

Morphological differences between close populations discernible by multivariate analysis: A case study of genus *Coilia* (Teleostei: Clupeiforms)

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Abstract – In order to understand the morphological differences between four populations of genus *Coilia* (Teleostei: Clupeiforms) and identify them conveniently, truss network data were used to conduct multivariate analysis. Nineteen morphometric measurements were made for each individual. Burnaby's multivariate method was used to obtain size-adjusted shape data. The cluster analysis and discriminant analysis were used to discriminate among populations. The results indicated that 1) the four populations were clustered into three distinct groups; the first group included Changjiang *C. mystus* and Taihu *C. ectenes*, the second one included Zhujiang *C. mystus*, the last one included Changjiang *C. ectenes*, and 2) discriminant analysis with selected 4 morphological parameters showed that the identification accuracy was between 88% and 100%, and global identification accuracy was 95%. Our result showed that populations of different *Coilia* species living in geographic proximity to one another are more similar than conspecifics living farther apart. Separation and adaption are important to morphological difference. The taxonomy of genus *Coilia* should be reconsidered. This study also showed that the method to obtain size-adjusted data is important to acquire right conclusion.

Key words: *Coilia ectenes* / *Coilia mystus* / Cluster analysis / Discriminant analysis / Stock identification

Résumé – Différences morphologiques entre populations proches, et déterminées par analyse multivariée : une étude de cas du genre *Coilia* (Téléostéens : Clupéiformes). Afin de comprendre les différences morphologiques entre quatre populations du genre *Coilia* (Téléostéens : Clupéiformes) et de les identifier de façon pratique, un réseau de données a été utilisé pour conduire l'analyse multivariée. Dix-neuf mesures morphométriques ont été faites sur chaque individu. La méthode multivariée de Burnaby's a été utilisée pour obtenir des ajustements des données. L'analyse par groupes (clusters) et l'analyse discriminante ont été utilisées. Les résultats montrent que : 1) les quatre populations sont regroupées en trois groupes distincts ; le premier groupe inclut le « changjiang » *C. mystus* et le « taihu » *C. ectenes*, le deuxième inclut le « zhujiang » *C. mystus*, le dernier le « changjiang » *C. ectenes*, et 2) l'analyse discriminante avec 4 paramètres morphologiques sélectionnés montre que la précision d'identification se situe entre 88 et 100 %, et la précision globale d'identification est de 95 %. Nos résultats montrent que les populations de différentes espèces de *Coilia* vivant à proximité géographique des unes des autres ont davantage de caractères communs que des individus de la même espèce mais plus éloignés géographiquement. La séparation et l'adaptation importent beaucoup dans les différences morphologiques. La taxonomie du genre *Coilia* devrait être reconsidérée. Cette étude montre aussi que la méthode d'ajustement est déterminante pour obtenir un résultat correct.

Introduction

Genus *Coilia* (Gray 1831) fishes are distributed mainly in the northwest and western Pacific, extending southward toward Canton in the north of southern China and northward to the Ariake Sound of southwestern Japan, including all of the Yellow Sea and the area off the western coast of Korea

(Whitehead et al. 1988). In China, four kinds of *Coilia* fishes were found (Zhang 2001). Two of them, namely, *C. ectenes* (Jordan et Seale 1905) and *C. mystus* (Linnaeus 1758), are of higher economic value (East China Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences and Shanghai Fisheries Research Institute 1990).

Due to great similarity, the taxonomic relationship between two ecotypes of *C. ectenes*, i.e., migrating Changjiang *C. ectenes* and resident Taihu *C. ectenes*, is controversial

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Table 1. Sampling details of *Coilia* fishes in this study. Range of standard length (SL), mean standard length (MSL), and standard deviations of MSL.

Population	Sampling location	Date of capture	Range of SL (cm)	MSL ± S.D. (cm)
DJ	Yangtze river estuary, Shanghai (N31° 37', E121° 80')	April 2003	16.9–24.7	21.09 ± 2.06
HJ	Taihu lake, Wuxi, Jiangsu province (N31° 38', E120° 10')	Dec. 2002	10.1–19.4	14.02 ± 2.45
CJ	Yangtze river estuary, Shanghai (N31° 37', E121° 90')	Mar. 2004	11.2–16.8	13.56 ± 1.51
ZJ	Pearl river estuary, Guangzhou (N22° 51', E113° 82')	Mar. 2004	8.6–16.9	12.17 ± 1.47

(Yuan et al. 1976; Yuan 1980; Liu 1995). Though they can be discriminated according to their physiological and ecological differences, it is very difficult to identify them with meristic index for they have many overlapping characters (Yuan et al. 1976). The physiological and ecological differences can be easily observed in spawning seasons. For example, the mature Changjiang *C. ectenes* has a longer standard length and larger diameter of mature eggs than does Taihu *C. ectenes* (East China Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences and Shanghai Fisheries Research Institute 1990). These differences are not consistently useful for they can be found only in spawning seasons and are not evident in other seasons. Different populations of *C. mystus*, such as, Changjiang *C. mystus* and Zhejiang *C. mystus*, are also difficult to identify with meristic index.

Moreover, only two meristic indices, i.e., numbers of anal spines and lateral lines, can be used to discriminate *C. ectenes* from *C. mystus* in traditional taxonomy (Cheng and Zheng 1987). In *C. ectenes*, anal spines number above 90 and lateral lines above 68 while in *C. mystus* anal spines number from 73 to 86 and lateral lines from 58 to 65. Given the difficulty in counting the numbers of anal spines and lateral lines to differentiate these two species they are not practical for use in everyday identification. Between February and April, *C. ectenes* is expensive, and delicious and tasteful at this season (East China Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences and Shanghai Fisheries Research Institute 1990); therefore due to the tremendous pressure to capture *C. ectenes* an illegal mix *C. ectenes* with *C. mystus* are often sold to consumers. This phenomenon not only damages the interests of the consumer, but is also very harmful to the protection and sustainable utilization of these two important fishery resources. Thus, it is necessary to discern their morphological differences and develop a convenient and practical method to identify them accurately. For the sake of convenience, Changjiang *C. ectenes*, Taihu *C. ectenes*, Changjiang *C. mystus* and Zhejiang *C. mystus* are coded in the text as DJ, HJ, CJ and ZJ, respectively.

Morphometric characters are continuous characters describing aspects of body shape. Morphometric variation between stocks can provide a basis for stock structure, and may be more applicable for studying short-term, environmentally induced variation and thus perhaps more applicable for fisheries management (Begg et al. 1999). Morphometric

characters have been successfully used for stock identification. Traditional measurements tended to concentrate along the body axis with only sampling from depth and breadth, and most measurements were taken from the head. Another system of morphometric measurements called the truss network system (Strauss and Bookstein 1982) has been increasingly used for stock identification (Corti et al. 1988; Junquera and Perez-Gandaras 1993; Silva 2003; Tzeng 2004; Turan 2004; Turan et al. 2004).

In a multivariate sense, morphology has two independent components: size and shape (Bookstein et al. 1985). Most of the variability in a set of multivariate characters is due to size (Junquera and Perez-Gandaras 1993). Thus, shape analysis should be free from the effect of size to avoid misinterpretation of the results (Strauss 1985).

Based on geographic variation in ontogenetic rates, morphometric differences are expected among *Coilia* populations. The objective of this study is to understand the morphological difference between four populations of genus *Coilia* fishes and identify them conveniently using multivariate statistical techniques. The results can provide a scientific basis for effective management and sustainable exploitation of *Coilia* fishes resources, optimizing their yield, and avoiding fraud.

Materials and methods

Sampling

A total of four populations of genus *Coilia*, two populations of *C. ectenes* and two populations of *C. mystus*, was collected between December 2002 and March 2004 (Table 1, Fig. 1). The sampling location and relative information are presented in Table 1. Forty animals were collected at each site, based on Reist's (1985) recommendation that at least 25 animals be used for morphological analyses. All samples were collected strictly following classification standard (Cheng and Zheng 1987).

Data collection

Nineteen morphological measurements were made on each specimen following the Truss method (Strauss and Bookstein 1982). They consisted of 18 morphological distances between

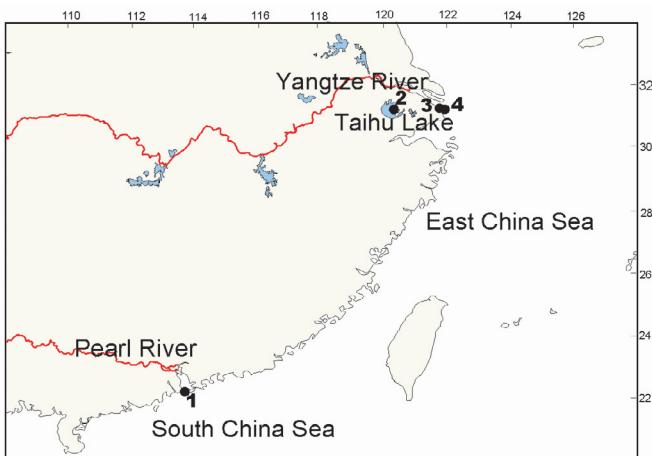


Fig. 1. Locations of sampling sites (numbers): 1. Pearl river (Zhujiang) estuary, Guangzhou; 2. Taihu lake, Wuxi, Jiangsu province; 3. Yangtze river (Changjiang) estuary, Shanghai; 4. Yangtze river estuary, Shanghai.

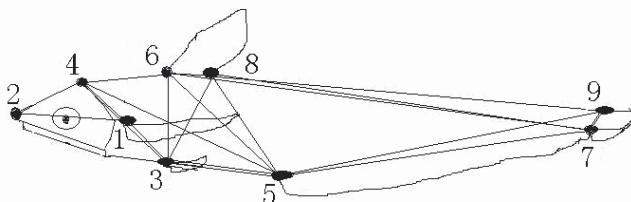


Fig. 2. Truss network of *Coilia* fish; 18 truss parameter measurements are the distances between the two of 9 landmark points. For example, D(1-2) denotes the distance between landmark points 1 and 2. Landmark points: 1. most posterior point of maxilla, 2. tip of snout, 3. origin of pelvic fin, 4. most anterior of scales on skull, 5. origin of anal fin, 6. origin of dorsal fin, 7. tremenus of anal fin, 8. tremenus of dorsal fin, 9. dorsal origin of caudal fin.

9 truss network landmark points plus standard length (SL). The morphological measurements were collected according to the method described by Elliott et al. (1995). Truss network of *Coilia* fish was shown in Figure 2.

Data analysis

To remove size-dependent variation, the data were adjusted prior to the analysis. Data were adjusted using Burnaby's multivariate size adjustment to test for shape differences among groups (Burnaby 1966; Rohlf and Bookstein 1987). The size-adjusted data were used in sequent analysis. Statistical analysis were performed with Statistica 6.0 software.

Dendrogram of four populations was constructed by hierarchical clustering of single linkage (nearest neighbor) by using Euclidean distance to assess the degree of similarity between the populations. The other linkage rules (i.e., complete linkage, unweighted pair-group average, unweighted pair-group centroid) and distance measures (i.e., Manhattan distance and Chebychev distance) were also tested to see if the results are robust to clustering method.

Table 2. The Euclidean distances between four *Coilia* fishes derived from size-free shape matrix.

Population	DJ	HJ	CJ	ZJ
DJ	0.00			
HJ	10.8	0.00		
CJ	11.3	1.2	0.00	
ZJ	13.5	3.3	2.5	0.00

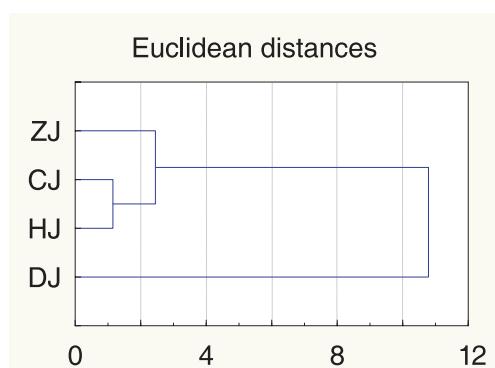


Fig. 3. Cluster dendrogram of four *Coilia* fishes derived from Euclidean distances.

A stepwise multivariate discriminant analysis was used to identify the combination of variables that best separate *Coilia* fishes. The relative importance of morphometric characters in discriminating populations was assessed using the F-to-remove statistic. Collinearity among variables used in the discriminant model was evaluated using the tolerance statistic. Accuracy of classifications was evaluated using extrinsic jackknife cross-validation, in which each specimen is removed from a discriminant function and classified to group (Marcus 1990). The proportion of individuals correctly reallocated was taken as a measure of the honesty of that population. In such a case the proportion of individuals that are misclassified is low if all groups discriminated by cluster analysis does not derive by chance alone (Soriano et al. 1988).

Results

Cluster analysis

18 characters were used to perform the cluster analysis. Different linkage rules (single linkage, complete linkage, unweighted pair-group average, unweighted pair-group centroid) and distance measures (Euclidean distance, Manhattan distance and Chebychev distance) were all tested and the results are robust to clustering method. That is to say, they produced the same cluster patterns (data not shown).

The Euclidean distance values between four samples derived from size-adjusted morphometric data were shown in Table 2. The Euclidean distance (13.5) between samples of DJ and ZJ was least similar, but the one (1.2) from the data sets of HJ and CJ was most similar. Figure 3 shows the Euclidean dendrogram of four samples.

Four samples were clustered into three distinct groups. The first group included HJ and CJ; the second group included ZJ,

Table 3. Selection of morphometric characters into discriminant model.

	Wilks'	Partial	F-remove	p-level	Toler.	1-Toler.
A(3-4)*	0.036 247	0.659 251	26.361	0.000 000	0.166 770	0.833 230
A(2-4)	0.028 089	0.850 740	8.948	0.000 017	0.780 065	0.219 935
A(3-8)	0.077 483	0.308 406	114.366	0.000 000	0.269 681	0.730 319
A(7-6)	0.103 019	0.231 959	168.866	0.000 000	0.104 404	0.895 596

*A(3-4) means the adjusted value of D(3-4).

Table 4. Classification functions of four samples of genus *Coilia*.

	DJ	HJ	CJ	ZJ
A(3-4)*	5.2134	5.9107	21.2591	26.2920
A(2-4)	24.0791	16.3567	17.0186	22.1484
A(3-8)	-1.9559	-2.3671	10.9296	31.1719
A(7-6)	4.8076	2.6504	-4.1072	-10.3668
Constant	-71.3830	-31.4751	-37.3470	-53.3471

*A(3-4) means the adjusted value of D(3-4).

Table 5. Results of discriminant analysis of four *Coilia* fishes based on size-adjusted shape data (bold values indicate correct classifications).

Population	Population predicted				Accuracy (%)	global accuracy (%)
	DJ	HJ	CJ	ZJ		
DJ	39	1	0	0	98	
HJ	2	38	0	0	95	
CJ	0	3	35	2	88	95
ZJ	0	0	0	40	100	
Total	41	42	35	42		

and the third group included DJ. Thus, it suggested that populations of HJ and CJ are closest in proximity, while the population of DJ is the farthest from other populations.

Discriminant analysis

All 18 morphological parameters are combined to perform stepwise discriminant analysis. The four variables which are most important in separating the groups were selected. The differences between groups were highly significant (Wilks' $\lambda = 0.02390$, approximate F (12, 405) = 104.70, $p < 0.0000$) (Table 3).

The classification functions of the four samples were listed in Table 4. Corresponding morphometric characters of a *Coilia* fish were substituted into these four classification functions respectively, the function with the largest resulting value is the population to which the sample belongs.

The result of the discriminant analysis was shown in Table 5. The most well-defined samples are from ZJ with zero misclassified individual (0%). The 12%, 5% and 2% of misclassifications were yielded separately for CJ, HJ and DJ samples.

Discussion

Results, obtained from size-adjusted shape analyses, reveal that four *Coilia* fishes were clustered into three distinct groups: the first group included HJ and CJ; the second group included ZJ, and the third group included DJ. The discriminant analysis confirmed the above results.

The results of this study were a little surprising. It was expected that the samples within *C. mystus* and *C. ectenes* were most likely to be similar. But the results suggest that CJ is closer to HJ, not closer to ZJ. Furthermore, DJ was found to be closer to ZJ, and not to HJ. Though the morphological similarity between HJ and DJ can not be ignored because they were misclassified as one another, the distance (10.8) between HJ and DJ is much farther than the distances between HJ and CJ(1.2) and ZJ(3.3). CJ is perhaps a middle ecotype between HJ and ZJ because some of CJ were misclassified as HJ(3) and the others as ZJ(2).

In general, fishes demonstrate greater variance in morphometric traits both within and between populations than other vertebrates, and are more susceptible to environmentally-induced morphological variation (Allendorf et al. 1987; Wimberger et al. 1992). The pattern of morphometric distinctness, detected among the genus *Coilia* samples, suggests a direct relationship between the extent of morphometric divergence and geographic separation.

The potential capacity of populations, to adapt and evolve as independent biological entities in different environmental conditions, is restricted by the exchange of individuals between populations. A sufficient degree of isolation may result in notable phenotypic and genetic differentiation among fish populations within a species, which may be recognizable as a basis for separation and management of distinct populations (Turan 2004).

Although, they are different geographic populations of *C. ectenes*, the great morphological difference between DJ and HJ is possible. DJ is a migrating group and HJ is a resident

group. HJ lives throughout its life in Taihu Lake, which is the third largest freshwater lake in China, and thus have almost no chance to exchange genes with DJ. Due to long-term separation and adaption to their respective environments, their morphological differences are remarkable. The great morphological difference between two geographic populations of *C. mystus*, CJ and ZJ, are also possible. The distance of about 1689 kilometers between Guangzhou and Shanghai gives ZJ and CJ almost no chance to exchange genes with each other, and due to long-term separation and adaption to their respective environments, their morphological differences are also quite remarkable. This result showed that populations of different *Coilia* species living in geographic proximity to one another are more similar than conspecifics living farther apart.

The incongruent morphometric results may suggest that the current taxonomy should be reconsidered. To confirm the hypothesis, more evidences drawn from molecular genetics and biochemical genetics, should be used to test if this holds.

Initially, we standardized all the individual morphometric characters using the formula by Elliott et al. (1995): $M_{adj} = M(L_s/L_0)^b$. We then use these adjusted data to perform cluster and discriminant analysis and concluded that the populations of DJ and CJ are the closest in proximity, and ZJ is the farthest of these four populations.

Though some scientists, such as Elliott et al. (1995), Young (2001), Tzeng (2004), Turan (2004), and Turan et al. (2004), have used the formula to adjust data and successfully discern morphological variation between different populations of some certain species, the method of removing size-dependent variation is generally ineffective for removing size variance from data because it only removes the effect of the standard distance, which is not a comprehensive measure of general size. The method implicitly assumes isometry between the independent and dependent variables, and multivariate analysis of ratios is statistically difficult (Cadrin 2000). The most effective approaches to size-correction are multivariate methods, like multiple-group principal components analysis (Thorpe 1988) and the associate size-adjustment (Burnaby 1966). In most morphometric studies, the size factor may account for 80% or more of the variation among a set of variables (Junquera and Perez-Gandaras 1993). Therefore, if size factor cannot be removed utterly, it will play a predominate role in morphometric analysis and result in erroneous result.

The conclusion from Elliott's formula is apparently different from the one obtained here. The different results stemming from same data purely reflect the differences between these two methods of data adjustment. It shows that different methods can lead to different results, despite the fact the data are the same. Thus, for acquiring a correct conclusion, it is very important to choose a suitable method for data analysis.

Discriminant analysis is a statistical method to look for objective discriminant evidence when the classification is already known (Ding 1981). Discriminant analysis has been widely applied to many fields due to its practicality (Zhang and Fang 1982). Stepwise discriminant analysis is a widely used method. It can set up a discriminant function by extracting the factors which are most necessary from all the known factors. Discriminant analysis is a common method used to identify fish populations (Li et al. 1990).

In traditional taxonomy, the criterion used to identify *C. ectenes* from *C. mystus* are mainly dependent on two indices, the numbers of anal spines and lateral lines. These two indices are not practical for everyday identification as it is very difficult to count them. DJ and HJ cannot be identified by using traditional morphological measurements for they overlap in these characters (Yuan et al. 1976). In this situation, physiological and ecological indices, such as standard length of mature fish and diameter of mature egg, can help to identify them (East China Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences and Shanghai Fisheries Research Institute 1990). Furthermore, because these indices can be observed only in spawning seasons, and can not be differentiated in other seasons, they represent an even less practical means of identification.

In this study, truss network parameters were used to conduct a discriminant analysis of four populations of the genus *Coilia*. Using only four truss-network characters, the identification accuracy was between 88% and 100%, and the accuracy of the global discriminant was 95%. So it showed that discriminant analysis is an effective and convenient method for identifying populations of closely related species. The discriminant formula supplies a scientific basis for discerning these populations accurately, and aides in protecting and sustainably utilizing the resources of fishes of the genus *Coilia*.

Morphometric variation is often related to behavioral or ontogenetic differences. Adaptation involves natural selection of those characters that improve the chance for survival and reproduction of individuals. Local environments vary, selecting for different characters in different areas. Differences in selected characters are maintained through reproductive isolation among groups (Cadrin 2004). Anadromous DJ inhabit a wide range of aquatic environments, and make a reproductive migration from aquatic areas near the ocean to freshwater areas every year during the reproductive season. HJ has no migratory habit and lives throughout its life in Taihu lake (East China Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences and Shanghai Fisheries Research Institute 1990). CJ and ZJ live at different latitudes. The ontogenetic rate of ZJ is quicker than that of CJ for they live in aquatic areas of higher temperature. These four important variables may be related to the different ecological or physiological patterns of these four populations.

The management implications of the detected morphological differences between genus *Coilia* fishes depend on the extent to which structuring persists over time. If the phenotypic differences found are genuine and not affected environmentally, then they should be repeatable in further analyses. Consistent differences in at least 2 repeated analyses between 2 groups of fish may indicate their temporal and spatial integrity.

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