fin rays, CFN = number of caudal fin rays, AFN = number of anal fin rays, SDRN = number of sub dorsal ring, TrRN = number of trunk ring, TaRN = number of tail ring, HL = head length, TrL = trunk length, TaL = tail length, DFL = dorsal fin base length, DFH = dorsal fin height, PFL = pectoral fin base length, PFH = pectoral fin height, TrD4 = trunk depth 4th, TrD9 = trunk depth 9th, TrW4 = trunk width 4th, TrW9 = trunk width 9th, AFL = anal ring depth, AFL = anal fin length, InOW = inter orbital width, HW = head width

in this lake has been as high as 20.3 t in 2014 and dropped to 8.8 t in 2019 (Department of Fisheries, 2014; 2019). Much of the market demand is driven by export to China, as pipefish is an important ingredient in traditional Chinese medicine. Pipefish have a varied chemical composition, which includes steroids and many essential trace elements (Xu et al., 2005). In addition, this fish has a rather high medical value and many pharmacological activities, including anti-fatigue, antitumor and sex hormone-like actions (Gao et al., 2018).

As identification of a fish stock is a basic requirement for the stock assessment and fisheries management of a targeted species, the current study gathered information on the morphological differences of *D. boaja* from two distinct habitats, namely between lentic and lotic environments. The study was based on the hypothesis that there is inter-species morphological variation between stocks from the two habitats. In addition, differences in the LWRs and well-being were tested to fundamentally describe the growth of the two stocks.

Materials and Methods

Study areas

Samples of *D. boaja* were collected from the local fishers of two inland water bodies: Songkhla Lake and the Bangpakong River. Songkhla Lake (Fig. 2) is a shallow coastal lagoon in southern Thailand ($7^{\circ}24'08.5''\text{N}$, $100^{\circ}15'42.3''\text{E}$), with an average depth of 2 m. The lake is influenced by the southeast (May–October) and the northeast (October–February) monsoons. The water body covers 1,018 km² and is classified into three distinct zones: inner (459 km²), middle (377 km²) and lower (182 km²). Salinity ranges from freshwater in the inner zone (0 practical salinity units; psu), to saline in the outer zone, with a maximum of 15 psu (Pradit et al., 2010). The lake is rich in faunal diversity; at least 450 fish species and 30 shrimp species have been reported (Pornpinatepong et al., 2010). The Bangpakong River ($13^{\circ}42'27.0''\text{N}$, $101^{\circ}08'08.9''\text{E}$; Fig. 2) is one of the major rivers in central Thailand and flows naturally with no dams for 231 km to the Gulf of Thailand (Boonphakdee and Fujiwara, 2008). The river basin is also influenced by the southeast and the northeast monsoons, and seawater intrusion is common between March and April. There has been a high level (270 species) of recorded fish species in this river (Sawangarreruks et al., 2003). Samples of *D. boaja* were collected from the inner zone of Songkhla Lake and from the lower portion of the Bangpakong River, near the estuary. These two inland water bodies were selected because they are

the main fishing ground of this fish in Thailand. The annual total catches of *D. boaja* fluctuates between 8,000 kg and 10,000 kg, of which more than 90% and more than 5% of the total catches are from the Songkhla Lake and the Bangpakong River, respectively (Department of Fisheries, 2019).

Sample handling and measurement

Samples of *D. boaja* were collected using a 2 cm stretched mesh gillnet and scoop net throughout 2020, except during the closed fishing season (October–December and May–August for the Songkhla Lake and Bangpakong River, respectively). Only complete samples consisting of the complete trunk, no broken snout and tail, with no torn dorsal and pectoral fins, were used for the study. Each individual was weighed (to the nearest 0.1 g) *in situ* and then positioned for digital photographing using a Sony Cyber-shot camera model DSC-HX200V (resolution: 18.2 megapixels). Morphological variables were measured (7 meristic traits and 16 morphometric variables) according to relevant references (Dawson, 1981; Matsunuma, 2017) using the ImageJ software in the laboratory (Table 1 and Fig. 1).

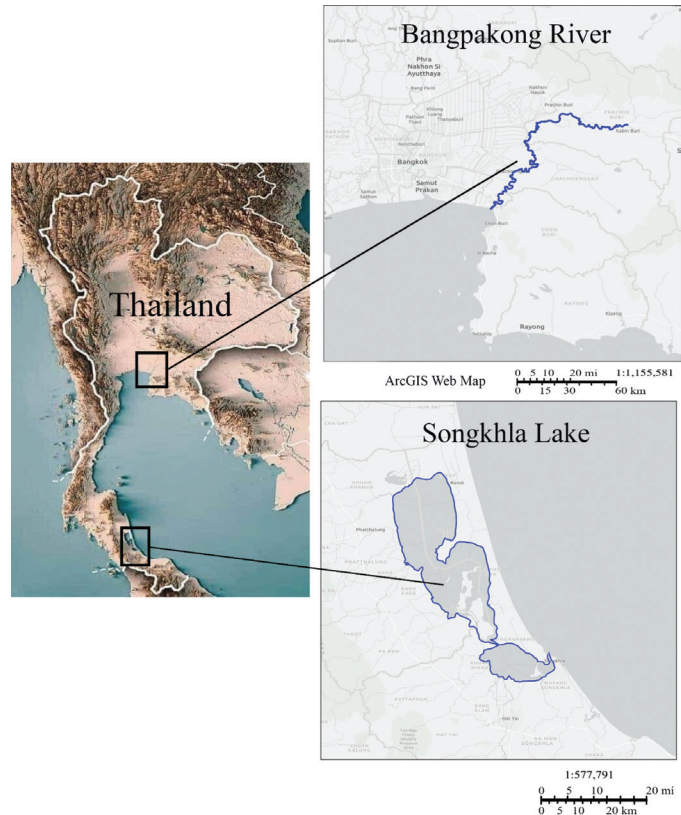


Fig. 2 Sampling locations for *Doryichthys boaja* in inner zone of Songkhla Lake and lower portion of Bangpakong River

Table 1 Meristic and morphometric variables used for separating *Doryichthys boaja* stocks, following Dawson (1981)

Variable	Abbreviation	Description
Number of dorsal fin rays	DFN	Number of the dorsal fin rays
Number of pectoral fin rays	PFN	Number of pectoral fin rays
Number of caudal fin rays	CFN	Number of caudal fin rays
Number of anal fin rays	AFN	Number of anal fin rays
Number of sub dorsal ring	SDRN	Number of rings under dorsal fin
Number of trunk ring	TrRN	From ring bearing pectoral fin base to ring bearing the anus
Number of tail ring	TaRN	From first ring behind anus to penultimate ring excluding terminal element bearing caudal fin
Head length	HL	Tip of lower jaw to posterior margin of operculum
Trunk length	TrL	Length of trunk
Tail length	TaL	Length of tail
Dorsal fin base length	DFL	Length of dorsal fin base
Dorsal fin height	DFH	Height of dorsal fin
Pectoral fin base length	PFL	Length of pectoral fin base
Pectoral fin height	PFH	Height of pectoral fin
Trunk depth 4 th	TrD4	Body height of trunk depth 4 th
Trunk depth 9 th	TrD9	Body height of trunk depth 9 th
Trunk width 4 th	TrW4	Body width of trunk depth 4 th
Trunk width 9 th	TrW9	Body width of trunk depth 9 th
Anal ring depth	AFD	Body height of anal ring
Anal fin length	AFL	Length of anal fin
Inter orbital width	InOW	Smallest bony width measured above centers of eyes
Head width	HW	Width of head

Note: First 7 items are meristic variables; the remaining 16 are morphometric variables.

Data analysis

Each of the morphometric variables was converted into a ratio to the total length. Analyses were split for meristic and morphometric characters. The normality of all variables was tested using the Shapiro-Wilk test. Permutational multivariate ANOVA (PERMANOVA) and the Kruskal-Wallis test were used to examine variation in morphological variables between sex and the environment. Dunn's post-hoc test was used when a significant difference was found among groups for each variable at $\alpha = 0.05$. Principal component analysis (PCA) was used to examine the variables important in separating the groups of fish by sex or environment. Linear discriminant function analysis was performed to examine the accuracy in sample classification by sex and environment.

The LWR values from the pipefish sampled in each environment were established using the power function (Equation 1) and estimated based on a logarithmic-transformed equation (Equation 2). Analysis of covariance (ANCOVA) was

applied to compare LWR values between stocks. The well-being of each stock was initially investigated using the relative condition factor (K_{rel} ; Equation 3; Le Cren, 1951). Then, the relative weight in relation to mean weight (W_{rm} ; Equation 4; Froese, 2006) was used to explore significant differences in well-being between stocks using the Mann-Whitney test. All data analyses were conducted using the R statistical software (R Development Core Team, 2020) with the packages ade4 (Dray and Dufour, 2007) and FSA (Ogle, 2016).

$$W = aL^b \quad (1)$$

$$\log(W) = \log(a) + b \log(L) \quad (2)$$

$$K_{rel} = W/aL^b \quad (3)$$

$$W_{rm} = 100(W/a_m L^{b_m}) \quad (4)$$

where W is the whole body wet weight (measured in grams); L is the total length (measured in centimeters); a and b are parameters; and a_m and b_m are the geometric means of a and b .

Ethics statement

Animal care and all experimental procedures were approved by the Ubon Ratchathani University Animal Care and Use Committee (Approval no. 47/2563/IACUC).

Results

In total 297 and 110 *D. boaja* individuals were collected from Songkhla Lake and the Bangpakong River, respectively. Length ranges (means \pm SD) of the respective stocks were 16.2–32.7 cm (25.3 ± 2.0 cm) and 15.6–33.7 cm (26.9 ± 2.9 cm). Weight ranges were 1.7–15.4 g (7.7 ± 2.2 g) and 0.7–21.5 g (7.4 ± 3.5 g). The morphometric variables were converted in to ratios to total length. Ranges and average values for all meristic

and morphometric variables are presented in Tables 2 and 3, respectively. None of the variables had a normal distribution ($p < 0.05$). The PERMANOVA results for the meristic variables revealed significant differences among groups by sex ($p = 0.01$) and environment ($p = 0.02$), but not their interaction ($p = 0.12$). All the measured morphometric variables were significantly different between factors, namely sex, environment and their interaction. The results from the Kruskal-Wallis tests showed highly significant ($p < 0.01$) differences in all meristic variables; explicit differences between environments were identified by Dunn's post-hoc test (Table 2). Except for head length ($p = 0.43$), all morphometric characters were also significantly ($p < 0.05$) different and Dunn's post-hoc test showed clear differences between environments, similar to the meristic variables (Table 3).

Table 2 Statistics for environment and sex of meristic characters of *Doryichthys boaja*

Code	Range	Mean \pm SD	Songkhla Lake		Bangpakong River	
			Female	Male	Female	Male
DFN	41–56	46.3 \pm 2.9	44.9 \pm 2.0 ^a	45.2 \pm 2.0 ^a	49.9 \pm 2.4 ^b	49.5 \pm 1.9 ^b
PFN	21–28	24.7 \pm 0.9	24.6 \pm 0.9 ^a	24.9 \pm 0.9 ^b	24.6 \pm 1.0 ^a	24.3 \pm 0.9 ^a
CFN	5–10	8.3 \pm 0.7	8.2 \pm 0.7 ^a	8.6 \pm 0.6 ^b	8.2 \pm 0.9 ^a	8.3 \pm 0.7 ^a
AFN	2–7	4.3 \pm 0.6	4.2 \pm 0.5 ^a	4.2 \pm 0.6 ^a	4.5 \pm 0.8 ^b	4.7 \pm 0.7 ^b
SDRN	7–11	8.8 \pm 0.7	8.5 \pm 0.5 ^a	8.5 \pm 0.5 ^a	9.7 \pm 0.5 ^b	9.7 \pm 0.5 ^b
TrRN	22–25	23.7 \pm 0.7	24.0 \pm 0.5 ^a	24.1 \pm 0.5 ^a	22.9 \pm 0.6 ^b	23.1 \pm 0.6 ^b
TaRN	25–38	33.3 \pm 1.4	33.0 \pm 1.1 ^a	32.8 \pm 1.0 ^a	34.4 \pm 1.6 ^b	33.4 \pm 2.4 ^c

Note: Mean \pm SD in a row superscripted with different lowercase letters are significant ($p < 0.05$) different.

Table 3 Statistics for environment and sex of morphometric characters of *Doryichthys boaja*

Code	Range	Mean \pm SD	Songkhla Lake		Bangpakong River	
			Female	Male	Female	Male
HL	26.05–66.33	44.28 \pm 4.77	43.30 \pm 4.41 ^a	43.41 \pm 2.98 ^{ab}	46.04 \pm 6.28 ^{ab}	49.78 \pm 4.65 ^b
TrL	52.31–132.76	98.20 \pm 10.52	97.09 \pm 10.76 ^a	98.33 \pm 7.65 ^b	97.61 \pm 13.38 ^c	107.52 \pm 8.54 ^a
TaL	37.37–139.00	105.06 \pm 10.80	102.14 \pm 9.77 ^a	101.86 \pm 8.27 ^a	112.34 \pm 11.45 ^b	117.44 \pm 7.03 ^b
DFL	4.65–94.46	26.95 \pm 5.21	25.55 \pm 6.45 ^a	25.30 \pm 1.96 ^a	30.57 \pm 4.25 ^b	33.14 \pm 2.31 ^b
DFH	1.82–6.70	3.79 \pm 0.73	6.36 \pm 0.60 ^a	3.72 \pm 0.60 ^{ab}	4.07 \pm 0.95 ^b	4.29 \pm 0.79 ^{ab}
PFL	2.79–9.47	5.50 \pm 0.81	5.40 \pm 0.77 ^a	5.33 \pm 0.53 ^a	5.76 \pm 1.08 ^a	6.33 \pm 0.65 ^b
PFH	2.39–7.26	4.08 \pm 0.71	3.89 \pm 0.57 ^a	3.95 \pm 0.49 ^a	4.47 \pm 0.95 ^b	4.81 \pm 0.67 ^b
TrD4	3.29–16.51	9.15 \pm 1.62	9.03 \pm 1.49 ^a	9.47 \pm 0.92 ^b	8.54 \pm 2.31 ^c	10.36 \pm 1.72 ^{ab}
TrD9	3.34–14.95	9.25 \pm 16.4	9.12 \pm 1.63 ^a	9.66 \pm 0.96 ^b	8.50 \pm 2.15 ^c	10.40 \pm 1.58 ^{ab}
TrW4	2.38–9.09	4.34 \pm 0.62	4.23 \pm 0.57 ^a	4.30 \pm 0.5 ^a	4.48 \pm 0.74 ^a	4.80 \pm 0.40 ^a
TrW9	2.29–9.95	4.17 \pm 0.60	4.11 \pm 0.55 ^a	4.18 \pm 0.67 ^a	4.18 \pm 0.60 ^b	4.53 \pm 0.32 ^{ab}
AFD	3.14–10.19	7.10 \pm 0.89	7.08 \pm 0.89 ^a	7.17 \pm 0.59 ^a	6.87 \pm 1.22 ^b	7.63 \pm 0.71 ^b
AFL	1.27–4.85	2.78 \pm 0.54	2.81 \pm 0.50 ^a	2.79 \pm 0.40 ^a	2.68 \pm 0.75 ^b	2.93 \pm 0.53 ^b
InOW	1.29–7.12	2.32 \pm 0.44	2.32 \pm 0.54 ^a	2.26 \pm 0.28 ^{ab}	2.36 \pm 0.45 ^b	2.62 \pm 0.34 ^a
HW	3.03–10.96	5.92 \pm 1.01	5.64 \pm 0.79 ^a	5.65 \pm 0.57 ^a	6.51 \pm 1.35 ^b	7.32 \pm 0.94 ^c

Note: Mean \pm SD in a row superscripted with different lowercase letters are significant ($p < 0.05$) different.

The first two axes of PCA (Figs. 3 and 4) explained 49.4% and 41.6% of variation in the meristic and morphometric variables, respectively. The PCA of meristic characters (Fig. 3) indicated that all variables had high loadings on one of the axes, displayed by all variables having long arms in their plots. The stock of Songkhla Lake had higher scores in TrRN, CFN and PFN, while TaRN, SDRN, DFN and APN were more important for the Bangpakong River stock. Using the meristic variables, the linear discriminant analysis (LDA) results showed high prediction accuracy in separating the two stocks (Table 4A), however there was low success in distinguishing the *D. boaja* samples by sex in the Bangpakong stock (Table 4B). With the exception of TaL, all the morphometric variables had high loadings in the PCA. The stock for the Bangpakong River had a higher score in length morphometry, while the stock

from Songkhla Lake had higher scores in trunk morphometry (Fig. 4). The LDA results based on morphometry showed a perfect result (100% accuracy) in predicting the stock origin of *D. boaja* (Table 4A) and also high accuracy in predicting the *D. boaja* samples according to the combination of sex and environment (Table 4B).

The original LWR and log-log transformed LWR relationships of the *D. boaja* samples of this study are presented in Fig. 5; the log-transformed relationships showed a linear trend. The equations representing stocks in Songkhla Lake (Equation 5) and Bangpakong River (Equation 6) were:

$$\log(W) = -8.145 + 3.147 \log(L) \quad (r^2 = 0.97) \quad (5)$$

$$\log(W) = -6.397 + 2.570 \log(L) \quad (r^2 = 0.61) \quad (6)$$

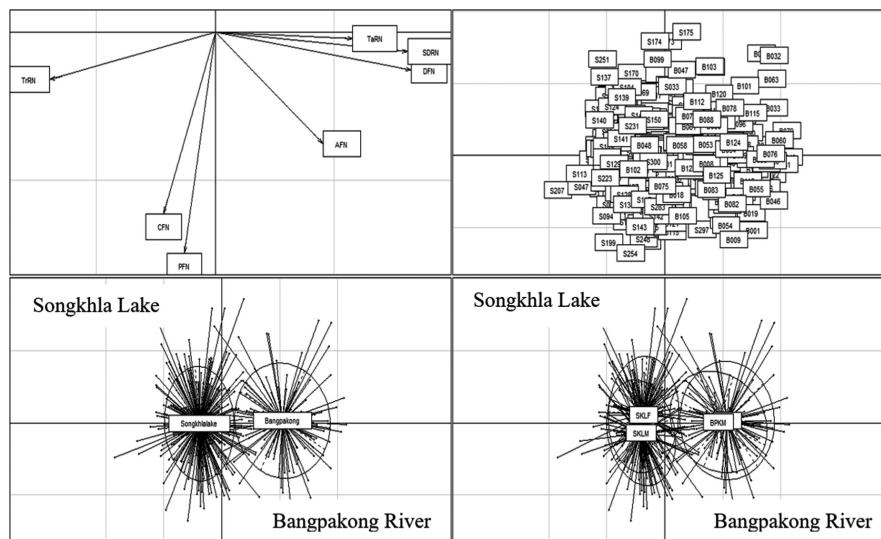


Fig. 3 Indicative display of principal component analysis of meristic variables of pipefish collected in two environments (Songkhla Lake and Bangpakong River)

Table 4 Cross-validated classification results of linear discriminant analysis (LDA) of *Doryichthys boaja* where individual samples were classified to (A) environment and (B) environment × sex based on meristic and morphometric characters, value and value in parentheses are actual and LDA estimate of number of samples, respectively.

(A) Environment

Character	Environment	
	Songkhla Lake	Bangpakong River
Meristic	297 (300)	110 (107)
Morphometric	297 (296)	110 (111)

(B) Environment × Sex

Character	Songkhla Lake		Bangpakong River	
	Female	Male	Female	Male
Meristic	148 (138)	149 (157)	89 (107)	21 (5)
Morphometric	148 (135)	149 (162)	89 (90)	21 (20)

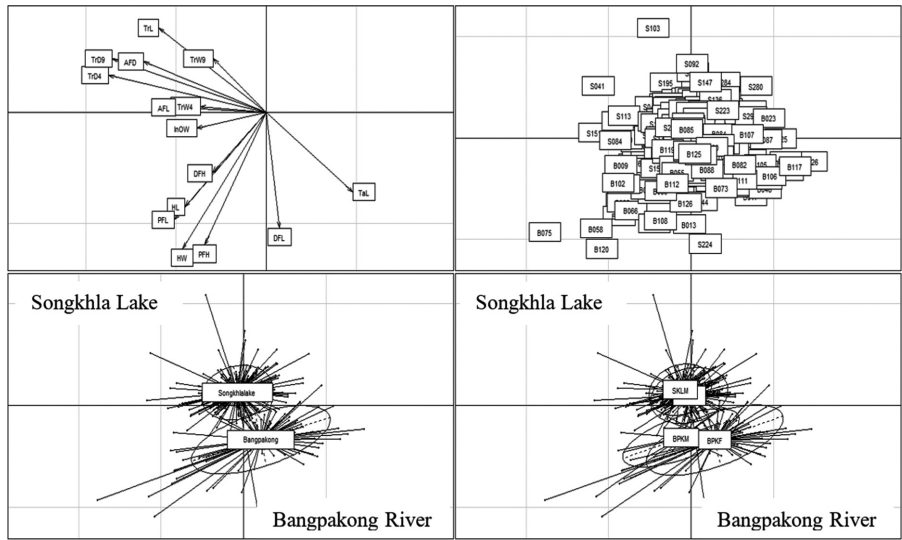


Fig. 4 Indicative display of principal component analysis of morphometric variables of pipefish collected in two environments (Songkhla Lake and Bangpakong River)

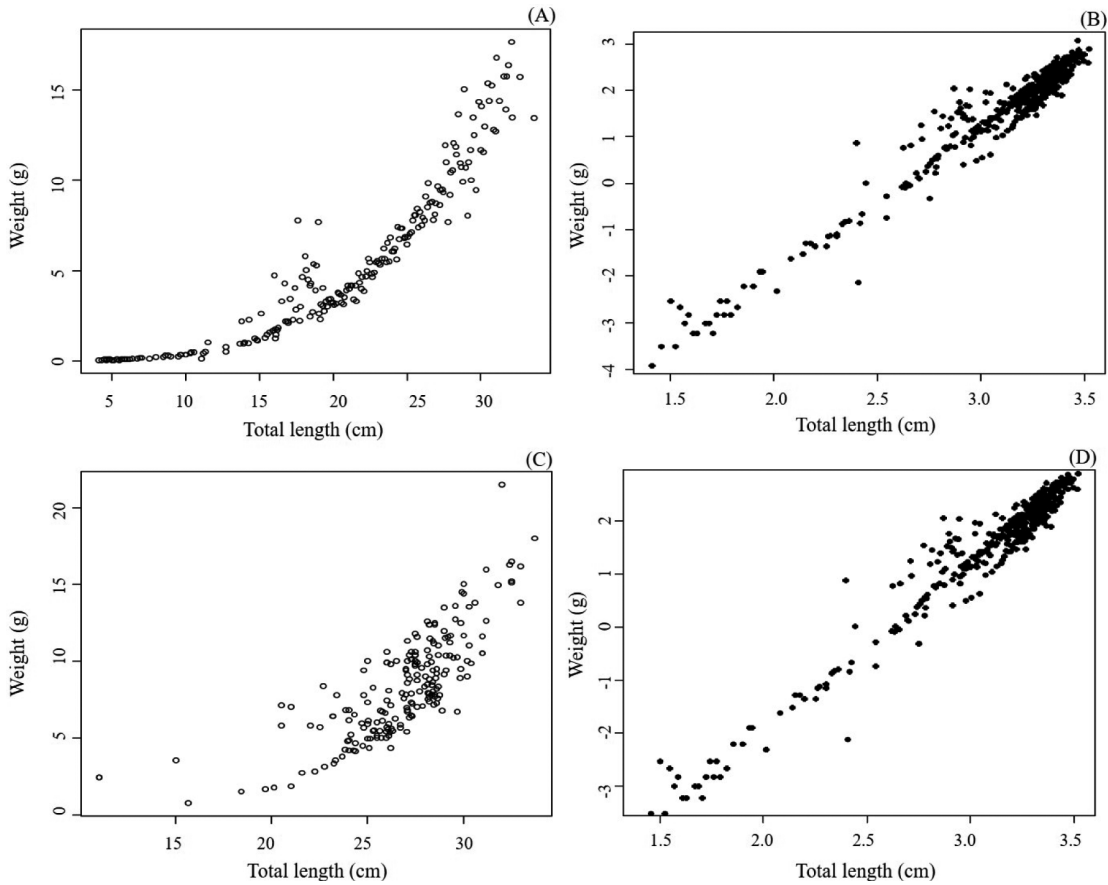


Fig. 5 Original length-weight relationships (LWRs) and log-log transformed LWRs of *Doryichthys boaja* samples from two environments (Songkhla Lake and Bangpakong River): (A) LWR for Songkhla Lake; (B) log-transformed LWR for Songkhla Lake; (C) LWR for Bangpakong River; (D) log-transformed LWR for Bangpakong River

The LWRs revealed positive and negative allometry for the Songkhla Lake and Bangpakong River stocks, respectively ($b \neq 3$, t-test, $p < 0.05$). ANCOVA indicated that the slopes (parameter b) between the two stocks were significantly ($p = 0.02$) different. The range and mean \pm SD of K_{rel} for the *D. boaja* samples from Songkhla Lake were 0.74–1.34 (1.01 ± 0.10) and for the Bangpakong River were 0.37–1.76 (0.88 ± 0.22). By applying W_{m} , it was noted that the samples from Songkhla Lake (111.3 ± 11.6) had significantly higher well-being ($p = 2.2 \times 10^{-6}$) than those from the Bangpakong River (86.1 ± 19.6).

Discussion

Taxonomic classification of Doryrhamphine pipefishes (species in the genus *Doryichthys*) is based on their morphological characters (Dawson, 1981). The current study identified stocks of *D. boaja* from two different environments (Songkhla Lake and the Bangpakong River) using the variables described by Dawson (1981). To study the stock discrimination using morphological characters, the sample size within each hypothetical stock should be greater than the number of variables measured, with a minimum of 50 individual samples (Tabachnick and Fidell, 1989; Cadrin, 2000). Based on these requirements, the samples in the current study work were sufficient. In the current study, the largest fish collected from the two localities (less than 35 cm TL) was smaller than the record for an adult *D. boaja* in Indonesia (over 40 cm TL) (Kottelat et al., 1993). This may reflect high exploitation pressure in the two localities due to the general shift in the catch toward smaller sizes of individuals (Ricker, 1981).

Morphological variation associations with habitats are common among natural populations. In addition, exploitation, which directly impacts fish growth, may further result in differentiation of fish morphological characters (Begg and Waldman, 1999; Pope et al., 2010; Gammanpila et al., 2017; Shuai et al., 2018). The current study detected significant shape differences between the two *D. boaja* stocks, implying that both meristic and morphometric characters can be used to discriminate the stocks of *D. boaja*, particularly from these habitats. By incorporating the results from Kruskal-Wallis analysis and PCA, four meristic variables (DFN, AFN, SDRN and TrRN) and five morphometric variables (DFL, PFH, AFD, AFL and HW) could be considered for use in the stock identification of *D. boaja* specimens. However, more accurate results would be obtained from the morphometric variables. Other studies also reported better success in classification

using morphometric variables; for example, success rates in classification exceeding 60% were achieved with meristic characters, and exceeding 80% with morphometric characters (Haddon and Willis, 1995; Hurlbut and Clay, 1998; Murta, 2000; Takács et al., 2016). Nevertheless, a concern has been raised by Murta (2000) that misclassification based on meristic characters is possible and could be due to the fact that they relate to the age and body size of fish.

Geladakis et al. (2018) observed that body shape differentiation is primarily influenced by body condition. Other studies showed both negative and positive allometry for pipefish according to the season and location (Gurkan and Taskavak, 2007; Ben Amor et al., 2011; Khrystenko et al., 2015). The current LWR results revealed negative allometry for the *D. boaja* stock from the Bangpakong River, implying that the fish become slimmer with increasing length. In contrast, the positive allometry found in the stock of Songkhla Lake suggest that the fish become heavier as the length increases, reflecting optimum conditions for growth (Froese, 2006; Jisr et al., 2018). Slow growth and relative thinness commonly occur when fish live in unfavorable conditions, such as freshwater fish in saline water (Boeuf and Payan, 2001). The negative allometry of the freshwater *D. boaja* from the Bangpakong River could be attributed to the intrusion of seawater, which extends more than 150 km up-river during the dry season (Okwala et al., 2020). This seawater intrusion could partly explain why the average condition factor of the Bangpakong River fish was lower than those from Songkhla Lake, which was confirmed by statistical analysis using the relative weight, as suggested by Froese (2006). In addition to the plumpness of fish, the relative weight can serve as a surrogate for estimating fish health and assessing prey abundance, as well as the favorability of the environment (Blackwell et al., 2000; Nahdi et al., 2016). In this case, the relative weights suggested that the conditions in Songkhla Lake were more favorable for *D. boaja*, perhaps due to the greater abundance of preferred foods or other factors of the lentic habitat.

Differences in morphological characters can be used to discriminate *D. boaja* stocks from different environments, such as the lentic Songkhla Lake and the lotic Bangpakong River. The morphometric characters provided greater accuracy in stock determination than the meristic characters. The LWR and relative weight of *D. boaja* suggested that this species grows more favorably in a lentic environment than a lotic one. Further work is suggested using other morphological methods such as truss networking to confirm the stock differentiation. Genetic study is also recommended to investigate the possibility of different species, not simply different stocks.

Conflict of Interest

The authors declare that there are no conflicts of interest.

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